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ON THE SYSTEMATICS OF *TRYPOXYLON SCROBIFERUM* RICHARDS AND *T. ANAPAIKE* AMARANTE WITH THE RECOGNITION OF A NEW SPECIES GROUP IN THE SUBGENUS *TRYPOXYLON* (HYMENOPTERA: CRABRONIDAE: TRYPOXYLINI)

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ABSTRACT

The males of Trypoxylon scrobiferum Richards and T. anapaïke Amarante are described for the first time and their genitalia illustrated. These species are demonstrated to represent a monophyletic group, and the scrobiferum species group is established for them. The scrobiferum species group is assigned to the subgenus Trypoxylon. This represents a new subgeneric combination for T. scrobiferum Richards.

KEYWORDS: Hymenoptera, Sphecidae, Crabronidae, Crabroninae, Trypoxylini, *Trypoxylon*, *Trypargilum*, Systematics.

INTRODUCTION

I described *T. (Trypargilum) anapaïke* based on one female (Amarante, 1991) and included it in the *fugax* subgroup of the *nitidum* group. I have since examined undescribed males of *T. anapaïke* and *T. scrobiferum* Richards and concluded that these species are closely related, sharing a character set that separates them from other species of the subgenus *Trypargilum*. Thus I have established the *scrobiferum* species group for them. Also, I present evidence that the new species group is properly assigned to the subgenus *Trypoxylon*.

The hitherto unknown males of *T. scrobiferum* and *T. anapaïke* are described and key characters that support the exclusion of these species from *Trypargilum* are noted. Relationships of the *scrobiferum* group with the other groups in the genus are described. The exclusion of these two species from *Trypargilum* requires

a redefinition of the subgenus. The current classification of *Trypoxylon* is reviewed because of the novel features of the new species group.

Abbreviations:

AA, distance between antennal sockets; AF, diameter of antennal socket; EA, least distance between inner eye margin and antennal socket; EC, least distance between eyes at clypeus; EE, distance between eye emarginations; EL, greatest length of eye; EV, least distance between eyes at vertex; FS, length of flagellomere I; FWL, forewing length; HL, length of head from clypeal apex to vertex; HW, width of head; IO, distance between hind ocelli; HO, diameter of hind ocellus; OO, least distance between hind ocellus and inner margin of eye.

Terms used to describe sculpturing follow Harris (1979). The material studied is housed in the fol-

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lowing institutions: The Natural History Museum, London (BMNH), (holotype of *T. scrobiferum* Richards); Instituto Nacional de Pesquisas da Amazônia, (INPA); Museu de Zoologia da Universidade de São Paulo (MZSP) (holotype of *T. anapaïke* Amarante); Departamento de Biologia, Universidade Federal de Viçosa, Viçosa (UFVB).

Species of the *scrobiferum* group

Trypoxylon anapaïke Amarante, 1991

(Figs. 1-3, 7-8, 10-11)

Trypoxylon (Trypargilum) anapaïke Amarante, 1991: 431, Figs. 3-4. Female. Holotype: Female; SURINAME; Marowije, Anapaïke (Lawa River) xi-1963; B. Malkin col. (MZSP); Amarante, 2002:49.

Description of male

Measurements. HW = 2.45-2.55 mm, FWL = 7.00 mm; Proportions: HW/HL = 1.14-1.16, HW/EV = 5.24-5.4, HW/EC = 6.24-6.47, EV/EC = 1.18-1.24, FS/EV = 0.71-0.75; Ratios: EL:EC:EV:EE = 1.05-1.09:0.21-0.23:0.26-0.27:1.00, OO:IO:HO = 0.06-0.13:0.49-0.51:1.00, AA:EA:AF = 0.24-0.26:0.25-0.38:1.00.

Color: Body black. Orange yellow are: ventral of scape, apex of pedicel, mandibular base, fore and mid tibiae and tarsi, apex of fore and midfemora, base of hindtibia, basal 0.5 of hindbasitarsus, apex of hindtarsomeres I-III, hindtarsomere IV, tibial spurs, basal 0.66 of tergum II, apex of terga III and IV, sternum II. Medial portion of mandible red. Dark reddish brown are: apex of mandible, dorsum of scape, pedicel basally, flagellum, apical margin of clypeus, fore, mid and hind trochanters and femora, hind tibia and tarsus, terga I, III-VI, apical 1/3 of tergum II, sterna I, III-VI. Hind margin of pronotal collar whitish yellow.

Vestiture: Silver to pale gold, except for white to yellowish white on tibiae and tarsi. Clypeus and frons below dorsal margin of the eye emargination with dense vestiture. Clypeus with scattered, downwardly oriented, long pale yellow setae. Gena densely covered by decumbent setae. Thorax laterally and ventrally with moderately dense decumbent setae. Scutum, scutellum and propodeal dorsum with erect short setae. Posterior surface and posterolateral angles of propodeum

with moderately dense decumbent setae. Terga pubescent, I and II more sparsely so.

Head: Frons and eye emargination narrow, dull, colliculate, with moderately close to sparse, very shallow foveolae. Frontal carina on an elevated frontal prominence, posterior truncation equal to diameter of median ocellus, bifurcating arms horseshoe shaped, with length about 2x length of lower branch. Supraantennal carina absent, dorsal margin of antennal socket elevated, deflexed, partially covering condyle of scape. Clypeus weakly convex; clypeus free margin reflexed, thin; apical rim distinct, polished, slightly convex; apical margin weakly sinuate, with two very weak lobes defined by indistinct median emargination. Anterior ocellus in moderate depression. Vertex with small swelling behind each hindocellus. Flagellomere I 0.75x as long as II+III, 3x as long as wide, flagellomeres II and III 2x as long as wide, IV 1.33x, V 1.14x, VI-X 1x, flagellomere XI sub conical as long as X+IX. Occipital carina interrupted behind hypostomal carina; horizontal area behind hypostomal carina 2x as broad as fore basitarsus width.

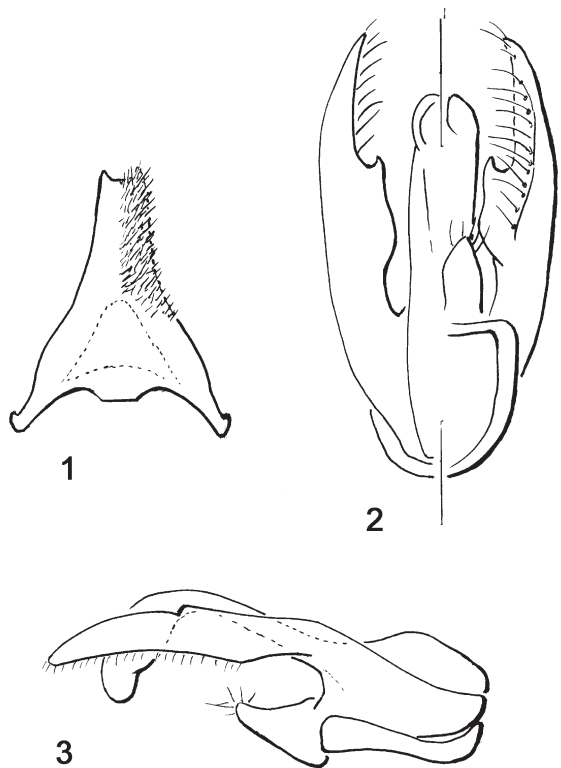


Plate 1: Figs. 1-3. *Trypoxylon anapaïke* Amarante, male: 1, sternum VIII, ventral view; 2 and 3, male genitalia; 2, left half, dorsal view, right half, ventral view; 3, lateral view.

Thorax: Dorsolateral angles of pronotal collar narrowly rounded, prominent. Pronotal collar with median dorsal prominence. Prosternal transverse carina sharp, reflexed and raised laterally, evanescent toward the middle. Scutum, scutellum and mesopleuron moderately shiny, finely and superficially reticulate, with moderately close to sparse, superficial and fine foveolae. Omalal area smoothly angulate, omalulus very weakly indicated below pronotal lobes, short, running by 0.15-0.17x of distance to episternal sulcus, subomalulus well developed, ending at episternal sulcus. Length of precoxal carina 0.5x length of mesopleural suture. Mesopleural wing process bordered by simple ridge, a little widened at hind margin. Metapleural flange narrow. Intercoxal carina arcuate, ventrolateral intercoxal carina present. Dorsoposterior carina of hindtibiae straight, uniformly elevated, abruptly ending subapically, well apart from trochanter emargination. Hindtibial anterior surface flattened, forming an angle with dorsal surface. Forewing vein R1 not extending beyond apex of marginal cell; forewing veinlet 1r-m of submarginal cell forming approximately 90° with vein sector RS+M. Outer row of hamuli on hindwing 1.7x its length apart from inner row.

Propodeum (Fig. 10): Dorsal surface of propodeum with diagonal ridges that become transverse toward apex, dorsal enclosure slightly depressed. Posterior surface with moderately broad, deep longitudinal sulcus, ending at short transverse carina, separated by 0.75x its length from border of petiole socket; depression above petiole socket subrectangular, well-defined, enclosed by risen sharp carina. Lateral surface shiny, with sparse, superficial foveolae and with fine diagonal ridges, more distinct near posterolateral and dorsolateral angles. Propodeal side delimited dorsally by longitudinal carina that extends from spiracle to middle of posterolateral angle. Dorsal border of petiole socket flat except for deep concavity above orifice of apodeme (Fig. 11) Propodeal sternite absent.

Gaster: Tergum I-IV moderately convex. Tergum I with well defined, and II and III with ill-defined subapical constrictions. Tergum I 3x as long as apical width, 2.5x as long as II, with sides slightly diverging at basal third, more strongly so on median, and slightly again in apical third; sternum VIII (Fig. 1) densely setose at apical half, with apical half narrow and elongated, about three times broader at base than at apex, with a shallow subtrapezoidal apical emargination, defining two short latero-apical spine-like processes; gonostyle of genitalia (Fig. 2-3) apically uniramous,

with mesal inner projection; volsellar lobes touching each other.

Notes on females

Since I described this species I have seen more specimens. I include here characters that I did not mention in the original description. The hindcoxa venter has a small subapical tuft of setae, hardly discernible under a light stereoscope. When viewed under a SEM, this structure is seen to be a depression with groups of minute pores interspaced by setae (Figs. 7 and 8).

The species is now known to occur southwest from Surinam to Acre, Brazil, and southeast to Espírito Santo, Brazil. Material examined: SURINAM: *Maronijne*: Anapaiké (Rio Lawa), xi.1963 (B. Malkin) female (Holotype, MZSP). BRAZIL: *Amazonas*: Rio Tarumã-mirim (3°2'S, 60°17'W), various dates (M.V.B. Garcia col.) 3 females, 4 males (MZSP, INPA, UFVB); BR 174 ZF 3 km 23, 2°26'S, 59°51'W, 20.x.1986 (M.V.B. Garcia col.) 1 female (MZSP); BR 174 km 70, 2°23'S, 59°56'W, 4.ix.1987 (M.V.B. Garcia col.) 1 female (MZSP). *Acre*: Rio Branco, 24.iv.1997, 1 female, 27.iv.1997, 1 female, 1 male, 10.v.1997, 1 female (S.F. Silva leg.) (MZSP). *Sergipe*: Santa Luzia do Itanhý, Crastro, 11°22'36,7"S, 37°24'58,2"W, Armadilha [trap] Malaise, trilha [trail], pto. 3 [point], 1-4.viii.2001 (M.T. Tavares & equipe col.). *Babia*: Mata de São João, Reserva de Sapiranga, 12°33'37,2"S, 38°02'55,3"W, Armadilha [trap] Malaise, trilha [trail], pto. 4 [point], 22-26.vii.2001 (M.T. Tavares & equipe col.). *Espírito Santo*: Linhares, Res. [Reserva] Biol. [Biológica] Sooretama, 18°58'02,8"S, 40°07'53,6"W, Armadilha [trap] de Malaise, trilha [trail], pto. 1 [point], 24-27.ii.2002 (C.O. Azevedo & equipe col.).

Trypoxylon scrobiferum Richards, 1934

(Figs. 4-6, 9)

Trypoxylon scrobiferum Richards, 1934: 253, Fig. 4. Holotype: female: Guyana: *Essequibo*: Essequibo River, Moraballi Creek, 22.ix.1929, (Oxf. Univ. Expedn.), (B.M. 1929-485; 2584; B.M. Type Hym. 21.481); Richards, 1936: 462; Vesey-Fitzgerald, 1938:191; Bohart & Menke, 1976:349; Amarante, 2002:51.

I examined the holotype, a female, five other females and one male, noticing some details imprecisely described by Richards (1934). I also present a description of the hitherto unknown male.

Description of Male

Measurements. HW = 1.63-2.00 mm, FWL = 4.3-5 mm; Proportions: HW/HL = 1.13-1.15, HW/EV = 4.5-5.5, HW/EC = 8.75-9.55, EV/EC = 1.8-1.9, FS/EV = 0.7-0.8; Ratios: EL:EC:EV:EE = 1.08-1.1:0.15-0.15:0.25-0.3:1.0, OO:IO:HO = 0.17-0.2:0.5-1:1.0, AA:EA:AF = 0.2-0.3:0.2-0.3:1.0.

Color: Body black. Pale to orange yellow are: scape, pedicel, anterior of flagellum or flagellomeres I-VIII and apex of XI, mandibular basal half, fore and mid tibiae and tarsi, apex of fore and midfemora, base of hindtibia, basal 0.5 of hindbasitarsus, apex of hindtarsomeres I-III, hindtarsomere IV, tibial spurs, basal 0.66 of tergum II, apex of terga II, III and IV, sternum II. Medial portion of mandible red. Dark reddish brown are: apex of mandible, dorsum of scape, posterior surface of flagellomeres I-VIII, whole flagellomeres IX and X and base of XI, apical margin of clypeus, trochanters and femora, hind tibia and tarsus, terga I, III-VI, apical 1/3 of tergum II, sternum I, III-VI. Hind margin of pronotal collar whitish yellow.

Vestiture: Silver to pale gold, except for white to yellowish white on tibiae and tarsi. Clypeus and frons below anterior ocellus with dense vestiture, denser and concealing sculpture below dorsal margin of eye emargination. Clypeus with scattered, downwardly oriented, long pale yellow setae. Gena densely covered by decumbent setae. Thorax laterally and ventrally with moderately dense decumbent setae. Scutum, scutellum and propodeal dorsum with erect, short setae. Patches of dense, decumbent setae on: hind dorsal margin of collar, lateral margin of scutum, mesopleura anteriorly to episternal sulcus and midcoxa, subalar area anteriorly, posterior surface and posterolateral angles of propodeum. Terga pubescent, through I and II more sparsely.

Head: Frons and eye emargination narrow, dull, colliculate. Supraantennal carinae sharp, long, markedly elevated, diverging from each other, forming an obtuse angle at its middle, reaching the tangent line of upper edge of eye emargination. Frontal prominence elevated, enclosed laterally by supraantennal carina; frontal carina fine, slightly elevated, posterior truncation equal to 0.5 diameter of median ocellus, bifurcating arms U-shaped, short, with length about 0.33x length of lower branch. Clypeal disc almost flattened; clypeus free margin reflexed, thin; apical rim distinct, shiny, superficially rugulose; apical border gently sinuate, with a short mid lobe gently concave at apical margin, excavated from beneath. Anterior ocellus in shallow depression. Vertex with small swelling behind each hindocellus. Flagellomere I 0.65x as long as II+III, 3x as long as wide, flagellomeres II and III 2x as long as wide, IV 1.5x, V 1.15x, VI-X 1x, flagellomere XI sub conical 1,15x as long as X+IX. Occipital carina interrupted behind hypostomal carina, interrupted tip connected to hypostomal carina by fine longitudinal carinulae; horizontal area behind hypostomal carina 1,7x as broad as fore basitarsus width.

Thorax: Dorsolateral angles of pronotal collar narrowly rounded, prominent. Pronotal collar with distinct median dorsal prominence. Prosternal transverse carina sharp, reflexed and raised, vanishing toward middle. Scutum, scutellum and mesopleuron moderately shiny, finely and superficially reticulate, with moderately close to sparse, superficial, fine punctures. Omaulus evanescent, indicated under pronotal lobes, short, running by 0.15x of distance to episternal sulcus, subomalous well developed, elevated, ending well beyond episternal sulcus. Length of precoxal carina 0.5x length of mesopleural suture. Mesopleural wing pro-

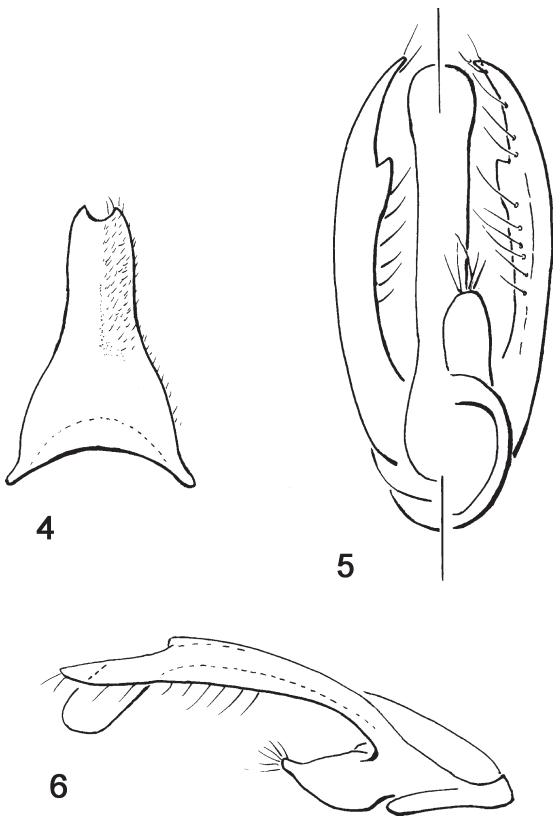


Plate 2: Figs. 4-6. *Trypoxylon scrobiferum* Richards, male; 4, sternum VIII, ventral view; 5 and 6, male genitalia; 5, left half, dorsal view, right half, ventral view; 6, lateral view.

cess bordered by simple ridge, a little widened on hind margin. Metapleural flange narrow. Intercoxal carina arcuate, ventrolateral intercoxal carina present. Dorsoposterior carina of hindtibiae straight, uniformly elevated, ending abruptly subapically, well apart from trochanter emargination. Hindtibial anterior surface flattened, forming an angle with dorsal surface. Forewing vein R1 not extending beyond apex of marginal cell; forewing veinlet 1r-m of submarginal cell forming approximately 90° with vein sector RS+M. Outer row of hamuli on hindwing 2x its length apart from inner row.

Propodeum: Dorsal surface of propodeum with longitudinal or diagonal ridges that become transverse toward apex, dorsal enclosure slightly depressed posteriorly. Posterior surface with broad, moderately deep longitudinal sulcus, ending at short transverse carina, separated by its length from border of petiole socket; depressed area above petiole socket subtrapezoidal, well-defined dorsally by fine and elevated carina. Lateral surface shiny, with sparse, superficial foveolae and fine diagonal ridges, more distinct near posterolateral and dorsolateral angles. Propodeal side delimited dorsally by longitudinal carina that extends from spiracle to petiole socket. Dorsal border of petiole socket flat except by a deep concavity above orifice of apodeme. Propodeal sternite present, forming Y-shaped sclerite that encircles the base of coxae and touches the ventral margin of propodeum.

Gaster: Tergum I-IV moderately convex. Tergum I with well defined, II and III with ill-defined subapical constrictions. Tergum I 3.2x as long as apical width, 1.45x as long as II, with sides slightly diverging at basal third, more strongly so on median, and slightly again in apical third; sternum VIII (Fig. 4) very similar to that of *T. anapaïke*, but narrower at base, about two times broader at base than at apex, 1.65x as long as broad at base, shallowly emarginate apically, with two blunt lateroapical tooth-like processes; gonostyle with inner subapical tooth (Fig. 5).

Notes on Females

Richards' description is sufficient to characterize the female, but the following important characters were overlooked or imprecisely described by him. The hindocelli almost touch the eyes (as corrected by Richards in a latter paper [1936]), the separation is less than 0.2x a hindocellar diameter. The antennal sockets are separated by 0.6x a socket diameter. The free clypeal margin has an ill-defined sub-rectangular median lobe.

The omaulus is present, although very short, almost indiscernible. The hindcoxa has a minute subapical ventral tubercle (Fig. 9). The propodeum has a dorsolateral carina (Richards described it as "[Propodeum] Sides well defined above"). A propodeal sternite is present.

Material examined: GUYANA: *Essequibo*: Essequibo River, Moraballi Creek, 22.ix.1929, (Oxf. Univ. Expedn.), (B.M. 1929-485; 2584; B.M. Type Hym. 21.481) 1 female (BMNH, Holotype). BRAZIL: *Amapá*: Rio Anicohi, 30.vi.1959, J. Lane col., 1 female (MZSP). *Pará*: Santarém, Curuá-Una, 17.xi.1997, bacía amarela [yellow pan], A.R. Lisboa. *Amazonas*: Manaus, Faz. Esteio, 2°24'26"S, 59°43'40"W, 11.ix.1989, E.F. Morato col., 1 female (MZSP) Rio Solimões, 3°15'S, 58°58'W, 19.viii.1991, M.V.B. Garcia col. (MZSP); Rio Tarumã-mirim, various dates, M.V.B. Garcia col. 2 females (INPA) 1 female (MZSP). *Goiás*: Serra da Mesa survey (Niquelândia), 14°1'3"S, 48°18'4"W, malaise across stream, N. Johnson col., 1 male (MZSP).

DISCUSSION

Comparative notes

Trypoxylon scrobiferum and *T. anapaïke* are easily distinguished from each other by the presence of the long and well developed supraantennal carinae in *T. scrobiferum*, and their absence in *T. anapaïke*; the flattened clypeal rim in *T. scrobiferum*, and convex rim in *T. anapaïke*; the free clypeal margin of with a very short sub-rectangular lobe in *T. scrobiferum*, with an uniformly convex outline in *T. anapaïke*. The males of the two species can also be separated by the shape of sternum VIII and male genitalia (compare Figs. 1-3 with Figs. 4-6). The dorsal carinulae of the propodeum are more delicate and sparser in *Trypoxylon scrobiferum* and the propodeal dorsum is not so depressed as in *T. anapaïke*.

Key to subgenera of *Trypoxylon* and species of the *scrobiferum* group

The following key can be used to identify the *scrobiferum* group and its species, and separate them from the other *Trypoxylon*. Also, it restricts the diagnostic characters for *Trypargilum*, as presented by Richards (1934) and Bohart & Menke (1976). I did not include

all species groups of both subgenera, as the revised key for species groups given by Bohart & Menke (*op. cit.*) is still satisfactory.

1. Dorsal border of petiole socket never convex, broadened, forming concave or flat band with small slightly more depressed crescent-like area above apodeme orifice (as in Figs 12 or 13); dorsolateral angles of propodeum without longitudinal carina; propodeal sternite absent; male sternum VIII with slender apicolateral processes, as long as half or more of sternum length; gonostylus uniramous, at most with mesal inner projection Subgenus *Trypargilum*
Dorsal border of petiole socket convex, narrowly bandlike or merely sharp edged, often with posterad projecting lamella or if flat and broadened with distinct impressed crescent-like area above petiole (Figs. 11); dorsolateral angles of propodeum with or without longitudinal carina; propodeal sternite present or absent; male sternum VIII at most with short apicolateral processes, when elongate, less than half of sternum length (in some Old World species); gonostylus bi- or uniramous *Trypoxylon* s.s.
2. Omaulus present, although very short and inconspicuous. Subomaulus crossing diagonally episternal sulcus. Dorsal border of petiole socket flat and broadened, with distinct impressed crescent-like area above petiole (Figs. 11); male sternum VIII with short lateroapical processes and distal half elongated, narrow, as in Figs. 1 and 4 *scrobiferum* group 3
Omaulus absent. Subomaulus absent or transverse near episternal sulcus. Dorsal border of petiole socket convex, narrowly bandlike or merely sharp edged, often with a posterad projecting lamella. Male sternum VIII various (when with distal half distinct, not so elongated and narrow as in Figs. 1 and 4, and with no apicolateral processes)
..... remaining species groups of *Trypoxylon* s.s. (see Bohart & Menke, 1976:344)
3. Supraantennal carina long and well-developed; clypeal rim flattened; the free margin of clypeus with a very short sub-rectangular lobe; female hindcoxa with a minute subapical ventral tubercle (Fig. 9); propodeal sternite present.
..... *T. scrobiferum* Richards
Supraantennal carina absent; clypeal rim convex; free margin of clypeus with uniformly convex outline; female hindcoxa with a minute subapical ventral spot (Figs. 7-8); propodeal sternite absent.
..... *T. anapaike* Amarante

The *scrobiferum* species group

The proper placement of *T. scrobiferum* and *T. anapaike* into the currently recognized and species groups of *Trypoxylon* is puzzling. They have character conditions that has been regarded exclusive either of *Trypoxylon* s.s. or of *Trypargilum*. Originally, Richards (1934) included *T. scrobiferum* as a new species in his *aureovestitum* subgroup, part of the *nitidum* species group of *Trypargilum*. Among the characters he listed to define the subgroup, only one was unique within the subgenus, the long and well developed supraantennal carinae ("limiting keels of the antennal scrobes") that enclose an area two times as long as broad. In fact, the shape of this carina is almost identical in *T. aureovestitum* and *T. scrobiferum*, but *T. scrobiferum* has characters that are only found in *Trypoxylon* s.s., as the dorsolateral carina of propodeum, the female hindcoxa with a ventral tubercle, the male VIII sternum shallowly emarginate apically with very short lateroapical apical processes, and the propodeal sternite. As in all other *Trypargilum*, *T. aureovestitum* has no dorsolateral carina of propodeum, the female hindcoxa lacks any ventral tubercle or pit, the male VIII sternum is deeply emarginate apically with long apical processes, and has no propodeal sternite. Furthermore, the same characters that suggest placement of *T. scrobiferum* in *Trypoxylon* s.s., are also found in *T. anapaike*, indicating that these two species constitute a natural group, the *scrobiferum* group.

Diagnosis

Trypoxylon scrobiferum and *T. anapaike* share the following unique combination of characters: (1) pronotal collar with triangular dorsoposterior median prominence; (2) omaulus present, although short and inconspicuous; (3) subomaulus well-developed, diagonally extending back beyond episternal sulcus; (4) dorsoposterior carina of hindcoxa straight and elevated, ending at coxal apex, not touching trochanter acetabulum; (5) hindcoxa with minute modified area on ventral surface (Figs. 7-9); (6) hind wing with two rows of hamuli separated from each other by more than length of apical row, forewing veinlet 1r-m of submarginal cell forming approximately 90° with vein sector RS+M; (7) propodeum with dorsolateral longitudinal carina (Fig. 10); (8) dorsal border of petiole socket broadened, flat but with deep impressed crescent-shaped area just above the petiole apodeme cavity (Fig. 11); (9) male sternum VIII with proximal half subtrapezoidal and posterior half elongated, with sides nearly parallel, apex shallowly emarginate, with short apicolateral processes

(Figs. 1 and 4); (10) gonostylus simple apically, with inner mesal tooth-like projection.

Among these conditions, only two can be regarded as unambiguous synapomorphies supporting the *scrobiferum* group: the shape of the petiole socket border and the shape of male sternum VIII. The remaining character states may be either symplesiomorphies or homoplasies.

Phylogenetic relationships of *scrobiferum* group

The *scrobiferum* group might be regarded as a new subgenus, having the structure of the petiole socket and the shape of sternum VIII as supporting autapomorphies. However, this proposal would be premature, as the infrageneric classification of *Trypoxylon* needs further study. The main problem is that *Trypoxylon*

s.s. may be paraphyletic (see Bohart & Menke, 1976; Coville, 1982). When Richards (1934) divided *Trypoxylon* in two subgenera, he listed unique character conditions for *Trypargilum* that excluded a heterogeneous assemblage of characters found in the nominal subgenus. That is, none of the characters listed in Richards' diagnosis for *Trypoxylon* s.s. are unique, and the taxon is a rather heterogeneous assemblage of species + species groups. At present, it is hard to find unambiguous synapomorphies supporting the subgenus, making *Trypoxylon* as defined today probably a paraphyletic or polyphyletic grouping. Therefore, the inclusion of the *scrobiferum* group in *Trypoxylon* s.s. should be viewed as tentative.

The *scrobiferum* group shares with some species of *Trypoxylon* s.s. the dorsolateral propodeal carina, modified areas on ventral surface of female hindcoxa, and male sternum VIII shallowly emarginate apically

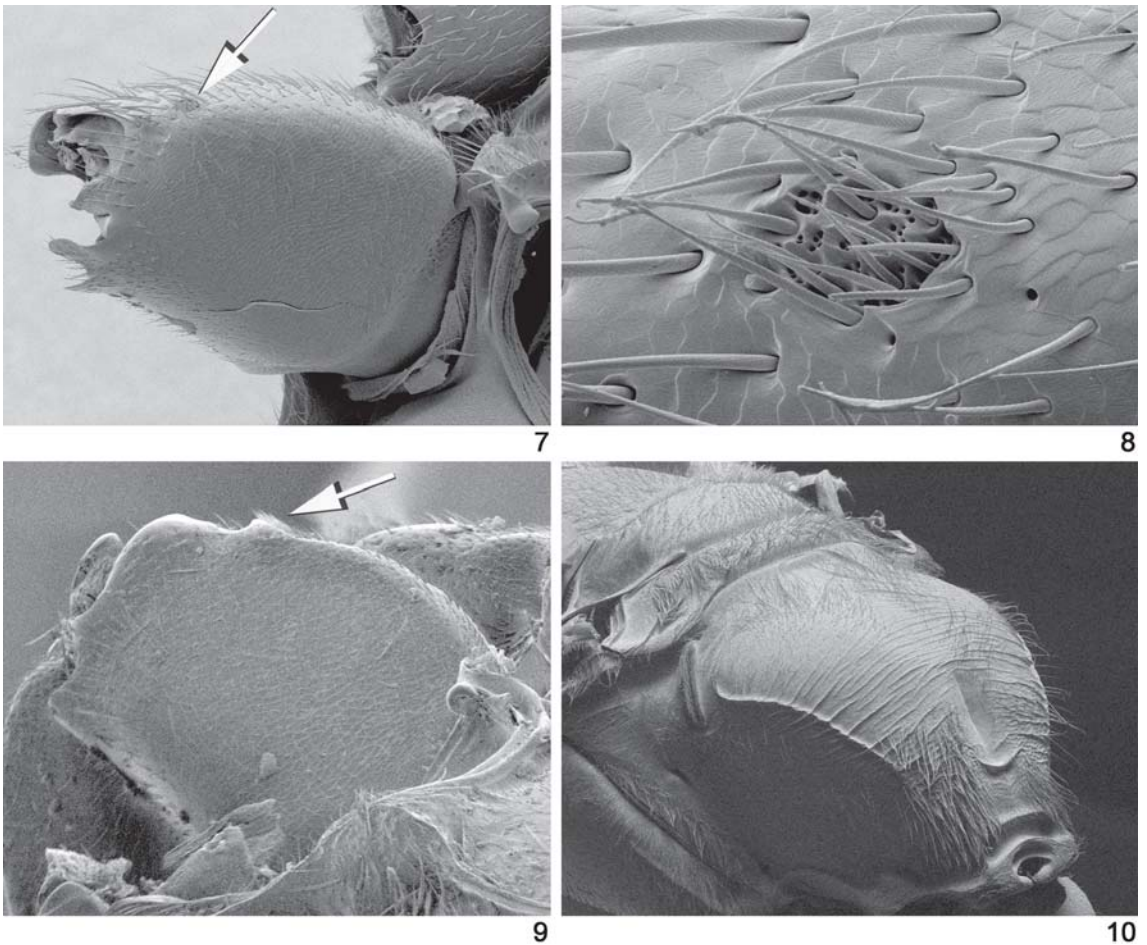


Plate 3: Figs. 7-10. *Trypoxylon anapaikae* Amarante, female, 7 and 8, right hindcoxa, oblique ventral view, arrow pointing apicoventral modified area, 8, detail of apicoventral modified area; *Trypoxylon scrobiferum* Richards, female, 9, right hindcoxa, lateroventral view, arrow pointing apicoventral tubercle; *Trypoxylon anapaikae* Amarante, female, 10, propodeum, oblique dorsal view.

with short lateroapical processes. Also, the shape of the submarginal cell, the space between the hindwing hamuli rows, the pattern of sculpture on propodeal enclosure agree best with *Trypoxylon* s.s., although I feel that these last three characters need to be studied for more species than I have seen (about 95 described and undescribed species of *Trypargilum* and near 140 species of *Trypoxylon* s.s., including a few species of the Old World; see also Bohart & Menke, 1976).

The *scrobiferum* group is certainly closely related to *Trypargilum*. Some character states shared with *Trypargilum* could be regarded as synapomorphic, supporting a sister group relationship between *Trypargilum* and the *scrobiferum* species group (see discussion on characters below). A list of tentative symplesiomorphies shared with *Trypoxylon* s.s. includes the propodeal lateral carina and the median prominence on the pronotal collar.

Here I discuss the phylogenetically significant characters of the *scrobiferum* group, which can be extended to the phylogeny of the genus.

(1) *pronotal collar with a dorsoposterior median prominence.*

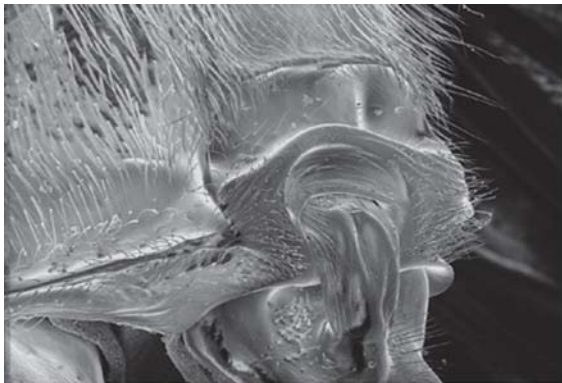
The pronotal collar with a distinct mesal prominence is found in some species of the *fabricator* group, as *T. cornigerum*. In other groups of *Trypoxylon* s.s. and *Trypargilum*, the dorsal outline of pronotal collar is smoothly convex or slightly angled in the middle.

(2) *omaulus present, although short and inconspicuous.*

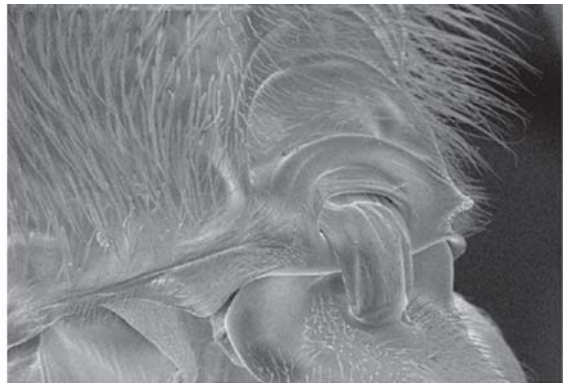
The omaulus is found in many species of *Trypargilum*, varying from well-developed to barely discernible. It is absent in all species groups of *Trypoxylon* s.s., except in the *scrobiferum* group.

(3) *subomaulus well-developed extending back beyond episternal sulcus.*

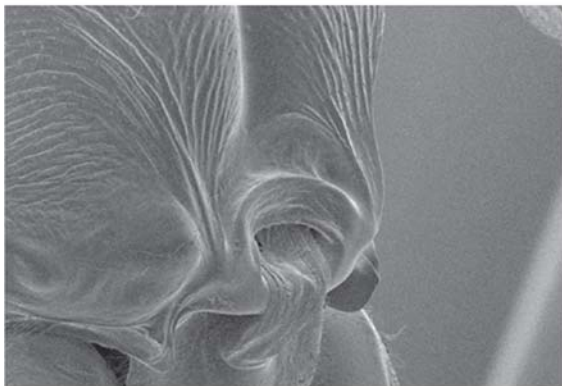
The subomaulus is found in *Trypargilum* in the species group *nitidum*, restricted to the species complexes of *punctulatum*, *spinosum*, *fugax* and to *Trypoxylon aureovestitum*. In these species complexes and in the *scrobiferum* group, it ends diagonally at or a little beyond the episternal sulcus. In *Trypoxylon* s.s. the



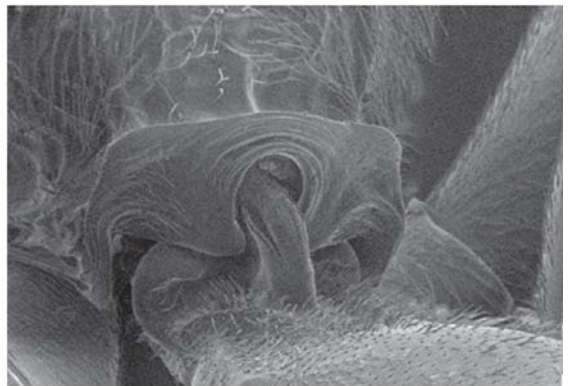
11



12



13



14

Plate 4: Figs. 11-14. Oblique posterior view of petiole socket: *Trypoxylon anapaikae* Amarante, 11; *Trypoxylon aureovestitum* Richards, 12; *Trypoxylon buchwaldi* Richards, 13; *Trypoxylon* sp. *rufidens* species group, 14.

submaulus becomes transverse near the episternal sulcus.

- (4) *dorsoposterior carina of hindcoxa straight and elevated, ending at apex of coxae, not touching trochanter acetabulum.*

In the *scrobiferum* group the dorsoposterior carina of hindcoxa resembles more that of the *excavatum* complex of the *nitidum* group and that of some other species in *Trypargilum* than the shape found in *Trypoxylon* s.s.. This character is very variable in *Trypoxylon* s.s. and it needs to be more carefully studied in other species of *Trypoxylon* s.s. to evaluate its significance for group diagnosing.

- (5) *Female hindcoxa with a minute modified area on ventral surface (Figs. 7-9).*

The presence of a modified area on the venter of the female hindcoxa is another character restricted to *Trypoxylon* s.s.. This feature has not been recorded in *Trypargilum*, and it is present in *Trypoxylon* s.s., except in the species groups *marginatum* and *rufidens*. The feature is not morphologically uniform in *Trypoxylon* s.s., the modified area may be constituted by a small tubercle, a pit or a membranous spot, and it may be near the apex or the base of the hindtibial ventral surface (Richards, 1934; see also Pulawski, 1984, Figs. 2b, c, d, 5d, e, f, 7b, c, d). In the *scrobiferum* group two different conditions are found, a minute pit in *T. anapaikae* and a small tubercle *T. scrobiferum*.

- (6) *hind wing with two rows of hamuli separated from each other by more than length of apical row, forewing veinlet 1r-m of submarginal cell forming approximately 90° with vein sector RS+M.*

These characters in the wings of the *scrobiferum* group agree with the prevailing conditions in *Trypoxylon* s.s.. In the *scrobiferum* group, the angle formed by the junction of the outer veinlet of the submarginal cell with RS+M is nearly a right angle and the outer hamuli row on hindwing is separated by more than its length from the inner row. Bohart & Menke (1976) discussed these characters, pointing out that they are not uniformly distributed within both subgenera.

- (7) *propodeum with dorsolateral longitudinal carina (Fig. 10).*

The dorsolateral carina of propodeum can be found in many species of all groups of species of *Trypoxylon* s.s. but the *fiebrigi* group, while in *Trypargilum* this carina is absent and the propodeal dorsolateral angles are at most transversely ridged. It is not clear if

this carina is a synapomorphy of *Pison* and *Trypoxylon* or has arisen independently in the two genera. Menke (1988) regarded the presence of a dorsolateral carina of the propodeum as apomorphic in the Larrini, Miscophini and Trypoxylini, in this last tribe occurring in *Pison* and *Trypoxylon*. Probably, this character state should be regarded as symplesiomorphic in the *scrobiferum* group, as it is shared with other species groups of *Trypoxylon*.

- (8) *dorsal border of petiole socket broadened, flat but with a conspicuous impressed crescent-shaped area just above the petiole apodeme cavity (Figs. 11).*

The character formerly used to include *T. scrobiferum* and *T. anapaikae* in *Trypargilum* (Richards, 1934; Amarante, 1992) was the dorsal margin of the petiole socket forming a broad and concave band (Figs. 11-13; see also Richards, 1934, fig. 21; Bohart & Menke, 1976, Fig. 108d). This character is loosely defined, with an apparently well defined state, found in *Trypargilum* and its multiform counterpart present in *Trypoxylon* s.s.. In *T. anapaikae* and *T. scrobiferum* the petiole socket border is broad, but has a contrasting concave area just above the apodeme cavity (Fig. 11). In *Trypargilum* the border of petiole socket is uniformly concave, or when a concave area above petiole socket is present it is at most a little more concave than the surrounding surface of the socket border (Fig. 12). Some species of *Trypargilum*, as *T. vagulum* Richards, may present the socket border similar to that of the *scrobiferum* group at first glance, but the concavity is not so large and deep. In *Trypargilum* the socket border is not so uniform, although it is always flat or concave. For instance, in the *albitarse* group and the *punctulatum* complex (a subgroup of the *nitidum* group, sensu Coville, 1982) the whole upper socket border is broadly and deeply concave (Fig. 13, *Trypoxylon buchwaldi* Richards, *albitarse* species group), while in most *Trypargilum* the socket border tends to be at most gently concave with a small crescent-shaped area a little more impressed (Fig. 12). These differences might even support a more precise delineation of states for this character within *Trypargilum*, splitting it in at least two different states. By contrast, the petiole border in *Trypoxylon* s.s. is primarily convex and in many cases narrow. These various shapes are clearly a reunion of a number of different character states that are difficult at the present to delineate within the subgenus, but it is clear that such character redefinition is mandatory for understanding the systematics of the subgenus. Anyway, the border of the petiole socket in a few groups of *Trypoxylon* s.s. morphologically ap-

proaches the form found in *Trypargilum* or in the *scrobiferum* group. For instance, in *T. mojuba* Amarante and some species of the *rufidens* group (Fig. 14), the petiole border has a slightly convex broad band. The difference between the forms in these two species groups with some *Trypargilum* or the *scrobiferum* group involves just a modification of the margin just above the apodeme cavity, which is convex rather than concave.

(9) *male sternum VIII with proximal half subtrapezoidal and posterior half elongated, with sides nearly parallel, apex shallowly emarginate, with short apicolateral processes (Figs. 1 and 4).*

The shape of male sternum VIII in the *scrobiferum* group better agrees with the diagnosis for *Trypoxylon* s.s. In *Trypoxylon* s.s. sternum VIII has a variable apex, but bears at most a short apical processes, while in *Trypargilum* these apical processes are slender and long, a putative synapomorphic condition for this subgenus. As apomorphic conditions for the *scrobiferum* group, the VIII sternum may present the narrow and elongated apical half, distinct from the subtrapezoidal basal half, and perhaps its vestiture, composed by short uniform setae densely arranged on the distal half. Among various shapes in *Trypoxylon* s.s., sternum VIII uniformly narrows toward the apex, as in *Trypoxylon nitidissimum* (see Richards, 1934: Plate VI, Fig. 5) and *T. gracilimum* (see Richards, 1934: Plate VI, Fig. 8), or present a median or subapical constriction before expanding toward the apex, as in many species of the *scutatum* group (as in Richards, 1934: Plate VI, Fig. 12), but it never assumes the shape seen in the *scrobiferum* group (for other examples, see Arnold, 1945; Leclercq, 1965; Tsuneki, 1981). In other species groups of *Trypoxylon* s.s., when the apical portion is narrow and distinct, it is very short. The dense covering of uniform, fine and short setae is more difficult to assume as an apomorphic condition, as similar covering is found in some species of *Pison* (see Menke, 1988) and in *Trypoxylon carpenteri* (see Richards, 1934: Plate VI, Fig. 7). In most species of *Trypoxylon* s.s. there is a tendency of sternum VIII to bear long setae apically, in many species forming apicolateral tufts of long setae. It is well beyond the scope of this paper to attribute different states to characters of sternum VIII for other species. However, a more comprehensive study of the genus will certainly delineate a number of states, leading to a conclusion that the condition exhibited by species of *Trypargilum* is merely a state that can be included in a character transformation series with other conditions found in *Trypoxylon* s.s..

(10) *gonostyli simple apically, with a inner mesal tooth-like projection (Figs. 2 and 5)*

The male genitalia in the *scrobiferum* group agree with those found in *Trypargilum* and the groups *rufidens* and *marginatum* of *Trypoxylon* s.s., differing from the remaining species groups in *Trypoxylon* s.s. by the uniramous gonostyle. A bifurcate gonostylus are found only in a few Crabronidae, in the Trypoxylini (some *Trypoxylon* and *Pison*) and in the monotypic subfamily Entomosericinae (Bohart & Menke, 1976). This character state is certainly apomorphic within the family, and might constitute a synapomorphic condition supporting the sister-group relationship of *Pison* and *Trypoxylon*. However, both genera present a number of species with uniramous gonostyli, and it is difficult to define the polarity of these states. In *T. anapaikae* and *T. scrobiferum* the gonostylus has a median inner projection that could be regarded as a rudiment of a lobe. It differs from the apical lobe seen in most *Trypoxylon* s.s. as it is located dorsally and on the inner side at about the middle of the gonostyle. Also, the shape of the gonostyle in the *scrobiferum* group is similar to those of some other species of *Trypargilum*, as *T. aureovestitum* and *T. fugax*. The volsellar lobes are partially fused in the *scrobiferum* group; an intermediary condition between the species of *Trypoxylon* s.s. with separated volsellar lobes and *Trypargilum* with fused lobes, although both *Trypoxylon* s.s. and *Trypargilum* present some variation in the degree of fusion.

Additional characters

The sculpture on the propodeal dorsum in the *scrobiferum* group resembles patterns seen in many species of *Trypoxylon* s.s., differing from a general tendency of patterns present in species of *Trypargilum*. In *Trypargilum*, when the propodeal dorsum is ridged, the ridges tend to be dense and diagonal or transverse, being restricted or more evident on propodeal enclosure. In the *scrobiferum* group, the ridges on propodeal enclosure are more spaced and runs mostly longitudinally. On the other hand, the *scrobiferum* group has conditions regarded till now to be present only in *Trypargilum*, the frons continuously flat but the frontal prominence, without any transverse sculpture and the frontal carina not extending ventrad between the antennal sockets.

Subgenera in *Trypoxylon*

The placement of the *scrobiferum* group in the subgenus *Trypoxylon* narrows the concept of

Trypargilum, and may even justify the synonymy of *Trypargilum* under *Trypoxylon*, with the species groups *albitarse*, *superbum* and *nitidum* as members of *Trypoxylon*. Alternatively, the ideas of Bohart & Menke (1976) could be adopted, who suggested that *Trypargilum* could be split into at least three subgenera – an opinion also shared by Coville (1982) – and some groups of *Trypoxylon* could be elevated to subgenera. The creation of the *scrobiferum* group adds offers support to these ideas, as I have shown here that some diagnostic characters of *Trypargilum* should be abandoned and others might be better regarded as the reunion of more than one character state into a single one. At the present, the autapomorphies of *Trypargilum* include the border of petiole socket uniformly concave or at most with an area slightly more depressed than its surrounding area and the male VIII sternum with long apical processes. However, if the shape of the petiole socket might be demonstrated to be a union of two or more distinct states, the male VIII sternum with long processes might be the only truly synapomorphic state supporting *Trypargilum*. Other conditions shared by the *scrobiferum* group and *Trypargilum* such as the frontal structure, presence of omaulus and subomaulus, gonostyli apically simple, might be regarded as symplesiomorphies retained within the subgenus.

RESUMO

Os machos previamente desconhecidos de Trypoxylon scrobiferum Richards e Trypoxylon anapaiké Amarante são descritos e a sua genitália ilustrada. Ambas espécies são transferidas do subgênero Trypargilum para o subgênero Trypoxylon, incluídas em um novo grupo de espécies, grupo scrobiferum, aqui criado para abrigá-las.

PALAVRAS-CHAVE: Hymenoptera, Sphecidae, Crabronidae, Crabroninae, Trypoxylini, *Trypoxylon*, *Trypargilum*, Systematics.

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