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Ultrastructure of *Antoonops*, a New, Ant-Mimicking Genus of Afrotropical Oonopidae (Araneae) with Complex Internal Genitalia

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ABSTRACT

Antoonops, a new genus of the spider family Oonopidae, is described from West Africa. The genus contains four new species, all known from both sexes: *A. corbulo* (type species), *A. bouaflensis*, *A. iita*, and *A. nebula*. All species mimic ants and exhibit a pronounced sexual dimorphism. Several new ultrastructural features are reported, including putative gland pores associated with the coxal insertions, specialized cheliceral setae, and peculiarly modified male endites. The potential of these and other traits as phylogenetically informative characters is discussed. SEM investigation of the internal female genitalia of *A. corbulo* reveals the presence of two peculiarly shaped sclerites embedded in the walls of the uterus externus and a reproductive tract with an apparent flow-through design.

INTRODUCTION

The Oonopidae or goblin spiders are a worldwide family of minute, haplogyne spiders whose greatest diversity occurs in the tropics and subtropics (Jocqué and Dippenaar-Schoeman, 2006). Several lines of evidence suggest that the presently recognized 491 species and 73 genera (Platnick, 2008) represent only a small fraction of actual

oonopid biodiversity. First, many geographical regions have been very poorly sampled. These may be exemplified by West Africa where no more than three species have been recorded, the most recent report dating back to 1907 (Platnick, 2008). Second, recent investigations have demonstrated the presence of an abundant, varied, and hitherto largely unexplored oonopid fauna living in the canopy of certain tropical forests. For exam-

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ple, in a species richness estimation study in a lowland forest in Ghana (W. Fannes, D. De Bakker, K. Loosveldt and R. Jocqué, unpubl. data), 12 canopy samplings yielded 11 morphospecies belonging to five genera. Finally, due to their small size oonopids have in the past not been optimally collected and studied and as a result their diversity has probably been underestimated even in those regions and habitats that were relatively intensely sampled. Renewed research efforts, specifically targeting the Oonopidae, could potentially lead to a tremendous increase in the number of nominal species, as hinted at by recent studies of Saaristo (2001, 2002), who documented 20 genera from the Seychelles where only nine were previously known to occur (Benoit, 1979).

The Oonopidae have been taxonomically and phylogenetically understudied despite their considerable morphological diversity (Saaristo, 2001). Simon established the family in 1890 and later classified the then-known genera according to their degree of body sclerotization, dividing them into two informal subgroups, the "Oonopidae loricati" and "Oonopidae molles" (Simon, 1890, 1893). The monophyly of these groups is, however, doubtful (Platnick, in litt.) and no other formal or informal classifications have been proposed, leaving the Oonopidae in a state of taxonomic chaos. Furthermore, the evolutionary relationships within the family were never examined using a cladistic approach. On a higher level, phylogenetic analysis of a large morphological data set (Platnick et al., 1991) suggested that the Oonopidae belong to the superfamily Dysderoidea and are the sister group of the Orsolobidae. Expanding Platnick et al.'s matrix by adding several characters dealing mainly with respiratory system anatomy confirmed this result (Ramírez, 2000). However, since these studies addressed the interrelationships between *all* families of haplogyne spiders the number of terminals included per family was necessarily limited (oonopids and orsolobids being represented by a single species each), making the analyses potentially highly susceptible to taxon-sampling effects. A thorough cladistic study of the Oonopidae, encompassing a wide selection of both ingroup and outgroup taxa, is therefore urgently needed to 1) rigorously test the

monophyly of the family and identify its synapomorphies, 2) resolve the major lineages within the Oonopidae, and 3) corroborate or refute the supposed sister-group relationship with orsolobids. Unfortunately, inferring a reliable phylogeny is presently unfeasible due to a conspicuous lack of ultrastructural data: only three genera have been more or less comprehensively studied by SEM (Platnick and Brescovit, 1995; Höfer and Brescovit, 1996; Ott and Brescovit, 2004).

The internal anatomy, biology, and behavior of oonopids are similarly poorly known, the available data being scarce, scattered, and often anecdotal. A noted exception is the recent work of Burger and coworkers (Burger et al., 2003, 2006; Burger, 2007) who studied the functional morphology of the female reproductive system in considerable detail.

Here we report four new, ant-mimicking species from West Africa whose assignment to a separate genus is proposed as a working hypothesis, to be tested by future cladistic analyses. The potential use of several traits as phylogenetically informative characters is discussed. In addition, the internal morphology of the female genital system is investigated by SEM.

MATERIALS AND METHODS

All measurements are in millimeters (precision = 0.01 mm) and are taken from the holotype (male) and allotype (female), unless explicitly noted otherwise. Total length is the sum of carapace length and dorsal scutum length. Measurements of legs are listed as: total length (femur + patella + tibia + metatarsus + tarsus). Eye diameters and distances between eyes were recorded from a frontal point of view. Most photographs were produced by taking several digital images at varying planes of focus with a Toshiba 3CCD camera mounted on a Leica MZ125 dissecting microscope and then integrating these images with Syncroscope's Automontage software, or by using a Leica MZ16A dissecting microscope, a DFC500 camera, and Leica Application Suite software. For SEM photos, specimens were cleaned ultrasonically, dried in HMDS, gold coated, and examined and photographed with a JEOL 6480 LV scanning electron microscope. The internal anatomy

was investigated by excising the ventral scuta and treating them for several hours with KOH or pancreatin. The remaining tissue was removed using fine needles and the scuta were then processed for SEM.

Pairs of specimens of *A. corbulo* have been deposited in the American Museum of Natural History (New York), the California Academy of Sciences (San Francisco), the Western Australian Museum (Perth), the Queensland Museum (Brisbane), and the Instituto Butantan (São Paulo).

TERMINOLOGY: We use the term *carapace* to denote the dorsal part of the prosoma. Following Saaristo (2001) and Saaristo and van Harten (2006) the two ventral scuta of females are simply called anterior ventral scutum and posterior ventral scutum, or anterior and posterior scutum for short. Many oonopids, including *Antoonops*, also have a semicircular scutum surrounding the ventral and lateral sides of the spinnerets. We agree with Saaristo (2001) that Simon's name for this structure, "inframammillary scutum", is cumbersome and introduce the term "spinneret scutum" instead. We refrain from adopting Saaristo's proposed replacement names, "anal scutum" (Saaristo, 2001) and "posterior ring" (Saaristo and van Harten, 2006) because a true anal scutum, clearly separated from the spinneret scutum and surrounding the dorsal and lateral sides of the anal tubercle, was found in *Antoonops* (see systematics section).

ABBREVIATIONS: ALE = anterior lateral eyes, ALS = anterior lateral spinnerets, CH = carapace height, CL = carapace length, CW = carapace width, DSL = dorsal scutum length, DSW = dorsal scutum width, MNHN = Musée Nationale d'Histoire Naturelle, Paris, MRAC = Musée Royal de l'Afrique Centrale, Tervuren, PLE = posterior lateral eyes, PLS = posterior lateral spinnerets, PME = posterior median eyes, PMS = posterior median spinnerets, SEM = scanning electron microscopy, TL = total length.

SYSTEMATICS

Antoonops, new genus

TYPE SPECIES: *Antoonops corbulo*, new species.

ETYMOLOGY: The masculine generic name refers to the antlike appearance of these oonopids.

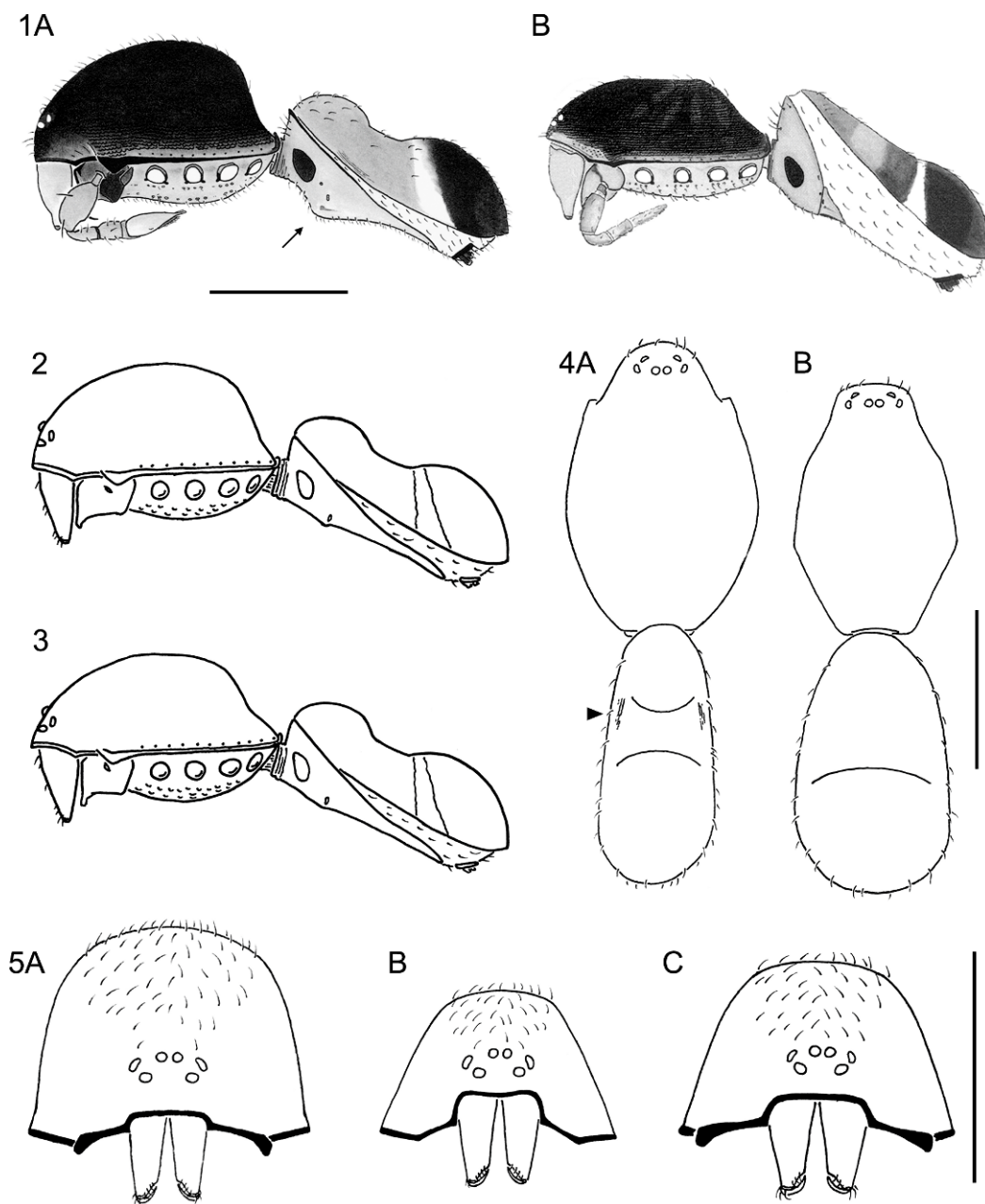
DIAGNOSIS: Both males and females of *Antoonops* can be easily distinguished from all other oonopids by the shape of the dorsum. With the exception of *A. nebula*, all species are also unique among the Oonopidae in having a white transverse band on a relatively darkly colored dorsal scutum. The specific modifications of the male endites also separate *Antoonops* from other known oonopid genera.

DESCRIPTION: Ant-mimicking oonopids with well-developed abdominal scuta. Moderate size (carapace length = 0.75–0.93, total length = 1.63–1.97). Sexual dimorphism pronounced, including major differences in both carapace and abdomen shape and in the morphology of the mouthparts.

Carapace: Shape sexually dimorphic: in females rather low and flat (fig. 13), in males higher and convex, more or less dome-shaped (figs. 15, 17); in both sexes markedly narrowed anteriorly (fig. 4). Carapace margin a dark red, sclerotized ridge; curls upward posteriorly, forming U-shaped channel termed sluice by Saaristo and van Harten (2006); immediately dorsal to outer ridge a horizontal row of very short hairs with modified base (figs. 21, 23), usually appearing as dark points under dissecting microscope. Outer ridge in males with downward-pointing, roughly triangular extension above posterior part of endites; pedipalps attached to endites immediately anteriorly to this prominent extension (fig. 19). Microsculpture (figs. 22, 23) present in both sexes, either covering entire carapace or only part of it. No lateral or dorsoventral constriction of prosoma discernible.

Eyes: Six small eyes, all clearly separated from each other and arranged in characteristic pattern with procurved posterior row (fig. 5). ALE elliptical (height 0.03, width 0.04), distance ALE-ALE 0.08–0.10. PME almost perfectly round, diameter 0.03; PLE appearing slightly kidney-shaped from frontal viewpoint. Distance PLE-PME 0.03–0.04, distance PLE-ALE 0.01; PME separated from each other by less than half their diameter.

Chelicerae: Without lamina. One small cheliceral tooth on promargin (examined: *A. corbulo*, *A. nebula*) (fig. 24, fig. 26). Chelicerae



Figs. 1–5. 1. Habitus of male (A) and female (B) *Antoonops corbulo*, n. sp. 2. Male *Antoonops bouaflensis*, n. sp. 3. Male *Antoonops iita*, n. sp. 4. Dorsal view of male (A) and female (B) *Antoonops corbulo*, n. sp. 5. Frontal view of male (A) and female (B) *Antoonops corbulo*, n. sp. and male *Antoonops iita*, n. sp. (C). Arrow: elevation of ventral scutum. Arrowhead: longitudinal grooves. Scale bars: 0.50 mm.

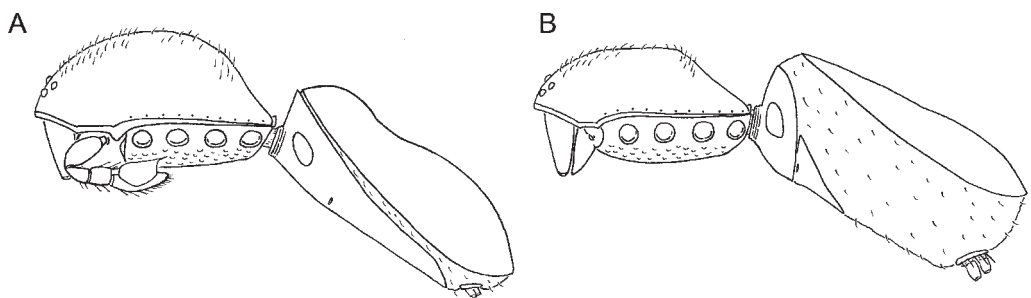


Fig. 6. *Antoonops nebula*, n. sp. (A) Male. (B) Female. Scale bar: 0.45 mm.

slightly constricted proximally. Promargin flanked by double row of modified hairs running toward fang base. Inner row consisting of four hairs (denoted i1–i4 with i1 most distal one; figs. 29, 31); hairs not immediately projecting upward but instead reclining, their most proximal part almost or actually touching cheliceral surface (figs. 29, 31); hair shafts with two rows of small cuticular teeth (fig. 31). Outer row consisting of four flattened, peculiarly shaped hairs (denoted o1–o4 with o1 most distal one); o1–o4 flanking i1–i4, respectively (figs. 29, 31). Long-stalked, medially directed plumose hair (anterior plumose hair, aph; fig. 29) originating between o1 and fang base. Two rather short hairs, often appearing somewhat flattened and blunt-ended, situated on distalmost anterior surface, close to fang base (short hairs, sh; figs. 28, 29). Proximal to double row a modified hair (mh1) flanked by spiniform hair (sph), their bases usually touching each other (fig. 27). Proximal to these a single modified hair (mh2; fig. 27). Inner surface of each chelicera giving rise to long, bent hair (fig. 27) originating proximally from mh2. Fang base flanked posteriorly by three hairs, innermost one plumose (posterior plumose hair, pph; fig. 28). Posterior surface with vertical row of five long, medially projecting hairs and group of usually three spines located close to outer margin of posterior surface (fig. 30).

Mouthparts: Sexually dimorphic. Male mouthparts heavily sclerotized, dark red to black. Endites large, strongly modified (figs. 32–36). Two ventrally projecting processes originating near inner margin of each endite; anterior one largest, its distal surface striking, appearing grooved; posterior one anteroposteriorly flattened, contacting poste-

rior surface of “grooved” process, distally giving rise to three thick, curved setae directed medially or posteromedially (figs. 33–36). Inner margin of each endite forming hollow hook pointing backward (figs. 33–36). Several hairs and short spines present on endites. A small, clear, round spot on each endite; using SEM a medially running band of ridged cuticle visible in this area; in some individuals also an irregular opening (examined: *A. corbulo*, *A. nebula*) (figs. 37, 38). Labium much wider than long; median part projecting forward; fused to sternum (fig. 40). Female mouthparts unsclerotized, not modified. Endites longer than wide, converging, frontal tips almost touching. Serrula with single row of teeth. Labium wider than long, anterior margin concave (fig. 41).

Sternum: Longer than wide, provided with round pits carrying hairs. Well-discernible radial furrows. Males with ridged structure (fig. 37) situated just in front of each anterolateral corner of sternum; structure connected posteriorly to pleura (fig. 37), sclerotized, appearing as small, dark red to black, anterolaterally projecting triangle under dissecting microscope.

Legs: Spineless, with club-shaped femora. Leg formula 4123. Base color white except metatarsus and tarsus pale brown-yellow; parts of some segments dark brown (*A. corbulo*, *A. bouaflensis*, *A. iita*) or dark green (*A. nebula*), giving legs banded appearance (fig. 9); pattern largely similar in all species, with only minor interspecific differences. Each leg with four dorsal trichobothria: one on proximal tibia, two on distal tibia, one on distal metatarsus. Bothrium with proximal hood that passes down sides of trichome aperture, not encircling it; hood completely

covered by numerous low, closely spaced ridges; articulating membrane also ridged (fig. 46). No variation in bothrium structure among legs or among positions on a given leg discernable. Tarsal organ similar on all legs, exposed: receptor region sunken, forming shallow, round to oval depression flanked by low rim only slightly elevated above tarsal surface. Internal border presenting three or more thin, low ridges. Receptor region consisting of group of usually three projected receptor lobes (fig. 47). Distalmost, toward onychium sloping part of tarsus provided with centrally located proprioceptor hair. Two tarsal claws on prominent onychium bearing many setae, some spatulated. Biseriate claws with outer row of about four to five large teeth (fig. 45A) and inner row situated distally along claw rim, close to claw tip; inner row consisting of series of small teeth, regularly spaced at very short distances from each other. Most proximal inner teeth small, becoming gradually larger distally (fig. 45B). Striated microsculpture of leg surface leaving open small, smooth, more or less oval patches; patches often forming a row.

Abdomen: Wider in females than in males (figs. 4, 8). Dorsal scutum large, covering entire dorsal surface of abdomen in both sexes. Shape of dorsal abdomen distinctly sexually dimorphic. Male abdomen with prominent dorsal constriction medially; dorsal scutum consequently with three parts: elevated, almost semispherical anterior part, depressed middle part and elevated, more or less elongated posterior part (figs. 16, 18). Female abdomen with posterior dorsal part raised; dorsal scutum consequently with flat anterior part and elevated posterior part (fig. 14). Ventral scutum of males long, almost reaching spinneret scutum (figs. 1A, 2, 3, 6A); a rather short lateral apodeme visible through integument on either side of sperm pore (fig. 12). Posterior ventral scutum of females triangular (fig. 10); posterior edge never reaching much further than halfway along abdomen, leaving posterior part of ventral abdomen uncovered (figs. 1B, 6B); anterior edge elevated (fig. 63). A lateral apodeme on either side of copulatory orifice (figs. 10, 11). No lateral constriction of either male or female abdomen discernible.

Respiratory system: Opercula large. A band of closely ridged cuticle arising from outer margin of each lung slit and spiracle and running toward lateral edge of ventral scuta (fig. 51). Males with very small opening on either side of sperm pore, close to spiracle (fig. 49); opening often slitlike (fig. 50).

Glands: Numerous small, more or less oval glands with low rim and minute central opening on legs and abdominal scuta (including petiolar tube); also some on carapace. Coxal gland opening a slit in basal part of coxa (fig. 39). A shallow groove where coxal insertions II, III, and IV meet the sternum (fig. 42); anteriormost part of each of these infracoxal grooves scattered with very small openings (figs. 42, 44). Anteriormost part sometimes forming deep, tube-shaped invagination. Coxal insertions I, II, and III each with two clusters of small openings situated just outside of their outer margin (figs. 42, 43); number of openings per cluster varying from two to five or even more. No clusters found associated with coxal insertion IV but may be concealed by folds.

Spinnerets: Small, sclerotized colulus sporting two hairs (fig. 57). ALS similar in both sexes, two-segmented, sclerotized, with one supposed major ampullate gland spigot and three piriform gland spigots, the anterior one clearly separated from two posterior ones (fig. 54). PMS single-segmented; in females more or less triangular in cross section, with four spigots: one (possibly minor ampullate gland) spigot located anterior to row of three aciniform gland spigots, the outer one separated from two inner ones (fig. 55); in males digitiform, with only one, presumably minor ampullate gland spigot (fig. 58). PLS two-segmented, sclerotized; in females as in figure 56, with six aciniform gland spigots; in males as in figure 59, with three aciniform gland spigots. Spinnerets ventrally and laterally enclosed by prominent semicircular spinneret scutum. Dorsal and lateral sides of anal tubercle surrounded by narrow, sclerotized anal scutum that is clearly separated from spinneret scutum (fig. 48). Both scuta bearing several setae.

Female genitalia: Copulatory orifice situated behind elevated anterior edge of posterior ventral scutum in depression (figs. 10, 60–63);

ranging from narrow vertical slit (*A. iita*; fig. 62) to rather large oval opening from which a short, very narrow groove extends anteriorly (*A. corbulo*; fig. 60). Group of setae on either side of copulatory orifice; many directed medially (fig. 63). Transverse structure looking like small stick with both ends slightly curved sometimes visible through posterior part of anterior ventral scutum (fig. 11). Pedipalp without claw; tibia with three trichobothria (structure as on legs). Palpal tarsal organ present; structure as on legs.

Male genitalia: Pedipalps as in figure 64. Palpal femur enlarged. Tibia with three trichobothria; structure as on legs. Cymbium with median tarsal organ (structure as on legs) and tuft of setae distally; fused with bulbous but borderline still clearly visible distally (fig. 64). Bulbous with small indentation on ventral surface and distal embolus and conductor (figs. 64, 65). Embolus tubular but tip flattened, opening to outside via broad slit (figs. 65, 66); tip with complex ultrastructure usually including very small denticles (fig. 67). Considerable intraspecific variation in tip shape. Tip often bent at almost 90° angle, sometimes forming hoodlike structure (fig. 68). Small projection near embolar tip (near tip projection, ntp; figs. 65, 68). Prolateral surface of embolus often with long groove or ridge. Conductor slender, usually broader at base; length variable, apparently even within species; situated approximately prolaterally of embolus (fig. 65). Sperm pore as in figure 69, with row of setae anterior to it.

NOTE: The MRAC collections from Ivory Coast contain at least one additional species of *Antoonops* that is not described due to the poor preservation of the specimens.

Antoonops corbulo, new species

Figures 1, 4, 5A, B, 7A, B, 8A, B, 9, 10A, 11, 13–16, 19, 21–26, 28–35, 38–41, 43, 45–47, 49–53, 57–60, 64, 69–80, 81B

TYPES: Male holotype: Ivory Coast, Apouesso, Forêt classée de la Bossematié, 6°35' North 3°28' West, forest, pitfall, Feb. 26, 1995, R. Jocqué and K. Tanoh (MRAC 204.544). Female allotype: same collection

data as holotype (MRAC 204.558). Paratype: same collection data as holotype except date Jan. 29, 1995 (MRAC 204.571), 1 ♂.

ETYMOLOGY: The specific name is a noun in apposition to the genus name and refers to the Roman general Corbulo (ca. A.D. 7–67), who served under the emperors Claudius and Nero.

DIAGNOSIS: Most similar to *A. bouaflensis* and *A. iita*, distinguished from both by the distinct elevation of the male ventral scutum at the level of the sperm pore and spiracles (fig. 1A) and by the shape of the copulatory opening (figs. 10A, 60); from the second also by the shape of the male carapace (fig. 1A).

MALE: TL 1.78, CL 0.87, CW 0.62, CH 0.39, DSL 0.91, DSW 0.44. Habitus as in figures 1A and 7A. Carapace high, dome-shaped, descending steeply posteriorly, dark brown to almost black, shiny; microsculpture limited to lower part (figs. 15, 19). Eye group width 0.22, distance ALE-ALE 0.10. Clypeus height 0.11. Shape of chelicerae as in figure 25, with slightly concave inner surface; fang tip resting on posterior surface. Boundary between inner and posterior surface distinct, giving way distally to group of very small teethlike structures (fig. 26). Outermost hair on posterior flank of fang base long and curved inward (fig. 28). Endital hooks as in figures 34 and 35, slender and protruding distinctly above anterior, "grooved" process. Sternum orange-yellow. Leg I 1.53 (0.46 + 0.22 + 0.35 + 0.32 + 0.18), leg II 1.52 (0.46 + 0.18 + 0.35 + 0.34 + 0.19), leg III 1.25 (0.40 + 0.16 + 0.25 + 0.26 + 0.18), leg IV 2.02 (0.61 + 0.26 + 0.46 + 0.46 + 0.23). Following areas on legs dark brown: leg I: large dark spot on proximal prolateral femur, small spot on ventral distalmost part of femur; ventral patella and tibia slightly dark; leg II: as leg I, but spot on prolateral femur less pronounced or absent; leg III: ventral femur, patella and tibia slightly dark; leg IV: pro- and retrolateral femur except proximal third; distalmost part of dorsal patella; pro- and retrolateral tibia except distalmost quarter. Dorsal scutum rather shiny, with anterior, middle, and posterior parts sharply delineated (fig. 16); a few rather short, shallow, longitudinal grooves near margin of scutum (fig. 4A). Anterior and middle parts brown, separated from darker

posterior part by conspicuous transverse white band; band usually less clearly delineated medially; posterior part usually dark brown to almost black laterally, much lighter medially; in most specimens two narrow, parallel white lines across entire length of middle part (figs. 1A, 8A). Ventral scutum orange-yellow, distinctly elevated at level of sperm pore and spiracles (fig. 1A); opercula usually dark orange to red. Pedipalps brown. Book lungs with very few lamellae (three to apparently only one) (fig. 52). From each spiracle stout tracheal trunk leading forward toward petiole. Narrower trachea arising from base of each main trunk; runs backward for short distance before splitting up in tracheoles (fig. 53). No evidence for transverse duct connecting main trunks.

FEMALE: TL 1.72, CL 0.78, CW 0.51, CH 0.24, DSL 0.94, DSW 0.56. Habitus as in figs. 1B and 7B. Carapace rather low and flat, dark brown, completely covered by micro-sculpture (fig. 13). Eye group width 0.22, distance ALE-ALE 0.09. Clypeus height 0.06. Chelicerae as in male but outermost hair on posterior flank of fang base short. Sternum orange-yellow. Leg I 1.41 (0.43 + 0.19 + 0.33 + 0.28 + 0.18), leg II 1.41 (0.42 + 0.20 + 0.30 + 0.30 + 0.19), leg III 1.15 (0.35 + 0.16 + 0.21 + 0.24 + 0.19), leg IV 1.84 (0.52 + 0.26 + 0.42 + 0.42 + 0.22). Following areas on legs dark brown: leg I: as in male except entire proximal third of prolateral femur dark, not limited to spot; retrolateral femur similar but less pronounced; tibia with most proximal and most distal part dark, especially ventrally, middle part white; leg II: as leg I except tibia which is as tibia of male leg I; leg III: as in male except pro- and retrolateral femur with dark middle third; leg IV: as in male (fig. 9). Dorsal scutum rather shiny; posterior part distinctly elevated (fig. 14). Anterior part brown, usually somewhat lighter across middle region; separated from darker posterior part by conspicuous transverse white band; band usually less clearly delineated medially; posterior part usually dark brown to almost black laterally, much lighter medially (figs. 1B, 8B). Ventral scuta orange-yellow; opercula dark orange to red. Pedipalps brown. Epigastric area as in figure 10A. Copulatory orifice a rather large oval opening from which short narrow groove

extends anteriorly (fig. 60). Book lungs and tracheae similar to male.

VARIATION: Measurements in five other males: TL 1.74–1.84 (mean = 1.79), CL 0.85–0.89 (mean = 0.88), CW 0.60–0.63 (mean = 0.61), CH 0.36–0.41 (mean = 0.38), DSL 0.89–0.95 (mean = 0.91), DSW 0.41–0.45 (mean = 0.43), tibia I 0.36–0.38 (mean = 0.37), tibia IV 0.47–0.50 (mean = 0.48). Measurements in five other females: TL 1.63–1.75 (mean = 1.69), CL 0.76–0.80 (mean = 0.78), CW 0.50–0.51 (mean = 0.51), CH 0.23–0.26 (mean = 0.25), DSL 0.87–0.95 (mean = 0.91), DSW 0.51–0.56 (mean = 0.54), tibia I 0.30–0.34 (mean = 0.32), tibia IV 0.41–0.43 (mean = 0.42).

OTHER MATERIAL EXAMINED: **Ivory Coast:** Appouesso, Forêt classée de la Bossematié, 6°35' North 3°28' West, forest, pitfall, Dec. 18, 1994 (MRAC 204.545, 204.557, 204.559, 204.568), 6 ♀; Jan. 2, 1995 (MRAC 204.539, 204.564, 204.566, 204.567), 4 ♂, 5 ♀; Jan. 15, 1995 (MRAC 204.543, 204.546, 204.562, 204.563, 204.577, 204.589), 6 ♂, 2 ♀; Feb. 12, 1995 (MRAC 204.552, 204.561, 204.569, 204.570), 3 ♂, 1 ♀; Feb. 26, 1995 (MRAC 204.572, 204.578), 2 ♂, 1 ♀; Mar. 12, 1995 (MRAC 204.547, 204.574), 1 ♂, 1 ♀; R. Jocqué and K. Tanoh. Same locality, rain forest, Jan. 3, 1994 (MRAC 202.220), 1 ♀; Jan. 31, 1994 (MRAC 202.209), 2 ♀; Feb. 16, 1994 (MRAC 202.231, 202.232), 3 ♀; Aug. 5, 1994 (MRAC 202.230), 1 ♀; Aug. 18, 1994 (MRAC 202.213), 1 ♂; Dec. 1, 1994 (MRAC 202.211, 202.239), 1 ♂, 1 ♀; R. Jocqué and N. Séabé. **Ghana:** Kakum forest, 5°20' North 1°23' West, secondary forest, Winkler extraction, Nov. 10, 2005, R. Jocqué, D. De Bakker and L. Baert (MRAC 217.500), 1 ♀.

DISTRIBUTION: Known from the type locality and from Kakum forest, Ghana.

Antoonops bouaflensis, new species

Figures 2, 10B, 42, 44, 61, 68

TYPES: Male holotype: Ivory Coast, Bouaflé, 6°59' North 5°45' West, pitfalls, Feb. 12, 1981, J. Everts (MRAC 219.428). Female allotype: Ivory Coast, "Pakodji near Degbézéré, 15 km E. Bouaflé", 6°59' North 5°39' West, pitfalls, Feb. 20, 1984, R. Schouten and J. Buysen (MRAC 219.429).

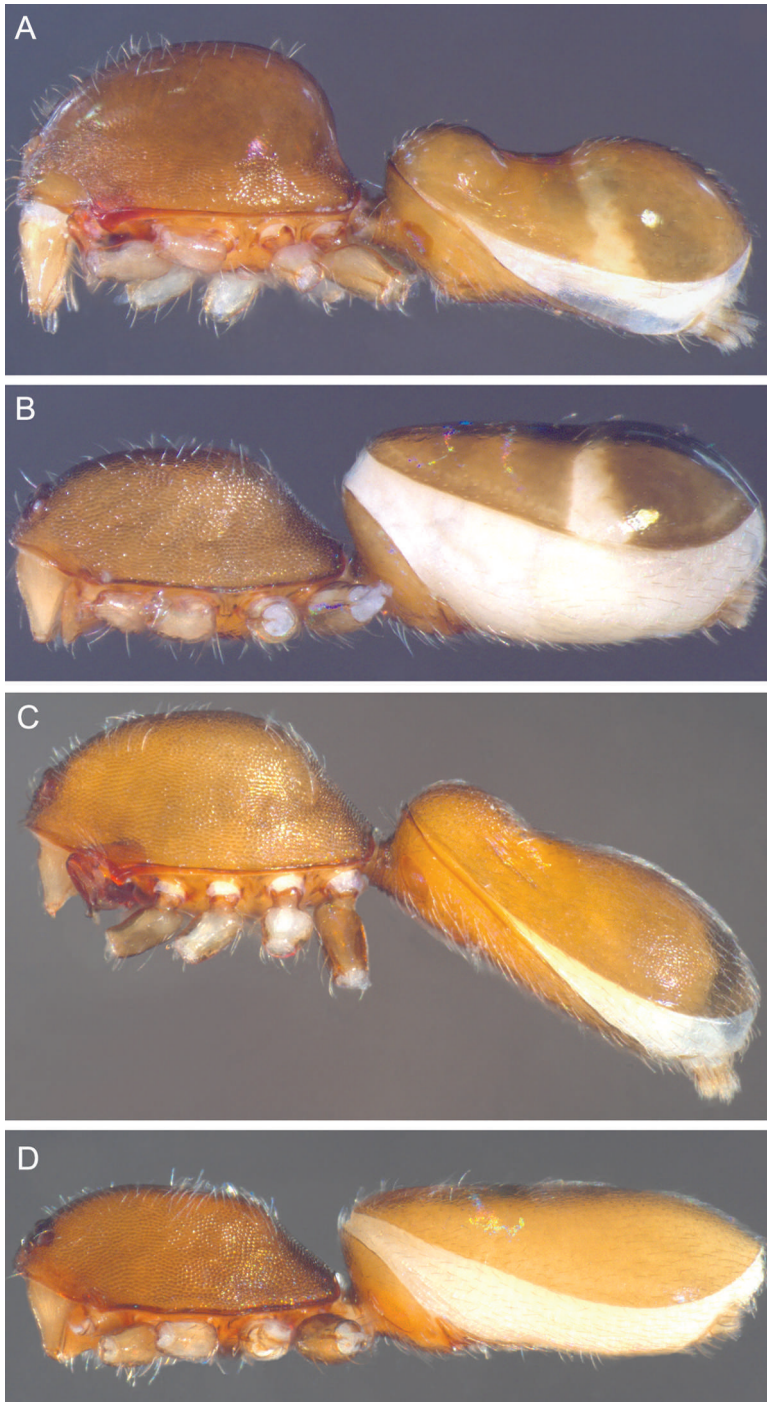


Fig. 7. Automontage images. A–B, *Antoonops corbulo*, n. sp., (A) male (magnification: 52 \times) and (B) female (56 \times). C–D, *Antoonops nebula*, n. sp., (C) male (magnification: 48 \times) and (D) female (50 \times).

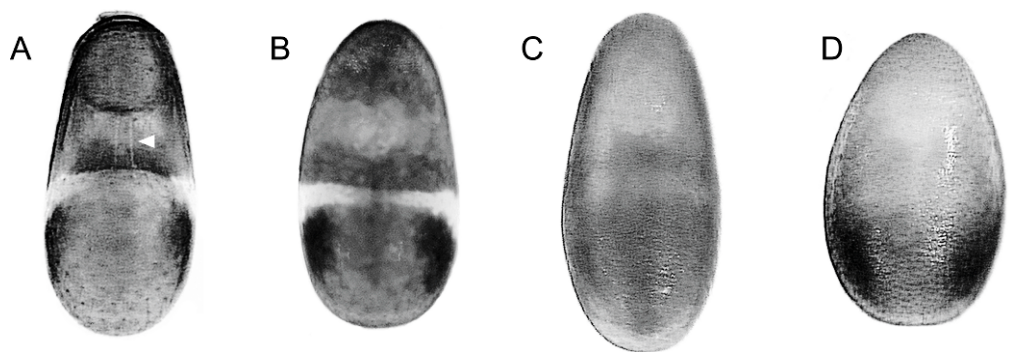


Fig. 8. Dorsal scuta. *Antoonops corbulo*, n. sp., (A) male and (B) female. *Antoonops nebula*, n. sp., (C) male and (D) female. White arrowhead: parallel lines. Scale bar: 0.40 mm.

Paratypes: same collection data as holotype (MRAC 174.111), 2 ♂. Paratypes: same collection data as allotype (MRAC 174.121), 4 ♀.

ETYMOLOGY: The specific name is an adjective referring to the type locality.

DIAGNOSIS: Most similar to *A. corbulo* and *A. iita*, distinguished from both by the shape of the copulatory opening (figs. 10B, 61); from the first by the male ventral scutum without an elevation (fig. 2); from the second by the shape of the male carapace (fig. 2).

MALE: TL 1.77, CL 0.86, CW 0.58, CH 0.35, DSL 0.91, DSW 0.46. Habitus as in figure 2. Carapace and sternum as in *A. corbulo* but carapace slightly lower (fig. 2). Eye group width 0.21, distance ALE-ALE 0.09. Clypeus height 0.09. Distal chelicerae somewhat anteroposteriorly flattened. Endital hooks not distinctly protruding above "grooved" process. Leg I 1.46 (0.44 + 0.19 + 0.33 + 0.30 + 0.20), leg II 1.4 (0.41 + 0.19 + 0.31 + 0.29 + 0.20), leg III 1.18 (0.36 + 0.15 + 0.22 + 0.26 + 0.19), leg IV 1.88 (0.55 + 0.25 + 0.45 + 0.40 + 0.23). Dorsal scutum as in *A. corbulo*. Ventral scutum orange-yellow, not elevated at level of sperm pore and spiracles (fig. 2). Pedipalps brown.

FEMALE: TL 1.65, CL 0.76, CW 0.51, CH 0.24, DSL 0.89, DSW 0.56. Carapace and sternum as in *A. corbulo*. Eye group width 0.20, distance ALE-ALE 0.08. Clypeus height 0.05. Leg I 1.34 (0.43 + 0.19 + 0.31 + 0.25 + 0.16), leg II 1.33 (0.39 + 0.19 + 0.29 + 0.30 + 0.16), leg III 1.12 (0.33 + 0.15 + 0.22 + 0.25 + 0.17), leg IV 1.73 (0.52 + 0.24 + 0.41 + 0.37 + 0.19). Abdominal scuta as in *A. corbulo*. Pedipalps brown. Epigastric area and copulatory orifice as in figs. 10B and 61.

VARIATION: Measurements in three other males: TL 1.71; 1.76; 1.79, CL 0.83; 0.87; 0.87, CW 0.58; 0.58; 0.59, CH 0.31; 0.33; 0.33, DSL 0.88; 0.89; 0.92, DSW 0.42; 0.44; 0.45, tibia I 0.31; 0.32; 0.34, tibia IV 0.43; 0.43; 0.44. Measurements in four other females: TL 1.64; 1.65; 1.69; 1.71, CL 0.75; 0.76; 0.76; 0.77, CW 0.51; 0.51; 0.52; 0.53, CH 0.21; 0.21; 0.22; 0.22, DSL 0.89; 0.89; 0.93; 0.94, DSW 0.40; 0.43; 0.50; 0.54, tibia I 0.30; 0.30; 0.32; 0.33, tibia IV 0.39; 0.41; 0.42; 0.42.

OTHER MATERIAL EXAMINED: **Ivory Coast:** Bouaflé, Koudougou, 6°56' North 5°40' West, "pièges", Jan. 1981, J. Everts (MRAC 166.264), 1 ♂.

DISTRIBUTION: Known only from the vicinity of Bouaflé, Ivory Coast.

Antoonops iita, new species

Figures 3, 5C, 10C, 27, 62, 67

TYPES: Male holotype: Nigeria, Ibadan, I.I.T.A, 7°14' North 3°30' East, riverine

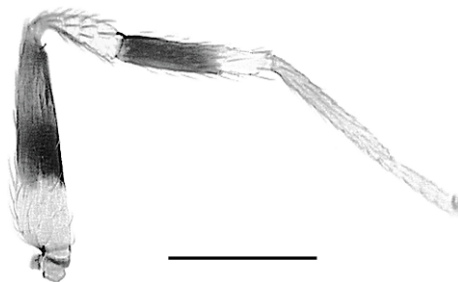


Fig. 9. *Antoonops corbulo*, n. sp. Leg IV, female, prolateral view. Scale bar: 0.40 mm.

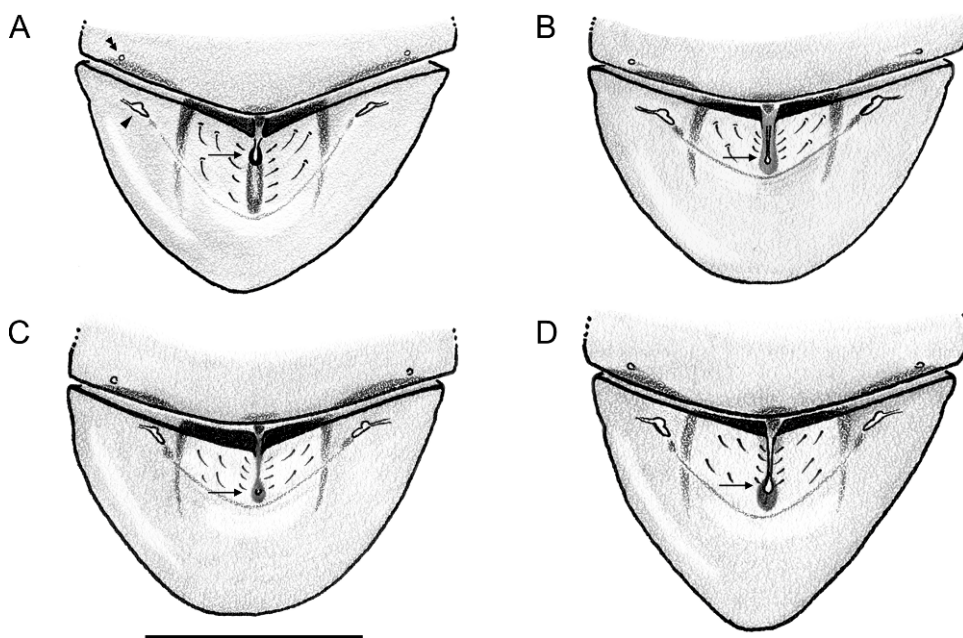


Fig. 10. Epigastric area: (A) *Antoonops corbulo*, n. sp. (B) *Antoonops bouaflensis*, n. sp. (C) *Antoonops iita*, n. sp. (D) *Antoonops nebula*, n. sp. Arrows: most posterior part of copulatory orifice. Arrowhead: spiracle. Double arrowheads: lung slit. Scale bar: 0.20 mm.

woodland, May 5, 1974, A. Russell-Smith (MRAC 219.426). Female allotype: same collection data as holotype (MRAC 219.427). Paratypes: same collection data as holotype (MRAC 160.358), 2 ♂, 2 ♀.

ETYMOLOGY: The specific name is a noun in apposition. It refers to the International Institute of Tropical Agriculture (I.I.T.A) on the grounds of which all hitherto known specimens were collected.

DIAGNOSIS: Most similar to *A. corbulo* and *A. bouaflensis*, distinguished from both by the shape of the copulatory opening (figs. 10C, 62) and the male carapace (fig. 3); from the first also by the male ventral scutum without an elevation (fig. 3).

MALE: TL 1.75, CL 0.85, CW 0.57, CH 0.30, DSL 0.90, DSW 0.45. Habitus as in figure 3; carapace declining posteriorly less sharply than *A. corbulo* and *A. bouaflensis*. Eye group width 0.20, distance ALE-ALE 0.09. Clypeus height 0.06. Sternum as in *A. corbulo*. Leg I 1.44 (0.43 + 0.19 + 0.32 + 0.30 + 0.20), leg II 1.4 (0.42 + 0.19 + 0.31 + 0.29 + 0.19), leg III 1.09 (0.37 + 0.16 + 0.22 + 0.20 + 0.14), leg IV 1.78 (0.52 + 0.23 + 0.42 + 0.38 +

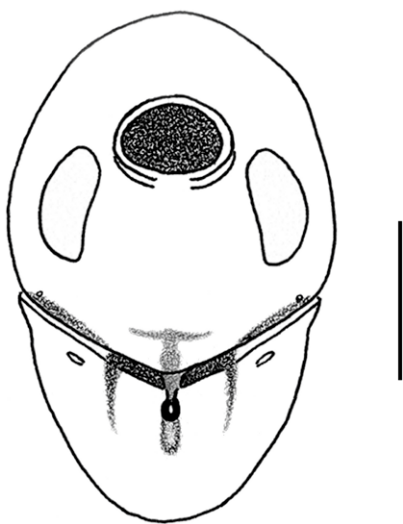
0.23). Abdominal scuta as in *A. bouaflensis* (fig. 3). Pedipalps brown.

FEMALE: TL 1.70, CL 0.78, CW 0.51, CH 0.27, DSL 0.92, DSW 0.54. Carapace and sternum as in *A. corbulo*. Eye group width 0.19, distance ALE-ALE 0.08. Clypeus height 0.04. Leg I 1.34 (0.41 + 0.19 + 0.30 + 0.26 + 0.18), leg II 1.31 (0.39 + 0.20 + 0.29 + 0.26 + 0.17), leg III 1.08 (0.32 + 0.15 + 0.21 + 0.23 + 0.17), leg IV 1.67 (0.48 + 0.23 + 0.38 + 0.37 + 0.21). Abdominal scuta as in *A. corbulo*. Pedipalps brown. Epigastric area and copulatory orifice as in figs. 10C and 62.

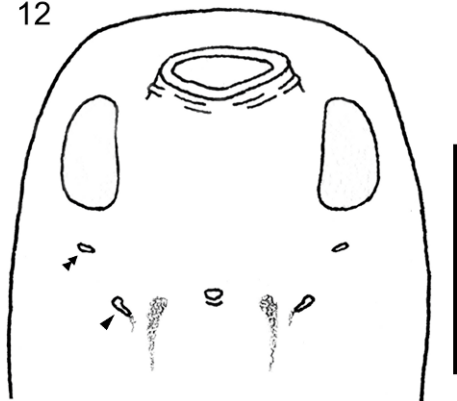
VARIATION: Measurements in three other males: TL 1.75; 1.81; 1.83, CL 0.85; 0.86; 0.87, CW 0.56; 0.57; 0.58, CH 0.30; 0.31; 0.34, DSL 0.89; 0.96; 0.96, DSW 0.44; 0.46; 0.47, tibia I 0.31; 0.32; 0.33, tibia IV 0.43; 0.43; 0.44. Measurements in two other females: TL 1.69; 1.81, CL 0.77; 0.80, CW 0.52; 0.52, CH 0.27; 0.27, DSL 0.92; 1.01, DSW 0.54; 0.57, tibia I 0.31; 0.31, tibia IV 0.41; 0.42.

OTHER MATERIAL EXAMINED: **Nigeria:** Ibadan, I.I.T.A, 7°14' North 3°30' East, riverine woodland, June 9, 1974, A. Russell-Smith (MRAC 160.324), 1 ♂.

11



12



Figs. 11, 12. **11.** *Antoonops corbulo*, n. sp. Oblique view on ventral scuta of female, showing sticklike sclerite. **12.** *Antoonops nebula*, n. sp. Anterior part of ventral scutum of male, showing lateral apodeme on either side of sperm pore. Arrowhead: spiracle. Double arrowheads: lung slit. Scale bar: 0.20 mm.

DISTRIBUTION: Known only from the type locality.

NOTE: Due to the limited number of available specimens only two males were investigated by SEM. Endital hooks were not immediately apparent in either of these. However, in one individual we found what appeared to be the basal part of a broken-off endital hook, suggesting that these structures may be present in *A. iita*.

Antoonops nebula, new species

Figures 6, 7C, D, 8C, D, 10D, 12, 17, 18, 20, 36, 48, 54–56, 63, 65, 66

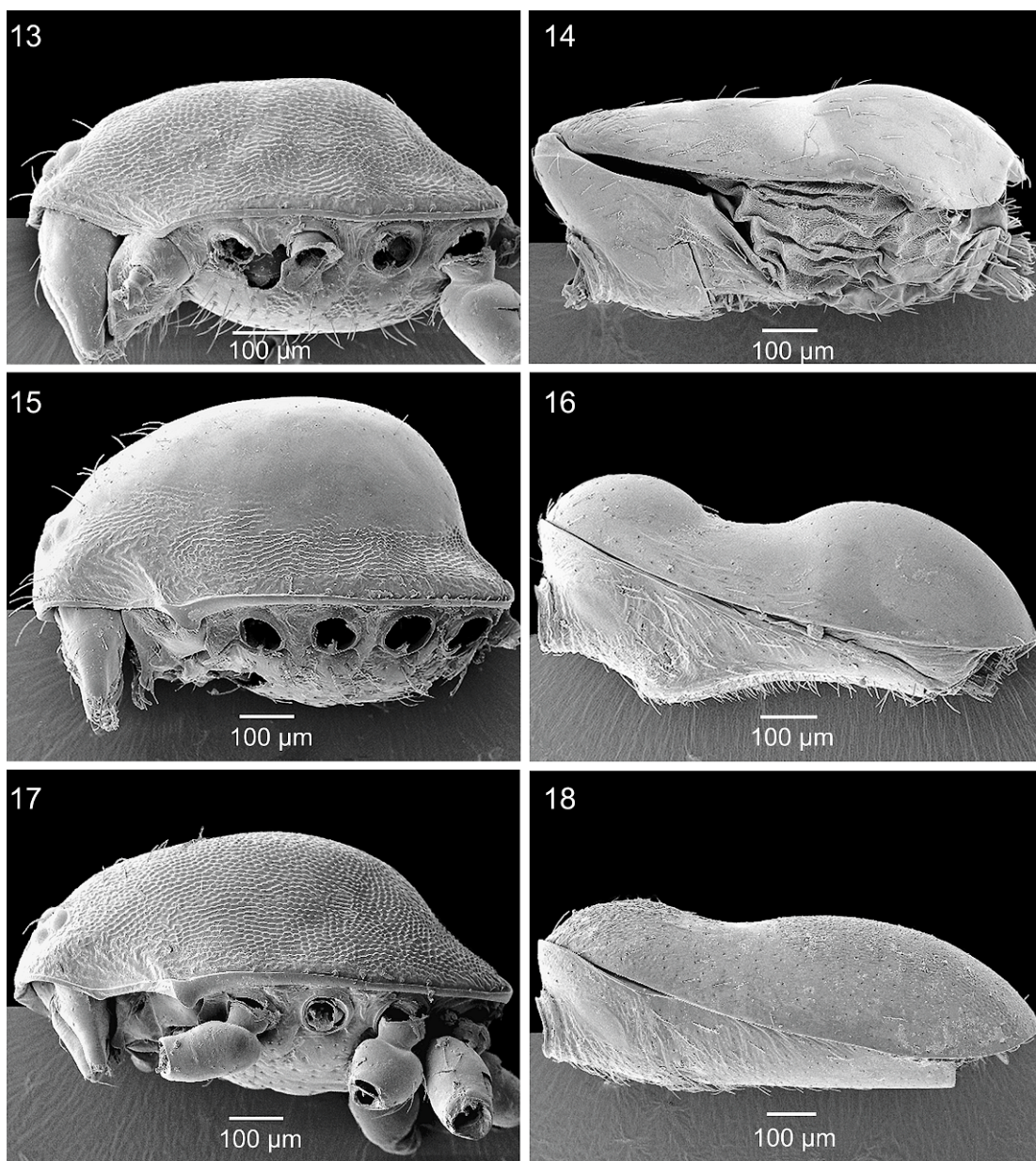
TYPES: Male holotype: Ghana, Kakum National Park, 5°20'55" North 1°23' West, 159 meters above sea level, lowland rain forest, Nov. 19, 2005, R. Jocqué, D. De Bakker and L. Baert (MRAC 219.422). Female allotype: same collection data as holotype except date Nov. 17, 2005 (MRAC 219.423). Paratypes: same collection data as holotype (MRAC 219.424), 6 ♂, 4 ♀.

ETYMOLOGY: The specific name is a noun in apposition meaning *cloud* or *fog* and refers to the original discovery of this species by canopy fogging.

DIAGNOSIS: Easily distinguished from all known congeners by the absence of a white transverse band on the dorsal scutum (fig. 8C, D), the shape of the abdomen of both males (figs. 6A, 7C, 18) and females (figs. 6B, 7D), the complete covering of the male carapace by microsculpture (fig. 17) and also by the shape of the copulatory opening (figs. 10D, 63).

MALE: TL 1.93, CL 0.93, CW 0.60, CH 0.34, DSL 1.00, DSW 0.49. Habitus as in figures 6A and 7C. Carapace dark brown, completely covered by microsculpture (fig. 17). Eye group width 0.22, distance ALE-ALE 0.09. Clypeus height 0.06. Endital hooks as in figure 36, not distinctly protruding above "grooved" process. Sternum yellow. Leg I 1.67 (0.50 + 0.24 + 0.39 + 0.33 + 0.21), leg II 1.63 (0.49 + 0.22 + 0.38 + 0.34 + 0.20), leg III 1.37 (0.43 + 0.18 + 0.28 + 0.28 + 0.20), leg IV 2.21 (0.68 + 0.31 + 0.53 + 0.45 + 0.24). Abdomen as in figure 18; anterior, middle and posterior parts of dorsal scutum readily discernible but transitions rather smooth; dorsal scutum dark brown to orange, without transverse white band (fig. 8C). Ventral scutum orange-brown, not elevated. Pedipalps greenish.

FEMALE: TL 1.80, CL 0.82, CW 0.52, CH 0.27, DSL 0.98, DSW 0.64. Habitus as in figures 6B and 7D. Carapace dark brown, completely covered by microsculpture (fig. 20). Eye group width 0.22, distance ALE-ALE 0.09. Clypeus height 0.04. Sternum orange-yellow. Leg I 1.63 (0.50 + 0.24 + 0.37 + 0.32 + 0.20), leg II 1.6 (0.47 + 0.23 +

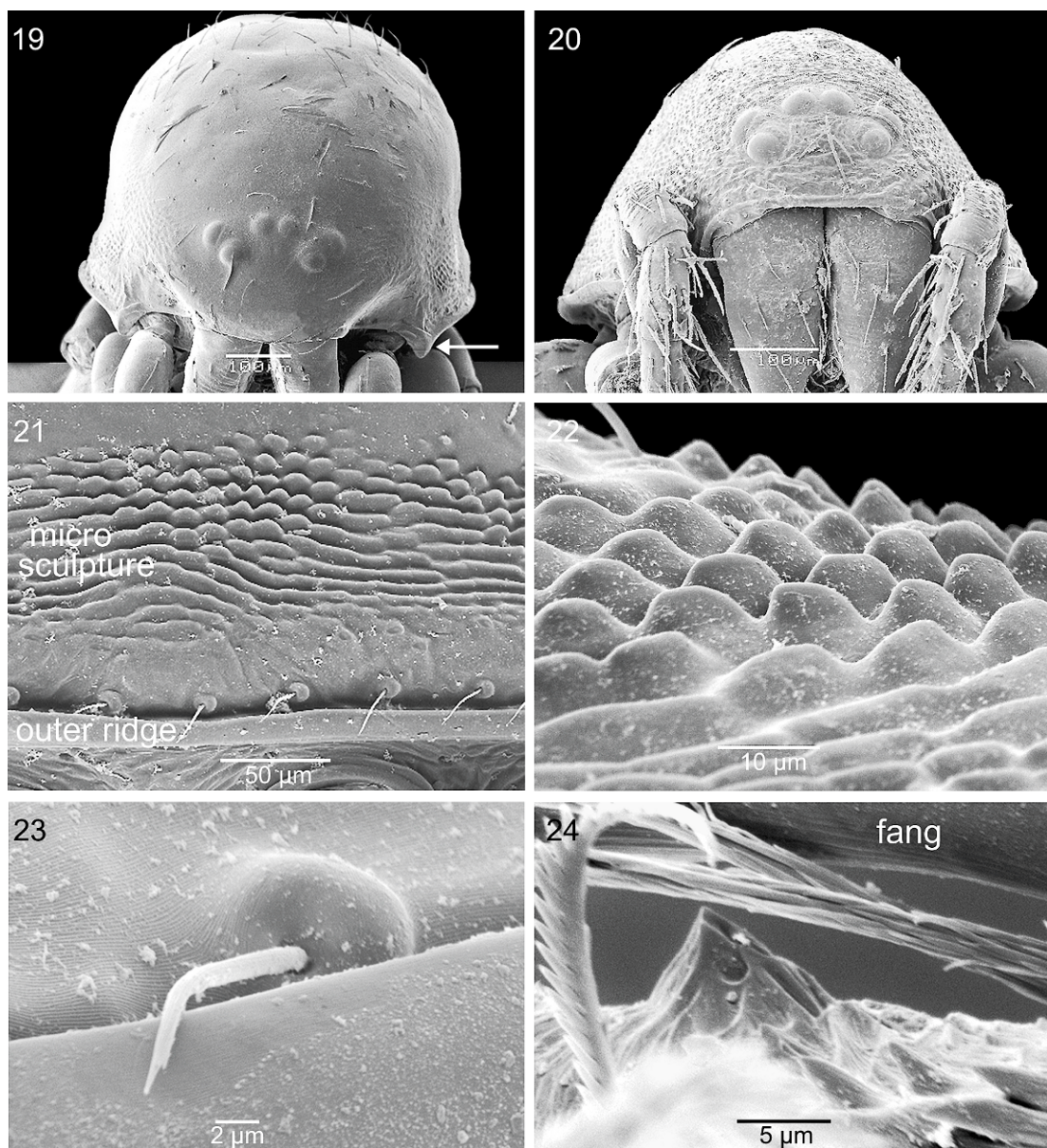


Figs. 13–18. 13–16. Female (13, 14) and male (15, 16) *Antoonops corbulo*, n. sp. 17, 18. Male *Antoonops nebula*, n. sp. **13, 15, 17.** Prosoma, lateral view. **14, 16, 18.** Abdomen, lateral view.

0.37 + 0.33 + 0.20), leg III 1.33 (0.40 + 0.18 + 0.27 + 0.28 + 0.20), leg IV 2.11 (0.62 + 0.31 + 0.50 + 0.43 + 0.25). Abdomen as in figures 6B and 7D; posterior part of dorsal abdomen only slightly elevated. Dorsal scutum grey to yellow, without transverse white band (fig. 8D). Ventral scuta orange-yellow.

Pedipalps greenish. Epigastric area and copulatory orifice as in figures 10D and 63.

VARIATION: Considerable variation in color (especially in males), including specimens with greenish carapace, sternum and scuta. Measurements in five other males: TL 1.89–1.97 (mean = 1.92), CL 0.89–0.92 (mean =

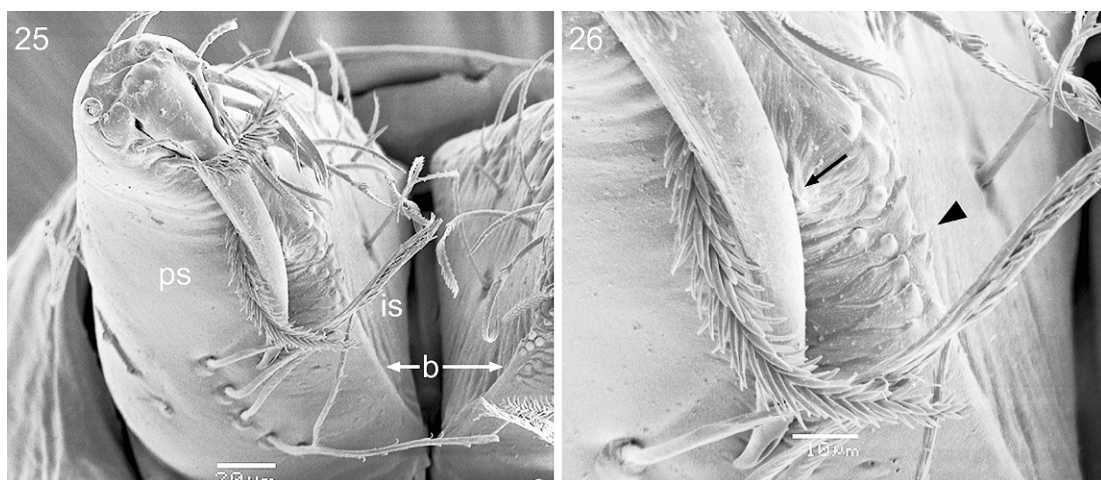


Figs. 19–24. 19, 21–24. *Antoonops corbulo*, n. sp. 20. *Antoonops nebula*, n. sp. 19. Frontal view, male. Arrow: triangular extension. 20. Frontal view, female. 21. Lower part of carapace, male, lateral view. 22. Microsculpture, female. 23. Hair with modified base, female. 24. Cheliceral tooth, male.

0.90), CW 0.57–0.61 (mean = 0.59), CH 0.31–0.34 (mean = 0.33), DSL 0.98–1.05 (mean = 1.02), DSW 0.47–0.50 (mean = 0.48), tibia I 0.37–0.40 (mean = 0.39), tibia IV 0.50–0.54 (mean = 0.53). Measurements in five other females: TL 1.76–1.92 (mean = 1.84), CL 0.80–0.85 (mean = 0.83), CW 0.52–0.55 (mean

= 0.53), CH 0.22–0.30 (mean = 0.26), DSL 0.96–1.07 (mean = 1.00), DSW 0.53–0.61 (mean = 0.58), tibia I 0.37–0.38 (mean = 0.37), tibia IV 0.50–0.53 (mean = 0.51).

OTHER MATERIAL EXAMINED: **Ghana:** Kakum National Park, 5°20'55" North 1°23' West, 159 meters above sea level, lowland rain



Figs. 25, 26. Chelicerae. *Antoonops corbulo*, n. sp., male. **25.** Posterior view. **26.** Detail showing boundary giving way to group of very small toothlike structures (arrowhead). Arrow: cheliceral tooth. Abbreviations: b, boundary between is and ps; is, inner surface; ps, posterior surface.

forest, Nov. 17, 2005, R. Jocqué, D. De Bakker and L. Baert (MRAC 219.425), 4 ♂, 4 ♀.

DISTRIBUTION: Known only from the type locality.

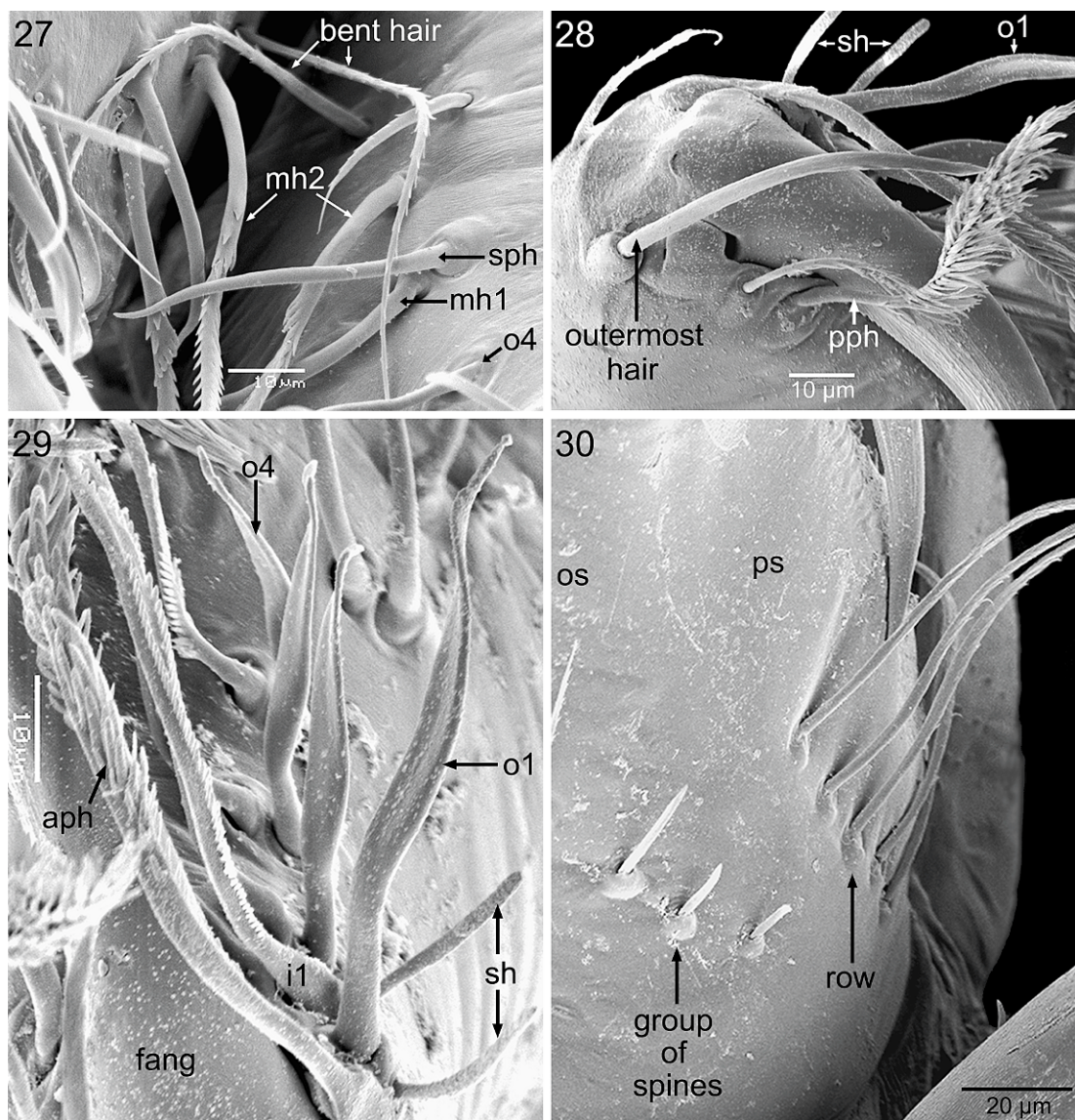
NATURAL HISTORY: This species was collected by canopy sampling using the pyrethrum knockdown method. The same two fogging sessions that resulted in the discovery of specimens of *A. nebula* also yielded large amounts of ants (various species), other oonopids (*Orchestina* Simon, 1882 and *Opopaea* Simon, 1891, among others) and some individuals of the ant-mimicking spider *Myrmarachne* MacLeay, 1839 (Salticidae) (D. De Bakker, personal commun.).

INTERNAL FEMALE GENITALIA

The copulatory opening of *A. corbulo* leads into a long duct that first runs posteriorly for a short distance but then turns back on itself forming a loop. The posterior running part has numerous small pores in its wall (fig. 73). The anterior running part of the duct initially rests on the dorsal surface of the wider posterior running part (fig. 73). After passing the level of the copulatory opening it contacts the scutal surface and acquires a globular appearance (figs. 70, 72, 73). The duct eventually reaches the median anterior edge of the

posterior ventral scutum (figs. 72, 73). Here the scutum gives rise to a rather slender, dorsally extending sclerite that is embedded within the posterior wall of the uterus externus (figs. 71–74); its distal part is shaped like an anteriorly directed hook (fig. 74). The globular duct ascends along the posterior surface of this sclerite and eventually enters the distal hook (fig. 74). A rather large, slitlike opening is present in the ventral surface of this hook (figs. 75, 76).

Embedded in the anterior wall of the uterus externus lies another peculiarly shaped sclerite. It is made up of two parts, a vertical stalk and a transverse, sticklike apodeme that is visible through the anterior ventral scutum (fig. 11). The stalk consists of a thin, roughly triangular plate that rests on the median posterior edge of the anterior ventral scutum (figs. 77–79). Distally it connects to the transverse apodeme (figs. 77–79). Medially this apodeme bears a remarkable dorsal extension that resembles a cylindrical cup whose posterior wall is missing (figs. 77–79). The cup has a well-developed dorsal rim (figs. 79, 80) and a hole in its floor (fig. 80). When dissecting specimens two slender muscle strands were observed to connect the left and right extremities of the transverse apodeme to the left and right lateral apodeme, respectively; these muscles attach to the lateral



Figs. 27–30. Cheliceral setae. 27. *Antoonops iita*, n. sp., male. 28–30. *Antoonops corbulo*, n. sp., male. 27. Hairs proximally of double row. 28. Posterior margin of fang base. 29. Double row on distal promargin. 30. Lateral view on posterior surface of right chelicera. Abbreviations: aph, anterior plumose hair; i, hair of inner row; mh, modified hair; o, hair of outer row; os, outer surface; pph, posterior plumose hair; sh, short hair; sph, spiniform hair.

apodemes near their posterior ends (not shown).

The sclerites embedded in the walls of the uterus externus are in close contact with each other, the distal hook of the posterior sclerite being situated dorsally of the transverse apodeme of the anterior sclerite (fig. 71).

DISCUSSION

ANT MIMICRY

A markedly narrowed and constricted abdomen, exhibited by the males of all four *Antoonops* species, is a morphological adaptation used by many spider species to achieve a

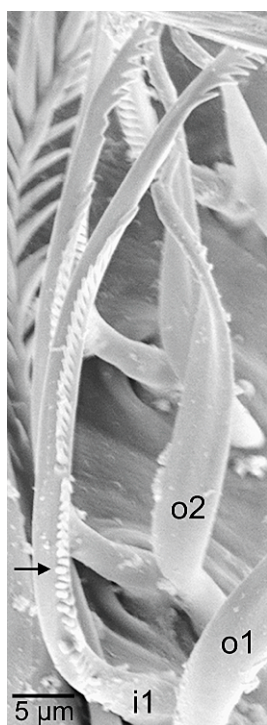


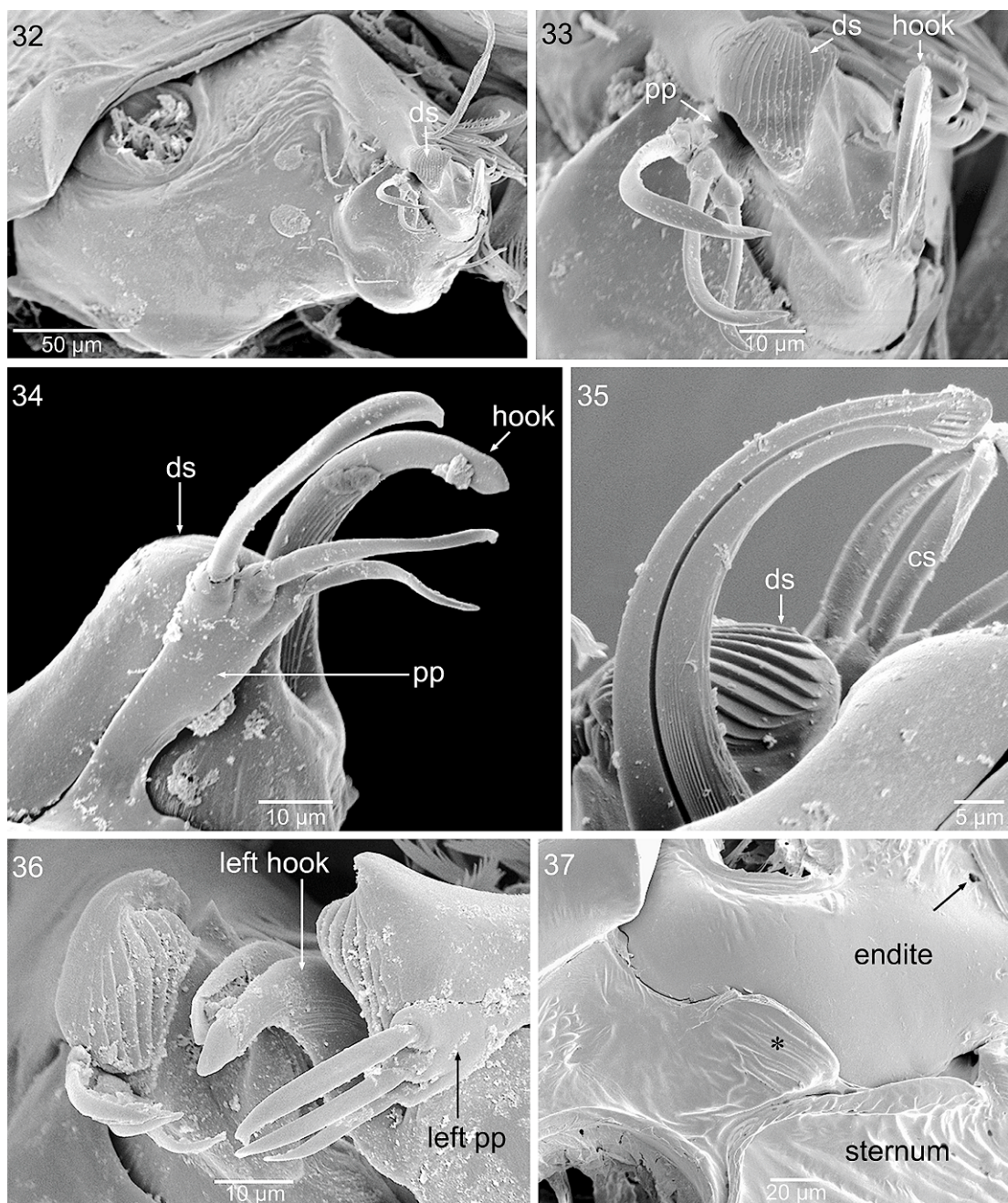
Fig. 31. Cheliceral setae. *Antoonops corbulo*, n. sp., male. Detail of double row. Arrow: cuticular teeth.

resemblance to ants, as is the presence of transverse white bands on the abdomen, found here in both sexes of *A. corbulo*, *A. bouaflensis*, and *A. iita*. Most ant-mimicking spiders are believed to be Batesian mimics, whose structural and/or behavioral correspondence to ants is a defensive adaptation, selected for by the need to deceive visually oriented predators such as sphecids wasps or salticid spiders (Cushing, 1997; McIver and Stonedahl, 1993).

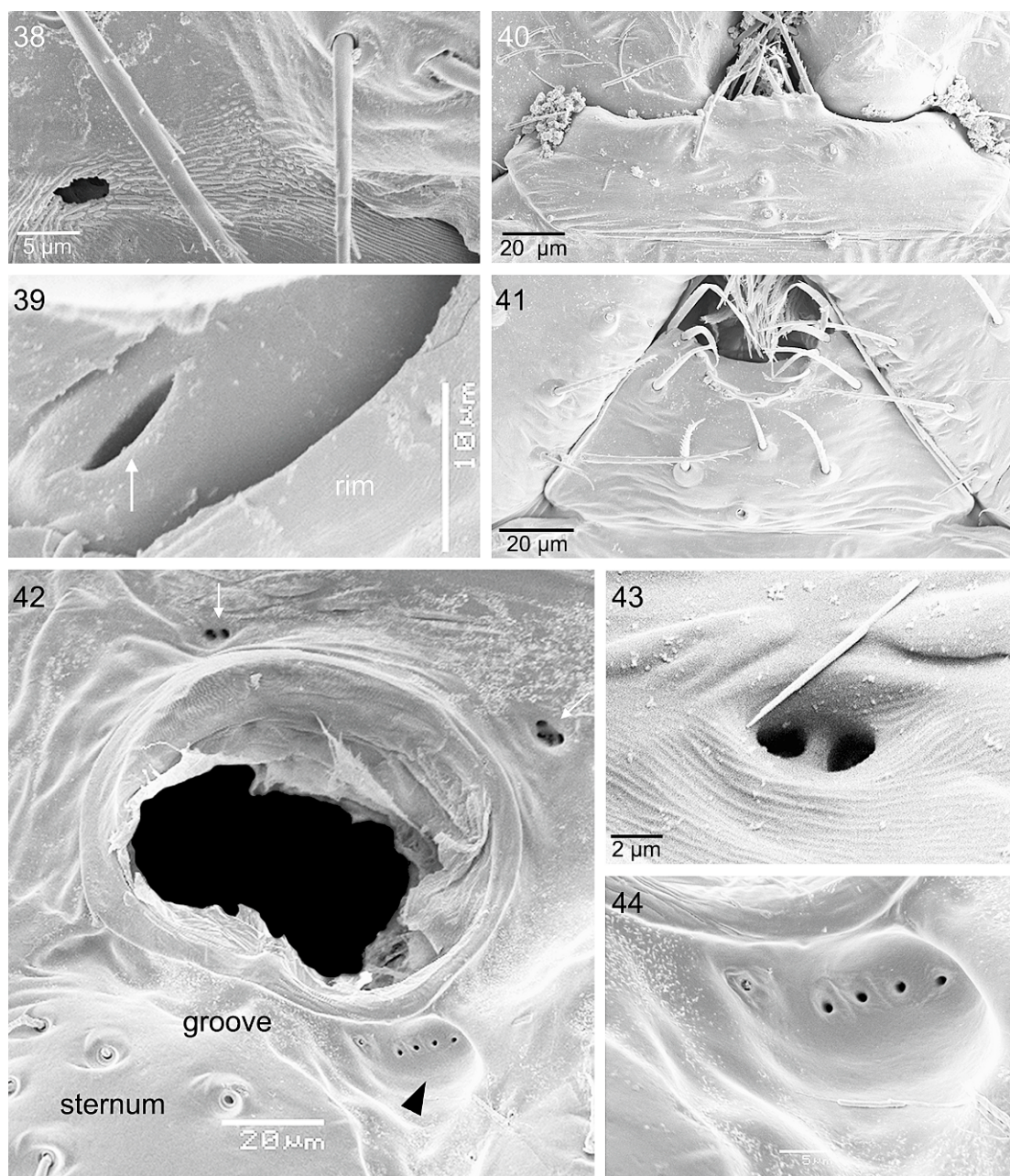
Hitherto, unambiguous examples of ant mimicry within the family Oonopidae appear to be limited to *Antoonops* and *Pescennina* Simon, 1914. As *Antoonops*, this American genus uses abdominal constriction and color patterning to produce the illusion of antlike form (N. Platnick, personal commun.). *Diblemma donisthorpii* O.P.-Cambridge, 1908, originally discovered in a hothouse at Kew gardens where it lived in close association with the ant *Wasmannia auropunctata* (Roger, 1863), was considered an ant-mimicking oonopid by Cushing (1997). Although *D. do-*

nisthorpii was indeed reported to resemble *W. auropunctata* in general appearance, length, and color, the two species may actually have been imported from different parts of the world and possibly do not coexist in nature (O.P.-Cambridge, 1908). This raises doubts on the validity of this case as an example of ant mimicry. Moreover, a recent redescription of this species by Saaristo (2001) does not provide any convincing evidence for a morphological resemblance to ants. This was confirmed further by our own examination of specimens of *D. donisthorpii* (MNHN, vial AR 5774, giving as locality "Vivant dans les serres de Kew"). Three other oonopids were originally discovered within or near ant nests and were supposed to be myrmecophiles, viz. *Pseudoscaphiella parasita* Simon, 1907, *Myrmecoscapheilla borgmeyeri* Mello-Leitão, 1926, and *Myrmopopaea jacobsoni* Reimoser, 1933. Some myrmecophiles mimic their hosts morphologically or behaviorally (Cushing, 1997; McIver and Stonedahl, 1993), but judging from the available data (Simon, 1907; Mello-Leitão, 1926; Reimoser, 1933; Jacobson, 1933) this does not seem to be the case in these three species. Examination of the type material (MNHN, vial AR 5779) supported this for *P. parasita*. Finally, it may be mentioned in this context that both Cushing (1997) and Hölldobler and Wilson (1990) list an unidentified *Gamasomorpha* species as another example of a myrmecophilic oonopid, referring to observations by Gray (1971). Gray's paper, however, mentions only *Canasonortha*, a name that is apparently not in use anywhere in the animal kingdom. Although *Canasonortha* may indeed be a misspelling of *Gamasomorpha*, the reported length of the spiders (4–6 mm) makes it doubtful whether they actually were oonopids.

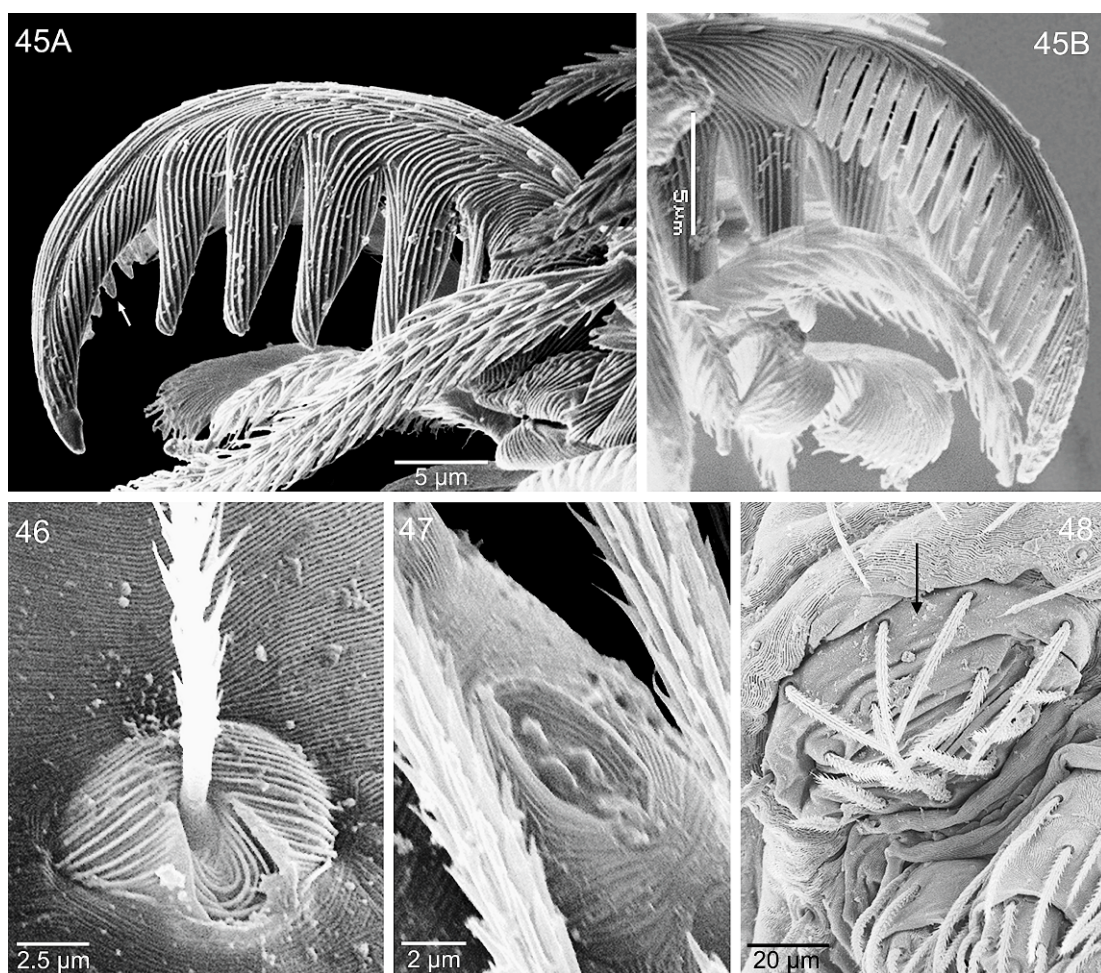
An interesting aspect of *Antoonops*' mimicry concerns its pronounced sexual dimorphism, the male being considerably more antlike in appearance due to its narrower and medially constricted abdomen. Several explanations might account for this dimorphism, though the different hypotheses are not necessarily mutually exclusive. One possible explanation is offered by the fact that some mimicry-enhancing traits are known to affect other functions or activities of the mimetic organism



Figs. 32–37. Male endites. 32–35, 37. *Antoonops corbulo*, n. sp. 36. *Antoonops nebula*, n. sp. **32.** Right endite, ventral view. **33.** Detail of innermost part. **34.** Lateral view showing outer surface of anterior process, posterior process and hook of right endite. **35.** Inner surface of hook. **36.** Ventral view on innermost part of right and left endites. **37.** Structure (asterisk) above anterolateral corner of sternum. Arrow: opening in endite. Abbreviations: cs, curved setae of pp; ds, distal surface of anterior process; pp, posterior process.



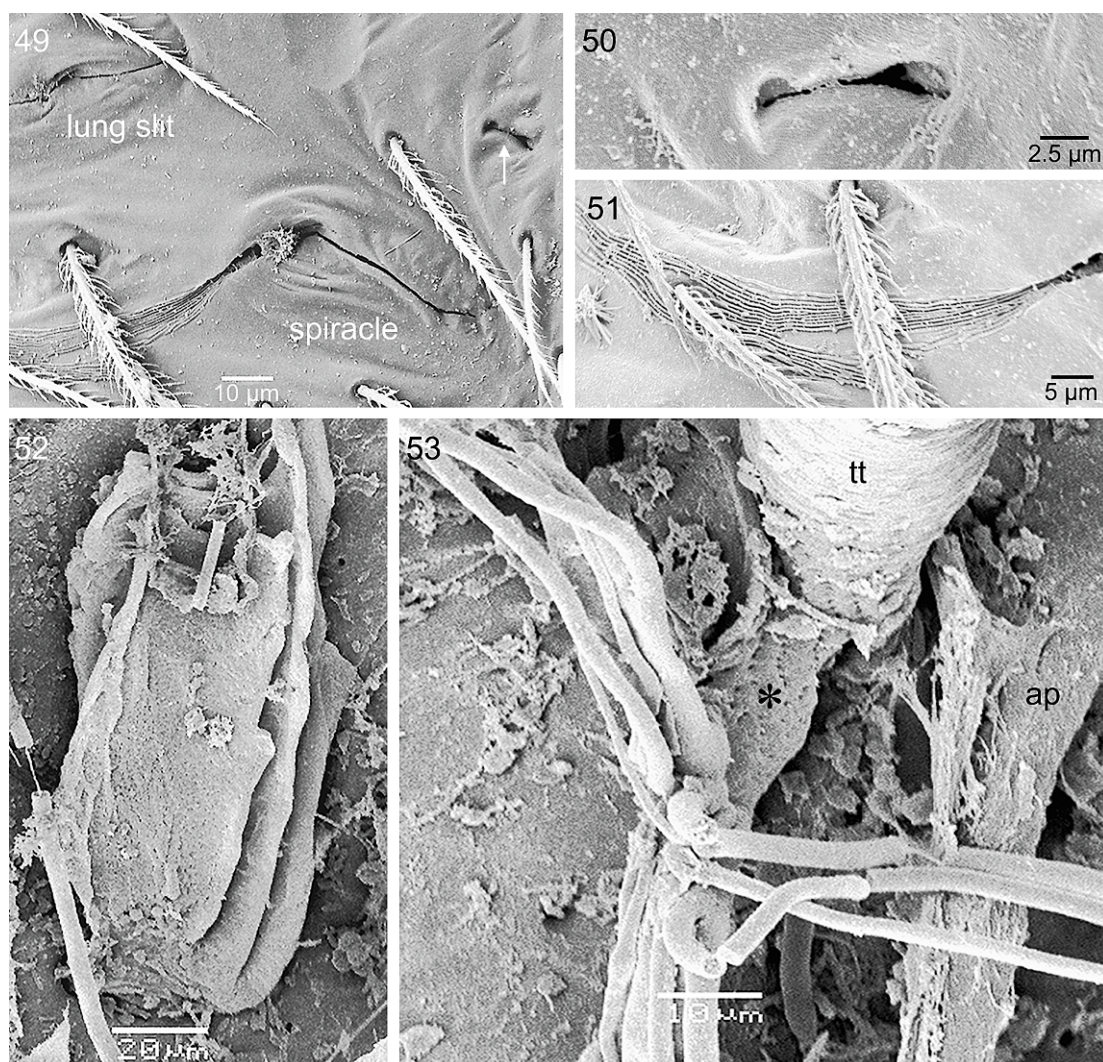
Figs. 38–44. 38–41, 43. *Antoonops corbulo*, n. sp. 42, 44. *Antoonops bouaflensis*, n. sp. 38. Band of ridged cuticle on male endite, with irregular opening. 39. Coxal gland opening (arrow), male. Rim: rim of coxal insertion. 40. Labium, male. 41. Labium, female. 42. Coxal insertion II, male. Arrows: clusters of openings. Arrowhead: anteriormost part of infracoxal groove. 43. Detail of cluster, male. 44. Detail of anteriormost part of infracoxal groove, male.



Figs. 45–48. 45–47. *Antoonops corbulo*, n. sp. 48. *Antoonops nebula*, n. sp. 45. Tarsal claw. (A) Outer row of teeth, female, leg II. Arrow: teeth of inner row. (B) Inner row, female, leg I. 46. Trichobothrium, male. 47. Tarsal organ, male. 48. Anal scutum (arrow), male.

in a negative way, making them costly to express (Holen and Johnstone, 2004). It is well known that the narrow body shape of ant-mimicking spiders such as *Myrmarachne* has resulted in reduced fecundity, with females laying fewer eggs per egg sac than their nonmimetic close relatives. Some species may have compensated for this limitation by producing more egg sacs, so that their lifetime fecundity equals that of nonmimics (Cushing, 1997; McIver and Stonedahl, 1993). However, the constraints exerted on females by the demands of egg production could alternatively lead to the evolution of sexually dimorphic ant mimics in which only the male's abdomen

becomes distinctly narrowed and constricted while the female largely retains its ancestral wide abdomen, exhibiting at best only a small degree of constriction. Such an evolutionary route might have been followed by the genus described here. In fact, the abdomen of female *Antoonops*, while characteristically modified, shows no obvious signs of constriction at all; its peculiarly shaped dorsal surface may originate from a gradual elevation of the posterior abdomen, possibly allowing successive generations of females to enhance their resemblance to ants without at the same time decreasing their fecundity. Still, many other factors could conceivably have contributed to



Figs. 49–53. Respiratory system. *Antoonops corbulo*, n. sp., male. **49.** Right lung slit, spiracle and small opening (arrow). **50.** Small opening. **51.** Band of ridged cuticle arising from outer margin of spiracle. **52.** Book lung with three leaves. **53.** Short, narrow trachea (asterisk) arising from base of tracheal trunk (tt) and splitting up in tracheoles. Abbreviation: ap, apodeme.

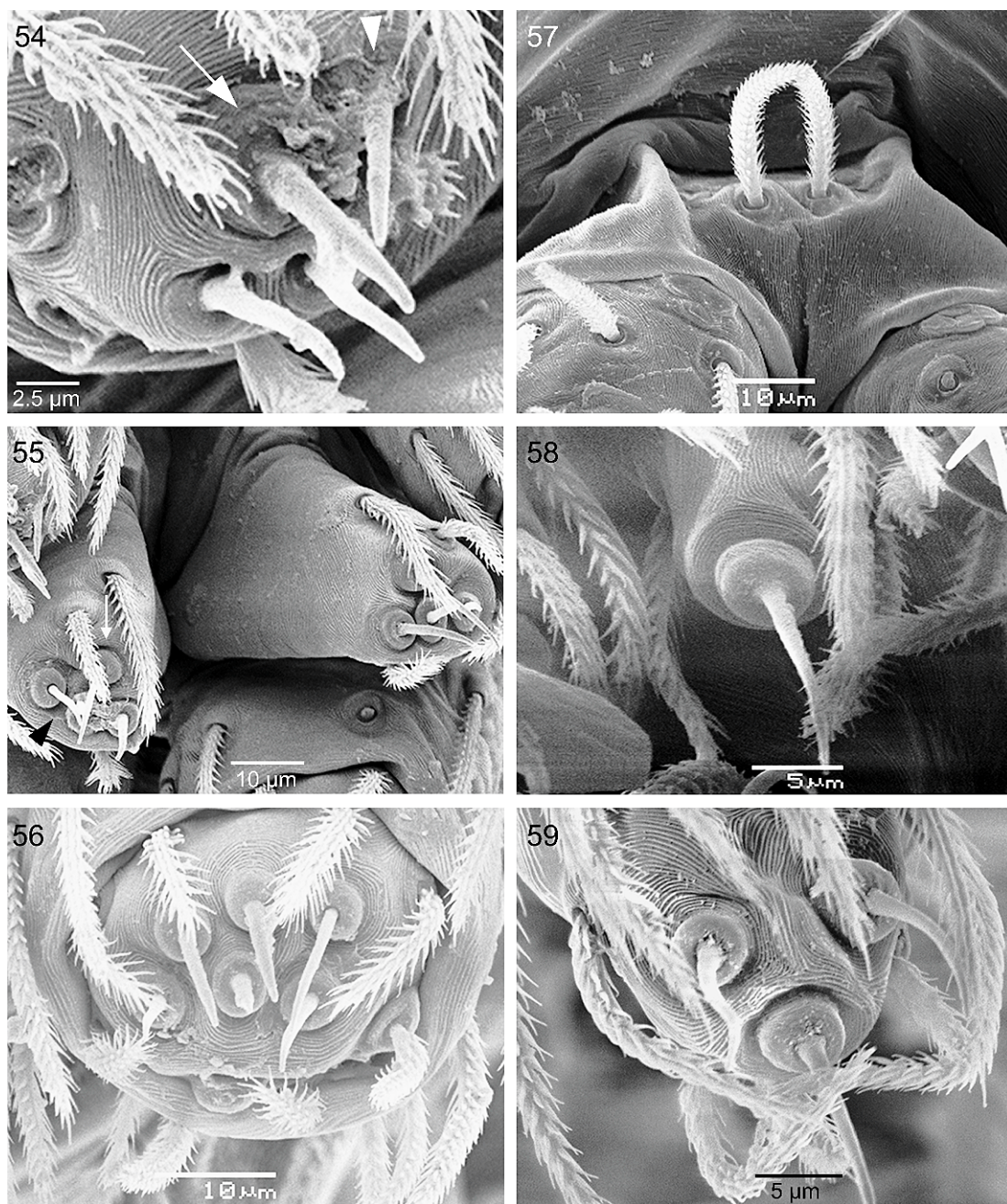
the origin and maintenance of *Antoonops*' mimetic dimorphism. For instance, differences between the sexes in behavior or microhabitat use could result in a higher predation pressure on males, making mimicry more advantageous to them than to females (Joron, 2005).

PHYLOGENETICALLY INFORMATIVE CHARACTERS

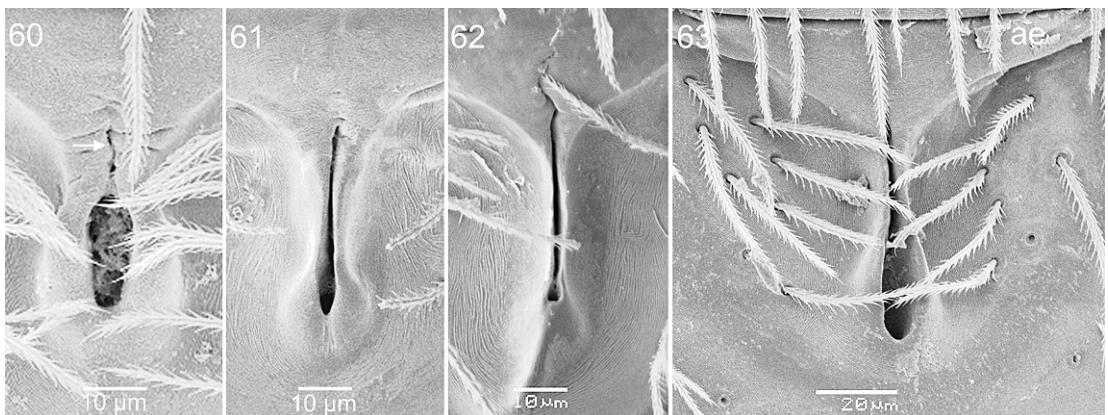
Comparison of our SEM results with the ultrastructural data available on oonopid

external morphology indicates the presence of considerable variation in many anatomical traits. We will here briefly discuss some of these traits and evaluate their potential use in the phylogenetic inference of higher-level relationships among oonopids.

The morphology, number, and spatial distribution of the cheliceral setae and spines described above are highly consistent among all *Antoonops* species. Previous authors have given very little or no attention to cheliceral



Figs. 54–59. Spinnerets and colulus. 54–56. *Antoonops nebula*, n. sp. 57–59. *Antoonops corbulo*, n. sp. **54.** ALS, female. Arrow: major ampullate gland spigot. Arrowhead: anterior piriform gland spigot. **55.** PMS, female. Arrow: spigot anterior to row of aciniform gland spigots. Arrowhead: space between outer and two inner aciniform gland spigots. **56.** PLS, female. **57.** Colulus, female. **58.** PMS, male. **59.** PLS, male.



Figs. 60–63. Copulatory orifice. **60.** *Antoonops corbulo*, n. sp. Arrow: narrow groove. **61.** *Antoonops bouaflensis*, n. sp. **62.** *Antoonops iita*, n. sp. **63.** *Antoonops nebula*, n. sp. Abbreviation: ae, anterior edge of posterior scutum.

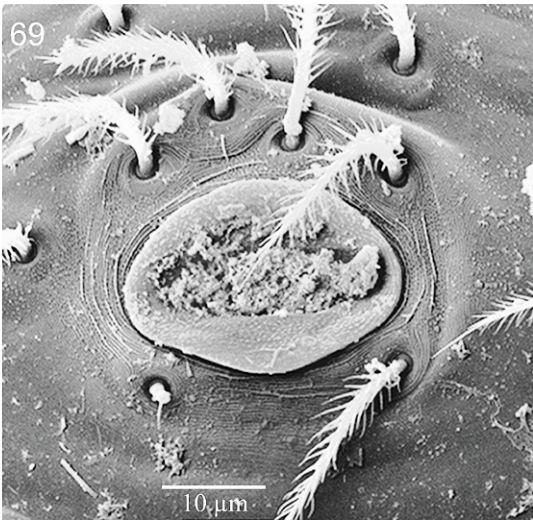
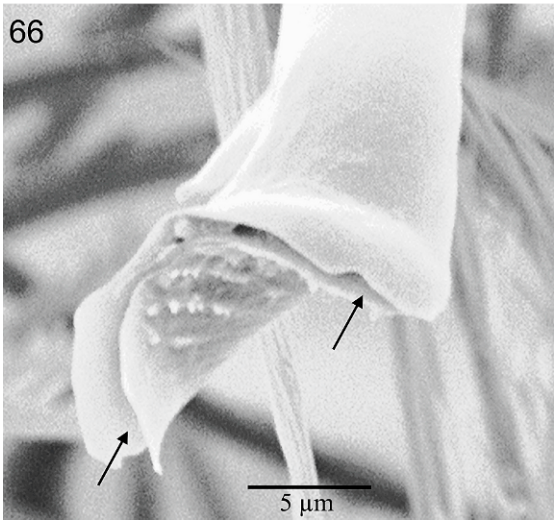
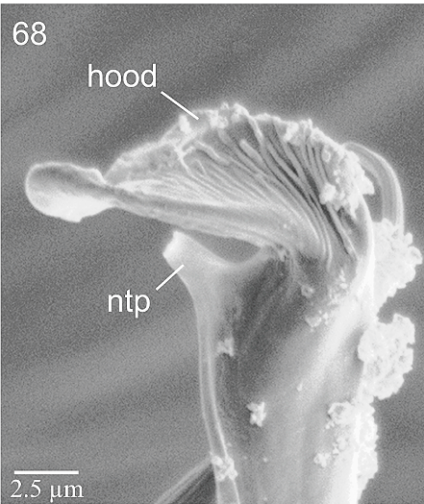
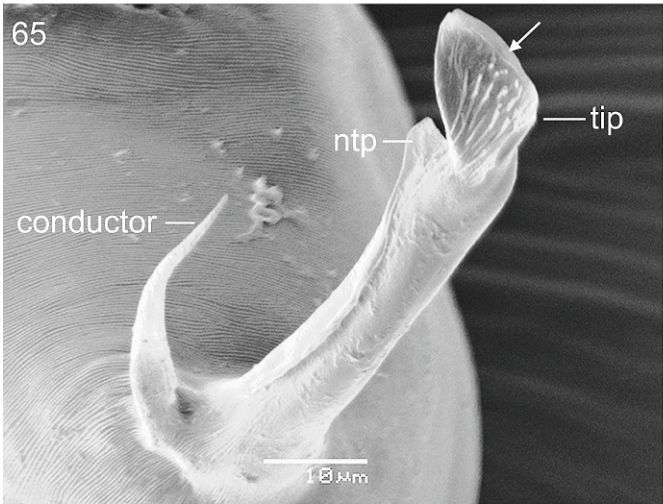
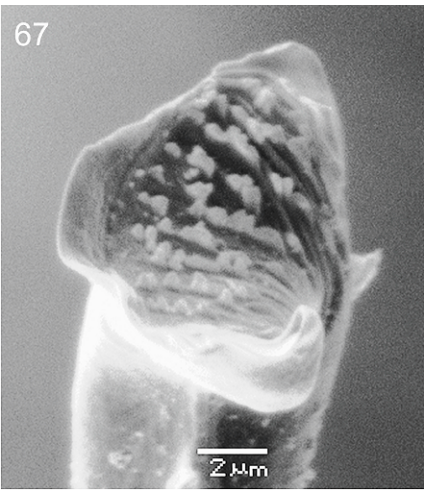
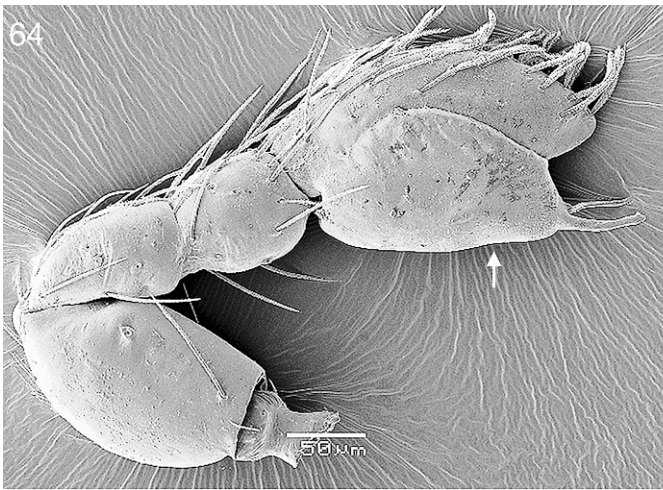
setae, but the few electron micrographs available in the literature (e.g., Forster and Platnick [1985]’s figure 877 of specialized hairs on the promargin of *Stenoonops nitens* Bryant, 1942) tentatively hint at considerable within-family variation. As a putative source of multiple synapomorphies, the cheliceral setae could potentially be of great value in oonopid systematics and should be an important feature of future work on this family.

Various modified male endites have been reported from numerous oonopids (e.g., Saaristo, 2001, 2002; Saaristo and van Harten, 2006; Höfer and Brescovit, 1996; Ott and Brescovit, 2004; Harvey, 1987; Cooke, 1972), but few of these equal *Antoonops*’ endites in complexity. Irrespective of their poorly understood function, endital elaborations could be informative at the genus level and possibly even higher, as the posterior, flattened process common to all *Antoonops* species may have a homologue in at least one other, currently undescribed African genus (W. Fannes and R. Jocqué, unpubl. obs.).

Several features pertaining to leg anatomy display possibly informative variation. A flat, exposed tarsal organ similar to the one in *Antoonops* was found in a number of other genera, including the type genus *Oonops* Templeton, 1835 (Forster and Platnick, 1985), but *Unicorn* Platnick and Brescovit, 1995 and *Xiombarg* Brignoli, 1979 exhibit a different, capsulate tarsal organ that may

unite these and possibly other genera as the sister group of the remaining Oonopidae (Platnick and Brescovit, 1995). The Australian *Grymeus* Harvey, 1987 may possess a tarsal organ that is morphologically intermediate between the flat and capsulate types (Harvey, 1987). Many oonopids possess uniseriate tarsal claws, but a biseriate dentition featuring a distally situated inner row of numerous closely spaced small teeth is shared by *Antoonops* and *Gamasomorpha* (see Forster and Platnick, 1985: fig. 838). The number and distribution of the trichobothria in *Antoonops* follow the pattern reported by Burger et al. (2002) for a species of *Opopaesa*. This pattern is very common among oonopids (W. Fannes and R. Jocqué, unpubl. obs.), but at least some intrafamilial variation exists, as *Unicorn* and *Xiombarg* have fewer trichobothria (Platnick and Brescovit, 1995) and a set of ventral trichobothria is present on tibia IV of *Coxapopha* Platnick, 2000 (Ott and Brescovit, 2004).

Spinneret morphology appears identical in all four species described here. This similarity even extends to such topological details as the separation between the outer and inner aciniform gland spigots of the female PMS (fig. 55). Comparison with published SEM photos (Platnick et al., 1991), on the other hand, brings to light considerable differences between *Antoonops*, *Dysderina plena* O.P. -Cambridge, 1894, and an unidentified species



of *Xyphinus* Simon, 1893. Thus, spinneret organization promises to provide useful characters at the generic level or higher.

The small openings associated with the coxal insertions (figs. 42–44) have, to the best of our knowledge, never been reported before. A role for these openings as exit pores of hitherto unknown prosomal glands seems an obvious interpretation, but definite assignment of a function evidently awaits further histological investigations. The phylogenetic importance of these previously unrecorded features is unclear. They could be unique to *Antoonops* and thus provide generic-level synapomorphies, or, as we suspect, they may be much more widespread and support a considerably larger clade. Detailed morphological studies of many more oonopids are obviously needed to resolve this issue.

INTERNAL FEMALE GENITALIA

Many recently published descriptions of oonopids have included information on the internal female genitalia (e.g., Harvey, 1987; Platnick and Brescovit, 1995; Höfer and Brescovit, 1996; Saaristo and van Harten, 2006; see also Forster and Platnick, 1985, for a discussion of dysderoid genital anatomy), but only two species have been the subject of detailed investigations using semithin serial sections and electron microscopy, viz. *Opopaea fosuma* Burger, 2002 and *Silhouettella loricatula* (Roewer, 1942) (Burger et al., 2002, 2003, 2006). Our discussion will therefore focus on a comparison of *A. corbulo*, *O. fosuma*, and *S. loricatula*, which reveals striking similarities as well as important differences (fig. 81).

Embedded within the anterior wall of the uterus externus of *O. fosuma* lies a sclerite that shows a remarkable resemblance to the anterior sclerite described above for *A. corbulo*: both consist of a triangular stalk and a transverse, sticklike apodeme that is connected to the lateral apodemes by two slender

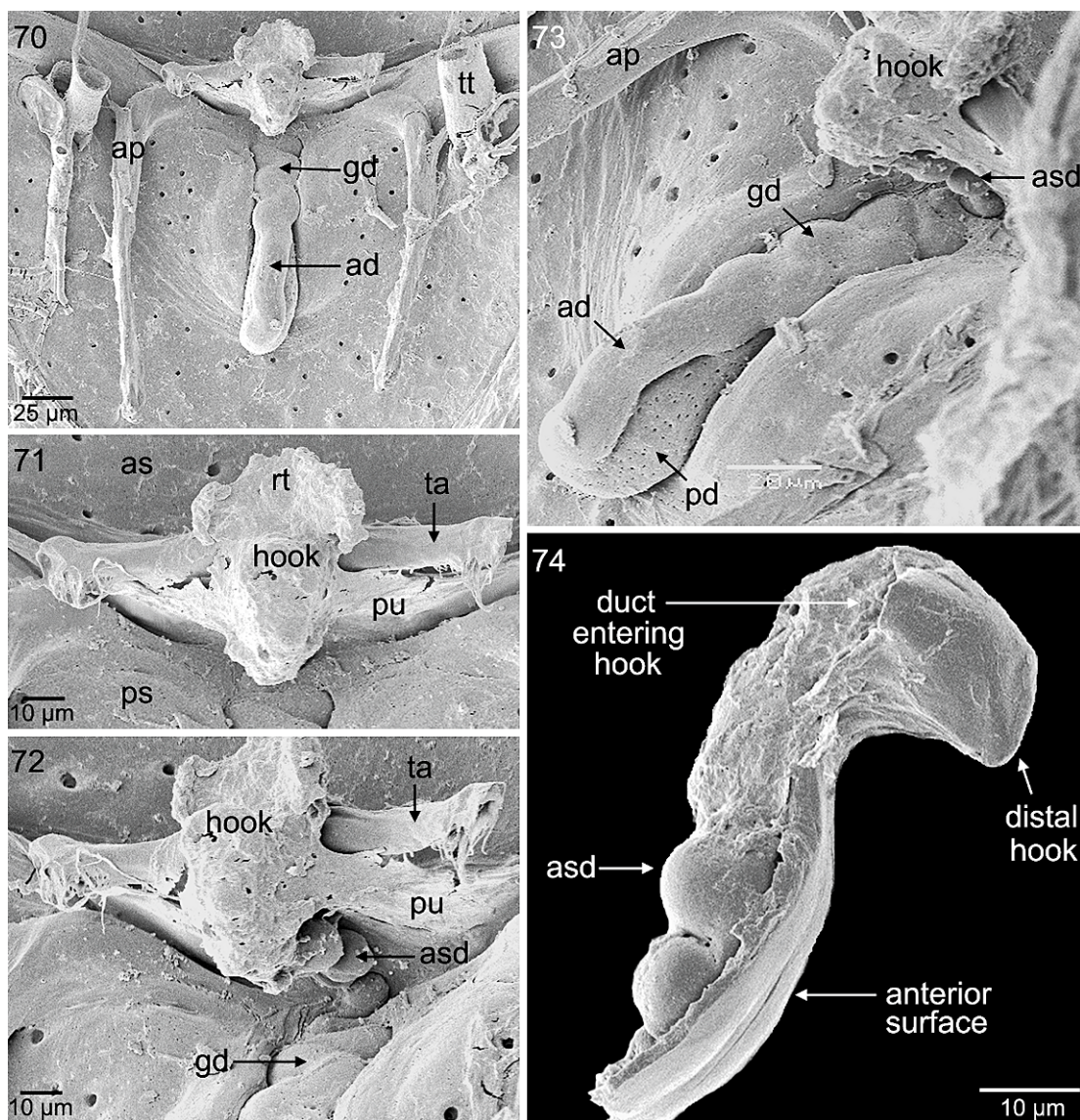
muscle strands. Judging from Ott and Brescovit (2004)'s figures, a comparable sclerite (called "anterior apodema" by these authors) is also present in the two-eyed genus *Coxapopha*. In *S. loricatula* the anterior sclerite is shaped rather differently but still displays a striking similarity in structure, position, and muscle attachments (Burger et al., 2006). Hence, the anterior sclerite of the female genital system represents a highly valuable candidate for a morphological homology and could potentially unite a very large clade within the Oonopidae, incorporating such anatomically disparate genera as *Antoonops*, *Opopaea*, *Coxapopha*, and *Silhouettella*.

Despite their similarity, the anterior sclerites of *A. corbulo* and *O. fosuma* are not identical as the transverse apodeme of the latter carries a posteriorly directed naillike extension instead of a dorsal cup (fig. 81). Muscle contractions presumably press this nail into a closely fitting hole present in the spermatheca's heavily sclerotized anterior wall, thereby effectively locking the uterus externus to prevent copulating males from transferring their sperm directly into it. A similar mechanism was proposed for *S. loricatula*. Embedded in the posterior wall of the uterus externus of this species lies a peculiarly shaped sclerite whose dorsalmost part, termed "globular appendix", bears a furrow in which the anterior sclerite is supposed to fit (Burger et al., 2003, 2006). In *A. corbulo* the hook- and sticklike sclerites are in close contact with each other (fig. 71) and may similarly serve females to lock the uterus externus (e.g., by pressing the hook into the cup), but further studies including histology are required to establish whether, and in which manner, they interact to form a locking mechanism.

The morphology of the internal female genitalia of *A. corbulo* as revealed by SEM strongly suggests that sperm cells are deposited in the duct via the copulatory orifice and are subsequently transferred along its entire

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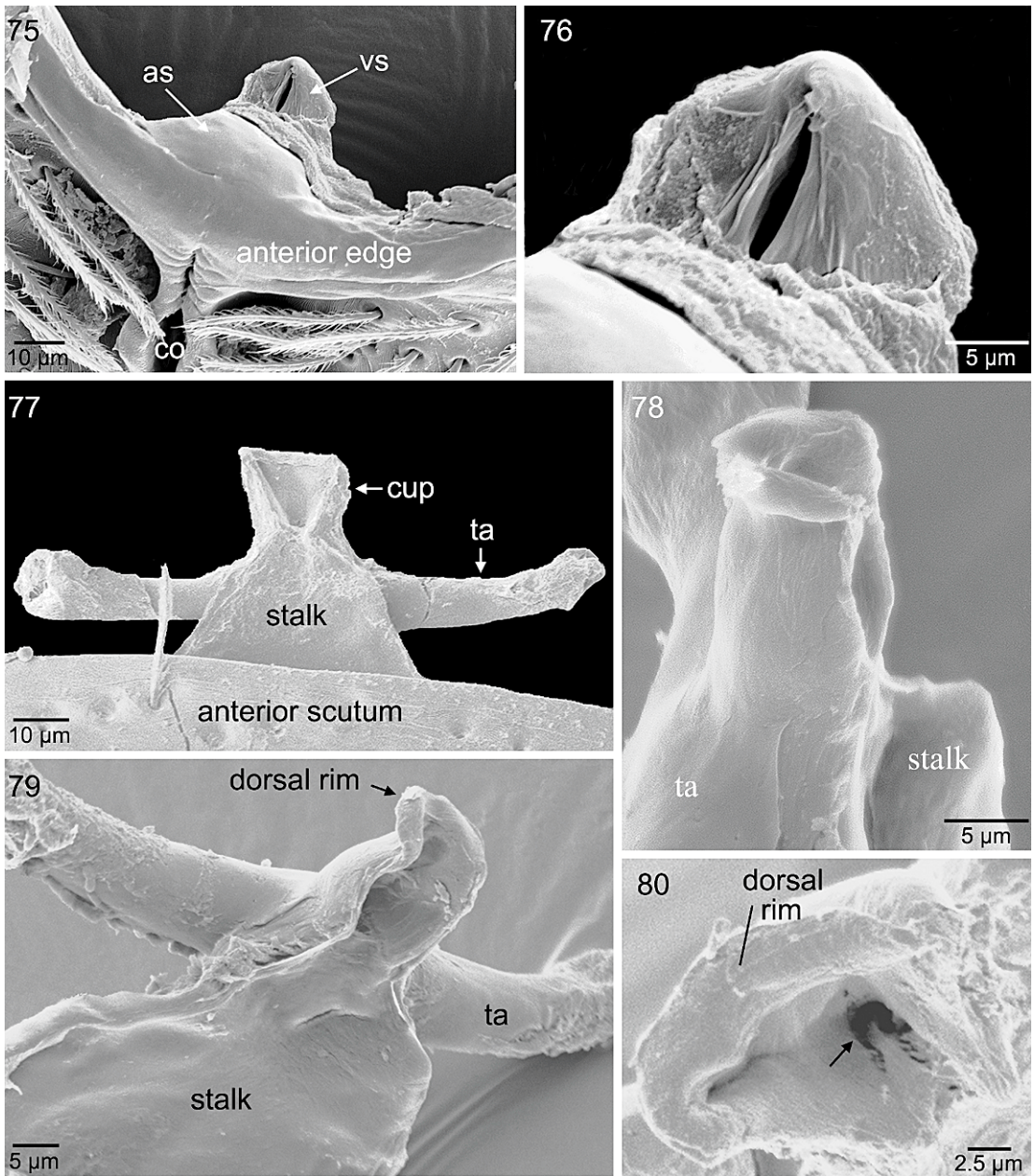
Figs. 64–69. 64, 69. *Antoonops corbulo*, n. sp. 65, 66. *Antoonops nebula*, n. sp. 67. *Antoonops iita*, n. sp. 68. *Antoonops bouaflensis*, n. sp. 64. Right palp, retrolateral view. Arrow: indentation on bulbus. 65. Embolus and conductor. Arrow: slit. 66. Embolar tip. Arrows indicate extremities of slit. 67. Embolar tip with small denticles. 68. Embolar tip forming hood. 69. Sperm pore. Abbreviation: ntp, near tip projection.



Figs. 70–74. Female internal genitalia. *Antoonops corbulo*, n. sp. **70.** Dorsal overview. **71.** Anterior and posterior sclerites embedded within the walls of the uterus externus. **72.** Side view on sclerites with ascending part of duct. **73.** Lateral view on duct. **74.** Dissected-out posterior sclerite with ascending duct. Abbreviations: ad, anterior running part of duct; ap, apodeme; as, anterior scutum; asd, ascending part of duct; gd, globose part of duct; pd, posterior running part of duct; pu, posterior wall of uterus externus; rt, residual tissue; ta, transverse apodeme; tt, tracheal trunk.

length to be finally released into the uterus externus through the slitlike opening in the distal hook of the posterior sclerite (fig. 81). This would make *A. corbulo* one of the very few reported cases of haplogyne spiders with entelegyne-like genitalia (see Huber, 1997,

2004, for another example). The two oonopids investigated by Burger and coworkers have a reproductive tract that differs markedly from *A. corbulo*'s. In *O. fosuma*, for example, the copulatory orifice leads into a posteriorly extending spermatheca that ends blindly and



Figs. 75–80. Female internal genitalia. *Antoonops corbulo*, n. sp. **75.** Ventral view on posterior sclerite arising from anterior edge of posterior scutum. **76.** Slitlike opening in ventral surface of distal hook. **77.** Posterior view on anterior sclerite in situ. **78.** Lateral view on cup. Open side faces posteriorly. **79.** Posterior view on dissected-out anterior sclerite. **80.** Hole (arrow) in floor of cup. Abbreviations: as, anterior surface of posterior sclerite; co, copulatory orifice; ta, transverse apodeme; vs, ventral surface of distal hook of posterior sclerite.

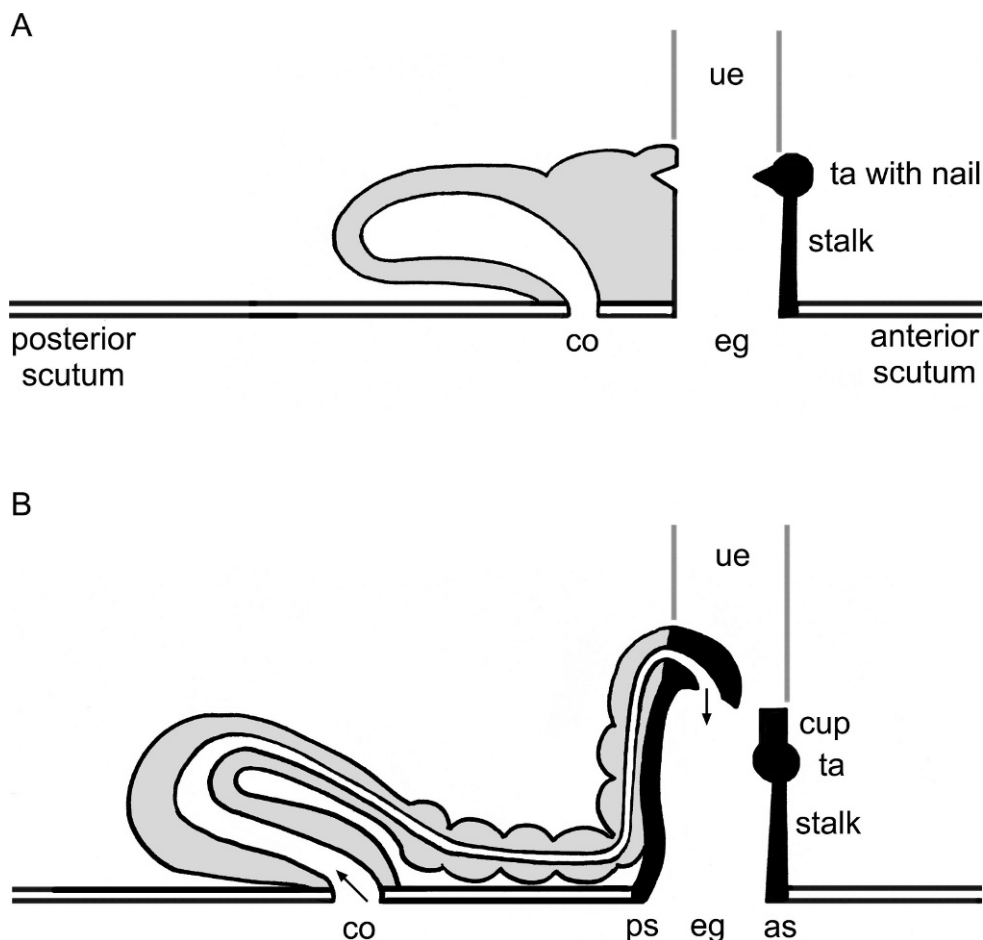


Fig. 81. Schematic drawing of internal female genitalia of (A) *Opopaea fosuma* Burger (after Burger et al., 2003) and (B) *Antoonops corbulo*, n. sp. Arrows indicate our hypothesis of sperm flow in *A. corbulo*: sperm is deposited in the duct via the co and finally enters the ue via the ventral opening in the distal hook of the posterior sclerite. Abbreviations: as, anterior sclerite; eg, epigastric groove; co, copulatory orifice; ps, posterior sclerite; ta, transverse apodeme; ue, uterus externus.

shows no connection to the uterus (Burger et al., 2003), making it presently unclear how fertilization is achieved in this species (fig. 81).

Female genital anatomy is one of the factors influencing the pattern of sperm priority in spiders (Eberhard, 2004; Uhl, 2002) and may be particularly important in oonopids where sperm mixing appears limited or even absent (Burger et al., 2006). If our interpretation is correct, *A. corbulo*'s reproductive tract has a flow-through design that may result in first-male sperm priority. The dead-end spermatheca of *O. fosuma*, on the other hand, might favor the last male to mate. Sperm-priority

patterns in turn have major implications for mating strategies (Eberhard, 2004). Continued comparative studies of the internal genitalia of Oonopidae will therefore not only contribute to resolving their phylogeny, but will also enhance our understanding of the mechanisms of sexual selection acting on these spiders.

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