Zootaxa 4657 (1): 057–096
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4657.1.2
http://zoobank.org/urn:lsid:zoobank.org:pub:F27CB967-C001-436A-9F25-184D5484363C

New Myxophagan water beetles from Madagascar (Coleoptera: Torridincolidae, Hydroscaphidae)

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Abstract

Myxophagan water beetles from Madagascar are comprehensively revised. Holotypes of the two previously known species are re-described and illustrated. Six new species of *Incoltorrida* Steffan and one new species *of Hydroscapha* LeConte are described and illustrated. The larvae of *Incoltorrida quintacostata* are illustrated and discussed. The presence of peritrich ciliates of the genus *Platycola* Kent on specimens of *Incoltorrida madagassica* Steffan is discussed and illustrated. Habitus, habitats, and male genitalia are illustrated, and distributions are mapped. The following new species are described (type localities parenthetic): *Incoltorrida benesculpta* **n. sp.** (Fianarantsoa, 3.2km S Ambohimanjaka); *I. galoko* **n. sp.** (Antsiranana, Diana, Ambilobe, Antsaba, Galoko mountains); *I. magna* **n. sp.** (Antsiranana, Diana, Ambilobe, Antsaba, Galoko mountains); *I. marojejy* **n. sp.** (Antsiranana, Sava, Marojejy National Park); *I. quintacostata* **n. sp.** (Fianarantsoa, 3.5km N Ivato); *I. zahamena* **n. sp.** (Toamasina, Alaotra-Mangoro, Zahamena National Park*)*; *Hydroscapha andringitra* **n. sp.** (Fianarantsoa, Ambilavao, Sendrisoa, approx. 10km N of Andringitra National Park).

Key words: Madagascar, Myxophaga, *Incoltorrida, Hydroscapha*, aquatic beetles, taxonomy, new species, peritrich ciliates, hygropetric habitat

Introduction

The Coleoptera suborder Myxophaga currently includes only four families: Hydroscaphidae, Lepiceridae, Sphaeriusidae and Torridincolidae (Hall 2000). Members of the suborder, which is microscopic in diversity and number of species compared with the much larger suborders Polyphaga and Adephaga, are usually regarded as having a relict distribution pattern. In Madagascar, three of the four known families of Myxophaga are found: Hydroscaphidae, Sphaeriusidae, and Torridincolidae. Prior to this contribution, one species in each family had been described: *Hydroscapha saboureaui* Paulian (1949); *Sphaerius madecassus* Paulian (1949); and *Incoltorrida madagassica* Steffan (1973).

Herein, the holotypes of the previously described species of Madagascar *Incoltorrida* and *Hydroscapha* are re-described, and habitus images and illustrations of the male genitalia are provided. Six new species of *Incoltorrida*, and one new species of *Hydroscapha* are described and illustrated, and distributions mapped. Habitats are discussed, and photographs of collecting localities are given.

Most of the specimens of the new species described herein were collected by J. Bergsten and co-participants in The Water Beetle Fauna of Madagascar project, during expeditions made between the years 2006 and 2018. Additional specimens were collected by M. Balke in 2004, and P. D. Perkins in 2014.

Habitats

All of the species of *Incoltorrida* in this study were found in hygropetric habitats, where water is flowing over rock

Accepted by W. Hall: 6 Jun. 2019; published: 16 Aug. 2019

substrates (Figs. 40–51). In many cases the water is a thin film, such as is present in seepage areas. In other habitats the water is a thicker layer, and is flowing faster, such as in small streams over bedrock, or large streams when water level is low.

One locality, where both *I. quintacostata* and *I. benesculpta* were collected, had both types of microhabitats (Figs. 42, 43). Specimens of *I. quintacostata* were collected in a small stream, flowing over bedrock. The beetles were collected just inches to a foot or more upstream from where the water tumbled over a small cascade. Only about two meters away from that collection area, specimens of *I. benesculpta* were collected on a vertical or near vertical seepage rock face at the side of the stream, that was also receiving a little spray water from the cascade. These two *Incoltorrida* species differ markedly both in size and dorsal sculpture (Figs. 1, 7, 8). The larger species, from faster water, *I. quintacostata*, has highly modified elytral sculpture, with reduced number of costae (=5), and strongly modified lateral areas of the elytra. The smaller species, *I. benesculpta*, from a slower, thinner layer of water, has strongly sculptured pronotum and elytra, the latter with the full complement of costae (=8) (see morphology section).

The *Incoltorrida* locality that was the largest in extent, and most complicated in angles and vertical drops (Fig. 40), had the most species collected in one locality: *I. galoko, I. magna,* and *I. quintacostata*.

Incoltorrida was collected literally from sea level on hygropetric rocks exposed to salt water wave-splash in stormy weather (Figs. 48, 49) to 1700m altitudes on the Central Highlands. Both *I. madagassica* and *I. quintacostata* were found in lowlands as well as on the central highlands, indicating tolerance of a large variation in climatic regime even within species.

The one species of *Hydroscapha* collected in the study was found in a very open, sunny area with much bedrock, and hygropetric flows (Figs. 52–55).

Morphological taxonomic characters of *Incoltorrida*

Head: In *Incoltorrida* the frons and clypeus are strongly joined to form what is herein termed a "frontoclyeal shield" (Fig. 4). This shield, when the beetle is facing upstream, is certainly the leading edge of the beetle's resistance to the strong, on-rushing flow of its microhabitat. The shield shows some variation among species. The shapes of the lateral margins vary slightly, and the degree to which the shield, in cross section, is more or less strongly bisinuate (shaped somewhat like a very flattened "W") varies moderately from species to species.

Pronotum: The pronotal sculpture varies considerably among species of *Incoltorrida*. These differences include the presence or absence of ridges, such as the anterior and posterior ridges (Fig. 2) and the midlongitudinal ridge (e.g., Fig. 10). The height of the pronotal reliefs and depth of the intervening depressions varies considerably, with *I. galoko* and *I. benesculpta* having the extreme condition.

Elytra: The elytral sculpture of *Incoltorrida* species provides useful taxonomic characters. Almost certainly the pleisomorphic condition of the genus is ten series of punctures, with intervals moderately elevated, or perhaps subcostate. In some species, such as *I. marojejy*, series #7 and #9 are reduced in length (i.e., reduced number of punctures; clearly visible in a transparency mount, Fig. 24). The reduction of the lateral series appears to be a general trend in the modification of the shape of the lateral area of the elytron. In the more derived condition, such as *I. quintacostata*, the intervals are flat, the serial punctures are very obscure, and costae (morphological) #4, #6, and #7 are absent, resulting in the elytron having only five well elevated costae, the morphological #8 being the strongest and most sinuate. The sinuation of costa #8 results in a large gap (depression) between the costa and the lateral elytral margin (Fig. 3). The curvature of, and comparatively large size of costa #8, in some species, with a large gap to the elytron margin (e.g., *I. magna*, Fig. 3), is probably a morphological adaptation to living in faster flowing water (also see microhabitat section). The total number of costae varies thusly: (8) *I. benesculpta, I. madagassica, I. magna, I. marojejy, I. zahamena*; (5) *I. galoko, I. quintacostata*. In some of the species interpreted to have eight costae, #6 and #7 are lower than the other costae.

Each elytron has, to a more or less degree, two transverse ridges which "link" the more lateral costae to one another (Figs. 2, 3). These ridges are sometimes offset one from the other (Fig. 2) and sometimes are in a line (Fig. 3).

Metaventrite: The large ventral tabella, present in all species of *Incoltorrida*, varies very little. There are very slight differences in the shape of the carina that defines the lateral limit of the tabella.

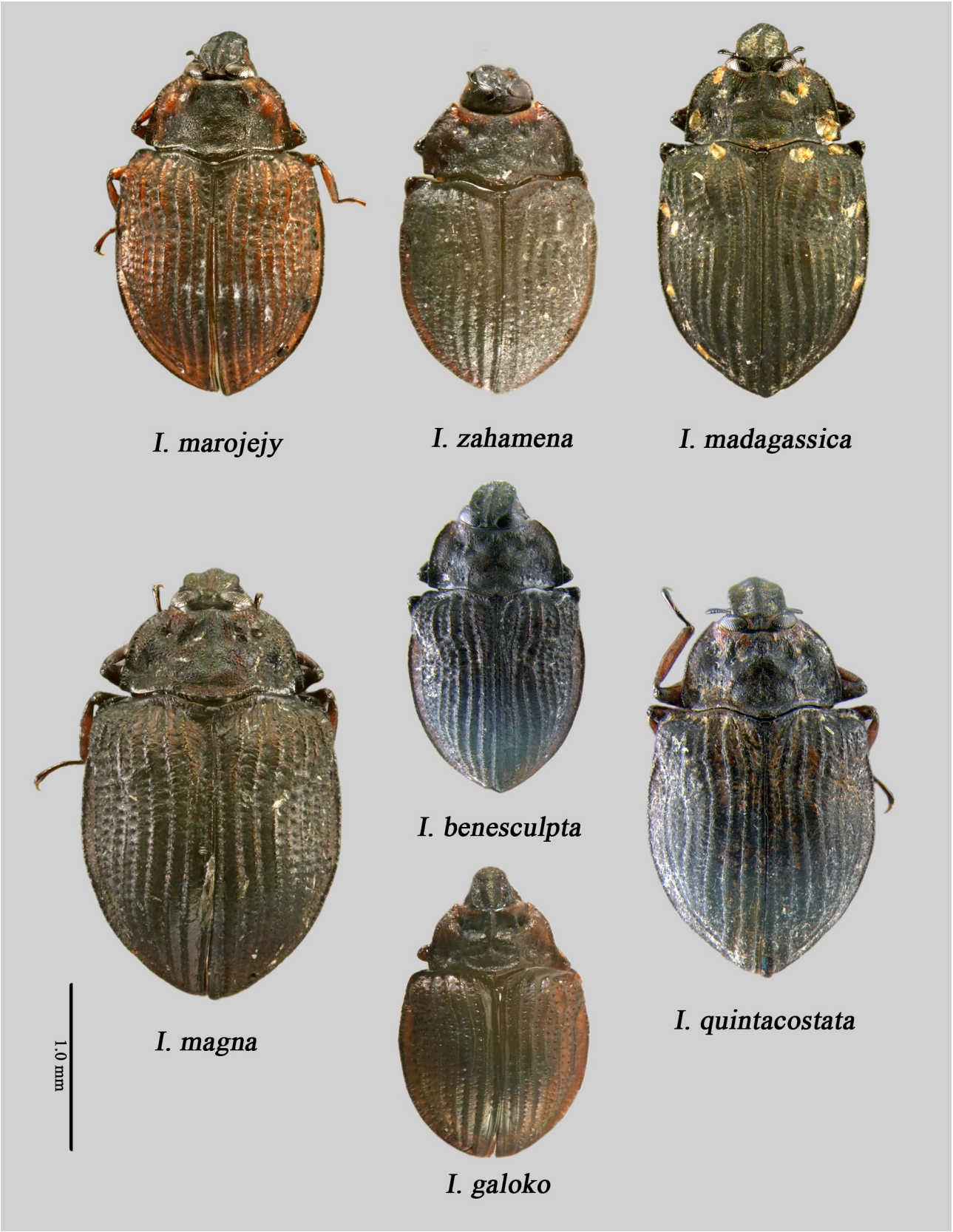
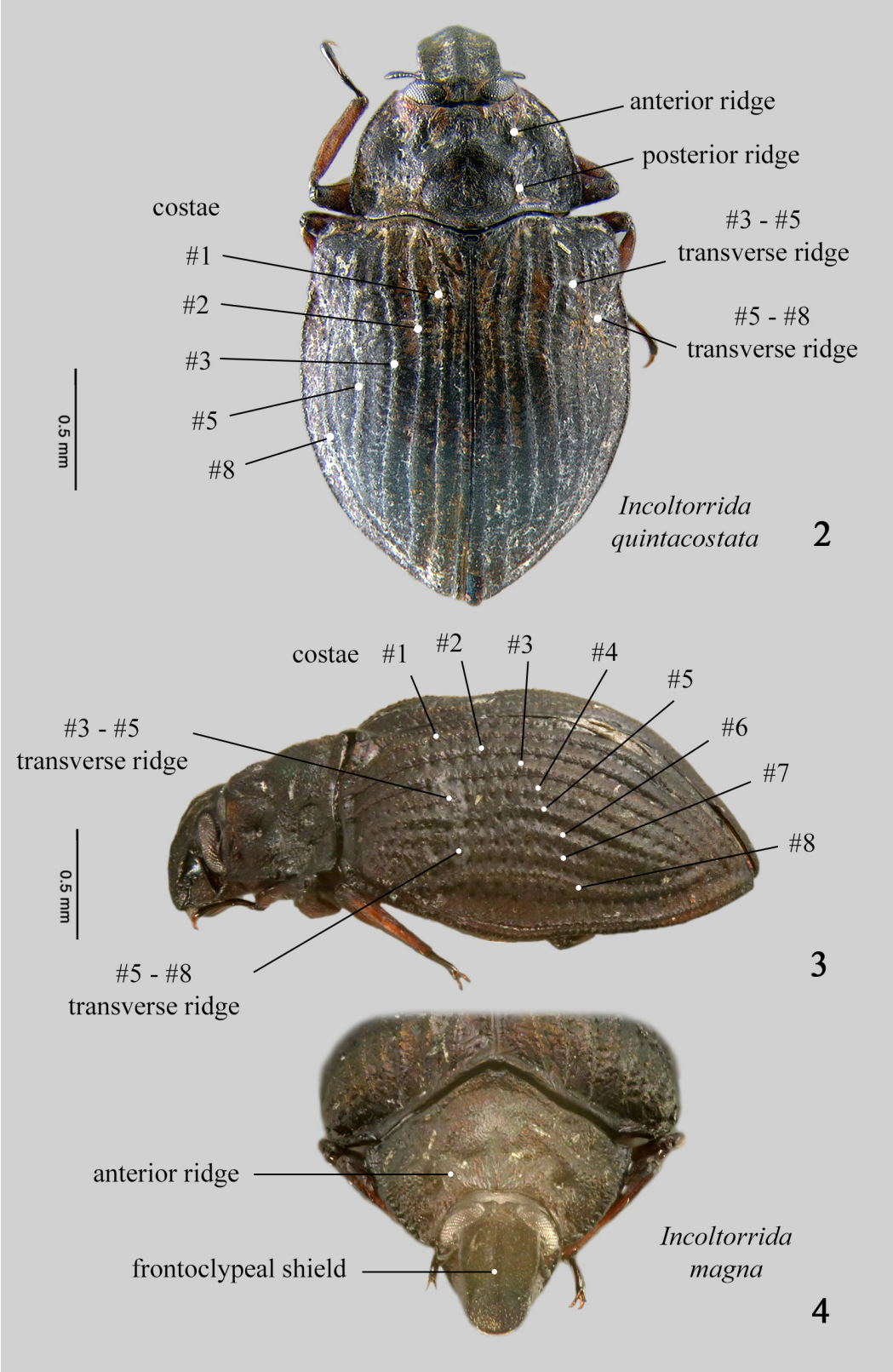


FIGURE 1. Dorsal habitus of *Incoltorrida* species.

Male genitalia: The male genitalia provide species specific differences in all *Incoltorrida* for which males are known (Figs. 12, 18–22). Differences among species include the length, shape (both in ventral and lateral views), and the presence/absence and size of sharply pointed spines on the distal areas of the aedeagus (Figs. 15–17). All

species have a single seta on each side near the base of the male genitalia, each seta being on a slightly enlarged, rounded basal lobe (e.g., Figs. 19, 20). These setae are the confirming clues that the basal lobes are the homologues of the parameres present in members of *Torridincola* Steffan, and are not expansions of the endophallus. Some species of the genus *Hydrochus* (Hydrochidae) have so-called pseudoparameres, which are attached to the base of the aedeagus, and are considered expansions of the endophallus (see Worthington *et al*., 2016); the pseudoparameres never have setae.



FIGURES 2–4. Dorsal morphology. (2) *Incoltorrida quintacostata*; (3–4) *I. magna*.

Larvae of *Incoltorrida*

Larvae of *Incoltorrida* were collected in association with the following species: *I. madagassica*, *I. marojejy*, and *I. quintacostata*. The larvae (e.g., Fig. 23) are quite similar to larvae of *Torridincola*, which were illustrated by Steffan (1964). The number (8) and placement of the spiracular gills is similar; each gill is 4-segmented in last instars, but are 3-segmented in early instars. The thorax is broader in *Incoltorrida*, and the posterior margin of the pronotum is arcuate, whereas in *Torridincola* (as figured by Steffan) the posterior border is bisinuate.

The last instar larva illustrated (Fig. 23) was collected in association with adults of *Incoltorrida quintacostata*. Larvae collected in association with other species do not significantly differ in structural details.

Epibiont peritrich ciliates of *Incoltorrida*

Several specimens of *Incoltorrida madagassica* had attached hollow urn-shaped structures, often found in the lateral intervals of elytral costae or in crevices on pronotum or head (Fig. 5). These are the lorica, or protective tests, of sessile peritrich ciliates. After consulting experts (see acknowledgements) these could be identified as belonging to the genus *Platycola* Kent, 1882 of the family Vaginicolidae Fromentel, 1874. All Vaginicolidae genera are loricate and solitary, some are stalked but *Platycola* is stalkless.

Platycola species occur both in marine and freshwater environments. They secrete a protective lorica with an anterior aperture onto a substratum that can be biotic (e.g. algae, plant or animal) or abiotic (Warren, 1982). There can be one, two or more zooids in a lorica (Warren, 1982). The lorica is typically attached decumbent onto the substratum with the aperture directed anteriorly and upwards (Warren & Carey, 1983). The zooid is trumpet-shaped or cylindrical and can extend beyond the lorica aperture (Warren, 1982). Reproduction occurs both asexually and sexually (Warren, 1982). On fixation, the zooids usually contract into the lorica and cannot be seen. The genus *Platycola* was taxonomically revised by Warren (1982) and he recognised 13 species, at least one of which has since been transferred to another genus (Jankowski, 2015). The taxonomy of the group was historically based on the morphology of the lorica; the size, shape, colour, neck of aperture, and striations (Warren, 1982; for detailed SEM images of the lorica of *Platycola decumbens* see Warren & Carey, 1983). But Kralik (1961) showed that the morphology of the lorica is highly variable and unreliable for species delineation on its own. Likewise, the substratum has been considered important, especially for epibiotic forms, but data are generally insufficient to evaluate host specificity. While some species are only known from a specific species, for instance a cave-dwelling isopod, the best studied species, *P. decumbens*, as currently defined, can be found on a variety of plant, animal and abiotic substrata (Warren, 1982; Cook *et al*, 1998). However, we have found no previous record of the genus *Platycola* as epibionts on aquatic beetles, or even on aquatic insects. The basibionts (animal substrata) we have found recorded in the literature for *Platycola* are crustaceans (isopods, amphipods, Cambaridae freshwater crayfish) and molluscs, although our literature search was not exhaustive. Other peritrich taxa such as *Vorticella* are well known to be epibionts on aquatic insects and are known from several insect orders including Coleoptera (Laird, 1959). More commonly reported epibiont ciliates on aquatic beetles belong to the subclass Suctoria however, and these have been reported from at least Hydraenidae, Dytiscidae, and Hydrophilidae (see references in Dovgal & Pesic, 2012 and Fernandez-Leborans, *et al*. 2017; Bameul, 1991).

Species-level identification of this *Platycola* on *Incoltorrida madagassica* is not possible based solely on the lorica. Furthermore, even though the substratum is new, we do not know if this species of *Platycola* is confined either to its host or to the habitat. Perhaps it occurs on all kinds of suitable biotic and abiotic substrata in these hygropetric environments. This is the first time *Platycola* is recorded from Madagascar, but arguably a non-insignificant proportion of microorganisms have a cosmopolitan distribution, captured in the microorganism metaphor "everything is everywhere" (Finlay 2002), although recent research is challenging this idea (see Foissner, 2006 and Fontaneto & Hortal, 2012 for reviews on biogeography and dispersal of microorganisms). This taxon on Madagascar may be endemic or it may be cosmopolitan. *Platycola decumbens* has indeed been recorded from both North and South hemispheres, from both Old and New World (Warren, 1982, Safi *et al*, 2014, Chandra *et al*, 2017, Cook *et al*, 1998). However, we note that there are no DNA sequences on GenBank of any *Platycola* species, hence the species concept has not been critically examined with DNA data.

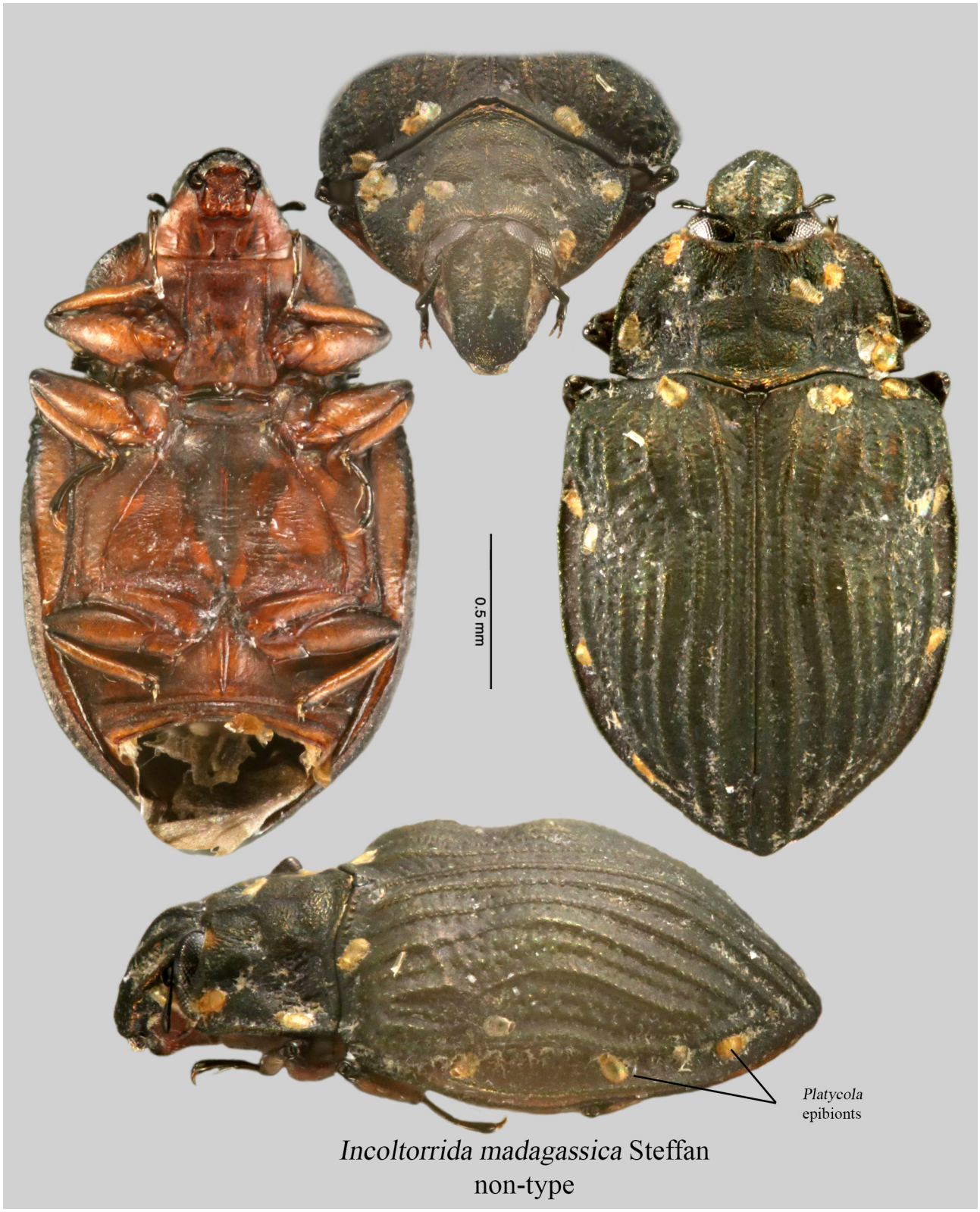


FIGURE 5. *Incoltorrida madagassica* Steffan, habitus views of non-type with attached *Platycola* epibionts.

Interestingly, when Spangler (1980) described a new Torridincolidae species from Brazil in the genus *Ytu*, he also noted attached epibionts identified as Vaginicolids. These loricae were of a rather different shape and were stalked (pedunculate) and not decumbent. Spangler suggested they may be closest to the genus *Pyxicola* Kent. He also noted they were most frequent on the ventral side of the beetles (in contrast to *Platycola* here reported which occurred on the dorsal side of the beetles) and argued they may take advantage of the beetle's foraging for food.

He suggested the relationship may be commensal, but it is unknown to what degree the beetle's fitness is affected, positively or negatively, by the epibiont. In general, potential advantages for the epibiont may include dispersal, increased supply of nutrients and protection against predators (Fernandez-Laborans, 2009). Potential advantages for the basibiont may include mimetic protection and cleansing, but may also be disadvantaged by restricted mobility, negative effect on growth and moult, and function of organs (Fernandez-Laborans, 2009).

It would be very interesting to find out if there is indeed a specific association between these epibionts and the beetle family Torridincolidae in particular. Is it more than a coincidence that vaginicolids were found on this old and poorly known family of aquatic beetles from both Brazil and Madagascar, and may there be a long coevolutionary history between the two?

Methods and Conventions

Locality records given herein are, with a few exceptions for clarity, as they appear on specimen labels. Specimen preparation and illustration techniques follow those used in Perkins (1997). Specimens of species represented by numerous individuals will be distributed among several of the institutions listed in the depositories section.

Some of the administrative divisions of Madagascar have changed since specimens were collected. The six former provinces of Antsiranana, Mahajanga, Toamasina, Antananarivo, Fianarantsoa and Toliara have been replaced by 22 administrative regions. The labels on the specimens reflect for the most part the administrative divisions at the time of collection (as do the captions on the habitat figures herein), but we also find it useful for faunistic continuity reasons to give the former provinces. Following are the more current administrative divisions of specimens that were collected by The Water Beetle Fauna of Madagascar project (collected by Bergsten, *et al*.), presented herein:

Coll. event P38: Sendrisoa, 27km S. of Ambalavao, approx. 10km N. of Andringitra National Park, brownish water seeping over rock, 22.0098S, 46.9504E, 1165m, 7 v 2006. Matsiatra Ambony region (former province Fianarantsoa).

Coll. Event MAD12-26: Galoko mountains, Antsaba, hygropetric rocks and water pools, 13.60974S, 48.72175E, 263m, 25 xi 2012. Diana region (former province Antsiranana).

Coll. event MAD12-31: Galoko mountains, stair-like hygropetric rocks 3.4 km NW of Antsaba village, 13.6093S, E48.7213E, 300m, 28 xi 2012. Diana region (former province Antsiranana).

Coll. Event MAD13-73: Manombo R.S., Parcelle I, Rearatra, Piste 56, forest stream with pools, 23.006183S, 47.7338833E, 21m, 14 xii 2013. Atsimo Antsinanana region (former province Fianarantsoa).

Coll. Event MAD14-02: 3km south of Ambalamanakana next to RN7, Ankazomivady forest, hygropetric rocks and marsh with vegetation, 20.7722S, 47.1809E, 1700m, 1 xi 2014. Amoron'i Mania region (former province Fianarantsoa).

Coll. Event MAD14-48: Marojejy NP, 800m N from Camp I, Humbert waterfall, hygropetric ex. bedrock pools atside of waterfall, 14.4333S, 49.773E, 550m, 8 xi 2014. Sava region (former province Antsiranana).

Coll. event MAD14-54: Marojejy National Park, hygropetric rocks (Andampimbazaha cascade) of Ambavaomby river below Camp II (Camp Marojejia), 14.4345S, 49.7606E, 710m, 9 xi 2014. Sava region (former province Antsiranana).

Coll. event MAD18-24: Marojejy National Park, hygropetric rocks upstream stream passing by camp II, traversing from Taktajania trail, 14.4369S, 49.7603E, 820m, 9 ii 2018. Sava region (former province Antsiranana).

Coll. event MAD18-25: Marojejy National Park, hygropetric rock by kitchen area of Camp II (Camp Marojejia), 14.4350S, 49.7601E, 770m, 9 ii 2018. Sava region (former province Antsiranana).

Coll. event MAD18-60: Masoala National Park, South side of Nosy Mangabe island, hygropetric rocks by the sea, 15.5056S, 49.7571E, sea level, 20 ii 2018. Analanjirofo region (former province Toamasina).

Coll. Event MAD18-111: Zahamena National Park, Antanandava Sect., midaltitude rainforest: Manambato river ~100m downstream of Camp Cascade, hygropetric rocks at night, 17.5438S, 48.7230E, 1280m, 10 iii 2018. Alaotra-Mangoro region (former province Toamasina).

Depositories

BMNH The Natural History Museum, London, UK (Christine Taylor)

CAS	California Academy of Sciences, San Francisco, CA, USA (D. H. Kavanaugh)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (P. D. Perkins)
MNHN	Museum national d'Histoire Naturelle, Paris (A. Taghavian-Azari)
MRAC	Royal Museum for Central Africa, Tervuren, Belgium (M. De Meyer)
NHRS	Swedish Museum of Natural History, Stockholm, Sweden (J. Bergsten)
UAZ	University of Arizona, Tucson, AZ, USA (W. Eugene Hall)
ZSMC	Zoologische Staatssammlung, Munich, Germany (M. Balke)
PBZT/MBC	Parc Botanique et Zoologique de Tsimbazaza/Madagascar Biodiversity Centre, Antananarivo, Madagascar (B. Rajemison)

Incoltorrida Steffan

Incoltorrida Steffan, 1973: 634. Type species *Incoltorrida madagassica* Steffan, 1973 (by original designation)

The following comments are given by Steffan (1973) as the differential diagnosis of *Incoltorrida*: "The members of *Incoltorrida* n. gen. differ from the members of *Torridincola* Steffan 1964, through the following characters: on average more robust body size and more pronounced sculpturing of the elytra; the proximally narrowed keel on frons and vertex; the length proportions of the tarsomeres (mesotarsi T4 approximately 1.5 times longer than T3, compared to twice as long in *Torridincola*); The absence of parameres and the prescence of a thorned saccus membranaceus in the male, and the lateral thorns on the styli of the female genital organ."

All of these diagnostic characters hold true for the new species described herein, except the presence in all species of a single seta on each side near the base of the male genitalia (e.g., Figs. 19, 20); these setae confirm that the basal lobes they are attached to are the homologues of the parameres present in members of *Torridincola*. Because of distortion, these setae are not visible on the permanent microslide mount of the holotype of *I. madagassica*, the only male available to Steffan at the time of the original description.

Identification key to species of *Incoltorrida*

1a.	Each elytron with five costae	2
1b.	Each elytron with eight costae	3
2a.	Larger species (>2mm) and more elongate body shape. Pronotum lacking distinct midlongitudinal carina anteriorly	*I. quintacostata*
2b.	Smaller species (<2mm) and shorter broader body shape. Pronotum with distinct midlongitudinal carina anteriorly	*I. galoko*
3a.	Apical part of male aedeagus without spines. Body length >2mm	4
3b.	Apical part of male aedeagus spinose. Body length above or below 2mm	5
4a.	Basal part of pronotum with two carinae. The two transverse ridges of elytron between costae #3-#5 and between costae #5 and #8 offset from each other. Aedeagus evenly wide along most of its length in ventral view and tips not diverging (Fig. 19)	*I. madagassica*
4b.	Basal part of pronotum without carinae. The two transverse ridges of elytron between costae #3-#5 and between costae #5 and #8 continuous. Aedeagus widest preapically and tips diverging (Fig. 21)	*I. magna*
5a.	Small species (<2mm). Basal part of pronotum with both a midlongitudinal carina and two lateral carinae	*I. benesculpta*
5b.	Medium-sized species (approx. 2mm). Basal part of pronotum without carinae.	6
6a.	Elytral costae strongly developed and anterior oblique carinae of pronotum distinct. Aedeagus in lateral view with apex distinctly narrowed (Fig. 22).	*I. marojejy*
6b.	Elytral costa less strong and anterior oblique carinae of pronotum not very distinct. Aedeagus in lateral view with apex expanded (Fig. 12)	*I. zahamena*

Incoltorrida madagassica Steffan

Figs. 5, 6 (habitus); 14, 15, 19 (genitalia); 38 (map); 48, 49 (habitat)

Incoltorrida madagassica Steffan 1973: 635.

Type material: Holotype (male) with labels: "HOLOTYPUS [red]//Madagascar (65) Cap Ambalasandra H. BER-

TRAND, 29.III.60//MUS. ROY. AFR. CENTR. caput fehlt! TO-ma-03. mikr prap: 03.01. = genital//Incoltorrida madagassica STEFFAN 1973 HOLOTYPUS male [red].” Now deposited, with permanent microslide of male genitalia, in MNHN; see remarks.

Material examined (52): Fianarantsoa, 20.7722S 47.1809E; Amoron’i Mania, 3km south of Ambalamanakana next to RN7, Ankazomivady forest, hygropetric rocks and marsh with vegetation, elev. 1700 m, 1 xi 2014, J. Bergsten, T. Ranarilalatiana & S. Holmgren (MAD14-02) (3 NHRS). **Toamasina**: Analanjirofo: S. side of Nosy Mangabe, Masoala National Park, hygropetric rocks by the sea, 15.5056S, 49.7571E, sea level, 20.II.2018, MAD18-60, J. Bergsten & T. Ranarilalatiana (49 NHRS, BMNH, MCZ, PBZT/MBC).

Differential Diagnosis. Similar in some characters to *I. magna*; differing therefrom by smaller size (ca. 2.31 vs. 2.62 mm), less convex elytra with a more gradual posterior declivity, slightly narrower elytral costae, smaller elytral serial punctures, more sinuate fifth elytral costa, and especially differing by having two carinae and a distinct impression between the carinae on the basal 1/2 of the pronotum. The elytron of *I. madagassica* has two transverse ridges, offset from one another, one linking costae #3 and #5 (located just behind the humeral umbo), and one linking costae #5 and #8 (located at the sinuation dip of costa #5). In *I. magna* these two ridges are located in the same plane, not offset from one another. The male genitalia of *I. madagassica* differ from that of *I. magna* in being less arcuate in lateral view, and shaped differently in ventral view (Figs. 14, 15, 19, 21).

Description. Size: holotype (length/width, mm): body (length to elytral apices) 2.31/1.29; head width 0.46; pronotum 0.50/0.96; elytra 1.51/1.29. Dorsum dark brown, venter brown to reddish brown, legs brown to reddish brown except tarsi and femoral-tibial articulations black.

Sides of frontoclypeal shield slightly arcuate toward midline at frontoclypeal suture, narrowest part slightly past midlength of shield, at frontoclypeal suture.

Short oblique carinae on the anterior 1/3 of the pronotum are well developed, but there is no indication of a midlongitudinal carina. Two short carinae and a distinct impression between carinae located on basal 1/2 of pronotum.

Elytron with eight costae; fourth costa interrupted by strong punctures; fifth costa strongly bisinuate; sixth and seventh costae very indistinct. Two transverse ridges, one linking costae #3 and #5 (located just behind the humeral umbo), and one linking costae #5 and #8 (located at the sinuation dip of costa #5).

Posterior 1/2 of metaventral tabella with closely spaced transverse grooves. Midlongitudinal groove in posterior 1/2 of metaventral tabella shallow, with ill-defined margins.

Midlongitudinal carina of first abdominal ventrite is strong and extends length of ventrite.

Male genitalia (Figs. 14, 15, 19) in lateral view slightly arcuate, aedeagal tips wide, apically rounded and with many pores (apparently without microsetae); in ventral view aedeagus nearly parallel-sided, with narrowed tips.

FIGURE 6. *Incoltorrida madagassica* Steffan, fragmentary holotype and labels.

FIGURE 7. *Incoltorrida quintacostata*, habitus views of holotype.

Remarks. In the original description, Steffan (1973) stated that the holotype was deposited in the MNHN. However, MNHN collection staff were unable to find the type. Search at other museums determined that the holotype was still with the paratypes, at the MRAC. Having permission of that museum, the holotype (fragmentary; Fig. 6) and the permanent slide mounted male genitalia were transferred to the MNHN.

In the original description (Steffan 1973), it is noted by the author that the head of the holotype is missing ("caput fehlt"). However, both the head and the prothorax are missing (Fig. 6). The two paratypes, both females, are from a different locality than the holotype ("Zentrales Hochland auf der Strecke Tananarie - Ambositra"). These

paratypes are larger than the holotype and have some sculptural differences; they probably represent a different species.

The original description gives “Cap Ambalasandra” as the type locality. Multiple searches online gave only one record with that geographical name, in a table in a paper on geological deposits. That locality is very near where the Mananara River enters the Indian Ocean (Fig. 38).

Thirty-three larvae were collected in association with adults at site MAD18-60.

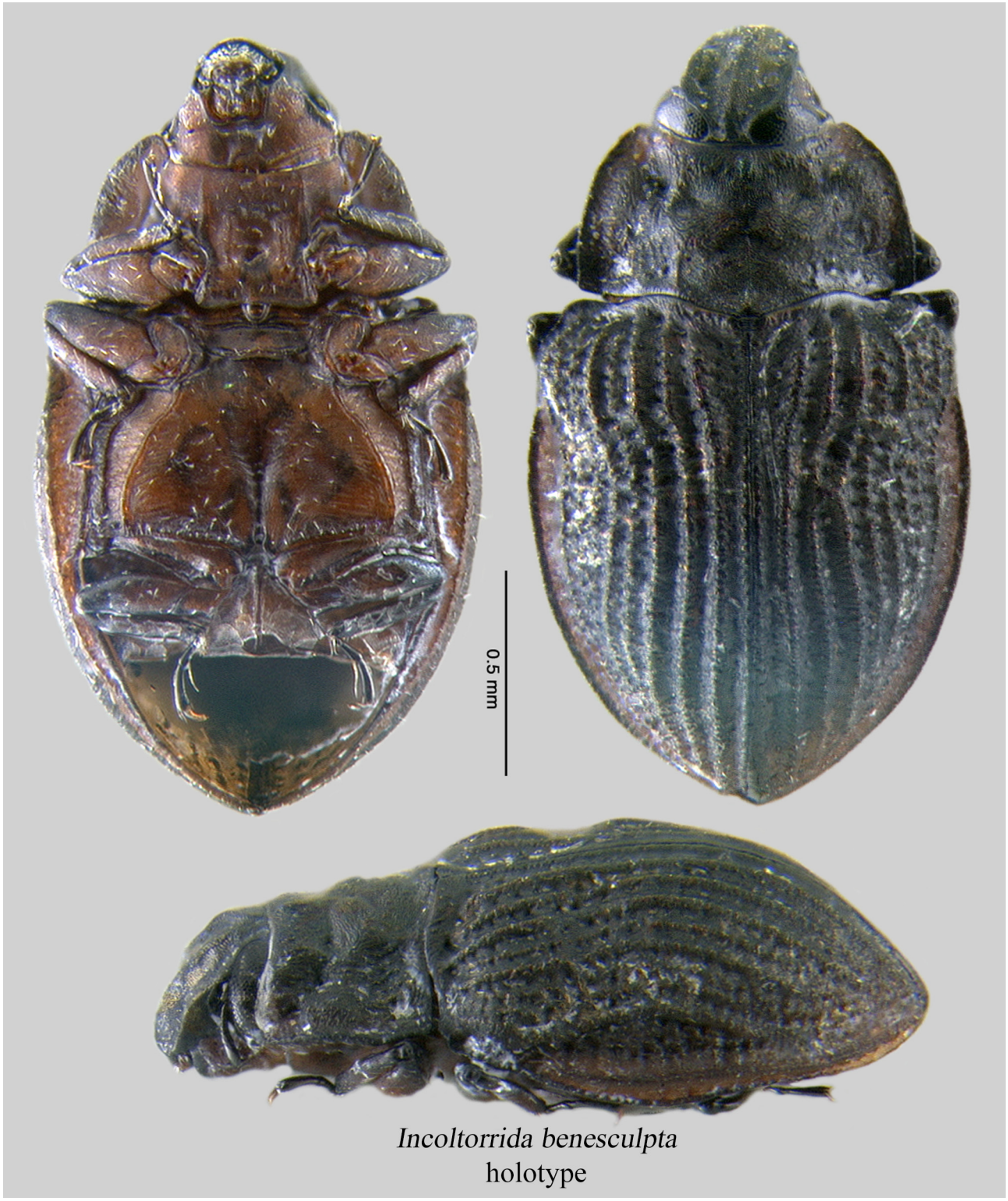


FIGURE 8. *Incoltorrida benesculpta*, habitus views of holotype.

FIGURE 9. *Incoltorrida marojejy*, habitus views of holotype.

***Incoltorrida quintacostata*, new species**
Figs. 2, 7 (habitus), 17, 18 (genitalia), 23 (larva), 34 (map), 42, 43 (habitat),

Type Material. Holotype (male): **Fianarantsoa**, 3.5km N Ivato, 20º 35.844' S 47º 12.78' E, rock face seep beside hwy. 7, elev. 1471 m, 5 xi 2014, P. D. Perkins (NHRS).

FIGURE 10. *Incoltorrida magna*, habitus views of holotype.

Paratypes (193): Same data as holotype (19: NHRS, MCZ); **Antsiranana**, Anjiabe Ambony: Ambilobe: Antsabe stairways-like cascade with vertical (!) steps, exposed, extremely hot day, N: -13.60930 E: 48.72120, elev. 303 m, 23 xi 2004, Balke *et al*. (P25MD16) (8 BMNH; 2 DNA extractions, #'s BMNH 670734, BMNH 670735); Diana:

Antsaba: Galoko mountains, 3.4 km NW from Anstaba, S13.60931 E48.72129, aspirator, forceps, sieves: hygropetric rocks and pools, elev. 296 m, 28 xi 2012, elev. 296 m, 28 xi 2012, J. Bergsten, R. Bukontaite, J.H. Randriamihaja & T. Ranarilalatiana (MAD12-31) (5 NHRS); Diana: Antsaba: Galoko mountains, S13.60974 E48.72175, sieves and aspirator: hygropetric rocks and water pools, elev. 263 m, 25 xi 2012, J. Bergsten, R. Bukontaite, J.H. Randriamihaja & T. Ranarilalatiana (MAD12-26) (62 NHRS, BMNH, PBZT/MBC); **Fianarantsoa**, 3.2km S Ambohimanjaka, 20º 14.0343' S 47º 5.59145' E, waterfall and hygropetric habitat near hwy. 7, elev. 1415 m, 5 xi 2014, P. D. Perkins (95 NHRS & MCZ); Atsimo Antsinanana: R.S. Manombo: Parcelle I, Rearatra, Piste 56: S23.006183 E47.7338833, GB nets and sieves, forest stream with pools, elev. 21 m, 14 xii 2013, J.H.Randriamihaja & T.Ranarilalatiana (MAD13-73) (3 NHRS); 20.7722S 47.1809E; Amoron'i Mania, 3km south of Ambalamanakana next to RN7, Ankazomivady forest, hygropetric rocks and marsh with vegetation, elev. 1700 m, 1 xi 2014, J. Bergsten, T. Ranarilalatiana & S. Holmgren (MAD14-02) (1 NHRS).

Differential Diagnosis. Differentiated from all other known *Incoltorrida*, except *I. galoko*, by the elytral sculpture. Each elytron has only five costae: #1, #2, #3, #5, and #8; costa #4, #6, and #7, which are present in other species, are absent in *I. quintacostata* (Fig. 2). The serial punctures are minute and very indistinct (microslide preparation necessary to see the punctures clearly). In this species the elytral costae are well developed in height, but comparatively narrow; the areas between the costae are quite flat. The transverse ridge that connects elytral costae #5 and #8 is more or less distinct (depending on the population). The anterior depressions of the pronotum are well developed and the foveae forming the medial margins of the ridges are narrowly separated and the intervening surface is transversely rounded, but there is no separate median carina. The pronotal sculpture and adult size of *I quintacostata* differ markedly from those of *I. galoko*, which also has five costae of each elytron. The ridges and impressions of the pronotum are similar to those of *I. benesculpta*, a much smaller species that has very different elytral sculpture; the aedeagi of the two species markedly differ (Figs. 18, 20).

Description. Size: holotype (length/width, mm): body (length to elytral apices) 2.33/1.32; head width 0.47; pronotum 0.51/0.93, elytra 1.50/1.32. Dorsum dark brown to black, venter brown to dark brown, legs brown except femoral-tibial articulations and tarsi black.

Sides of frontoclypeal shield very slightly arcuate, almost parallel-sided, and only very slightly and gradually narrowed from frons vertex to the transverse anterior margin of the clypeus.

Short oblique carinae on anterior 1/3 of pronotum are well developed; no indication of a midlongitudinal carina. Basal 1/3 of pronotum with distinctive carina on each side, each slightly oblique toward midline.

Each elytron with only five costae: #1, #2, #3, #5, and #8; costae #4, #6, and #7 absent. Areas between costae quite flat, and serial punctures minute, very indistinct, a unilinear row located adjacent to the lateral margin of each costa. Transverse ridge linking costae #5 and #8 present, but more distinctive in some populations than others.

Lateral margins of the metaventral tabella straight for most of their length, arcuate only very near base. Midlongitudinal groove in posterior 1/2 of the metaventral tabella is narrow and parallel-sided.

Midlongitudinal carina of the first abdominal ventrite is moderately strong but usually does not extend the full length of the ventrite.

Male genitalia long and slender (Figs. 17, 18); see remarks.

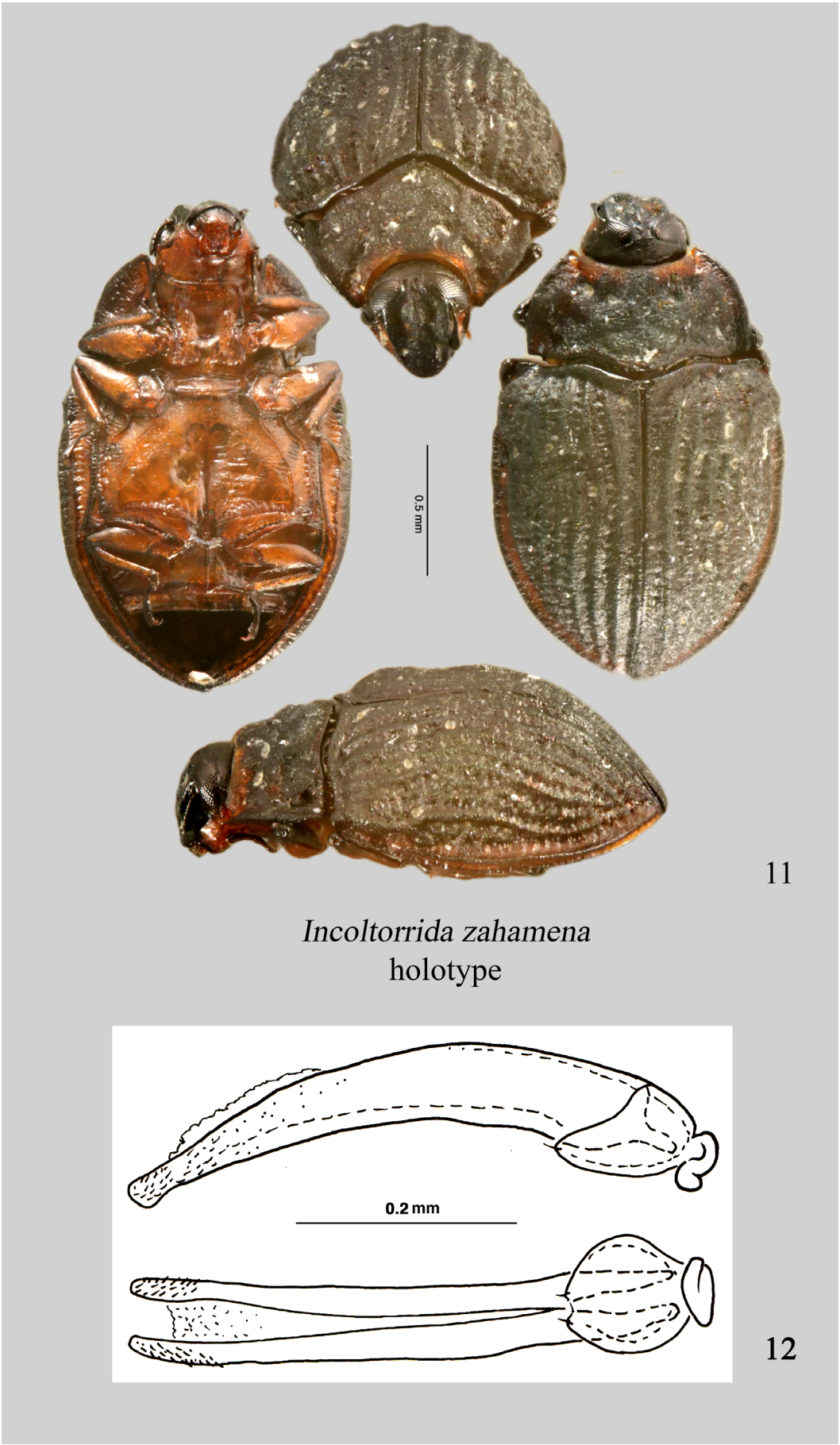
Etymology. Named in reference to the five costae of each elytron.

Remarks. Some specimens, such as the holotype, have the posterior angles of the pronotum very weakly shallowly notched; other specimens do not have this weak indentation, and some specimens have it only on one side.

The male genitalia in ventral view is long and comparatively slender, with a quite spinose apical tip (Figs. 17, 18). Males vary considerably in body length, ca. 2.09–2.39 mm. The length of the aedeagus varies, roughly, in proportion to the body size; for example: (aedeagus length/body length): 0.73/2.18 (=0.33); 0.75/2.15 (=0.35); 0.77/2.09 (=0.37);0.80/2.24 (=0.36); 0.93/2.39 (=0.39, the holotype). The shape of the aedeagus does not vary significantly. This is the most commonly collected species of *Incoltorrida* (Fig. 34).

Four larvae (NHRS) were collected at the type locality, and 54 larvae (NHRS) were collected at site MAD12-26.

DNA sequences of partial CO1 (Acc. Nos. FJ819700 (BMNH670734) and FJ819701 (BMNH670735)) and partial 28S (FJ818156 (BMNH670734) and FJ818157 (BMNH670735)) published by Monaghan *et al* (2009) are based on adult specimens, and are available in Genbank.



FIGURES 11–12. *Incoltorrida zahamena*, holotype, habitus and aedeagus.

FIGURE 13. *Incoltorrida galoko*, habitus views of holotype.

***Incoltorrida benesculpta*, new species**
Figs. 8 (habitus); 16, 20 (genitalia); 35 (map); 42, 43 (habitat)

Type Material. Holotype (male): **Fianarantsoa**, 3.2km S Ambohimanjaka, 20º 14.0343' S 47º 5.59145' E, waterfall and hygropetric habitat near hwy. 7, elev. 1415 m, 5 xi 2014, P. D. Perkins (NHRS). Paratypes (19): Same data as holotype (13: NHRS, MCZ, BMNH, PBZT/MBC); **Antsiranana**, Sava, Mad.; Antsirana; Marojejy NP, 800m N from Camp I, Humbert waterfall; hygropetric; 14.4333S 49.773E; MAD14-48, ex. bedrock pools at side of waterfall, elev. 550 m, 8 xi 2014, P. D. Perkins (MAD14-48) (6 MCZ).

Differential Diagnosis. Together with *I. galoko* the smallest known member of the genus (l/w ca. 1.85/1.05). The elytral costae are high and strong, and are more sinuate than in other species. The serial punctures are large and in sulcate grooves. The sculpture of the pronotum is similar to that of *I. quintacostata*, but *I. benesculpta* has a more distinct midlongitudinal carina in the basal half, and the sides of the pronotum in the anterior half are more arcuate. The elytra and the aedeagi of the two species are quite dissimilar.

Description. Size: holotype (length/width, mm): body (length to elytral apices) 1.85/1.05; head width 0.40; pronotum 0.40/0.81; elytra 1.17/1.05. Dorsum black, venter dark brown, legs brown except femoral-tibial articulations and tarsi black.

Sides of frontoclypeal shield slightly arcuate toward the midline, such that apical part is slightly wider than the width at midlength, and slightly narrower than the posterior area of the frons.

Short oblique carinae on anterior 1/3 of pronotum are well developed, no indication of midlongitudinal carina. The basal 1/3 has a short carina on each side, and a very low narrow midlongitudinal carina.

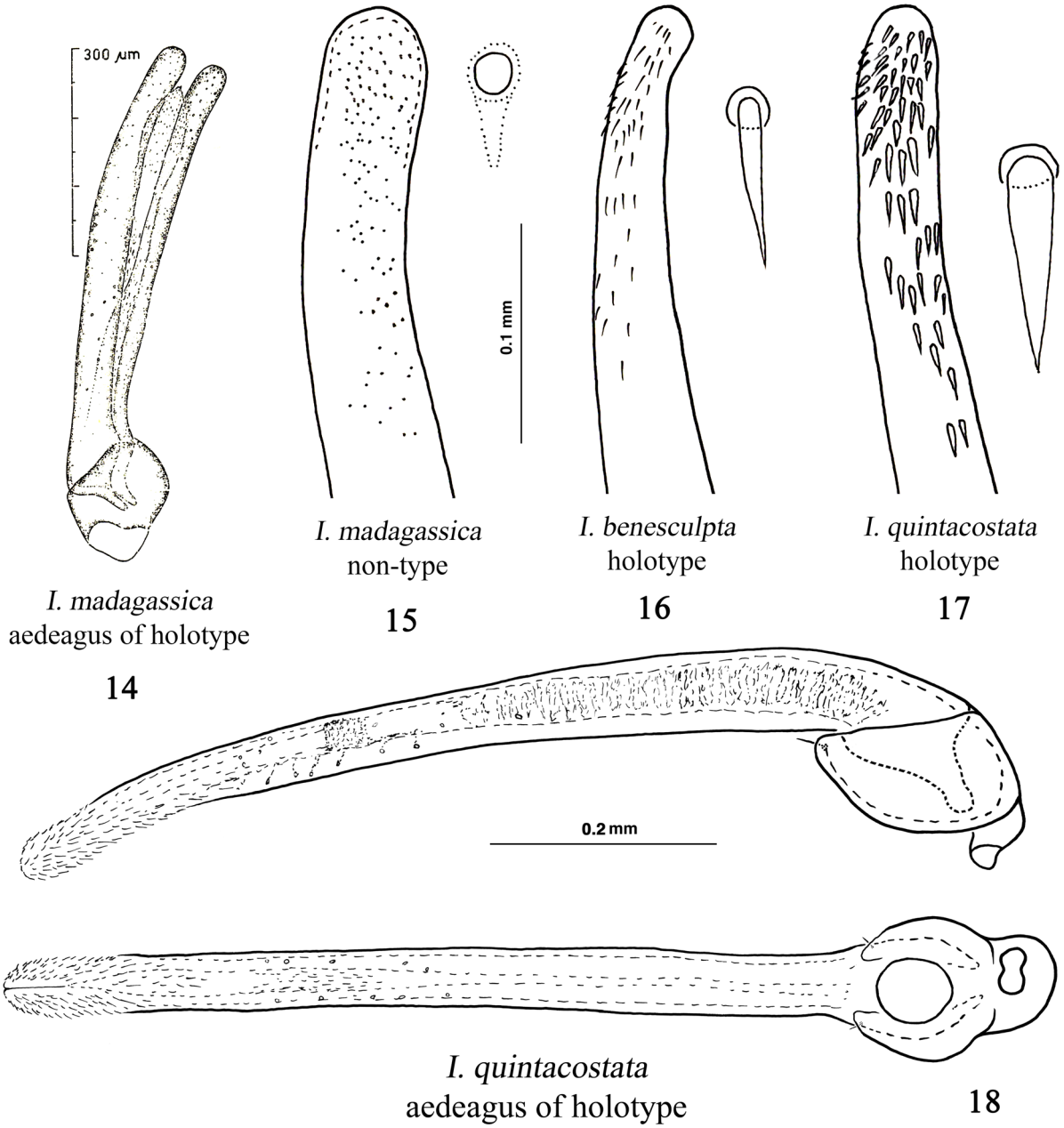
Elytron with eight strong high costae; fourth costa interrupted with strong punctures; fifth costa weakly bisinuate; sixth and seventh costae very indistinct. Serial punctures large and distinct.

Sides of metaventral tabella more distinctively arcuate than in other species. Midlongitudinal groove in the posterior 1/2 of metaventral tabella gradually widens from posterior to anterior.

Midlongitudinal carina of first abdominal ventrite strong and extends length of ventrite.

Male genitalia very short, with the apical part narrowed and spinose (Figs. 16, 20).

Etymology. Named in reference to the markedly sculptured pronotum and elytra.



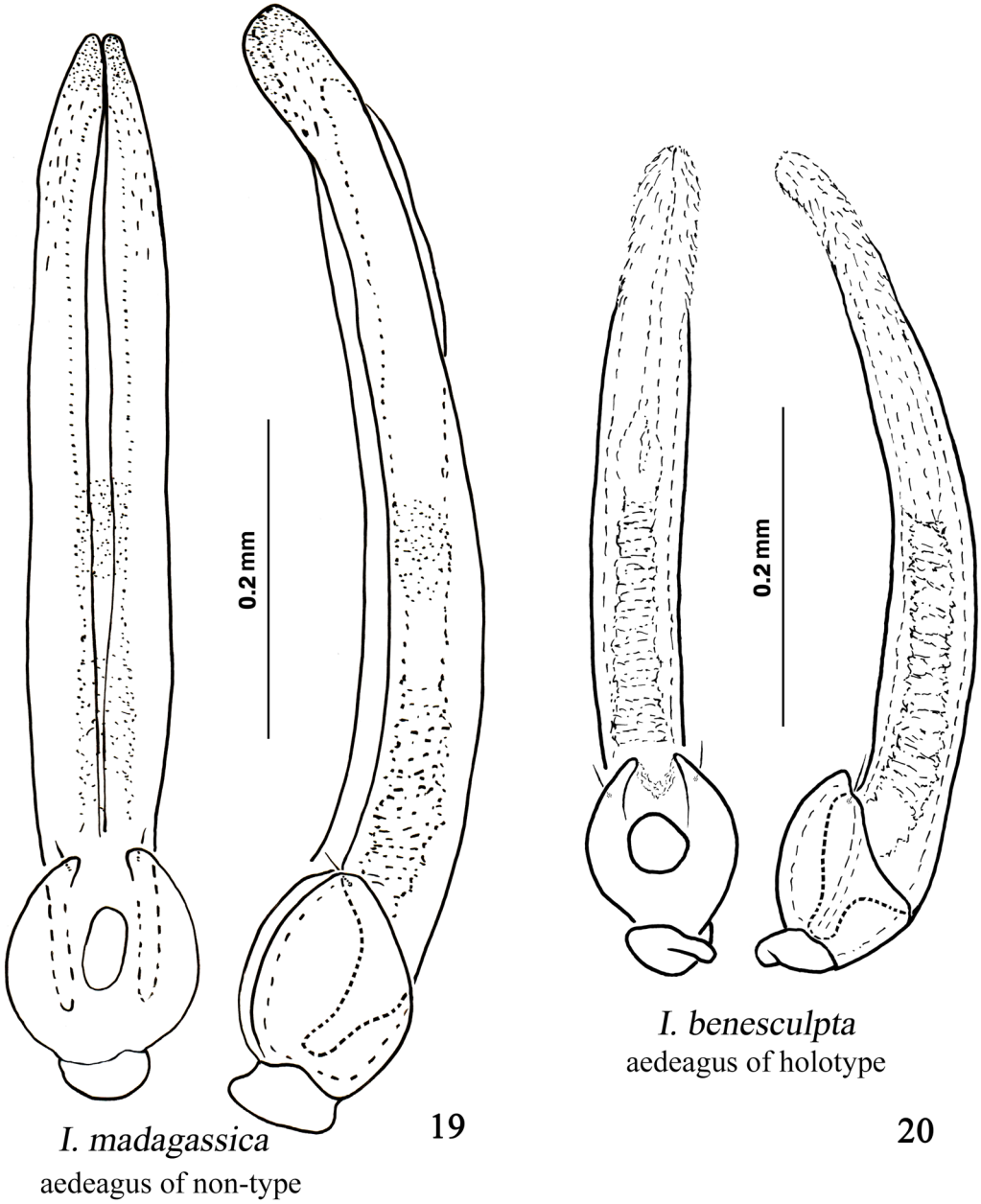
FIGURES 14–18. *Incoltorrida* spp.; (14) *I. madagassica*, male genitalia of holotype (after Steffan 1973, permanent slide mount). (15–17) male genitalia apex showing pores of *I. madagassica* and spines of *I. benesculpta* and *I. quintacostata*; (18) *I. quintacostata*, aedeagus of holotype.

***Incoltorrida marojejy*, new species**

Figs. 9 (habitus); 22 (genitalia); 24 (elytron); 37 (map); 41, 44–47 (habitat)

Type Material. Holotype (male): **Antsiranana**, 14.4345S 49.7606E Sava Marojejy National Park, Camp II, wide river forming hygropetrick rocks and rockpools, elev. 710 m, 9 xi 2014, J. Bergsten, R. Bukontaite, J.H. Randriamihaja, T. Ranarilalatiana & S. Holmgren (MAD14-54) (NHRS). Paratypes: **Antsiranana**: Sava : Marojejy National Park: midaltitude rainforest: MAD18-24: upstream on stream by camp II, traversing from Taktajania trail, 14.4369S, 49.7603E, 820m, 09.II.2018, J.Bergsten & T.Ranarilalatiana (98 NHRS, MCZ, BMNH, PBZT/MBC).

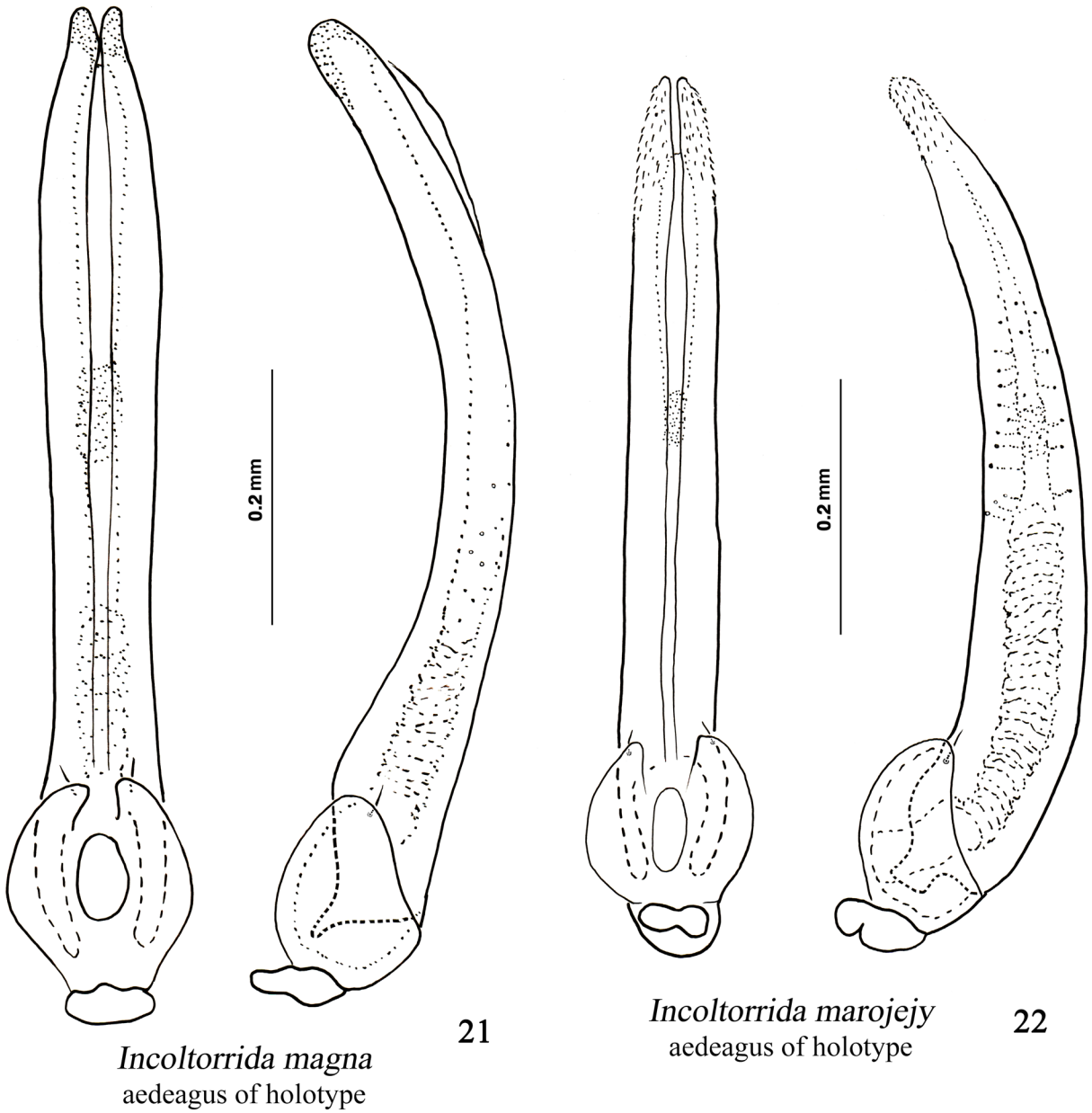
Differential Diagnosis. Pronotal sculpture similar to *I. magna*; both species lack ridges on each side near the base. Differing therefrom by the smaller size (ca. 2.19 vs. 2.62 mm), the presence of transverse grooves on the metaventrite tabella, the shape of the frontoclypeal shield, and the larger serial elytral punctures. The aedeagi of the two species differ markedly (Figs. 21, 22).



FIGURES 19–20. (19) *Incoltorrida madagassica*, male genitalia of non-type; (20) *Incoltorrida benesculpta*, male genitalia of holotype.

Description. Size: holotype (length/width, mm): body (length to elytral apices) 2.19/1.26; head width 0.41; pronotum 0.47/0.89; elytra 1.40/1.26. Dorsum brown to reddish brown, venter reddish brown, legs reddish brown except femoral-tibial articulations and tips of tarsi black.

Sides of frontoclypeal shield slightly arcuate toward midline, such that apical part is slightly wider than width at midlength, and slightly narrower than posterior of frons.



FIGURES 21–22. *Incoltorrida*, male genitalia of holotypes. (21) *I. magna*; (22) *I. marojejy*.

Short oblique carinae on anterior 1/3 of pronotum well developed, no indication of midlongitudinal carina, and area posterior to carinae is transversely rounded and shows no indication of ridges or depressions.

Elytron with eight strong costae; costae #6 and #7 interrupted by distinct transverse ridge that connects #5 and #8. Serial punctures large and deep.

Posterior 1/2 of metaventral tabella with distinctive, closely spaced transverse grooves; midlongitudinal groove in posterior 1/2 of metaventral tabella gradually widens from posterior to anterior.

Midlongitudinal carina of first abdominal ventrite strong and extends length of ventrite.

Male genitalia in lateral view distinctively thickened in basal 1/2, apical tip abruptly distinctively narrowed and spinose (Fig. 22).

Etymology. Named in reference to the type locality.

Remarks. Four larvae were collected in association with adults at site MAD18-24.

***Incoltorrida magna*, new species**
Figs. 3, 4, 10 (habitus); 21 (genitalia); 36 (map); 40 (habitat)

Type Material. Holotype (male): **Antsiranana**, Diana: Antsaba: Galoko mountains, 3.4 km NW from Anstaba, S13.60931 E48.72129, aspirator, forceps, sieves: hygropetric rocks and pools, elev. 296 m, 28 xi 2012, elev. 296 m, 28 xi 2012, J. Bergsten, R. Bukontaite, J.H. Randriamihaja & T. Ranarilalatiana (MAD12-31) (NHRS). Paratypes (36): Same data as holotype (1 NHRS); **Antsiranana**, Anjiabe Ambony: Ambilobe: Antsabe stairways-like cascade with vertical (!) steps, exposed, extremely hot day, N: -13.60930 E: 48.72120, elev. 303 m, 23 xi 2004, Balke *et al*. (P25MD16) (35 BMNH, NHRS, MCZ, PBZT/MBC; 2 DNA extractions, #'s BMNH 670732, BMNH 670733).

Differential Diagnosis. This is the largest known *Incoltorrida* species: l/w ca. 2.62/1.58. The elytral serial punctures are very distinct, as is the transverse ridge that links costae #5 and #8. The pronotum lacks the basal ridges seen in *I. quintacostata*, *I. benesculpta*, and *I. madagassica*. It is much larger than *I. marojejy* (2.62 vs. 2.19); *I. marojejy* lacks the pronotal midlongitudinal carina that is present in *I. magna*, and the frons plate is shaped differently in the two species. The male genitalia (Fig. 21) distinctively differ from that of the other species in the genus. See also the diagnosis of *I. madagassica*.

Description. Size: holotype (length/width, mm): body (length to elytral apices) 2.62/1.58; head width 0.50; pronotum 0.55/1.12; elytra 1.78/1.58. Dorsum dark brown to black, venter brown to reddish brown, legs brown to reddish brown except tarsi and femoral-tibial articulations black.

Frontoclypeal shield narrowest at anterior 1/3, with sides of frons slightly arcuate; apical 1/3 is slightly wider than area of frontoclypeal suture.

Short oblique carinae on anterior 1/3 of pronotum are well developed; a midlongitudinal carina is present, though not as developed as the oblique carinae; the area posterior to the carinae is transversely rounded and shows no indication of ridges or depressions, except for a basal impression in front of scutellum.

Elytra quite convex, declivity steep. Each elytron with eight wide and high costae; #4 continuous, not interrupted by punctures; #5 weakly bisinuate; #6 and #7 distinct, though crossed by transverse ridge that connects #5 and #8. Second transverse ridge links #3 and #5, in nearly same plane as the #5-#8 ridge.

Posterior 1/2 of metaventral tabella without distinctive, closely spaced transverse grooves; midlongitudinal groove in posterior 1/2 of metaventral tabella narrow and parallel-sided.

Midlongitudinal carina of first abdominal ventrite not especially strong and extends only 1/2 length of ventrite.

Male genitalia in lateral view distinctively arcuate; in ventral view widest at about apical 1/4, and then narrowed, with tips pointing slightly outward (Fig. 21).

Etymology. Named in reference to the relatively large size.

Remarks. DNA sequences of partial CO1 (Acc. Nos. FJ819703 (BMNH 670732) and FJ819702 (BMNH 670733)) and partial 28S (FJ818159 (BMNH 670732) and FJ818158 (BMNH 670733)) published by Monaghan *et al.* (2009) are based on adult specimens, and are available in Genbank.

***Incoltorrida zahamena*, new species**
Figs. 11 (habitus); 12 (genitalia); 36 (map); 50, 51 (habitat)

Type Material. Holotype (male): Madagascar: Toamasina: Alaotra-Mangoro: Zahamena National Park, Antanandava Sect., midaltitude rainforest: Manambato river ~100m downstream of Camp Cascade, hygropetric rocks at night, 17.5438S, 48.7230E, 1280m, 10.III.2018, MAD18-111, Leg. J. Bergsten & T. Ranarilalatiana (NHRS). Paratypes, same data as holotype (2 females NHRS, BMNH).

Differential Diagnosis. Differentiated from other members of the genus by the combination of small size (ca. 1.97 mm), oval habitus (Fig. 11), pronotum without median longitudinal ridge, and elytron with eight costae. The elytral series are irregular, giving the elytra a scabrous appearance.

Description. Size: holotype (length/width, mm): body (length to elytral apices) 1.97/1.19; head width 0.39; pronotum 0.43/0.92; elytra 1.21/1.19. Dorsum dark brown to black, venter reddish brown, legs reddish brown except femoral-tibial articulations and tarsi dark brown.

Sides of frontoclypeal shield slightly arcuate. Clypeus about as long as frons.

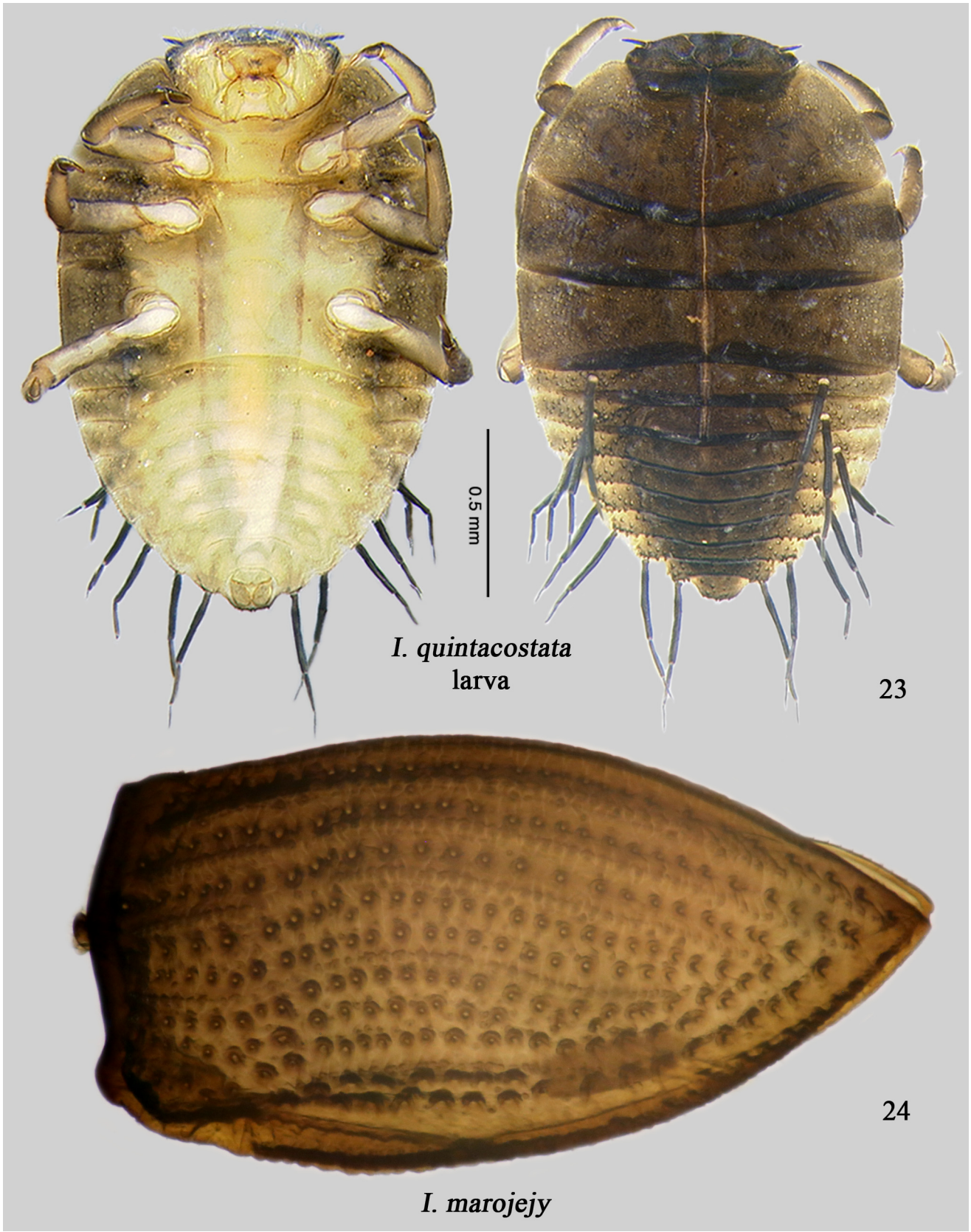


FIGURE 23–24. (23) Last instar larva of *Incoltorrida quintacostata*; (24) transparency mount of elytron of *I. marojejy*.

FIGURE 25. *Hydroscapha saboureaui*, habitus and labels of holotype.

Pronotum with short oblique carinae on anterior 1/3 moderately developed, no indication of midlongitudinal carina, area posterior to carinae transversely rounded, with no indication of ridges or depressions. Cuticle rough, subgranulate.

FIGURES 26. *Hydroscapha andringitra*, habitus of holotype.

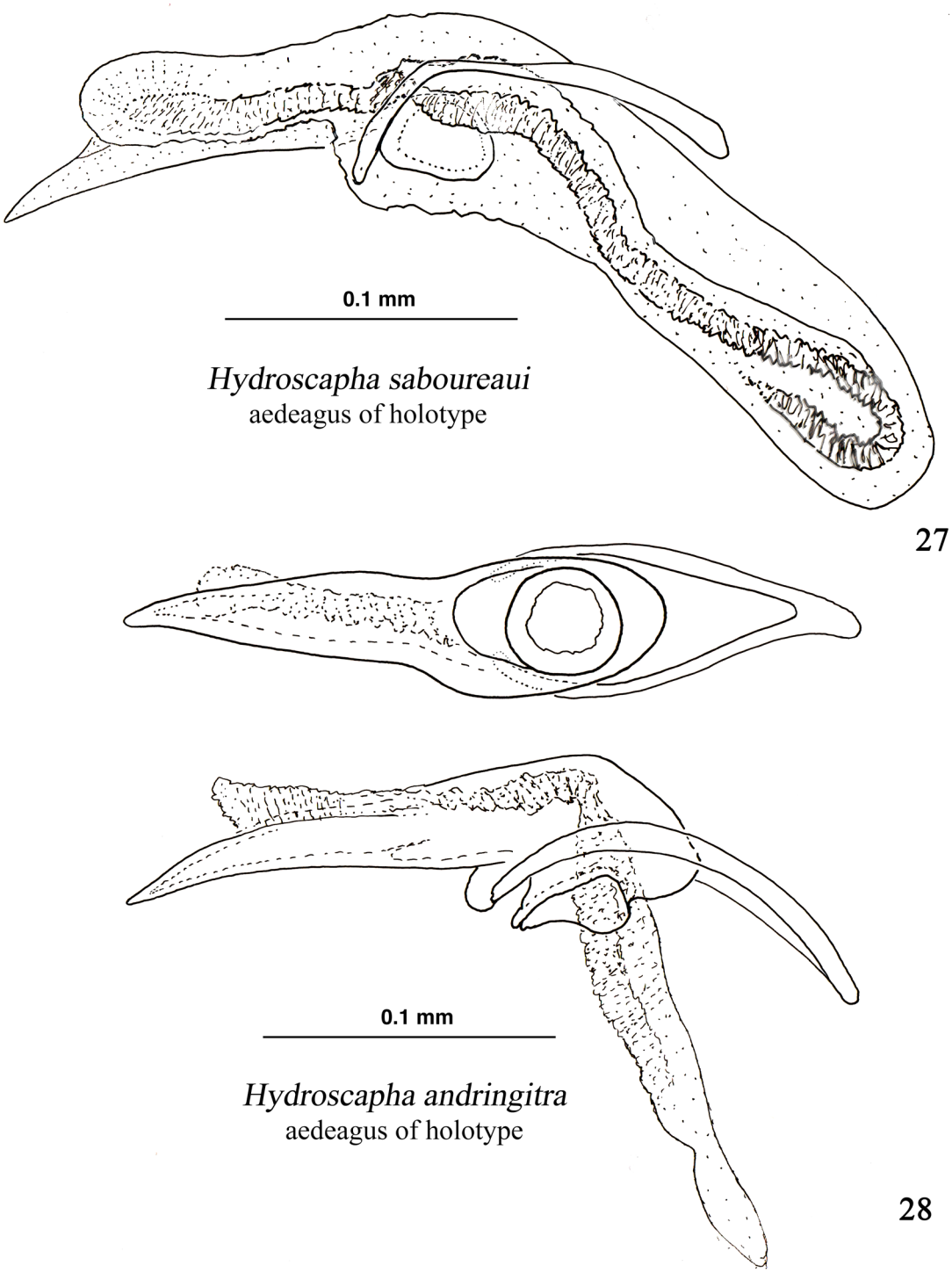
Elytron with eight costae of varying height; costa #6 very low and short, costa #8 generally higher and stronger than other costae; transverse ridges between costae absent or very indistinct. Serial punctures large and coarse, producing scabrous appearance.

Metaventral tabella with very faint, indistinct transverse grooves; midlongitudinal groove in posterior 1/2 of metaventral tabella widest at about midlength.

Midlongitudinal carina of first abdominal ventrite strong and extends length of ventrite.

Male genitalia in lateral view distinctively thickened in basal 1/2, apical 1/2 narrowing, with tip slightly widened and spinose (Fig. 12).

Etymology. Named in reference to the type locality.



FIGURES 27–28. (27) *Hydroscapha saboureaui*, male genitalia of holotype, lateral view; (28) *Hydroscapha andringitra*, male genitalia of holotype, dorsal and lateral views.

Incoltorrida galoko, new species

Figs. 13 (habitus); 36 (map); 40 (habitat)

Type Material. Holotype (female): **Antsiranana**, "Anjiabe Ambony: Ambilobe: Antsabe stairways-like cascade with vertical (!) steps, exposed, extremely hot day, N: -13.60930 E: 48.72120, elev. 303 m, 23 xi 2004, Balke *et al*. (P25MD16)" // DNA extraction, # BMNH 670736 (BMNH).

Differential Diagnosis. An abundantly distinct species, differentiated from other members of the genus by the combination of small size, broadly oval body form, extreme pronotal sculpture, and each elytron with five costae. Currently know only from the female holotype, which is distinct morphologically, and also distinct according to DNA sequence data published by Monaghan *et al.* (2009) (Genbank Accession Nos. FJ819704 (partial COI) and FJ818160 (partial 28S)) from the two coexisting species *I. magna* and *I. quintacostata*.

Description. Size: holotype (length/width, mm): body (length to elytral apices) 1.74/1.14; head width 0.36; pronotum 0.43/0.76; elytra 1.07 /1.14. Dorsum dark brown, venter brown to reddish brown, legs brown to reddish brown except tarsi and femoral-tibial articulations black. Body form very broad, oval (Fig. 13).

Sides of frontoclypeal shield very slightly arcuate, narrowest, but only slightly so, at frontoclypeal suture. Head slightly concave in front of eyes.

Pronotal sculpture extreme (Fig. 13), ridges distinctly raised and depressions deep; anterior part with three carinae, midlongitudinal carina and oblique carinae on each side. Midlongitudinal carina terminating where, on each side is transverse timidity. Together, sculptural elements on disc somewhat resemble a snarling lion's face.

Each elytron with only five distinct well separated, granulate costae: #1, #2, #3, #5, and #8; costae #4, #6, and #7 absent. Merest hint of two transverse ridges, one linking costae #3 and #5 and one linking costae #5 and #8, later located just behind the humeral umbo. Nine rows of small serial punctures, two rows each between costae #4 and #5, #5 and #6, #6 and margin; three other rows single.

Midventral area of metaventral tabella with distinct, widely spaced transverse grooves. Midlongitudinal carina of first abdominal ventrite, strong, extends length of ventrite.

Etymology. Named in reference to the type locality.

Remarks. The holotype female, which has been extracted for DNA, is unfortunately in pieces, and is missing several leg parts. The parts were glued together for the habitus figures (Fig. 13).

Hydroscapha LeConte

Hydroscapha LeConte, 1874: 45. Type species *Hydroscapha natans* LeConte (by original designation)

Hydroscapha saboureaui Paulian

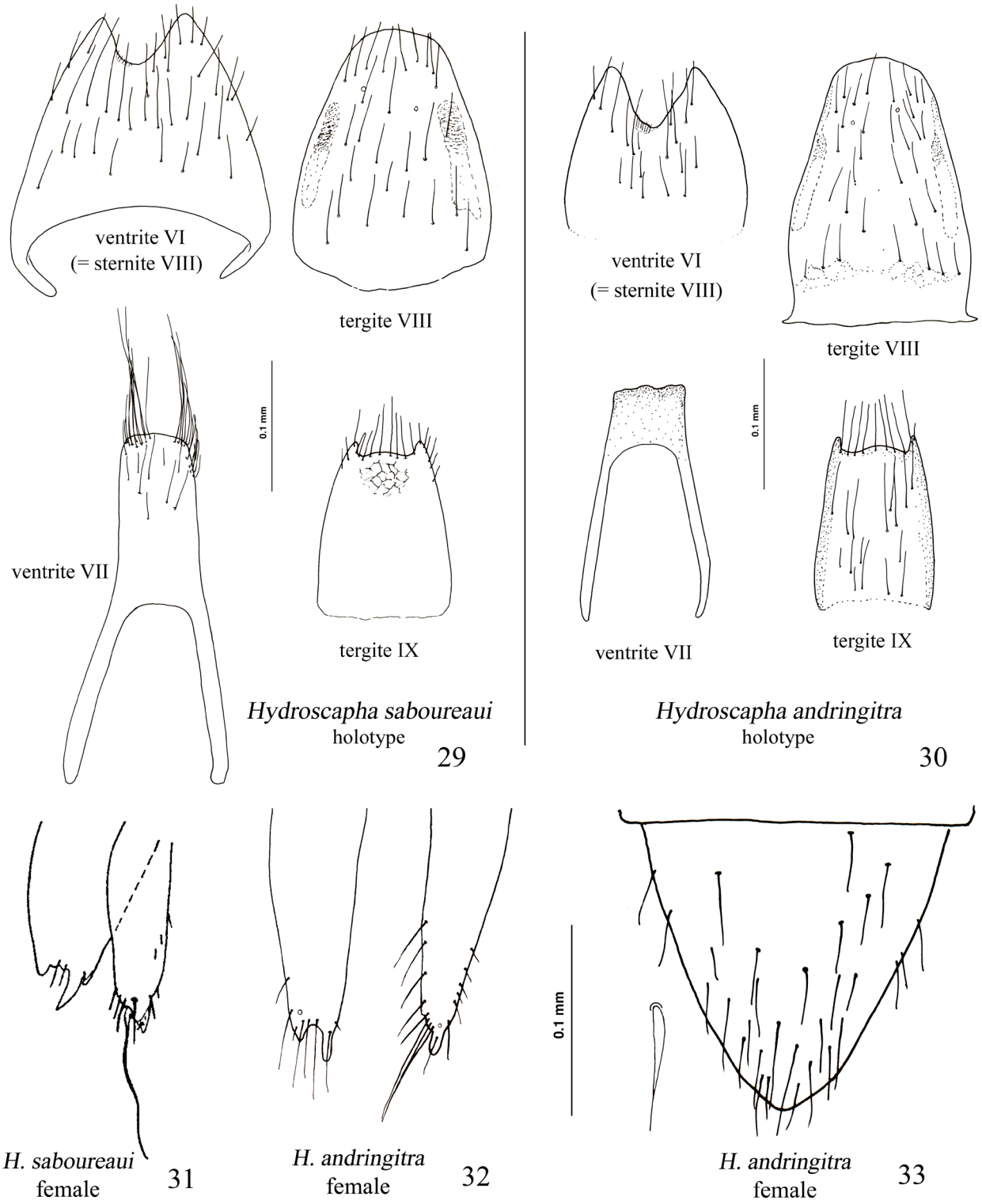
Figs. 25 (habitus), 27 (aedeagus), 29, 31 (terminal abdominal segments), 39 (map)

Hydroscapha saboureaui Paulian, 1949: 371.

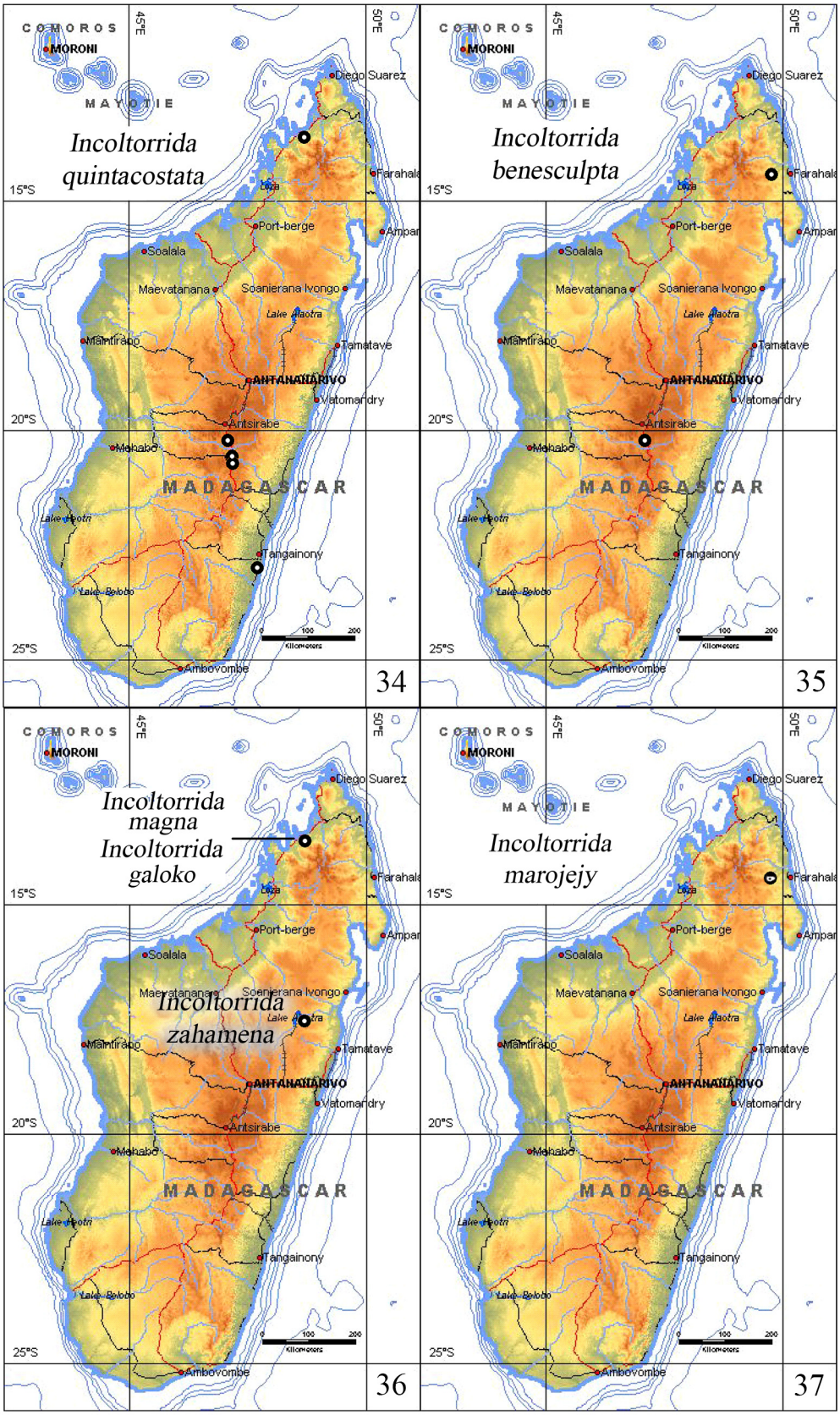
Type Material. Holotype (male): Labels (Fig. 25): "S. Ankavandra sables VII 49 R P//Hydroscapha saboureaui n.sp. Type//MNHN EC7800" (MNHN). Type locality notes in original description: "60 km. au sud d/Ankavandra, sur la piste de Miandrivazo, dans une mare tres superficielle formee par suintement sur le sable; l/eau, surchauffee, cache par un dense tapis d'algues colle au sable."

Differential diagnosis. Habitus as in Fig. 25 (imaged pre-dissection). Slightly smaller in size than *H. andringitra* (length to elytral apices ca. 0.79 vs. 0.82 mm), but with a larger aedeagus, which has a much larger internal sac (Figs. 27, 28). The total body length, including the telescoping terminal abdominal segments is slightly greater in *H. saboureaui* (ca. 1.14 vs. 0.99 mm). The two species also have distinctive differences in the terminal abdominal segments of males (see comparative notes following) and in females (Figs. 29–33).

Description (holotype male): Size (mm): length to elytral apices 0.79, total length 1.14 (variable due to telescoping last abdominal segments), width 0.51. Color brown, with legs, palpi and antennae lighter, testaceous in parts.



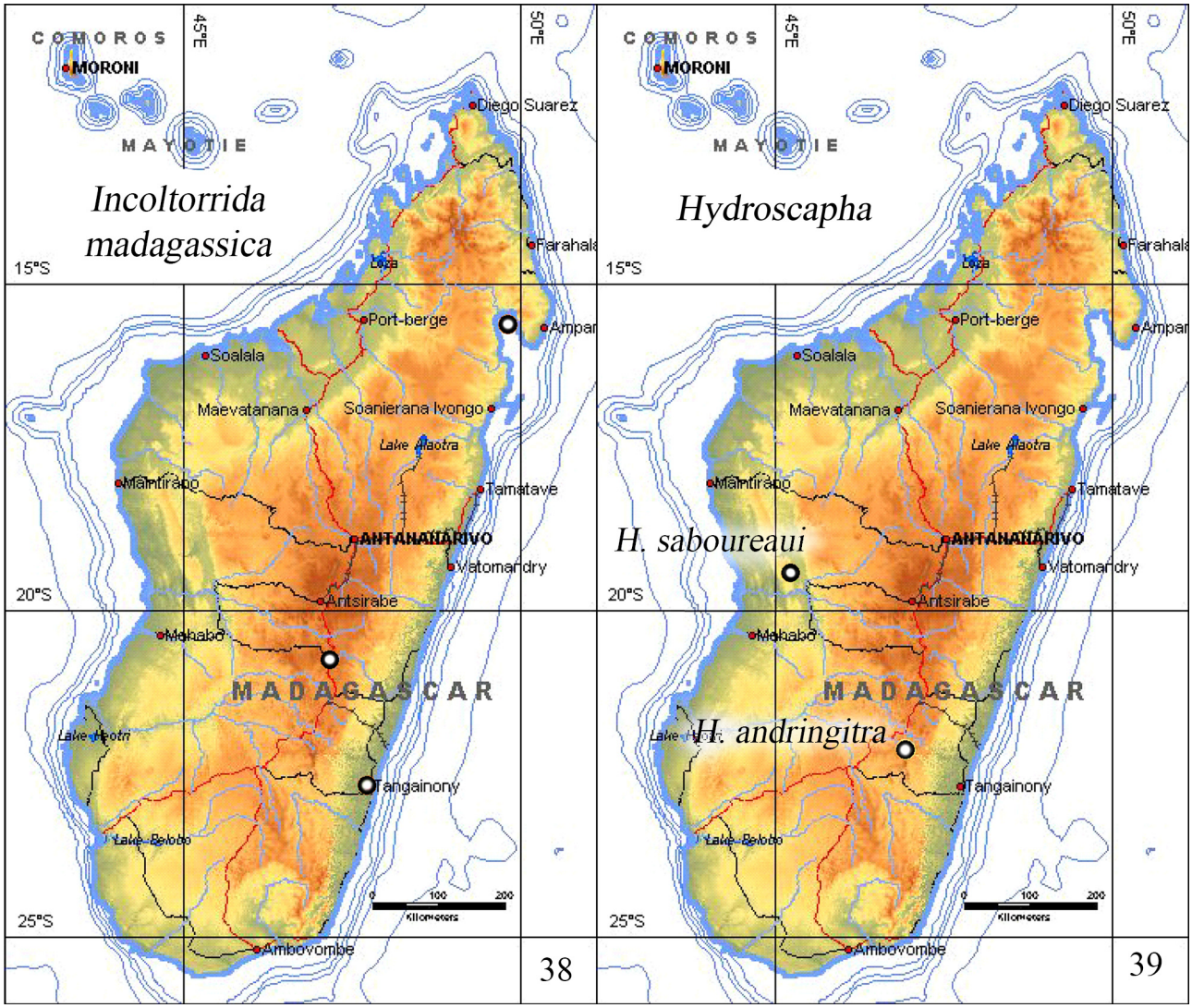
FIGURES 29–33. (29–30) *Hydroscapha* males, ventrites and tergites. (29) *H. saboureaui*, holotype; (30) *H. andringitra*, holotype. (31– 33) *Hydroscapha* females, terminal abdominal segments. (31) *H. saboureaui*, last abdominal segments, right side, dorsal aspect (from Paulian 1949); (32) *H. andringitra*, last abdominal segments, right side, dorsal aspect; (33) *H. andringitra*, last visible ventrite.



FIGURES 34–37. *Incoltorrida* distribution maps.

Habitus as illustrated (Fig. 25). Aedeagus and terminal abdominal segments as illustrated (Figs. 27, 29, 31). Dorsum very finely sparsely punctate and with very indistinct short sparse setae. Body shape and configuration of ventral morphology typical for genus (material for making slide mounts unavailable).

Comparative notes: The aedeagi of the two Malagasy species differ most notably in the size of the internal sac (= endophallus), which in *H. saboureaui* is at least twice as large as the sac of *H. andringitra*. In addition, the shape of the aedeagal apex differs slightly in the two species, with *H. saboureaui* being slightly wider at the area of the distal extreme of the internal sac (Figs. 27, 28).



FIGURES 38–39. Distribution maps. (38) *Incoltorrida madagassica*; (39) *Hydroscapha* species.

The following differences are seen in the abdominal sclerites of males of the two species:

Ventrite VI: In *H. saboureaui* the apical notch is shallower and the ventrite has lateral setae; in *H. andringitra* the notch occupies more of the ventrite, and lateral setae are lacking.

Tergite IX: In *H. saboureaui* the apical indentation is slightly narrower, setae are restricted to the apical area, behind which the cuticle is microreticulate and does not have setae. In *H. andringitra* the apical indentation is wider, the setae at the apex are slightly longer, and the area posterior to the apex has setae and is not microreticulate.

Ventrite VII: This is the most curious of the differences. In *H. andringitra* ventrite VII is truncate apically, and lacks the distinctive two clusters of long setae seen in other species of *Hydroscapha*. The apical margin is sclerotized, not membranous, indicating that the apical portion was not accidentally removed during dissection. Also, the habitus images (Fig. 26), which were taken pre-dissection, show that the setal clusters of ventrite VII are not present. Additional specimens are needed to confirm that this is the actual condition, or if it is a deformity.

Tergite VIII: The tergite has a shorter broader shape in *H. saboureaui* and with basal corners rounded (Fig. 29). In *H. andringitra* the shape is more elongate and lateral sides are sinuate before acuminate basal corners (Fig. 30).

In females, the shapes of the terminal abdominal segments differ in the two species (Figs. 31, 32).

The first three abdominal ventrites of the *H. saboureaui* holotype appear to be longer than those of the *H. andringitra* holotype (Figs. 25, 26). However, this might be due to some telescoping of segments in the later species. More specimens are needed to make reliable comparisons.

Historical perspective. Over time, various numberings and designations have been used for the terminal abdominal segments of Hydroscaphidae (see below). In many species of the genus, including the two Malagasy species, the penultimate ventrite is deeply notched (Figs. 29, 30); herein, this is considered to be ventrite VI (= sternite VIII). The segment considered ventrite VII (Figs. 29, 30) is held within the cavity formed by sternite VIII (= ventrite VI)) and tergite VIII.

Reichardt & Hinton (1976), in a comprehensive paper, elected to use the anatomical, non-homologous, terms "last visible sternite" (= ventrite VI), and "invaginated sternite" (= ventrite VII) for the male ventral terminal segments. Also, in reference to the terminal abdominal structures of females, they stated that, "We have not attempted to homologize any of these structures with the parts of the genitalia in other beetles."

Löbl (1994) labeled the deeply notched male ventrite of two species as "sternite V" (his figure 12) for one species and "sternite VI" (his figure 18) for the other species. Löbl referred to the last male segments as "segment génital."

Fikáček and Šípková (2009) considered these segments to be "sternite VI" (the deeply notched ventral segment) and "sternite VII", respectively.

In two more recently published papers, Hall and Short (2010) and Short *et al.* (2015) the sixth visible ventral abdominal segment is treated as sternite VIII. These differences are due to anatomical numbering (= ventrite VI) versus morphological numbering (= sternite VIII).

Hydroscapha andringitra new species

Figs. 26 (habitus), 28 (aedeagus), 30, 32, 33 (terminal abdominal segments), 39 (map)

Type Material: Holotype (male): Fianarantsoa, Ambilavao, Sendrisoa, approx. 10km N of Andringitra NP, hygropetric, brownish muddy water seeping over rock (+ standing water with vegetation next to it), 22.00975S, 46.9504E, elev. 1165m, 7.v.2006, leg. J. Bergsten (NHRS). Paratypes: 10 females, same data as holotype (NHRS, MCZ, BMNH, PBZT/MBC).

Differential diagnosis. Habitus as in Fig. 26 (imaged pre-dissection). Slightly larger in size than *H. saboureaui* (length to elytral apices ca. 0.82 vs. 0.79 mm), but with a smaller aedeagus, which has a much smaller internal sac (Figs. 27, 28). Also refer to the differential diagnosis of *H. saboureaui*, and see comparative notes following that species.

Description (holotype male): Size (mm): length to elytral apices 0.82, total length 0.99 (variable due to telescoping last abdominal segments), width 0.46. Color dark brown to black, with legs, palpi and antennae lighter, testaceous in parts.

Habitus as illustrated (Fig. 26). Aedeagus and terminal abdominal segments as illustrated (Figs. 28, 30, 32-33). Dorsum very finely sparsely punctate and with very indistinct short sparse setae. Configuration of ventral morphology typical for the genus. See comparative notes in section on *H. saboureaui*.

FIGURE 40. The incredible stair-like hygropetric habitat at the type locality of *Incoltorrida magna* and *Incoltorrida galoko*. Jacquelin Herisahala Randriamihaja seen close to top.

FIGURE 41. The expansive hygropetric habitat, low water, at the type locality of *Incoltorrida marojejy*.

FIGURES 42–43. (42) Kelly B. Miller collecting at a locality of *Incoltorrida quintacostata* and the type locality of *Incoltorrida benesculpta*; (43) Same locality, slightly upstream. Photos by Robert Sites.

FIGURES 44–45. Hygropetric habitats of *Incoltorrida marojejy*. Guide Desiré Razafimahatratra collecting with forceps.

FIGURES 46–47. Hygropetric habitats of *Incoltorrida marojejy*. Guide Desiré Razafimahatratra collecting with a pipette.

FIGURES 48–49. Hygropetric habitats of *Incoltorrida madagassica*, water flowing into the sea at Nosy Mangabe, Masoala National Park.

FIGURES 50–51. Hygropetric habitats at type locality of *Incoltorrida zahamena*. Tolotra Ranarilalatiana collecting with a pipette.

FIGURES 52–53. Hygropetric and pond habitats at the type locality of *Hydroscapha andringitra.*

FIGURES 54–55. Hygropetric and pond habitats at the type locality of *Hydroscapha andringitra.* Tolotra Ranarilalatiana seen holding a D-frame aquatic net.

Acknowledgements

We are grateful to Ministère de l'Environment, de l'Ecologie et des Forets for authorising the fieldwork as well as to Madagascar National Parks, Madagascar Biodiversity Centre, IPSIO and Université d'Antananarivo for continuous support and collaboration. The curators of the collections listed in the depositories section are warmly thanked for providing specimens for this project. Special thanks to A. Taghavian-Azari (MNHN) and M. De Meyer (MRAC) for providing the historical types, which are absolutely essential to establishing the identity of old (and new) species. We thank the following people for generous help with contacts and protist expertise that made possible a genus-level identification of the epibionts: Diego Fontaneto, Edward Mitchell, Enrique Miguel Lara Pandi, Helmut Berger, Gregorio Fernandez Leborans and Alan Warren, the last author also for feedback on an early draft on the epibiont text. Sibylle Häggqvist kindly provided help with the translation of Steffan's publications. The participants of The Water Beetle Fauna of Madagascar project are thanked for their efforts and field fellowship during the expeditions, including but not limited to Tolotra Ranarilalatiana, Jacquelin Herisahala Randriamihaja, Rasa Bukontaite, Sandra Holmgren and Desiré Razafimahatratra. Michael Monaghan is thanked for organizing the 2006 collecting trip resulting in the discovery of *Hydroscapha andringitra*, and Michael Balke *et al.* for discovering the excellent Galoko mountains hygropetric locality with three of the new species in 2004, one of which (*Incoltorrida galoko*) is only known from the female holotype collected that year.

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