

The genus *Cultrobates* (Acari: Oribatida: Ceratokalummidae) in the Galapagos Islands and Central America

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Original research

ABSTRACT

The species *Cultrobates heterodactylus* Willmann, 1930 is known from Central America and has erroneously been reported from the Galapagos archipelago. A comparison with findings of this species from Panama has highlighted morphological differences between the specimens from Galapagos and *C. heterodactylus*. Herein, two new species from Galapagos, *Cultrobates ermilovi* n. sp. and *Cultrobates subiasi* n. sp. are described and illustrated. Also, differences in colonization of different islands as well as preferences in occupation of different habitats of the two species in Galapagos were noted, whereby *C. subiasi* was found almost exclusively in epiphytic habitats, predominantly in moss, and *C. ermilovi* occurs in various microhabitats in ground litter. *Cultrobates heterodactylus* occurs in Panama in lowland tropical rainforests, mainly in moist forest floor and litter in epiphytic bromeliads. Additional taxonomical remarks on *C. heterodactylus* are presented. Corrections to previous distribution data are given.

Keywords oribatid mites; systematics; morphology; Neotropical region; Ecuador; Panama; new species; distribution

Zoobank <http://zoobank.org/0743C54E-56E2-4A31-BA9C-C5915466DA9B>

Introduction

The oribatid mite genus *Cultrobates* was proposed by Willmann (1930) with *Cultrobates heterodactylus* Willmann, 1930 as type species. Although Willmann (1930) did not assign this genus to any known oribatid family, he related it to *Tectoribates* Berlese, 1910. Jacot (1934) suspected a classification of *Cultrobates* into “Oribatellinae” and Balogh (1961, 1965) placed the genus *Cultrobates* near Oribatelloidea. Woolley (1967) questioned the inclusion of *Cultrobates* (and other genera) into Oribatellidae and suggested a relationship with Ceratozetidae. Balogh (1970) erected the family Ceratokalummidae (as member of the superfamily Galummoidea [sic!]) with the type genus *Ceratokalumma* Balogh, 1970. In his catalogue of “Oribatid genera of the world” (Balogh 1972) he still placed the genus *Cultrobates* in the family Oribatellidae, and the family Ceratokalummidae into the superfamily Galummoidea.

Mahunka (1983) listed *Cultrobates heterodactylus* as member of the newly erected family Genavensiidae Mahunka, 1983. Marshall *et al.* (1987) placed this family, including the genus *Cultrobates*, in the superfamily Oribatelloidea. In their revision of the family Ceratokalummidae Balogh and Balogh (1988) did not make a commitment on the higher systematic position of the family – similarities with Galumidae were mentioned. In the same paper the authors synonymized the family name Genavensiidae Mahunka, 1983 (including the erroneous name Genaviidae Mahunka *nomen nudum* in Balogh and Mahunka 1981), and placed all known genera and species of Genavensiidae into Ceratokalummidae. Balogh and Balogh (1992) still

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placed the family Ceratokalummidae, also including the genus *Cultrobates*, in the superfamily Galumnoidea. Lee (1991) placed the family Ceratokalummidae together with Epactozetidae and Parakalumidae in the “Parakalummid complex” of the superfamily Oripodoidea.

Subías (2004) changed the family placement of Ceratokalummidae again to Oribatelloidea, which classification is still retained in his updated online catalogues (Subías 2022). However, this placement has been doubted before (e.g., Woolley 1967). Norton and Behan-Pelletier (2009) included the family Ceratokalummidae tentatively in the superfamily Ceratozetoidea “because adults share ceratozetoid character states such as a genal notch, axillary saccule of the subcapitulum, and a large pedotectum I.”, though “this placement is tentative pending discovery of immatures and/or phylogenetic analysis using molecular data” (Behan-Pelletier and Walter 2013). Ermilov *et al.* (2021) presented generic traits of the genus *Cultrobates* and described a new species from Peru. Prior to the present study four species were placed in this genus (*C. heterodactylus* Willmann, 1930, *C. lehmanni* Ermilov, Subías, Shtanchaeva & Friedrich, 2021, *C. nipponicus* Aoki, 1982, *C. quadricuspidatus* (Ewing, 1909)).

In the course of investigating oribatid mites in the Galapagos archipelago, numerous specimens of *Cultrobates* belonging to two morphologically distinct species were found. One of these species has similarities to *C. heterodactylus* and was mentioned under this name in Schatz (1998) and in subsequent publications, as far as findings from the Galapagos Islands are concerned (Schatz 2006, Baert 2011, Ermilov *et al.* 2021, Revelo-Toblar 2022, Revelo-Toblar *et al.* 2022). During further studies on oribatid mites in Panama, specimens of *Cultrobates heterodactylus* were identified that are morphologically identical to previous findings in Central America (Willmann 1930, Mahunka 1983). A detailed examination revealed that the Galapagos specimens, previously considered to be *C. heterodactylus*, show consistent differences. Thus, there are hitherto two unknown species of *Cultrobates* in the Galapagos Islands. These are described here and compared with *C. heterodactylus* from Panama.

Material and methods

Most of the material from the Galapagos Islands was collected during several expeditions to all the major and most of the minor islands of the archipelago by Heinrich and Irene Schatz in the years 1985–1988 (Schatz 1998), supplemented by further collections by Sandra Abebedrabbo, and the group of Leon Baert, Konjev Desender, and Jean-Pierre Maelfait. The Galapagos material was collected more than 30 years ago. Due to the difficulty of obtaining suitable preservation fluid on the remote islands at that time, and the age of the preserved material, several individuals are now damaged. Although this allows morphological studies, it is questionable whether this material is still suitable for molecular analyses. The material from Panama was collected during two extended field trips of Heinrich and Irene Schatz in the years 1996 and 1997 (Schatz 1997, 2006). Details of samples are given in the respective records of the different species.

The soil and organic litter samples from the Galapagos Islands were extracted in the Charles Darwin Research Station in Galapagos with a modified Tullgren–Berlese extraction apparatus (details see Schatz 1998), the extraction of the samples from Panama was done with the same method in Gamboa, Panama. For microscopic studies the specimens were mounted in lactic acid on temporary cavity slides for illustration, and subsequently preserved in ethanol. Drawings were made with a camera lucida attached to a transmission light microscope “Nikon Eclipse E400”. Each measured parameter was oriented to the particular optimal parallax-free perspective. Measurements of total body length was done in lateral view, from tip of the rostrum to the posterior edge of the notogaster. Body width refers to the maximal width of notogaster in dorsal aspect (without pteromorphs). Measurements indicated are ranges between maximum and minimum value, mean in brackets; all measurements are given in micrometers (µm). Females are recognizable by the presence of ovipositor and/or eggs, males by the small spermatopositor under the genital plates (Grandjean 1956). The terminology of

morphological features used in this paper follows that of Grandjean (summarized by Travé and Vachon 1975, Travé *et al.* 1996, Norton and Behan-Pelletier 2009). For scanning electron microscopy specimens were air dried and mounted on aluminum support with Depex and sputtered with 15 nm gold/palladium. Micrographs were made with a field emission scanning electron microscope (DSM 982 GEMINI Zeiss) at the Institute of Histology and Embryology, Medical University of Innsbruck by K. Pfaller.

In the text and figures the following abbreviations were used: *Prodorsum*: rostral (*ro*), lamellar (*le*), interlamellar (*in*), bothridial (*bs*), exobothridial (*ex*) setae, nasiform structure (*no*), tutorium (*tu*), dorsosejugal porose area (*Ad*), dorsophragma (*Dp*), pleurophragma (*Pp*). *Notogaster*: porose areas (*Aa*, *A₁*, *A₂*, *A₃*), notogastral setae (*c*, *l*-, *h*-, *p*-series), lyrifissures (*ia*, *im*, *ip*, *ih*, *ips*), opisthonotal gland opening (*gla*). *Gnathosoma*: subcapitular setae (*a*, *m*, *h*), axillary sacculae (*as*), adoral setae (*or*), cheliceral setae (*cha*, *chb*), Trägårdh's organ (*To*), palp setae (*sup*, *inf*, *d*, *l*, *cm*, *acm*, *lt*, *vt*, *ul*, *su*), solenidion (*ω*), postpalpal seta (*pps*). *Epimeral, lateral podosomal regions*: pedotecta I, II (*PtI*, *PtII*), genal tooth (*gt*), humeral porose areas (*Ah*, *Am*, *Ai*), transverse tubercles arc (*ta*), custodium (*cus*), discidium (*dis*), circumpedal carina (*cp*), epimeral setae (*1a*–*1c*, *2a*, *3a*, *3b*, *4a*, *4b*). *Anogenital region*: genital, aggenital, anal, adanal setae (*g₁*–*g₅*, *ag*, *an₁*, *an₂*, *ad₁*–*ad₃*), adanal lyrifissure (*iad*), preanal organ (*po*), postanal porose area (*Ap*). *Legs*: leg setae (*ft*, *tc*, *it*, *p*, *u*, *a*, *s*, *pv*, *pl*, *d*, *l*, *v*, *bv*, *ev*), leg solenidia (*ω₁*, *ω₂*, *φ₁*, *φ₂*, *σ*), leg famulus (*ε*), porose area (*pa*).

Taxonomy

Genus *Cultrobates* Willmann, 1930

Cultrobates ermilovi n. sp.

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Cultrobates sp.: Schatz 1998, p. 387.

(Figs 1–6, 10 C)

Diagnosis

Adults of *Cultrobates ermilovi* n. sp. differ morphologically from their congeners by the following combination of characters: Body size: 300–330 x 150–215. Rostrum with lateral teeth and nasiform protuberance. Lamellar cusp incised, with two teeth almost equal in length. Interlamellar seta usually shorter than prodorsum. Bothridial seta long, proximally thickened with filiform apex distally. Pteromorph movable, well developed. Ten pairs of very short notogastral setae, four pairs of small porose areas. Circumpedal carina, custodium and triangular discidium present. About 30 small tubercles forming convex transverse arc on anterior coxisternal region. Epimeral setal formula 3–1–2–2, genito-anal setal formula 5–1–2–3. Leg tarsus I with one claw, tarsi II–IV with three claws each.

Description of adult

Measurements. females (n=18): L 310–(320)–330, W 190–(203)–215, males (n=12): L 300–(310)–330, W 185–(195)–205.

Integument. Body colour medium to dark brown (“chestnut brown”), notogaster, ventral plate, genital, anal plates finely granulated. Anterior part of epimeral region with thin longitudinal striae. Distal surface of pedotecta I and II striated. Pteromorph light brown, lateral edge indistinctly striated.

Prodorsum. Rostrum appearing rounded in dorsal aspect, with small attenuating teeth laterally, protruding nasiform structure (*no*) forming a tunnel-shaped fold with small tongue directed anteriorly. In anterodorsal aspect rostrum appearing concavely rounded between lateral teeth (Figs 2 B, C). Lamella long blade (70–85), cusp distally bifurcate, deeply incised, inner tooth broader, outer attenuating (both teeth ~8–12). No distinct transverse ridges between



Figure 1 *Cultrobates ermilovi* n. sp., adult: dorsal aspect. Scale bar 100 μ m.

lamellae. Prodorsal setae setiform with small bristles, rostral seta (*ro*, 40–45) inserted underneath ventro-distal end of tutorium, directed anteromediad. Lamellar seta (*le*, 30–35) inserting in indentation of cusp, curved and directed anteromediad. Interlamellar seta (*in*, 55–65) mostly shorter or maximally of equal length as prodorsum, directed anteriad, insertion underneath anterior margin of notogaster, distance between insertions 18–25. Bothridium cup-shaped with large scales, medial scale under bothridial seta, directed anteromediad towards lamellar edge. Bothridial seta (*bs*) of medium length (stem ~10, head 45–60), head slightly thickened proximally (width 4–6), distally terminating with filiform apex, directed

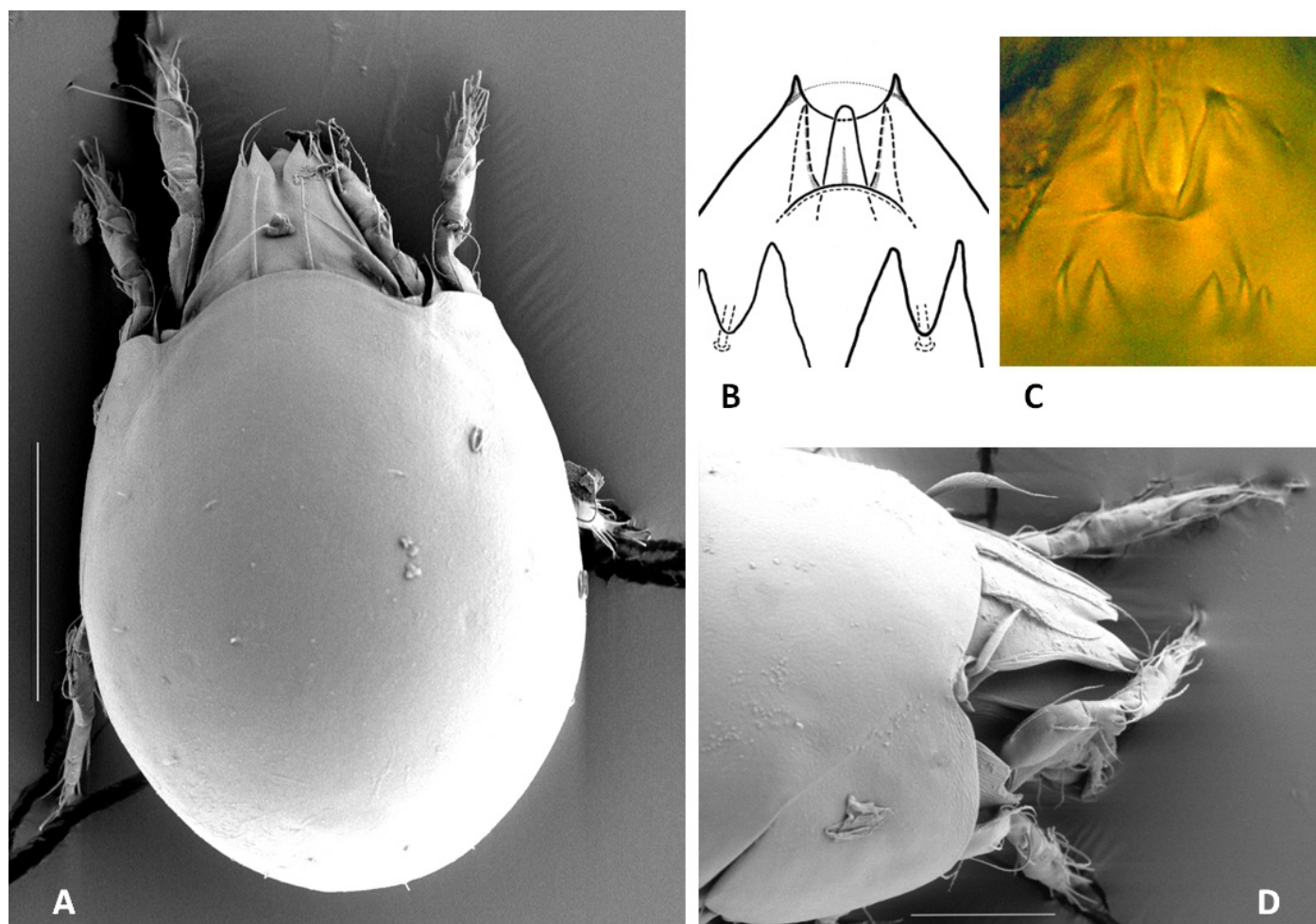


Figure 2 *Cultrobates ermilovi* n. sp., adult: A – dorsal aspect, SEM. Scale bar 100 µm; B – Anterior part of prodorsum, anterodorsal aspect (lamellar setae omitted); C – same aspect, microscope photograph; D – prodorsum, lateral aspect SEM. Scale bar 50 µm.

anteromedial. Tutorium long and small blade (*tu*, 70–75) with distinct apex anterodistally. Genal tooth (*gt*) large, distally attenuating. Dorsosejugal porose area (*Ad*) posterolateral to insertion of *in*, small, oval (~10 x 4). Internal apophyses distinct, dorsophragmata (*Dp*) small, fused medially, pleurophragmata (*Pp*) larger, posterior to bothridia. Exobothridial seta (*ex*, 4–5) on posterior end of bothridium, hidden under pteromorph, in some specimens not observable.

Notogaster. Oval, about 1.15–1.25 x longer than wide. Anterior margin slightly projecting anteriorly. Pteromorph well developed, movable, projecting anteriorly at level of anterior notogastral margin, triangular, laterally rounded, posterior with obtuse apex, length 105–130 (34–40% of body length). Posterior tectum present. Ten pairs of short notogastral setae, attenuating, *c* longest (10–12), others 4–6. Four pairs of porose areas, well visible, *Aa* largest (9–12 x 5–6), oval (in some specimens slightly triangular, apex directed anterodistad), others smaller (4–7), *A₁*, *A₂* round to oval, *A₃* round. Lyrifissures distinct, best visible in lateral and posterior view, *ia* situated posterior to *c*, *im* anteromedial to *h₃*, *ip* lateromedial to *p₁*, *ih* laterad to *A₁*, *ips* laterad to *h₂*. Opisthonotal gland (*gla*) opening located between *A₁* and *ih*.

Gnathosoma. Subcapitulum diarthric, large mentum (50–57 x 55–60). Subcapitular setae *h*, *a* (~5–7), *m* (8–12) smooth, attenuating. Adoral setae on conical lateral lips, smooth (*or*, 4–5). Chelicerae chelate-dentate, size (n=6) 80–90 x 25–30. Cheliceral setae (~15) attenuating with small bristles, *cha* inserted near dorsal margin, directed anteriorly, *chb* inserted abaxially.

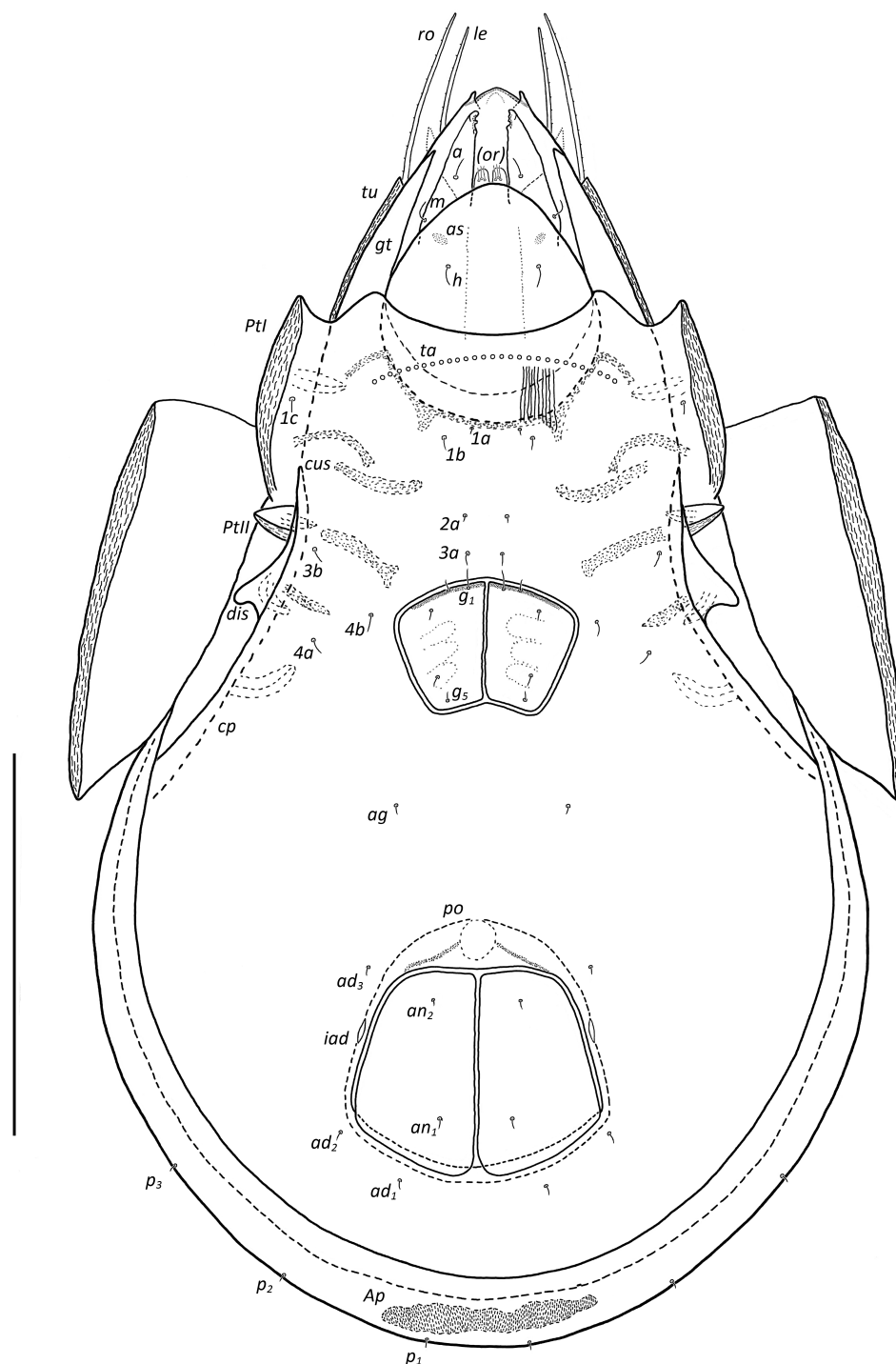
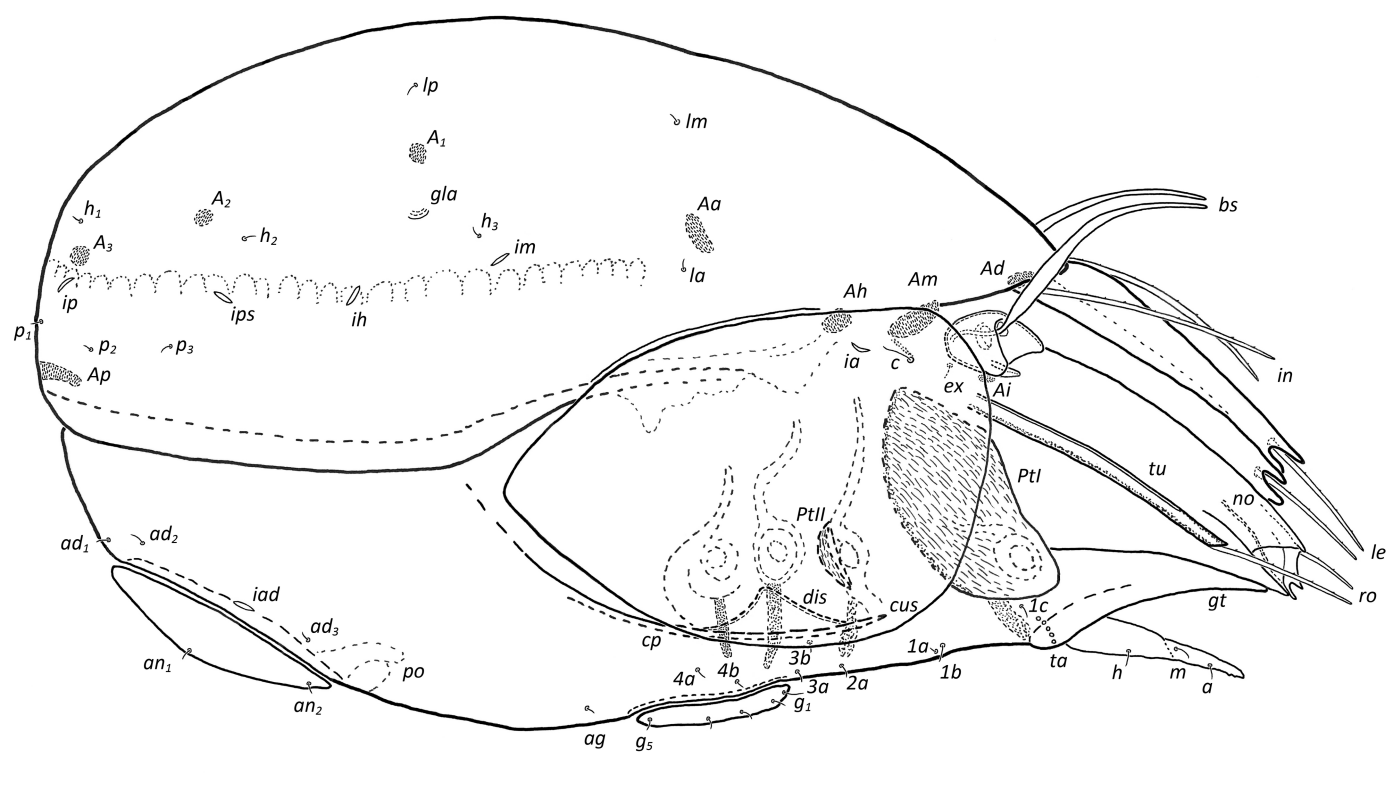


Figure 3 *Cultrobates ermilovi* n. sp., adult: ventral aspect (legs not shown). Scale bar 100 μ m.

Length of movable digit 15–20. Palp (50–60) with long femur and long tarsus, setal formula 0–2–1–3–9 (+ solenidion ω), setae with short bristles. Length of ω 8, attached to eupathidial seta *acm*. Postpalpal seta spiniform (*pps*, 4–5). Axillary sacculus posterior to palptrochanter, oval elongated (*as*, 6–8 x 3).

Lateral aspect of podosoma. Pedotectum I (*Ptl*) large, pedotectum II (*PtlI*) small scale



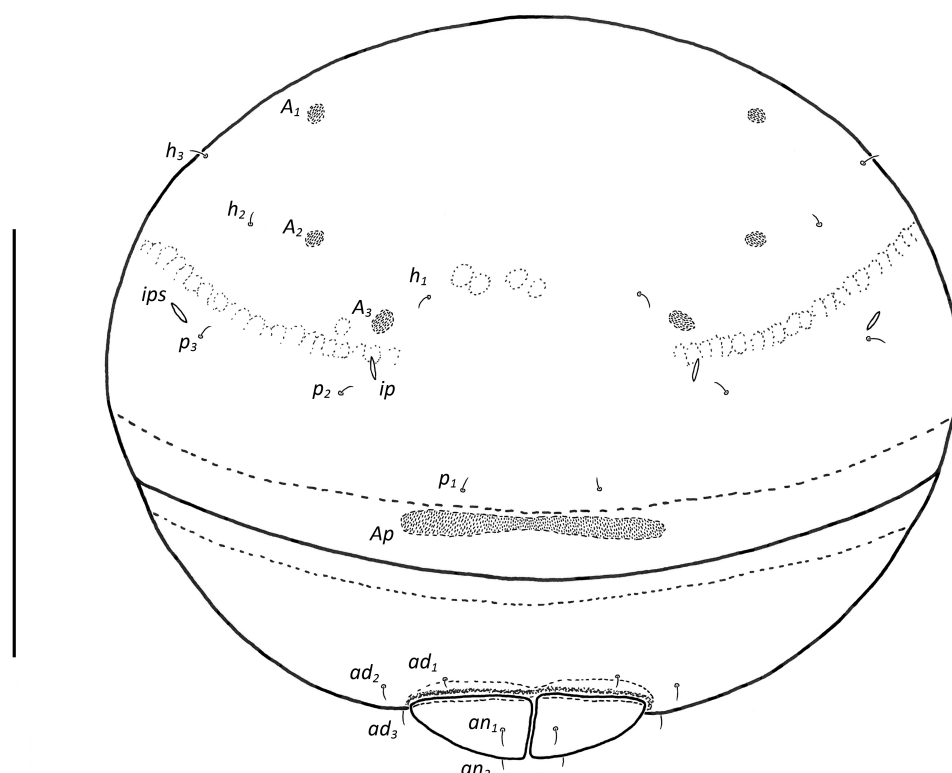


Figure 5 *Cultrobates ermilovi* n. sp., adult: posterior aspect. Scale bar 100 μ m.

II 30–40. Position and length of setae as in Fig. 6. Large porose areas (*pa*) on all femora (in paraxial position) and on trochanters III, IV.

Immatures

Unknown.

Sexual dimorphism

Females slightly larger than males, ranges overlapping. Length of female genital plates ($n=17$) 33–38. Most females with ovipositor, few specimens carrying one or two large eggs, size ($n=7$) 105–130 x 50–70. Shape of eggs oval to elliptical. Length of male genital plates ($n=12$) 26–32, longitudinal cross section of spermatopositor 9–11. Apart from size differences, no external sexual dimorphism could be observed.

Type locality – Material examined

Galapagos Islands, Fernandina Island, western part, moist *Psychotria* zone, below “Green Crater”, moist decayed leaf litter with humus under ferns and grass under *Zanthoxylum fagara* and *Psychotria rufipes* (16. March 1985, 480 m a.s.l., 0°23.57'S, 91°36.08'W, leg. H. Schatz). Holotype female, ten paratypes (four females, six males). Additionally, several specimens from other sites and islands were used for measurements and morphological analyses.

Type deposition

The holotype and eight paratypes (four females, four males) from the type locality, preserved in ethanol, are deposited in the collection of the Senckenberg Museum, Görlitz, Germany

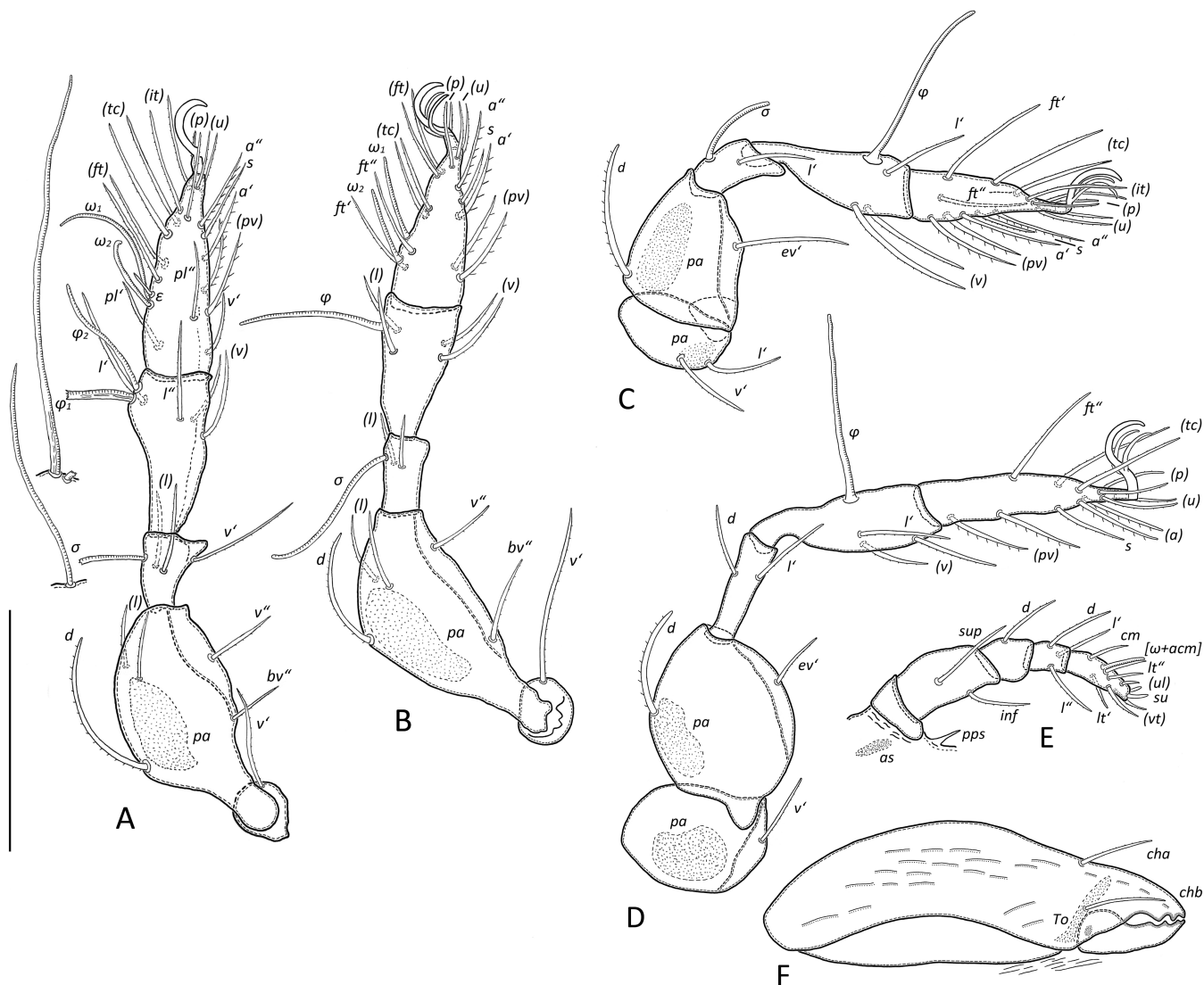


Figure 6 *Cultrobates ermilovi* n. sp., adult: legs, antiaxial aspect. A – Leg I, right. B – Leg II, right. C – Leg III, left. D – Leg IV, left. E – right palp. F – right chelicera. Scale bar 50 µm.

(SMNG). Additional material is deposited in the collection of the author, which will finally also be placed in the Senckenberg Museum, Görlitz.

Etymology

The new species is gratefully dedicated to my friend and colleague Dr. Sergey G. Ermilov, Tyumen, Russia, in recognition to his extensive research on morphology, taxonomy, life cycles and biogeography of oribatid mites throughout the world. His work significantly improves the modern morphological taxonomy.

Records from the Galapagos Islands

H. and Irene Schatz coll., unless other names given.

Cultrobates ermilovi n. sp. was found on three islands of the Galapagos archipelago (Fig. 11). No morphological differences between the populations on different islands and sites were observed.

Isla Fernandina — Western part of the island, moist (*Psychotria*) zone – Elfin Forest / Fern-sedge zone: Below “Green Crater”, moist decayed leaf litter with humus under ferns and grass under *Zanthoxylum fagara* and *Psychotria rufipes* (16. March 1985, 480 m a.s.l., 78 adults); *ibid.*, same place (9. May 1991, 230 adults, S. Abedrabbo coll.); above “Green Crater”, in dry to moist decayed fern litter and grass (15. March 1985, 560 m a.s.l., Fig. 12 A, 14 adults); *ibid.*, decayed leaf and fern litter under *Croton scouleri* (7. May 1991, 47 adults, S. Abedrabbo coll.); *ibid.*, in decayed fern and grass litter (7. May 1991, 800 m a.s.l., 3 adults, S. Abedrabbo coll.); western part of crater rim in fumarole, in moist to wet decayed fern litter (15. March 1985, 1280 m a.s.l., 0°22.48'S, 91°34.32'W, 3 adults); *ibid.*, in pad of moss under *Lycopodium cernuum* (Fig. 12 B, 1 adult).

Isla Isabela — *Volcano Wolf*. Moist (*Psychotria*) zone – Elfin Forest / Fern-sedge zone: open forest with *Bursera graveolens*, *Psidium galapageium*, *Zanthoxylum fagara*, in moist decayed leaf litter and humus (23. March 1988, 800 m a.s.l., 50 adults, L. Baert, K. Desender, J.P. Maelfait coll., loc. 71); *ibid.*, open forest with *Zanthoxylum fagara*, *Tournefortia* sp., *Cordia lutea*, *Macraea laricifolia*, *Psidium galapageium*, lava boulders with thick litter layer, in moist, decayed leaf litter with humus (23. March 1988, 1000 m a.s.l., 141 adults, L. Baert, K. Desender, J.P. Maelfait coll., loc. 72); *ibid.*, open forest with *Zanthoxylum fagara*, *Croton scouleri*, *Scalesia microcephala*, *Macraea laricifolia*, *Psidium galapageium*, *Ipomoea* sp., *Opuntia insularis*, ferns, lava boulders with soil, in moist leaf litter and decayed pieces of wood (23. March 1988, 1200 m a.s.l., 65 adults, L. Baert, K. Desender, J.P. Maelfait coll., loc. 73).

Isla Isabela — *Volcano Darwin*. Moist (*Psychotria*) zone – Elfin Forest / Fern-sedge zone: shrubs and grass with *Macraea laricifolia*, *Scalesia* spp., *Zanthoxylum fagara*, *Croton scouleri*, in dry to moist grass litter (28. March 1988, 1000 m a.s.l., 5 adults, L. Baert, K. Desender, J.P. Maelfait coll., loc. 86); *ibid.*, shrubs and ferns with *Macraea laricifolia*, *Zanthoxylum fagara*, in dry to moist leaf litter, pieces of wood and lichens under ferns and grasses (28. March 1988, 1200 m a.s.l., 1 adult, L. Baert, K. Desender, J.P. Maelfait coll., loc. 88).

Isla Isabela — *Volcano Alcedo*. Moist (*Psychotria*) zone – Elfin Forest / Fern-sedge zone: Northeastern slope at upper end of the Encañada in open forest with *Trema micranta*, *Scalesia microcephala* and *Tournefortia rufo-sericea*, in dry to moist leaf and grass litter with pieces of wood and humus (25. March 1988, 780 m a.s.l., 1 adult); inner edge of southwestern crater rim near fumarole, under *Pteridium aquilinum* and *Ipomoea* sp., in moist decayed fern litter and humus (21. March 1988, 1030 m a.s.l., Figs 12 C, D, 152 adults); at southwestern crater rim in Elfin Forest of *Zanthoxylum fagara*, *Psychotria rufipes*, *Scalesia microcephala*, in moist decayed fern litter with roots and humus (23. March 1988, 1060 m a.s.l., 6 adults); at western crater rim in dense bush vegetation of *Psychotria rufipes*, *Zanthoxylum fagara*, *Scalesia microcephala*, in dry to moist decayed leaf litter with pieces of wood and humus under dead trunk (24. March 1988, 1090 m a.s.l., Fig. 12 E, 20 adults); at southern crater rim, under *Cyathea weatherbyana* and *Pteridium aquilinum*, in moist fern litter with pieces of wood and roots (23. March 1988, 1100 m a.s.l., 9 adults); at eastern crater rim in Elfin Forest, under *Psychotria rufipes*, in dry to moist decayed leaf litter, pieces of wood and humus (25. March 1988, 1100 m a.s.l., 23 adults).

Isla Santa Cruz — *Scalesia* forest around Los Gemelos: in moist to wet leaf litter and moss under *Zanthoxylum fagara* (16. April 1985, 590 m a.s.l., 7 adults).

***Cultrobates subiasi* n. sp.**

Zoobank: 0105B879-801A-4FC9-90BA-D0309EEFB289

Cultrobates heterodactylus: Schatz 1998, pp. 387, 396; Schatz 2006, p. 282; Baert 2011, p. 32; Ermilov *et al.* 2021, p. 2414 (findings from the Galapagos Islands); Revelo-Toblar 2022, p. 83; Revelo-Toblar *et al.* 2022, p. 27 (findings from the Galapagos Islands).
(Figs 7–9, 10 A, B)

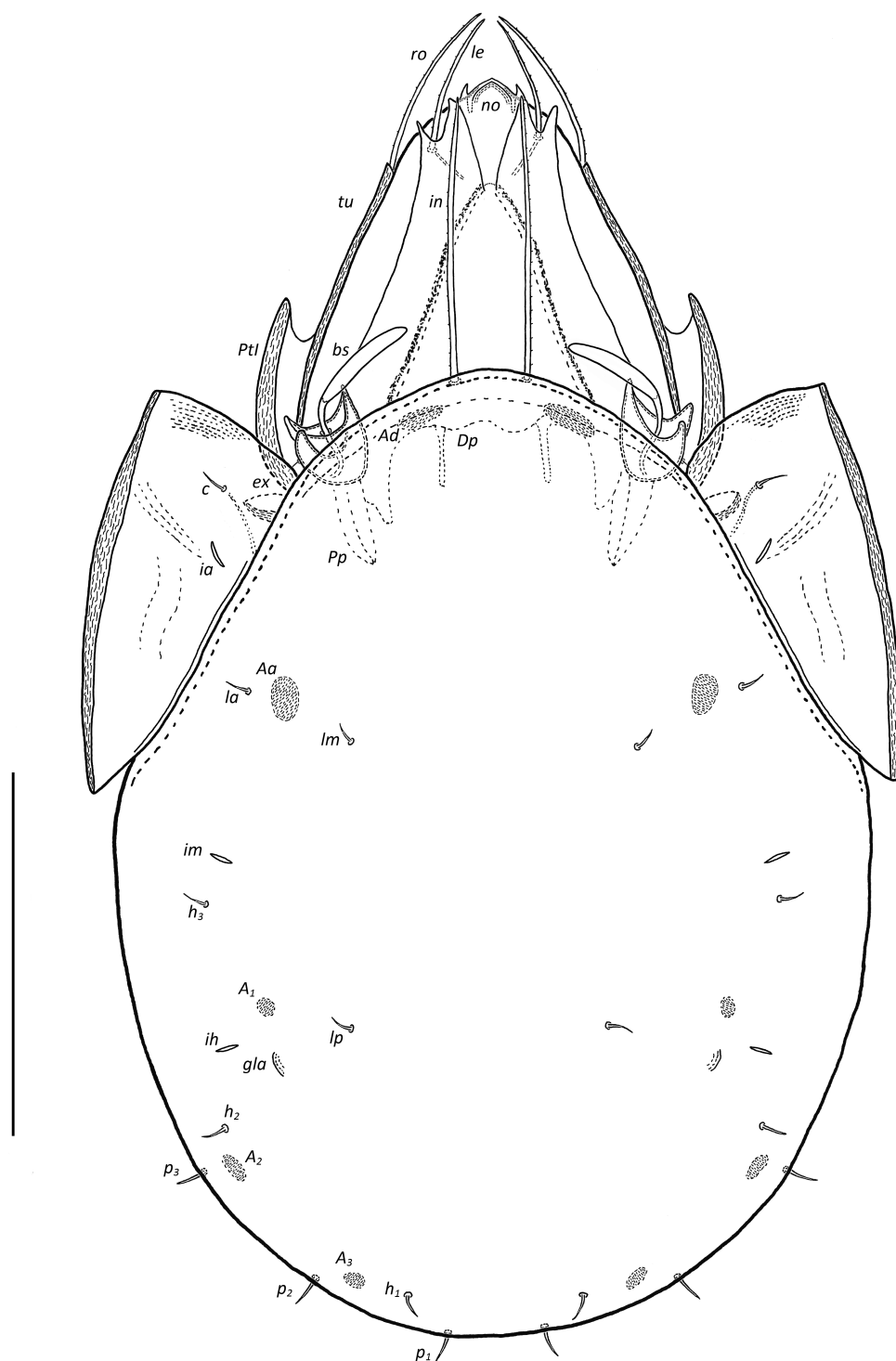


Figure 7 *Cultrobates subiasi* n. sp., adult: dorsal aspect. Scale bar 100 µm.

Diagnosis

Adults of *Cultrobates subiasi* n. sp. differ morphologically from their congeners by the following combination of characters: Body size: 318–365 x 195–240. Rostrum with lateral teeth and nasiform protuberance. Lamellar cusp incised, inner tooth mostly slightly longer

Figure 8 *Cultrobates subiasi* n. sp., adult: ventral aspect (legs not shown). Scale bar 100 μ m.

than outer tooth. Interlamellar seta as long or longer than prodorsum. Bothridial seta slightly curved and thickened, peapod-shaped, with rounded or slightly pointed tip. Pteromorph movable, well developed. Ten pairs of short notogastral setae, four pairs of small porose areas. Circumpedal carina, custodium and triangular discidium present. About 30 to 35 small

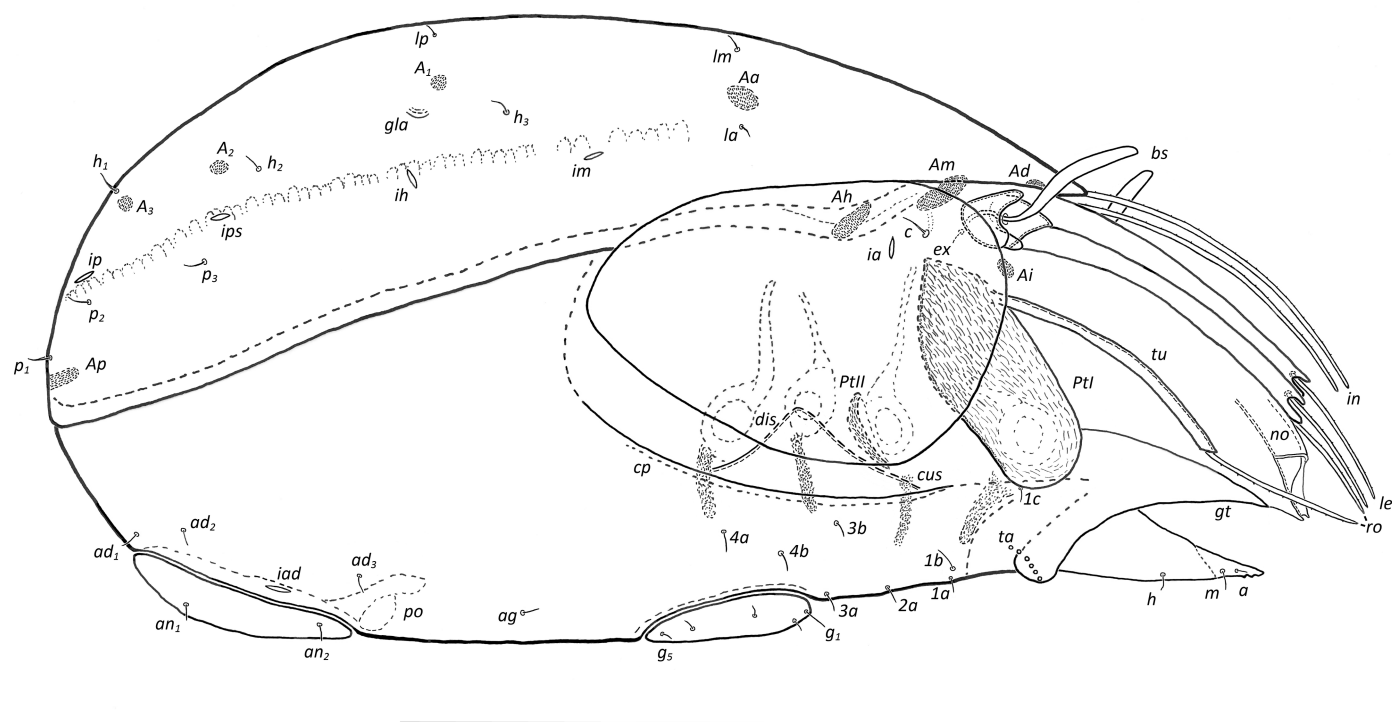


Figure 9 *Cultrobates subiasi* n. sp., adult: lateral aspect (legs not shown). Scale bar 100 μ m.

tubercles forming convex transverse arc on anterior coxisternal region. Epimeral setal formula 3–1–2–2, genito-anal setal formula 5–1–2–3. Leg tarsus I with one claw, tarsi II–IV with three claws each.

Description of adult

Body size. females (n=17): L 320–(346)–365, W 195–(217)–240, males (n=13): L 318–(331)–345, W 195–(209)–220.

Integument. Body colour light brown (“orange brown”), surface granulate. Anterior part of epimeral region with thin longitudinal striae. Distal surface of pedotecta I and II striated. Pteromorph light brown, lateral edge striated.

Prodorsum. Rostrum with small attenuating teeth laterally, appearing rounded in dorsal aspect, with protruding nasiform structure (no). Lamella long blade (75–95), cusp distally bifurcate, deeply incised, inner tooth broader and triangular, outer attenuating, tip of inner tooth (~8–14) mostly anterior of tip of outer tooth (~6–10). Prodorsal setae setiform with small bristles, rostral seta (ro, 43–50) inserted underneath ventro-distal end of tutorium, directed anteromediad. Lamellar seta (le, 25–35) inserting in indentation of cusp, curved and directed anteromediad. Interlamellar seta (in, 70–80) most often as long or longer than prodorsum, directed anteriad, insertion underneath anterior margin of notogaster, distance between insertions ~20–25. Bothridium cup-shaped with large medial and two lateral scales, medial scale directed anteriad toward lamella. Bothridial seta (bs) rather short to medium length, head (30–35, rarely 40), peapod-shaped, slightly curved and thickened over entire length (width 4–5), tip rounded or slightly pointed, directed anteromediad. Tutorium long and small blade (tu, 70–75) with distinct apex anterodistally. Genal tooth (gt) large, distally attenuating. Dorsosejugal porose area (Ad) posterolateral to insertion of in, small, oval (10–12 x 4–6). Internal apophyses distinct, dorsophragmata (Dp) small, fused medially, pleurophragmata (Pp) larger, posterior to bothridia. Exobothridial seta (ex, ~5) posterolateral of bothridium.

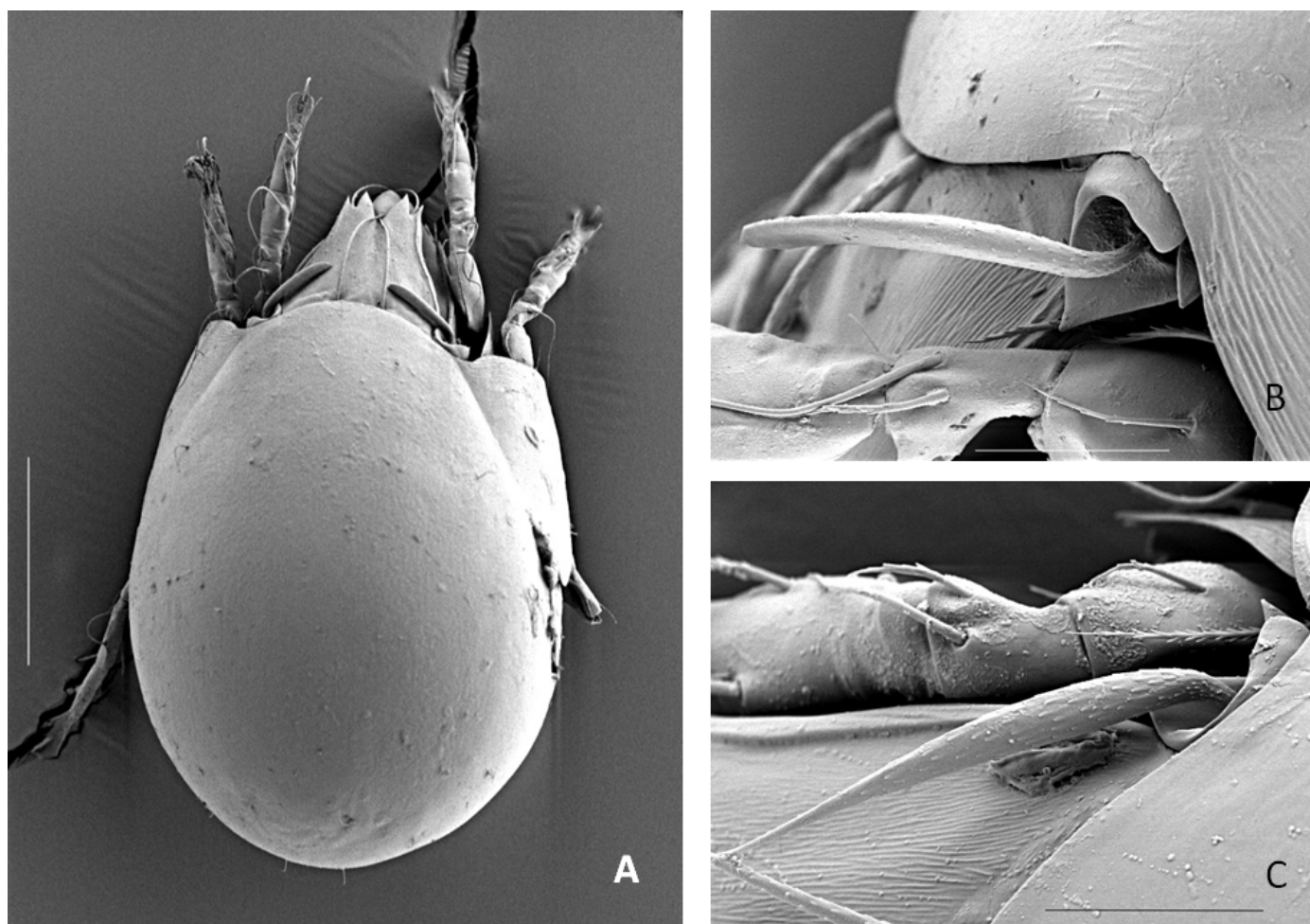


Figure 10 *Cultribates subiasi* n. sp., adult, SEM: A – dorsal aspect. Scale bar 100 μ m; B – bothridial seta. Scale bar 20 μ m; C – *Cultribates ermilovi* n. sp., adult, SEM: bothridial seta. Scale bar 20 μ m.

Notogaster. Oval, about 1.15–1.40 x longer than wide. Anterior margin slightly projecting anteriad. Pteromorph well developed, movable with hinge, triangular, projecting anteriad at level of anterior notogastral margin, anteriorly and laterally rounded, posteriorly with obtuse apex, length 120–140 (33–42% of body length). Posterior notogastral tectum present. Ten pairs of short notogastral setae, attenuating (8–12). Four pairs of small porose areas, *Aa* largest (10–14 x 6–8), oval, others smaller, round to oval (4–6). Lyrifissures and opisthonotal gland (*gla*) distinct, situated as in previous species.

Gnathosoma. Generally, similar to that of *C. ermilovi* n. sp., except sizes. Mentum large (60 x 53–56). Subcapitular setae *h*, *m* (8–12), *a* (5–8) smooth, attenuating, adoral setae (*or*, 6–9) smooth. Chelicerae chelate-dentate, size (n=6) 95–105 x 27–30. Cheliceral setae with small bristles, ~15–20. Length of movable digit 18–22. Palp 54–60, length of ω 10, attached to eupathidial seta *acm*. Postpalpal seta spiniform (*pps*, 5). Axillary saccule oval elongated, directed diagonally (*as*, 6–8 x 3–4).

Lateral aspect of podosoma. Pedotectum I (*PtI*) large, pedotectum II (*PtII*) small scale posterior to trochanter II projecting abaxially. Discidium (*dis*) large, triangular, projecting laterally. Circumpedal carina (*cp*) merging into custodium. Custodium (*cus*) pointing anteroventrad, acute tip toward pedotectum I. Humeral porose areas *Am* (~20 x 7), *Ah* (11 x 5) indistinct, oval, *Ai* small (~3 x 6), oval to slightly triangular, ventral to bothridium.

Epimeral region. Slightly convex transverse arc (*ta*) consisting of about 30–35 small tubercles on anterior coxisternum. Apodemes I complete and fused medially, apodemes II and III and sejugal apodemes medially incomplete. Anterior part of epimeral region with very thin longitudinal striae (almost invisible in some specimens after long preservation in ethanol). Epimeral setal formula 3–1–2–2, all setae attenuating, length of *1a* 3, *1b* 10–12, *2a* 5, others 7–8.

Anogenital region. Genito-anal setal formula, shape and position as in *C. ermilovi* **n. sp.**, 5–1–2–3, sizes of g_1 10–12, g_2 ~6–7, other genital setae 3–5, aggenital, anal and adanal setae 3–6. Postanal porose area elongate (*Ap*, ~10 x 60–70).

Legs. Generally, similar to those of *C. ermilovi* **n. sp.**, except sizes. Legs of medium length (35–50% of body size), length (with claws) of leg I 140–155, II 140–150, III 125–135, IV 155–170. Leg I monodactylous, legs II–IV heterotridactylous, with stronger median and thin lateral claws. Shape and setal formula of legs as in previous species. Solenidia ϕ_1 on tibia I 90–100, ϕ on tibia II 45–50, σ on genu I 50–55, σ on genu II 40–45.

Immatures

Unknown.

Sexual dimorphism

Females slightly larger than males, ranges overlapping. Length of female genital plates ($n=17$) 37–42. Most females with ovipositor, few specimens carrying one or two large eggs, size ($n=12$) 80–160 x 55–80. Shape of eggs oval to elliptical, some kidney shaped, surface punctate. Length of male genital plates ($n=13$) 30–34, longitudinal cross section of spermatopositor 9–11. Apart from size differences, no external sexual dimorphism could be observed.

Type locality – Material examined

Galapagos Islands, Santa Cruz Island, *Scalesia* forest around “Los Gemelos” (590 m a.s.l., 0°37.53'S, 90°23.18'W), on bough of *Piscidia carthagenensis*, in pads of *Peperomia inaequalifolia*. Holotype female, two paratypes (one female, one male, 16. April 1985); *ibid.*, on trunk of *Scalesia pedunculata* var. *parviflora*, in dry to moist moss (one female, two males, 8. March 1987, leg. H. Schatz). In addition, all encountered specimens (see Records) were used for measurements and morphological analyses.

Type deposition

The holotype and two paratypes (one female, one male) from the type locality, preserved in ethanol, are deposited in the collection of the Senckenberg Museum, Görlitz, Germany (SMNG). Additional material is deposited in the collection of the author, which will finally also be placed in the Senckenberg Museum, Görlitz.

Etymology

The new species is gratefully dedicated to my friend and colleague Dr. Luis S. Subías, Madrid, Spain. His research on morphology, taxonomy, biogeography, and classification of oribatid mites are of profound influence.

Records from the Galapagos Islands

H. and Irene Schatz coll.

Cultrobates subiasi **n. sp.** was found on four islands of the Galapagos archipelago (Fig. 11). No morphological differences between the populations on different islands and sites were observed.

Isla Isabela — *Volcano Alcedo*. Moist (*Psychotria*) zone – Elfin Forest / Fern-sedge zone: at southern crater rim in Elfin Forest of *Psychotria rufipes*, *Tournefortia rufo-sericea*, *Piscidia*

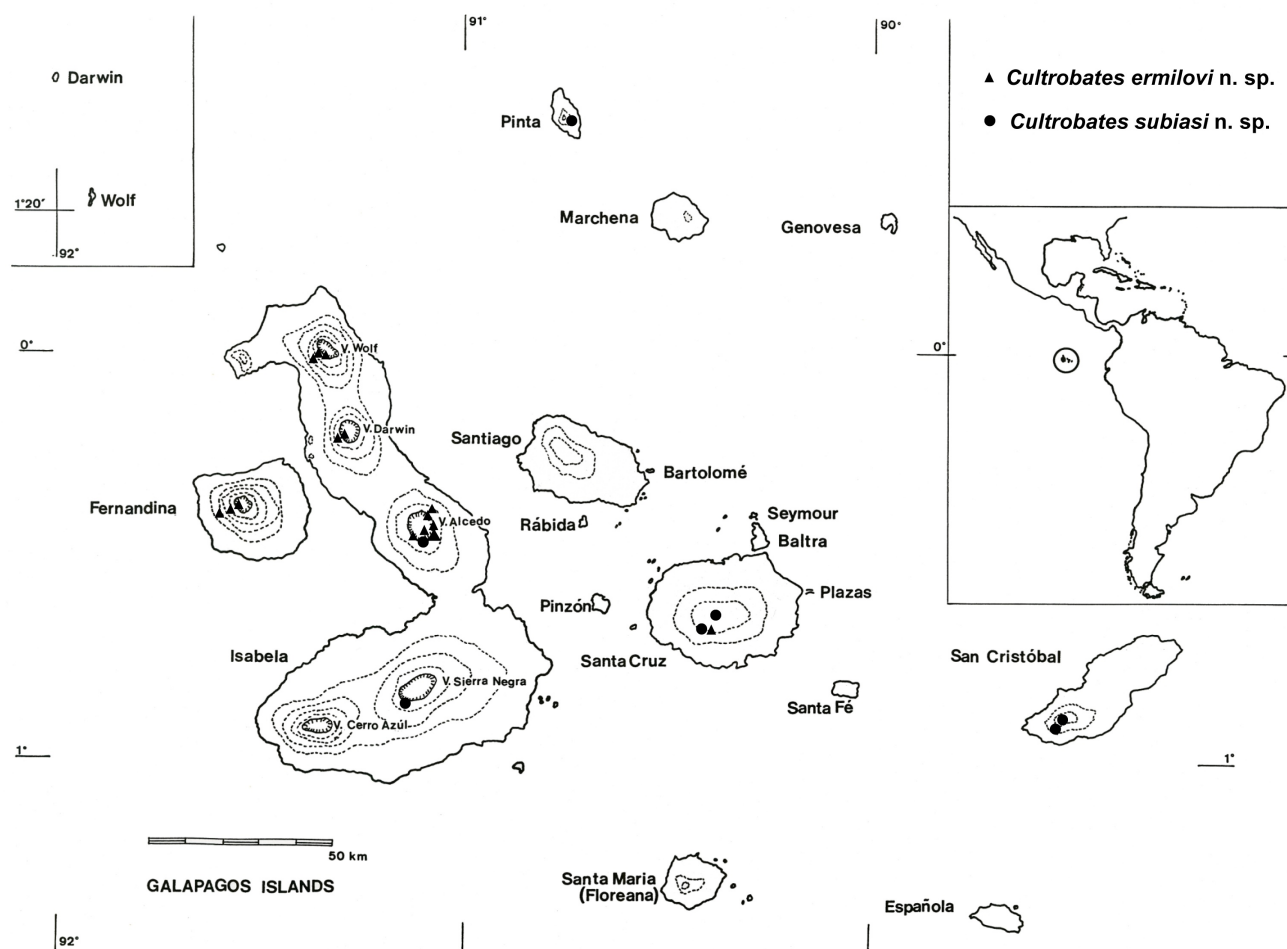


Figure 11 Records of *Cultrobates* species from the Galapagos Islands.

carthagenensis in moist epiphytic moss, lichens and fungi (21. March 1988, 1040 m a.s.l., Fig. 13 B, 2 adults).

Isla Isabela — *Volcano Sierra Negra*. Moist (*Psychotria*) zone – Elfin Forest / Pasture zone: Pampa at southwestern crater rim, in moist lichens and moss on barks of *Sapindus saponaria* (11. Feb. 1987, 910 m a.s.l., 6 adults).

Isla Pinta — Moist (*Psychotria*) zone, forest: at eastern slope of the main crater, in moist moss on ground under *Zanthoxylum fagara* and *Pisonia floribunda* (1. April 1988, 530 m a.s.l., 1 adult).

Isla San Cristóbal — Moist (*Miconia*) zone / Fern-Sedge zone: around lake El Junco, 650 m a.s.l., in moist hanging pads of moss and *Lycopodium dichotomum* on boughs of *Psidium guajava* and *Miconia robinsoniana* (28. March 1985, 650 m a.s.l. 8 adults); *ibid.*, small cataract at river southeast of El Junco, in moist hanging pads of moss and *Lycopodium dichotomum* on bough of *Psidium guajava* (3. Jan. 1987, 630 m, Fig. 12 F, 6 adults).

Isla Santa Cruz — *Scalesia* forest around “Los Gemelos:” in moist to wet leaf litter and moss under *Zanthoxylum fagara* (16. April 1985, 590 m a.s.l., 3 adults); *ibid.*, on bough of *Piscidia carthagenensis*, in pads of *Peperomia inaequalifolia* (16. April 1985, 590 m a.s.l., 3 adults); *ibid.*, on dead *Scalesia* tree, in moist moss (13. Jan. 1987, 1 adult); *ibid.*, on trunk of *Scalesia pedunculata* var. *parviflora*, in dry to moist moss (8. March 1987, 590 m a.s.l., Fig. 13 A, 3 adults); *Scalesia* forest near Cerro Crocker, on *Scalesia pedunculata* var. *parviflora*

and *Zanthoxylum fagara*, in moist moss from boughs with pads of *Peperomia inaequalifolia* (6. March 1987, 700 m a.s.l., 12 adults).

***Cultrobates heterodactylus* Willmann, 1930**

Willmann 1930: p. 242, fig. 4; Mahunka 1983: p. 723, figs 32, 33; Balogh and Balogh 1990: 133, figs 122 D, E; Balogh and Balogh 2002a: p. 359; Balogh and Balogh 2002b: fig. 473:6; Schatz 2006: p. 282.

The original description (Willmann 1930), based on two specimens from Guatemala is short and lacks information about some morphological structures. Mahunka (1983) found another specimen in Tikal, Guatemala, and provided additional morphological information. I was able to study this specimen. Until further findings in Panama (Schatz 2006) no other records of *C. heterodactylus* were known (for erroneous and unproven reports see chapter “Corrections to previously stated distribution data”). I found this species in four different sites in the lowlands of Central and Northwest Panama. Later, additional reports from Panama were given by Basset *et al.* (2012). Recently, *Cultrobates heterodactylus* has also been reported from Mexico (Revelo-Tobar *et al.* 2022).

The examined specimens from the populations in Panama were morphologically consistent with the specimen from Guatemala and with the descriptions by Willmann (1930) and Mahunka (1983). Some additional morphological features which were not given in detail in previous descriptions are presented here on the basis of specimens from Panama. Comparable species-specific differential characters among the species *C. heterodactylus*, *C. ermilovi* **n. sp.** and *C. subiasi* **n. sp.** are given in the remark (#1).

Body size. females (n=25): L 265–(277)–290, W 153–(162)–175, males (n=13): L 250–(267)–270, W 145–(152)–165.

Supplementary description

Body colour light to medium brown (“copper brown”), surface finely granulated. Rostrum corresponds to the above described species *C. ermilovi* **n.sp.** with small lateral teeth and protruding naso. Rostral (35–40) and lamellar setae (25–30) directed anteromediad. Inter-lamellar setae shorter or maximally of equal length as prodorsum, length 60–70 (80–100% of prodorsum length). Inner tooth of lamellar cusp (8–12) equal or slightly longer than outer tooth (6–10). Bothridium with large scales. Bothridial seta long (40–55) and narrow (5) (almost “ensiform”), directed anteromediad, at base slightly incrassate, distally rounded or slightly acuminate, dorsally with spoon-shaped indentation. Exobothridial seta 4–5. Notogastral setae very short, *c* longest (7–8), others 4–7. Epimeral setal formula 3–1–2–2, length of setae *1a* and *2a* 2, *1b* 5, others 2–3. Epimeral plate with fine longitudinal stripes. Length of genital setae *g*₁ 8–10, *g*₂–*g*₅ 3, aggenital seta 2, anal and adanal setae 3–4, gnathosomal setae *h*, *m*, *a* 3–4, adoral setae 3. Legs of medium length (40–60% of body size), length (with claws) of leg I 105–110, II 110–120, III 120–130, IV 145–155. Setal formula of legs and shape as in *C. ermilovi* **n. sp.** Solenidia *φ*₁ on tibia I 70–80, *φ* on tibia II 40–45, on tibia III 30–35, on tibia IV 30–35, *σ* on genu I 45–50, on genu II ~30, on genu III 10–12. Setae *d* on femora long (15–25) and spiniform.

Sexual dimorphism

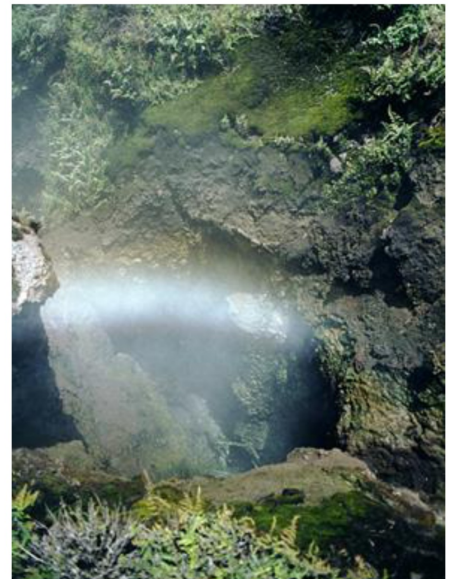
Among the examined individuals, females predominate. Females larger than males, ranges slightly overlapping. Length of female genital plates 27–32, most females with ovipositor, no eggs detected. Length of male genital plates 22–26, longitudinal cross section of spermatopositor 10–12. Apart from size differences, no external sexual dimorphism could be observed.

Records from Panama

H. and Irene Schatz coll



A



B



C



D



E



F

Figure 12 Some sampling localities of *Cultrobates* spp. in the Galapagos Islands (all photos Irene and Heinrich Schatz). A – Fernandina Island, “Green Crater”, western slope of the island, type locality of *C. ermilovi* n. sp. (15. March 1985). B – Fernandina Island, fumarole at crater rim in lava fissure (15. March 1985). C – Isabela Island, Volcano Alcedo, western part of the crater rim (24. March 1988). D – ibid., fumarole at inner edge of crater rim (21. March 1988). E – ibid., Elfin Forest at crater rim (24. March 1988). F – San Cristóbal Island, small cataract at river southeast of El Junco (2. Jan. 1987).

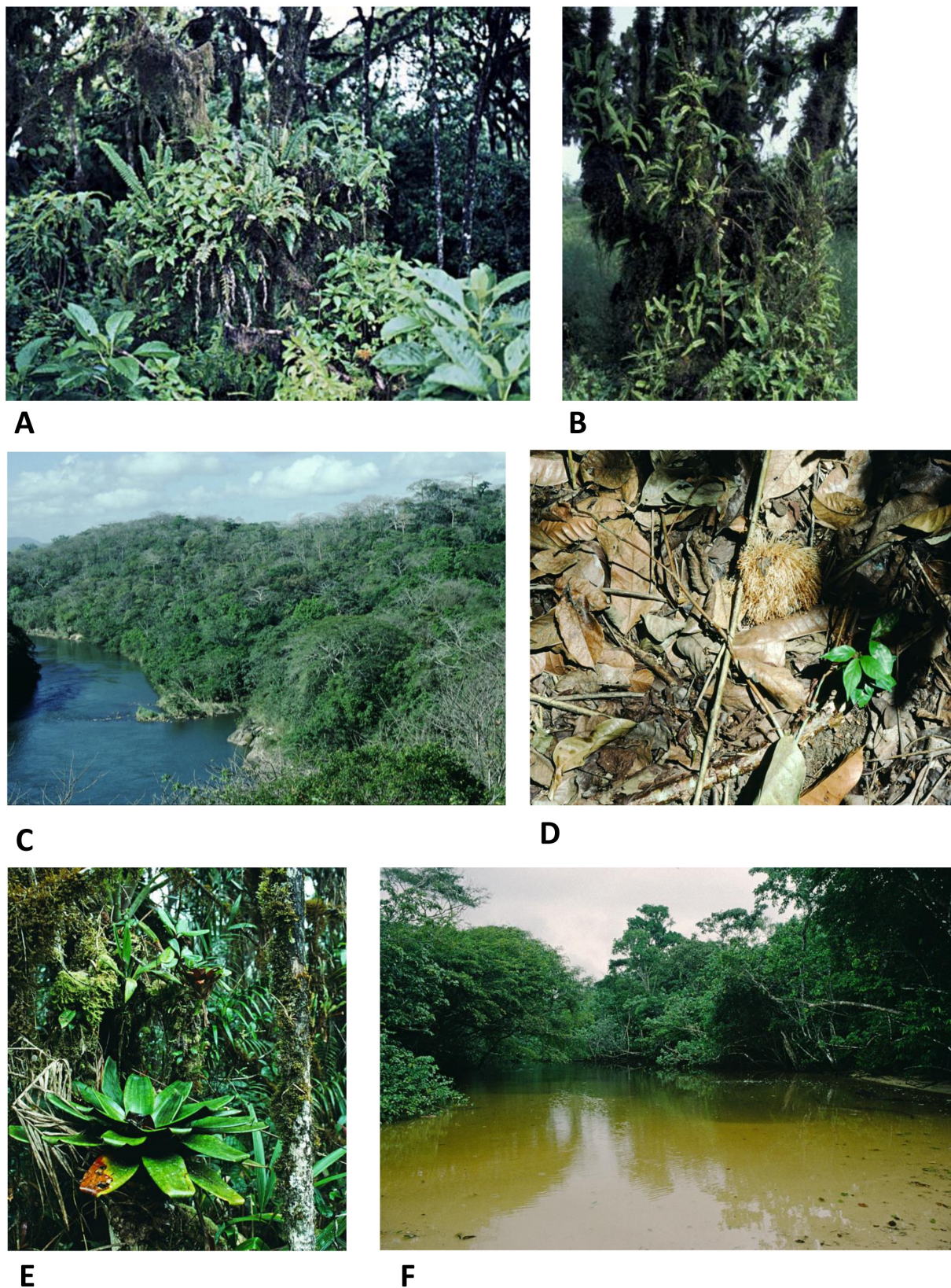


Figure 13 Some sampling localities of *Cultrobates* spp. in the Galapagos Islands (A, B) and Panama (C–F) (all photos Irene and Heinrich Schatz). A – Santa Cruz Island, *Scalesia* forest near Los Gemelos, epiphytes on trunk of *Scalesia pedunculata*, type locality of *C. subiasi* n. sp. (8. March 1987). B – Isabela Island, Volcano Alcedo, epiphytes on trunk of *Piscidia carthagenensis* (23. March 1988). C – Deciduous dry forest at Rio Chagres near Madden Dam (8. Feb. 1996). D – ibid., ground leaf litter (8. Feb. 1996). E – Costa Abajo, San Lorenzo Protected Forest, epiphytic bromelia and moss in tropical wet forest (26. Jan. 1996). F – Isla Bastimentos, Playa Larga, mangrove lagoon in coastal rain forest (1. Feb. 1996).

Soberania — Soberania National Park (Panamá Province) – Tropical Moist Forest: Camino de Cruces, near entrance, under rotting tree, organic litter and humus on bromelia (20. Jan. 1996, 50 m a.s.l., 18 adults); Semaphor Hill, at Quebrada, partially well-decayed moist leaf litter and roots on ground under uppermost layer (24. Jan. 1997, 160 m a.s.l., 1 adult); Sendero La Plantación at Rio Chico Masambi, between buttressed roots, well-decayed moist leaf litter with humus on ground (24. Jan. 1997, 50 m a.s.l., 1 adult).

Madden Dam area (Colón Province) – Deciduous Dry Forest: near hydrographic station at Rio Chagres, well-decayed leaf litter and humus below uppermost level on ground, sample slightly moist (8. Feb. 1996, 40 m a.s.l., Figs 13 C, D, 1 adult).

Costa Abajo (Colón Province) – Tropical Wet Forest: 5 km east of Piña, moss scratched from tree (26. Jan. 1996, 20 m a.s.l., 1 adult); between the hamlets Achiote and Piña: in epiphytic bromelia at about 3 m altitude, with bark and moss; dry (26. Jan. 1996, 30 m a.s.l., Fig. 13 E, 26 adults); *ibid.*, well-decayed moist leaf litter on ground under *Monstera* and *Philodendron* (26. Jan. 1996, 30 m a.s.l., 26 adults). The finds of Basset *et al.* (2012, Supplementary material, coll. N. Winchester, det. V. Behan-Pelletier) date from the adjacent San Lorenzo Protected Area, in the canopy and understorey of a lowland tropical rainforest (Basset *et al.* 2007).

Archipelago de Bocas del Toro: Isla Bastimentos National Marine Park (Bocas del Toro Province) – Coastal Rain Forest: Playa Larga, ca. 100 m behind beach in dense forest, well-decayed deep and wet leaf litter and humus (4. Feb. 1996, 20 m a.s.l., 16 adults); *ibid.*, mangroves in littoral zone, in moist leaf litter, algae and seagrass at beach in a lagoon (1. Feb. 1996, 0 m a.s.l., Fig. 13 F, 1 adult).

Remarks

1. Morphological differences between *C. heterodactylus* and the new species

The most striking morphological differences between the three taxa are in body colour and size, shape and size of bothridial seta (“sensillum”), relative length of interlamellar seta, and length of notogastral setae.

- **Colour** — *C. heterodactylus* – cuticula light to medium brown (“copper brown”), *C. ermilovi* n. sp. – medium to dark brown (“chestnut brown”), *C. subiasi* n.sp. – light brown (“orange brown”). Although the brown coloration of *C. heterodactylus* and *C. subiasi* n.sp. is similar, there is a notable difference in direct comparison. Other congeners (data from literature): *C. quadricuspispidatus* – light brown, *C. nipponicus* – not mentioned, *C. lehmanni* – “brown”.

- **Body length** — *C. heterodactylus* – 250–290, *C. ermilovi* n. sp. – 300–330, *C. subiasi* n.sp. – 318–365. There is slight overlap in size between *C. ermilovi* n. sp. and *C. subiasi* n.sp., but these taxa are characterized by other morphological differences. There is a large gap between the size ranges of *C. heterodactylus* and *C. subiasi*. Other congeners: *C. quadricuspispidatus* – 320, *C. nipponicus* – 260, *C. lehmanni* – 265–273.

- **Size and shape of bothridial seta** — *C. heterodactylus* – 40–55 (~55–79% of prodorsal length), long and narrow, nearly straight, at base slightly incrassate (Mahunka 1983, fig. 32), *C. ermilovi* n. sp. – 45–60, proximally slightly thickened, distally with filiform apex (Fig. 10 C), *C. subiasi* n.sp. – 30–40 (~35–55% of prodorsal length), peapod-shaped, slightly curved and thickened over entire length, tip rounded or slightly pointed (Fig. 10 B). The bothridial seta of *C. heterodactylus* and *C. subiasi* n.sp. is similar, but much shorter in the latter (although this taxon has a larger body size). Other congeners: *C. quadricuspispidatus* – “very large, clavate”, *C. nipponicus* – long (48, ~82% of prodorsal length), head proximally small, distally swollen, pointed at tip, *C. lehmanni* – 45–49 (60–70% of prodorsal length), fusiform, narrowly elongate, roughened head having narrowed distal part.

- **Length of interlamellar seta** — *C. heterodactylus* – 60–70 (80–100% of prodorsal length), *C. ermilovi* n. sp. – 55–65 (80–100%), *C. subiasi* n.sp. – 70–80 (90–113%). The interlamellar seta is shorter or at most the same length as the prodorsum in *C. heterodactylus*

and *C. ermilovi* **n. sp.**, but longer in *C. subiasi* **n.sp.** (also in relation to the prodorsum). Other congeners: *C. quadricuspidatus* – “long”, *C. nipponicus* – “very short” (9, ~15% of prodorsal length), *C. lehmanni* – 69–73 (96–102% of prodorsal length).

- **Length of notogastral setae** — (except for the longer seta *c*, the lengths of other notogastral setae are usually quite similar in the same individuals). *C. heterodactylus* (individuals from Panama) – 4–7 (Mahunka 1983, fig. 32: 7–8, own measurement on this specimen from Tikal, Guatemala: 6–8), *C. ermilovi* **n. sp.** – 4–7, *C. subiasi* **n.sp.** – 8–12. Other congeners: *C. quadricuspidatus* – “rather small”, *C. nipponicus* – “short and fine” (7–9), *C. lehmanni* – 8.

2. Rank of the taxa – species or subspecies?

Compared to other known *Cultrobates* species, both newly described taxa share morphological characters with *C. heterodactylus*. The most obvious common features of the three taxa are the lamellar cusps with two similar teeth and the number of leg claws. However, once invariable differences are present between *C. heterodactylus*, *C. ermilovi* **n. sp.** and *C. subiasi* **n.sp.** (see remark #1), the species status was preferred for the following reasons:

- The term “subspecies”, the division of the population of a species on the ground of incomplete reproductive isolation, is frequently used for taxa with minor morphological differences which usually occur in different geographically defined populations (Hale *et al.* 2005).
- In both taxa males were found, so that sexual reproduction can be assumed. Subspecies might interbreed, which is not proven for the taxa from Galapagos.
- In cases where both taxa occur side by side (one sample from Santa Cruz contains both taxa with both sexes each), no hybrids were found.

3. Tubercle row on anterior coxisternal region

Among the known *Cultrobates* species this “necklace” is reported from *C. lehmanni* (~13 tubercles according to fig. 1 in Ermilov *et al.* 2021), *C. heterodactylus*, *C. ermilovi* **n. sp.** and *C. subiasi* **n. sp.** (about 30–35 tubercles each). Ventral structures on other known *Cultrobates* species (*C. quadricuspidatus* and *C. nipponicus*) are not mentioned in the respective descriptions, but tubercle rows are likely to be present in all species of the genus. *Cultrobates* sp. from Florida has a row of about 30 tubercles (Norton and Behan-Pelletier 2009, fig. 15.59E), specimens from New Brunswick, Canada (unpublished, probably *C. quadricuspidatus*, Behan-Pelletier, pers. comm.) show also tubercles. These tubercle rows were not observed in other taxa of Ceratokalummidae. Behan-Pelletier and Walter (2013) found a similar necklace structure in species of the genera *Tectoribates* and *Pseudotectoribates* (Tegoribatidae). In those taxa the band is concave, following the contour of epimere I (vs. rather convex in *Cultrobates* species) and longer, extending between epimeral setae *1c* (vs. shorter in *Cultrobates* species, hardly broader than the subcapitulum). The function of these tubercles is unknown (Behan-Pelletier and Walter 2013).

4. Custodium

Ermilov *et al.* (2021) mentioned in the generic traits of *Cultrobates* that the custodium is absent in the genus. The species studied here exhibit a custodium. According to Norton and Behan-Pelletier (2009) a custodium is present in Ceratozetoidea (the presumed assignment of Ceratokalummidae to Ceratozetoidea is pointed out in the introduction). As far as known, a custodium is also present in other species of Ceratokalummidae genera.

5. Claw formula

The number of claws on legs I–IV in the hitherto known *Cultrobates* species is different: *C. heterodactylus* Willmann, 1930, *C. ermilovi* **n. sp.** and *C. subiasi* **n. sp.** bear 1–3–3–3 claws, *C. nipponicus* Aoki, 1982 and *C. lehmanni* Ermilov, Subías, Shtanchaeva et Friedrich, 2021 2–2–2–2, *C. quadricuspidatus* (Ewing, 1909) 2–3–3–3 claws (cf. comment in Ermilov *et al.*

2021). Species of other genera of the family bear 1-1-1-1 (*Achipterina* spp., according to original descriptions), or 3-3-3-3 claws (*Arcozetes* spp., *Genavensia* spp. and *Guaranozetes* spp., according to original descriptions, resp. Balogh and Balogh 1992).

Key to known species of *Cultrobates*

Ermilov *et al.* (2021) presented a key of all Ceratokalummidae species known at that time. Inserting the two new species, an updating of this key for the genus *Cultrobates* is proposed:

11. Leg tarsus I with two claws 12
— Leg tarsus I with one claw, leg tarsi II–IV with three claws (1-3-3-3) 14
12. Leg tarsi II–IV with three claws (2-3-3-3)
..... *Cultrobates quadricuspidatus* (Ewing, 1909). Distribution: North America.
— All leg tarsi with two claws (2-2-2-2) 13
13. Interlamellar seta long, inner tooth on cusp much longer than outer, head of bothridial seta fusiform, narrowed distally; body length: 265–273
... *Cultrobates lehmanni* Ermilov, Subías, Shtanchaeva & Friedrich, 2021. Distribution: Peru.
— Interlamellar seta very short, both cusp teeth almost of same length, head of bothridial seta proximally small, distally swollen; body length: 260
..... *Cultrobates nipponicus* Aoki, 1982. Distribution: Japan.
14. Bothridial seta peapod-shaped, slightly curved and thickened over entire length, tip rounded or slightly pointed 15
— Bothridial seta proximally swollen, distally with filiform apex
..... *Cultrobates ermilovi* **n. sp.** Distribution: Galapagos Islands.
15. Bothridial seta long (>55% of prodorsal length), notogastral setae (except seta c) very short (4–7); body length: 250–290
..... *Cultrobates heterodactylus* Willmann, 1930. Distribution: Mexico and Central America.
— Bothridial seta of medium length (<55% of prodorsal length), notogastral setae (except seta c) short (8–12), body length: 318–365
..... *Cultrobates subiasi* **n. sp.** Distribution: Galapagos Islands.

Corrections to previously stated distribution data

- The distribution information of *Cultrobates heterodactylus* in Lesser Antilles and Colombia (Schatz 2006) was obtained from Balogh and Balogh (1988, 2002a) (“Guadeloupe, Guatemala, Columbia”). In fact, no published record of that species from Guadeloupe or other Antilles islands could be found, neither from Colombia or “Columbia” (regarding the geographical confusion, see Norton and Kethley 1989), therefore these distribution statements are not proven.

- The records of “*Cultrobates heterodactylus*” in Galapagos (Schatz 1998 and subsequent publications) belong to the above-described species *C. subiasi* **n. sp.**

- The records of “*Cultrobates* sp.” (= *C. ermilovi* **n. sp.**) on the Galapagos islands San Cristóbal and Pinzón (Schatz 1998, Ermilov *et al.* 2021) belong to other species. Thus, the occurrence of both *Cultrobates* species on San Cristóbal Island as mentioned in Schatz (1998) is not proven. On that island only *C. subiasi* **n. sp.** has been recorded up to now, and on Pinzón no *Cultrobates* species are recorded yet.

Table 1 Overview of the sampling conditions for the treated *Cultrobates* species.

Table 1a. *Cultrobates heterodactylus* - Panama

altitude (m a.s.l.)	sample	moisture (sample)	indiv. (adults)
<i>Soberania – tropical moist forest</i>			
50	epiphytic - rotting wood, litter, humus in bromeliad	moist	18
160	ground - leaf litter, wood	moist	1
50	ground - leaf litter, humus	moist	1
<i>Madden Dam area – deciduous dry forest</i>			
40	ground - leaf litter, humus	moist	1
<i>Costa Abajo – tropical wet forest</i>			
20	epiphytic - moss on tree	moist	1
30	epiphytic - bromelia, moss, wood	moist	26
30	ground - leaf litter	moist	26
<i>Isla Bastimentos – coastal rain forest</i>			
20	ground - leaf litter	wet	16
0	ground - leaf litter, seagrass at beach	moist	1
			91

Table 1b. *Cultrobates ermilovi* sp.n. – Galapagos Islands

altitude (m a.s.l.)	sample	moisture (sample)	indiv. (adults)
<i>Isla Fernandina – moist (Psychotria) zone</i>			
480	ground - leaf-, fern-, grass litter, humus	dry to moist	308
560	ground - fern litter	dry to moist	14
600	ground - fern-, leaf litter	moist	47
800	ground - fern-, grass litter	moist	3
1290	ground (fumarole) - fern litter	moist to wet	3
1290	ground (fumarole) - moss	moist to wet	1
<i>Isla Isabela – Volcán Wolf, moist (Psychotria) zone</i>			
800	ground - leaf litter, wood, humus	moist	50
1000	ground - leaf litter	moist	141
1200	ground - leaf litter, rotten wood	moist	65
<i>Isla Isabela – Volcán Darwin, moist (Psychotria) zone</i>			
1000	ground - grass litter	dry to moist	5
1200	ground - leaf litter, wood, lichens	dry to moist	1
<i>Isla Isabela – Volcán Alcedo, moist (Psychotria) zone</i>			
780	ground - leaf litter, wood, humus	dry to moist	1
1030	ground - fern litter, humus	moist	152
1060	ground - fern litter, humus	moist	6
1090	ground - leaf litter, wood, humus	dry to moist	20
1100	ground - fern litter, moss, wood	moist	9
1100	ground - leaf litter, wood, humus	dry to moist	23
<i>Isla Santa Cruz – moist (Scalesia) zone</i>			
590	ground - leaf litter, moss	moist to wet	7
			856

Table 1c. *Cultrobates subiasi* sp. n. – Galapagos Islands

altitude (m a.s.l.)	sample	moisture (sample)	indiv. (adults)
<i>Isla Isabela – Volcán Alcedo, moist (Psychotria) zone</i>			
1040	epiphytic - moss, lichens	moist	2
<i>Isla Isabela – Volcán Sierra Negra, moist (Psychotria) zone</i>			
910	epiphytic - lichens, moss on bark	moist	6
<i>Isla Pinta</i>			
530	ground - moss	moist	1
<i>Isla San Cristóbal</i>			
650	epiphytic - fern litter, moss	dry to moist	8
630	epiphytic - fern litter	moist	6
<i>Isla Santa Cruz – moist (Scalesia) zone</i>			
590	ground - leaf litter, moss	moist to wet	3
590	epiphytic - fern litter, moss	dry	3
590	epiphytic - moss	dry	1
590	epiphytic - moss on trunk	dry to moist	3
700	epiphytic - moss on bough	dry to moist	12
			45

Distribution and microhabitats

As indicated previously (Schatz 1998), the two new *Cultrobates* species from the Galapagos Islands differ in their occurrence in different microhabitats and partially also on different islands. This might be an indication of speciation by occupying different habitats. A comparative overview of the sample conditions for each species is compiled in Tables 1 and 2.

Cultrobates heterodactylus was found in Guatemala from surroundings of Guatemala City, in moss from trunks in about 1500 m a.s.l. (Willmann 1930) as well as in the lowland rain forest of Tikal (Departamento Petén), in 200 m a.s.l., without detailed habitat data (Mahunka 1983). The reports from Mexico (Revelo-Tobar *et al.* 2022) are from forest floors in three different localities (coniferous and oak forest floor in about 25 m a.s.l. near Tomatlan, State of Jalisco, pine and oak forests in approximately 1900 m a.s.l., San Juan Nuevo, State of Michoacán, tropical sub-deciduous forest floor in about 2800 m a.s.l. near San Salvador el Verde, State of Puebla). In Panama, the species occurs in lowland tropical forests. With few exceptions (Guatemala, Mexico), most finds of this species were made in lowland rainforests. It is noteworthy that *C. heterodactylus* has not been encountered in Belize and Costa Rica yet, despite numerous samplings in these countries (Schatz 1997, 2006), and likewise not at higher elevations or mountain chains of Costa Rica and Panama (Schatz 2007).

Findings in Panama (91 adult, Tables 1a, 2) are primarily from moist to wet conditions, from moss, fern and leaf litter, from samples containing dead wood, and from litter in epiphytic bromeliads. Almost the same number of individuals was found in epiphytic habitats and on forest floor. The reported single individual in leaf litter and seagrass in the littoral zone might have dropped from the surrounding trees. According to our current knowledge, *C. heterodactylus* prefers moist forested habitats in Central America, often in epiphytic habitats and in moss.

In contrast, the two species in Galapagos have been found exclusively in the moister higher elevations of the islands. *Cultrobates ermilovi* n. sp. is hitherto only known from the Galapagos Islands. It was found in considerable numbers (>800 adult individuals) on different volcanoes of the westernmost islands Fernandina and Isabela (volcanoes Wolf, Darwin, Alcedo), and on the island Santa Cruz, always on the floor in mainly vegetated and moister areas in higher

Table 2 Comparative overview of sample conditions for the *Cultrobates* species *C. heterodactylus* (samples from Panama), *C. ermilovi* n. sp. and *C. subiasi* n. sp. (samples from the Galapagos Islands).

sample	<i>C. heterodactylus</i>		<i>C. ermilovi</i> n. sp.		<i>C. subiasi</i> n. sp.	
indiv. total	91	%	856	%	45	%
ground	46	50.5	856	100	4	8.9
epiphytic	45	49.5	0	0	41	91.1
dry	0	0	0	0	4	8.9
dry to moist	0	0	372	43.5	23	51.1
moist	75	82.4	473	55.3	15	33.3
moist to wet	0	0	11	1.3	3	6.7
wet	16	17.6	0	0	0	0
fern	0	0	542	63.3	17	37.8
moss	27	29.7	17	2	37	82.2
leaf	46	50.5	663	77.5	3	6.7
grass	1	1.1	316	36.9	0	0
wood	45	49.5	160	18.7	0	0
lichens	0	0	1	0.1	8	17.8
bromeliad	44	48.4	0	0	0	0

vegetation belts (Table 1b, Fig. 11). This species was found primarily in samples containing leaf and fern litter, but also grass and dead wood, but rarely encountered in moss (Table 2).

Also, *C. subiasi* **n. sp.** is hitherto only known from the Galapagos Islands. A few individuals were found on the western island Isabela (volcanoes Alcedo and Sierra Negra), on Pinta, and in slightly higher individual numbers on the central and eastern islands San Cristóbal and Santa Cruz (Table 1c, Fig. 11). Almost all findings of this species are from epiphytic habitats (over 90% of all individuals), mainly from mosses and ferns or lichens. The few records from the forest floor were found in mossy samples under trees (Table 2). A notable finding of both species was made in the forest floor near los Gemelos, Santa Cruz Island. The individuals of *C. subiasi* **n.sp.** probably dropped from the surrounding epiphytic trees, where they were also detected.

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