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First Tropical American Species of the “Relict” Genus *Litoleptis*, and Relationships in Spaniinae (Diptera: Rhagionidae)

DAVID A. GRIMALDI¹

ABSTRACT

The genus *Litoleptis* has consisted of nine described species, seven of them Asian and only two in the New World: *L. alaskensis* Chillcott, known from two specimens from northwest Alaska, and *L. chilensis* Hennig, known from a male specimen from near Santiago, Chile. A third New World species is described here, *Litoleptis tico*, n. sp., based on a single female from Costa Rica. The species is unique for the genus in having a vestigial proboscis and lacking spermathecal accessory ducts and glands. Female terminalia are unknown for the other two New World species. A morphologically based, preliminary phylogeny of spaniines is provided, indicating *Litoleptis* is recently derived among spaniines and thus Rhagionidae; the Early Cretaceous *Litoleptis fossilis* is a stem group to the living species. A derived position of the genus, its apparently broad distribution, and an abundance in Japan where *Litoleptis* has been bred from liverworts (Imada and Kato, 2016a), all indicate that these flies are probably not at all relict, simply vastly undersampled because of a reliance on mass-collecting techniques.

INTRODUCTION

Rhagionidae is a family of some 500 species in 16 genera, more than half of them in the genus *Chrysopilus* Macquart, making it the second largest family of the Tabanomorpha after the Tabanidae, with some 4400 species (Kerr, 2010). The fossil records of these two families differ greatly: the oldest known tabanids are seven stem-group species from the Cretaceous

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FIG. 1. Global distribution records of the genus *Litoleptis*. Numbers correspond to records in table 1.

(Grimaldi, 2016); Rhagionidae are among the most diverse and abundant Mesozoic Brachycera (reviewed in Evenhuis, 1994), extending to the Early Jurassic. The geological antiquity of Rhagionidae *sensu lato* suggests a particularly archaic group, providing that the many fossils known merely from wings are accurately assigned. Antiquity may reflect the biogeography of Rhagionidae, which display more disjunction than, for example, Tabanidae, particularly southern austral (*Austroleptis* [now in Austroleptidae: Kerr, 2010], *Arthroteles*, *Atherimorpha*) and Laurasian (*Arthroceras*, *Rhagio*, and many Spaniinae) (Kerr, 2010) distributions. The subject of this paper is Spaniinae, a relatively small group of six genera with ca. 80 species, most in the genus *Symphoromyia* Frauenfeld (Kerr, 2010).

Litoleptis Chillcott consists of nine described extant species, seven of them Asian (six in Japan) and only two in the New World (fig. 1, table 1), *L. chilensis* Hennig from Chile, and *L. alaskensis* Chillcott from northwest Alaska, known from only one and two specimens respectively. Such disjunction and geological age has led some authors to regard the distribution of *Litoleptis* as relict, the result of extensive extinction (Arillo et al., 2009; Saigusa, 2006). The oldest spaniine is *Litoleptis fossilis* in San Just amber from the Escucha Formation of Teruel Province, Spain, ~105 mya (Arillo et al., 2009), discussed below.

The natural history of spaniines is a dramatic departure from that of the rest of the Tabanomorpha, a group whose larvae are typically predators and occasionally known or presumed to be saprophages. Three genera of spaniines are now known to be bryophagous, feeding on liverworts (Marchantiophyta) and/or mosses (Musci): *Ptiolina*, *Spania*, and *Litoleptis*. Life histories of the Holarctic genus *Omphalophora* and the Australian genus *Spaniopsis* are unknown. Scattered reports of bryophagy in a few species have been in the literature for over a century: *Spania nigra* mining the leaflike thalli of the liverwort *Pellia neesiana* (Mik, 1896; Nartshuk,

TABLE 1. Global Records of *Litoleptis* species (for map, see fig. 1).

Species	Locality	Reference
1. <i>alaskensis</i>	Cape Thompson,* Alaska	Chillcott, 1963; Kerr, 2010
2. <i>tico</i>	Zurquí de Moravia, Costa Rica	herein
3. <i>chilensis</i>	near Santiago, Chile	Hennig, 1972
4. <i>asterelaphile</i>	Honshu, Japan	Imada and Kato, 2016a
<i>himukaensis</i>	Honshu, Japan	Imada and Kato, 2016a
<i>izuensis</i>	Honshu, Japan	Imada and Kato, 2016a
<i>japonica</i>	widespread in Japan	Imada and Kato, 2016a
<i>kiiensis</i>	Honshu, Japan	Imada and Kato, 2016a
<i>niyodoensis</i>	Honshu, Japan	Imada and Kato, 2016a
5. <i>orientalis</i>	Luzon, Philippines	Frey, 1954
6. “sp.”	Xiaguan, Yunnan, China	Yang et al., 1997
7. “n. sp.”	Nepal	Nagatomi, 1982
8. <i>fossilis</i>	San Just, Spain [amber]	Arillo et al., 2009

* Near Point Hope, Alaska, according to Kerr (2010).

1995), and the green larvae of *Ptiolina* feeding on mosses (Brauer, 1883; Brindle, 1959) as well as the liverwort *Marchantia polymorpha* (Nartshuk, 1995). The studies by Imada and Kato (2016a, 2016b) have transformed our understanding of spaniines.

In Japan, a species of *Spania* and six species of *Litoleptis* feed as larvae on liverworts, and a species of *Ptiolina* feeds on mosses (Imada and Kato, 2016a, 2016b). Each of the Japanese *Litoleptis* species feeds on only one of three liverwort genera: *Conocephalum* (Conocephalaceae) (*Litoleptis japonica*); *Reboulia* (Aytoniaceae) (*L. kiiensis*, *L. niyodoensis*, *L. himukaensis*, *L. izuensis*); and *Asterella* (Aytoniaceae) (*L. asterelaphile*). A species of *Spania* mines thalli of the liverwort *Pellia* (Pelliaceae), and a species of *Ptiolina* bores the axis of mosses (Imada and Kato, 2016a, 2016b). Larval lifespan is approximately 11 months, with adults emerging in early spring (generally April). As expected, larval morphology of the bryophagous spaniines differs significantly from the typical, predatory morphology (Imada and Kato, 2016b). *Spania* and *Litoleptis* (but not *Ptiolina*) lack creeping welts; the mandibles are reduced in size (not the typical bladellike hooks), with the preapical orifice shifted from the adoral surface to a dorsal position (the central canal is retained), and the mandibular brush is lost, including in *Ptiolina*. The labrum of the larva has biserial rows of coarse, retrorse teeth (Imada and Kato, 2016b).

I am providing the description and a discussion of a new species from Costa Rica because of its distinctive features, the biogeographic significance, and the uncertainty as to whether this species will be found again.

METHODS AND MATERIALS

The unique specimen was found in Malaise trap samples from Zurquí de Moravia, near San José, Costa Rica (see locality data under holotype, and commentary of the locality in Dis-

cussion). The traps were set by Paul Hanson (University of Costa Rica) in the early 1990s at the edge of a very dense cloud forest surrounded by pasture, the traps positioned on a slope close to and at the same level as the forest canopy. The specimen was critical-point dried en masse with other Diptera selected from the samples. The right wing was removed and temporarily slide mounted in glycerin for photomicrography. To observe internal reproductive organs the apex of the abdomen was removed and macerated in hot lactic acid, rinsed in distilled water, briefly soaked in 70% ethanol, then liquid glycerin, and temporarily slide mounted in glycerin-jelly for study and photomicrography at 200–400 \times . Photomicrography used a Nikon SMZ1500 with 16 MP camera and NIS Elements software, and a Nikon Eclipse compound microscope. Details of the head and mouthparts were studied using a Zeiss Evo60 Variable Pressure scanning electron microscope, without any gold or carbon coating of the specimen, at 10kV voltage between 500 \times and 2500 \times magnifications.

SYSTEMATICS

Litoleptis Chillcott

Litoleptis Chillcott, 1963: 1186. Type species: *L. alaskensis* Chillcott; Kerr, 2010 (redialagnosis of genus); Imada and Kato, 2016a, 2016b (revision, life histories, larvae).

EMENDED DIAGNOSIS: Like closely related spaniine genera, antenna with single flagellomere (usually tapered or abruptly narrow apically) (fig. 2C), laterotergite bare of fine setulae (fig. 2B); bases of cerci widely separated in female (figs. 5, 6), connected to epandrium in male; adult mandibles lost (except *Spaniopsis*); thickened portion of vein C ending at/near apex of R₅ or M₁; spermathecae lightly to weakly sclerotized (figs. 5, 6). Larvae graze/mine bryophytes, mandibular brush absent, creeping welts absent. *Litoleptis* is unique among spaniines by loss of all tibial spurs, proboscis reduced, pseudotracheae highly reduced, wing with membrane having very dense microtrichia (fig. 4B) and costal margin with long setulae (fig. 4A); vein M₃ absent, crossvein dm-cu lost (no discal cell), base of M spectral in living species; apex of vein CuA abruptly incomplete in most species (fig. 4).

Litoleptis tico, new species

Figures 2–6

DIAGNOSIS: Small, grayish-brown fly with thorax small, wings large (slightly longer than body) (fig. 2A), venation as in other *Litoleptis*; tibial spurs absent, empodium pulvilliform; abdomen slender (figs. 2A; 5A, B), cercus 2-segmented (figs. 5, 6). Best distinguished from other members of the genus by reduced proboscis, the labellum and theca much smaller than palps (figs. 2C, 3A); maxillary palp with one segment, base connected directly to head capsule (fig. 3A); wing with branches of M₁-M₂ fork curved (vs. virtually straight), crossvein cua-m significantly shorter than r-m (vs. slightly longer) (fig. 4A); spermatheca completely lacking accessory glands (ducts and sacs) (figs. 5C, 6).

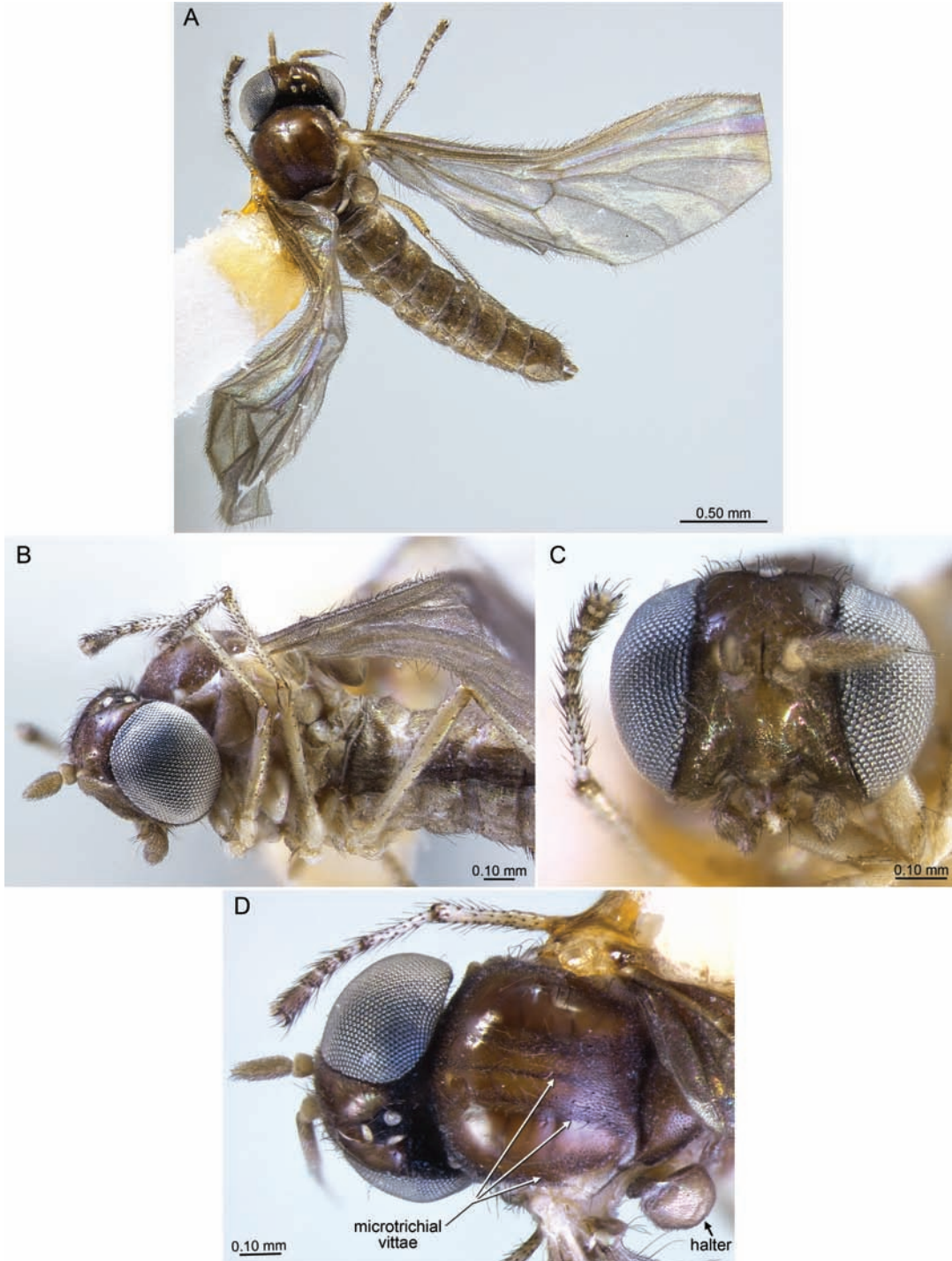


FIG. 2. *Litoleptis tico*, new species, holotype. A. Dorsal habitus of intact specimen, prior to dissection of terminalia and removal of wing. B. Anterior half of body, lateral view. C. Frontal view of head. D. Dorsal view of head and thorax.

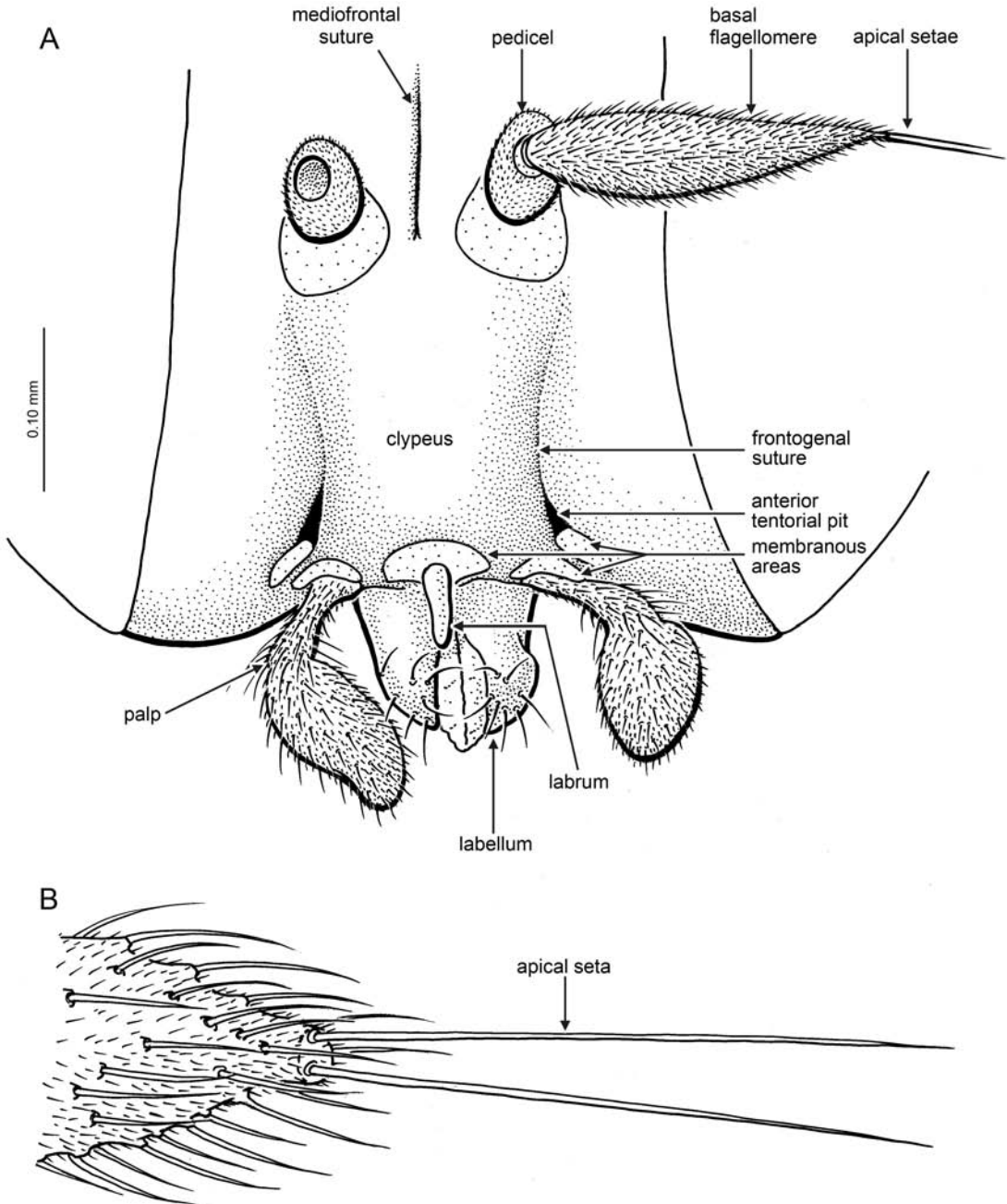


FIG. 3. *Litoleptis tico*, holotype. **A.** Drawing of facial region. **B.** Detail of antennal tip (based on scanning electron micrographs of uncoated holotype).

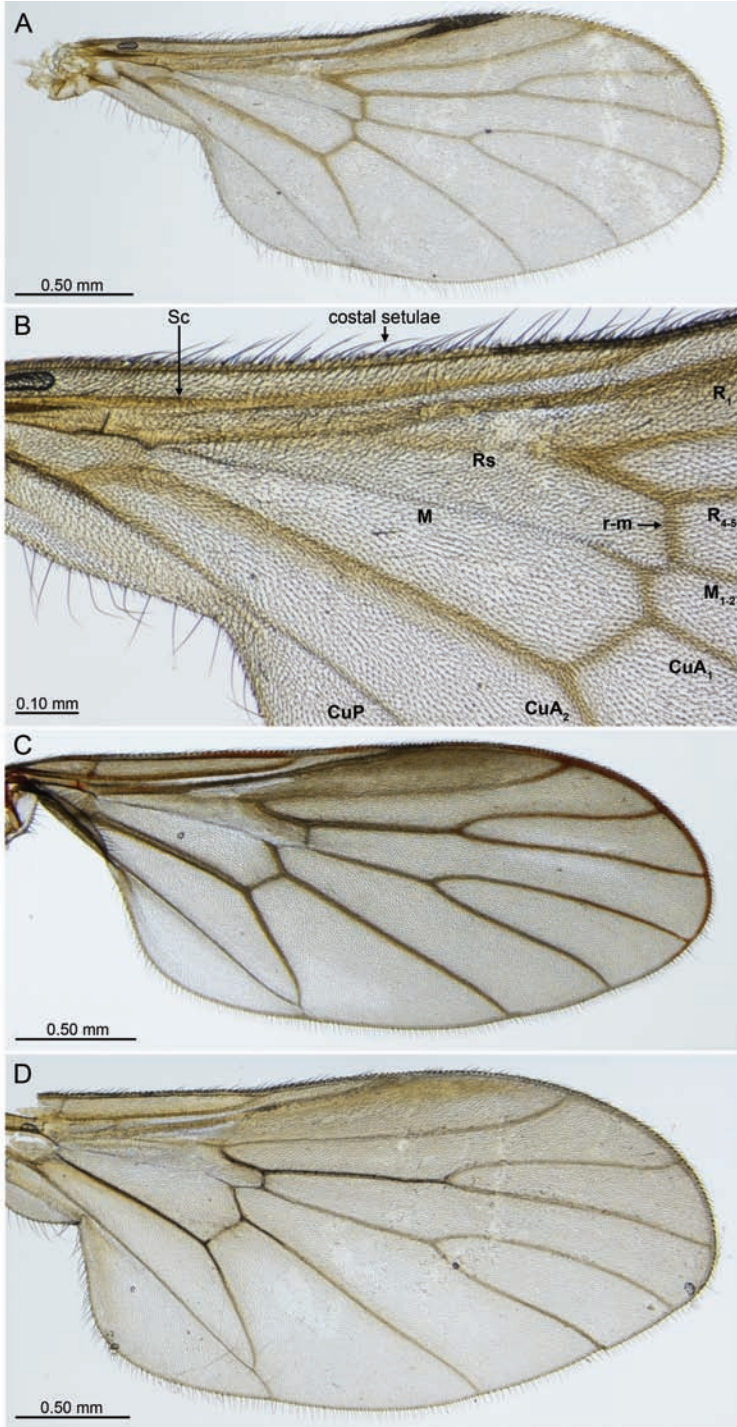


FIG. 4. Wing of *Litoleptis* species. **A, B.** *L. tico*, holotype. **A.** Entire wing. The dark pseudostigma is only preservational, due to air trapped in this swollen area. **B.** Base of wing. **C.** *L. kiensis* Imada and Kato. **D.** *L. japonica* Imada and Kato.

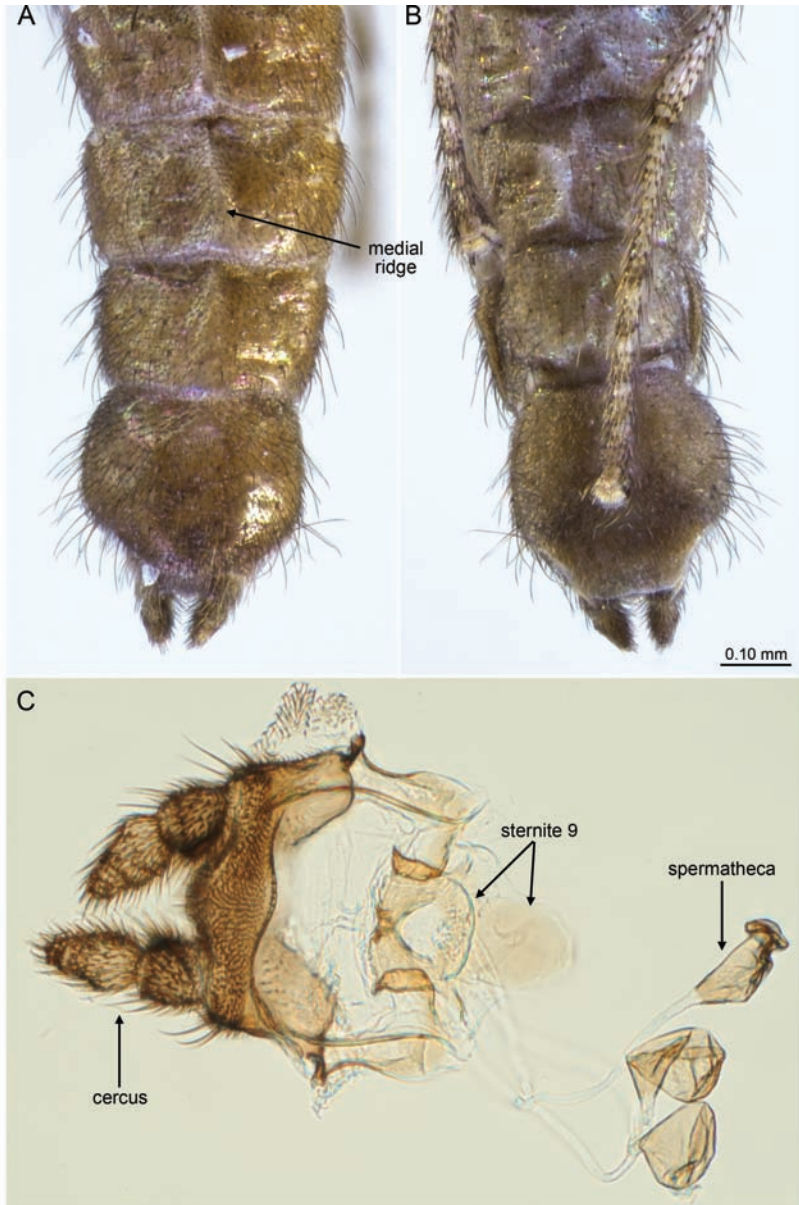


FIG. 5. Terminalia of *L. tico*, holotype. **A, B:** Abdominal apex of intact specimen, prior to dissection. **A.** Dorsal. **B.** Ventral. **C.** Macerated dissection. Spermathecae are collapsed.

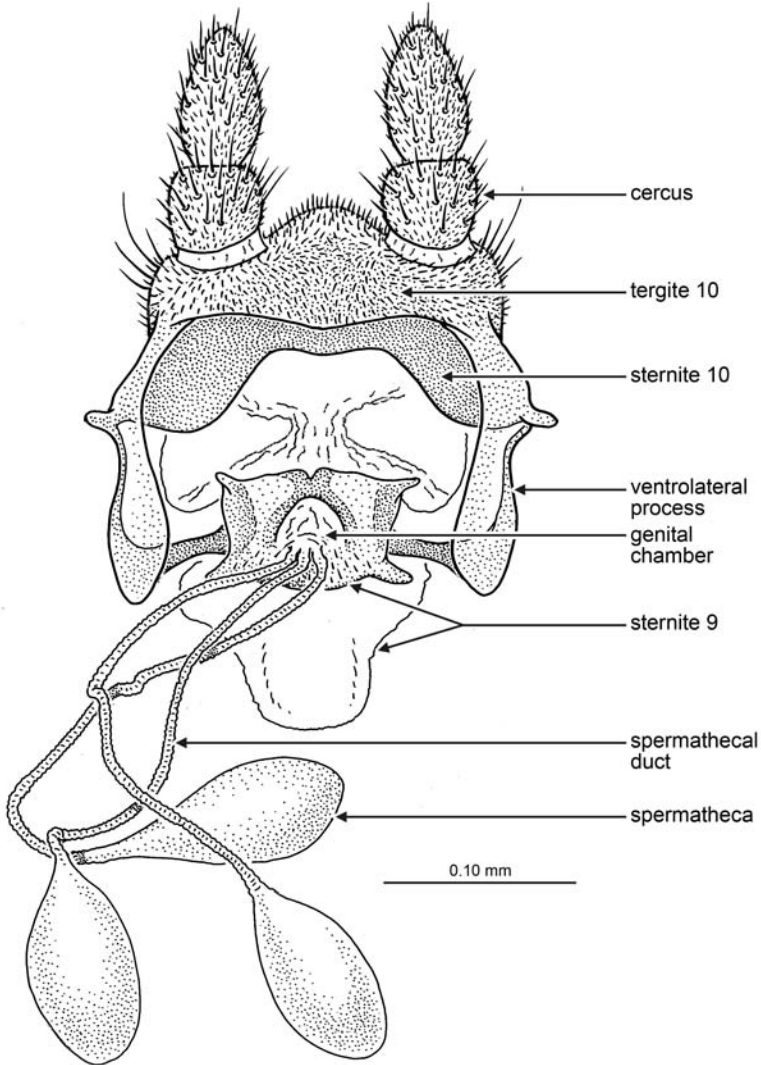


FIG. 6. Drawing of *L. tico* terminalia (cf. fig. 5C). Spermathecae have been reconstructed to their original shape.

DESCRIPTION: Body length 2.7 mm (not including antennae); abdomen length 1.75 mm; thorax length 0.70 mm; head width 0.61 mm; frontal width (between eye margins, at level of antennae) 0.29 mm; wing length 2.8 mm; wing width 1.2 mm. HEAD: Broader than tall; eyes dark, silvery gray, large, occupying entire lateral portion of head (no cheek exposed laterally); no differentiation of facets (only female known), eye completely bare; inner margins on frons nearly parallel, margins bordering face slightly diverging ventrad, no emargination. Frons dark brown, slightly raised above level of eyes; shiny, with scattered, fine, long setulae (lengths ca. $2.5\times$ diameter of facet). Lower part of frons and area between antennal bases with faint, vertical median furrow. Ocelli light, large, of equal size; lying on shallow, velvety-black tubercle; ocellar triangle/tubercle slightly recessed into vertex of head. Occiput concave; dorsal portion with dark, fine, stiff setulae pointing upward. Antennal bases widely separated, by distance slightly greater than diameter of scape; scape ringlike, hidden frontally by pedicel, encircled by larger, exposed membranous area; pedicel short, slightly conical, without apical ring of setulae; basal flagellar article long, tapered, heavily setulose; apex lacking style, with pair of stiff, needlelike setae at apex, length ca. $0.4\times$ that of basal flagellar article. Face broad, slightly broader than frons, dark brown; clypeus slightly swollen, paraclypeal sulci faintly impressed. Palp one-segmented; base slender, ca. $0.3\times$ width of apex, which is swollen; base with longer setulae; palp connected directly to head capsule (membranous articulation visible frontally). Proboscis very small, length approximately equal to that of basal palpomere, labellum very small, appears nonfunctional, with 5–6 fine setae per lobe; labrum tiny, whitish, membranous. Anterior tentorial pit deep, well defined; located just above base of palp.

THORAX: Short, broad, scutum slightly wider than long. Scutum shiny, dark brown, with two large glabrous/shiny patches laterally, two smaller paramedian glabrous patches; other portions of scutum with dense, dark microtrichia forming trident shape; scutellum entirely matte. Stiff, fine, dark setae on paramedian stripes, and laterally on notopleural and supraalar areas. Transverse suture barely developed. Area between notopleura and pleura, and surrounding wing base, whitish. Pleura entirely glabrous, devoid of setae, setulae, microtrichia; sclerite proportions and sizes shown in figure 2B. Mesothoracic spiracle a large vertical slit. Legs slender but relatively short; coxal lengths $cx1 > cx2 > cx3$, bases of $cx1$ by posterior portion of head; coxae with 5–6 setulae on each. Legs with fine, scattered dark setulae; lengths slightly greater than podite width; apices of all podomeres except femora are dark. Femoral lengths $f3 > f2 > f1$; profemur shorter than protibia; meso- and metafemur about same length as tibiae; hind femur slightly swollen apically. All tibiae lack apical spurs. Tarsus shorter than respective tibiae; basitarsomere slightly shorter than distal tarsomeres combined (2–5), distal tarsomere widest. Claws, pulvilli well developed; empodium pulvilliform, slightly larger than pulvilli.

WINGS: Large, slightly longer than body, uniformly dusky, with dense microtrichia (fig. 4B). Venation very similar to the other two New World species, with differences as noted: like *alaskensis* with R_3 slightly curved costad (vs. straight, as in *chilensis*); like *chilensis* with fork of R_{4+5} only slightly divergent, lengths of branches nearly equal (R_4/R_5 0.82 in *tico*, 0.84 in *chilensis*, 0.75 in *alaskensis*). Unique to *tico* are branches of M_1 - M_2 fork curved (vs. virtually straight); crossvein *cua-m* very short (ca. $0.5\times$ length of *r-m* crossvein, vs. slightly longer than *r-m* in

chilensis, *alaskensis*, and species from Japan; fig. 4C, D). Halter large, length approximately equal to width of scutum, length of knob and stalk approximately equal; knob very swollen, with dense covering of microtrichia (fig. 2D).

ABDOMEN: Slender, with very broad attachment to thorax (essentially no constriction), only slightly tapered in width apicad. Tergites lightly sclerotized, light brown, with subtle ridge running down middle of abdomen (fig. 5A); tergite 1 approximately 0.5× length of other tergites (2–7). Tergites with microtrichia plus scattered, very fine setulae. Pleural membrane well exposed, spiracles in membrane at level of segment divisions. Sternites approximately same size as tergites (fig. 5A, B), with similar vestiture but lighter and less sclerotized; lateral margins of sternite 8 with apical third tapered, posterior margin slightly concave. Cercus short, two-segmented, apical cercomere slightly conical (figs. 5C, 6).

ETYMOLOGY: As a noun in apposition, taken directly from “ticos,” a familiar and affectionate name that Costa Ricans give to each other, in reference to their tendency to add the diminutive “tico” to the end of words.

TYPE: Holotype, female: COSTA RICA: San José, Zurquí de Moravia, 1600 m., VII/92, P. Hanson, Malaise trap. Latitude 10.047 N, longitude 84.008 W. In AMNH. The specimen is in excellent condition, originally critical-point dried from alcohol; originally fully intact (except for loss of setae on one antennal tip). The right wing and terminalia were removed for temporary slide mounting (using glycerin-jelly) and photography; they are stored in a genitalia vial in glycerin on the pin with the type.

RELATIONSHIPS

Below is a list of characters used in reconstructing spaniine relationships. The original sources of most characters are cited accordingly, including Chillcott (1963), Hennig (1972), Kerr (2010), and Imada and Kato (2016a, 2016b), along with the character number used in that study (e.g., Kerr, 2010: 109) and a number in brackets after that signifies the character state. Figure 7 depicts relationships; the matrix table of character-state distributions is in the appendix.

Spaniinae (including *Symphoromyia*):

1. Genital chamber in female well defined by median sclerotization of sternite 9 (Kerr, 2010: 109) (vs. sternite 9 without median sclerotization).
2. Tergite 9 in female with pair of forward-projecting apodemes (“ventrolateral processes”) flanking sternite 9 (Kerr, 2010: 64) (vs. processes absent).
3. Larval thoracic segment 1 with anterior edge having scalelike lobes (Imada and Kato, 2016b) (vs. without lobes).

Symphoromyia synapomorphies:

4. Basal flagellomere reniform (vs. oblong).
5. Scape enlarged (Kerr, 2010: 7[3]).

Omphalophora + rest of spaniines except *Symphoromyia*:

6. Flagellum with one article, usually gradually tapered or abruptly narrowed apicad, no apical style (Hennig, 1972; Kerr, 2010: 10) (figs. 2C, 3).
7. Laterotergite bare of fine setulae (Kerr, 2010: 28).
8. Bases of male cerci adjacent (Kerr, 2010: 64).
9. Base of male cercus connected directly to epandrium (Kerr, 2010: 59).
10. Bases of female cerci separated by a distance \geq width of cercus (Kerr, 2010: 90) (figs. 5C, 6).
11. Adult mandibles lost (except in *Spaniopsis*) (Kerr, 2010: 16; Nagatomi and Soroida, 1985).

Ptiolina + *Spaniopsis* + *Spania* + *Litoleptis*:

12. Larvae graze on/mine bryophytes (Imada and Kato, 2016b) (may also include *Omphalophora*, but its larva and that of *Spaniopsis* are unknown).
13. Larval mandibular brush lost (Imada and Kato, 2016b) (larva of *Spaniopsis* unknown).
14. Basal cercomere of female radially symmetrical, narrow, no lobes (figs. 5C, 6) (vs. asymmetrical, with one side enlarged into a small lobe).
15. Vein C circumambient but thickened portion ending at apex of vein R₅ or near (fig. 4A, C, D) (vs. gradually tapered).
16. *Ptiolina* synapomorphy: tergite 9 of female narrow and rectangular (Kerr, 2010: 85) (vs. broad, semicircular).

Spaniopsis + *Spania* + *Litoleptis*:

17. Hind tibial spur lost (vs. present).
18. Larva with creeping welts lost (Imada and Kato, 2016b) (larva of *Spaniopsis* unknown) (vs. present).
19. Spermathecae moderately to weakly sclerotized (figs. 5C, 6) (vs. heavily sclerotized, dark).
20. Maxillary palp with a single palpomere. The palp in *Litoleptis* is variously reported to be one- or two-segmented: two in *alaskensis* (Chillcott, 1963); one in *chilensis* (Hennig, 1972) and other members of the genus (Kerr, 2010; Imada and Kato, 2016a). Courtesy of Yume Imada, I was able to examine specimens of *L. japonica* and *L. kiiensis*, for which I dissected and slide-mounted the mouthparts, confirming one-segmented palps. Palp segmentation is obscure on intact specimens, since the palp base is slender and has longer setulae, giving the appearance of two segments, which is why I suspect that Chillcott's (1963) observation is probably incorrect. The closely related genera *Spania* and *Spaniopsis* are reported to have one-segmented palps, and *Ptiolina* to have one- and two-segmented palps (Kerr, 2010).
21. *Spaniopsis* synapomorphies: cornu fused apically to pharyngeal pump (Kerr, 2010); adult mandibles present (Kerr, 2010).

Spania + *Litoleptis*:

22. Wing membrane with dense microtrichia (fig. 4B); vein C (or at least the thick, leading edge) with long, fine setulae, length of setulae greater than thickness of C (fig. 4B).
23. *Spania* synapomorphy: Sternite 8 of female lacking medial emargination (Kerr, 2010: 83).

Litoleptis, including *fossilis*:

24. Tibial spurs lost (Chillcott, 1963), though hind tibial spur apparently present and minute in *L. fossilis* (Arillo et al. 2009). This needs to be carefully checked in the fossil since hind tibial spurs do not occur in any living *Litoleptis* nor in the closely related genera *Spania* and *Spaniopsis*, and small spurs (i.e., articulating in the intersegmental membrane) are sometimes difficult to discern even in modern specimens.

25. Vein M_3 lost (Chillcott, 1963; Kerr, 2010: 50[3]) (fig. 4).

26. Discal cell lacking (crossvein dm-cu lost) (Chillcott, 1963) (fig. 4).

Litoleptis, excluding *fossilis*:

27. Base of vein M highly reduced, spectral and foldlike (fig. 4B) (vs. tubular).

28. Apex of CuA_2 vein incomplete, usually abruptly (fig. 4A), sometimes just weakened (i.e., *L. kiiensis*, *izuensis*). The apex of CuA_2 seems complete in *L. japonica*, but there is actually a small gap between it and CuP , best seen in an oblique view.

29. Pseudotracheae: Great reduction or loss. The pseudotracheae are described as lost in the two *Litoleptis* species that Kerr (2010) examined; the condition in *orientalis* and *fossilis* is unknown. The vestigial labellum in *L. tico* would have required dissection of the proboscis in the unique specimen (the mesal surfaces of the labellar lobes are not exposed); the pseudotracheae are presumably absent in it given the vestigial proboscis. Imada and Kato (2016a) mentioned the loss of pseudotracheae in the generic diagnosis, but my dissection of a *L. japonica* female found five very fine tracheae on the inner surface of each labellar lobe, and I suspect that this may be the situation in most other *Litoleptis*. Determining whether these are functional pseudotracheae will probably require SEM, but these structures should probably be best described as highly reduced, which seems to be a reliable synapomorphy of *Litoleptis*. Arillo et al. (2009) did not mention the presence/absence of pseudotracheae in *L. fossilis* (they probably are too obscure), but I am assuming that they are developed and functional, given the long proboscis.

30. Proboscis short, length \leq length of palp (e.g., fig. 3A). Dissection of a *L. japonica* specimen found the cibarium to be poorly developed, evidence in addition to the vestigial pseudotracheae that the proboscis is probably nonfunctional. The proboscis in *L. tico* is more reduced than in the other species, including the labrum. The labrum of *L. tico* is minute and barely sclerotized; in *L. japonica* it is slender and shaped like a chemistry spatula.

Arillo et al. (2009) indicated that the holotype of *L. fossilis* was a female, but based on the large, “nearly holoptic” eyes, this specimen is almost certainly a male. Those authors may have been misled by the small, obscure male genitalia of the specimen, typical of *Litoleptis* in general.

Litoleptis japonica + *tico* + *orientalis* + *chilensis*:

31. One or two long setae at apex of gradually tapering flagellomere (figs. 2C, 3B). For *L. orientalis* this condition is based on the original description by Frey (1954). Hennig (1972) illustrated the antennal apex in *chilensis* as having two minute, peglike setae, but in the photograph by Kerr (2010: fig. 12) these are clearly setiform, though distinctly shorter than the long setae in *tico*. These setae are easily dislodged, but their absence in all the Japanese species except

japonica (which has a single terminal seta) is no doubt real since Imada and Kato (2016a) studied pristine, reared specimens.

All Japanese species of *Litoleptis* except *japonica*:

32. Lateral ejaculatory process present, in all Japanese species except *L. japonica* (it is also absent in *L. chilensis* and *L. alaskensis*) (Imada and Kato, 2016a).

33. Basal (and only) flagellomere not tapered to point, but oblong, which is found in many species from Japan.

There are several characters that probably will define species groups in *Litoleptis*, but were not included in the phylogeny, because either character states are uncertain for some terminals or the sampling of sexes thus far is incomplete (i.e., no females in *L. alaskensis*, *L. chilensis*, and *L. izuensis*; no male in *L. tico*):

(1) Spermathecal accessory gland sacs highly reduced to lost. Reduced accessory gland sacs occur in all of the Japanese species, although these were shown only in the figure for *L. niyodoensis* (Imada and Kato, 2016a) (gland sacs readily disintegrated in preparations of the Japanese species, Y. Imada, personal commun., to D.A.G., April 2018). In *L. tico* there is absolutely no trace of even a vestigial accessory gland duct.

(2) Duct of spermathecal accessory gland a short, sclerotized collar. This occurs in all the Japanese species (Imada and Kato, 2016a).

(3) Bases of spermathecal ducts do not connect to a common duct or trunk, but rather emerge separately from the genital chamber (fig. 6). This condition occurs in three Japanese species (*L. kiiensis*, *L. niyodoensis*, and *L. asterallaphile*), as well as in *L. tico*, n. sp. The common duct/trunk is very short in *L. japonica*.

(4) Ejaculatory apodeme present, as reported for all of the Japanese species (Imada and Kato, 2016a), although existence of the structure is surely plesiomorphic.

(5) Apex of aedeagus with “numerous tiny pustulae,” as reported for all the Japanese species (Imada and Kato, 2016a).

DISCUSSION

Kerr (2010) did not include *Litoleptis* in his phylogenetic analysis because at that time females were unavailable, and his study found that female terminalia have a rich array of systematic characters for Rhagionidae. My cladogram (fig. 7) differs from Imada and Kato's (2016b) 28S rRNA phylogeny, with *Spania* + *Litoleptis* as sister groups, rather than *Spaniopsis* + *Litoleptis*. The most important point, though, is that in both schemes *Litoleptis* is a highly derived genus of Spaniinae, and according to Kerr's (2010) analysis, Spaniinae is a highly derived group within Rhagionidae (Stuckenberg [2001] notwithstanding). Also, the Cretaceous fossil *L. fossilis* is clearly a stem group to the living species, lacking characters 26–28 (above) that define living species in the crown group. Crown-group *Litoleptis* may be Late to post-Cretaceous in age.

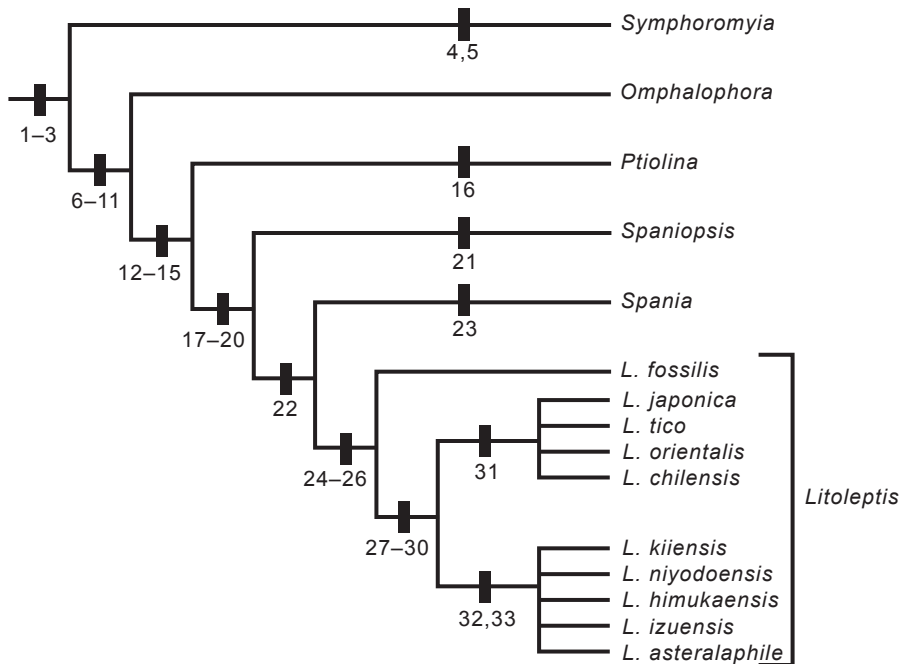


FIG. 7. Cladogram of genera of spaniine Rhagionidae and species of *Litoleptis*. See text for description of numbered characters.

Litoleptis is very rarely captured as adults using general collecting techniques such as Malaise traps and sweep netting. Prior to the work of Imada and Kato (2016a, 2016b) on the Japanese species, the three described species as well as several undescribed ones have been known entirely on the basis of one or two specimens for each. Incredibly, *Litoleptis tico* escaped detection by over 20 entomologists, myself included, who intensively surveyed the patch of cloud forest that is its type locality in Zurquí de Moravia, Costa Rica (Borkent et al., 2018; Brown et al., 2018). That survey, called ZADBI (Zurqui All-Diptera Biodiversity Inventory), recovered hundreds of thousands of fly specimens collected over 13 months using various trapping methods (Malaise, emergence, yellow-pan, bait, and light traps, as well as sweeping by hand), finding 4348 Diptera species in 72 families (Borkent et al., 2018; Brown et al., 2018). The only rhagionids from the ZADBI project were *Chrysopilus*. The unique specimen of *Litoleptis tico* was captured in a Malaise trap set 20 years earlier, a striking example of the difficulty in sampling some species.

The chance discovery of *Litoleptis* in Costa Rica—well distant between the two other New World records in Alaska and Chile—and the work of Imada and Kato (2016a, 2016b) in Japan indicate that the genus probably has a very widespread distribution and can be locally abundant. These flies are simply far undersampled. As a genus, *Litoleptis* in Japan is not particularly rare or regionally restricted, based on over 220 specimens collected from 24 localities throughout the country (Imada and Kato, 2016a, 2016b), though four of the six Japanese species are known from 10 or fewer individuals from a single locality. These authors report that *Litoleptis* adults live for

“only a few days” and were not observed feeding (although oviposition was observed), and that adults are “seldom found in the field.”

This situation in *Litoleptis* is reminiscent of flies in the unrelated family Axymyiidae, which fits all criteria for relict status. There are seven species in three living genera of axymyiids sporadically distributed throughout the Holarctic Region, Taiwan, and southern China (Sinclair, 2013); the family may be the sister group to the very diverse clade Bibionomorpha (Wiegmann et al, 2011); their fossil record extends to nearly 175 million years (Zhang, 2010; Guifeng et al., 2013). Adults are very rarely captured (e.g., Sinclair, 2013), but in an intensive survey of the larvae of the North American species, *Axymyia furcata* (which bore into partially submerged, decaying logs in streams) was found to be more widespread and far more abundant than previously thought (Wihlm and Courtney, 2011). There can be up to 200 larvae of *A. furcata* in a log (Wihlm and Courtney, 2011). The nonfeeding adults are rarely found because they have brief lives, the result of a vestigial labellum, as in *Litoleptis tico*.

It seems that the apparent rarity of *Litoleptis* is due not merely to their small size and obscurity, but like *Axymyia* in their fidelity to a very specific habitat and especially because of an ephemeral adult life and flight period. I predict that *Litoleptis* is actually widespread in Holarctic boreal forests and in wet, cool montane forests rich in bryophytes, from western North America to Central America and Andean South America. Further fieldwork is essential.

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APPENDIX

CHARACTER MATRIX

See text for character number and descriptions.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34			
<i>Symphoromyia</i> spp.	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Omphalophora</i> spp.	1	1	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Ptiolina</i> spp.	1	1	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Spaniopsis</i> spp.	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Spania</i> spp.	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Litoleptis fossilis</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Litoleptis japonica</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	
<i>Litoleptis tico</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	
<i>Litoleptis orientalis</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Litoleptis chilensis</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Litoleptis kiinensis</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Litoleptis niyodoensis</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Litoleptis himukaensis</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Litoleptis izuensis</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
<i>Litoleptis asteralaphile</i>	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0

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