A revision of the genus *Telomerina* Roháček (Diptera, Sphaeroceridae)

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ABSTRACT. The genus *Telomerina* Roháček (Diptera: Sphaeroceridae) is revised to include twelve species: five Palaearctic, five Nearctic, one Holarctic and one cosmopolitan. The five Neartic species, *chillcotti*, *orpha*, *submerda*, *cana* and *pengellyi* are described as new. The male of *T.eburnea* Roháček is described; *T.gracilipennis* (Spuler) is synonomized with *T.flavipes* (Meigen) and *T.antonini* Roháček is synonomized with *T.levifrons* (Spuler). The larva and pupa of *T.flavipes* are described. A phylogenetic hypothesis for the genus is presented along with a discussion of its zoogeography.

Introduction

The genus *Telomerina* was erected by Roháček (1983) to contain seven Palaearctic species including *T.levifrons* (Spuler) (as *T.antonini* sp.n., see below) and *T.flavipes* (Meigen) which are also found in the Nearctic. *Telomerina* is equivalent to the *Limosina minutissima* group of Richards (1930).

Species of Telomerina are easily recognized by their small eyes, the very long male surstylus and paramere, and the absence of a male subanal plate and sternite 10 (intraperiandrial sclerite). Diagnostic features of the female include a short abdomen, tergite 8 narrowed dorsally and expanded laterally, sternite 6 narrow and weakly sclerotized, hypoproct complex, and each spermatheca usually with a long terminal evagination. The wing venation, with a long discal cell and the costa produced beyond R_{4+5} , is also diagnostic. Telomerina is clearly a monophyletic taxon, distinct from the rest of the Limosininae. The most clearly related genus is probably Opalimosina Roháček, 1983. The

Correspondence: Dr S. A. Marshall, Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1. one species of *Opalimosina* which has small eyes, and thus resembles *Telomerina*, is *Opalimosina mirabilis* (Collin, 1902). *O.mirabilis*, however, is easily recognized by its huge, curved hind tibial spur and differs markedly from *Telomerina* species in characters of the male and female terminalia.

The purpose of the present paper is to revise the Nearctic and east Palaearctic species, to supplement Roháček's (1983) discussion of the west Palaearctic species using material not available at that time (such as the male of *T.eburnea* and the larva of *T.flavipes*), to provide an illustrated key to the Holarctic species and to discuss the relationships of the entire genus *Telomerina*.

Collection abbreviations. MCZ: Museum of Comparative Zoology, Cambridge, Mass.; CNC: Canadian National Collection, Biosystematics Research Institute, Ottawa, Canada; USNM: United States National Museum, Washington, D.C.; TMB: Természettudományi Múzeum Allatara, Budapest, Hungary; SMO: Slezske Muzeum, Opava, Czechoslovakia; JRO: J. Roháček collection, Opava, Czechoslovakia; GUELPH: University of Guelph, Guelph, Ontario, Canada; FSC: Florida State Collection of Arthropods, Gainesville, Florida; FLD: Field Museum, Chicago.

Morphology and terminology

The authors of this paper have previously used different terminology when describing male and female genitalia in this family. Marshall (i.e. 1982a, b) used the terminology established by McAlpine (1981) in the Manual of Nearctic Diptera, which has become a standard reference for North American dipterists. Roháček (1982) described male terminalia using terminology based on Griffiths' (1972) periandrial theory. Although the periandrial theory seems to be well supported by Chvala's (1983) recent study of the superfamily Empidoidea, a strong argument can still be made for describing Muscomorpha using the more familiar terms found in the Manual of Nearctic Diptera. For this reason, the present paper uses the term 'surstylus' instead of 'telomere' (Roháček, 1982) or 'gonostylus' (Griffiths, 1981; Chvala, 1983); the term 'paramere' is used instead of 'postgonite' (Roháček, 1982) or 'gonostylus' (Griffiths, 1981; Chvala, 1983); the term 'epandrium' is used instead of 'periandrium' (Roháček, 1982). The term 'epandrium' is used to refer to the large, saddle-shaped posterodorsal sclerite of the male abdomen although this sclerite is actually the fusion product of the true epandrium (or true periandrium) and the inverted sternite 8 (Griffiths, 1972). The interperiandrial sclerite of Roháček (1982) (interepandrial sclerite of Anderson, 1966) is here referred to as sternite 10.

Discrepancies have also arisen in naming the bristles of the top of the head. Terms used here (Fig. 120) agree with Roháček & Marshall (1982) with two exceptions. The inner occipitals of Roháček & Marshall are termed paraverticals to conform with McAlpine (1981). These bristles are the same as those called inner occipitals by Hendel (1928) and Hennig (1958); however, they were renamed by Steyskal (1976) whose usage has been accepted by North American dipterists. Similarly, the postverticals of Roháček & Marshall are here termed the postocellars in keeping with McAlpine (1981) who has followed Steyskal in considering 'postocellar' a preferred synonym of 'postvertical'.

Roháček & Marshall have also differed in naming the last sclerites of the female terminalia. Roháček (1982) has referred to these as tergite 9 and sternite 9. The terms 'epiproct' and 'hypoproct' are used here to conform with McAlpine (1981).

Other differences in terminology are as follows: phallophore = basiphallus; sternopleuron = katepisternum; ta = r-m; tp = dm-cu; ads = orbital setulae.

TELOMERINA Roháček

Telomerina Roháček, 1982: 224. Type-species Borborus flavipes Meigen, 1830.

Generic diagnosis. Small flies, 1.0-1.7 mm in length, eye small; 3-5 short interfrontal bristles; a well-developed pair of postocellar bristles (Fig. 120) between the paravertical bristles. Mid tibia with an anterodorsal bristle on basal third and a relatively large dorsal bristle on distal third above which are smaller anterodorsal and posterodorsal bristles. Dorsocentral bristles in two pairs, anterior pair very short; one pair of prescutellar acrostichal setulae. Wing with costa extending beyond the more or less straight R_{4+5} , cell dm long, distally angulate with projections of both M_{1+2} and CuA_1 ; alula small and narrow. Sternite 5 of male with membranous posteromedial area flanked by setulose lobes; epandrium of male with only short bristles; cerci reduced, not connected medially by subanal plate, each cercus with a long bristle. Sternite 10 (interperiandrial sclerite) absent, at most 2 minute remnants preserved. Surstylus long and slender; hypandrium as long as or longer than aedeagal apodeme. Basiphallus short but wide, frame-like; distiphallus simple, largely membranous; paramere very long. Female abdomen with pale but well-sclerotized sclerites; terminal segments (postabdomen) short and wide; sixth tergite narrower and paler pigmented than the following ones; eighth tergite short dorsally, expanded laterally. Epiproct small but distinct; hypoproct larger and patterned with setulose or weakly pigmented areas. In most species, each spermatheca with slender apical projection. Cercus of female usually short and broad, its setosity hair-like to spine-like.

Discussion. The species of this genus are very similar except for the characters of the abdomen. It is therefore usually necessary to remove and clear the abdomen to facilitate identification.

Key to the species of Telomerina Roháček

- R₂₊₃ apically strongly curved up to costa (Fig. 103). Mid femur of male with a row of curved spines. Sternite 5 of male with a knob-like projection in front of membranous posteromedial region (Fig. 1). Spermatheca smoothly rounded, without terminal evagination (Fig. 6). . .levifrons
- 2 Eye diameter more than 2.2 times narrowest genal width. Surstylus with 2 stout apical spurs (Fig. 44) and lobes flanking posteromedial region of sternite 5 of male short and simple (Fig. 3).

ursina

- Females (females of orpha and kaszabi not known)
 13
- 4 MALES: Mid tibia with a row of short ventral spines on distal half (Figs. 95, 99). Surstylus either with an anterobasal lobe which is longer than wide (Figs. 22, 34) or with stout apical spurs (Figs. 8, 17).....5
- Mid tibia without central spines; usually with a small anteroventral bristle below middle. Surstylus simple, without apical spurs and with at most a short, broad anterobasal lobe 8

- 6 Posteromedial region of sternite 5 flanked by two clusters of stout spines; posterior lobes thin, bare except for medial setulae (Fig. 20) kaszabi
- Sternite 5 lacking clusters of spines; lobes thick, covered by dark, scale-like bristles; outer edge of each lobe dark and heavily sclerotized (Fig. 11) submerda
- 7 Sternite 5 with broad, setulose posterior lobes (Fig. 25). Paramere widest before apex (Fig. 24) pengellvi
- Sternite 5 with thin bare medial lobes (Fig. 36). Paramere clubbed, widest at apex (Fig. 31)

pseudoleucoptera

- 8 Posterior lobes of sternite 5 narrow and separated by 8 times their width (Fig. 37). Surstylus setulose posterodorsally (Fig. 38). *flavipes*
- Posterior lobes broad, separated by less than 3 times their width. Surstylus bare posterodorsally
 9
- 9 Katepisternum with 2 setulae anterior to posterodorsal bristle. Surstylus broad, blade-shaped (Fig. 50). Paramere strongly arched (Fig. 52). Lobes of sternite 5 weakly differentiated (Fig. 53).

chillcotti

- Katepisternum with a single setula anterior to posterodorsal bristle, Surstylus narrow, Parameres straight or weakly concave on anterior surface. Lobes of sternite 5 strongly differentiated, 10 Anterior surface of surstylus with an anterobasal lobe or a cluster of tubercle-based bristles (Fig. 59) orpha - Anterior surface of surstylus without tubercles 11 Epandrium with eight or nine bristles on anteroventral region, otherwise very sparsely haired (Figs. 73, 74). Setulae of posteromedial region of sternite 5 equal in size to those of posterior lobes Epandrium uniformly and sparsely haired. Setulae of posteromedial region of sternite 5 smaller than those of posterior lobes (Figs. 65, 86) 12 12 Surstylus slightly constricted in basal third (Figs. 83, 84). Sternite 5 with large, flat posterior lobes Surstylus not constricted, evenly tapering to tip (Fig. 64). Sternite 5 with smaller posterior lobes 13 FEMALES: Spermatheca with slender and long terminal evagination which is curved or twisted - Spermatheca with a minute, apical evagination (Fig. 15) or apical evagination twisted and recurved to body of spermatheca (Fig. 29). . . . 18 14 Apical evagination shorter than body of spermatheca (Figs. 42, 48). Cercus short, with 2 short, slightly curved bristles (Figs. 39, 41) . . . flavipes - Apical evagination longer than body of spermatheca and strongly recurved apically (Figs. 57, 80). Cercus either long (Fig. 91) or with a sinuate 15 Cerci long and tapering, each with two stout, upwardly curving, closely arising, apical bristles Cerci short and stout, with sinuate apical and 16 Katepisternum with two setulae anterior to posterodorsal bristle. Mid tibia with only minute setulae anteroventrally (Fig. 97). Tergite 7 medially shorter than tergite 8, with only short Katepisternum with one setula anterior to posterodorsal bristle. Mid tibia with an anteroventral bristle below middle. Tergite 7 medially longer than tergite 8, with 2 long bristles (Fig. 17 Sternite 7 with a transverse, darkly pigmented stripe (Fig. 69). Hypoproct with a transverse anterior sclerite separated from larger, posterior - Sternite 7 more uniformly pigmented (Fig. 78). Hypoproct with a quadrate anterior part (Fig. 78) cana

18 Mid tibia with only small setulae anteroventrally (Fig. 100). Sternite 8 with a distinct dark, scalelike sclerite posteromedially (Fig. 27). Tergite 8 divided into 2 sclerites (Fig. 26). pengellyi

- Spermatheca with a minute apical evagination (Fig. 15). Sternites 7 and 8 lightly pigmented. Hypoproct larger than sternite 8, setulose on posterior quarter; anterior two-thirds bare and medially indented into a large groove (Fig. 13) submerda

Telomerina levifrons (Spuler, 1925) comb.n. (Figs. 1–6, 103)

- Leptocera (Scotophilella) levifrons Spuler, 1925:77. Holotype 9, U.S.A.: Idaho, Kendrick, 17.vi.1910 (Melander) (USNM).
- Telomerina antonini Roháček, 1983: 131. Holotype &, CZECHOSLOVAKIA: Moravia, Rasna nr. Telc, 8.ix.1978, sifting Sphagnum (Roháček) (WRO). Syn.n.

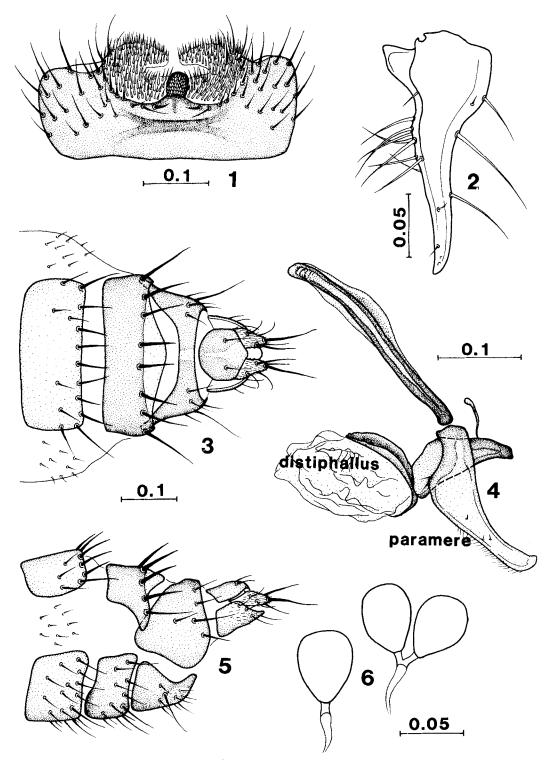
Description. Length 1.4-1.6 mm; colour brownish black with grey dusting. Interfrontal bristles in 4-5 subequal pairs, anterior pair slightly shorter. Face concave, strongly carinate at middle. Eye diameter 1.7 times smallest genal width. Postocellar bristles subequal in length to paravertical bristles. Orbital setulae well developed, in a long row extending below eye. Scutum with 2 pairs of dorsocentral bristles, the anterior pair short; acrostichal setulae in 6 rows. Katepisternum with a short posterodorsal bristle and a minute setula anterior to posterodorsal bristle. Scutellum relatively long, roundly triangular. Mid tibia of male with a long row of short, stout dark spines and a small ventral bristle at apex. Mid leg of female lacking rows of ventral spines, tibia with a distinct anteroventral bristle below middle and a larger apicoventral bristle. Wing with pale brownish membrane, veins except costa pale brown; costa dark brown. R2 + 3 apically strongly curved to costa (Fig. 103); second costal sector slightly shorter than third (0.87-0.94 times as long in male, 0.89-0.94 times as long in female). Supler's (1925) description of T.levifrons emphasizes that R_{4+5} is curved down at the middle. It is (Fig. 103), but not to the degree illustrated by Spuler (1925: Fig. 13). Neither the holotype nor the paratypes show the strongly bent R_{4+5} illustrated by Spuler.

Male abdomen. Sternite 5 (Fig. 1) with a membranous posteromedial area covered with small flat setulae, extended posteriorly into two flat, wide lobes, and overlapped at middle by an anterior, knob-like projection composed of small cuticular excrescenses. Surstylus (Fig. 2) long and slender, posteriorly with only three long, hair-like bristles. Paramere short and thick, with setulose anterior margin (Fig. 4). Basiphallus flat, broad, almost as long as distiphallus; distiphallus with a large unadorned membranous part (Fig. 4).

Female abdomen. Tergite 7 of female darker and wider than tergite 6; with stout spine-like posterior bristles, tergite extends behind bristle bases as a broad, pale lobe (Fig. 3). Tergite 8 medially shortened and weakly pigmented (Fig. 3). Epiproct long, with a pale median stripe (Fig. 3). Sternite 8 large, convex, with a small, oval depigmented medial area and with two long ventral bristles. Hypoproct with a very small transverse aperture at middle and a deep anterior incision separated from above aperture by a small stripe. Each spermatheca (Fig. 6) smooth, egg-shaped. Cercus short, with two weakly sinuate bristles and some short, curved hairs (Fig. 5).

Material examined. U.S.A.: 1 9, Washington, Lake Cushman, 22.vii.1910 (Melander) (USNM) (paratype of *levifrons*); 1 9 Washington, Vashon, 28.v.1917 (Melander) (USNM) (paratype of *levifrons*); 1 ^o, Oregon, Corvallis, 1950 561 (no other data) (USNM); 1 d, 1 φ , Michigan, Somerset Junction, 30.v.1936 (Sabrosky) (USNM); 1 9, Michigan, East Lansing, 21.vi.1936 (Sabrosky) (USNM); 1 o, Maryland, Glen Echo, 11.v.1954 (Stone) (USNM). CZECHOSLOVAKIA: 1 9, Moravia, Trest-Loucky, 3.ix.1974, on human feces (Roháček) (JRO); 1 9, Moravia, H. Jesenik Mts, Peat-bog Rejviz, 12.ix.1979, on decayed fungi (Roháček) (SMO); 1 9, Moravia, H. Jesonik Mts, Peat-bog Skritek, 30.viii.1977, on decayed fungi (Roháček) (SMO); 1 d, Slovakia, Kremnické pohorie Mts, Turček env., 24.vi.1979, on bear excrement (Roháček) (SMO); (all paratypes of antonini).

Comments. The holotype of *T.levifrons* was mistakenly listed by Spuler as a male, but



FIGS. 1-6. Telomerina levifrons: 1, sternite 5 of male; 2, left surstylus, lateral; 3, terminalia of female, dorsal; 4, aedeagal complex, left lateral; 5, terminalia of female, left lateral; 6, spermathecae.

is a female. Only two of Spuler's paratypes are conspecific with the holotype; the others are a male *Minilimosina fungicola* and a female *Spelobia* sp.

This species is associated with sphagnum bogs in Europe but specific habitat information is not available for North American specimens. Its rarity in collections and its wide distribution together suggest a restricted habitat.

T.levifrons retains more plesiomorphic features than any congener and is tentatively placed as the sister taxon to the rest of the *pseudoleucoptera* group (Fig. 126).

Telomerina submerda sp.n. (Figs. 7–15, 93–95, 104)

Description. Length 1.3-1.5 mm; colour light brown. Interfrontal bristles in 4-5 subequal pairs. Face narrowly tuberculate between antennae, concave and weakly carinate below. Postocellar bristle much smaller than paravertical bristle. Orbital setulae very weakly developed, forming an indistinct row from just above lower orbital to below eye. Eye diameter 1.4 times narrowest genal width. Scutum with two pairs of dorsocentral bristles, anterior pair small, subequal to prescutellar acrostichal setulae; five rows of acrostichal setulae between anterior dorsocentrals. Katepisternum with two bristles on dorsal part, posterior one reaching three-quarters of distance to wing base, anterior one minute, sometimes subtended by another minute setula. Scutellum blunt-triangular, 1.5 times as wide as long. Mid tibia of male (Fig. 95) with a row of small spines ventrally on distal half, mid tibia of female (Figs. 93, 94) with a large mid ventral bristle. Wing of male and female similar (Fig. 104), second costal sector slightly longer than third (1.13–1.20 times as long in male; 1.13-1.14 times as long in female). Wing membrane brownish, costa dark brown, other veins pale brown.

Male abdomen. Central desclerotized area of sternite 5 with a patch of setae centrally and some small setae at anterior margin; posterior lobes of sternite 5 complex, with heavily sclerotized outer margins, and covered with dark, scale-like clusters of flat bristles (Fig. 11). Surstylus (Figs. 7-9) elongate-triangular, tipped with two stout spurs. Paramere (Fig. 10) broad, distal portions minutely setulose ventrally. Basiphallus long, frame-like, longer than distiphallus. Distiphallus very broad at apex, with small spines in membrane (Fig. 10).

Female abdomen. Tergite 7 shorter, wider and darker than tergite 6; tergite 8 depigmented medially; hypoproct with a depigmented medial region in posterior two-thirds (Fig. 12). Sternite 8 rounded, convex, entirely setulose but weakly pigmented over posterior twothirds, a small bare, deflexed plate behind sternite 8 (Fig. 13). Hypoproct longer than sternite 8, setulose on posterior quarter, bare and indented into large medial groove anteriorly (Fig. 13). Each spermatheca oval, without apical process, surface reticulate (Fig. 15). Cercus robust, short; dorsobasal bristles cruciate and longer than apical or preapical bristles (Fig. 14).

Holotype, &, U.S.A.: Florida, Alachua Co., 18.viii.1980, under cow dung (Sivinski) (CNC).

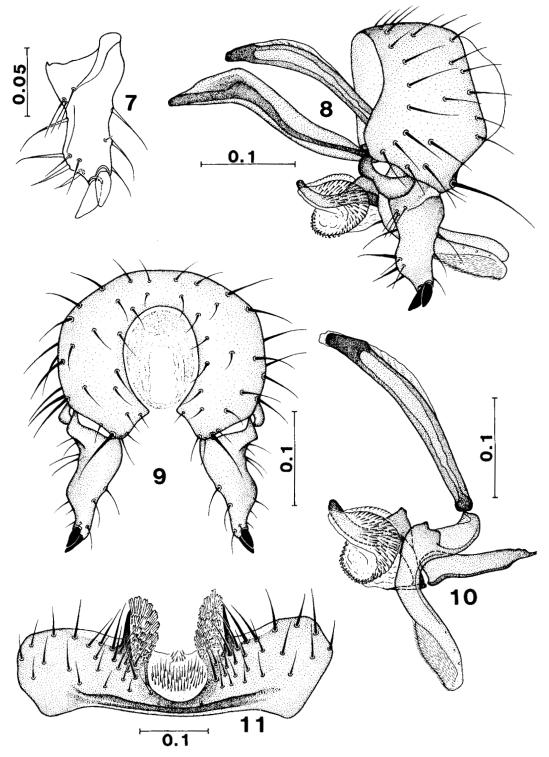
Paratypes. U.S.A.: 20, 39, collected with holotype (GUELPH, JRO); 2d, Florida, Alachua Co., 15.ii.1983, under pig dung (Marshall) (GUELPH); 1 °, Florida, Clay Co., Gold Head Branch State Park, 4-14.iv.1971, carrion (Newton) (MCZ); 2 d, Louisiana, 11 miles SW Alexandria, 21.iii,1960 (Chillcott) (CNC); 1d. Arkansas, Polk Co., 13 miles NW Mena, Rich Mtn 2800 ft, 1-3.vi.1979 (Peck) (GUELPH); 10, 29, Arkansas, Washington Co., 3 miles S Devil's Den State Park, 28-31.v.1979 (*Peck*) (GUELPH); 1°, 2°, Mississippi, Scott Co., Bienville Nat. For., 10-14.iv.1972, dung traps in pine forest (Newton) (MCZ); 14 d, 99, Oklahoma, Latimer Co., 5 miles W Red Oak, 9.iii.1977, pig dung trap (Stephen) (GUELPH, FSC).

Etymology. The Latin *submerda* refers to the type habitat, under dung.

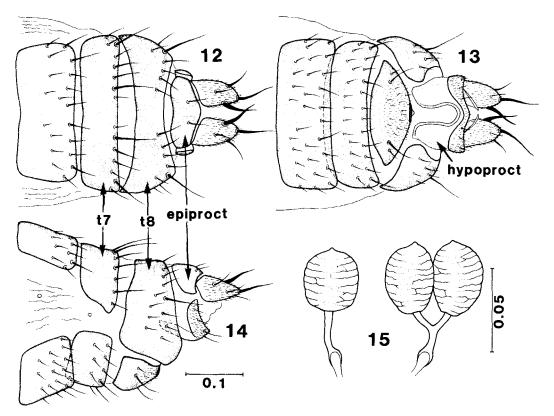
Telomerina kaszabi (Papp, 1973b) (Figs. 16–20, 105)

Limosina kaszabi Papp, 1973b; 396. Holotype &, MONGOLIA: Bulgan aimak, 11 km W von Somon Bajannuur an see Bajannuur, 1000 m, Exp. Dr Z. Kaszab, 1968, Nr 958, 14.vi. - 24.vii.1968 (TMB).

Telomerina kaszabi (Papp); Roháček, 1983. Description. Length 1.35 mm (taken from Papp, 1973b); colour dark brown, pruinose.



FIGS. 7-11. Telomerina submerda, male: 7, left surstylus; 8, terminalia, left side; 9, epandrium and surstyli, caudal view; 10, aedeagal complex, left lateral; 11, sternite 5.



FIGS. 12–15. Telomerina submerda, female: 12, terminalia, dorsal; 13, terminalia, ventral; 14, terminalia, lateral; 15, spermathecae.

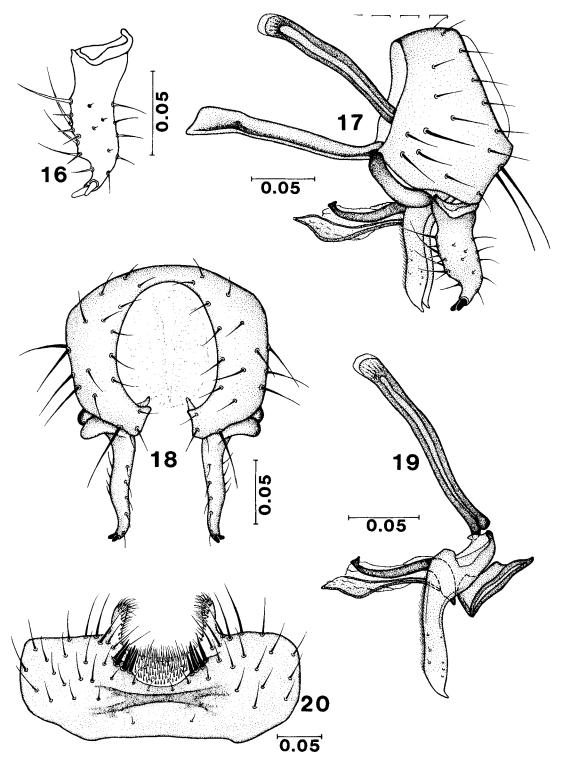
Head cannot be described (lost). Thorax of type largely de-bristled, with two dorsocentral bristles and about six rows of acrostichal setulae between anterior dorsocentrals. Scutellum roundly triangular, narrower than in related species. Probably two katepisternal bristles but only posterior scar visible. Chaetotaxy of mid tibia similar to congeners, bristles short; dorsally with bristle in apical sixth longest; ventrally with a row of short spines, apicoventral bristle very short. Wing (Fig. 105) with greyish membrane; veins pale brown. Second costal sector 1.10 times as long as third.

Male abdomen. Sternite 5 with unusually slender, internally finely haired posterior lobes and two groups of robust spines situated on sides of finely spinulose posteromedial membranous area (Fig. 20). Epandrium (Figs. 17, 18) rather sparsely haired, bearing some thicker bristles lateroventrally. Surstylus (Figs. 16, 17) flattened laterally; apically tapered and with two thick, blunt spines. Aedeagal complex (Fig. 19) with robust basiphallus and narrow distiphallus without spicules in membrane. Parameres with short, pointed apex, densely pubescent anterior margin and inner side and with some minute setulae on outer side. Female unknown.

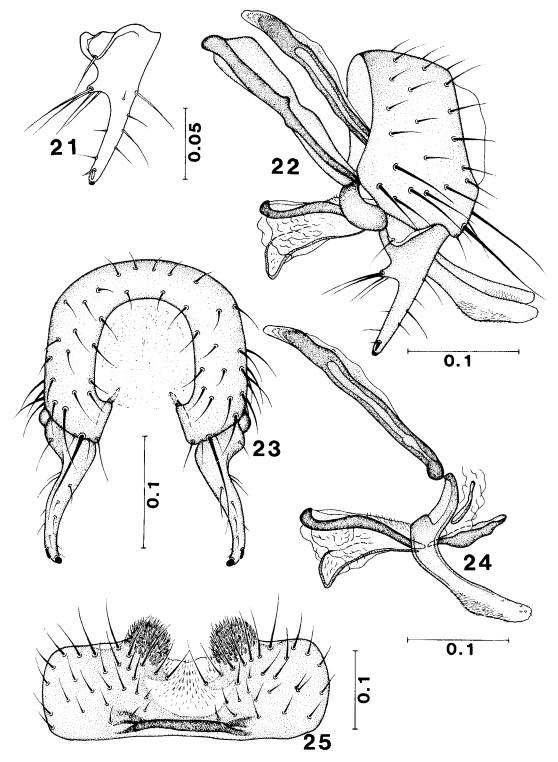
Comments. The holotype and only known specimen is severely damaged (head, some legs or their parts and most bristles missing). Its abdomen is detached and preserved in a plastic tube with glycerine; one wing and one midleg are on a microslide pinned on the same pin below the specimen (examined).

Telomerina pengellyi sp.n. (Figs. 21-29, 98, 99, 100, 106, 121, 122, 124)

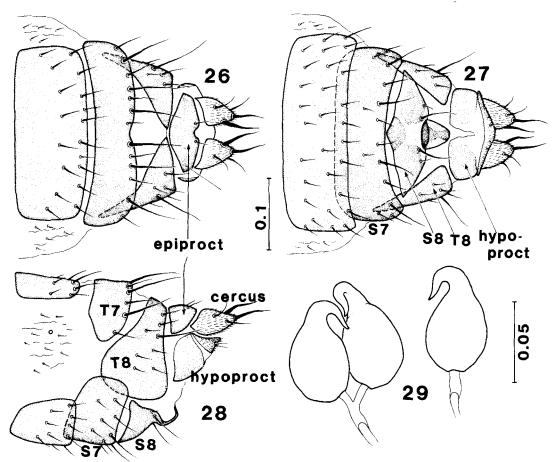
Description. Length 1.1-1.5 mm; colour brown with heavy grey dusting. Interfrontal bristles in four subequal pairs, the lower slightly smaller. Postocellar bristle about half as long as paravertical bristle. Orbital setulae



FIGS. 16–20. Telomerina kaszabi, male: 16, left surstylus; 17, terminalia, left lateral; 18, epandrium and surstyli, caudal view; 19, aedeagal complex, left lateral; 20, sternite 5.



FIGS. 21–25. Telomerina pengellyi, male: 21, left surstylus; 22, terminalia, left lateral; 23, epandrium and surstylus, caudal view; 24, terminalia, left lateral; 25, sternite 5.



FIGS. 26-29. Telomerina pengellyi, female: 26, terminalia, dorsal; 27, terminalia, ventral; 28, terminalia, left lateral; 29, spermathecae.

long but sparse, in a row extending below eye (Figs. 121, 122). Face broadly tuberculate between antennae, concave and weakly carinate below. Eye diameter slightly greater than 1.9 times smallest genal width. Scutum with two pairs of dorsocentral bristles, anterior pair subequal to prescutellar acrostichal setulae. Acrostichal setulae in five rows between anterior dorsocentrals. Scutellum broad, twice as wide as long, truncate. Katepisternum with two posterodorsal bristles, the anterior minute, the posterior one reaching threequarters of way to wing base. Mid tibia of male (Figs. 98, 99) with a distal row of small ventral spinules and a small apicoventral bristle, mid tibia of female (Fig. 100) with an anteroventral bristle below middle and a large apicoventral bristle. Wing (Fig. 106) membrane clear, costa brown, other veins yellowish; alula very narrow, almost linear. Second costal sector slightly longer than third (1.16-1.29 times as long in male, 1.00-1.08 times as long in female).

Male abdomen. Sternite 5 with bare, membranous posteromedial region flanked by two heavily setulose lobes (Fig. 25). Surstylus long, slender with a narrow anterior lobe basally, bearing several long bristles apically (Figs. 21, 22). Basiphallus small, half as long as distiphallus (Fig. 24). Distiphallus simple, membrane unadorned. Paramere broad, widened and with anteroventral surfaces setulose from middle to just before apex (Figs. 22, 24, 123).

Female abdomen. Tergite 7 darker and wider than tergite 6; tergite 8 constricted medially, divided into two plates. Epiproct darkly pigmented, with a posteromedial notch (Fig. 26). Sternite 8 membranous posteromedially, a small, scale-like sclerite just behind this membranous area, scale-like sclerite dark and shining in dried specimens (Fig. 27). Hypoproct small, membranous, setulose on posterior quarter, depigmented medially and incised anteromedially (Fig. 27). Each spermatheca with a thick, recurved apical process (Fig. 29). Cercus very short, apical and preapical bristles similar in length (Fig. 28).

Holotype &, CANADA: Alberta, Lower Kananaska Highway, 5.viii.1980, on cow dung (Marshall) (CNC).

Paratypes CANADA: 50, 99, collected with holotype (GUELPH, JRO); 13 d, 8 9, New Brunswick, St Andrews, 25.vii.1978, 15-30. vii.1978 and 14.vii.1978, dung-baited and unbaited traps (Marshall) (GUELPH); 8 d, 11 9, Ontario, Chaffey's Locks, Queen's University Biological Station, 12.ix.1980, on wet cow dung near lake shore (Marshall) (GUELPH); 1 d, Ontario, Lanark, 1.ix.1979, on decayed mushroom (Marshall) (GUELPH); 2d, 29, Ontario, Marmora, 11.vi.1952 (Vockeroth) and 15.viii.1952, (McAlpine) (CNC); 12d, 79, Alberta, Cypress Hills, 15.vii.1980, on cow dung (Marshall) (GUELPH, SMO). U.S.A.; 1 \circle , Massachusetts, Medford, 7.ix-5.x.1969, dung trap in deciduous forest (Peck) (GUELPH); 29, West Virginia, Pendleton Co., Spruce Knob, 4600 ft, conifer forest, 27.vii-9.viii.XXX (Newton) (MCZ); 4 d, Arkansas, Washington Co., 3 miles S of Devil's Den State Park, 28-31.v.1979, oak-hickory forest (Peck) (GUELPH).

Etymology. This species is named after Dr D. H. Pengelly, who has given much encouragement to the senior author.

Telomerina pseudoleucoptera (Duda, 1924) (Figs. 30–36, 106)

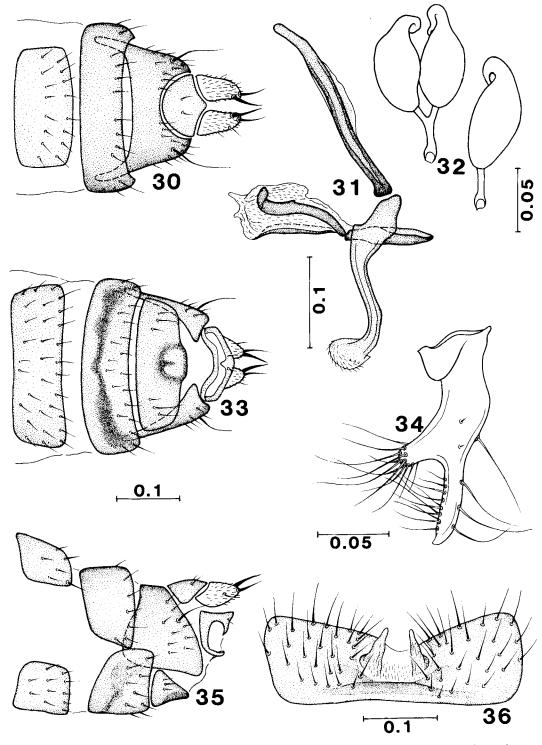
- Limosina (Scotophilella) pseudoleucoptera Duda, 1924: 175. Lectotype & F.R.G., Herten, Westfalen (Duda) (labelled '25 516' (ZMB). [designated by Roháček, 1983].
- Leptocera (Scotophilella) pseudoleucoptera Duda, 1925: 159.
- Leptocera (Limosina) pseudoleucoptera (Duda); Richards, 1930: 297.
- Limosina (Limosina) pseudoleucoptera (Duda); Duda, 1938: 139.

- Limosina pseudoleucoptera (Duda); Papp, 1973a: 51.
- Telomerina pseudoleucoptera (Duda); Roháček, 1983: 136.

Description. Length 1.0-1.3 mm; colour blackish brown, greyish brown dusted. Postocellular and paravertical bristles subequal. Orbital setulae well developed, in a long row extending below eye. Interfrontal bristles small, in 4 or 5 pairs, anterior pair shortest. Facial cavity and strongly protruding carina subshining. Eye diameter about 1.4 times smallest genal width. Dorsocentral bristles in 2 pairs, the anterior pair short. Acrostichal setulae in 6 rows between anterior dorsocentrals, prescutellar acrostichals slightly enlarged. Scutellum roundly trapezoidal, 1.5 times as wide as long. Katepisternum with a posterodorsal bristle reaching half way to wing base and a minute anterior setula. Mid tibia of male with a row of short ventral spines in distal half, apicoventral bristle little larger than ventral spinules. Mid tibia of female with an anteroventral bristle below middle and a distinct apicoventral bristle only. Wing (Fig. 106) with pale but distinctly brownish membrane, veins pale brown, costa darker brown, second costal sector thickened (especially in female) but usually not as thick as in Duda's photograph (1938, Fig. 32). Second costal sector subequal to or slightly longer than third (0.91 -1.04 times as long in female; 0.94-1.29 times as long in male).

Male abdomen. Sternite 5 with membranous medial area small, very finely pubescent, two lobes arising from the middle of this area (not its posterolateral margins as in congeners); these lobes long, slender and tapering distally (Fig. 36). Surstylus (Fig. 34) long, slender, with a large anterior lobe; both lobes with a number of long hair-like setae. Basiphallus flat but broad, much shorter than distiphallus; distiphallus simple, membrane weakly granulate (Fig. 31). Parameres long, slender, S-shaped, with enlarged and finely pubescent apex bearing about 3 minute setulae.

Female abdomen. Tergite 7 short, broad, laterally extended, much wider than tergite 6. Tergite 8 short, uniformly pigmented (Fig. 30). Epiproct short, uniformly pigmented, with 2 minute dorsal setulae. Sternite 7 with transverse band-like pigmentation; sternite 8



FIGS. 30-36. *Telomerina pseudoleucoptera*: 30, terminalia of female, dorsal; 31, aedeagal complex, left lateral; 32, spermathecae; 33, terminalia of female, ventral; 34, left surstylus; 35, terminalia of female, lateral; 36, sternite 5 of male.

with a small, posterior, ring-like pigmented area (Fig. 33). Hypoproct narrow, with large medial aperture, frame-like. Spermatheca (Fig. 32) elongated and terminally with slender, strongly twisted projection. Cercus with 2 short spines (Fig. 35), these shorter than cercus.

Material examined. In addition to the material listed by Roháček (1983) the following specimens have been examined. CZECHO-SLOVAKIA: 7 d, 12 \, Slovakia, Brzotin nr Roznava, 4.ix.1980 (*Roháček*) (JRO, GUELPH). HUNGARY: 1 d, Kiskunsag, Bugac, 18.ix.1980 (*Papp*) (JRO).

Comments. This species is widespread in Europe but rarely collected. It is recorded from England, Finland, Sweden, Denmark, Germany, Holland, Hungary and Czechoslovakia. Laurence (1955) bred it from older, dry cow droppings and most other records are from ungulate dung at high altitudes during the summer months (Roháček, 1983).

Telomerina flavipes (Meigen, **1830**) (Figs. 37–42, 108, 109, 116–120, 123)

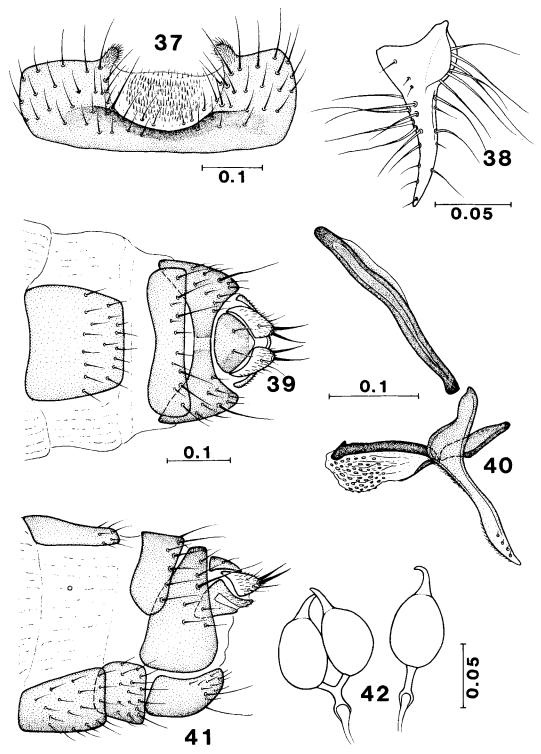
- Borborous flavipes Meigen, 1830: 208. Lectotype &, 'flavipes Coll.Winth.' (NMW) [Designated by Roháček, 1983].
- Leptocera (Scotophilella) gracilipennis Spuler, 1925: 78. Holotype & U.S.A.: Washington, Friday Harbour (Melander) (USNM). Syn.n.
- Limosina (Limosina) flavipes (Meigen); Duda, 1938: 122.
- Leptocera (Limosina) flavipes (Meigen); Harrison, 1959: 269; Richards, 1951: 81; 1967: 14; 1973: 372.
- Limosina flavipes (Meigen); Papp, 1973a: 55.
- Limosina minutissima Zetterstedt, 1847: 2505. Specimen from which description made is lost, known syntypes are in other taxa. (Synonymized by Duda, 1938.)
- Leptocera (Limosina) minutissima (Zetterstedt); Richards, 1930: 296.
- Leptocera minutissima (Zetterstedt); Seguy, 1934: 467.
- Limosina retracta Rondani, 1880: 25. Lectotype & labelled '1931' (catalogue number) [designated by Roháček, 1983] (Synonymized by Duda, 1938.)
- Limosina (Scotophilella) retracta (Rondani); Duda, 1918: 140.

- Leptocera (Scotophilella) retracta (Rondani); Duda, 1925: 161.
- Telomerina flavipes (Meigen); Roháček, 1983: 134.
- ? Limosina (Limosina) ventruosella Venturi, 1965: 7. Type (not located), ITALY: Sicily, Mt Etna, Grotta di S. Gregorio (cave), 31.viii.1961 (La Greca).

Description. Length 1.2-1.6 mm; colour brown with grey dusting. Interfrontal plate bordered by 4 or 5 equal interfrontal bristles. Postocellar bristle subequal in length to paravertical bristle (Fig. 120). Orbital setulae very well developed, in a long row extending below eye. Face narrowly tuberculate between antennae, concave-carinate below. Eye diameter about 1.6 times smallest genal width. Scutum with 2 pairs of dorsocentral bristles, anterior pair short; acrostichal setulae in 5 or 6 rows. Katepisternum with posterodorsal bristle reaching about half way to wing base, a much smaller bristle present anterior to this bristle. Scutellum large, 1.5 times as wide as long. Mid tibia with a very small, indistinct anteroventral bristle below middle and a small ventral bristle at apex, both these bristles small in male, larger in female. Wing slightly opalescent, veins other than costa weakly pigmented. Wing (Figs. 108, 109) narrower in female than in male; alula very narrow. Second costal sector subequal to or slightly longer than third (0.92-1.34 times as long in male, 0.98-1.23 times as long in female).

Male abdomen. Sternite 5 with a large membranous posteromedial area, central part covered by semicircular patch of short setae; this area flanked by flat, finely haired lobes (Fig. 37). Surstylus long, slender, apically pointed and with no adornment other than long hair-like bristles (Figs. 38, 123). Paramere long, acute at apex, with some minute setulae apically and on inside margin (Fig. 40).

Female abdomen. Tergite 7 darker and wider than tergite 6; tergite 8 medially very short and with narrow, pale pigmented stripe; epiproct small, slightly wider than long; darkest laterally (Fig. 39). Sternite 8 large, convex. Hypoproct membranous medially and anteriorly, with short, dark posterior sclerite dark; triangular lateral sclerites; and an indistinct, lightly pigmented anterior sclerite. Each spermatheca oval, with slender, slightly curved terminal portion (Fig. 42). Cercus short;



FIGS. 37-42. Telomerina flavipes: 37, sternite 5 of male; 38, left surstylus; 39, terminalia of female, dorsal; 40, aedeagal complex, left lateral; 41, terminalia of female, left lateral; 42, spermathecae.

inner, preapical bristle shorter and thicker than outer, apical bristle (Figs. 39, 41).

Third instar larva. About 3.6 mm in length; colour white. Head (Fig. 116) with antennomaxillary lobes well separated; oral ridges with rows of comb-like structures. Cephalopharyngeal skeleton (Fig. 118) mostly dark; mandibles heavily sclerotized except for a central, window-like, weakly pigmented Hypopharyngeal sclerite elongate, patch. slightly longer than mandibles, H-shaped in dorsal view. Parastomal bars slender, fused with tentoropharyngeal sclerite and projecting over two-thirds of hypopharyngeal sclerite. Dorsal bridge narrow basally, widened and perforated dorsally. Dorsal cornua long, slender, almost parallel-sided except posterior one-third which is slightly swollen and divided into 2 pointed lobes, the lower lobe smaller than the upper. Ventral cornua weakly pigmented in posterior two-thirds; pharyngeal ridges in the usual 9 rows.

Thorax with anterior spiracles held at right angles to body (Fig. 117), composed of a single main stem with 7-8 branches. Ventral creeping welts of thoracic segments weak, without a distinct central row of spines.

Abdomen with anteroventral creeping welts on segments 1-8; those on segments 2-8 consisting of a few large anterior teeth, about 3 irregular rows of minute, sometimes bilobed teeth packed closely into comb-like ridges, a central row of large truncate or weakly bifid teeth, and posteriorly with another 3 irregular rows of minute teeth packed into comb-like ridges (Fig. 116). Perianal pad bulbous, bearing a cluster of 4 large, hook-shaped teeth on its posterior margin. Posterior spiracular processes about twice as long as basal width, constricted at two-thirds of length, the distal onethird darkly pigmented, appearing spherical in lateral view. Spiracular plates slanted inward, almost facing each other; each plate with 3 elongate spiracular slits, each slit with 2 parallel rows of about 6 spiracular openings. Spiracular plate fringed with 4 tufts of long, branched hairs.

Puparium. Length about 2.3 mm; colour reddish-brown, body covered with transverse wrinkles. Creeping welts lost or invaginated into wrinkles, not visible. Anterior spiracles situated at anterolateral corners, atrophied and darkly pigmented at base. Features of cephalopharyngeal skeleton and posterior spiracles as described for larva.

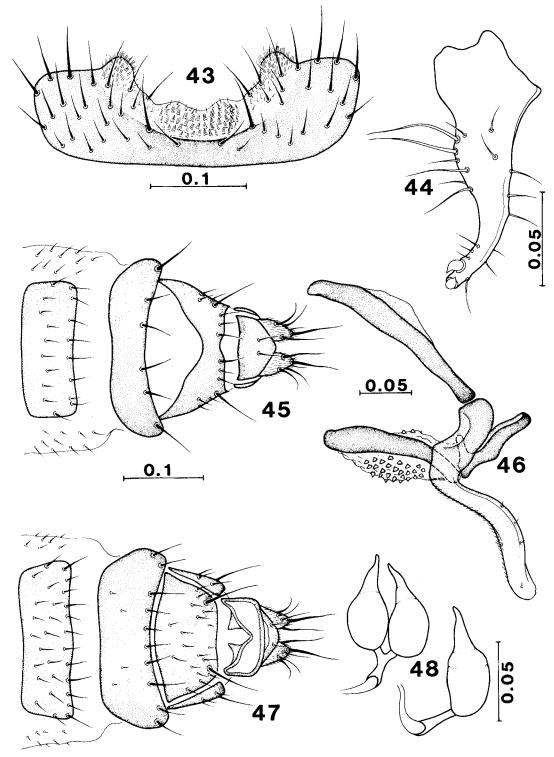
Material examined. Paratypes of Leptocera (Scotophilella) gracilipennis (4 specimens, 1 d dissected, USNM); U.S.A.: Idaho, Moscow (Melander) (USNM); Illinois, Illinois University (USNM); Massachusetts, Boston (Melander) (USNM). Other material examined. Over 500 specimens from the following regions: CANADA: Nova Scotia, New Brunswick, Quebec, Ontario, Manitoba, Alberta, British Columbia. UNITED STATES: Illinois, New York, Massachusetts, Tennessee, Virginia, Florida, Arizona, Arkansas, Colorado, New Mexico, Wyoming. ENGLAND, NETHER-LANDS, CZECHOSLOVAKIA, HUNGARY, ROMANIA, BULGARIA, SPAIN, ITALY, GREECE, FINLAND, ICELAND. Specimens from Mongolia were misidentified by Papp (1973b) and listed as paratypes of T.paraflavipes (see data for that species). T.flavipes had not previously been recorded from the East Palaearctic.

Comments. This is a very common fly, not only in North America and Europe, but also in South Africa (Hackman, 1965), South America (Richards, 1967), Australia (Richards, 1973), and New Zealand (Harrison, 1959). This species has previously been recorded in North America only as *Leptocera gracilipennis* Spuler. Most of the specimens examined were collected in carrion traps, but the species is also known from dung (Roháček, 1983), decaying fungi (Papp, 1973a), caves (Duda, 1928) and mammal burrows (Hackman, 1963). It has been reared from housefly medium by A. Norrbom at State College, Pennsylvania.

Telomerina ursina Roháček, 1983 (Figs. 43–48, 110)

Telomerina ursina Roháček, 1983: 132. Holotype d, CZECHOSLOVAKIA: Slovakia, Kremnické pohorie Mts, Turček env. 850 m, 27.vi.1979, on bear excrement (*Roháček*) (SMO).

Description. Length 1.0-1.5 mm; colour brownish black, pruinose. Head bristles small. Postocellar bristles distinct and almost cruciate. Orbital setulae well developed, in a long row.



FIGS. 43-48. Telomerina ursina: 43, sternite 5 of male; 44, left surstylus; 45, terminalia of female, dorsal; 46, aedeagal complex, left lateral; 47, terminalia of female, ventral; 48, spermathecae.

Interfrontals in 3-4 subequal pairs, anterior pair shortest. Facial cavity blackish and shiny, carina very distinctly protruding between antennal bases. Eye larger than in all related species, with diameter 2.3-2.4 times smallest genal width. Dorsocentral bristles in 2 pairs, anterior short; acrostichal setulae in 6 rows, prescutellar pair slightly enlarged. Scutellum relatively short, with short marginal bristles, the apicals hardly longer than scutellum. Katepisternum with a posterodorsal bristle and a minute setula in front of posterodorsal bristle. Mid tibia with an anteroventral bristle below middle and a weak ventral bristle at apex, these bristles stronger in female. Wing (Fig. 110) with pale, whitish membrane; costa brownish, other veins pale. Second costal sector shorter than or equal to third (0.78 -0.98 as long in male, 0.86-1.02 as long in female).

Male abdomen. Sternite 5 with an isolated patch of spinules at middle of posteromedial area; posterior lobes short and with only weak spinules (Fig. 43). Surstylus (Fig. 44) long, slender, apically tapering, with long hairs only anteriorly; apically with 2 short, curved spurs. Aedeagal complex large, especially the parameres which project posteroventrally and are visible even in dry specimens (Fig. 46). Paramere large, S-shaped, apically flattened and rounded, with finely haired anterior margin. Basiphallus broad and flat, much shorter than distiphallus. Distiphallus simple, composed of dorsal sclerite and ventral membranous part dotted with distinct, thorn-like spicules (Fig. 46).

Female abdomen. Tergite 7 wider than tergite 6; sparsely haired and darkly pigmented (Fig. 45). Tergite 8 medially incised and very short, but not divided or depigmented. Epiproct short, basally with 2 lateral darker pigmented spots (Fig. 45). Sternite 8 large, long, posteromedially with triangular membranous and pale area and posterolaterally with a long bristle on each side (Fig. 47). Hypoproct frame-shaped, anterior edge bent posteriorly and with 2 triangular swellings (Fig. 47). Spermatheca (Fig. 48) similar to T.flavipes, but apical projections slightly longer. Cercus short, with 2 long, slightly sinuate bristles and 3 shorter, weaker preapical bristles (Fig. 45).

Material examined. No further material

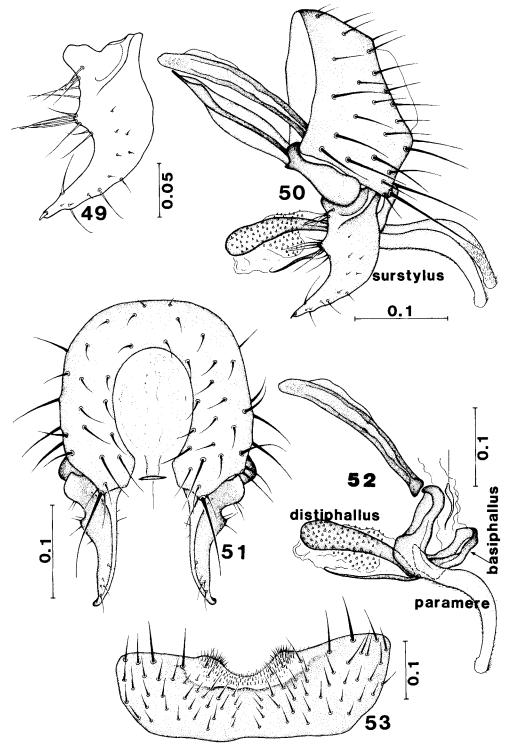
has become available since Roháček (1983) described this species based on thirty-seven specimens collected in Czechoslovakia.

Comments. Most of the type series of this species was collected from 4-6-day-old bear dung.

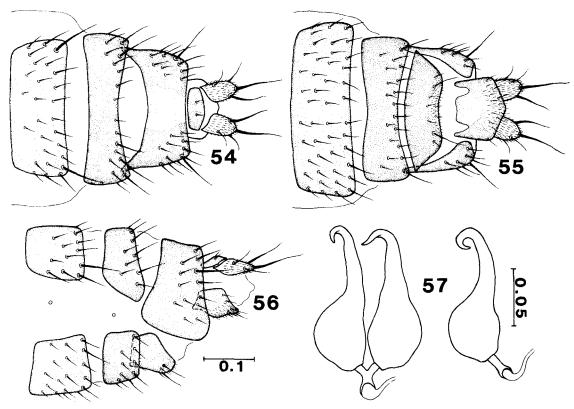
Telomerina chillcotti sp.n. (Figs. 49–57, 96, 97, 111, 125)

Description. Length 1.4–1.7 mm; colour pruinose brown. Interfrontal plate more distinctly raised than in other species, bordered by 4-5 (usually 5) interfrontal bristles. Postocellar and paravertical bristles subequal. Orbital setulae well developed, in a long row. Eye diameter 1.4 times narrowest genal width. Face narrowly tuberculate between antennae, deeply concave and carinate below. Scutellum broadly rounded, 1.6 times as wide as long. Dorsal part of katepisternum with posterior bristle reaching half-way to wing base, 2 smaller bristles (rarely only 1) present anterior to this bristle. Scutum with 2 pairs of dorsocentral bristles, anterior pair barely longer than acrostichal setulae. Mid tibia of male with only short setulae in mid ventral regions, mid tibia of female (Figs. 96, 97) with a small anteroventral bristle at middle; apicoventral bristle of male small, only slightly larger than the anteroapical setula; apicoventral bristle of female large. Wing (Fig. 111) broad in both sexes, alula unusually broad for this group, truncate at tip. Second costal sector 1.3-1.5 times as long as third (1.25-1.43) times as long in male, 1.29-1.33 times as long in female). Wing membrane whitish, costa brown, other veins almost without pigment.

Male abdomen. Sternite 5 indented posteromedially and with a small, minutely setulose posteromedial area; indented area flanked by small setulose lobes (Fig. 53). Surstylus long and pointed but much broader than in related species, with a broad anterior lobe basally (Figs. 49, 50, 125). Paramere long and thin, arched medially, not tapering, with a broadly rounded tip, anteroventral surfaces setulose (Fig. 52). Basiphallus frame-shaped, much smaller than the distiphallus which has a very large dorsal sclerite, a thin ventral sclerite and a spicule-covered membrane (Fig. 52).



FIGS. 49-53. Telomerina chillcotti, male: 49, left surstylus; 50, terminalia, left lateral; 51, epandrium and surstyli, caudal view; 52, aedeagal complex, left lateral; 53, sternite 5.



FIGS. 54-57. Telomerina chillcotti, female: 54, terminalia, dorsal; 55, terminalia, ventral; 56, terminalia, lateral; 57, spermathecae.

Female abdomen. Tergite 7 darker and wider than tergite 6; tergite 8 long, not medially shortened but with a large medial depigmented area (Fig. 54). Epiproct small, with a median pale stripe. Sternite 8 uniformly pigmented except setulose posterior margin. Hypoproct slightly smaller than sternite 8, setulose on posterior half, anterior half bare and folded medially into a large groove (Fig. 55). Each spermatheca with apical process longer than body of spermatheca (Fig. 57). Cercus (Fig. 56) short, all bristles thin and sinuate, apical bristle longer than cercus, dorsopreapicals shorter than apicals, sometimes cruciate.

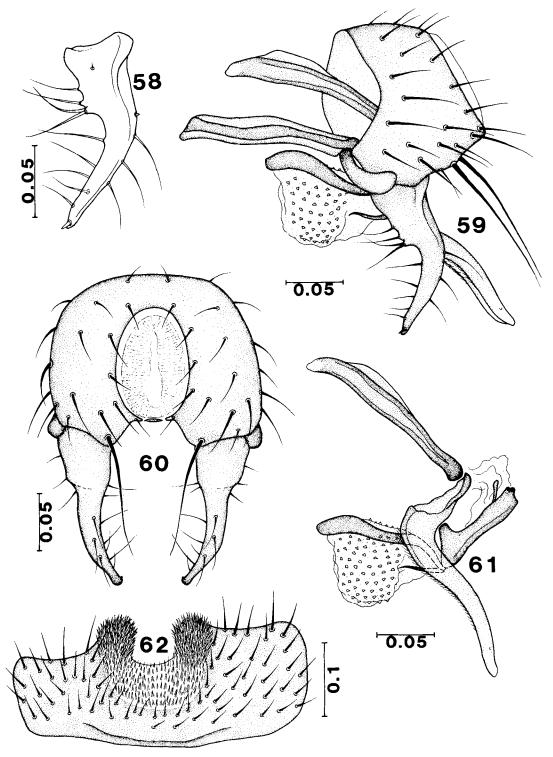
Holotype &, U.S.A.: Louisiana, 11 miles SW Alexandria, 30.iii.1960 (*Chillcott*) (CNC).

Paratypes USA.: 11 Å, 22 Ŷ, collected with holotype (CNC, GUELPH, JRO); 1 Å, 1 Ŷ, Tennessee, Nancy's Ferry Cave, Newmarket, 13.vi.1952 (Ives) (USNM); 1 Å, Tennessee, Great Smoky Mountain National Park, 20.v. 1957, on ground among Carex roots (Vockeroth) (CNC); 4 Å, 5 Ŷ, Tennessee, Bedford Co., Reese Cave, Guano, 12.iii.1965 (Peck) (GUELPH, CNC); 1 Å, Louisiana, 3 miles S Oak Grove, 31.iii.1960 (Chillcott) (CNC); 1 Ŷ, Louisiana, 11 miles SW Alexandria, 1.iv.1960 (Chillcott) (JRO); 1 Ŷ, Texas, Davis Bat Cave, Blanco Co., 12.vi.1959 (Mason) (CNC). Specimens not designated paratypes: CANADA: 1 Ŷ, Ontario, Marmora, 11.vi.1952, on mashed Malacosoma larvae (Vockeroth); 1 Ŷ, New Brunswick, St Andrews, 15.viii.1978 (Marshall).

Etymology. This species is named after the late Dr J. Chillcott, who collected most of the type series of this species and many other valuable sphaerocerids.

Telomerina orpha sp.n. (Figs. 58-62, 101, 102, 112)

Description. Male: Length 1.4 mm; colour brown, slightly pruinose. Interfrontal bristles



FIGS. 58-62. Telomerina orpha, male: 58, left surstylus; 59, terminalia, left lateral; 60, epandrium and surstyli, caudal view; 61, aedeagal complex, left lateral; 62, sternite 5.

in 3-4 pairs, middle 2 longest. Postocellar bristle slightly shorter than paravertical. Orbital setulae well developed, in a long row extending below eye. Face concave-carinate; tuberculate between antennae. Eye diameter 1.5 times smallest genal width. Scutum with 2 pairs of dorsocentral bristles, anterior pair weak; acrostichal setulae in 6 rows between anterior dorsocentrals, one pair of slightly enlarged acrostichal setulae between posterior dorsocentrals. Scutellum relatively short, 1.5 times as wide as long. Mid tibia (Figs. 101, 102) with a weak ventral bristle below middle and a slender apicoventral bristle. Wing broad, membrane slightly browned, costa brown, other veins yellow, costal sectors subequal (Fig. 112). Sternite 5 with broad posterior lobes; dense setulosity of lobes continuous with rows of setulae covering posteromedial area; setulae of lobes subequal in size to setulae of posteromedial region (Fig. 62). Surstylus with setulose anterobasal lobe broader than high, distal part of surstylus long and narrow (Figs. 58, 59). Paramere long and narrow, tapering to a rounded tip, apical third very lightly sclerotized, finely setulose on inside margin (Fig. 61). Basiphallus as long distiphallus; distiphallus with ventral as sclerite minute; membrane with triangular spicules (Fig. 61).

Holotype & U.S.A.: Illinois, Champaign Co., Mahomet, Hart Woods, 20-26.v.1979, Malaise-interception trap in oak woods (*Peck*) (CNC).

Paratypes U.S.A.: 2 Å, collected with holotype (JRO, GUELPH); Å, Massachusetts, Middlesex Co., Medford, 7.ix-5.x.1969, carrion trap (Newton) (MCZ).

Telomerina eburnea Roháček, **1983** (Figs. 63–71, 113)

Telomerina eburnea Roháček, 1983: 133 (female only). Holotype ⁹, CZECHOSLO-VAKIA: Moravia, Studence, 8.iv.1962 (*Rozkosny*) (JRO).

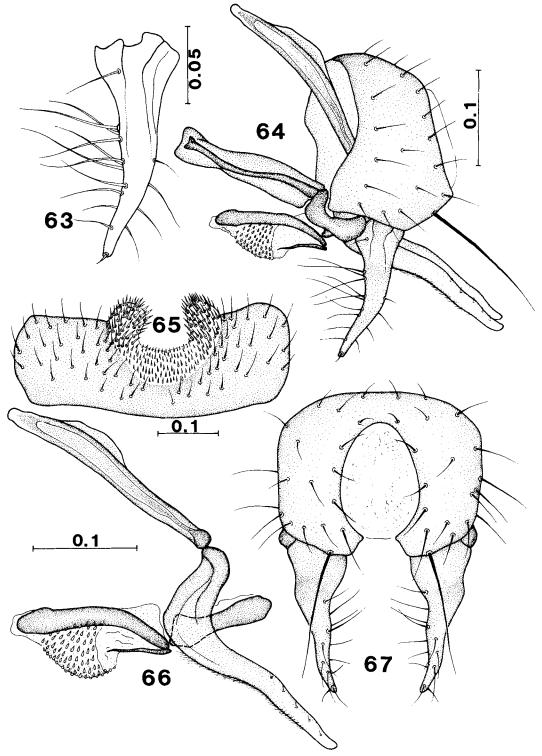
Description. Length 1.3-1.6 mm; colour dark brown, pruinose. Interfrontal bristles in 4-5 short, subequal pairs. Paravertical bristle slightly shorter than paravertical; paravertical

short. Orbital setulae in a long row extending below eve. Face concave, carina strongly protruding between antennae. Eye diameter 1.8-1.9 smallest genal width. Scutum with 2 pairs of dorsocentral bristles, the anterior short, acrostichal setulae in 6 rows, the medial prescutellar pair enlarged, as long as anterior dorsocentral bristles. Scutellum roundly triangular, with long marginal bristles. Katepisternum with a posterodorsal bristle and a minute anterior setula. Mid tibia in both sexes with a well-developed anteroventral bristle below middle and a distinct apicoventral bristle. Wing membrane conspicuously white, veins hyaline, costa pale yellowish brown. Second and third costal sectors subequal (Fig. 112) (second 0.96-0.98 times as long as third in female, 0.97 times as long in male).

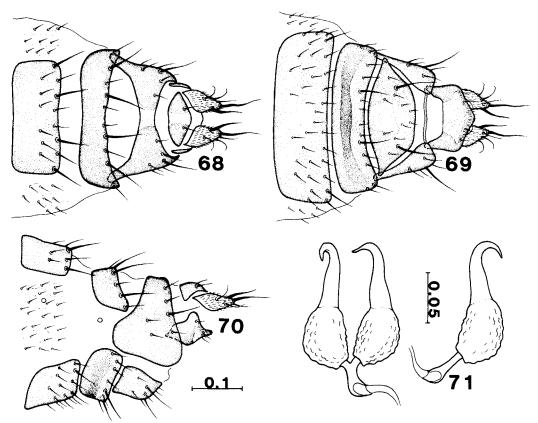
Male abdomen. Sternite 5 with 2 wide, flat posterior appendages covered with small setae and connected by a finely setulose, membranous posteromedial area (Fig. 65). Epandrium (Fig. 64) uniformly and sparsely haired. Cerci reduced and fused with epandrium, each with a long caudal bristle. Surstylus (Figs. 63, 64) long, slender, pointed, with numerous long setae on anterior margin and with only short hairs on posterior margin; these restricted to apical half. Parameres long, slender, distally tapering but blunt at apex. Basiphallus compact, frame-like, shorter than distiphallus. Distiphallus simple, formed by larger dorsal and small ventral sclerite; membranous part connecting them armed by thorn-like spicules (Fig. 66).

Female abdomen. Tergite 7 short, wide, darkly pigmented (Fig. 68). Tergite 8 medially shortened, with pale median stripe. Epiproct short, small, with a pale median stripe. Sternite 7 with a pigmented transverse band (Fig. 69). Sternite 8 large, convex; hypoproct laterally heavily sclerotized and dark, medially with large, membranous area and anteriorly with a narrow stripe connecting its anterior corners. Spermathecae (Fig. 71) large, each with finely tuberculate basal part and long, curved terminal projection. Cerci short, each with a stout, sinuate, apical and dorsopreapical bristle.

Material examined. Roháček (1983) described this species on the basis of 1 \bigcirc (Holotype) from Czechoslovakia and another 2



FIGS. 63-67. Telomerina eburnea, male: 63, left surstylus; 64, terminalia, left lateral; 65, sternite 5; 66, aedeagal complex, left lateral; 67, epandrium and surstyli, caudal view.



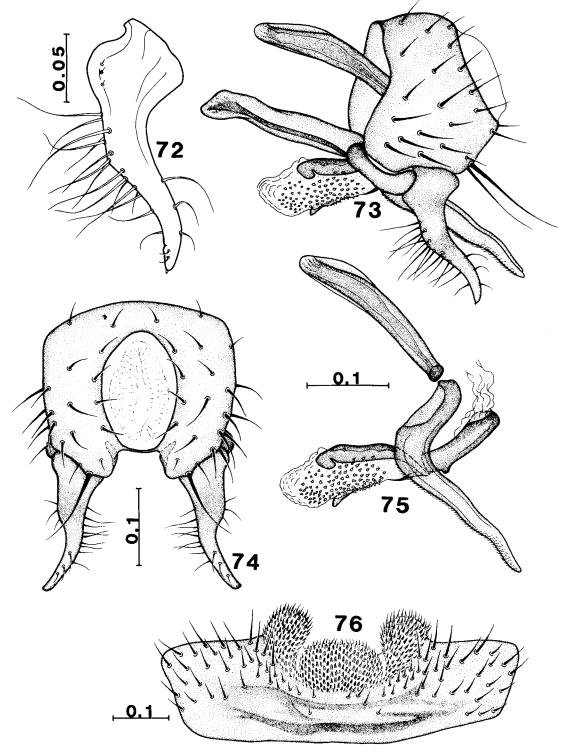
FIGS. 68-71. Telomerina eburnea, female: 68, terminalia, dorsal; 69, terminalia, ventral; 70, terminalia, left lateral; 71, spermathecae.

from Denmark. Other material examined: 1 d, FINLAND: Oulanka Biol. Stat., NL. 66.3 meat trap, 20.vii.1967 (*Mihalyi*) (TMB).

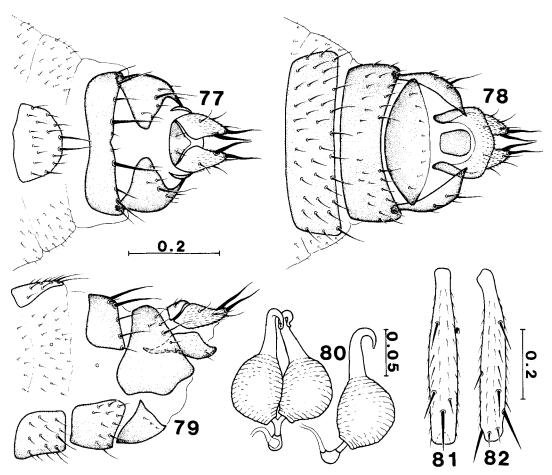
Telomerina cana sp.n. (Figs. 72-82, 114)

Description. Length 2.0-2.5 mm; colour yellow brown. Interfrontal bristles in 4 subequal pairs, lower 2 pairs weakly cruciate. Postocellar bristle present but minute, less than half as long as paravertical bristle. Orbital setulae well developed, but in a short row ending before ventral eye margin; some minute setulae below eye. Lower frons and interantennal area strongly convex, face deeply concave. Eye diameter 1.3-1.6 times smallest genal width. Scutum with 2 pairs of dorsocentral bristles, anterior pair half as long and just as thick as posterior pair; acrostichal setulae in 5 or 6 rows, proscutellar pair slightly enlarged, half as long as anterior dorsocentrals. Katepisternum with posterodorsal bristle reaching one-half way to wing base, a much smaller bristle present anterior to this bristle. Scutellum broad, 1.2 times as wide as long. Mid tibia (Figs. 81, 82) with a distinct anteroventral bristle below middle and a long ventral bristle at apex; anteroventral bristle shorter in female. Wing (Fig. 114) slightly opalescent, costa light brown, other veins yellowish. Second costal sector slightly longer than third (1.05-1.20 times as long in female, 1.20 times as long in male).

Male abdomen. Sternite 5 (Fig. 76) with a large membranous posteromedial area, central part densely covered by flat, scale-like setae; this area flanked by broad lobes very densely covered with similar setae. Epandrium (Fig. 73) with posterodorsal and posteroventral bristles and 7 or 8 bristles on anteroventral portion. Cerci reduced and fused with epandrium, each with a long caudal bristle (Fig.



FIGS. 72-76. T.cana, male: 72, left surstylus; 73, terminalia, left lateral; 74, epandrium and surstyli, caudal; 75, aedeagal complex, left lateral; 76, sternite 5.



FIGS. 77-82. *T.cana*, female: 77, terminalia, dorsal; 78, terminalia, ventral; 79, terminalia, left lateral; 80, spermathecae; 81, mid tibia, dorsal; 82, mid tibia, anterior.

74). Surstylus (Fig. 72) long, narrow, weakly S-shaped, with no adornment other than long, hair-like bristles; several of these bristles on anterior surface, 3 posterior bristles on distal one-third, basal two-thirds of surstylus bare posteriorly (in contrast to *flavipes*).

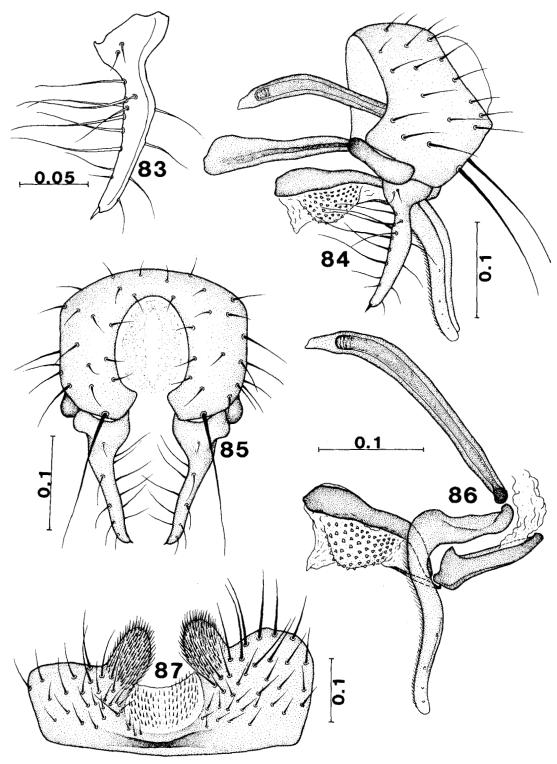
Parameres (Fig. 75) long, slender, distally tapering to a point, distal one-fifth transparent. Basiphallus subequal to distiphallus (Fig. 75). Distiphallus simple, with a small ventral and large dorsal sclerite; membranous part armed by quadrate spicules.

Female abdomen. Tergite 7 short, wide, darkly pigmented (Fig. 77). Epiproct short, small, with a pale median stripe. Sternite 7 darkly pigmented, lighter anteromedially and posteriorly. Sternite 8 large, convex; hypoproct simple, bare on anterior half and setulose on posterior half, a quadrate anteromedial portion surrounded by membranous area (Fig. 78). Spermathecae large, each with a finely tuberculate basal part and long, curved terminal projection (Fig. 80). Cerci short, each with a stout, sinuate apical and dorsopreapical bristle (Figs. 77, 79).

Holotype &, U.S.A.: Alabama, Marshall Co., 4 miles N Union Grove, Merrill Cave, 10.vii.1967 (Peck & Fiske) (CNC).

Paratypes U.S.A.: 4 Å, 5 Ŷ, collected with holotype (JRO, GUELPH, CNC); 4 Å, 3 Ŷ, Tennessee, Shell Mound, Nickajack Cave, 1.vii.1937 (*Dierolf*) (FLD); 1 Å, Oklahoma, Kansas Bat Cave, 10.vi.1938 (*Dierolf*) (FLD).

Etymology. The specific name is from the Latin for 'whitish grey', and refers to the opalescent wing membrane.



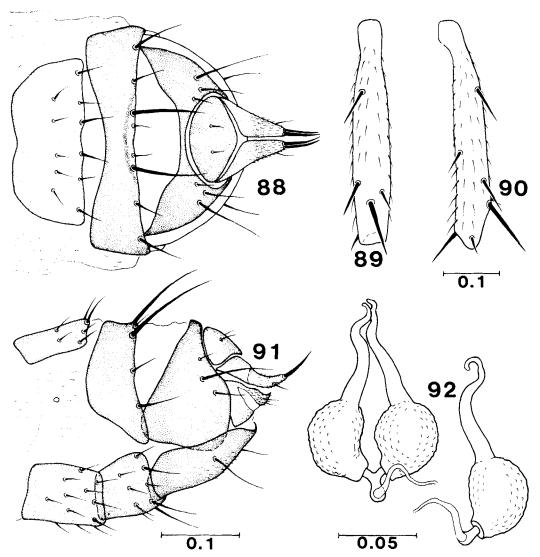
FIGS. 83-87. Telomerina paraflavipes, male: 83, left surstylus; 84, terminalia, left lateral; 85, epandrium and surstylus, caudal view; 86, aedeagal complex, left lateral; 87, sternite 5.

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Telomerina paraflavipes (Papp, 1973b) (Figs. 83–92, 115)

Limosina paraflavipes Papp, 1973: 401. Holotype &, MONGOLIA: Bulgan aimak, 11 km W von Somon Bajannuur am see Bajannuur, 1000 m, nr 958, 14.vi-24.vii.1968 (Kaszab) (TMB).

Description. Length 1.1-1.3 mm; colour brown to blackish brown, pruinose. Interfrontal plate bordered by 4-5 short, subequal interfrontal bristles. Eye diameter about 1.5 times narrowest genal width. Postocellar bristle present but minute. Orbital setulae well developed, in a long row extending below eye. Dorsocentral bristles in two pairs, anterior pair short. Acrostichal setulae in 6-8 rows between anterior dorsocentrals. Scutellum long. Mid tibia of male with a small anteroventral bristle below middle and a distinct apicoventral bristle; these bristles longer in female (Figs. 89, 90). Wing (Fig. 115) long and narrow, with whitish membrane; costa brown, other veins yellowish. Second costal sector longer than third (1.16-1.40 times as



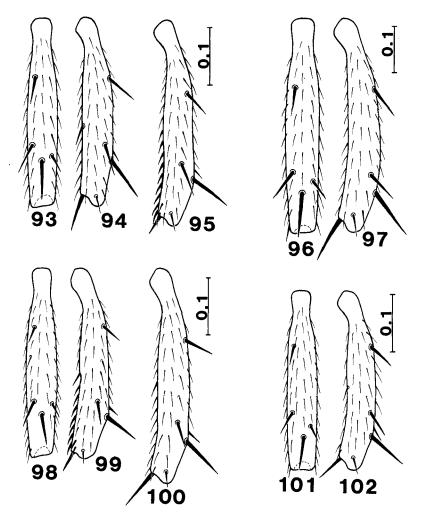
FIGS. 88-92. Telomerina paraflavipes, female: 88, terminalia, dorsal; 89, mid tibia, dorsal; 90, mid tibia, anterior; 91, terminalia, lateral; 92, spermathecae.

long in male, 1.11-1.27 times as long in female).

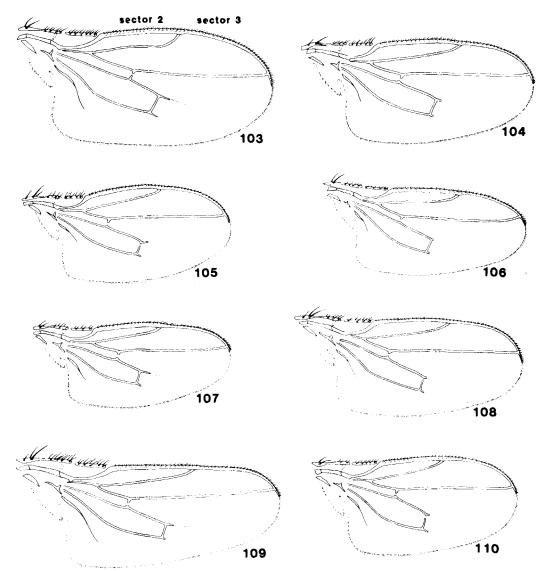
Male abdomen. Sternite 5 (Fig. 87) with large, flat, densely setulose lobes at posterior margin flanking weakly setulose, membranous posteromedial region. Surstylus (Figs. 83, 84) long and slender, with a short apical spine. Aedeagal complex (Fig. 86) large; paramere large, somewhat S-shaped, with finely haired anterior margin. Basiphallus broad and flat, subequal in length to distiphallus. Distiphallus simple, membranous part dotted with spicules.

Female abdomen. Tergite 7 short and wide, transverse, with a pair of strikingly long.

bristles at middle of posterior margin (Fig. 88). Tergite 8 constricted but sclerotized dorsally; laterally greatly enlarged. Epiproct short, oval; medially with pale pigmented stripe and 2 setulae. Sternite 7 short, more darkly pigmented than sternite 6. Sternite 8 very long (longer than in any congener), rounded posteriorly, with 2 long bristles in addition to short setulae. Hypoproct complex, partly membranous. Each spermatheca (Fig. 92) with finely tuberculate body and long terminal process, apex of process twisted. Cerci very different from congeners, long and slender; in profile strikingly upcurved and



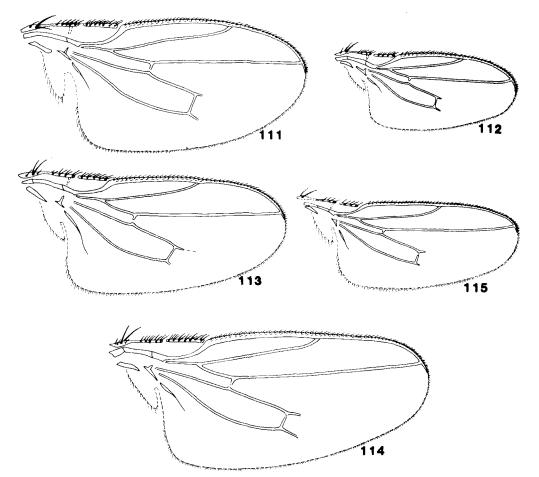
FIGS. 93-102. Nearctic Telomerina spp., mid tibiae. 93-95, submerda: 93, female, dorsal; 94, female anterior; 95, male anterior. 96-97, chillcotti female, anterior. 98-100, pengellyi: 98, male, dorsal; 99, male, anterior; 100, female, anterior. 101-102, orpha, male: 101, dorsal; 102, anterior.



FIGS. 103-110. Telomerina spp., wings: 103, levifrons, male; 104, submerda, male; 105, kaszabi, male; 106, pengellyi, male; 107, pseudoleucoptera, female; 108, flavipes, male; 109, flavipes, female; 110, ursina, male.

each bearing 2 apical spines which look like a single spine in profile.

Material examined. MONGOLIA: 19, collected with holotype, poor condition; 1 d, 19, Chovsgol aimak, 3 km SW von Somon Burenchaan, 1650 m, Exp. Dr Z. Kaszab, 1968, Nr 993, 21.vi-16.vii.1968 (TMB); 19, Central aimak, 11 km S vom Pass Zosijn davaa, 90 km S von Ulan-Baator, 1650 m, Exp. Dr Z. Zaszab, 1967, Nr 768, 7.vi.1967 (TMB) (all paratypes of *paraflavipes*). Other paratypes mentioned by Papp (1973b) are not conspecific with the holotype and belong to *T.flavipes*. These are as follows: 4 d, same data as holotype; 1 d, 1 ♀, MONGOLIA: Central aimak, Ulan-Baator, Nucht im Bogdo ul, 1600 m, Exp. Dr Z. Kaszab, 1965, Nr 297A, 22.vii-27.viii.1965 (TMB).



FIGS. 111-115. Telomerina spp., wings: 111, chillcotti, female; 112, orpha, male; 113, eburnea, female; 114, cana, female; 115, paraflavipes, male.

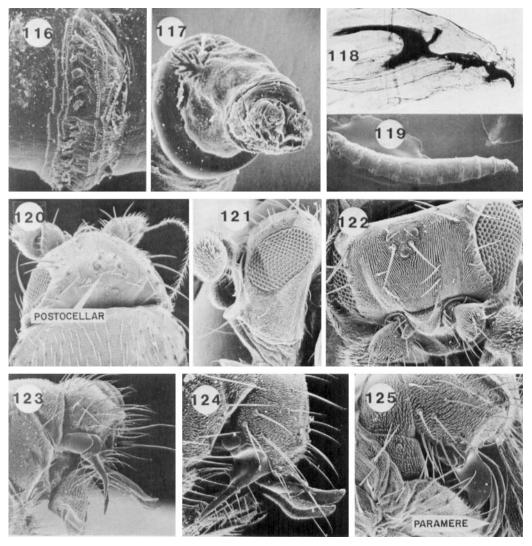
Other species possibly in Telomerina

Leptocera (Scotophillela) cellularis Spuler, 1925: 79. Holotype d, U.S.A.: Texas, Austin (Melander).

Although the type material of this species cannot be found, Spuler's wing figure and, to a lesser extent, his comments on eye size indicate that it belongs in *Telomerina* (see also Roháček, 1983: 130). His description of eye size is difficult to interpret, since in one sentence he says 'eyes rather small, occupying but little more than half the distance from mouth margin to vertex' (i.e. eye height equal to genal height), then proceeds to say 'cheeks, at vibrissal angle, half as high as eye' (i.e. eye height double genal height). No specimens were seen that fit Spuler's description of a species with 3 katepisternal bristles (as in *chillcotti*) and a mid tibial mid ventral bristle (as in *flavipes*). Spuler's description is so inadequate that, in the absence of type material, it is not possible to be certain that *cellularis* belongs in *Telomerina*.

Phylogeny

Telomerina, as defined in the present paper, is clearly a monophyletic group with a number of autapomorphic characteris. Although Roháček (1982) suggested its affinity to the genus Opalimosina Roháček, there is no well-



FIGS. 116–119. *T.flavipes*, larva: 116, ventral creeping welt; 117, head and thorax, anterolateral; 118, cephalopharyngeal skeleton; 119, habitus, left lateral.

FIGS. 120–122. Telomerina heads: 120, flavipes, posterodorsal; 121, pengellyi, lateral; 122, pengellyi, anterodorsal.

FIGS. 123-125. Telomerina, male terminalia, left lateral: 123, flavipes; 124, pengellyi; 125, chillcotti.

supported sister-group relationship between *Telomerina* and any other genus of the Limosininae. This gap in our knowledge of higher classification can be attributed to the virtually unknown nature of much of the world's sphaerocerid fauna. The study of Neotropical Limosininae in particular can be expected to yield informative taxa.

As shown by the list below, the monophyly of *Telomerina* is most strongly supported by a number of characters of the male and female terminalia. Other features, such as chaetotaxy, are highly conservative throughout the subfamily. Characters are enumerated below as on the cladogram (Fig. 126). In the absence of a clearly defined sister taxon, character polarity was determined using the remainder of the Limosininae as a generalized outgroup.

- - apomorphic; - plesiomorphic.
- ■, □ interpretation uncertain.
- 1. - Subanal plate and sternite 10 absent.

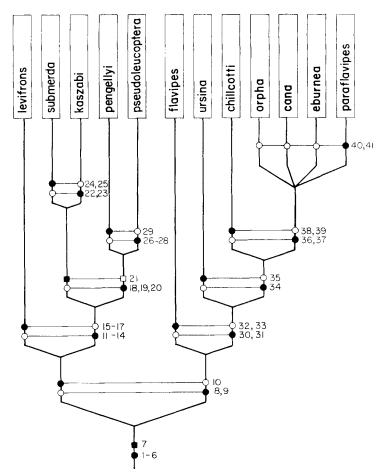


FIG. 126. A phylogenetic hypothesis for the genus Telomerina.

- 2. - Paramere long and slender.
- Surstylus anteriorly and internally public pu
- Female sternite 6 narrow and weakly sclerotized.
- 5. - Female hypoproct of complex form.
- Spermathecae usually with slender terminal projection.
- 7. - Costa produced far beyond R_{4+5} and discal cell long.
- e distiphallus with spicules in membranous part (*flavipes*-group);
 - – distiphallus without such armature (*pseudo-leucoptera*-group).
- 9. spermathecae with slender and long terminal projection curved or twisted only apically (*flavipes*-group);
 - spermathecae simple or with short, strongly twisted projection (*pseudoleucoptera*group).
- 10.• male mid tibia ventrally with a row of short spines (pseudoleucoptera-group);

 male mid tibia ventrally without short spines and usually with a small anteroventral bristle below middle (*flavipes*group).

Only a single character (10) is used to support the monophyly of the *T.pseudoleucoptera* group including *T.levifrons*, and furthermore this character is one subject to convergent development throughout the Limosininae. The inclusion of the strongly plesiomorphic *T.levifrons* in the *pseudoleucoptera* group is thus poorly supported, and there is a possibility that *T.levifrons* is the sister group to the rest of *Telomerina*. The monophyly of the *pseudoleucoptera* group excluding *levifrons* is well supported by several characters, listed below along with the autapomorphies of *T.levifrons*.

- 11.• paramere long and slender;
- – paramere short, thicker.
- 12.• female tergite 9 long;
- − female tergite 9 shortened, transverse.
- 13. spermathecae either with terminal twisted projection or this indicated by a small terminal tubercle;
 - \circ spermathecae completely simple.
- 14. - R_{2+3} very slightly bent apically;
- $\circ R_{2+3}$ strongly bent apically.
- 15.• male cerci projecting below epandrium;
 - \circ male cerci more reduced.
- 16.• distiphallus with reduced sclerites;
- • distiphallus with larger sclerites.
- 17. male sternite 5 with medial knob-like projection;
 - — male sternite 5 medially without projection.

Within the *pseudoleucoptera* group, 2 clades include Nearctic-Palaearctic sister species. *T.submerda* and *T.kaszabi* share striking similarities of the male terminalia; but since the female of *kaszabi* is unknown, we can only predict that *kaszabi* will exhibit the plesiomorphic form of (19), a female character found in its apomorphic form in the sister group *pengellyi* and *pseudoleucoptera*. Characters of these 2 clades are as follows:

- 18.• spermathecae with twisted terminal projection;
 - spermathecae without terminal projection.
- 19.• basiphallus reduced to a slender frame;
- basiphallus more robust.
- 20.• surstylus with an anterobasal, long-haired lobe;
- – surstylus simple anterobasally.
- 21.• surstylus widened and bearing 2 apical robust spines;
 - surstylus slender, simple apically.

Autapomorphic characters of the above four *pseudoleucoptera* group species are as follows:

- 22. – paramere pointed apically;
- – paramere rounded (blunt) apically.
- 23. male sternite 5 with 2 groups of thick spines;
 - \circ male sternite 5 without such spines.
- 24. - surstylus and its apical spines very robust;
- surstylus more slender and its apical spines smaller.
- 25.• distiphallus finely spinulose;
- − distiphallus unarmed.
- 26. apex of paramere flattened and strongly widened;
 - \circ apex of paramere simple in shape.
- 27.• surstylus with larger anterior projection and without apical short spines;

- - surstylus with smaller anterior projection and with 2 small blunt bristles on apex.
- 28. female cerci with shortened apical setae;
 female cerci with longer apical setae.
- 29.• female sternite 8 with posterior medial lobe;
 - female sternite 8 simple.

The other main group of *Telomerina* is the *flavipes* group with seven species. In this group a much greater homogeneity of male and female abdomens is found than is the case in the *pseudoleucoptera* group. Derived characters of the *flavipes* group as a whole include the strongly spinose distiphallus membrane and the apically elongated spermathecae. *T.flavipes*, presumed sister taxon to the rest of the species group, shows the above characters in a weakly developed, presumably primitive state. Characters defining the clades within the *flavipes* group are listed below.

- 30.• membrane of distiphallus with distinctive thorn-like armature;
 - \circ distiphallus with finer grains in membrane.
- 31.• spermathecae with long terminal projection;
 - - spermathecae with shorter terminal projection.
- 32. proximal part of surstylus with long posterior hairs;
 - - proximal part of surstylus bare posteriorly.
- 33. paramere with pointed apex;
- paramere with rounded apex.
- 34.

 spermathecae with very long and narrow terminal projection, apically hook-like curved;
 - - spermathecae with shorter, more robust and simple terminal projection.
- 35.• surstylus with 2 short robust spines on apex;
 - - surstylus at most with small apical spine.
- 36. male sternite 5 with 2 distinctive posterior lobes;
 - - distinct posterior lobes of male sternite 5 not developed.
- 37. -spermathecae with wrinkled and tuberculate bodies;
 - - spermathecal bodies with plain (smooth) surface.
- 38.• surstylus flattened, broad;
- surstylus narrow, slender.
- 39. mid tibia without anteroventral bristle below middle;
 - – mid tibia with anteroventral bristle (sometimes small) below middle present.
- 40.● female cerci modified, slender, with 2 closely arising spines;
 - - female cerci robust and with 2 thick sinuate hairs besides small setulae.

41.● - female sternite 8 very enlarged;
○ - female sternite 8 smaller.

The relationships between orpha, eburnea, cana and paraflavipes are not clear. T. paraflavipes stands apart from the other three species on the basis of a number of striking autapomorphies such as the pointed, upturned female cerci. T. orpha, eburnea and cana, on the other hand are almost identical. This apparent similarity is due to plesiomorphic characters and the expected close sisterspecies relationships are not supported by apomorphies. For this reason, this group of four species is treated as unresolved in Fig. 126.

Discussion

Although some aspects of the above phylogeny are highly speculative, some proposed sister-group relationships stand out as strongly supported hypotheses. Almost all of these are between Nearctic and Palaearctic species pairs such as submerda-kaszabi, or pengellyipseudoleucoptera. This seems to be a general phenomenon within the Limosininae and has been documented in the genera Aptilotus (Marshall, 1983) and Rudolfia (Marshall, 1982b). Within the genera of Limosininae which have been examined on a Holarctic basis, most of the clearly supported species pairs are Nearctic-Palaearctic. Although all of the species pairs previously known were Nearctic-western Palaearctic, they were seen as reflecting relatively recent faunal interchange across Beringia, and the lack of related East Palaearctic species was thought to represent our lack of knowledge of that area. The close relationship between kaszabi (Mongolia) and submerda (southeast U.S.A.) supports the expectation that the East Palaearctic fauna will show strong Nearctic affinities. Although the habits of kaszabi are unknown, submerda is associated with the dung of large herbivores and appears to be restricted to the interstices between the dung and the soil. Its apparent restriction to the southeast may be merely a reflection of the disinclination of insect collectors in other areas to carefully examine the interstices beneath ungulate dung.

This general problem of inadequate distribution of data for species in restricted habitats also hinders our interpretation of *T.levifrons*.

T.levifrons is unique in Telomerina and unusual in the Limosininae in being a nonsynanthropic fly of probable low vagility with a Holarctic distribution. Since it is associated with bogs, we can suggest that it is either a relict species left in isolated boreal-type patches upon the retreat of the last glaciation, or it is a widely distributed Holarctic species in bog and boreal habitats today. A boreal habitat could have allowed T.levifrons to maintain a trans-Beringian fauna in a fairly uniform habitat while other, previously Holarctic species were divided into disjunct Palaearctic and Nearctic ranges. The possibility must also be recognized that levifrons actually consists of morphologically identical but genetically distinct Nearctic and Palaearctic species equivalent to the more usual morphologically divergent species pairs commonly encountered in the Limosininae.

Although a number of zoogeographic scenarios could be suggested to account for the primary division of Telomerina into two clades, one intriguing possibility is that this reflects vicariance of eastern North America and the western Palaearctic about 50 million years ago. North Atlantic faunal interchange and subsequent vicariance of eastern North America and the western Palaearctic provides a plausible explanation for higher level sistergroup disjunctions in less speciose groups such as Nearcticorpus-Puncticorpus (Roháček & Marshall, 1982) and Ceroptera (Marshall, 1982a). Perhaps the primary division of Telomerina was into a flavipes-like western Palaearctic species and a levifrons-like eastern Nearctic species. Subsequent speciation may have been triggered by vicariance events such as those caused by changes in Beringia, habitat shifts such as a shift from the moist bog environment to the more restricted moist microhabitats under ungulate dung or in caves, or combinations of both factors.

Conclusions

Although there is a clear pattern of disjunct Nearctic-Palaearctic sister-species relationships within this genus, lack of extensive distributional data and microhabitat information stands in the way of a detailed reconstruction of a zoogeographic history for *Telomerina*. Further data from the eastern Palaearctic and northwestern Nearctic are needed, along with elucidation of specific microhabitats of each species and careful study of those microhabitats throughout the potential ranges. It is hoped that this paper has provided both the stimulation and the necessary taxonomic framework for such further study.

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