# A revision of the *Sclerocoelus galapagensis* group (Diptera: Sphaeroceridae: Limosininae)

### S. A. Marshall

Department of Environmental Biology, University of Guelph, Guelph, Ontario, N1G 2W1, Canada.

Abstract: The Sclerocoelus galapagensis group is defined and revised, including the description of S. galapagensis new species from the Galapagos Islands; S. caribensis new species from the Caribbean and adjacent areas; S. brasilensis new species from Brazil, Ecuador, Colombia, and Panama; S. hemorrhoidalis new species from Ecuador and Venezuela; and S. andensis new species from Argentina, Bolivia, and Venezuela. The south Atlantic species Sclerocoelus subbrevipennis (Frey), new combination, is redescribed as a member of the S. galapagensis group, and is considered the sister species to the rest of the species group. A key to species, character matrix, and cladogram are provided.

### Introduction

The genus *Sclerocoelus* Marshall is abundant in the New World, with over 40 species distributed from Canada to Argentina, and with one species, *Sclerocoelus subbrevipennis* (Frey) from the south Atlantic. The latter species is a member of the distinctive *Sclerocoelus galapagensis* group, and is here redescribed from Tristan da Cunha. The *S. galapagensis* group also includes five other new species from the Galapagos Islands, Mexico, the Caribbean, Central America, and South America (Map).

Most Sclerocoelus are associated with wet, decaying vegetation in cloud forests, where they are often collected in large numbers by sweeping a net over moist dead leaves. The species group revised here, the S. galapagensis group, is the most distinctive and easily diagnosed group of Sclerocoelus. All species in the group can easily be distinguished from congeners by the conspicuous, sclerotized male perianal pads or by the spinose apical bristles of the female cerci. They are also generally larger than congeners and, as outlined in the diagnosis below, form a clearly monophyletic group characterized by other striking apomorphic characters.

Other than the 6 species considered here, the only described species of *Sclerocoelus* are the widespread, Nearctic, type species, *S. sordipes* (Adams), and the Neotropical species *S. plumiseta* (Duda) and *S. regularis* (Malloch).

### Sclerocoelus Marshall

Sclerococlus Marshall, 1995: 283. Type species Limosina sordipes Adams 1904

Diagnosis of the genus *Sclerocoelus*: Members of the genus *Sclerocoelus* can be recognized by the combination of a very broad alula, an enlarged intra-alar bristle just anterior to the prescutellar dorsocentral bristle, a very broad lunule and characteristic tibial chaetotaxy including a mid ventral bristle only in the female. Characteristics of the male genitalia, especially the complex subcerci and genital pouch, are defining for the genus (Marshall, 1995).

Diagnosis of the *Sclerocoelus galapagensis* group: All members of the species group have strongly developed male perianal pads, characteristically shaped surstyli, and one (or rarely 2) stout apical bristle on each female cercus. All Neotropical species have setae on the membrane flanking the prosternum.

Description of the Sclerocoelus galapagensis group: Dark, heavily pollinose limosinines. 2.0-3.0mm, usually ca. 2.5mm. Interfrontal area tapered, width at top equal to height; 3 equal interfrontal bristles. Lunule prominent, broadly rounded. Fore coxa with 3-4 short, stout medial preapical bristles. Acrostichal bristles in 8 rows between anterior dorsocentrals; prescutellar acrostichal bristle and posterior intra-alar bristle twice as long as anterior dorsocentral bristle; anterior dorsocentral bristle slightly longer than acrostichal setulae. Scutellum 1.3-1.5X as wide as long, four apical bristles 1.8-2.0X as long as scutellum. Dorsal surface of mid tibia with 2 large anterodorsal bristles and 1 small posterodorsal bristle proximally, posterodorsal bristle midway between anterodorsals; 2 anterodorsal bristles distally, the lower one twice as long as the upper; 1 very large posterodorsal distal bristle; 1 very small distal dorsal bristle at level of upper anterodorsal. Mid tibia of female with a midventral bristle; ventral surface of male mid tibia with a patch of short, stout bristles distally; mid tibia of both sexes with a strong apicoventral and weaker posteroventral and anteroventral apical bristles. Mid femur with short, stout anteroventral and posteroventral bristles basally; mid basitarsus with an enlarged ventral bristle in basal half. Wing with second and third costal sectors equal;  $R_{9+3}$  sinuate, strongly curved up to costa.

**Abdomen:** Syntergite 1+2 with broad, short, anterior pale area with a narrow posterior extension. Sinistral flange of synsternite 6+7 short, weakly developed; synsternite completely separated from sternite 8. Inner ventral corners of epandrium widely separated, forming narrow, truncate lobes. Sternite 10 (subepandrial sclerite) complete medially. Subcercus complex, with an outer (upper) part usually projecting posteriorly into the perianal pad and anteriorly to the posterior surstylar-epandrial junction, and an inner (lower) part often with a long posterior arm; junction of inner and outer parts of subcercus with posterior bristles: left and right subcerci meeting or almost meeting near posteromedial part of sternite 10 (subepandrial sclerite). Distiphallus short, broad, dorsoventrally flattened, with broad, laterally-directed basal sclerites, a basal ring, and a distal part comprising two curved lateral sclerites and a medial sclerite which is usually distally bifid. Three spermathecae, single one largest; swollen apically with a shallow invagination; ducts short, inserted near invagination; surface striate.

# Phylogeny of the Sclerocoelus galapagensis species group

Analysis of a matrix of 22 characters, using Hennig 86, yielded three equally parsimonious cladograms (consistency index 82, retention index 87, length 35) which differed only in the placement of the two island endemics, the Atlantic subbrevipennis and the Pacific galapagensis. I prefer the cladogram treating subbrevipennis as the sister group to the rest of the genus, and placing galapagensis as the sister group to the rest of the New World species (Fig. 1, table 1). The latter sister group relationship is supported by two unusual, independent characters (16,17) which probably represent good synapomorphies. An alternative cladogram treats the phenetically very similar island endemics as sister species based on two wing char

acters (18,19). The short, brown wings of galapagensis are extremely similar to those of subbrevipennis; however, shortening and darkening of wings is common in insular sphaerocerids and these characters are therefore considered especially subject to homoplasy. The third cladogram treats galapagensis as the sister group to the rest of the genus, and links the Atlantic subbrevipennis to mainland Neotropical and Caribbean species on the basis of two characters of equivocal polarity (6,21). Character 21, the presence of a single stout apical bristle at the apex of the female cercus, is probably a synapomorphy for the whole species group and is reversed in galapagensis by the enlargement of the inner preapical cercal bristle found in all members of the species group.

The relationships between the remaining four species, all found in mainland South America and the Caribbean basin, are well supported. Sclerocoelus brasilensis is the most plesiomorphic of the mainland species, with superficial similarities to the island endemics. Sclerocoelus brasilensis is treated as the sister group to the other mainland and Caribbean species on the basis of six weak synapomorphies (7,9,13,14,20,22), which are not conflicted elsewhere on the cladogram. The monophyly of a group containing the remaining three species in the group (caribensis, andensis, hemorrhoidalis) is much more strongly supported. Relative to other Sclerocoelus, members of this group seem to be characterized by progressive reduction of the complicated set of genital pouch sclerites (Character 1). Most members of the genus have an apparently homologous series of sclerites including 4 or 5 separate sclerites between the left side of synsternite 6+7 and the spiracular sclerite on the right side of the abdomen. In the basal lineages of the galapagensis species group, 3 of these sclerites are clearly visible, and 2 (sclerites C and D) are separate as in other Sclerocoelus. These sclerites disappear in the highly distinctive Neotropical clade including caribensis, andensis, and hemorrhoidalis, and are replaced with a deep, evenly sclerotized pouch. This group is also characterised by a number of other unique synapomorphies of the male and female genitalia, and the monophyly of this clade of three species seems unequivocal.

# Zoogeography of the Sclerocoelus galapagensis species group

As is the case for the genus as a whole, members of the *Sclerocoelus galapagensis* group are almost

always associated with wet leaf litter in cloud forests or similar habitat. This might seem to suggest that these species are less likely to colonize islands than are littoral species. It is possible, however, that association with wet litter predisposes Sclerocoelus species to inclusion in flood debris washed out to sea after heavy rains. Peck (1994) found abundant fluvial debris in pleuston net samples taken between the Galapagos Islands during the strong 1992 El Niño event. The same pleuston net samples included almost 4,000 arthropods. Although none were identified as Sphaeroceridae, transport in riverine flood debris is a plausible mechanism for the dispersal of cloud forest species to islands. Sclerocoelus subbrevipennis is the only endemic sphaerocerid in the remote Tristan da Cunha group, and S. galapagensis is one of a very few endemic sphaerocerids on the Galapagos islands, so the group appears to be preadapted to overwater dispersal. Sclerocoelus subbrevipennis probably originated from an eastern South American population of the common ancestor of the whole group, subsequent to which the ancestral species of the new world clade acquired synapomorphies 16 and 17. Western South American populations of this species served as the source for the ancestor of Sclerocoelus galapagensis, which is now restricted to wet Scalesia forest on the Galapagos Islands. Division of the mainland ancestral species into the eastern South American brasilensis, and a western Neotropical-Caribbean clade must have been the next occurrence in the zoogeographic history of the group. The western Neotropical-Caribbean clade then split into caribensis in the Caribbean basin, and an Andean species ancestral to andensis and hemorrhoidalis. Today, andensis is common in relatively undisturbed southern Andean cloud forests, and has been collected in cloud forests as far north as Venezuela. Sclerocoelus hemorrhoidalis is known from relatively few specimens, mostly from disturbed sites such as pasture and a riverbank in an urban area near Merida, Venezuela.

# Key to species of the Sclerocoelus galapagensis group

- Posterodorsal katepisternal bristle fine, hair-like, reaching at most one-third of the way to wing base.

- 3. Wing membrane brown, especially above and below R<sub>2+3</sub>. Cerci of female dorsally concave, shining, terminating in 2 strong bristles (Fig. 38). Galapagos......

- Sternite 5 of male longer than genital pouch and subequal in length to sternite 4, with two setose posteromedial lobes; setosity of posterolateral area sparse (Fig. 45). Genital pouch well developed, but relatively small and lightly sclerotized ...... Sclerocoelus hemorrhoidalis, new species.

### Sclerocoelus andensis, new species (Figs. 2-12)

**Description:** Length 2.2-3.0mm; dark brown to black; legs, pleuron, and gena reddish-brown, tarsi paler; interfrontal strips black, lower frons

otherwise reddish; vibrissal angle reddish brown like anterior gena and lateral parts of face, middle part of face darker. Minimum interantennal distance 1.7X width of ocellar triangle. Eye height 3.2-3.5X genal height; anterior genal bristle as long as genal height.

Prothorax with 3 small, bristle-bearing sclerites in membrane beside prosternum. Katepisternum with a short, fine posterodorsal bristle and a minute anterodorsal setula. Male mid tibia strongly curved; ventral surface with a row of slightly enlarged bristles on distal half, apical fifth covered with stout, curved bristles. Male mid femur with a row of 4 stout anteroventral and a patch of ca. 10 stout posteroventral bristles at base. Wing length 2.5x width; membrane clear.

Male abdomen: Tergite 5 with middle posterior bristles short but with 2 or 3 pairs of other posterior marginal bristles 1.5X tergite length. Sternite 5 similar in size to sternite 4; uniformly dark brown except for short, pale, striate portion normally telescoped over sternite 4; posteromedially with a setulose patch from which arise 2 very dark, posteriorly directed lobes. Synsternite 6+7 almost symmetrical, right side (spiracular sclerite) similar in size and shape to ventral part of left side. middle part forming a continuous narrow band ventral to a deep, sclerotized central pouch. Ring sclerite well developed, posterior to but separate from spiracular sclerite. Epandrium with two posterior bristles as long as epandrium and a posteroventral bristle twice as long as epandrium. Length of dorsal part of epandrium greater than height of anal fissure. Perianal pads strongly developed, longer than epandrium, expanded ventrally; anterior and dorsal parts well sclerotized but posteroventral part membranous, bulbous and setulose. Pseudocercus small, bearing 3 short bristles; connected to epandrium by a pale band of tissue. Halves of sternite 10 (subepandrial sclerite) uniformly narrow except at middle where they are slightly expanded and fused, middle part with weak ventrolateral lobes. Subcercus with large inner lobe, ventrally expanded into posterior and anterior lobes; outer part of subcercus narrow, with anterior arm only. Surstylus large, twice as long as deep in lateral view; anterior part with a digitate anterodorsal process, anteroventrally with 3 inner bristles, a tooth-like apical process, and laterally directed ventral ridge; posterior part of surstylus long, tapered. Paramere very broad basally, apically with a narrow, anteriorly hooked process. Basiphallus short, simple, posteriorly carinate; distally slightly expanded at point of contact with distiphallus. Distiphallus with distally expanded and serrate laterally directed basal sclerites; central sclerite broad, distally pale and bifid.

Female abdomen: Tergite 7 dark; tergite 8 divided into 2 large, dark lateral sclerites and an indistinct, pale dorsal sclerite. Epiproct minutely setulose, tapered between cerci; cerci tapered, with long, stout apical bristle and short stout dorsal preapical bristle. Sternite 7 strongly convex posteromedially. Main sclerite of sternite 8 troughlike; narrow anteriorly, broader posteriorly; anterior and lateral margins dark, middle part bare, pale and concave; 2 small setae on sclerotized bases present in membrane on each side. Hypoproct projecting ventrad and densely long-setose on posterior third.

**Holotype**(♂,CNC) and 43 Paratypes (22♂,21♀,GUE,INESALT): Argentina. Salta. 1500m, 40kmN Salta, Camino La Cornisa, sweep in roadside forest remnant, 27.ii.1992, S.A. Marshall.

Other paratypes: ARGENTINA. Salta. 15kmW Chicoana, Canyada Gotera, 18.ii.1992, sweep in forest remnant, S.A. Marshall (11♂,1♀,GUE); 30kmE Campo Quijano, 18-28.1992, Flight intercept trap and sweep in forest remnant, S.A. Marshall (10,49, GUE); La Caldera, 1500m, forest sweep, 27.ii.1992, S.A. Marshall (6♂,9♀,GUE); 22kmN LaCaldera, El Ucumar, malaise, subtropical humid forest, 2-30.xii.1987. S.&J. Peck (10, CNC). BOLIVIA. Sta. Barbara, N. Coroico, Yungas, 4-5.i.1976, 1100m, L.E. Pena (4♂,3♀, CNC). VENEZUELA. Merida. Los Chorros, 2100m, Flight intercept trap and sweep among debris, 1-5.v.1988, S.A. Marshall (17♂,2♀,GUE,MIZA); Merida, 1500m, Calle Sta. Rosa trail, Flight intercept trap near spring, 24-30.iv.1988, S.A. Marshall (8♂,3♀,GUE).

Comments: Sclerocoelus andensis is most easily separated from other Sclerocoelus on the basis of the 2 pairs of long posterior bristles on male tergite 5. This species is found in Andean cloud forests from Venezuela south to northern Argentina. In the northern part of its range it occurs sympatrically with the closely related S. hemorrhoidalis.

# Sclerocoelus brasilensis, new species (Figs. 13-23)

**Description:** Length 2.4-2.6mm; dark brown to black; legs and gena dark reddish-brown, tarsi paler; lower frons usually luteous only along nar-

row anterior margin; vibrissal angle reddish, contrasting in colour with the dark gena and face. Minimum interantennal distance 1.3X width of ocellar triangle. Eye height 2.8-3.3X genal height; anterior genal bristle as long as genal height. Prothorax with 2-3 small, bristle-bearing sclerites in membrane beside prosternum. Katepisternum with a short, fine posterodorsal bristle and a minute anterodorsal setula. Male mid tibia strongly curved; ventral surface with a row of slightly enlarged bristles on distal half, apical fifth covered with stout, curved bristles. Male mid femur with a row of 6 stout anteroventral and a patch of ca. 10 stout posteroventral bristles at base, anteroventral bristles stouter. Wing length 2.4X width; membrane clear.

Male abdomen: Tergite 5 with middle posterior bristles short but with 3 pairs of posterior bristles ca. 1.1X tergite length and 1 pair of posterolateral bristles ca. 1.3X tergite length. All sternites with a medial longitudinal pale stripe. Sternite 5 equal in width and length to sternite 4; posteromedially with short, wide, pale area, each side bulging and with a pigmented, setose patch. Three small dark sclerites behind posteromedial part of sternite 5, of these the most sinistral (sclerite D) small and apparently fused with sternite 5, the other 2 (sclerites C and E) heavily sclerotized, with dextrally curved, tapered, posterior parts. Spiracular sclerite large, bilobed sinistrally, similar in size to remainder of genital pouch; ring sclerite large, anterior edge fused to spiracular sclerite, posterior edge thin. Right side of sternite 8 cleft; anteroventral part contiguous with spiracular sclerite. Epandrium sparsely setose dorsally, more densely long-setose ventrally, longest posterior bristles shorter than epandrium. Dorsal part of epandrium slightly shorter than anal fissure. Perianal pads flat, dark; tapered and bare ventrally, otherwise microsetulose; ventral lobe articulating with subcercus. Pseudocercus small, brown, free from epandrium, with 3 bristles, upper bristle twice as long as others and half as long as longest epandrial bristle. Each half of sternite 10 (subepandrial sclerite) long, narrow, weakly arched; flattened, expanded and fused medially into a quadrate middle part. Subcercus with inner part ventrally extended into a distally expanded lobe but without prominent posterior process; outer part with prominent anterior and posterior arms, posterior arm articulating with sclerotized part of perianal pad. Surstylus twice as long as deep in lateral view; setulose on ventral half; posterior part flat; anterior part thick,

deeper than posterior part, with 3 or 4 enlarged bristles and a small flat, carina on inner surface; inner anterior corner with a narrow, sharply tapered lobe. Paramere broad basally; distal half narrow, strongly bent posteriorly; apex swollen, with a narrow, anteroventrally recurved part. Basiphallus simple, cylindrical, basally enlarged. Distiphallus short, dorsoventrally flattened, with laterally directed basal sclerites broad but pale and with only 2 or 3 serrations distally; central sclerite narrow, distally bifid.

Female abdomen: Tergite 7 dark, shortened medially; tergite 8 divided into 2 elongate, dark lateral sclerites and an indistinct, pale dorsal sclerite. Epiproct setulose, tapered between cerci; cerci tapered, with stout apical bristle and short stout dorsal preapical bristle. Sternite 7 short, posterior margin appearing slightly concave because of pale posteromedial area. Sternite 8 almost egg-shaped, posterior margin weakly pigmented and appearing concave, lateral margins folded under; 2 small setae on sclerotized bases present in membrane on each side. Hypoproctprojecting ventrad and densely long-setulose on posterior half, anterior part with medial and lateral bare, pigmented areas.

Holotype (o',CNC) and 26 paratypes (15o',11o,GUE,MNR) paratypes BRAZIL. Parana. Curitiba, under fallen epiphytes near Natural History Museum, 5.ii, 1990, S.A. Marshall.

Other paratypes: Bolivia. Coroico Yungas de La Paz, 6-7.i.1976, 1100-1600m, L.E. Pena (1º,CNC). Brazil. Rio de Janeiro, Jacara Pagua, wet litter by stream, 22.i.90, S.A. Marshall (6♂,14♀,GUE); Mury, near Nova Friburgo, 1000m, swept off goat dung in wet area, 11.iii, 1990, S.A. Marshall (1♀,GUE); São Paulo, Jaragua, 8.ii. 1990, S.A. Marshall (30,19,GUE); Parana, Londrina, Parque Arthur Thomas, sweep, 1.ii. 1990, S.A. Marshall (3♂,1♀,GUE); Curitiba, Flight intercept trap in woods behind Natural History Museum (1♂,1♀,GUE); sweep of creek debris east of Curitiba, 8.ii. 1990, S.A. Marshall (1°, GUE). ECUADOR. Pichincha prov., Rio Palenque Station, 47kmS Sto. Domingo, 29.iv-5.v.1987, L.Coote and B. Brown, 180m, Malaise trap, lowland rain forest (1♀,GUE). PANAMA. Barro Colorado Island. Canal Zone. 1.5.1929, C.H. Curran (1♂,1♀,AMNH).

Comments: Males of this species are easily separated from other mainland species by the form of the perianal pads and the separate sclerites behind sternite 5. The name *brasilensis* reflects the abundance of this species in southern Brasil.

### Sclerocoelus caribensis, new species (Figs. 24-33)

**Description:** Length 2.2-2.5mm, dark brown to black, legs dark reddish-brown, lower frons usually red only lateral to interfrontal strips; vibrissal angle reddish, contrasting with darker gena and face. Minimum interantennal distance 1.5X width of ocellar triangle. Eye height 3.5X genal height; anterior genal bristle as long as genal height.

Prothorax with 2-4 small, bristle-bearing sclerites in membrane beside prosternum. Katepisternum with a short, fine posterodorsal bristle and a minute anterodorsal setula. Male mid tibia strongly curved; ventral surface with a row of slightly enlarged bristles on distal half, apical fifth covered with stout, curved bristles and with a large apicoventral bristle. Male mid femur with 2-3 stout anteroventral bristles and 6-8 smaller posteroventral bristles at base. Wing length 2.4X width; membrane clear.

Male abdomen: Tergite 5 with 1 pair of median posterior marginal bristles 1.5X tergite length, other posterior bristles 0.5X tergite length. Sternite 5 0.5X as long as sternite 4; dark except anterolateral corners and posteromedial area; longsetose posterolaterally and posteromedially. Area behind posteromedial part of sternite 5 occupied by a deep sclerotized pouch (sclerite D), with a dark sinistral lobe (sclerite C) and a spinulose patch (sclerite E) posterior to sac. Right side of sclerotized sac with a posterior lip contiguous with spiracular sclerite. Spiracular sclerite very large, well sclerotized. Ring sclerite small, fused to posterolateral corner of spiracular sclerite. Epandrium with dense, short bristles, posterior bristles longer and bristle at posteroventral corner as long as epandrium. Length of dorsal part of epandrium greater than height of anal fissure. Perianal pads strongly developed but shorter than epandrium, expanded ventrally; anterior and dorsal parts well sclerotized but posteroventral part membranous, bulbous and setulose. Pseudocercus small, weakly pigmented, free from epandrium, with 3 small bristles. Halves of sternite 10 (subepandrial sclerite) dark, narrow; contiguous medially, medial part with weak ventral lateral lobes. Subcercus with a broad, elongate inner lobe, posteroventrally extended into a pointed, prominent process; outer part of subcercus with a short posterior arm and a longer anterior arm. Surstylus large, with a scoop-shaped posterior lobe with 4-6 short, stout posterior bristles; anterior part complex, with enlarged ventral bristles, an

anterodorsal inner lobe, and a broad, carinate lobe on medial surface. Paramere short, broad basally, sharply tapered on apical half. Basiphallus short, simple, compressed, partly contiguous with ventral part of distiphallus. Distiphallus with broad, distally serrate, laterally directed basal sclerites; central sclerite narrow, distally pale and bifid.

Female abdomen: Tergite 7 dark; tergite 8 divided into 2 large, dark lateral sclerites and an indistinct, pale dorsal sclerite. Epiproct setulose, truncate; cerci tapered, with long, stout apical bristle and short stout dorsal preapical bristle. Sternite 7 strongly convex posteromedially. Sternite 8 narrow anteriorly, broadened and concave posteriorly; 2 small setae on sclerotized bases present in membrane on each side. Hypoproct projecting ventrad and densely long-setose on posterior half.

Holotype (o',CNC) and 24 paratypes (10o',14o,GUE): DOMINICAN REPUBLIC. Near Cabo Rojo, 1300m, Las Abejas, cloud forest, 19.i.1989, S.A. Marshall.

Other paratypes: Costa Rica. Monteverde Reserve, 1500m, 15-20.viii.1986, L. Masner (18♂,15♀,CNC); Estrella Valley, Pandora, 19.ii. 1984, Malaise trap, H. & A. Howden (1♀, GUE); Cartago, 500m., Turrialba, Catie, 4.ix.1986, L. Masner (1여, GUE); San Jose, San Antonio de Escazu, 25 Mar. to 9 April, 1984, Malaise trap, S.A. Cameron (SNOW, 1♂,1♀); Puntarenas, Monte Verde, ca. 1500m, lower montane wet forest, 4-11.ii.89, D. Grimaldi (10', AMNH). Cuba. Pinar del Rio, Prov. Soroa, 27-28.iv.1983, W.N. Mathis (1♀,USNM). Dominica, W.I. Trafalgar Falls, 6.iii.1965, W.W. Wirth (10, USNM); Clarke Hall Est., 31.v, 1.vi, 2.vi, 3.vi, 4.vi, 1966, G. Steyskal (3♂,2♀,USNM); Manets Gutter, 5.iii.1965, W.W. Wirth (10,2,2,USNM). El Salvador. Los Chorros, 20.vi.1963, D.Q. Cavagnaro & M.E. Irwin (13°,CAS). Guatemala. Isabal, 300m, Las Escobas at light, 14-16.xi. 1986, M. Sharkey (11♂, 13♀, CNC). Jamaica. Hardwar Gap, 10.iii.1970, stream margin, Wirth & Farr (10♂,3♀,USNM); Hardwar Gap, 25.vii.1966, 4000', Howden & Becker (19,CNC); Runaway Bay, ii.1969, W.W. Wirth, stream bed (4♂,2♀, USNM). MEXICO. Tepic, Navarit, 3000', viii.1964, light trap, Blanton & Broce (3♂,1♀,USNM); SLP, 20kmW. Xilitia, 1600m, 12.vi-6.viii, 1983, cloud forest flight intercept trap, S. &J. Peck (10, GUE); SLP, 40kmW. Xilitla, 12.vi-6.viii.1983, 1700m, Pine-Oak forest, Flight intercept trap, S.&J. Peck (19,GUE); Chiapas, Union Juarez, 4kmN., 22.iv.1983, W.N. Mathis (10, USNM). Puerto Rico. Aguas Buenas Census,

Aguas Buenas Cave, 14.v.1973, 250m., S. Peck (19,BERK). St. Kitts, W.I. Mt. Misery, 4-20.xii.1985, 730m, pond/rainforest, L.D. Coote (1°,49,GUE). Venezuela. Aragua, Rancho Grande, Parque Nacional Henry Pittier, 4.iii.1967, flight trap, 1100m, M.E. Irwin (3°,CAS); Rancho Grande, Malaise intercept, 2-30.xii.1987, M. Sanborne (1°,GUE); Caripe, Guachero caves, 20.iv.1986, oilbird refuse piles, S.A. Marshall (1°,MIZA).

Other specimens examined (approx. 400, GUE): Dominican Republic. Las Abejas Valley, near Cabo Rojo; trail to Pico Duarte, near La Cienaga; Barahona: Puerto Plata.

**Comments:** This species is easily separated from congeners by the exceptionally distinctive male postabdomen with spinose surstyli and a short sternite 5. The name *caribensis* reflects the great abundance of this species throughout the Caribbean region.

### Sclerocoelus galapagensis, new species (Figs. 34-41)

**Description:** Length 2.0-2.2mm, dark brown to black, legs and gena reddish-brown, lower frons extensively reddish; vibrissal angle concolorous with reddish gena and face. Minimum interantennal distance 2.0X width of ocellar triangle. Eye height 2.5-3.0X genal height; anterior genal bristle shorter than genal height.

Prothorax with 1 or 2 small bristles in membrane beside prosternum. Katepisternum with posterodorsal bristle reaching one third of way to wing base; anterodorsal bristle minute. Male mid tibia weakly curved; ventral surface with double row of slightly enlarged bristles on distal fifth. Male mid femur with 3 stout anteroventral and 6 or 7 stout posteroventral bristles at base. Wing length 1.9X width; membrane, especially above and below  $R_{2+3}$  heavily brown-tinted.

Male abdomen: Tergite 5 with three pairs of marginal bristles as long as or longer than tergite, other posterior bristles 0.5X tergite length. Sternite 5 as long as sternite 4; setose posterolaterally, bare medially; posteromedial area bilobed, darkly pigmented, densely setulose. Area behind posteromedial part of sternite 5 with three separate, subquadrate, heavily sclerotized sclerites overlapping each other (sclerites C,D, and E); anteriormost of these sclerites fused with inside surface of sternite 5. Spiracular sclerite large, pale, contiguous with well sclerotized ring sclerite. Epandrium with short bristles; posterior bristles longer and bristle

at posteroventral corner half as long as epandrium; anteroventral bristles stout. Length of dorsal part of epandrium subequal to height of anal fissure. Perianal pad strongly developed, almost entirely sclerotized, shorter than epandrium, setulose, ventral part with a narrow lobe articulating with subcercus. Pseudocercus small, weakly pigmented, fused with corner of epandrium, with 3 bristles, the lower 2 very small, upper bristle as long as longest epandrial bristle. Halves of sternite 10 (subepandrial sclerite) dark, narrow; contiguous medially, medial part deeply U-shaped and weakly lobate at middle. Subcercus with a broad, elongate inner part; outer part of subcercus with a very broad anterior lobe and a quadrate posterior lobe articulating with sclerotized part of perianal pad; inner and outer parts of subcercus broadly joined. Surstylus large, with a scoop-shaped posterior lobe with small, densely packed posterior bristles; anterior part with four slightly enlarged ventral bristles on outer surface and a pair of stout ventral bristles on inner surface; anterior lobe of surstylus quadrate, flattened. Paramere relatively broad, with a deep anterior notch near base, apex boot-shaped. Basiphallus with a short, quadrate epiphallus, distal part expanded dorsally. Distiphallus short and broad, with basal, laterally directed sclerites bladelike, distally smooth; central sclerite broad, short.

Female abdomen: Tergite 7 dark; tergite 8 divided into 2 large, dark lateral sclerites and a pale dorsal sclerite. Epiproct bare except for 4 small bristles; cerci tapered, with two long, stout apical bristles. Sternite 7 straight posteromedially. Sternite 8 with a central, pale sclerite with posteromedial part produced into 2 prominent, dark, laterally flattened processes; a minute bristle on sclerotized base present in membrane on each side. Hypoproct large, rounded, pale and bare except along dark, setulose posterior margin.

Holotype (o',CNC) ECUADOR. Galapagos, St. Cruz, Los Gemelos, 600m, forest dung trap, 31.i-4.ii.1989, B.J. Sinclair.

Paratypes: ECUADOR. Galapagos, St. Cruz, Los Gemelos, 31kmN Santa Rosa, 23.vi. 1985, Scalesia forest, 570m, Flight intercept trap and Malaise, S.J. Peck (5°,2°,GUE); 1kmN Puntado, 650m, ii. 1989, Malaise in Scalesia forest 89-26, S. Peck (1°,1°,CNC); St. Cruz, 4kmN Bellavista, Media Luna, 620m, Miconia Zone Flight intercept trap, 14.v-13.vii. 1985, S. &J. Peck (3°,3°,GUE); Isabela, Sierra Negra Pampas, 1000m, Dec. 1986, S. Aberdrabbo (1°,CNC).

Comments: Sclerocoelus galapagensis is highly distinctive in both male and female genitalia, and forms the sister group to the rest of the Neotropical members of the species group. It is named for its restriction to the Galapagos islands.

## Sclerocoelus hemorrhoidalis, new species (Figs. 42-51)

Description: Length 2.1-2.3mm, dark brown to black, legs reddish-brown, lower frons usually reddish only at corners; vibrissal angle reddish, contrasting with dark gena and face. Minimum interantennal distance 1.5X width of ocellar triangle. Eye height 3.5X genal height; anterior genal bristle as long as genal height. Prothorax with 3-5 small, bristle-bearing sclerites in membrane beside prosternum. Katepisternum with a short, fine posterodorsal bristle one third as long as distance between bristle base and wing base, and a minute anterodorsal setula. Male mid tibia strongly curved; ventral surface with apical fifth covered with stout, curved bristles and with a large apicoventral bristle. Male mid femur with 2 or 3 stout anteroventral bristles and 6 or 7 stout posteroventral bristles at base. Wing length 2.5X width; membrane clear.

Male abdomen: Tergite 5 with posterior margin straight, 2 or 3 pairs of posterior marginal bristles equal to tergite length, other posterior bristles 0.5X tergite length. Sternite 5 slightly longer than sternite 4; darkest along anterior margin; long-setose posterolaterally; posteromedially produced into two long-setose lobes. Ventral part of synsternite 6+7 almost symmetrical, left side developed as usual, right side with a similar sclerotized area made up of a large spiracular sclerite, a narrow anterior sclerite (sclerite E) and possibly another sclerite (sclerite F) fused with the spiracular sclerite. Ring sclerite small, contiguous with posterolateral corner of spiracular sclerite. Middle part of synsternite 6+7 forming a continuous narrow band ventral to a deep, sclerotized central pouch. Epandrium with dense, short bristles laterally, posterior bristles longer and bristle at posteroventral corner twice as long as epandrium. Inner ventral corners of epandrium with a broad, short Perianal pads strongly developed, longer than epandrium, broad ventrally; anterior and dorsal parts well sclerotized but posteroventral part membranous, bulbous and setulose. Pseudocercus small, weakly pigmented, free from epandrium, with 3 small subequal bristles. Halves of sternite 10 (subepandrial sclerite) dark, narrow; contiguous

medially with weak ventral lobes. Subcercus with a broad, elongate inner lobe, posteroventrally extended into a pointed, prominent process; outer part of subcercus small, with an anterolateral arm but not produced posteriorly. Surstylus large, with a scoop-shaped posterior lobe with 4-6 short, stout posterior bristles on the tapered apex; anterior part complex, with enlarged ventral, apically curled bristles, an anterodorsal inner lobe, and a broad, carinate lobe on medial surface. Paramere short, broad basally, sharply tapered on apical half. Basiphallus short, simple, compressed, partly contiguous with ventral part of distiphallus. Distiphallus with laterally directed, basal, distally serrate sclerites; central sclerite thin, apically bifurcate.

Female abdomen: Tergite 7 dark; tergite 8 divided into 2 large, dark lateral sclerites and an indistinct, pale dorsal sclerite. Epiproct setulose, truncate; cerci tapered, with long, stout apical bristle and short stout dorsal preapical bristle. Sternite 7 strongly convex posteromedially. Sternite 8 trough-shaped, depressed medial part paler than margins; anterior part narrower than posterior part; 2 minute setulae in membrane flanking sternite. Hypoproct projecting ventrad and densely long-setose on posterior half.

HOLOTYPE (o',CNC) and 5 paratypes (1o',4o,GUE): Venezuela. Merida, La Punta, sweep along Rio Chama, 25.iv.1988, S.A. Marshall.

Other paratypes: Ecuador, Napo Prov., Baeza, screen sweep in wet montane forest, 1500-1700m, forest-pasture, 18.v.1987, L.D. Coote (2°, ROM #870013); Pichincha, 47kmS Sto. Domingo, Rio Palenque Biological Station, 1.v.1987, at light, B.V. Brown (1°,GUE). Venezuela. Merida, Sta. Rosa Trail, flight intercept trap along spring, 1500m, 24-30.iv.1988, S.A. Marshall (1°,GUE).

Comments: Sclerocoelus hemorrhoidalis is named for the strongly bulging areas flanking the anus. It can be most easily separated from sympatric congeners by the short, stout posterior surstylar bristles.

# Sclerocoelus subbrevipennis (Frey), new combination (Figs. 52-61)

Limosina subbrevipennis Frey, 1954:35

**Description:** Length *ca.* 2.2mm, dark brown to black, legs, face, vibrissal angle, and anterior part of gena reddish-brown, lower frons usually extensively reddish. Minimum interantennal dis-

tance 1.5X width of ocellar triangle. Eye height 3.5X genal height; anterior genal bristle as long as genal height. Prosternum bare, without bristles. Katepisternum with posterodorsal bristle reaching half way to wing base; anterodorsal bristle minute. Male mid tibia strongly curved; ventral surface with double row of slightly enlarged bristles on distal third. Male mid femur with a row of 3-4 stout anteroventral and 6 or 7 stout posteroventral bristles at base. Wing length 2.0X width; membrane brownish, lightly tinted.

Male abdomen: Tergite 5 with 3 pairs of median posterior marginal bristles 1.5X tergite length, other posterior bristles 0.5X tergite length. Sternite 5 almost as long as sternite 4; setose posterolaterally, bare medially; posteromedial area bilobed, pale, densely covered with short, flat setulae. Area behind posteromedial part of sternite 5 with three separate, subquadrate, heavily sclerotized sclerites overlapping each other (sclerites C. D, and E); anteriormost of these sclerites fused with inside surface of sternite 5. Spiracular sclerite large, pale, contiguous with well sclerotized ring sclerite. Epandrium with short bristles; posterior bristles longer and bristle at posteroventral corner almost as long as epandrium; anteroventral bristles stout. Length of dorsal part of epandrium subequal to height of anal fissure. Perianal pad strongly developed, almost entirely sclerotized, shorter than epandrium, setulose, ventral part with a narrow lobe articulating with subcercus. Pseudocercus small, weakly pigmented, fused with corner of epandrium, with 3 bristles, the lower 2 very small, upper bristle as long as longest epandrial bristle. Halves of sternite 10 (subepandrial sclerite) dark, narrow; contiguous medially, medial part deeply U-shaped and weakly lobate at middle. Subcercus with a broad, elongate inner part; outer part of surstylus with a very broad anterior lobe and a quadrate posterior lobe articulating with sclerotized part of perianal pad; inner and outer parts of subcercus broadly joined. Surstylus large. with a scoop-shaped posterior lobe with small, densely packed posterior bristles; anterior part with four large ventral bristles on outer surface and a pair of enlarged ventral bristles on inner surface; anterior corner produced into a broadly rounded lobe. Paramere sinuate, broad basally, narrow and dorsoventrally flattened distally, apex foot-like. Basiphallus narrow, simple. Distiphallus short and broad, with laterally directed, distally smooth, basal, blade-like sclerites, otherwise mostly membraneous; central sclerite not developed.

Female abdomen: Tergite 7 dark; tergite 8 divided into 2 large, dark lateral sclerites and an indistinct, pale dorsal sclerite. Epiproct setulose, truncate; cerci tapered, with long, stout apical bristle and short stout dorsal preapical bristle. Sternite 7 straight posteromedially. Sternite 8 hour-glass shaped, laterally compressed with concave sides separated by a narrow flat area, ventral surface thus with 2 prominent ridges; 2 small setae on sclerotized bases present in membrane on each side. Hypoproct with a short, setulose posterior margin narrowly connected with a bare, tonguelike, anteroventrally curved anterior part.

Lectotype (type #14347 Helsinki) by current designation and 9 paralectotypes (lectotype ♥ originally minuten pinned, remounted on card by G. Ståhls in 1995) and 9 paralectotypes ♥ ♥ in alcohol, Oslo): South Atlantic, Tristan da Cunha group, NIGHTINGALE ISLAND, 7.II. 1938. Collected from the rotting remains of plants, on the beach running along the eastern side of the island.

Other material examined: (Albany Museum, Grahamstown, South Africa, all from South Atlantic, Inaccessible Island, 37°02'S 12°12'W) Malaise trap, *Phylica* woodland, 18.x.1989, H.M. Barber and A.J. Gardiner; Plateau in vegetation, edge of Ringeye burrow, 16.x.1989, H.M. Barber (10); Malaise trap with light, open area below hut, 19.x.1989, H.M. Barber and A.J. Gardiner (1♀); Plateau, near pool in river, parallel to The Long Ridge, 19.x. 1989, H.M. Barber (19); Plateau, Yellow-nosed Albatross nest, 12.x. 1989, H.M. Barber (10; 3♂,1♀ minuten pinned on one block, 3♂,1♀ minuten pinned on one block, 19 pointed); Plateau. top of west road, 17.x.1989, A.J. Gardiner (10,19 minuten pinned on one block); SW of Denstone Hill. 14.x.1989, H.M. Barber (10); just before summit, top of West road, 23.x. 1989, A.J. Gardiner (19).

Comments: This species was described from females only, and species in this group are very difficult to separate based only on female characters. Male specimens from islands other than Inaccessible are required to investigate the possibility that more than one species are grouped under the name *subbrevipennis*. Inaccessible and Nightingale are separated by only 22km of relatively shallow water, and 11 of the 17 fly species Frey (1954) reported from Nightingale are also recorded from the lesser known fauna of Inaccessible Island. It is most likely that the same species of *Sclerocoelus* occurs on both islands.

Sclerocoelus subbrevipennis is apparently the sister species to the rest of the galapagensis species

group, although it is very similar in appearance to *S. galapagensis*. Both species have shortened, brown wings and similar subcerci, and both have sclerotized perianal pads identical to those of *S. brasilensis*. The latter characters are interpreted as plesiomorphy, but the similarity in wings is a striking homoplasy.

Frey (1954) listed 28 species of Diptera from Tristan da Cuna, of which 7 were widespread synanthropic species. Of the remaining 21, 15 were treated as endemics, 3 were shared with the Palaearctic, 1 with the Nearctic, and 2 with the Neotropical region, and none with Africa. The two sphaerocerids listed as having Palaearctic affinities, Pullimosina heteroneura and Thoracochaeta brachystoma are now known to be common throughout the New World, as is the sphaerocerid listed as having a Nearctic affinity, Thoracochaeta seticosta. Both of these Thoracochaeta are common on the east coasts of North and South America (unpublished data), and are easily dispersed seaweed flies, as is the other fly listed as of Palaearctic affinity (Fucel*lia maritima*). The sphaerocerid listed by Frey as having Neotropical affinities, Leptocera abdominiseta Duda, was described from South America, but the extra-Palaearctic species of the genus Leptocera remain in such a state of confusion that records of this and other Leptocera species remain questionable pending a revision of the genus. It seems unlikely that any of the species listed by Frey as showing affinities between Tristan da Cunha and major zoogeographic regions really reflect natural affinities, and it seems that the search for such affinities must take place at a higher level. The sister group relationship between S. subbrevipennis and the Neotropical galapagensis group is strongly supported, and represents such a higherlevel relationship.

Acknowledgements and collection abbreviations: I thank the curators of the Canadian National Collection, Ottawa (CNC), the United States National Museum, Washington (USNM), the American Museum of Natural History (AMNH), the Museo Nacional, Rio (MNR), the Royal Ontario Museum, Toronto, Ontario (ROM), and the Albany Museum, Grahamstown South Africa, the Instituto de Investigaciones Entomologicas, Salta, Argentina (INESALT), and the Museo del Instituto de Zoologia Agricola, Venezuela (MIZA) for the use of their specimens. Unless otherwise specified specimens are deposited in the University of Guelph collection (GUE). I would particularly like to thank Dr. David Barraclough (Natal Museum, South Af-

rica) for bringing the newly collected specimens of *S. subbrevipennis* to my attention, and Dr. Knut Rognes (Zoologisk Museum, Oslo, Norway), and G. Ståhls (Museum of Zoology, Helsinki, Finland) for sending me the type series of that species. David Montagnes and Ian Smith prepared the illustrations. Drs. S.B. Peck and T.A. Wheeler kindly reviewed the manuscript.

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caribensis	11111 21121 11211 11001 12
galapagensis	00000 00000 02000 11110 00
hemorrhoidalis	21011 21121 21211 11001 12
subbrevipennis	00000 10000 00000 00110 10

 ${\bf Table~1.~Character~matrix~for~the~\it Sclerocoelus~galapagensis~group.}$ 

### Character matrix list, Sclerocoelus galapagensis group

### Male terminalia

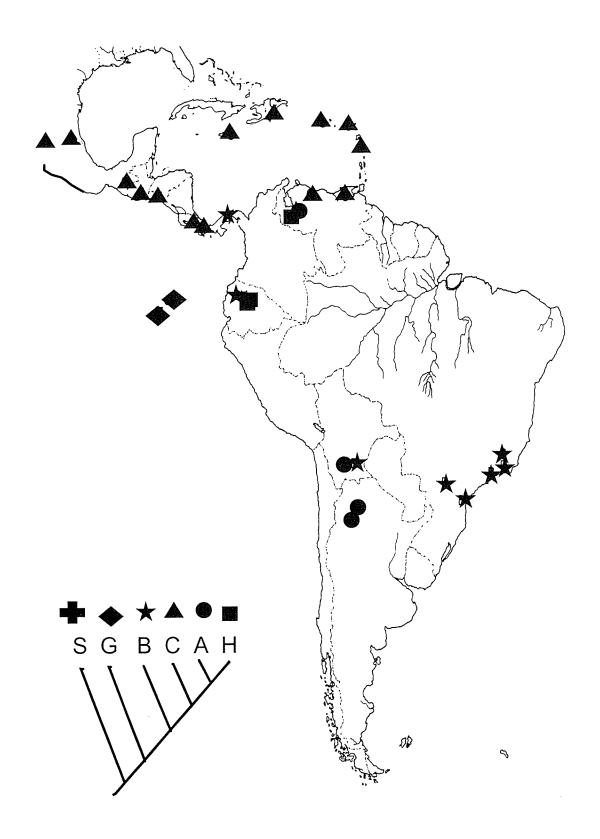
- 1) Sclerites C and D behind sternite 5: 0, present and separate; 1, present and fused; 2, absent.
- 2) Deep, sclerotized pouch above posteromedial part of sternite 5: 0, absent; 1, present.
- 3) Surstylus with stout apical bristles on posterior lobe:0, absent; 1, present.
- 4) Surstylus with a narrow, finger-like anterodorsal lobe: 0, absent; 1, present.
- Surstylus with anteromedial crest: 0, weak or absent; 1, prominent.
- 6) Posteroventral epandrial bristle: 0, short, like other epandrial bristles; 1, longer than other epandrial bristles but shorter than epandrium; 2, prominent, longer than epandrium.
- Large setulose area behind perianal pad: 0, absent;
  prominent.
- 8) Perianal pad with finger-like posteroventral extension: 0, present; 1, absent.
- 9) Middle part of sternite 10: 0, medially rounded; 1, quadrate with lobes at corners.
- Inner (ventral) part of subcercus: 0, rounded, not projecting posteriorly; 1, with long, blade-like posterior lobe.
- 11) Outer (upper) part of subcercus: 0, with posterior lobe articulating with apex of perianal pad; 1, with short posterior lobe not articulating with perianal pad; 2, without posterior lobe.
- 12) Basiphallus: 0, broad basally and narrow distally; 1, short, laterally compressed; 2, with short epiphallus and distal expansion (unordered).
- 13) Basal lateral arms of distiphallus: 0, without teeth; 1, with 3 teeth; 2, with over 5 teeth.
- 14) Middle part of distiphallus: 0, short and undeveloped; 1, long and distally bifurcate.
- 15) Pseudocercus with three bristles: 0, upper bristle much longer than others; 1, all three bristles small.

#### External characters

- 16) Membrane beside prosternum: 0, without bristles; 1, with bristles.
- 17) Posterior katepisternal bristle: 0, reaching half way to wing base; 1, minute, fine, reaching less than one-third of distance to wing base.
- 18) Wing membrane: 0, clear; 1, brown.
- 19) Wing length: 0, ca. 2.5X width; 1, ca. 2.0X width (conspicuously shortened).
- 20) Face and subvibrissal angle colour: 0, yellow brown; 1, face dark brown to black and vibrissa contrastingly pale.

#### Female abdomen

- 21) Cerci: 0, with two or more apical bristles; 1, terminating in a single apical spine.
- 22) Sternite 8: 0, lateral parts more extensive than ventral part; 1, lateral parts smaller than ventral part; 2, lateral parts absent or folded under large concave ventral part.



Map. Distribution of species in the Sclerocoelus galapagensis group. S, S. subbrevipennis; G, S. galapagensis; B, S. brasilensis; C, S. caribensis; A, S. andensis; H, S. hemorrhoidalis.

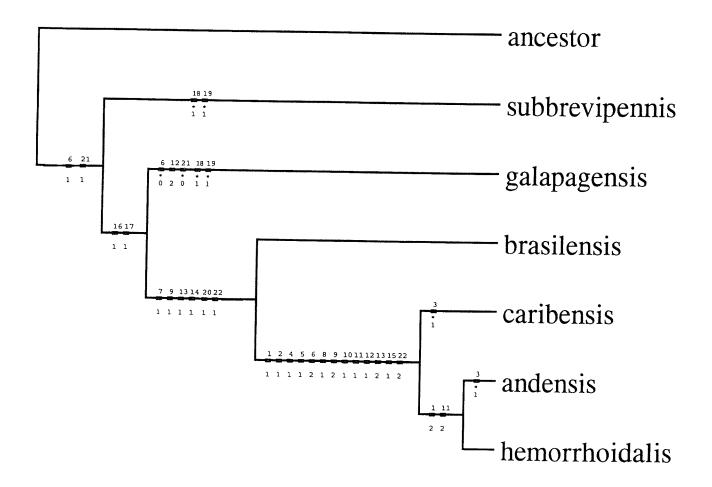
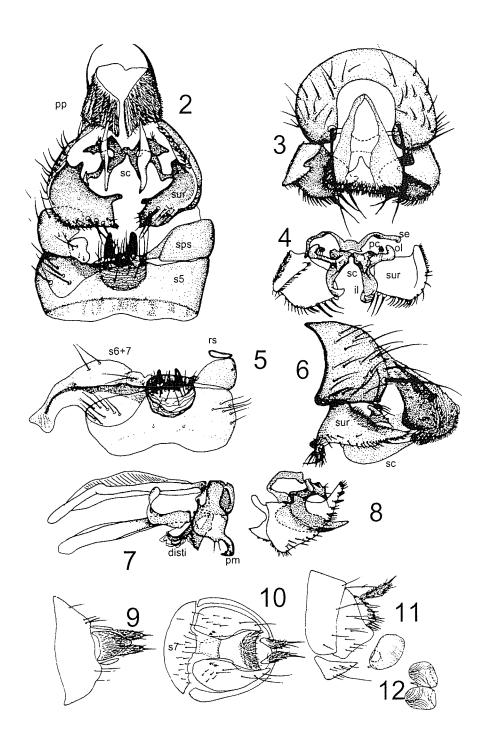
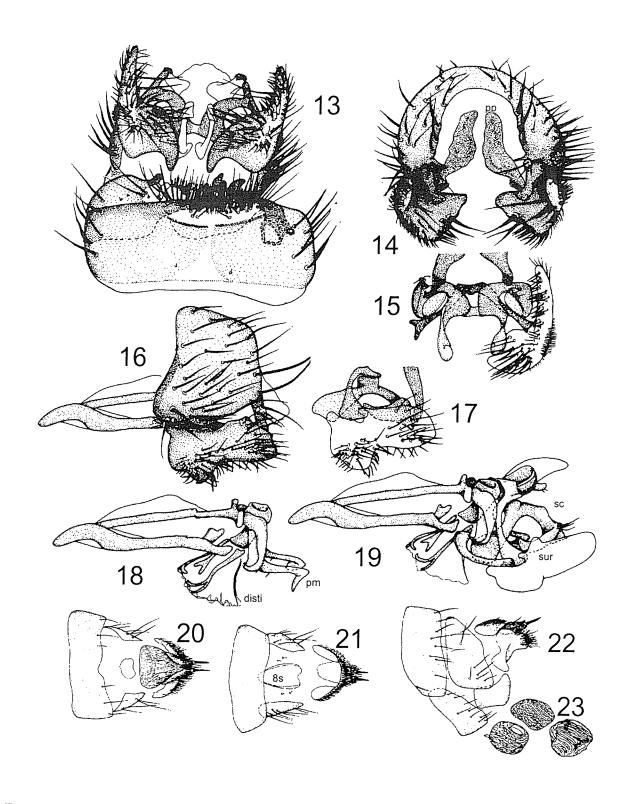


Fig. 1. Phylogeny of the Sclerocoelus galapagensis group. States marked with an asterisk are homoplasies; numbers on right side are character states.

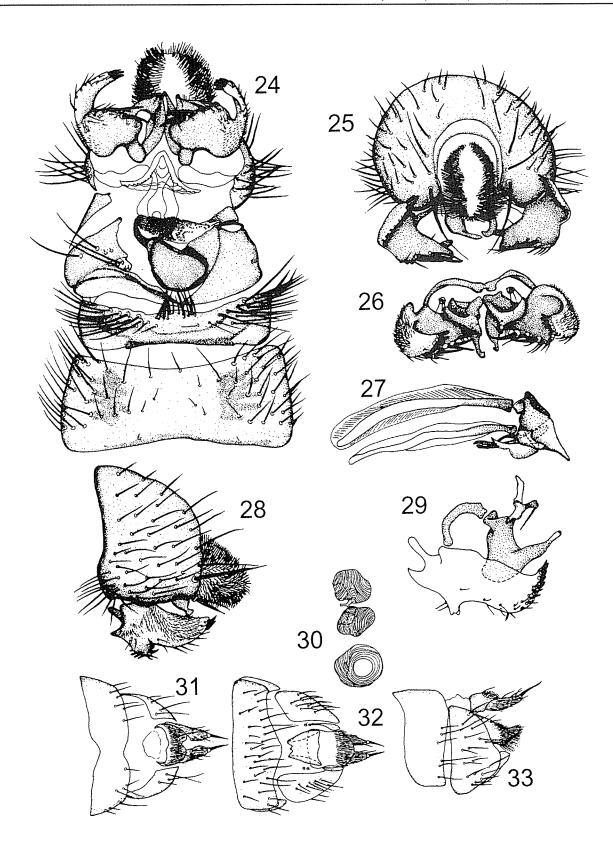


Figs. 2-12. Sclerocoelus andensis. 2, Male terminalia, ventral; 3, Male terminalia, posterior; 4, Subcerci, surstyli, and subepandrial sclerite, posteroventral; 5, Male sternites 5-7, ventral; 6, Male terminalia, left lateral; 7, Aedeagus and associated structures; 8, Subcerci, surstyli, and subepandrial sclerite, left lateral; 9, Female terminalia, dorsal; 10, Female terminalia, ventral; 11, Female terminalia, lateral; 12, Spermathecae.

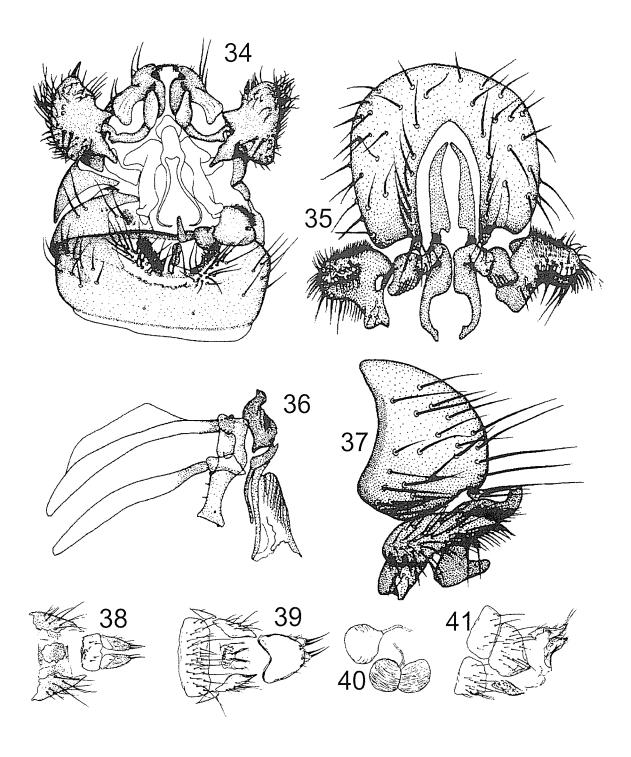
Abbreviations: pp, perianal pad; sc, subcercus; sur, surstylus; sps, spiracular sclerite; s5, sternite 5; se, subepandrial sclerite; pc, pseudocercus; ol, outer lobe of subcercus; il, inner lobe of subcercus; s6+7, synsternite 6+7; rs, ring sclerite; disti, distiphallus;pm, paramere; s7, sternite 7.



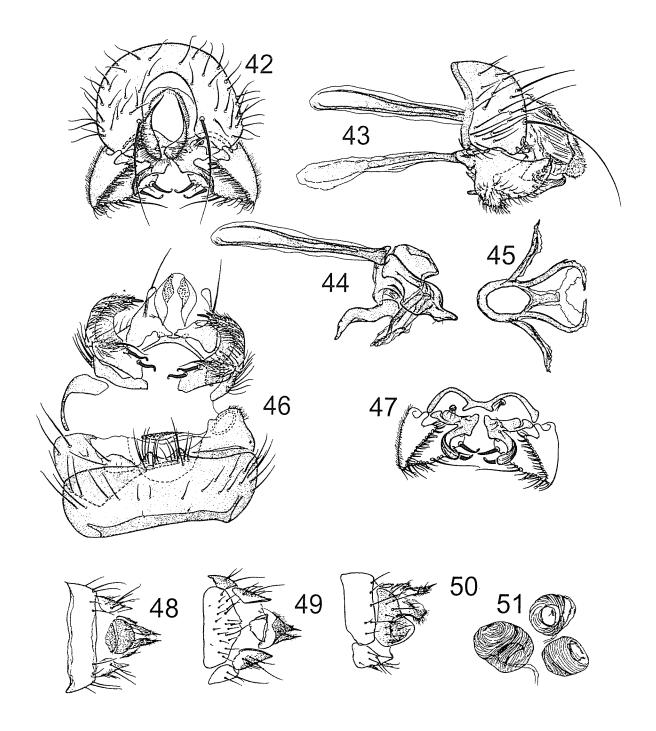
Figs. 13-23. Sclerocoelus brasilensis. 13, Male terminalia, ventral; 14, Male terminalia, posterior; 15, Subcerci, right surstylus, and subepandrial sclerite, posteroventral; 16, Male terminalia, left lateral; 17, Subcerci, surstyli, and subepandrial sclerite, left lateral; 18, Aedeagus and associated structures, lateral; 19, Terminalia, left dorsolateral, epandrium removed; 20, Female terminalia, dorsal; 21, Female terminalia, ventral; 22, Female terminalia, lateral; 23, Spermathecae. Abbreviations: disti, distiphallus;pm, parameres; sc, subcercus; sur, surstylus; 8s, sternite 8.



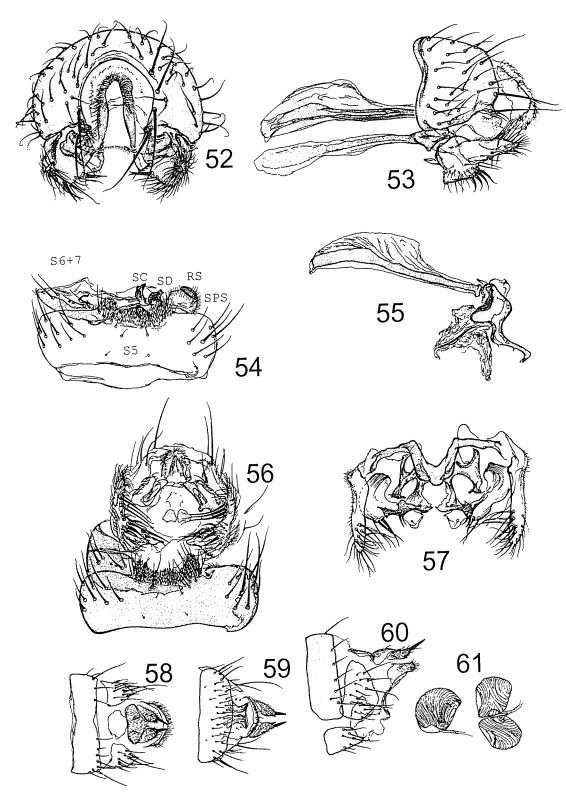
Figs. 24-33. Sclerocoelus caribensis. 24, Male terminalia, ventral; 25, Male terminalia, posterior; 26, Subcerci, right surstylus, and subepandrial sclerite, posteroventral; 27, Aedeagus and associated structures; 28, Male terminalia, left lateral; 29, Subcerci, surstyli, and subepandrial sclerite, left lateral; 30, Spermathecae; 31, Female terminalia, dorsal; 32, Female terminalia, ventral; 33, Female terminalia, lateral.



Figs. 34-41. Sclerocoelus galapagensis. 34, Male terminalia, ventral; 35, Male terminalia, posterior; 36, Aedeagus and associated structures; 37, Male terminalia, left lateral; 38, Female terminalia, dorsal; 39, Female terminalia, ventral; 40, Spermathecae; 41, Female terminalia, lateral.



Figs. 42-51. Sclerocoelus hemorrhoidalis. 42, Male terminalia, posterior; 43, Male terminalia, left lateral; 44, Aedeagus and associated structures; 45, Distiphallus, ventral; 46, Male terminalia, ventral; 47, Subcerci, right surstylus, and subepandrial sclerite, posteroventral; 48, Female terminalia, dorsal; 49, Female terminalia, ventral; 50, Female terminalia, lateral; 51, Spermathecae.



Figs. 52-61. Sclerocoelus subbrevipennis. 52, Male terminalia, posterior; 53, Male terminalia, left lateral; 54, Male sternites 5-7; 55, Aedeagus and associated structures; 56, Male terminalia, ventral; 57, Subcerci, right surstylus, and subepandrial sclerite, posteroventral; 58, Female terminalia, dorsal; 59, Female terminalia, ventral; 60, Female terminalia, lateral; 61, Spermathecae.

Abbreviations: S6+7, synsternite 6+7; SC, sclerite C; SD, sclerite D; RS, ring sclerite; SPS, spiracular sclerite; RS, ring sclerite; S5, sternite 5.