

Revision of the Taiwanese millipede genus *Chamberlinius* Wang, 1956, with descriptions of two new species and a reclassification of the tribe Chamberlinini (Diplopoda, Polydesmida, Paradoxosomatidae, Paradoxosomatinae)

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Abstract

The millipede genus *Chamberlinius* is basically confined to Taiwan, with only one of the four known species presumably introduced to southern Japan. Both previously known species are redescribed, based on new material: *C. hualienensis* Wang, 1956 (the type species) and *C. piceofasciatus* (Gressitt, 1941), the latter being a new subjective senior synonym of *Chamberlinius shengmui* Wang, 1957, **syn. n.** Two further congeners are described as new: *C. pessor* **sp. n.** and *C. sublaevus* **sp. n.** The genus is re-diagnosed, all of its four species are keyed, and their distributions mapped. The tribe Chamberlinini is reclassified and, based on gonopod traits, shown to comprise the following five genera: *Chamberlinius* Wang, 1956, *Haplogonosoma* Brölemann, 1916, *Riukiupeltis* Verhoeff, 1939, *Aponedyopus* Verhoeff, 1939 and *Geniculodesmus* Chen, Golovatch and Chang, 2008.

Keywords

Millipede, *Chamberlinius*, Chamberlinini, taxonomy, new species, key, distribution, Taiwan

Introduction

The genus *Chamberlinius* Wang, 1956 was first erected, based on the single species *C. hualienensis* Wang, 1956, taken from Taruko, Hualien, Taiwan (Wang 1956). A year later, Wang (1957) described another new congener, *C. shengmui* Wang, 1957, and he also proposed a new subfamily, Chamberlininae. Jeekel (1968) placed *Chamberlinius* in the tribe Sulciferini, subfamily Paradoxosomatinae. He compared the illustrations of *Orthomorphella pekuensis* (Karsch, 1881), the type species of *Orthomorphella* Hoffman, 1963, which Hoffman (1963) had validated, with the poor line drawings of both *Chamberlinius hualienensis* Wang, 1956 and *C. shengmui* Wang, 1957 as presented by Wang (1956, 1957), to conclude that *Chamberlinius* was a senior synonym of *Orthomorphella*. This opinion has since been shared by Wang and Mauriès (1996). Furthermore, Jeekel (1968) referred to *Chamberlinius* as containing four species: *C. cristatus* (Takakuwa, 1942), *C. hualienensis* Wang, 1956 (the type species), *C. pekuensis* (Karsch, 1881) and *C. shengmui* Wang, 1957.

Soon after that, Hoffman (1973), disagreeing with Jeekel (1968), resurrected *Orthomorphella* as an independent genus, removed *Chamberlinius* from the tribe Sulciferini, and downgraded the subfamily Chamberlininae to the tribal status, Chamberlinini in Paradoxosomatinae. This tribe was stated to encompass only *Chamberlinius* and *Riukiupeltis* Verhoeff, 1939. He was also the first to assign *C. piceofasciatus* (Gressitt, 1941), another species from Taiwan, to *Chamberlinius*. He redescribed both *C. hualienensis* and *C. piceofasciatus*, simply listing *C. shengmui* as a third congener. More recently, Hoffman (1980) spoke already of “about five species” in this genus, which is a slightly puzzling estimate because only the above trio has hitherto been known to compose *Chamberlinius*.

Regrettably, since all of the diplopod material Wang (1956, 1957) claimed to have deposited in the Department of Zoology (now incorporated into the Department of Life Science) of the National Taiwan University and/or Taiwan Museum seems to be lost, it appears necessary to amass new samples, including topotypes, and build up a modern collection of Taiwanese Diplopoda.

The present study is a revision of the millipede genus *Chamberlinius*, based not only on new material, including some topotypes, but also on a few old types. As a result, all previously described species could be re-assessed, two new species added, and a new synonym established. In addition, the tribe Chamberlinini could be reclassified due to the present revision of the type genus *Chamberlinius*.

In his Nomenclator, Jeekel (1971, p. 219) corrected Chamberlininae to Chamberliniinae, because family-group names are derived from the stem of the genitive singular of the genus name, which in this case is Chamberlinii, stem Chamberlini-. Similarly, the correct form of Chamberlinini is Chamberliniini. We are keeping Chamberlininae and Chamberlinini because Jeekel’s correction was not widely adopted and these names are in prevailing usage (ICZN section 29.5).

Material and methods

New extensive collections of millipedes covering most parts of Taiwan were made between 1986 and 2010, using hand-sorting of the soil and litter. Specimens were preserved in 70% ethanol. External morphology was examined and the drawings prepared with a LEICA MZ 16 stereomicroscope as well as with a HITACHI S2400 scanning electron microscope. Coloration of the specimens is described from alcohol material. This material has been shared between the collections of Department of Life Sciences, National Chung-Hsing University (NCHUL), Taiwan; National Museum of Natural Science (NMNS), Taiwan; the Department of Biological Sciences, National Sun Yat-Sen University (NSYSU), Taiwan; Department of Life Science, National Taiwan Normal University (NTNU), Taiwan; Taiwan Forestry Research Institute (TFRI), Taiwan; California Academy of Sciences (CAS), San Francisco, U.S.A.; National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C., U.S.A.; Field Museum of Natural History (FMNH), Chicago, Illinois, USA, and Zoological Museum of the State University of Moscow (ZMUM), Russia.

Systematic account

Genus *Chamberlinius* Wang, 1956

<http://species-id.net/wiki/Chamberlinius>

Chamberlinius Wang, 1956: 156; Wang, 1957: 103; Jeekel, 1968: 73; Jeekel, 1971: 219; Hoffman, 1973: 377; 1980: 170; Korsós, 2004: 22.

Diagnosis (amended): Large-sized *Chamberlinini* (25–37 mm long). Paraterga very well-developed, paraterga 2 not lower, but as high as adjacent paraterga. Pleurosternal carinae well-developed. Both a lobe between ♂ coxae 4 and adenostyles missing. A pair of ridge-like spiracles flanking gonopod aperture.

Gonopod coxae long, subcylindrical, setose distodorsally, cannula as usual. Telopodites very slender and long, in situ their distal parts crossing medially. Femorite especially long, longer than acropodite, simple, devoid of outgrowths, apically with a clear cingulum demarcating a mesally directed, elongate postfemoral part; the latter branching near base (just distal to cingulum) into a long, thick and simple solenomere and a shorter to longer, similarly thick solenophore supplied with a dentiform outgrowth at base. Seminal groove running mostly on medial face of femorite to move laterally only towards, and to return back to medial side near, cingulum.

Type species: *Chamberlinius hualienensis* Wang, 1956, by original designation.

Remarks. Hoffman (1973), when outlining the tribe *Chamberlinini*, included only two genera therein: *Chamberlinius* and *Riukiupeltis* Verhoeff, 1939, with three and one species, respectively. They show very well-developed paraterga resembling those of some *Xystodesmidae*, both a lobe between ♂ coxae 4 and adenostyles missing,

and the gonopods being peculiar in the entire terminal half of the telopodite (distal to the cingulum) representing a single element with several subterminal branches, one of which carries the seminal groove.

Such a description of gonopod structure actually means that, unlike many other tribes of Paradoxosomatidae, which have a long and flagelliform solenomere more or less strongly sheathed/protected by a complex, rather membranous solenophore, the solenomere in the Chamberlinini is a thick, strong and long branch accompanied by a similarly thick, strong and long solenophore branch. The above new diagnosis of *Chamberlinius* emphasizes its peculiar gonopod conformation. Regrettably, the gonopod conformation of *Riukipeltis* still remains to be clarified to properly rediagnose this genus (Jeekel 1968).

Jeekel (1968) included the following species in *Chamberlinius*: *C. cristatus* (Takakuwa, 1942) from Japan, *C. pekuensis* (Karsch, 1881) from Japan, Korea, continental China and Taiwan, *C. hualienensis* (misspelled as *hauensis*) Wang, 1956 and *C. sheng-mui* Wang, 1957, both latter taxa from Taiwan. Hoffman (1973) later transferred *pekuensis* into *Orthomorphella* (see above). As regards *C. cristatus*, originally described as *Orthomorpha cristatus* Takakuwa, 1942 from near Tokyo, Japan (Takakuwa 1942), this species badly needs a revision (Jeekel 1968), but the sketch of its gonopod structure alone, showing a flagelliform solenomere and a complex membranous solenophore, prevents its assignment to Chamberlinini altogether. So *O. cristatus* is here formally ejected from *Chamberlinius*, but its current generic relationships remain obscure.

As a result, presently only three species can be considered as belonging to this genus (Hoffman 1973, Korsós 2004). Our contribution puts on record two new congeners from Taiwan and establishes the synonymy of one of the older species, altogether providing a revision of *Chamberlinius*.

Distribution: All *Chamberlinius* species are believed to be native to Taiwan (Hoffman 1980), but one congener seems to have been introduced to Japan (Higa and Kishimoto 1986, 1989, Yamaguchi et al. 2000, Nijima and Arimura 2002, Nakamura and Korsós 2010).

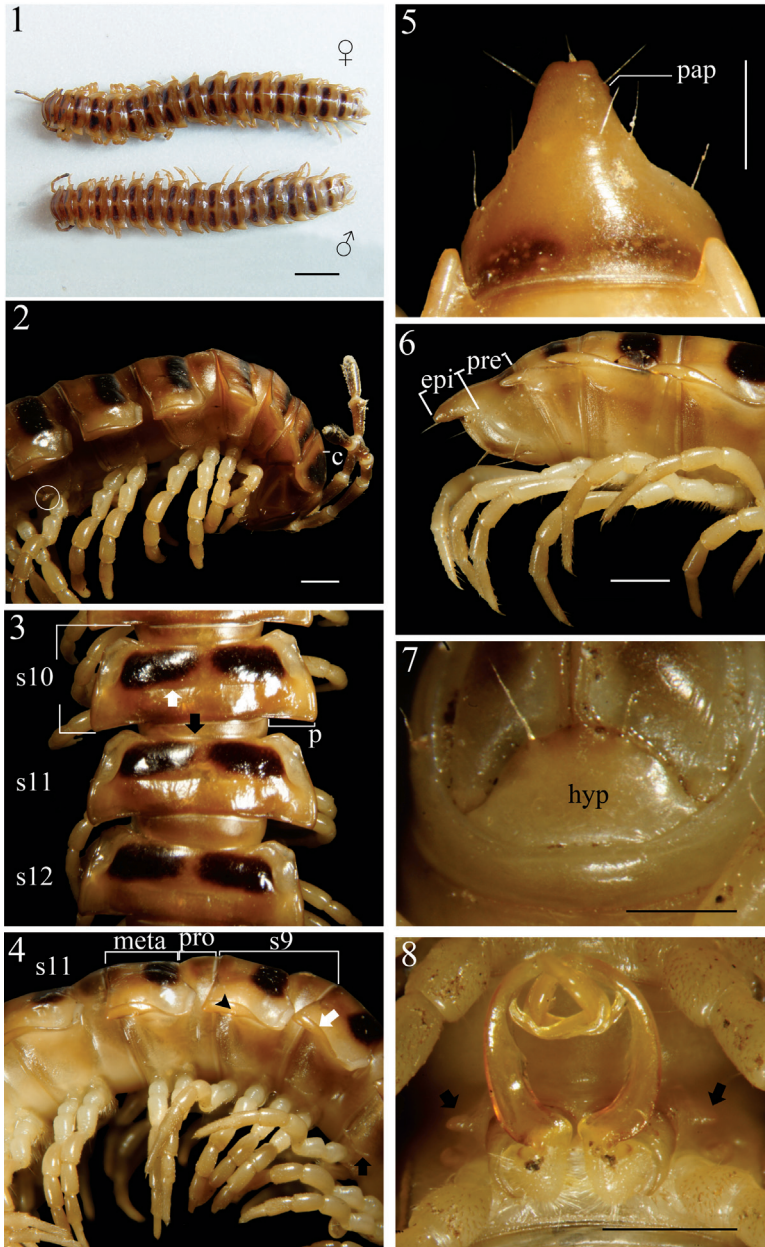
***Chamberlinius hualienensis* Wang, 1956**

http://species-id.net/wiki/Chamberlinius_hualienensis

Figs 1–8, 33–35

Chamberlinius hualienensis Wang, 1956: 155, fig. 1; 1958a: 341; 1958b: 881; 1963: 90; 1964: 69; Jeekel, 1968: 70; 1971: 219; Hoffman, 1973: 379, figs 19–21; Higa and Kishimoto, 1986: 62–72, figs 3, 9–14; Wang & Mauriès, 1996: 87; Korsós, 2004: 32.

Material examined: 1 ♀ (NSYSUB-DI 38), Taipei City (台北市), Yangmingshan National Park (陽明山國家公園), Rd. BaLaKa (巴拉卡公路), under decayed leaves in a gutter, ca. 850 m a.s.l., 10 September 2002, leg. S. Y. Wu. 1 ♂ (NSYSUB), same locality, the first staff dormitory, 24 June 2003, leg. J. L. Chao. 1 ♂ (NSYSUB-DI 01),



Figures 1–8. *Chamberlinius huailienensis* Wang, 1956, ♂ and ♀ from Siji forest path (四季林道) (1) and ♂ from Basianshan Forest Recreation Area (八仙山森林遊樂區) (2–8). **1** Entire body, dorsal view **2** Anterior body portion, lateral view. Circle: caudal tooth of pleurosternal carinae **3** Segments 10–12, dorsal view. up arrow: transverse sulcus; down arrow: stricture **4** Segments 9–11, lateral view. down arrow: calluses; up arrow: pleurosternal carinae; triangle: ozopore **5**, **6** Epiproct, dorsal and lateral views, respectively **7** Hypoproct, ventral view **8** Spiracle-bearing cones lateral to gonopod aperture (arrows). Scale bars: 5.0 mm (1); 1.0 mm (2–6, 8); 0.5 mm (7). **c**: collum; **epi**: epiproct; **hyp**: hypoproct; **meta**: metatergum; **p**: paraterga; **pap**: pre-apical papillae; **pro**: prozona; **s9–s12**: segments 9–12 separately.

New Taipei City (新北市), Wulai District (烏來區) (formerly: Taipei County 台北縣, Wulai Township 烏來鄉), Wulai (烏來), 5 November 2001, same collector. 1 ♀ (NSYSUB-DI 07), same place, Neidong (內洞), ca. 500 m a.s.l., 16 August 2002, leg. C. C. Chen. 1 ♀ (NSYSUB-DI 06), Taoyuan County (桃園縣), Fushing Township (復興鄉), Hualing (華陵), 1,060 m a. s. l., 19 August 2002, leg. J. N. Huang. 2 ♂, 2 ♀ (NSYSU), Taichung City (台中市), Hoping District (和平區) (formerly: Taichung County 台中縣, Heping Township 和平鄉), Anmashan Forest Rd. (鞍馬山林道), 2,000–2,500m a.s.l., 1 June 2003, leg. J. D. Lee. 2 ♂, 1 ♀ (NSYSU), same district, Basianshan Forest Recreation Area (八仙山森林遊樂區), 900–1,500 m a.s.l., 23 June 2010, leg. H. D. Zhu. 1 ♂ (NCHUL), Nantou County (南投縣), Yuchi Township (魚池鄉), Lake Sun Moon (日月潭), ca. 750 m a.s.l., 16 July 2004, leg. S. H. Wu. 1 ♂, 1 ♀, same county, Lugu Township (鹿谷鄉), Siitou (溪頭), ca. 1,200 m a. s. l., 15 November 2002, leg. J. D. Lee. 4 ♂, 3 ♀ (NSYSU), same county, Xinyi Township (信義鄉), Tongfu Village (同富村), Provincial Highway # 21 (another name: New Central Cross-Island Highway 新中橫公路), in soil, 1,280 m a.s.l., 23°34'09"N, 120°53'29"E, 8 September 2004, leg. H. D. Zhu. 3 ♂, 2 ♀, 1 juvenile (NSYSUB), same township, Dongpu (東埔), Shalisian Stream (沙里仙溪), in soil under stones, ca. 1,020 m a.s.l., 23°33'24"N, 120°55'19"E, 9 April 2004, same collector. 2 ♂, 1 ♀ (NSYSU), same county, Zhushan Township (竹山鎮), Shanlinsi Stream (杉林溪), ca. 1,600–2,000 m a.s.l., 7 October 2004, leg. S. Y. Wu. 1 ♂, 2 juveniles (NCHUL), Chia-i County (嘉義縣), Alishan Township (阿里山鄉), 65 road-km of Provincial Highway # 18, near Shihjhuo (石卓), ca. 1,350 m a.s.l., 28 October 2000, leg. H. Z. Liang. 1 ♂, 1 ♀, 1 ♂ juvenile (NSYSUB-DI 02-04), same county, Fanlu Township (番路鄉), Longtou (龍頭), in bamboo forest, ca. 1,300 m a.s.l., 21 April 2002, leg. J. L. Chao. 1 ♂ (NTNUL-My 70), Kaohsiung City (高雄市), Maolin District (茂林區) (formerly: Kaohsiung County 高雄縣, Maolin Township 茂林鄉), Shanping (扇平), ca. 700 m a.s.l., 7–9 July 1986, leg. S. H. Chen. 3 ♂, 6 ♀ (NTNUL-My 16–24), 26 January 1989, same place and collector. 1 ♀ (NSYSUB-DI 05), same place, 13 May 2002, leg. C. H. Yang. 1 ♀ (NSYSUB), same place, 1 October 2006, leg. M. H. Hsu. 1 ♂ (NSYSU), same district, Duona Township Rd. (多納林道), 1,600 m a.s.l., 11 August 2004, leg. T. Y. Tei. 1 ♀ (NSYSUB-DI 58), same city, Taoyuan District (桃源區) (formerly: Taoyuan Township 桃源鄉), Tengjhih (藤枝), ca. 1,450 m a.s.l., 21 October 2001, leg. S. Y. Wu. 1 ♂, 2 ♀ (NSYSUB-DI 35–37), Pingtung County (屏東縣), Shihzih Township (獅子鄉), Neiwun (內文村), in humus under decayed wood, ca. 400–500 m a.s.l., 5 October 2002, same collector. 5 ♂, 3 ♀, 6 juveniles (NSYSU), same county, Mudan Township (牡丹鄉), Dongyuan (東源), about 300 a.s.l., 4 July 2006, leg. H. W. Chang. 1 ♀ (NSYSU), Ilan County (宜蘭縣), Jiaoxi Township (礁溪鄉), Ilan village street (宜6鄉道), Linmeishipan forest path (林美石盤林道), 200 m a.s.l., 8 September 2009, leg. C. C. Cheng. 9 ♂, 3 ♀ (NSYSUB-DI 18–29), same county, Datong Township (大同鄉), Ciilan Forest Amusement Park (棲蘭森林遊樂園), 460–480 m a.s.l., 20 August 2002, leg. C. C. Chen and Y. H. Lin. 2 ♂, 5 ♀ (NSYSU), same township, Renze Warning Spring (仁澤溫泉), 560 m a.s.l., 24°32'42"N, 121°30'16"E, 29 August 2004, leg. H. D. Zhu. 1 ♂, 4 juve-

niles (NSYSUB-DI 30-34), same township, Taipingshan Working Station (太平山工作站), under decayed leaves, ca. 480 m a.s.l., 20 August 2002, leg. C. C. Chen, Y. H. Lin, J. N. Huang etc. 8 ♂, 2 ♀ (NSYSUB-DI 08-17), same township, Sihji Forest Rd. (四季林道), ca. 1,060 m a.s.l., under fallen bamboo leaves, 20 August 2002, leg. C. C. Chen and Y. H. Lin. 2 ♂, 1 ♀ (ZMUM), 2 ♂, 1 ♀ (FMNH 6673-6675), 2 ♂, 1 ♀ (NMNS 4418-001), same place, date and collectors. 1 ♂, 1 ♀ (NSYSU), same township, Sihji Village (四季村), ca. 780 m a.s.l., 24°29'32"N, 121°25'43"E, 9 April 2006, leg. M. H. Hsu. 1 ♂ (NSYSU), same township, Nanshan Village (南山村), ca. 1,380 m a.s.l., 24°27'08"N, 121°22'51"E, 8 April 2006, same collector. 3 ♂, 2 ♀ (NSYSU), Hualien County (花蓮縣), Xiulin Township (秀林鄉), Tongmen Village (銅門村), Provincial Highway # 14 (台14線), ca. 210 m a.s.l., 23°58'39"N, 121°28'28"E, 13 February 2007, same collector. 1 ♀ (NSYSU), same county, Xincheng Township (新城鄉), Beipu Village (北埔村), productive road (產業道路), ca. 80 m a.s.l., 24°03'22"N, 121°35'35"E, 1 March 2007, same collector. 2 juveniles (NSYSU), same county, Fengbin Township (豐濱鄉), Hualien village street 51 (花51鄉道) (Baliwan Productive Road 八里灣產業道路), ca. 250 m a.s.l., 23°35'15"N, 121°30'15"E, 6 May 2009, same collector. 16 juveniles (NSYSU), same place, 23°35'06"N, 121°30'04"E, same date and collector. 3 juveniles (NSYSU), same county, Rueisuei Township (瑞穗鄉), Rueigang Highway (瑞港公路), Houzihshan (猴子山), ca. 130 m a.s.l., 23°29'50"N, 121°25'23"E, 7 May 2009, same collector. 2 juveniles (NSYSU), Taitung County (台東縣), Changbin Township (長濱鄉), Sanjianwn (三間屋), ca. 150 m a.s.l., 23°21'37"N, 121°27'33"E, 7 May 2009, same collector. 2 ♂, 3 ♀ (NSYSU), same county, Haiduan Township (海瑞鄉), Xiangyang (向陽), mine, under stones mixed with fallen leaves, ca. 1,280 m a.s.l., 26 June 2003, leg. S. Y. Wu. 2 ♂ (NSYSU), same township, South Cross-island Highway 175 k (near Lidao 利稻), ca. 1,070 m, a.s.l., 26 June 2003, same collector. 1 ♀ (NSYSU), same township, tunnel entrance of Wulu (霧鹿隧道口), in fallen leaves in a gutter, ca. 710 m a.s.l., 26 June 2003, same collector. 1 ♂ (NSYSU), same county, Beinan Township (卑南鄉), Lijia Forest Rd. (利嘉林道, also called Lijia Productive Road 利嘉產業道路), ca. 1,340 m a.s.l., 22°49'56"N, 121°00'34"E, 18 August 2004, leg. Y. J. Fan. 9 juveniles (NSYSU), same township, Yanping Forest Rd. (延平林道), ca. 1,070 m a.s.l., 22°52'58"N, 121°02'18"E, 3 June 2009, leg. M. H. Hsu. 1 ♂, 1 ♀ (NSYSU), same place, 22 February 2007, leg. S. Y. Wu. 1 ♂, 1 juvenile (NSYSU), same county, Taimali Township (太麻里鄉), Yima forest path (依麻林道), 6 December 2004, < 800 m a. s. l., same collector. 1 ♀ (NSYSU), same county, Jinfeng Township (金峰鄉), Forestry Research Institute Forest Rd. (林試分所林道), ca. 850 m a.s.l., 30 August 2003, leg. M. H. Hsu.

Description: Length 30–34 (♂, n=5) and 32–37 mm (♀, n = 5); width of mid-body metaterga 10 ca. 4.0–5.0 (♂) and 5.0–5.2 mm (♀). Coloration of both sexes in alcohol (Fig. 1) almost uniformly very light brown to brown in both sexes; head, collum (except posterior edge), anterior end of metaterga 2–4, sometimes also of 19th, brown, subtrapeziform (Fig. 3) on presulcus halves of metaterga 5–18, separated by an axial line, closer to axial line with narrower sides but closer to paraterga with wider

sides; antennae entirely light brown to increasingly blackish distally; tip contrastingly pallid.

In width, head < collum (c) (Fig. 2) = segment 2 > 3 < 4 < 5 < 6–9 < 10 < 11 < 12 < 13 < 14 < 15 ≥ 16 in ♂, but head < collum = segment 2 > 3 < 4 < 5 < 6–9 < 10 < 11 < 12 < 13 < 14 in ♀; thereafter body gradually and gently tapering both in width and height towards telson. Antennae medium-sized to long, slender, reaching behind middle to posterior end of metatergum 4 (Fig. 2) dorsally in ♂, or posterior end of segment 3 to anterior edge of segment 4 in ♀. Surface generally shining and smooth, rugulose on metazona (Figs 3, 4), also evidently and densely granular below paraterga 2–19 in both sexes. Paraterga (**p**) (Fig. 3) very well-developed, sometimes slightly more strongly in ♂ as compared to ♀, calluses (Fig. 4, down arrow) delimited by a sulcus dorsally and ventrally on segments 2–19, ventral sulcus finer than dorsal one; paraterga like high ridges, subhorizontal, extending increasingly beyond caudal tergal margin on segments 2–19 in both sexes, especially strongly spiniform caudally on segments 17–19 (♂) (Fig. 5) or 18 and 19 (♀); anterior corner of paraterga thinner dorsoventrally and depressed much more obviously in ♂ (Fig. 4). Axial line (Fig. 3) absent or traceable in places, usually present. Transverse sulcus (Fig. 3, up arrow) evident on metaterga 5–17, poorly traceable to evident on metatergum 18, wanting on segment 19 in both sexes, narrow, shallow, slightly deeper in ♂, neither beaded at bottom nor reaching bases of paraterga in both sexes. Limbus thin, caudal margin entire. Segments poorly constricted. Stricture (Fig. 3, bottom) dividing pro- and metazona (Figs 3, 4) shallow, moderately wide, densely and roughly beaded at bottom dorsally down to paratergal level, contrastingly more roughly so in ♀ as compared to ♂. Pleurosternal carinae (Figs 2, 4) well-developed, contrastingly more strongly so in ♂ as compared to ♀, well-developed on segments 2–9(10), traceable on segments 10–14, like low bosses on segments 15 and 16 to sometimes only traceable on segments 11–17 in ♂, or well-developed on segments 2–10, traceable on segments 11 and 12, like low bosses on segments 13–15 to sometimes only traceable on segments 11–16 in ♀, with small caudal teeth on segments 3–7(8) (♂) (Fig. 2, left) or (2)3–8 (♀), thereafter wanting. Tergal setae fully abraded, pattern untraceable in both sexes. Ozopores (Fig. 4, triangle) lateral, lying on callus ca. one-third metatergal length in front of caudal edge. Epiproct (**epi**) (Figs 5, 6) flattened dorsoventrally, long, somewhat longer in ♂ as compared to ♀, curved (especially well so in ♂) and directed caudoventrad in lateral view (Fig. 6), ratio of epiproct length to pre-epiproct (**pre**) length of telson 1:1.8 in ♂ (Fig. 6), tip subtruncate to slightly concave (♂) or emarginate (♀) in dorsal view (Fig. 5); pre-apical papillae (**pap**) evident (Fig. 5), situated close to apex. Hypoproct (**hyp**) (Fig. 7) subtrapeziform, caudally rounded (♂) or convex to rounded (♀), 1+1 setae at caudal corners situated on well-separated knobs, sides slightly concave at base in both sexes.

Sterna moderately setose in ♂, more sparsely so in ♀; an obvious, short, round ridge supporting spiracles lateral to gonopod aperture (Fig. 8, arrows); each cross-impression with an evident transverse sulcus, but without axial groove. Legs (Fig. 4) without tarsal brushes, long, ca. 1.5 times as long as midbody height in ♂, slightly shorter in ♀. Each ♂ coxa 2 perforated by a vas deferens with a very small pore opening apically.

Gonopods (Figs 33–35) simple; coxae (**co**) long, subcylindrical, setose distodorsally; prefemur (**prf**) large, short, almost 1/4 femur length, densely setose; femorite (**f**) about midway evidently thinner and broadened, with a thin membranous lobe on mesal side (**l**); cingulum marking the end of femorite very clear, especially so on lateral side, common stem of postfemoral region (**pof**) short, very quickly branching into a remarkably long and strong solenomere (**sl**) crowned with a narrow apical lamina (**m**), and a similarly long, simple, less strong and unequally bifid solenophore (**sph**) with a short, strong, dentiform process (**dp**).

Distribution: *C. hualienensis* Wang, 1956 is currently known from Taiwan, as well as on Kyushu Island and on most of the islands of the Ryukyu Archipelago, Japan (Higa and Kishimoto 1986, 1989, Yamaguchi et al. 2000, Nijima and Arimura 2002, Nakamura and Korsós 2010). The occurrences of *C. hualienensis* in Japan are likely to be introduced from Taiwan through human agency. Moreover, it is this species in Japan, but not in Taiwan, that occasionally shows swarming, like repeated massive outbreaks in Okinawa (Higa and Kishimoto 1986) or one at Kagoshima in early winter 2000 which caused serious railway traffic problems (Nijima and Arimura 2002).

Such a distribution pattern vividly reminds of that demonstrated by still another basically Taiwanese paradoxosomatid genus, *Aponedyopus* Verhoeff, 1939. Of its three currently known species (Chen et al. 2010), only one, the most widespread *A. montanus* Verhoeff, 1939, has been recorded in the Ryukyus, Japan, but its identity still requires verification (Nakamura and Korsós 2010).

In Taiwan, *C. hualienensis* is likewise the most common and widespread among its congeners, with altitudes ranging from about 80 m to ca. 2,500 m a.s.l. (Map).

***Chamberlinius piceofasciatus* (Gressitt, 1941)**

http://species-id.net/wiki/Chamberlinius_piceofasciatus

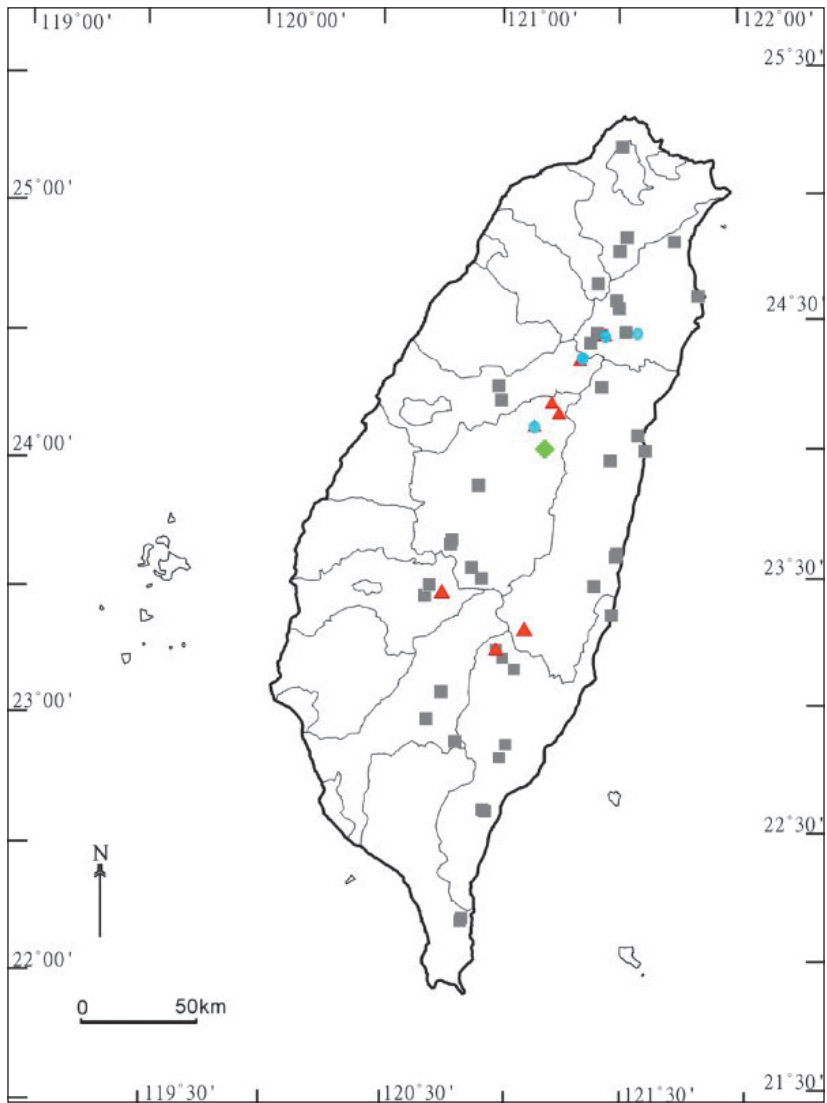
Figs 9–16, 39–41, 45, 46, 53

Prionopeltis piceofasciatus Gressitt, 1941: 59; Wang, 1964: 69; Jeekel, 1968: 69.

Chamberlinius piceofasciatus Hoffman, 1973: 381, figs 23–27; Wang and Mauriès, 1996: 87; Korsós, 2004: 32.

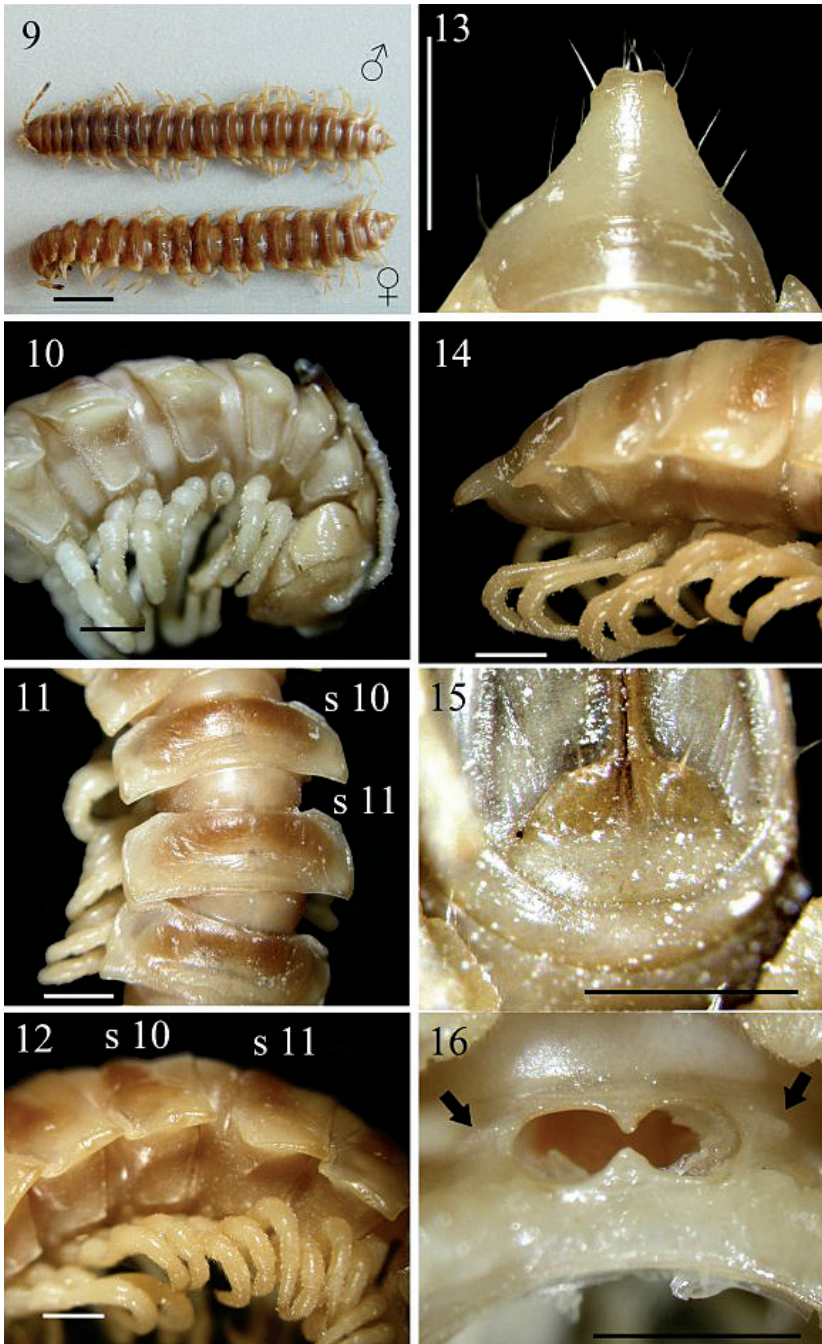
Chamberlinius shengmui Wang, 1957b: 103, fig. 4; Hoffman, 1973: 382; Korsós, 2004: 22. **New Synonymy!**

Material examined: 1 ♂, 1 ♀ (CAS, type series number # 5617 of *Prionopeltis piceofasciatus*: contrary to Hoffman's (1973) presentation, it is the female that Gressitt (1941) had labeled as the holotype, while the male is a paratype), central Taiwan (臺灣中部), Arisan (阿里山), 2,000 m a.s.l., 24 May, 1934, leg. J. L. Gressitt. 1 ♂, 1 ♀ (NMNH, *Chamberlinius shengmui*, det. & ded. Y. H. M. Wang), Alisan Kiayi (阿里山, 嘉義縣), August, 1957, leg. Y. H. M. Wang. 1 ♀ (TFRI), Taichung City (台中市), Hoping District (和平區) (formerly: Taichung County 台中縣, Heping Township 和平鄉), Shengguang (勝光), 2,000–2,300 m a.s.l., 21 August - 24 September 2002, leg. W. C. Yeh. 1 ♂ (TFRI), same place, date and



Map. Distribution of *Chamberlinius* species in Taiwan. *C. hualienensis* Wang, 1956: filled grey squares; *C. piceofasciatus* (Gressitt, 1941): filled red triangles; *C. pessior* sp. n.: filled light-green diamond. *C. sublaevus* sp. n.: filled blue circles.

collector. 1 ♀ (TFRI), same place, 24 November - 24 December 2002, same collector. 1 ♂ (TFRI), same place, 26 March - 25 April 2003, same collector. 1 ♂ (TFRI), same place, 24 July 2003, same collector. 1 ♂ (TFRI), same place, date and collector. 1 ♀ (NTNUL-My 42), Nantou County (南投縣), Renai Township (仁愛鄉), Hehuanshan (合歡山), 3,100 m a.s.l., 30 August 1988, leg. S. H. Chen. 1 ♂ (NCHUL), same township, Meifeng (梅峰), ca. 2,000 m a.s.l., 2 April 2002, leg. S. H. Wu. 1 ♂, 2 ♀, 3 juveniles (NSYSUB-DI 44-49), same township, HuaGer water source (華岡水源), ca. 2,600 m a.s.l., 22 August 2002, leg.



Figures 9–16. *Chamberlinius piceofasciatus* (Gressitt, 1941), ♂ and ♀ from HuaGer water source (華岡水源) (9) and ♂ from AliShan (阿里山) (10–16). **9** Entire body, dorsal view **10** Anterior body portion, lateral **11, 12** segments 10 and 11, dorsal and lateral views, respectively **13, 14** Epiproct, dorsal and lateral views, respectively **15** Hypoproct, ventral view **16** Spiracle-bearing cones/ridges lateral to gonopod aperture (arrows). Scale bars: 5.0 mm (9); 1.0 mm (10–16). **s10** and **s11**: segments 10 and 11 separately.

C. C. Chen and J. N. Huang. 3 ♂, 2 ♀ (NTNUL-My 1-5), Chia-I County (嘉義縣), AliShan (阿里山), 2,260 m a.s.l., 3 July 1989, leg. S. H. Chen. 1 ♂, 1 ♀ (NTNUL-My 59-60), same place, 2,250 m a.s.l., same date and collector. 1 ♂ (TFRI), Ilan County (宜蘭縣), Datong Township (大同鄉), Lakes Jialuohu (加羅湖), ca. 2,300 m a.s.l., 24 May 2002, leg. W. C. Yeh. 1 juvenile (TFRI), same place, 23 August 2002, same collector. 1 ♂ (NCHUL), Hualien County (花蓮縣), Zhuoxi (卓溪), 2,500 m a.s.l., 15 February 2008, leg. S. H. Wu. 1 ♂ (NTNUL-My 43), Taitung County (台東縣), Haituan Township (海端鄉), Siangyang (向陽), on wall, ca. 2,270 m a.s.l., 3 September 2002, leg. J. H. Chen.

Diagnosis: Closest to *C. hualienensis*, but differs in often a lighter general coloration; in metaterga 2–19 with only a slightly infusate (brown), subtrapeziform band in the anterior half (versus 1+1 darker, axially separated spots in *C. hualienensis*); in the paraterga like low ridges (versus higher ridges in *C. hualienensis*); by the pleurosternal carinae with small caudal teeth on segments 3–5(9, 10) (♂) (versus 3–7(8) in *C. hualienensis*); in the epiproct shorter; in the smaller spiracle-bearing ridges lateral to the gonopod aperture; and in the gonopods, in which the solenophore is rounded apically and considerably shorter than the solenomere, while the parbasal dentiform process is stouter and more solid (versus longer and membranous in *C. hualienensis*), always placed behind the solenomere in ventral view.

Description: Length 29–33 (♂, n = 4) or 31–34 mm (♀, n = 3); width of metazonite 10 ca. 4–4.5 (♂) or 4.5–5.0 mm (♀). Specimens in NMNH: Length ca. 32 (♂, n = 1) and 38 mm (♀, n = 1); width of midbody metaterga 10 ca. 4.0 (♂) and 4.3–4.5 mm (♀).

Coloration in alcohol (Fig. 9) light yellow-brown to light brown from head to end of epiproct, as well as from dorsum down to paraterga, sterna and legs; collum and metaterga 2–19 with a slightly infusate (brown), subtrapeziform band in anterior half (Fig. 11); a lighter or darker anterior part of epiproct; colour pattern similar in both sexes, but ♀ darker; antennae increasingly blackish distally, but tip contrastingly pallid.

In width, head < collum < 2 > 3 < 4 < 5 < 6 < 7 < 8–16 in ♂, or head < collum ≤ 2 > 3 < 4 < 5 < 6 < 7 < 8 < 9–16 in ♀; thereafter body gradually and gently tapering both in width and height towards telson. Antennae (Figs 9, 10) moderately long to long in ♂, slender, reaching either behind posterior end of metatergum 4 to anterior end of metatergum 5 (♂), or anterior edge to end of metatergum 3 (♀) dorsally. Surface smooth throughout, rugulose on metaterga (Figs 10, 12) and below paraterga where evidently and densely granular on segments 2–19 in ♂; sometimes so only on segments 2–5, suddenly not so densely on segments 6 and 7, then wanting on segments 8–14, but traceable again on segments 15 and 16 in ♂ or on segments 2–18 in ♀. Paraterga (Fig. 11) very well-developed, calluses (Fig. 12) delimited by a sulcus only dorsally on segments 3 and 4, both dorsally and ventrally on segments 5–19; like low ridges always extending beyond caudal tergal margin on segments 2–19 (Fig. 9), spiniform caudally (Fig. 13) on segment 19 in both sexes or on segments 18 and 19 only in ♀. Axial line wanting to traceable in places. Transverse sulcus (Fig. 11) evident on segments 5–18 in ♂, likewise evident on segments 5–17, but only traceable on 18th in ♀, narrow, shallow, neither beaded at bottom nor reaching bases of paraterga. Stricture (Fig. 11) between pro- and metazona very faintly beaded at bottom dorsally. Pleurosternal carinae (Figs 10, 12) well-developed on segments 2–(9)10, traceable

on (10)11–14(15), like low bosses on segments 15–17 in ♂, well-developed on segments 2–(9)10, visible on segments (10)11–(13)16, like low bosses on segments (14–16)17 in ♀, thereafter virtually absent in both sexes; with small caudal teeth (Fig. 10) on segments 3–5(9, 10) (♂) or 3(4)–5(7) (♀). Tergal setae fully abraded, pattern untraceable. Ozopores (Fig. 12) lateral, lying on callus ca. one-third metatergal length in front of caudal edge. Epiproct (Figs 13, 14) digitiform, flattened dorsoventrally, moderately long in lateral view, ratio of epiproct length to pre-epiproct length of telson 1: 2.2 in ♂ (Fig. 14); subtruncate and slightly concave to emarginate in dorsal view (Fig. 13); pre-apical papillae (Fig. 13) present, situated close to apex. Hypoproct (Fig. 15) roundly subtrapeziform caudally, 1+1 setae at caudal corners situated on well-separated knobs, sides straight to slightly concave.

Sterna moderately setose, not modified; a short, round, spiracle-bearing ridge flanking gonopod aperture (Fig. 16, arrows); each cross-impression with an evident transverse sulcus, but without axial groove. ♂ legs (Fig. 12) without tarsal brushes, ca. 1.5 times as long as midbody height, slightly shorter in ♀.

Gonopods (Figs 39–41, 45, 46, 53) peculiar in solenophore (**sph**) being rounded apically and considerably shorter than solenomere (**sl**), while its dentiform process (**dp**) more solid, and both **sph** and **dp** always placed behind solenomere in ventral view.

Remarks: The sketch of a gonopod of *C. shengmui* by Wang (1957) showed the solenophore being strongly broadened distad, while the solenomere broadened at midway. Apparently due to these distinctions, this species has since been considered as valid. We have been privileged to examine the specimens of *C. shengmui* deposited at NMNH (without catalogue number) by Wang, and found the gonopod sketch of the solenomere accompanying the original description (Wang 1957) misleading. Having also re-examined the ♀ holotype and ♂ paratype of *C. piceofasciatus*, both housed in CAS, and compared them side-by-side with *shengmui*, we found that these species are identical. Therefore, *C. shengmui* is a new junior subjective synonym of *C. piceofasciatus*.

Distribution: *C. piceofasciatus* seems to be endemic to Taiwan, being restricted to higher elevations (2,000 to > 3,000 m a.s.l.) (Map).

Chamberlinius pessior sp. n.

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http://species-id.net/wiki/Chamberlinius_pessior

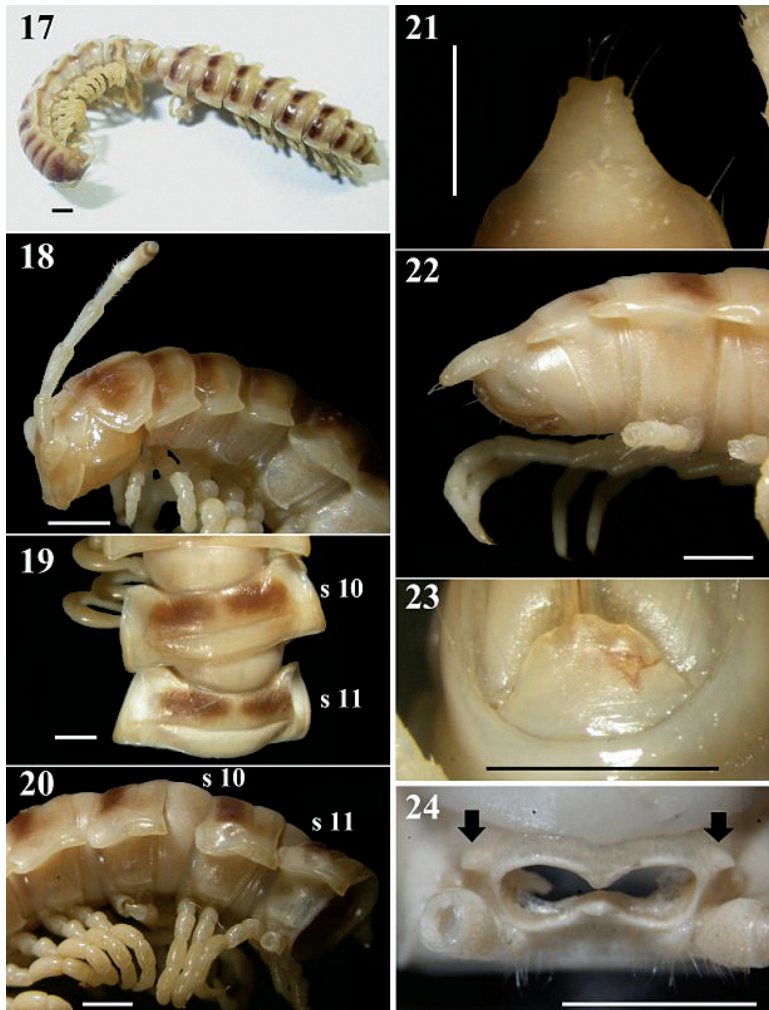
Figs 17–24, 36–38, 49–52

Holotype ♂ (NTNUL-My 74), Taiwan, Nantou County (南投縣), Renai Township (仁愛鄉), Lushan warm spring (廬山溫泉), ca. 1,200 m a.s.l., 29 August 1988, leg. S. H. Chen.

Paratypes: 1 ♂, 5 ♀ (NTNUL-My 75–80), same locality and date, together with holotype.

Name: To emphasize the lower paraterga.

Diagnosis: Closest to *C. hualienensis*, but differs in being obviously smaller, with paraterga like low ridges (versus higher ridges in *C. hualienensis*), the pleurosternal carinae are



Figures 17–24. *Chamberlinius pessior* sp. n., holotype. **17** Entire body, dorsal view **18** Anterior body portion, lateral **19, 20** segments 10 and 11, dorsal and lateral views, respectively **21, 22** Epiproct, dorsal and lateral views, respectively **23** Hypoproct, ventral view **24** Spiracle-bearing cones lateral to gonopod aperture (arrows). Scale bar: 1.0 mm. **s10** and **s11**: segments 10 and 11 separately.

with small caudal teeth on segments 3–10 (versus 3–7(8) in *C. hualienensis*), legs with tarsal brushes (versus without in *C. hualienensis*) and the gonopods showing the tip of the solenophore pointed and simple (versus bifid in *C. hualienensis*).

Description: Length 25–26 (♂, n = 2) or 27–29 mm (♀, n = 5), width of metazonite 10 ca. 3.5–3.8 (♂) or 3.8–4.0 mm (♀). Coloration in alcohol (Fig. 17) almost entirely light yellow-brown in ♂, but infusate (brown) in ♀ compared with ♂; colour pattern same as in *C. hualienensis*.

In width, head < collum = segment 2 > 3 < 4 < 5 < 6 < 7 < 8 < 9 < 10 < 11 < 12 < 13 < 14 < 15 < 16 in ♂, or head < collum = segment 2 > 3 < 4 < 5 < 6 < 7 < 8 < 9 < 10 < 11–16

in ♀; thereafter body gradually and gently tapering both in width and height towards telson. Antennae (Figs 17, 18) long and slender, reaching behind middle of metatergum 4 (♂) or 3 (♀) dorsally. Surface generally shining and smooth, rugulose (**r**) (Figs 18, 20, 49) on metaterga on place and below paraterga 2–19, metazona below paraterga evidently and densely granular on segments 2–19 in both sexes. Paraterga (Fig. 19) very well-developed, calluses (Figs 19, 20) delimited by a sulcus dorsally and ventrally on segments 2–19; paraterga like low ridges (Figs 20, 49), slightly extending beyond caudal tergal margin on segments 2–4, obviously beyond it on segments 5–19 (Fig. 17), spiniform caudally (Fig. 22) on segments 17–19 in both sexes; anterior corner of paraterga thinner dorsoventrally and depressed only in ♂. Axial line traceable to evident on pro- and metaterga from collum to anterior part of segment 19 in ♂, fainter in ♀. Transverse sulcus (Figs 19, 49) evident on segments 5–17, traceable on segment 18, wanting on segment 19 in both sexes, narrow, shallow (markedly shallower in ♂ as compared to ♀), neither beaded at bottom nor reaching bases of paraterga. Limbus thin, caudal margin entire. Stricture (Fig. 19) between pro- and metazona roughly beaded, evidently more roughly so in ♀ as compared to ♂. Pleurosternal carinae (Figs 18, 20) well-developed on segments 2–10, traceable on segments 11–15 in ♂, well-developed on segments 2–12, visible on segments 13–17 in ♀, thereafter wanting, with small caudal teeth on segments 3–10 (♂) or 3–9 (♀). Tergal setae fully abraded, pattern untraceable in both sexes. Ozopores (Figs 20, 49) lateral, lying on callus about one-third metatergal length in front of caudal edge. Epiproct (Figs 21, 22) digitiform, long, flattened dorsoventrally, curved and directed caudoventrad in lateral view (Fig. 22), ratio of epiproct length to pre-epiproct length of telson 1: 2.0 in ♂ (Fig. 22), subtruncate and emarginated (♂) or slightly concave (♀) in dorsal view (Fig. 21); pre-apical papillae (Fig. 21) evident, situated close to apex. Hypoproct (Fig. 23) subtrapeziform, caudally convex, 1+1 setae at caudal corners situated on well-separated knobs, sides slightly concave in both sexes.

Sterna moderately setose in ♂, sparsely so in ♀; an obvious, short, round, spiracle-bearing ridge flanking gonopod aperture (Fig. 24, arrows); each cross-impression with an evident transverse sulcus, without axial groove. Legs (Fig. 49) with tarsal brushes, long, ca. 1.2 times midbody height in ♂, slightly shorter in ♀.

Gonopods (Figs 36–38, 50–52) as in *C. hualienensis*, but solenophore (**sph**) not bifid, being simple and pointed.

Remarks. *C. pessior* sp. n. is endemic to Taiwan, being known from a single locality at 1,200 m a.s.l. (Map).

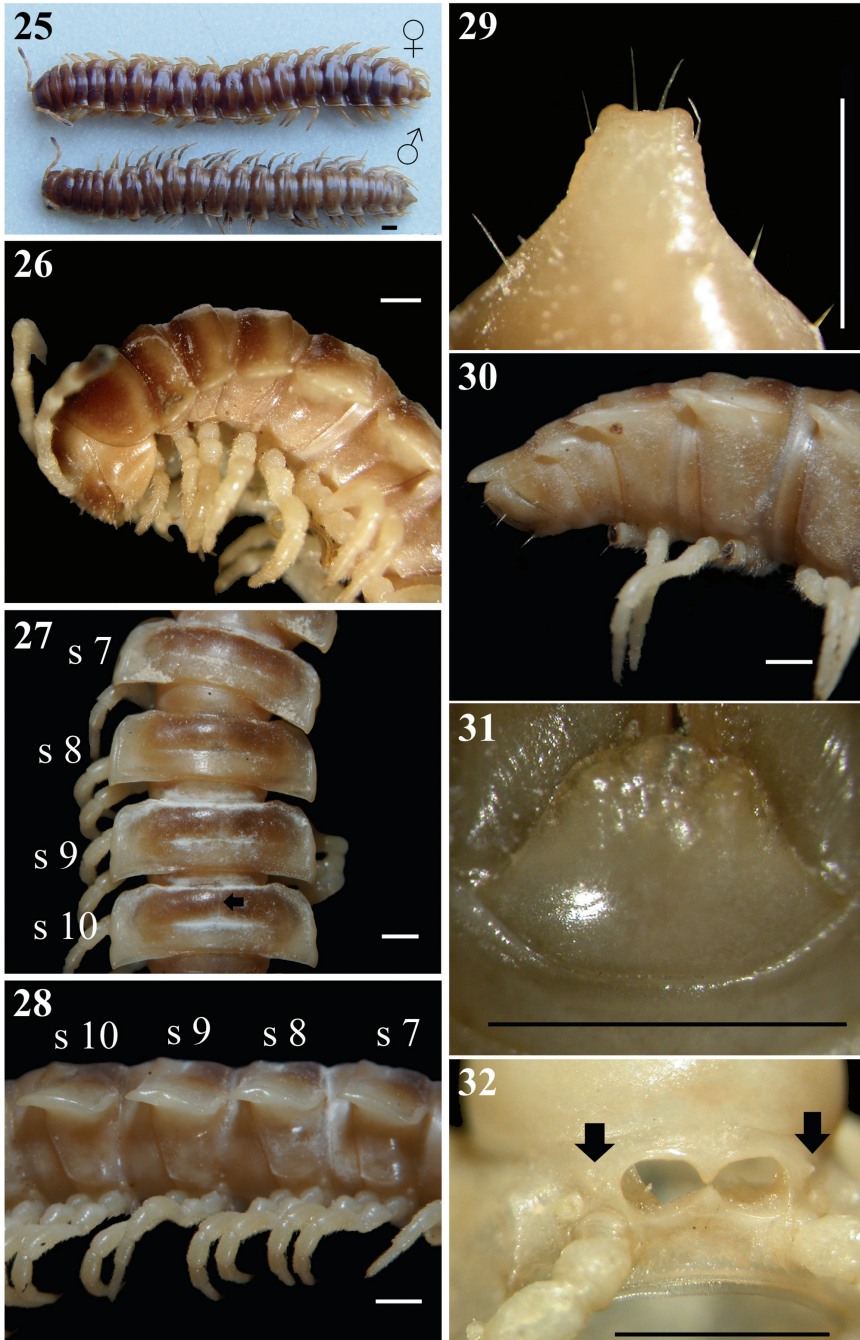
Chamberlinius sublaevus, sp. n.

urn:lsid:zoobank.org:act:6AC5346F-0657-44A1-9452-59B2A1AC9B61

http://species-id.net/wiki/Chamberlinius_sublaevus

Figs 25–32, 42–44, 47, 48, 54–57

Holotype ♂ (NSYSUB-DI 50), Taiwan, Taichung County (台中縣), Heping Township (和平鄉), Syuan (思源), 1.5 km away from the entrance of forest path no. 710, ca. 2,050–2,100 m a.s.l., 21 August 2002, leg. C. C. Chen and Y. H. Lin.



Figures 25–32. *Chamberlinius sublaevus* sp. n., ♀ and ♂ paratypes from Yuanping forest path (元平林道) (25–31) and Syuan (思源) (32), respectively. **25** Entire body, dorsal view **26** Anterior body portion, lateral **27, 28** Midbody segments, dorsal and lateral views, respectively. arrow: axial line **29, 30** Epiproct, dorsal and lateral views, respectively **31** Hypoproct, ventral view **32** Cones lateral to gonopod aperture (arrows). Scale bar: 1.0 mm. **s7–s10**: segments 7–10 separately.

Paratypes: 3 ♂, 1 ♀, 2 juveniles (NSYSUB-DI 51-57), same locality and date as in holotype. 1 ♂, 1 ♀ (NCHUL), Nantou County (南投縣), Renai Township (仁愛鄉), Meifeng (梅峰), ca. 2,000 m a.s.l., 2 April 2002, S. H. Wu. 1 ♂ (TFRI), Ilan County (宜蘭縣), Datong Township (大同鄉), Lakes Jialuohu (加羅湖), ca. 2,300 m a.s.l., 22 April 2001, leg. W. C. Yeh. 1 ♂ (TFRI), same place, 26 April 2002, same collector. 1 ♂ (TFRI), same place, 4 June 2003, same collector. 1 ♂, 1 ♀ (NSYSUB-DI 451-452), same township, Yuanping forest path (元平林道), 4 km, on a dirty wall, ca. 1,990 m a.s.l., 29 August 2004, leg. H. D. Zhu.

Name: To emphasize the elevated paraterga.

Diagnosis: Closest to *C. piceofasciatus*, but differs in the smaller size and higher paraterga; by the pleurosternal carinae with small caudal teeth either on segments 3–8(10) (♂) or 3–4, or without any caudal teeth (♀) (versus segments 3–5(10) (♂) or 3(4)–5(7) (♀) in *C. piceofasciatus*); and in gonopod structure, with the solenophore being slender, its tip pointed and placed ventrad under the solenomere (versus the solenophore being much stouter, blunt and remaining fully behind and above the solenomere in ventral view in *C. piceofasciatus*).

Description: Length 29–30 (♂, n = 5) or 28 mm (♀, n = 1); width of metazonite 10 ca. 4–5 mm (♂) or 4–5.5 mm (♀). Coloration in alcohol (Fig. 25) pallid to light brown from head to end of epiproct, as well as from dorsum down to paraterga, sterna and legs; most of head (except for occipital part), anterior 2/3rds of collum (Fig. 27), and most of epiproct darker, colour pattern same as in *C. piceofasciatus* (Gressitt, 1941) and similar in both sexes, but ♀ darker; antennae increasingly blackish distally, but tip contrastingly pallid.

In width, head < collum ≤ segment 2 > 3 = 4 < 5 < 6 < 7 < 8 ≤ 9 = 10 < 11–15 in ♂, or head < collum < segment 2 > 3 = 4 < 5–16 in ♀; thereafter body gradually and gently tapering both in width and height towards telson. Antennae (Figs 25, 26) long, slender, reaching either middle to end of metatergum 4 dorsally in ♂, or end of metatergum 3 in ♀. Surface generally shining and rather smooth, sometimes rugulose on metaterga, rugulose, finely and densely granular below paraterga 2–19 (Figs 26–28, 55). Paraterga (Fig. 27) very well-developed, calluses delimited by a sulcus only dorsally on segments 3–4, both dorsally and ventrally on segments 5–19; paraterga like high ridges (Fig. 28) extending beyond caudal tergal margin on segments 5–19 (Fig. 25), spiniform caudally (Fig. 30) on segments 17–19 in both sexes. Axial line (Fig. 27, arrow) wanting to sometimes traceable (on prozona), visible also at anterior edge of collum to end of segment 19, or on segments 5–19, better so on ♂ metaterga than in ♀. Transverse sulcus (Figs 27, 55) evident on segments 5–18, wanting on segment 19 in ♂, present on segments 5–18(19) in ♀, narrow, shallow, neither beaded at bottom nor reaching bases of paraterga. Limbus thin, caudal margin entire. Stricture (Figs 27, 55) between pro- and metazona faintly beaded at bottom dorsally. Pleurosternal carinae (Figs 26, 28, 55) well-developed on segments 2–10, traceable on segments 11–13 in ♂, reduced to low bosses on segments 14–17 in ♂, well-developed on segments 2–8, visible on 9–16 (17) in ♀, thereafter virtually absent in both sexes; with small caudal teeth either on segments

3–8 or 3–10 (♂), or either on segments 3 and 4, or without any caudal teeth (♀). Tergal setae fully abraded, pattern untraceable. Ozopores (Figs 28, 55) lateral, lying on callus about one-third metatergal length in front of caudal edge. Epiproct (Fig. 29) digitiform, long, flattened dorsoventrally, ratio of epiproct length to pre-epiproct length of telson 1: 2.3 in ♂ (Fig. 30); subtruncate or emarginate in dorsal view; pre-apical papillae almost wanting, situated close to apex. Hypoproct (Fig. 31) subtrapeziform, caudally narrowly to broadly rounded, 1+1 setae at caudal corners situated on well-separated knobs, sides concave at base.

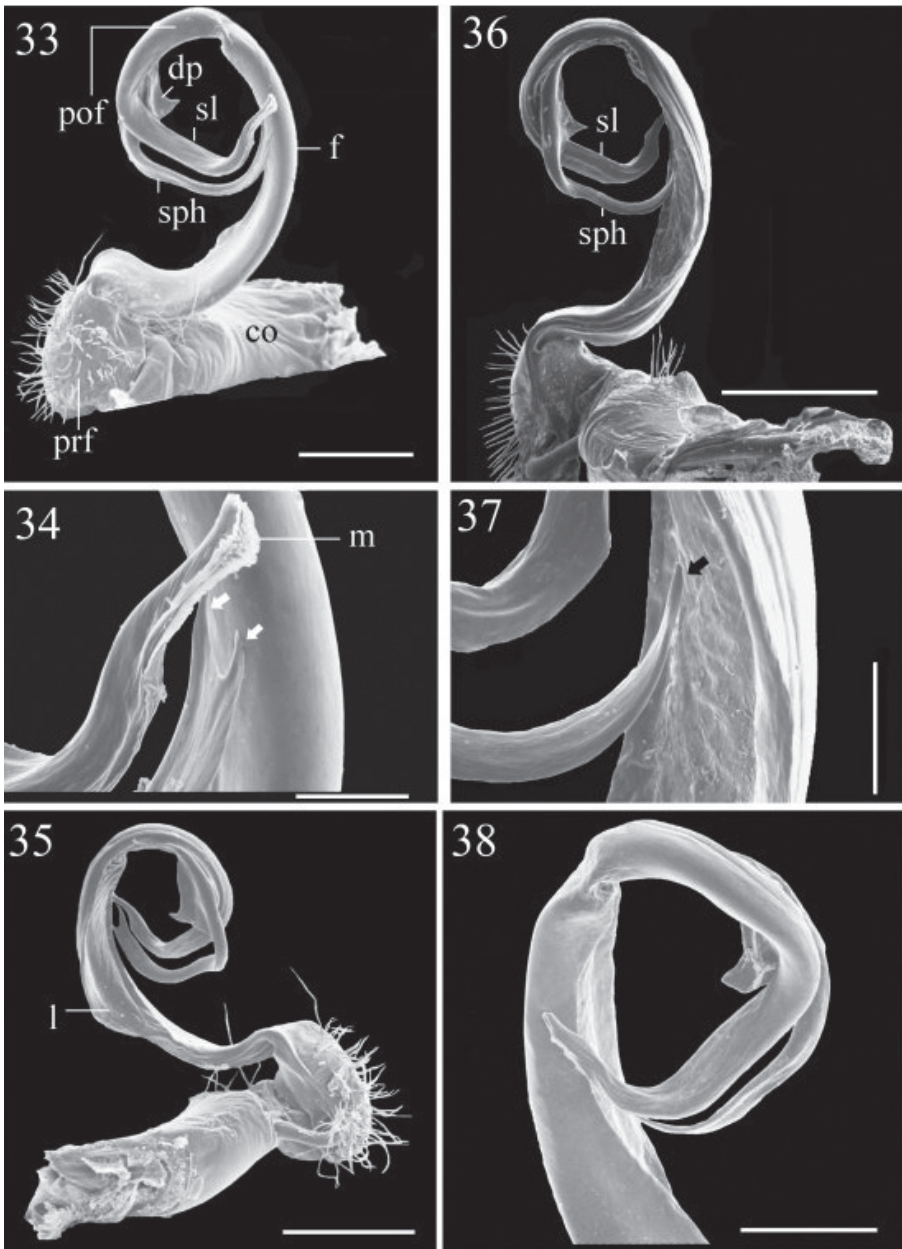
Sterna moderately setose, not modified; a pair of small, short, round, spiracle-bearing ridges flanking gonopod aperture (Fig. 32, arrows); each cross-impression with an evident transverse sulcus, without axial groove. ♂ legs (Figs 28, 55) evidently incrassate, especially so due to dorsally swollen prefemora, without tarsal brushes, ca. 1.7 times as long as midbody height, a little shorter and slenderer in ♀.

Gonopods (Figs 42–44, 47, 48, 54, 56, 57) very similar to those of *C. piceofasciatus*, differing in solenophore (**sph**) being slender, elongate, pointed and directed ventrad under solenomere (**sl**).

Distribution: This new species is also endemic to Taiwan, being high-montane (2,000–2,300 m a.s.l.) (Map).

Key to *Chamberlinius* species (based mainly on adult males):

- 1 Dark brown subtrapeziform markings on presulcus halves of metaterga 5–18 divided by a light axial line; solenophore as long as solenomere, parabasal dentiform process of gonopod membranous **2**
- Brown subtrapeziform markings on presulcus halves of metaterga 2–19 not divided by axial line; solenophore considerably shorter than solenomere, parabasal dentiform process of gonopod stout and more solid..... **3**
- 2 Body much longer and wider (length 30–34 mm, width 4.5–5.0 mm); paraterga like high ridges; pleurosternal carinae with small caudal teeth on segments 3–7(8); solenophore with a bifid tip *C. hualienensis*
- Body shorter and narrower (length 25–26 mm, width 3.5–3.8 mm); paraterga like low ridges; pleurosternal carinae with small caudal teeth on segments 3–10; solenophore with one pointed end..... *C. pessior* sp. n.
- 3 Larger (length 29–33 mm); paraterga like low ridges; parabasal dentiform process and solenophore of gonopods always placed behind solenomere in ventral view *C. piceofasciatus*
- Smaller (length 29–30 mm); paraterga like high ridges; parabasal dentiform process placed behind solenomere, but solenophore pointed and directed ventrad under solenomere in ventral view *C. sublaevus* sp. n.



Figures 33–38. **33–35** *Chamberlinius hualienensis* Wang, 1956, ♂ from CiiLan Forest Amusement Park (棲蘭森林遊樂園), left gonopod (33–35). **33** Entire gonopod, sublateral view **34** Tip of telopodite, sublateral view. Arrows: a bifid solenophore **35** Entire gonopod, medial view. **Figures 36–38.** *Chamberlinius pessior* sp. n., holotype, right gonopod. **36, 37** Entire gonopod and tip of solenophore (arrow), respectively, submedial view **38** Apical part of telopodite, medial and slightly ventral view. Scale bars = 0.5 mm (33, 35, 36); 0.1 mm (34, 37); 0.25 mm (38). **co**: coxa; **dp**: dentiform process; **f**: femur; **m**: apical lamina; **l**: membranous lobe; **po**: postfemoral region; **prf**: prefemur; **sl**: solenomere; **sph**: solenophore.

Distribution

The distribution of *Chamberlinius* species in Taiwan shows that only one species, *C. hualienensis*, is truly widespread across Taiwan, ranging from lowlands (ca 80 m a.s.l.) to high in the mountains (up to 2,500 m a.s.l.) (Map). Unsurprisingly, it is *C. hualienensis* that seems to have become introduced to southern Japan. Another species, *C. pes-sior* sp. n., has only been encountered at a single midmontane locality at 1,200 m a.s.l., while the remaining two congeners are far more local in distribution, being restricted to high elevations (> 2,000 a.s.l.) both in the northern and central parts of the island. Allopatry or parapatry are prevailing, but syntopic occurrences of two species, one of them usually *C. hualienensis*, are not too rare, e.g. at Alishan, Hoping etc.

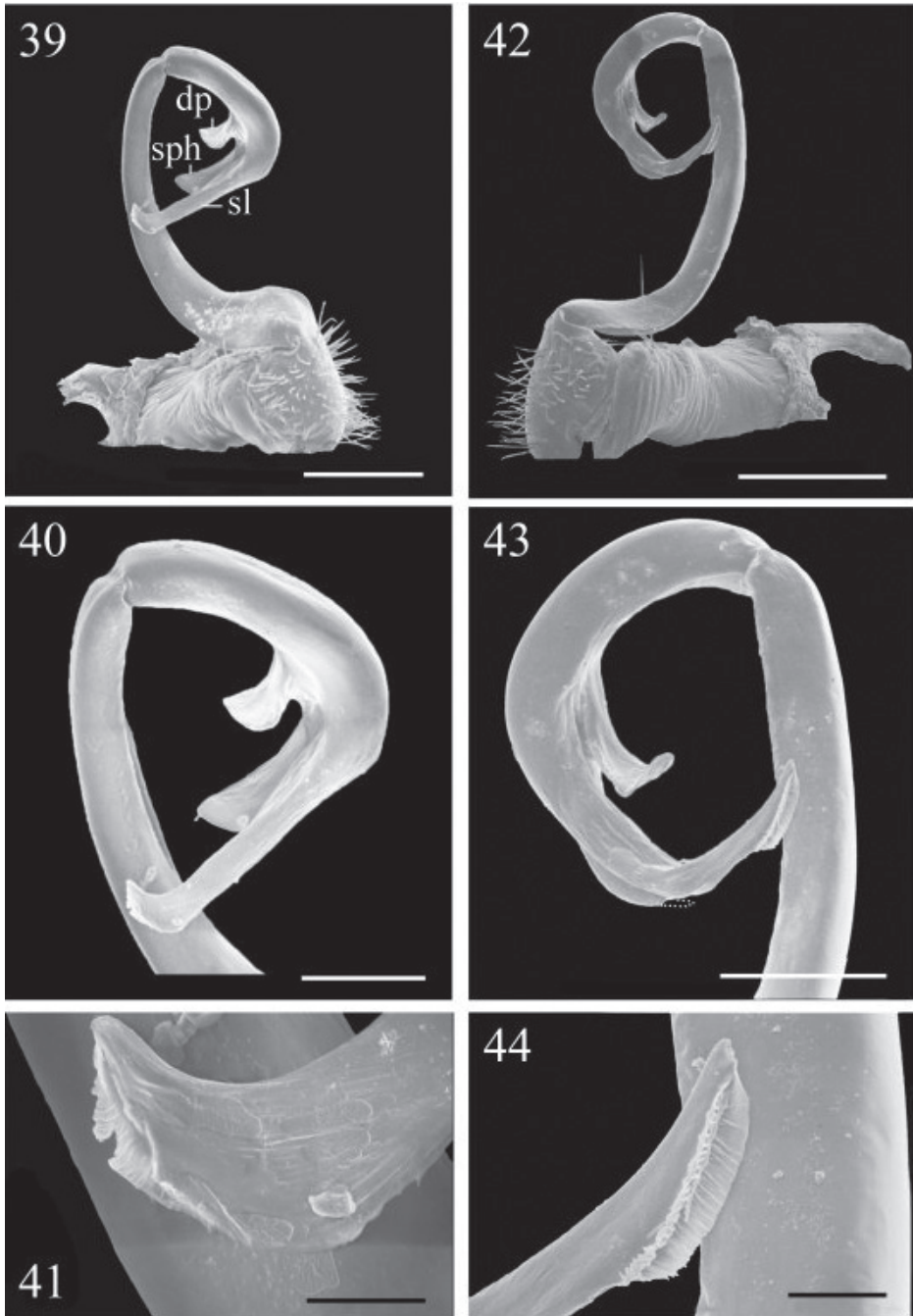
To our mind, it seems more logical to surmise that high-montane species in Taiwan tend to be more local in distribution, more inclined to endemism and less liable to introduction than those showing vaster distributions, including lowland habitats. So we are inclined to interpret the presence of the especially common and eurytopic *C. hualienensis* in Japan as likely introduced from Taiwan.

Reclassification of the Chamberlinini

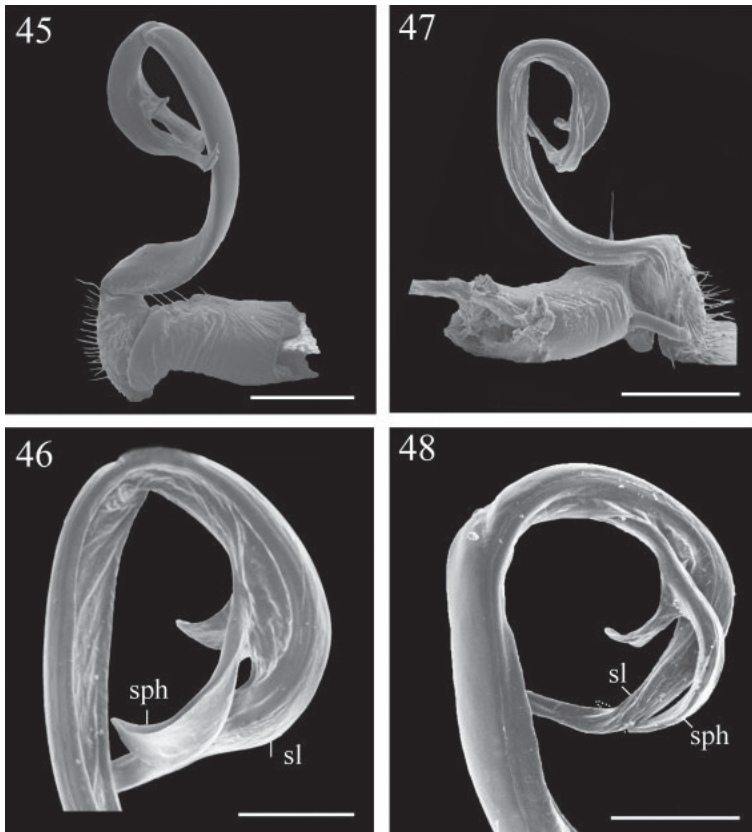
The subfamily Chamberlininae, proposed by Wang (1957) for *Chamberlinius* alone, was originally diagnosed as showing a distally “toothed” seminal groove branch (= solenomere). Because this statement was incorrect, Hoffman (1973), who was the first to revise *Chamberlinius*, downgraded the Chamberlininae to the tribe Chamberlinini and reshaped it as comprising both *Chamberlinius* and *Riukiupeltis*. He reformulated the tribe’s diagnosis to emphasize that the terminal part of the gonopod lying distally of the postfemoral cingulum represents a single element with several subterminal branches, one of which carries the seminal groove. This diagnosis still holds valid and, based on several recent revisions, including the present one, now allows for another few East to Southeast Asian genera and species to be formally added to the tribe.

Thus, the genus *Haplogonosoma* Brölemann, 1916, with presumably two valid species (one ranging from central Honshu, Japan to Kurile Island, Russia, the other from Kyushu, Japan to ?Sumatra, Indonesia) shows highly elongate gonopods, in which the slender femorite is supplied with a distinct lateral sulcus. Distally of it, there is a cingulum demarcating a clear-cut geniculation followed by a very long, mesally directed, complex and strongly coiled postfemoral region. The latter is split from its base into a very long, flagelliform, fringed solenomere supported by an undivided, similarly long, slender, membranous lamina (= solenophore). The solenophore carries a pronounced basal outgrowth distodorsally.

Golovatch et al. (1995), who revised *Haplogonosoma*, referred this genus, albeit with hesitations, to the basically Papuan tribe Eustrongylosomatini. At present, however, we believe it is better placed in Chamberlinini.



Figures 39–44. 39–41 *Chamberlinius piceofasciatus* (Gressitt, 1941), ♂ from AliShan (阿里山), right gonopod, subventral view. 39 Entire gonopod 40 Apical part of telopodite 41 Tip of solenomere, respectively. **Figures 42–44.** *Chamberlinius sublaevis* sp. n., ♂ paratype from Syuan (思源), left gonopod, sublateral view. 42 Entire gonopod 43 Apical part of telopodite, dotted line shows a broken tip of solenophore 44 Tip of solenomere. Scale bars: 0.5 mm (39, 42); 0.25 mm (40, 43); 0.05 mm (41, 44).

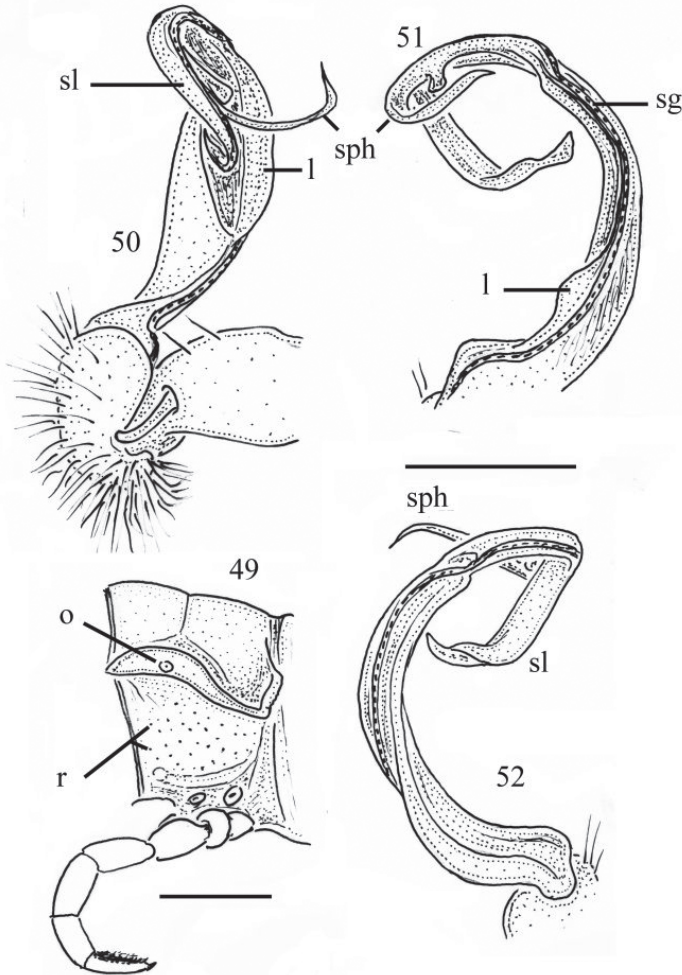


Figures 45–48. **45–46** *Chamberlinius piceofasciatus* (Gressitt, 1941), ♂ from AliShan (阿里山), left gonopod, submedial view. **45** Entire, lateral view **46** Apical part of telopodite, submedial view. **Figures 47–48.** *Chamberlinius sublaevus* sp. n., ♂ paratype from Syuan (思源), left gonopod, submedial view. **47** Entire, dotted line shows a broken tip of solenomere **48** Apical part of telopodite. Scale bars: 0.5 mm (45, 47); 0.25 mm (46, 48). **sl**: solenomere; **sph**: solenophore.

Aponedyopus Verhoeff, 1939, with three species from Taiwan, shows moderately elongate gonopods, in which the femorite is enlarged parabasally, supplied by a distoventral outgrowth, but devoid of a sulcus before a clear-cut cingulum and geniculation. The latter is followed by a long, mesally directed, complex and moderately coiled postfemoral region split from its base into a very long, simple and flagelliform solenomere supported by an only subterminally biramous, similarly long, slender, membranous lamina (= solenophore). The solenophore carries an evident basal outgrowth distoventrally.

Chen et al. (2010), in their recent revision of *Aponedyopus*, have suggested transfer of this genus from the Tonkinosomatini to the Chamberlinini. This transfer is formalized below.

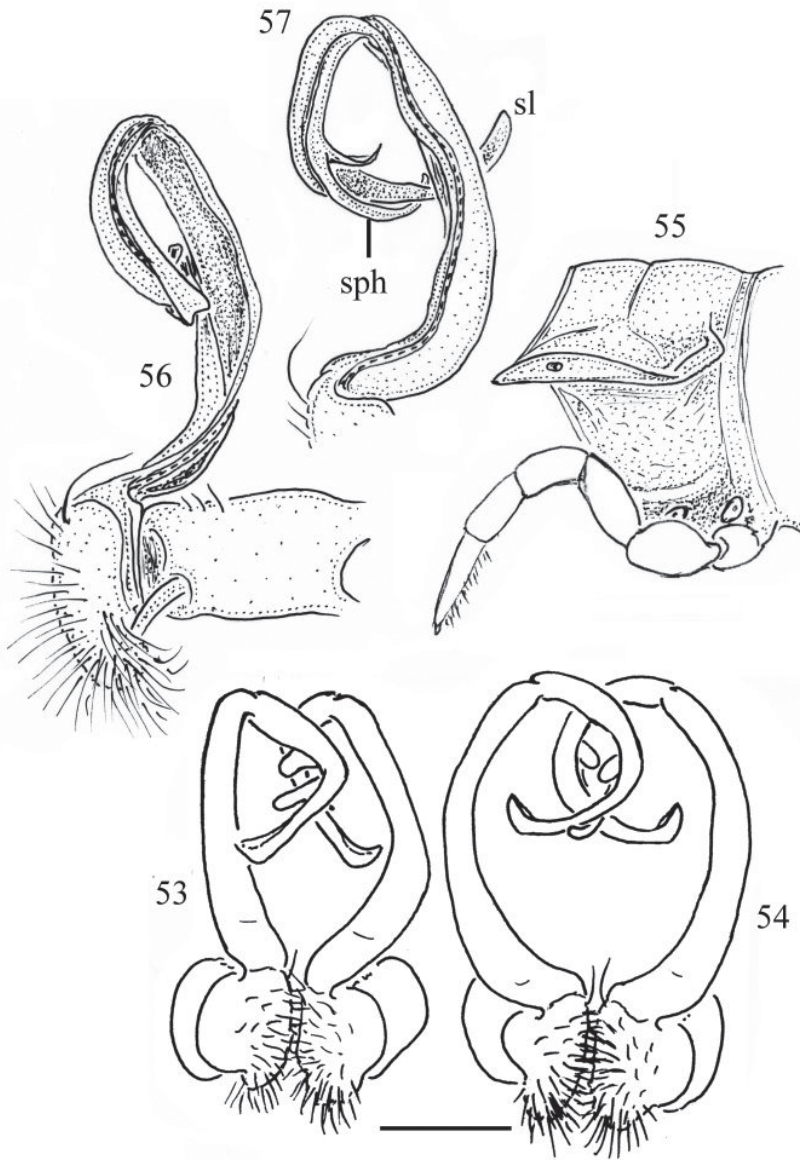
The genus *Geniculodesmus* Chen, Golovatch & Chang, 2008 has recently been erected (Chen et al. 2008) to accommodate a single species, *G. inexpectatus* (Attems, 1944), described from Mt Takao, Hachiojishi, Tokyo Prefecture, Japan and also recorded as likely



Figures 49–52. *Chamberlinius pessor* sp. n., holotype. **49** Segment 10, lateral view **50–52** Right gonopod, medial, dorsal and sublateral views, respectively. Scale bars: 1.0 mm (49); 0.5 mm (50–52). **l**: membranous lobe; **sg**: seminal groove; **sl**: solenomere; **sph**: solenophore; **o**: ozopore; **r**: rugulosity.

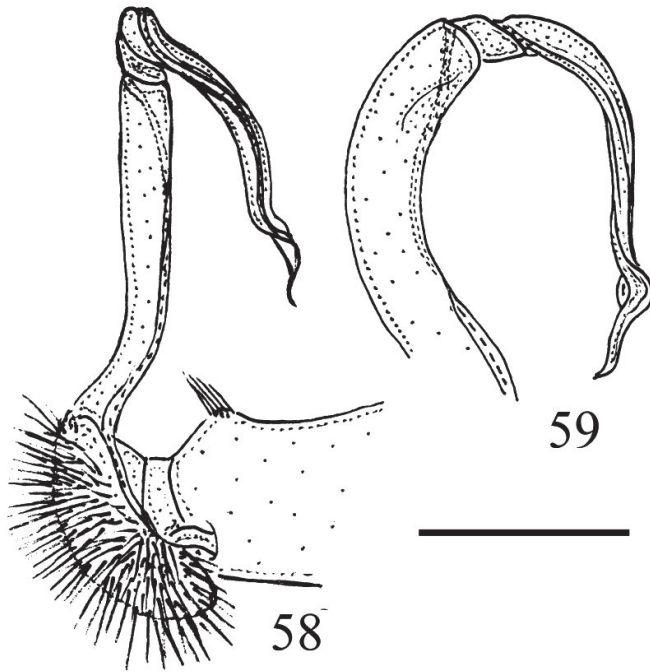
an introduction at Kaohsiung, Taiwan. Its gonopods are elongate, the femorite is slender and devoid of both a distal outgrowth and a sulcus before a clear-cut cingulum and geniculation. The latter is followed by a long, mesally directed, rather simple and moderately coiled postfemoral region split from its base into a long, simple and flagelliform solenomere supported by an only subterminally bifid, similarly long, slender, membranous lamina (= solenophore). The solenophore carries a basal, caudally directed outgrowth.

Geniculodesmus has initially (Chen et al. 2008) been considered as being especially similar to both *Haplogonosoma* and *Aponedyopus*, so its formal assignment to Chamberlinini is likewise fully warranted.



Figures 53–57. **53** *Chamberlinius piceofasciatus* (Gressitt, 1941), ♂ from AliShan (阿里山), entire gonopods, ventral view. **Figures 54–57.** *Chamberlinius sublaevus* sp. n., ♂ paratypes from Meifeng (梅峰) (54) and Syuan (思源) (55–57). **54** Entire gonopods, ventral view **55** Segment 10, lateral view **56–57** Right gonopod, medial and dorsal views, respectively. Scale bars: 0.5 mm (53, 54); 1.0 mm (55–57).

As regards *Riukiupeltis* Verhoeff, 1939, its scope and diagnosis remain rather obscure. The type-species *R. yamashinai* Verhoeff, 1939, from the Ryukyus, Japan has been described as showing the gonofemorite long and slender, devoid of both a sulcus



Figures 58–59. Right gonopod of *Riukiupeltis falcatus* (Attems, 1953), ♂ from Bi Doup National Park, southern Vietnam, medial and ventral views, respectively. Scale bar: 0.5 mm.

and a distal outgrowth before a clear-cut cingulum and geniculation. The postfemoral part is very long, slender, probably directed mesad, moderately coiled, devoid of any basal outgrowth, gradually attenuating towards a pointed tip. A solenomere is only depicted as likely broken off, branching off from the distal half of the solenophore (Verhoeff 1939).

Such a conformation seemed so improbable that Jeekel (1968) doubted it altogether, especially as regards the extent and position of the solenomere. The more so as in another species, *R. falcatus* (Attems, 1953), from Laos and Vietnam, he also formally placed in *Riukiupeltis* the gonopods show a condition readily reminding of that observed in *Chamberlinius*: the solenomere is not flagelliform, but thick and long, gradually attenuating towards a pointed tip (Figs 58, 59). Yet, pending a revision of the type species *R. yamashinai*, it appears impossible to unequivocally state that *Riukiupeltis* is indeed characterized by the gonopod postfemoral portion being normal, non-split, devoid of any additional solenophore, being represented instead solely by a thick, long and helicoidally twisted solenomere.

To accommodate the above five genera into the tribe Chamberlinini, and to properly rediagnose it, only a few slight amendments to Hoffman's (1973) definition are necessary, as follows.

Tribe Chamberlinini Wang, 1957

Diagnosis: Gonopod femorite usually long and slender, only rarely somewhat expanded parasally and supplied with a distal outgrowth (*Aponedyopus*) or carrying a lateral sulcus (*Haplogonosoma*) before a clear-cut cingulum and geniculation. Post-femoral portion directed mesad, long, slender, more or less coiled, either entirely a thick solenomere devoid of any outgrowths (*Riukiupeltis*) or split at base into a thick (*Chamberlinius*) or thin, long, truly flagelliform solenomere and a membranous, more or less complex solenophore (remaining three genera).

Included genera: *Chamberlinius* Wang, 1956, *Riukiupeltis* Verhoeff, 1939, *Aponedyopus* Verhoeff, 1939, *Haplogonosoma* Brölemann, 1916 and *Geniculodesmus* Chen, Golovatch & Chang, 2008.

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References

- Chen CC, Golovatch SI, Chang HW (2008) Identity of the east Asian millipede *Habrodesmus inexpectatus* Attems, 1944 (Diplopoda: Polydesmida: Paradoxosomatidae). *Journal of Natural History* 42(39–40): 2547–2556. doi:10.1080/00222930802354118
- Chen CC, Golovatch SI, Chang HW (2010) Revision of the endemic Taiwanese millipede genus *Aponedyopus* Verhoeff, 1939, with descriptions of two new species (Diplopoda, Polydesmida, Paradoxosomatidae). *ZooKeys* 72: 1–21. doi:10.3897/zookeys.72.743
- Golovatch SI, Mikhaljova EV, Tanabe T (1995) Review of the East Asian millipede genus *Haplogonosoma* Brölemann, 1916 (Diplopoda, Polydesmida, Paradoxosomatidae). *Proceedings of the Japanese Society of Systematic Zoology* 53: 71–80.
- Gressitt JL (1941) New myriopods from Formosa and Hainan Island. *Annals and Magazine of Natural History, Series 11*, 8: 55–61.

- Higa Y, Kishimoto T (1986) Unusual outbreak and control of millipedes, *Chamberlinius haulienensis* Wang in Okinawa. Annual Report of Okinawa Prefectural Institute of Public Health 20: 62–72. [In Japanese]
- Higa Y, Kishimoto T (1989) Expansion of distribution area of millipede, *Chamnerlinius haulienensis* Wang, in Okinawa. Annual Report of Okinawa Prefectural Institute of Public Health 23: 72–76. [In Japanese]
- Hoffman RL (1963) A contribution to the knowledge of Asiatic strongylosomoid Diplopoda (Polydesmida, Strongylosomidae). Annals and Magazine of Natural History, Series 13, 5: 577–593.
- Hoffman RL (1973) Descriptions and allocation of new or poorly known genera and species of Paradoxosomatidae from south-eastern Asia (Diplopoda: Polydesmida). Journal of Natural History 7: 361–389. doi:10.1080/00222937300770281
- Hoffman RL (1980) Classification of the Diplopoda. Genève: Muséum d'histoire naturelle, 237 pp. [for 1979]
- Jeekel CAW (1968) On the classification and geographical distribution of the family Paradoxosomatidae (Diplopoda, Polydesmida). Academisch Proefschrift, Rotterdam, 162 pp. [privately published]
- Jeekel CAW (1971) Nomenclator generum et familiarum Diplopodorum. A list of the genus and family-group names in the Class Diplopoda from the 10th edition of Linnaeus, 1758, to the end of 1957. Monografieën van de Nederlandse Entomologische Vereniging 5, i–xii + 1–412 [for 1970]
- Korsós Z (2004) Checklist and bibliography of millipedes (Diplopoda) of Taiwan. Collection and Research 17: 11–32.
- Nakamura Y, Korsós Z (2010) Distribution and diversity of millipedes of the Ryukyu Archipelago, with the Senkaku and Daito island groups: A literature review (Arthropoda: Diplopoda). Acta Arachnologica 59(2): 73–86.
- Nijijima K, Arimura T (2002) Obstruction of trains by the outbreaks a millipede *Chamberlinius haulienensis* Wang (Diplopoda: Polydesmida). Edaphologia 69: 47–49. [In Japanese]
- Takakuwa Y (1942) Die *Orthomorpha*-Arten aus Japan. Transactions of the Natural History Society of Formosa 32: 44–47.
- Verhoeff KW (1939) Zur Kenntnis ostasiatischer Diplopoden. III. Zoologischer Anzeiger 127(5/6): 113–125.
- Wang YHM (1956) Serica 1e: Records of myriapods on Formosa with description of new species (2). Quarterly Journal of the Taiwan Museum 9: 155–159.
- Wang YHM (1957) Serica 1g: Records of myriapods on Taiwan Islands (4). Six new polydesmides. Quarterly Journal of the Taiwan Museum 10: 103–111.
- Wang D, Mauriès JP (1996) Review and perspective of study on myriapodology of China. In: Geoffroy JJ, Mauriès JP, Nguyen Duy-Jacquemin M (Eds) Acta Myriapodologica. Mémoires du Muséum national d'Histoire naturelle 169: 81–99.
- Yamaguchi T, Izumi S, Takemura K, Torigoe H, Matunaga T, Nagata K (2000) Annual occurrence of *Chamnerlinius haulienensis* Wang on Amami-Oshima Island and possible chemicals for controlling it. Proceedings of the Association for Plant Protection of Kyushu 46: 118–122. [In Japanese]

Systematics and biology of the new genus *Macrosaccus* with descriptions of two new species (Lepidoptera, Gracillariidae)

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Abstract

The new genus *Macrosaccus* Davis & De Prins is proposed for three species formerly assigned to the genus *Phyllonorycter*: *M. robiniella* (Clemens), *M. morrisella* (Fitch), and *M. uhlerella* (Fitch); two new, closely related species: *M. neomexicanus* Davis and *M. gliricidius* Davis, are also proposed. Descriptions of the adults, pupae, larvae, life histories, and distributions are supplemented with photographs, line drawings, and scanning electron micrographs. Larvae of all species are serpentine/blotch leaf miners on various genera of the plant family Fabaceae. The genus is endemic to the New World, with the invasive species *M. robiniella* now widely established in Europe.

Keywords

Biogeography, DNA barcodes, host plants, hypermetamorphosis, genital morphology, larval morphology, Lithocolletinae, pupal morphology, leaf mining, taxonomy

Introduction

The gracillariid subfamily Lithocolletinae includes 503 species (De Prins and De Prins 2011) assigned to 7–9 genera according to different authors (Kumata 1993; Davis and Robinson 1998; Kuznetsov and Baryshnikova 2001). Lithocolletinae are very small moths (less than 10 mm in wing expanse) with often brilliantly coloured forewings of ochreous-orange or reddish-brown ground colour, marked by white or silvery white striae and fasciae (Chapman 1902; Vári 1961; Kumata 1961, 1963, 1993; Watkinson 1985; Kuznetsov 1981; Kuznetsov and Stekol'nikov 1987, 2001; Davis and Robinson 1998; Kuznetsov and Baryshnikova 2001). The subfamily has a worldwide distribution, but is more species-rich in temperate zones: 273 species are known from the Palaearctic, 142 species from the Nearctic, 49 species from the Oriental, 26 species from the Afrotropical, 16 species from the Neotropical, and only 8 species from the Australasian region (De Prins and De Prins 2005, 2011). The hostplant range within this subfamily is broad. Lithocolletinae feed on no less than 36 families of plants (De Prins and De Prins 2005, 2011). Approximately 32 families of dicotyledonous plants serve as hosts for *Phyllonorycter* moths, compared to 11 families for *Cameraria* (De Prins and De Prins 2005, 2011). Deschka (1993) lists 13 hostplant families for *Cameraria*, but we failed to find any published record related to *Cameraria* larvae feeding on either Oleaceae or Sapotaceae. Seven lithocolletine genera (*Cameraria*, *Phyllonorycter*, *Chrysaster*, *Hyloconis*, *Neolithocolletis*, *Porphyrosela* and *Protolithocolletis*) mine plants of the family Fabaceae, with the latter five genera feeding exclusively on Fabaceae (Robinson et al. 2007; De Prins and De Prins 2011). Probably many more taxa will be discovered in the southern hemisphere. However, even in the seemingly well-known European and North American Lithocolletinae fauna the generic assignment of some lithocolletine species is still questionable; for example, the species-rich genus *Phyllonorycter*, comprising about 400 species and having a world-wide distribution, has served for some time as a depository for several species of uncertain phylogenetic placement.

Characters defining genera within the Lithocolletinae are still being investigated. Most of these concern the life history and morphology of the preimaginal stages (Kumata 1993). With regards to adult morphology, Kumata (1993) diagnosed Lithocolletinae genera by the following characters: 1) wing venation, in particular the parallel condition of veins Rs and M near the base of the hindwing; 2) number of setae on apical part of tegumen in male genitalia; 3) development of the transtilla in male genitalia; 4) number and shape of signa in female genitalia; and 5) dark margins of whitish fasciae on forewings. Adult morphology does not always clearly separate genera: for example, 1) the wing venation in *Phyllonorycter* and *Cameraria* is identical (with the exception of *C. fasciata*); 2) a pair of setae on the apical part of the tegumen is present in *Cameraria*, *Chrysaster* and *Porphyrosela* (absent in *Phyllonorycter*); more than two pairs of tegumenal setae are found in *Hyloconis* and *Cremastobombycia*; 3) transtilla is incomplete in *Hyloconis* and *Cameraria* (with the exception of *C. magnisignata*, *C. milletiae*, *C. palawanensis*, *C. pongamiae*, and *C. virgulata*); 4) signa of the corpus bursae

show a variety of shapes in *Phyllonorycter*; 5) most of the species in both *Cameraria* and *Cremastobombycia* show black margins distally on the whitish fasciae (Busck 1909; Ely 1918; Braun 1925; Kumata 1963, 1993, 1995; Opler and Davis 1981; Powell and Opler 2009). Recently, a multidisciplinary approach was undertaken which incorporates adult morphology, chemical communication and DNA barcoding to resolve the generic assignment within Lithocolletinae (De Prins et al. 2009). Although this approach appears useful to assess the generic limits of Gracillariidae, it is applicable only to those few groups of species for which chemical communication has been studied (De Prins et al. 2009; Liblikas et al. 2009 and the references therein). Collecting efforts are beginning to reveal the existence of several previously unknown Lithocolletinae genera in the tropics. An evaluation of generic apomorphies will only be accomplished after a thorough phylogenetic study of Lithocolletinae genera, based on both molecular and morphological characters, is completed.

The purpose of this paper is to propose and diagnose a new lithocolletine genus, *Macrosaccus*, and to document the five species we recognize within this New World group. This study is long overdue because one species, *Macrosaccus robiniella* (Clemens), has become a serious invasive pest on the introduced *Robinia pseudoacacia* L. (Fabaceae) over much of Europe. With this contribution we also attempt to broaden the understanding of the generic definitions within Lithocolletinae. We transfer three previously known *Phyllonorycter* species to *Macrosaccus*, clarify the synonymy, and designate lectotypes whenever possible for the species-group taxa. Additionally, we provide DNA barcodes as identification aids and descriptions of two new congeneric species which also were reared from Fabaceae.

Methods

Collecting and rearing. Field investigations were carried out in Europe (Belgium), Canary Islands (La Palma), and in several states within the United States (Arizona, Illinois, Maryland, New Mexico). All specimens examined in this study were reared from species of Fabaceae which are summarized in Table 1.

Leaves containing mines with larvae were placed in plastic bags or rearing containers periodically moistening the lids protecting the specimens from drying out. Specimens were pinned, spread and mounted in the usual way for morphological examination. Some voucher samples of reared specimens were fixed in 100% ethanol for DNA analysis. Larvae and pupae collected on *Robinia pseudoacacia* L. were preserved in 75% ethanol.

Morphology

Adults were examined externally using either MZ12.5 or Nikon SMZ 1500 stereomicroscopes (maximum magnification 200×). Genitalia were prepared following

Table 1. *Macrosaccus* and four *Phyllonorycter* species that feed on Fabaceae.

| Moth species | Host plant species | Country | Reference |
|---|--|--------------------------|------------------------------|
| <i>Macrosaccus gliricidius</i> Davis, sp. n. | <i>Gliricidia sepium</i> (Jacq.) | Guadeloupe, Honduras | Present study |
| <i>Macrosaccus morrisella</i> (Fitch, 1859) | <i>Amphicarpa bracteata</i> (L) Fernald | Canada | Present study |
| <i>Macrosaccus morrisella</i> (Fitch, 1859) | <i>Amphicarpa bracteata</i> (L) Fernald | U.S.A. | Chambers 1878: 111 |
| <i>Macrosaccus morrisella</i> (Fitch, 1859) | <i>Amphicarpa</i> sp. | Canada | Present study |
| <i>Macrosaccus morrisella</i> (Fitch, 1859) | <i>Strophostyles leiosperma</i> (Torrey & A. Gray) | Canada | Present study |
| <i>Macrosaccus neomexicanus</i> Davis, sp. n. | <i>Robinia neomexicana</i> Gray | U.S.A. | Present study |
| <i>Macrosaccus robiniella</i> (Clemens, 1859) | <i>Robinia hispida</i> L. | U.S.A. | Chambers 1878: 111 |
| <i>Macrosaccus robiniella</i> (Clemens, 1859) | <i>Robinia pseudacacia</i> L. | Belgium | De Prins & Groenen 2001: 159 |
| <i>Macrosaccus robiniella</i> (Clemens, 1859) | <i>Robinia pseudacacia</i> L. | U.S.A. | Clemens 1859: 320. |
| <i>Macrosaccus robiniella</i> (Clemens, 1859) | <i>Robinia viscosa</i> Vent | U.S.A. | Chambers 1878: 111 |
| <i>Macrosaccus uhlerella</i> (Fitch, 1859) | <i>Amorpha fruticosa</i> L. | U.S.A | Chambers 1878: 110 |
| <i>Phyllonorycter cytisifoliae</i> (M. Hering, 1927) | <i>Chamaecytisus proliferus</i> (L.) Link | Canary Islands: La Palma | Hering M 1927: 419 |
| <i>Phyllonorycter foliolosi</i> Walsingham, 1908 | <i>Adenocarpus foliolosus</i> (Ait.) DC | Canary Islands: La Palma | Walsingham 1908: 978 |
| <i>Phyllonorycter medicaginella</i> (Gerasimov, 1930) | <i>Medicago sativa</i> L. | Belgium | Kuchlein et al. 2002: 89 |
| <i>Phyllonorycter nigrescentella</i> (Logan, 1851) | <i>Vicia sepium</i> L. | Belgium | Fologne 1862: 24 |

Robinson (1976) with some modifications. After maceration of the abdomen in 10% KOH for 24 hours or by heating in hot 10% KOH for ~ 30 minutes, and subsequent cleaning and deionization, the male genitalia were stained with 2% eosine B, a mixture of 2% azophloxine and 2% acid fuchsin; the female genitalia were stained with a 1% chlorazol black E solution and embedded in Euparal or Canada balsam. Genital morphology was examined using a Leica DMLB microscope under magnifications of 150×, 200×, and 400×. The terminology follows Vári (1961), Klots (1970), Kumata (1993, 1995), and Kristensen (2003). Microslides for studies of wing venation were prepared following the technique suggested by Vári (1961) and applying modifications used by Hoare (2000). Some wing slides were cleaned, stained with saffranin, and mounted dry beneath a glass coverslip.

For scanning electron microscopy, the immatures were immobilized by moment freezing at -27°C. Pupae were sputtered-coated with gold using a Bal-TEC/SCD 005

Sputter Coater. The images were taken with a Jeol MP 35060 camera combined with a Jeol JSM-5400 LV Electron Scanning Microscope and processed using the Orion 4 High Resolution Image Grabbing System software. Larval terminology follows Davis (1987).

The spellings of all species names were retained as originally proposed.

Molecular analysis

Sequences of the 658bp Cytochrome Oxidase I were generated at the Biodiversity Institute of Ontario, University of Guelph, Canada. DNA was extracted from legs or entire bodies of adult moths using a QIAGEN DNeasy Extraction Kit (Qiagen, Inc., Valencia, CA). Primers LepF1 and LepR1 (Herbert et al. 2004) were used to obtain the barcoding fragment of COI following methods previously described (Hajibabaei et al. 2006). Sequences are available at the National Center for Biotechnology Information GenBank database and at the Barcode of Life Database (BOLD). A neighbor-joining (NJ) tree was generated utilizing the Kimura 2-parameter model via the BOLD web-site (<http://www.boldsystems.org/>; Ratnasingham and Hebert 2007) to illustrate the genetic divergences between species. A compressed version of this tree was produced (Fig. 1) using Molecular Evolutionary Genetics Analysis (MEGA) version 4 (Tamura et al. 2007).

Museum collections

Whenever possible the primary types of every species were examined. Lectotypes were designated from the syntypic series whenever available.

Abbreviations of Institutions from which specimens were examined are:

- ANSP** Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
- BMNH** The Natural History Museum (formerly the British Museum (Natural History)), London, United Kingdom.
- CCDB** Canadian Centre for DNA Barcoding, University of Guelph, Canada
- CNC** Canadian National Collections of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, Ottawa, Canada.
- CU** Cornell University, Ithaca, New York, USA.
- INHS** Illinois Natural History Survey, Champaign, Illinois, USA.
- MCZ** Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.
- RMCA** Royal Museum for Central Africa, Tervuren, Belgium
- USNM** Collections of the former United States National Museum, now deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

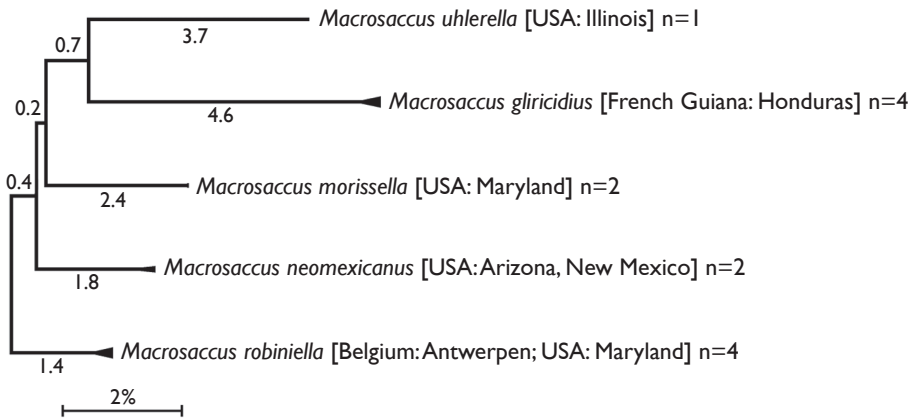


Figure 1. Compressed subtree sequenced data for cytochrome c oxidase I (COI) of *Macrosaccus*, derived from 13 samples among 5 species based upon neighbor-joining analysis with Kimura 2-parameter model. Numbers above branches indicate branch length. Sequence lengths obtained for all samples were 658bp each.

Table 2. Mitochondrial DNA (COI) sequence divergence (%) among species of *Macrosaccus*. Uncorrected average pairwise distances are shown for the barcoding region of (COI). Shaded cells contain means within species distances. Cells below shaded diagonal contain mean between species distances. Species abbreviations in the heading refer to species listed in left column.

| | <i>gliri</i> | <i>morri</i> | <i>robi</i> | <i>neom</i> | <i>uble</i> |
|---------------------------------|--------------|--------------|-------------|-------------|-------------|
| <i>Macrosaccus gliricidius</i> | 0.4 | | | | |
| <i>Macrosaccus morissella</i> | 8.1 | 0.0 | | | |
| <i>Macrosaccus robiniella</i> | 8.1 | 4.7 | 0.4 | | |
| <i>Macrosaccus neomexicanus</i> | 7.1 | 4.5 | 4.1 | 0.5 | |
| <i>Macrosaccus uhlerella</i> | 8.6 | 6.7 | 6.5 | 7.3 | 0.0 |

Systematic Account

Macrosaccus Davis and De Prins, gen. n.

urn:lsid:zoobank.org:act:2451DAED-FEB2-4E03-B86C-88F10584A067
<http://species-id.net/wiki/Macrosaccus>

Type species: *Lithocolletis robiniella* Clemens, 1859, by original designation.

Macrosaccus is assigned to the subfamily Lithocolletinae on the basis of the following putative morphological synapomorphies: hindwing vein Rs parallel to vein M and costal margin; adults rest with body parallel to surface; adult head with occipital tuft; and pupation occurring within the mine.

Diagnosis. Superficially, *Macrosaccus* is similar to nearly all other genera of Lithocolletinae, sharing such characters as a well developed occipital tuft; a forewing pattern

accentuated with oblique, whitish strigulae; and by the mode of pupation which occurs inside a silken cocoon within the whitish blotch mine usually on the underside of the host leaf without any prepared exit opening. However, in contrast to the typically solitary larvae and pupae of other Lithocolletinae genera, those of *Macrosaccus* are often gregarious inside a single, composite mine. The wing venation of *Macrosaccus* is similar to that of *Cameraria* and *Phyllonorycter* in possessing five apical veins, but it differs from the two latter genera in having Rs4 rising either from the base of Rs3 or stalked with Rs3. The hindwing venation is similar to *Cameraria*, *Chrysaster*, *Leucanthiza*, *Neolithocolletis*, and *Phyllonorycter*, but differs from *Cremastobombycia*, *Hyloconis*, *Porphyrosela*, and *Protolithocolletis* in the absence of vein M2. In the male genitalia, the sternum 8 is not produced caudally as in *Chrysaster*, *Leucanthiza*, and *Protolithocolletis*. In *Cameraria*, *Cremastobombycia*, *Hyloconis*, *Neolithocolletis*, *Phyllonorycter*, and *Porphyrosela*, the sternum 8 forms a large flap underlying the valvae. The apex of the tegumen in *Macrosaccus* possesses a pair of tiny setae as in *Cameraria*, *Chrysaster* and *Porphyrosela*, but unlike *Phyllonorycter* which lacks apical setae. The transtilla of *Macrosaccus* is complete like that of other lithocolletine genera, but it differs from that of *Cameraria* and *Hyloconis* where it is incomplete. The female genitalia of *Macrosaccus* are characterized by numerous, microscopic spine-like signa which are scattered within the subcaudal part of corpus bursae (in other lithocolletine genera the corpus bursae bears other types of signa). Though the adult head of *Macrosaccus* is very similar to that of *Protolithocolletis*, the venation between these two genera differs with the forewing of *Protolithocolletis* more developed in possessing veins Rs1 and M2. The pupae provide perhaps the best characters for generic distinction, with that of *Protolithocolletis* lacking the spinose accessory cremaster ridge on sternum 7, which is characteristic for *Macrosaccus*.

Adult. *Head* (Figs 10, 11). Vertex covered with long dense tuft of piliform scales; frons with smooth appressed scales; eyes of midsize; interocular index (= vertical eye diameter/interocular distance) $\sim 0.75\text{--}0.96$. Antenna about $0.7\times$ the length of forewing ($n=9$), smooth scaled, with a single row of scales per segment; scape with dense pecten. Proboscis well developed, naked, ca. $1.8\text{--}2.5\times$ length of labial palpus. Maxillary palpus very short, rudimentary, $\sim 0.5\times$ length of labial palpomere II, and directed laterally; consisting of 2 articulated segments; basal 2 segments fused; segment 3 free, spherical. Labial palpus slender, drooping, with ratio of segments from base 1.5: 1: 2.

Thorax (Fig. 12). Forewing slender, maximum width/length ratio ca. 0.2, narrow at apex. Venation with 8 veins, apical part with 5 veins; Sc strong, extending nearly to costa, basal half of R indistinct, Rs2 present, Rs3 arises from apex of the cell, position of Rs4 variable, arising either from base of Rs3 or stalked with Rs3, M and CuA1 separate, CuP indistinct (fold) for entire length, 1A strong, separate, discal cell either open (with absence of crossvein between Rs2 and Rs3) or closed, extending ~ 0.78 of wing length. Hindwing lanceolate, maximum width 0.12 that of length, venation reduced, similar to *Phyllonorycter*; Sc very short, Rs very long, extending almost to apex; basal $2/3$ of M indistinct, parallel to Rs, distal part of M ends near distal $3/5$; basal half of Cu strong, distal half indistinct, ending slightly before

midway along dorsum; frenulum a single stout bristle in male, 2 tightly appressed bristles in female, retinaculum in male consisting of a broadly triangular curved fold from the ventral base of Sc and a few stiff, forward directed scales situated on the posterior part of Cu.

Abdomen. The margins of the abdominal opening strongly sclerotized and broad laterally, the sclerotized margination of abdomen opening unconnected on T2, S2 apodemes long, ~ half the length of S2, generally slender but more stout at basal 1/3 and very slender at distal 2/3; two pairs of tiny spinules on S2 sublaterally, and a pair of tiny spinules on S3–S6 sublaterally. Sternum 8 in male undeveloped.

Male genitalia. Tegumen relatively short, broad, moderately sclerotized laterally. Caudal portion covered with numerous tiny setae. A pair of long, slender setae present at apex of tegumen. Vinculum broad, U-shaped with very slender, elongate saccus which ranges from 1.1–1.7× the length of valva. Valvae symmetrical, moderately broad, costal margin nearly straight to slightly curved; ventral margin variable between species from slightly convex to slightly concave over distal half with apex varying from fully round to abruptly narrowing; median surface of valva with sparse setae of medium length; apex of valva densely covered with longer, more stout setae. Transtilla complete and well developed, laterally expanded into rounded lobes. Aedeagus very long, nearly as long as entire genital capsule (from apex of tegumen to anterior end of saccus), straight and slender, of uniform diameter along its length; caudal end of vesica usually with long, slender cornuti; phallobase ~ ¼ total length of aedeagus.

Female genitalia. Papillae anales flattened, strongly interconnected, covered with short setae mostly along apical margin; basal bar broad but weakly sclerotized. Posterior apophyses slightly longer than width of papillae anales, straight and slender. Segment 8 short, weakly sclerotized. Anterior apophyses as long or slightly shorter than posterior apophyses, with moderately broad bases, then slender extending to caudal 1/3 of segment 7. Ostium bursae opens medially, near caudal margin of segment 7; sterigma simple, without cuticle folds, antrum funnel-shaped, narrowing anteriorly. Subcaudal area of segment 7 mottled with numerous tubercles. Ductus bursae ~ 2× times longer than segment 7; a membranous accessory bursae ~ 2/3 the length of corpus bursae, arising from middle to anterior 1/3 of ductus bursae, with a smaller lateral pouch arising ~ midway along side of accessory bursae. Corpus bursae 1.0–2.0× the length of segment 7, subcaudal region of corpus bursae usually with scattered spicules or with spicules arranged in linear rows in *M. robiniella*.

Larva. Hypermetamorphic with five larval instars. Earliest instars (1–3) highly modified sapfeeders with strongly depressed bodies and reduced chaetotaxy; 3 pairs of stemmata arranged in a lateral, anterior cluster on head; labrum short and broad, bilobed; anterior margin broadly concave, roughened, with minute dentations along inner margin of lateral lobes; maxillary and labial palpi absent. Later instars (4 and 5) tissue feeders, with cylindrical bodies. Head approximately round with full complement of mouthparts; 4 pairs of stemmata present; antenna 3-segmented with first segment moderately long; labrum strongly bilobed with raised median portion on each lobe; M1 absent; numerous secondary spines visible from inner, ventral perimeter of

labrum. Thorax with SD1 elongate, immediately ventral to XD2; SD2 absent on T1, present on T2–3L group bisenose on T1–3. SV unisetose on T1–3. Legs relatively short but fully developed; coxae widely separated, with 4 coxal setae. Abdomen with D and SD groups bisetose on A1–8, 10; unisetose on A9; L group bisetose on A1–5, unisetose on A6–10; prolegs present on A3–5, 10; crochets of A3–5 arranged in a uniordinal circle; anal proleg with crochets arranged in a uniordinal semicircle opened caudally; anal plate with 4 pairs of setae.

Pupa. Head with vertex terminating in a relatively short, broadly triangular, acute frontal process (cocoon cutter). Abdomen mostly covered dorsally and ventrally with dense, minute spines; dorsum of A2–7 with a single anterior row of short, stout spines; caudal half of sternum 7 with a transverse ridge (accessory cremaster) bearing ~ 18–21 mostly longitudinal rows of short, blunt spines; cremaster of A10 greatly reduced, nearly absent, consisting of 1–2 pairs of minute tergal spines.

Etymology. The generic name is derived from the ancient Greek μακρο- (long) and σάκκος (bag) in reference to the elongate saccus in the male genitalia. Gender masculine.

Generic relationships and species diversity. Several morphological specializations closely associate *Macrosaccus* with the genera *Chrysaster*, *Cremastobombycia*, and *Phyllonorycter*. Some of these involve the moderately produced proboscis (~ 2× the length of the labial palpi) and the very reduced, two-segmented (with basal segment relatively enlarged), broad maxillary palpi (Figs 10, 11). The wing venation of all three genera is nearly identical and is among the most reduced within Gracillariidae. Only three branches of Rs are present in the forewing, accompanied by single branches of M and Cu (Fig. 12). Venation in the lanceolate hindwings is similarly reduced with only three major veins usually preserved (Rs, M, and Cu) in addition to the extremely basal Sc+R1. The position of Rs4 in *Macrosaccus* differs somewhat from that in the aforementioned three genera in arising either from the base of Rs3 or stalked with Rs3. Perhaps more significantly is that the discal cell is usually open in *Macrosaccus* due to the total or near absence of the Rs2–Rs3 crossvein. This crossvein is usually present in the other genera.

The most distinguishing feature in the male genitalia of *Macrosaccus* is the extremely long, rodlike saccus, whence the generic name is derived. The male saccus in *Chrysaster*, *Cremastobombycia*, and *Phyllonorycter* is either undeveloped or much shorter and stouter (except in two Afrotropical species *P. farensis* and *P. obandai*). Likewise sternum 8 in all males of these three genera is extended caudally as a variably lengthened plate beneath the genitalia, compared to being unmodified in *Macrosaccus*. The female genitalia of *Macrosaccus* typically possess a relatively large, variably shaped accessory bursa arising approximately midway along the long, slender ductus bursae. The corpus bursae contains dense patches or faint rows of minute spines. The accessory bursae in *Phyllonorycter* originates more caudally near the ostium, and usually two, circular and variably sclerotized signa are present (Davis and Deschka 2001).

The pupa of *Macrosaccus* is characterized by an accessory cremaster on abdominal sternum 7 that is unlike that of any other known gracillariid genus. This consists of a raised transverse ridge bearing ~ 18–21 mostly longitudinally oblique rows of short, blunt spines (Figs 84, 85). The accessory cremaster when present in *Phyllonorycter* dif-

Table 3. Diagnostic comparisons between adults and pupae of *Macrosaccus* and *Phyllonorycter*.

| Character | <i>Macrosaccus</i> | <i>Phyllonorycter</i> |
|--|--|---|
| Sternum 8 | Unmodified (not extended) | Caudally extended |
| Male genitalia: apex of tegumen | With 2 setae | No setae |
| Male genitalia: saccus | Saccus longer than valva in all species | Saccus shorter than valva except in two Afrotropical species |
| Male genitalia: setation of valva | Only apex of valva densely covered with elongate, stout setae | Other types of setation |
| Male genitalia: aedeagus | ca. 2× as long as genital capsule from apex of tegumen to anterior end of vinculum | Significantly shorter except in three Afrotropical species |
| Female genitalia: signum | Consisting of numerous microscopic spicules scattered or in linear series on subcaudal part of corpus bursae | Signa not scattered, often confined to 1–2 moderately sclerotized, oval areas |
| Forewing venation | Rs4 arises either from base of Rs3 or is stalked with Rs3 | Rs3 and Rs4 separate |
| Pupa: accessory cremaster of sternum 7 | An elongate, transverse ridge bearing 18–21 oblique rows of minute spines | No transverse ridge; instead located midventrally, with 1–2 pairs of lateral spines |

fers greatly in consisting of a raised triangular area located midventrally on sternum 7 with 1–2 pairs of stout spines projecting laterally (Davis and Deschka 2001).

In addition to the foregoing morphological characters, a preliminary molecular phylogeny based on ten genes also strongly places *Macrosaccus* apart from *Phyllonorycter* (Kawahara 2010). Morphological characters distinguishing *Macrosaccus* from *Phyllonorycter* are summarized in Table 3.

Five species, all indigenous to the New World, are currently recognized in the new genus *Macrosaccus*. The high sequence divergence of the barcoding region of COI (> 7%) between species (Fig. 1, Table 2) further confirms the species concepts previously determined by morphological and larval host information. Sequence divergences within species for the 12 samples with multiple specimens were low and varied between 0–0.62% (*M. gliricidius*), 0% (*M. morrisella*), 0–0.46% (*M. neomexicanus*), and 0–0.71% (*M. robiniella*). The latter included specimens from Belgium and the United States.

Key to species of *Macrosaccus* (based primarily on male genitalia and larval host)

- 1 Valva of male of uniform width to broadly rounded apex (Fig. 32); host *Gli-ricidia sepium* ***M. gliricidius***
- Male valva narrowing before apex **2**
- 2 Valva gradually tapering to narrow apex (Fig. 23); host *Robinia neomexi-cana*..... ***M. neomexicanus***
- Valva constricted before apex **3**

- 3 Valva strongly constricted at middle (Fig. 28); distal half less than half the width of sacculus; host *Amorpha fruticosa*..... ***M. ublerella***
- Valva slightly constricted near apex4
- 4 Forewing with a short, oblique white streak from base of costa; median white fascia complete, slightly curved outward (Fig. 5). Valva constricted before apex; arms of transtilla reduced (Fig. 18); hosts *Amphicarpa bracteata*, *Strophostyles leiosperma* ***M. morrisella***
- Forewing without basal white costal streak; median white fascia usually broken, strongly oblique (Figs 2–4). Valva constricted closer to apex; arms of transtilla broader (Fig. 13); hosts *Robinia pseudoacacia*, *R. hispida*, *R. viscosa* ***M. robiniella***

***Macrosaccus robiniella* (Clemens), comb. n.**

http://species-id.net/wiki/Macrosaccus_robiniella

Figs 1–4, 10–17, 36–40, 59–98, Tables 1, 2, 4, 5.

Lithocolletis robiniella Clemens 1859 (Nov.): 318; 1872: 66.- Chambers 1871: 54, 87, 163, 183, 185; 1872: 9, 107; 1875: 228; 1877: 137.- Zeller 1875: 348.- Frey and Boll 1878: 275.- Riley 1891: 109, No. 5889.- Busck 1903: 189.- Dyar 1902 [1903]: 551, No 6267.- Braun 1908: 291.- Meyrick 1912a: 7; 1912b: 32.- Braun 1914: 110.- Forbes 1923: 192.- McDunnough 1939: 95, No. 9191.- Weaver and Dorsey 1965: 934; 1967: 178.

Phyllonorycter robiniella (Clemens).- Ely 1918: 59.- Davis 1983: 10.- Maier and Davis 1989: 15.- Leraut 1997: 96.- De Prins and De Prins 2005: 342.- De Prins and De Prins 2011.

Argyromiges pseudacaciella Fitch 1859: 836, No. 335.

Lithocolletis pseudacaciella (Fitch).- Riley, 1891: 109, No. 5889 (synonym of *Lithocolletis robiniella*).- Dyar 1902 [1903]: 551, No 6267.- Braun 1908: 291.- Meyrick 1912a: 7; 1912b: 32.- Ely 1918: 59.- Barnes and McDunnough 1917: 187, No. 7915.- McDunnough 1939: 95, No. 9191.- Davis 1983: 10.- Leraut 1997: 96.- De Prins and De Prins 2005: 342.- De Prins and De Prins 2011.

Diagnosis. The overall appearance of this widespread eastern North American (and now well established European) species most closely resembles that of the more southwestern US species, *M. neomexicanus*. The more abruptly constricted apical region of the valvae and the minute, longitudinally oriented striae and spicules of the corpus bursae readily distinguish it from *M. neomexicanus*.

Adult (Figs 2–4). Forewing length 2.3–3.1 mm.

Head: Frons smooth, shiny white. Vertex extremely rough; vestiture consisting of a tuft of elongate, piliform, mostly dark brown, intermixed with white, scales. Labial palpus white. Antenna mostly dark fuscous dorsally for most its length, with dark area narrowing to a more slender dark streak toward basal 1/4–1/3 its length; antenna mostly white ventrally; apical segment entirely white.



Figures 2–9. Adults **2–4.** *Macrosaccus robiniiella*. **2** ♂, USA: Maryland, (2.8 mm) **3** ♂, USA: Maryland, (3.0 mm) **4** BELGIUM: Antwerp, (3.0 mm) **5** *M. morrisella*, ♂, USA: Maryland, (2.5 mm) **6** *M. neomexicanus*, USA: Arizona, (3.2 mm) **7** *M. uhlerella*, USA: Illinois, (2.5 mm) **8** *M. uhlerella*, USA: Illinois, (3.0 mm) **9** *M. gliricidius*, ♂, HONDURAS: Morazán, (2.4 mm). (Forewing lengths in parentheses).

Thorax: Dark brown dorsally, white ventrally; tegula dark brown, with pale grey to white suffusion anteriorly. Forewing pattern complex, costal half mostly light orange brown crossed by 4 equally spaced, white costal strigulae, each bordered basally, sometimes faintly, by black to dark grey and distally by light grey scales; basal 2 strigulae strongly oblique; a fifth, minute, white strigula sometimes arising from black apical spot before forewing apex. Basal third and dorsal half of forewing usually darker, mostly black to sometimes pale golden grey between strigulae; slender white streak from base of wing usually indistinct or absent; a greyish, oblique strigula often evident near base of wing which connects with a larger, more distinct greyish strigula from dorsal margin; dorsal margin also with 3, usually less distinct white strigulae approximately opposite to distal 3 white strigulae from costa; basal dorsal strigula usually contiguous with second costal strigula. Apex of forewing with a large black apical spot, which is rarely reduced; fringe mostly light grey. Hindwing, including fringe, uniformly grey. Foreleg mostly dark fuscous dorsally, white ventrally, with 2 white annuli around basal tarsomeres; midleg with 2 oblique bands of white dorsally over tibia; tarsomeres more broadly banded with white dorsally; hindleg mostly white with much of tibia pale fuscous dorsally, and with 3 broad, pale fuscous annuli dorsally over tarsomeres.

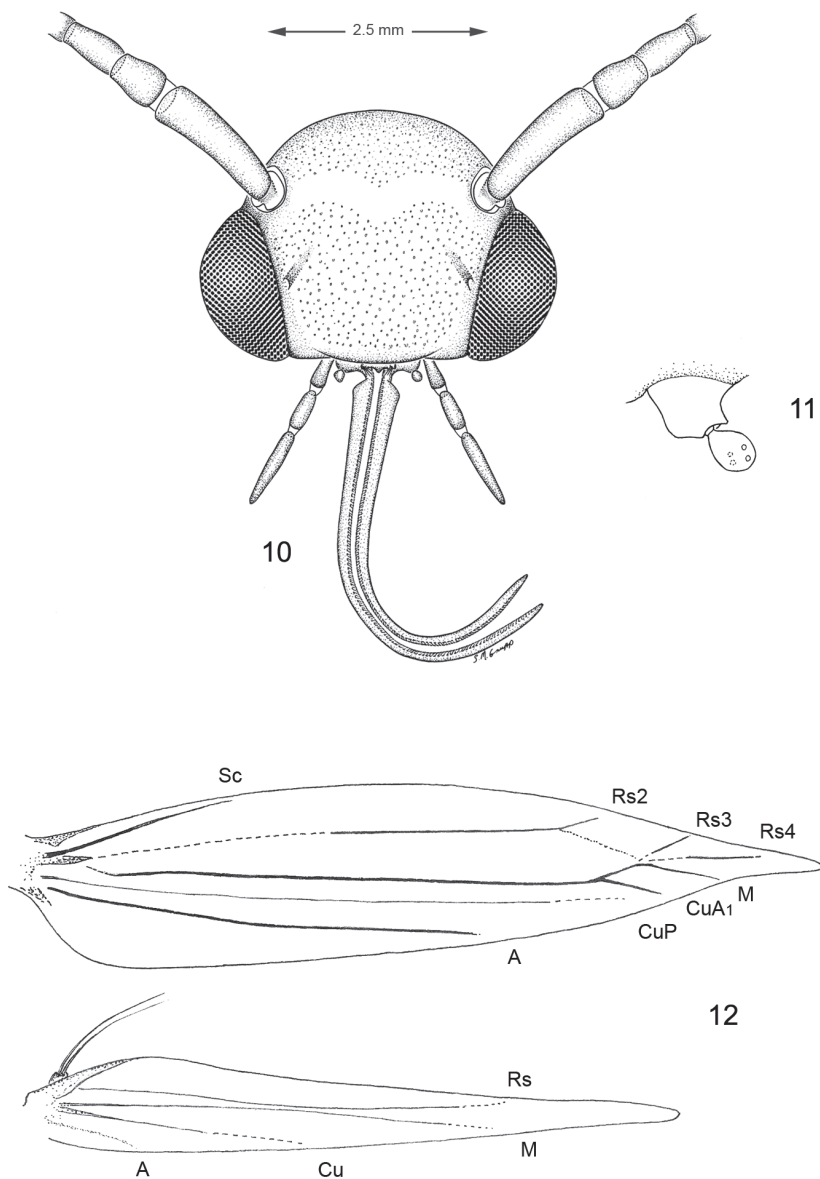
Abdomen: dark fuscous dorsally and white ventrally with greyish suffusion on anterior portion of segments 2–7 laterally and sometimes ventrally on A8.

Male genitalia (Figs 13, 14): Valva relatively simple, similar to *M. morrisella* in form, gradually constricted before apex; apex rounded, densely setose; base of costa fused to moderately thickened, arched transtilla; transtilla with rounded knoblike lateral projections that extend anteriorly in repose (more caudally when valvae are spread widely apart); saccus a slender, elongate rod $\sim 1.2\times$ length of valva. Aedeagus very long and uniformly slender, $\sim 2.1\times$ length of valva.

Female genitalia (Figs 15–17): Ductus bursae long and slender, nearly half the length of elongate corpus bursae. Accessory bursae $\sim 2/3$ the length of corpus bursae, arising from anterior 1/3 of ductus bursae; with a smaller lateral pouch arising \sim midway along side of accessory bursae. Corpus bursae gradually broadening anteriorly, with faint longitudinal striae in wall which bear longitudinal rows of low, dentate ridges around anterior third of corpus bursae; walls of anterior end (distal 1/5) of corpus bursae entirely membranous.

Larva (Figs 59–80, 90–96). Hypermetamorphic; five larval instars. Earliest instars (1–3) highly modified sapfeeders with strongly depressed bodies and reduced chaetotaxy; maximum length 3.7 mm, width (T1): 0.9 mm. Later instars (4 and 5) tissue feeders, with cylindrical bodies; maximum length: 4.7 mm, width: 0.7 mm; body colour pale green to white with notal plates and pinnacula smooth, reduced and unpigmented (indistinct).

Sap-feeding instars. **Head:** Maximum width (third instar) 0.4 mm; greatly depressed, triangular. Most setae lost or reduced; 3 pairs of stemmata arranged in a lateral, anterior cluster on head. Labrum (Fig. 60) short and broad, bilobed, with 2 pairs of extremely reduced, peglike dorsal setae; anterior margin broadly concave, roughened, with 4–5 minute dentations along inner margin of lateral lobes. Mandibles



Figures 10–12. Adult morphology, *Macrosaccus robiniella*. **10** Head **11** Detail of left maxilla **12** Wing venation.

broadly rounded, flattened, with 2 short cusps lateral to relatively large inner plate. Labium smooth, lateral margins subparallel; anterior margin shallowly notched at middle; spinneret absent. Maxillary and labial palpi absent. Hypopharynx broad, densely covered with minute spines along anterior margin; with margin slightly excavated at

middle. Antenna 3-segmented, with short basiconic sensilla as shown (Fig. 62). *Body*: Setae generally reduced. Legs, prolegs, and crochets absent.

Tissue-feeding instars. *Head*: Approximately round with full complement of mouthparts; brown; maximum width (fifth instar) 0.35 mm. Frons elongate, $\sim 0.85\times$ the distance to epicranial notch. Ecdysial line terminating near epicranial notch. Chaetotaxy (Figs 91–92) relatively complete; all three MD setae present, arising caudad to P1. P1 arising adjacent to ecdysial line. P2 reduced, arising slightly caudad to reduced L1. Setae AF1–2 absent. A2 arising near A3 in a line between P1 and A3. C1 and 2 reduced, closely adjacent. Four stemmata present. Antenna 3-segmented; first segment moderately long; sensilla as shown in Fig. 70. Labrum (Figs 68, 95) strongly bilobed with raised median portion on each lobe; M1 absent; numerous secondary spines visible from inner, ventral perimeter of labrum. Mandible (Figs 71, 96) with three large median cusps and one smaller median and two lateral cusps; mandibular setae variable (1–2) and located on anterior surface. Hypopharynx with dense, well developed dorsal spines. Maxilla as shown in Fig. 69. Spinneret a relatively short tube with a simple, rounded apex. Labial palpus with a relatively long basal segment bearing one short sensillum and a much shorter ($\sim 0.25\times$ length of basal segment) apical bearing a single long apical sensillum $\sim 2\times$ length of apical segment. *Thorax*: Setae XD1 and 2 short, of equal lengths on prothorax (T1). SD1 elongate, immediately ventral to XD2; SD2 absent on T1, present on T2–3L group bisetose on T1–3. SV unisetose on T1–3. Legs (Fig. 76) relatively short but fully developed; coxae widely separated, with 4 coxal setae; pretarsal claw moderately curved. *Abdomen*: D and SD groups bisetose on A1–8, 10; unisetose on A9; L group bisetose on A1–5, unisetose on A6–10. Prolegs present on A3–5, 10; crochets of A3–5 consisting of 17–24 small hooks arranged in a uniordinal circle; anal proleg with crochets consisting of 15–18 small hooks arranged in a uniordinal semicircle opened caudally (Fig. 79). Anal plate with 4 pairs of setae.

Larval mine (Figs 36–40). The mine begins as an elongate serpentine track (Fig. 37) which enlarges to an elongate-oval, whitish blotch (Fig. 36, 38) located on one side of the midrib and usually on the under (abaxial) side of the leaflet. Eventually the mine becomes slightly tentiform due to the silk laid down by the later instar larvae.

Hosts. (Table 1). Fabaceae: *Robinia pseudoacacia* L. (Clemens 1859: 320), *Robinia viscosa* Vent. (Chambers 1878: 111), *Robinia hispida* L. (Chambers 1878: 111; Needham et al. 1928: 288). The primary host, *Robinia pseudoacacia*, is believed once to have occurred primarily in two regions within the United States – one centered in the Appalachian Mountains from central Pennsylvania to northern Georgia and Alabama, and the other in the Ozark Plateau of southern Missouri, eastern Arkansas to eastern Oklahoma. This tree has since spread over much of the continental United States, portions of northeastern Canada, and parts of South America, Europe, Asia, Africa, and Australia (Stone 2009).

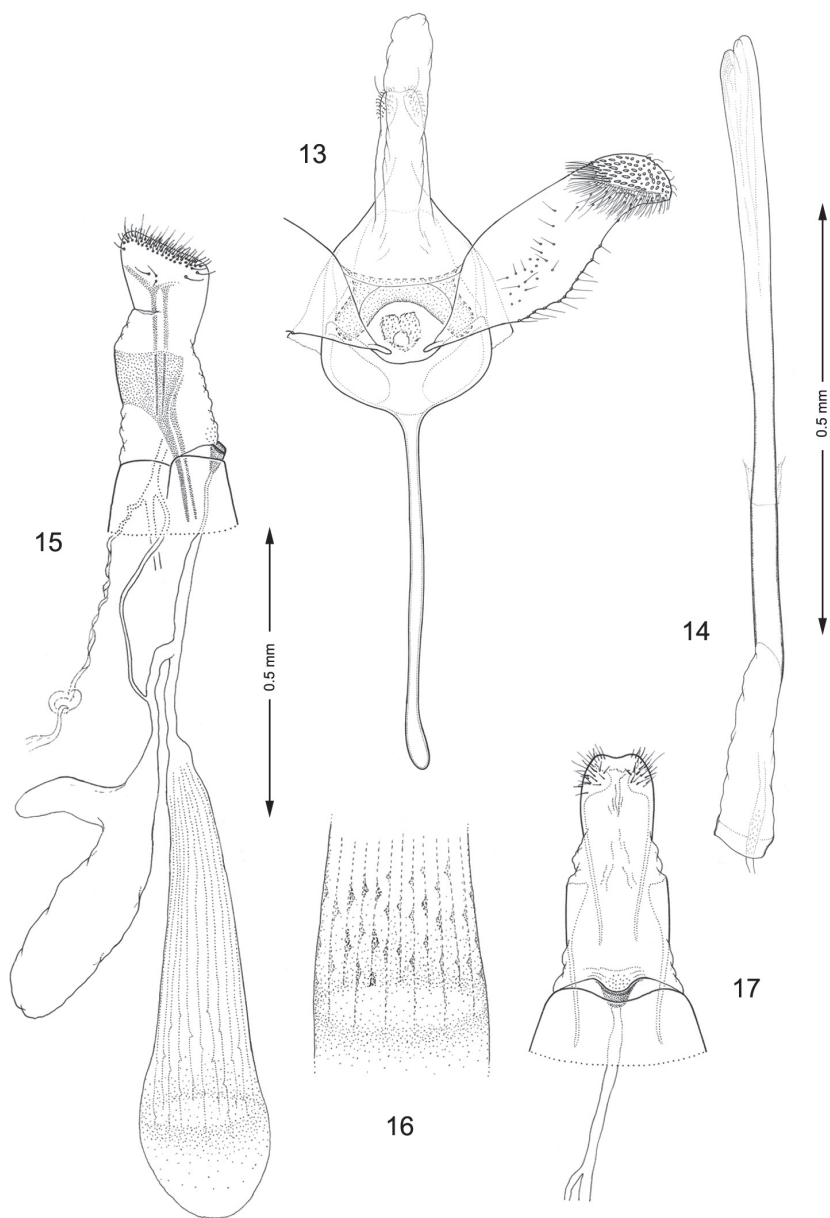
Life history (Figs 36–40). The egg of *M. robiniella* is deposited externally usually some distance from the leaf edge or midrib. Five larval instars have been observed by counting head capsules within mines in North America and Belgium. Kasch and Nicolai (2002) reported up to six instars based on head capsule measurements in Germany.

The larvae typically form elongate-oval, whitish blotch mines on usually the under (abaxial) side of the leaflets. Upon eclosion, the apodal, prognathous sap-feeding larva enters the leaf and begins a slender, subepidermal, serpentine mine (Fig. 37). Eventually the mine is expanded into an oval blotch (Fig. 38) which usually encompasses and obliterates the previous serpentine mine. As is true for the larvae of *Phyllonorycter* (Davis and Deschka 2001), the last sap-feeding instar probably begins expanding the mine laterally. Initiation of the tissue-feeding instar is indicated by deeper feeding into the spongy and palisade tissue layers of the leaflet as the larva begins to ingest solid tissue. The resulting injury becomes visible from the opposite leaf surface, particularly in the underside mines, as dense, whitish punctures. As the tissue-feeding larva matures, it begins to lay down silken strands across the inner surface of the mine causing the leaflet to roll inwards and the mine to become tentiform (Fig. 39). Pupation occurs inside a silken cocoon (Fig. 40) within the mine without any pre-cut exit opening. Especially during heavy infestations, the mines of adjacent larvae may coalesce resulting in multiple pupal cocoons. The phenology of this species has not been accurately determined over its range within North America. Normally two to three generations per year have been reported in Europe, which can occasionally reach as many as four (Nicolai 2005).

Braun (1908) noted that the mines could occur on both leaf surfaces. Weaver and Dorsey (1967) described the larval mining behaviour of *M. robiniella* in great detail and observed several differences between the upper side mines, which reportedly were more common at higher elevations (~ 760 m), and the under side mines. The latter were found most frequently at elevations of ~ 270 m at their West Virginia study sites. Some of the distinctions they observed were that upper side mines occurred usually more basal on the leaflet and often extended across the midrib, with the larval frass concentrated more basally within the mine. Under side mines are situated less basally and usually restricted to one side of the midrib, with frass scattered more uniformly throughout the mine. Only a single, somewhat loosely woven cocoon was observed in the upper side mines, compared to as many as three, densely woven cocoons in the lower mines. DRD compared males reared from the upper and lower side mines and found no significant morphological differences (Weaver and Dorsey 1967). A search for the Weaver specimens in the collections of the University of West Virginia at Morgantown yielded no material associated with the upper side mines from the higher elevation sites (~ 760 m). Hopefully specimens from the higher elevation, upper side mines can be collected in order to examine their genetic distances.

In addition to Hymenoptera parasitoids, other Lepidoptera larvae have been noted within the mines of *M. robiniella* (Weaver and Dorsey 1967). These were observed to alter the appearance of the mine by removing all mesophyll and largely destroying the frass pattern created by *M. robiniella*. Packard (1890) identifies a species of Gelechiidae, *Filatima pseudacaciella* (Chambers), which sometimes feeds within the mine in addition to feeding externally.

Natural enemies. (Table 4). Fifty seven species (including two unidentified) of Hymenoptera, the great majority of which are members of Eulophidae (Noyes 2010),



Figures 13–17. Genitalia, *Macrosaccus robiniella*. **13–14** Male. **13** Genital capsule, ventral view **14** Aedeagus. **15–17** Female. **15** Lateral view **16** Detail of signa within corpus bursae **17** Segments 7–10, ventral view.

have been reported as parasitoids of *Macrosaccus robiniella* in Europe and North America. Weaver and Dorsey (1967) also list two species of predators in the families Reduviidae and Vespidae that preyed on *M. robiniella*.

Table 4. Parasitoids of *Macrosaccus robinella*.

| Parasitoid name | Family | Country | Reference |
|--|------------|----------------|--------------------------------|
| <i>Achrysocharoides cilla</i> (Walker, 1839) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Achrysocharoides gahani</i> (Miller, 1962) | Eulophidae | Italy | Navone 2003: 79 |
| <i>Achrysocharoides gahani</i> (Miller, 1962) | Eulophidae | Switzerland | Girardoz et al. 2007: 606 |
| <i>Achrysocharoides robiniae</i> Hansson & Shevtsova, 2010 | Eulophidae | Austria | Hansson and Shevtsova 2010: 34 |
| <i>Achrysocharoides robiniae</i> Hansson & Shevtsova, 2010 | Eulophidae | Germany | Hansson and Shevtsova 2010: 34 |
| <i>Achrysocharoides robiniae</i> Hansson & Shevtsova, 2010 | Eulophidae | Hungary | Hansson and Shevtsova 2010: 34 |
| <i>Achrysocharoides robiniae</i> Hansson & Shevtsova, 2010 | Eulophidae | Italy | Hansson and Shevtsova 2010: 34 |
| <i>Achrysocharoides robiniae</i> Hansson & Shevtsova, 2010 | Eulophidae | U.S.A. | Hansson and Shevtsova 2010: 34 |
| <i>Achrysocharoides robinicolus</i> Hansson & Shevtsova, 2010 | Eulophidae | U.S.A. | Hansson and Shevtsova 2010: 34 |
| <i>Ageniaspis testaceipes</i> (Ratzeburg, 1848) | Encyrtidae | Hungary | Csóka et al. 2009: 407 |
| <i>Apanteles nanus</i> Reinhard, 1880 | Braconidae | Italy | Bolchi Serini 1990: 142 |
| <i>Astichus trifasciatiipennis</i> (Girault, 1913) | Eulophidae | Italy | Noyes 2010: Internet |
| <i>Baryscapus nigroviolaceus</i> (Nees, 1834) | Eulophidae | Czech Republic | Girardoz et al. 2007: 608 |
| <i>Baryscapus nigroviolaceus</i> (Nees, 1834) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Baryscapus nigroviolaceus</i> (Nees, 1834) | Eulophidae | Italy | Gibogini et al. 1996: 16 |
| <i>Baryscapus nigroviolaceus</i> (Nees, 1834) | Eulophidae | Switzerland | Girardoz et al. 2007: 606 |
| <i>Chrysocharis laomedon</i> (Walker, 1839) | Eulophidae | Italy | Gibogini et al. 1996: 16 |
| <i>Chrysocharis nephereus</i> (Walker, 1839) | Eulophidae | Switzerland | Whitebread 1990: 349 |
| <i>Chrysocharis pentheus</i> (Walker, 1839) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Chrysocharis pentheus</i> (Walker, 1839) | Eulophidae | Switzerland | Girardoz et al. 2007: 606 |
| <i>Cirrospilus elegantissimus</i> Westwood, 1832 | Eulophidae | Italy | Gibogini et al. 1996: 16 |
| <i>Cirrospilus lyncus</i> Walker, 1838 | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Cirrospilus talitzkii</i> Bouček, 1961 | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Cirrospilus variegatus</i> (Masi, 1907) | Eulophidae | Italy | Gibogini et al. 1996: 16 |
| <i>Cirrospilus viticola</i> (Rondani, 1877) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Cirrospilus viticola</i> (Rondani, 1877) | Eulophidae | Italy | Gibogini et al. 1996: 16 |

| Parasitoid name | Family | Country | Reference |
|---|---------------|----------------|--------------------------------|
| <i>Closterocerus cinctipennis</i> Ashmead, 1888 | Eulophidae | U.S.A. | Weaver and Dorsey 1965: 934 |
| <i>Closterocerus</i> sp. | Eulophidae | Czech Republic | Girardoz et al. 2007: 608 |
| <i>Closterocerus trifasciatus</i> Westwood, 1833 | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Closterocerus trifasciatus</i> Westwood, 1833 | Eulophidae | Italy | Bolchi Serini 1990: 143 |
| <i>Colastes braconius</i> Haliday, 1833 | Braconidae | Italy | Bolchi Serini 1990: 142 |
| <i>Colastes braconius</i> Haliday, 1833 | Braconidae | Switzerland | Whitebread 1990: 349 |
| <i>Elachertus inunctus</i> Nees, 1834 | Eulophidae | Italy | Zhu and Huang 2001: 343 |
| <i>Eupelmus urozonus</i> Dalman, 1820 | Eupelmidae | Hungary | Csóka et al. 2009: 407 |
| <i>Hockeria unicolor</i> Walker, 1834 | Chalcididae | Italy | Gibogini et al. 1996: 16 |
| <i>Horismenus fraternus</i> (Fitch, 1856) | Eulophidae | U.S.A. | Weaver and Dorsey 1965: 934 |
| <i>Mesochorus</i> sp. | Ichneumonidae | USA | Weaver and Dorsey 1967: 180 |
| <i>Minotetrastichus frontalis</i> (Nees, 1834) | Eulophidae | Czech Republic | Girardoz et al. 2007: 608 |
| <i>Minotetrastichus frontalis</i> (Nees, 1834) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Minotetrastichus frontalis</i> (Nees, 1834) | Eulophidae | Italy | Bolchi Serini et al. 1990: 143 |
| <i>Minotetrastichus frontalis</i> (Nees, 1834) | Eulophidae | Switzerland | Whitebread 1990: 349 |
| <i>Necremnus hungaricus</i> (Erdős, 1951) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Neochrysocharis formosus</i> (Westwood, 1833) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Pediobius bucculatricis</i> (Gahan, 1927) | Eulophidae | Canada | Peck 1985: 677 |
| <i>Pediobius liocephalatus</i> Peck, 1985 | Eulophidae | Canada | Peck 1985: 675 |
| <i>Pediobius saulius</i> (Walker, 1839) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Pediobius saulius</i> (Walker, 1839) | Eulophidae | Italy | Gibogini et al. 1996: 16 |
| <i>Pholetesor circumscriptus</i> Nees, 1834 | Braconidae | Italy | Bolchi Serini 1990: 142 |
| <i>Pholetesor nanus</i> (Reinhard, 1880) | Braconidae | Czech Republic | Girardoz et al. 2007: 608 |
| <i>Pholetesor nanus</i> (Reinhard, 1880) | Braconidae | Hungary | Csóka et al. 2009: 407 |
| <i>Pholetesor nanus</i> (Reinhard, 1880) | Braconidae | Italy | Bolchi Serini 1990: 142 |
| <i>Pholetesor nanus</i> (Reinhard, 1880) | Braconidae | Switzerland | Girardoz et al. 2007: 606 |
| <i>Pholetesor ornigis</i> Weed, 1887 | Braconidae | U.S.A. | Weaver and Dorsey 1965: 934 |
| <i>Pnigalio agraulis</i> (Walker, 1839) | Eulophidae | Switzerland | Girardoz et al. 2007: 606 |
| <i>Pnigalio pectinicornis</i> (Linnaeus, 1758) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Pnigalio pectinicornis</i> (Linnaeus, 1758) | Eulophidae | Italy | Bolchi Serini 1990: 143 |
| <i>Pnigalio pectinicornis</i> (Linnaeus, 1758) | Eulophidae | Switzerland | Girardoz et al. 2007: 606 |

| Parasitoid name | Family | Country | Reference |
|---|--------------|----------------|-----------------------------|
| <i>Phygadeuonidius soemius</i> (Walker, 1839) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Phygadeuonidius soemius</i> (Walker, 1839) | Eulophidae | Italy | Bolchi Serini 1990: 143 |
| <i>Pteromalus chrysos</i> Walker, 1836 | Pteromalidae | Italy | Gibogini et al. 1996: 16 |
| <i>Pteromalus</i> sp. | Pteromalidae | Czech Republic | Girardoz et al. 2007: 608 |
| <i>Sympiesis acalle</i> (Walker, 1848) | Eulophidae | Hungary | Szabóky and Csóka 1997: 570 |
| <i>Sympiesis acalle</i> (Walker, 1848) | Eulophidae | Italy | Bolchi Serini 1990: 143 |
| <i>Sympiesis dolichogaster</i> Ashmead, 1888 | Eulophidae | Switzerland | Girardoz et al. 2007: 607 |
| <i>Sympiesis gordius</i> (Walker, 1839) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Sympiesis gordius</i> (Walker, 1839) | Eulophidae | U.S.A. | Weaver and Dorsey 1965: 934 |
| <i>Sympiesis marylandensis</i> Girault, 1917 | Eulophidae | U.S.A. | Maier 1988: 731 |
| <i>Sympiesis sericeicornis</i> (Nees, 1834) | Eulophidae | Czech Republic | Girardoz et al. 2007: 608 |
| <i>Sympiesis sericeicornis</i> (Nees, 1834) | Eulophidae | Hungary | Csóka et al. 2009: 407 |
| <i>Sympiesis sericeicornis</i> (Nees, 1834) | Eulophidae | Italy | Bolchi Serini 1990: 143 |
| <i>Sympiesis sericeicornis</i> (Nees, 1834) | Eulophidae | Switzerland | Girardoz et al. 2007: 607 |
| <i>Sympiesis sericeicornis</i> (Nees, 1834) | Eulophidae | U.S.A. | Weaver and Dorsey 1965: 934 |

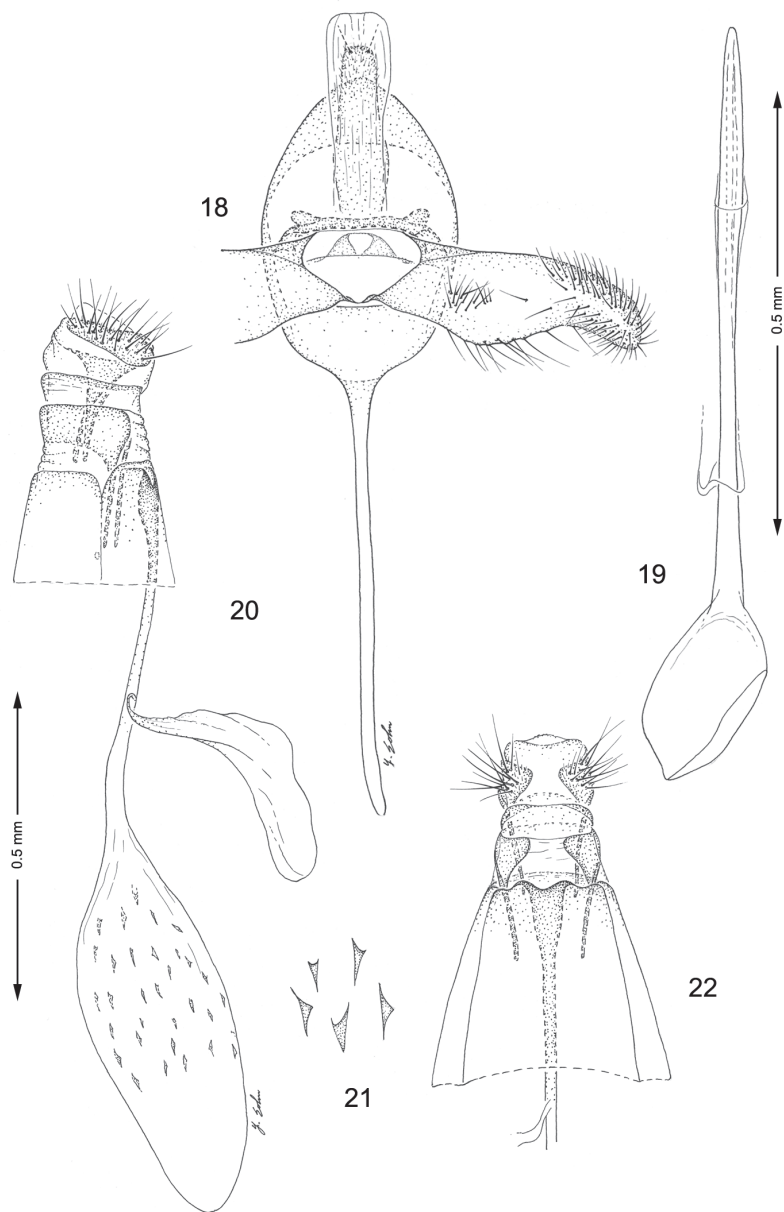
Pupa (Figs 82–89, 97, 98). Maximum length 3.6 mm; width 0.9 mm. Vertex with frontal process (cocoon cutter) relatively short, broadly triangular, acute (Figs 81, 82). Forewing extending to anterior margin of A6; antenna slightly longer to middle of A6; hindleg extending to A7. Abdomen mostly covered dorsally and ventrally with dense, minute spines; dorsum of A2–7 with a single anterior row of short, stout spines (Figs 83, 98); caudal half of sternum 7 with a transverse ridge (accessory cremaster) bearing ~ 18–21 mostly longitudinal rows of short, blunt spines (Figs 84, 85). Cremaster of A10 greatly reduced, nearly absent, consisting of 1–2 pairs of minute tergal spines.

Types. *Lithocolletis robiniella* Clemens: Lectotype ♀ (present designation): “14”; “*Lithocolletis robiniella* Clemens, Type ! A.B. 1902; Type 7505 *Lithocolletis robiniella* B. Clemens”; “Lectotype ♀ by D. R. Davis”, (ANSP). [The abdomen, right forewing, and distal part of right hindwing are missing].

Paralectotypes 3 ♂ and 1 specimen without abdomen “Syntype”, “*Lithocolletis robiniella* Clem. 1/4”, “Clemens det. ex Clemens coll.”, “Stainton coll. Brit. Mus. 1893–134”; same labels except nrs. 2/4, 3/4 and 4/4. The specimen with nr. 4/4 carries an extra label in Stainton’s handwriting: “*Lithocolletis robiniella* Clemens, Proc. N. S. Phil. 1859 p. 319, n.s. unlike any European species”, (BMNH).

Argyromiges pseudacaciella Fitch: Lectotype ♀ (present designation): “*Argyromiges Pseudacaciella*; Type No. 514 U.S.N.M.”; “Lectotype ♀ by D. R. Davis.” (USNM).

Material examined. BELGIUM: Province of Antwerp: Postal: 15 ♂, 23 ♀, 7 Sep 2009, em. 15–22 Sep 2009, J. and W. De Prins, leafmine on *Robinia pseudoacacia*, USNM slides 34257, 34258, 34263, DNA/BOLD ID RDOPO090-09, GenBank GU669590, DNA/BOLD ID RDOPO091-09, GenBank GU669591, (USNM).



Figures 18–22. Genitalia, *Macrosaccus morrisella*. **18–19** Male. **18** Genital capsule, ventral view **19** Aedeagus **20–22** Female. **20** Lateral view **21** Detail of signa within corpus bursae **22** Segments 7–10, ventral view.

CANADA: ONTARIO: Ancaster: 1 ♂, 24 Jul 1964, T. N. Freeman, Host: *Robinia pseudoacacia*, 64–20, (CNC). Bobcaygeon: 1 ♂, 23 Jul 1932, J. McDunnough, reared on *Robinia*, (CNC). Ottawa: 1 ♂, 26 Aug 1955, G. G. Lewis, Host: *B. locust*, 55–8, (CNC). Walsh: 1 ♂, 23 Sep 1966, T. N. Freeman, Host: *Bl. Locust*, (CNC). UNITED

STATES: DISTRICT OF COLUMBIA: 1 ♀, 7 Jul 1879, Host: *Robinia*, V.T. Chambers, (USNM); 3 ♂, 2 ♀, 9 Aug 1898, (USNM); 1 ♀, 24 Aug 1899 (USNM); 4 UNK, 18 Sep 1899, Host: *Robinia*, (USNM); Rock Creek Park: 1 ♂, 22 May 1984, W. E. Steiner, (USNM). ILLINOIS: Adams Co: Quincy: 3 ♂, 3 ♀, 15–21 Feb 1948; 2 ♂, 2 ♀, 6 Apr 1947; J. P. Nielson (INHS). Coles Co: Fox Ridge State Park: 1 ♂, 1 Jun 1991, em. 9 Jun, 1991; 1 ♀, 29 Jun 1991, em. 5 Jul 1991; 3 ♂, 1 ♀, 14 Jul 1991, em. 16–20 Jul 1991, T. Harrison, leafmine on *Robinia pseudoacacia*, (INHS); 1 ♂, 7 Jun 1991, at UV light T. Harrison, (INHS). Putnam Co: 1 ♀, 15 Apr 1996; 1 ♂, 24 Apr 1963; 1 ♂, 29 Apr 1969; 1 ♂, 2 Jun 1966; 1 ♀, 11 Jul 1959; 1 ♀, 3 Sep 1951, M. O. Glenn, (INHS); 1 ♀, 3 May 1953; 1 ♂, 1 ♀, 10 May 1953; 1 ♂, 26 Aug 1961; 2 ♂, 10 Sep 1948; 2 ♂, 10 Oct 1948, M. O. Glenn, reared from *Robinia pseudoacacia*, (INHS). Vermilion Co: Kickapoo State Recreation Area: 1 ♂, 13 Jun 1991, em. 14 Jun 1991, T. Harrison, leafmine on *Robinia pseudoacacia*, (INHS). KENTUCKY: Fayette Co: Lexington: 1 ♂, 6–13 Oct 1975, malaise trap, (USNM). MARYLAND: Garret Co: Deep Creek. Lake State Park: 15 ♂, 12 ♀, 16 Sep 1990, em. 23 Sep – 7 Oct 1990, D. and S. Davis, DRD 821, Host: *Robinia pseudoacacia* L. USNM slides 33282, 30903, 30895, 30894, DNA/BOLD ID RDOPO088-09, GenBank GU669592, DNA/BOLD ID RDOPO089-09, GenBank GU669593, (USNM). Montgomery Co: Fort Washington, vicinity Henson Creek: 1 ♂, 19 Sep 1990, em. 13 Oct 1993, D. Davis, DRD 1376, Host: *Robinia pseudoacacia* L., (USNM). MASSACHUSETTS: Essex Co: Beverly: 1 ♂, 2/69, Burgess, (BMNH). MICHIGAN: Clinton Co: T6N-R1W S10: 3 ♂, 2 Oct 1997, em. 9–13 Oct 1997, R. J. Priest, Host: *Robinia pseudoacacia* L., (USNM). Wayne Co: Detroit: 1 ♂, 2 ♀, 20 Nov 1995, T. Wallenmeier, (USNM). MISSOURI: Boone Co: Columbia: 1 ♂, 25 Nov 1995, slide USNM 17047, 1 ♀, 14 Dec 1969, W.S. Craig, under bark of sycamore, (USNM). NEW HAMPSHIRE: Cumberland Co: Hampton: 1 ♀, 16 Feb 1906, S.A. Shaw, (USNM). NEW JERSEY: Burlington Co: Moorestown: 2 ♂, 22 Aug 1902, W.D. Kearfott, Host: Locust, (USNM). NEW YORK: Specific locality unknown: 1 ♀, lectotype, *Argyromiges pseudacaciella* Fitch, (USNM). Clinton Co: Peru: 2 ♂, 2–18 May 1977, R. Weires, caught in pheromone trap, slide USNM 20912, (USNM). Essex Co: Crown Point: 2 ♂, 4–20 May 1977, 1 ♂, 20 May–17 Jun 1977, R. Weires, caught in pheromone trap, slide USNM 20910, (USNM). Livingston Co: Letchworth State Park: 12 ♂, 8 ♀, 21–22 Jun 1986, E. R. Hoebeke, reared from mines of *Robinia pseudoacacia*, (CU). Thompkins Co: Ithaca: 1 ♂, 15 Feb; 1 ♂, 1 ♀, 8 Apr 1945, Renwick, (CU). NORTH CAROLINA: Macon Co: Highlands, 3865': 6 ♂, 5 ♀, 1–24 Aug 1958, R. W. Hodges, (CU); 11 ♂, 5 ♀, 27 Jul–25 Aug 1958, R.W. Hodges, (USNM). OHIO: Hamilton Co: Cincinnati: 1 ♂, 29 Apr 1905, 6806, (CNC); 1 ♀, 29 Apr 1903, 7 ♂, 4 May 1904, 1 ♂, 23 July 1903, 1 ♂, 1 ♀, 25–27 Sep 1902, 1 ♂, 1 ♀, 30 Sep 1911, slide USNM 97837, 2 ♀, 10–22 Oct 1903, 3 ♂, 15–20 Nov 1903, Annette F. Braun, (USNM). PENNSYLVANIA: Specific locality unknown: 1 ♀, lectotype, *Lithocolletis robinella* Clemens, (ANSP). Allegheny Co: Oak Station: 1 ♂, 1 ♀, 1 Oct 1910, Fred Marloff, (CU); 1 ♀, 10 Apr 1910, 3 ♂, 5 ♀, 3–22 May 1910, 1 ♀, 12 Jun 1908, Fred Marloff, (USNM). Erie Co: Girard: 3 ♂, 1 ♀, 9 Oct 1920, reared from black locust, (CU). Franklin Co: Mont Alto: 1 ♀, 5 Oct 1971, reared Black locust seedling,

slide USNM 17166, (USNM). Indiana Co: Strongstown: 1 ♀, 23 Sep 1971, reared Black locust seedling, (USNM). Monroe Co: Sciota: 1 ♂, 21 Jul 1965, T. N. Freeman, Host: *Robinia pseudoacacia*, 65–27, (CNC). SOUTH CAROLINA: Oconee Co: Cherry Hill Rec. Area, Rt.107, 2000' [610m]: 2 ♂, 1 ♀, 11 Aug 1958, R.W. Hodges, (CU); 3 ♂, 11 Aug 1958, R.W. Hodges, slide USNM 17017, (USNM). TEXAS: 1 ♀, Boll, (USNM). VIRGINIA: Arlington Co: Rosslyn: 1 ♂, A. Busck, underside mine on Hog peanut, (USNM). Madison Co: Shenandoah Nat. Park, Skyline: 3 ♀, 12 Aug 1972, E. Jäckh, Host: *Robinia pseudoacacia* L., (USNM). WEST VIRGINIA: Marion Co: Morgantown: 5 ♂, 3 ♀, [no date], Host: *Robinia*, slide USNM 97835, (USNM). WISCONSIN: Dane Co: Madison: 1 ♂, 1 ♀, 24 Aug 1958, L. J. Bayer, Host: *Robinia*, (USNM).

Distribution. *Macrosaccus robiniella* occurs naturally over much of eastern North America from Ontario, Canada south to South Carolina and west to Missouri and Texas. *Macrosaccus robiniella* was first reported in Europe in 1983, near Basel, Switzerland (Whitebread 1990: 344) and has since spread through 23 European countries (Table 5).

Remarks. The synonymous names *Lithocolletis robiniella* Clemens and *Argyro-miges pseudacaciella* Fitch were both published in 1859. The month of publication

Table 5. Discovery and general distribution of *Macrosaccus robiniella* in Europe.

| Country | First year of occurrence | Reference to the first record |
|-------------------------|---|--|
| Albania | not recorded | Lopez-Vaamonde et al. 2010: 645 |
| Austria | 1991 | Huemer et al. 1992: 199 |
| Belgium | 2001 | De Prins and Groenen 2001: 159 |
| Bosnia and Herzegovina | 1999 | Dimić et al. 2000: 7 |
| Bulgaria | 2001 | Tomov 2003: 105 |
| Croatia | 2000, unpublished observations, Aleš Laštůvka & Hana Šefrová, pers. comm. | Lopez-Vaamonde et al. 2010: 645 |
| Czech Republic | 1992 | Laštůvka et al. 1993: 31 |
| Denmark | 2003 | Buhl et al. 2005: 79 |
| France | 1984 | Whitebread and Joos 1986: 117 |
| Germany | 1988–1989 | Whitebread 1990: 345 |
| Hungary | 1992 | Szabóky and Csóka 1997: 569 |
| Italy | 1988 | Bolchi Serini and Trematerra 1989: 193 |
| Lithuania | 2007 | Noreika 2008: 35 |
| Moldova (Pridnestrovje) | 2006 | Antyukhova 2007: 65 |
| Netherlands | 1999 | De Prins and Groenen 2001: 160 |
| Poland | 1999 from Šefrová 2002: 10 | Buszko and Novacki 2000: 25 |
| Romania | 2002 | Nețoiu 2003: 154 |
| Serbia | 1998 | Dimić et al. 1999: 34 |
| Slovakia | 1992 | Buszko 1996: 53 |
| Slovenia | 1994 | Seljak 1995: 78 |
| Spain | 2001 | Olivella 2002: 35 |
| Switzerland | 1983 | Whitebread and Joos 1986: 117 |
| Ukraine | 2002 | Bidzilya and Budashkin 2004: 61 |

for *robiniella* is clearly indicated as November in the Proceedings of the Academy of Natural Sciences of Philadelphia for that year. The month of publication for *pseudacaciella* Fitch cannot be determined as precisely. With the assistance of Tim McCabe of the New York State Museum, we were able to resolve an approximate date of printing for the Fifth report of Fitch's Report on the noxious, beneficial and other insects of the state of New York (Fitch 1859), but we were not able to determine the actual distribution date. From such dated sections of that Report, particularly a "Notice " to the farmers of New York, McCabe deduced that the Fifth Report most likely was printed in March, 1859. Attempts to locate receivership stamps for this report in various libraries to determine an approximate distribution date have been unsuccessful.

Thus, available evidence now suggests that *pseudacaciella* Fitch preceded the publication of *robiniella* Clemens by a few months. Because it is known that (1) Riley (1891) first treated *pseudacaciella* as a junior synonym of *robiniella* and no subsequent author has considered it otherwise, and (2) that the name *robiniella* has been recognized as the valid name for this taxon in more than 25 publications (141 publications using *robiniella* as the valid name are actually known) by more than 10 authors, this name must be preserved as the valid name for this taxon in accordance with the provisions of article 23.9.1 of the International Code of Zoological Nomenclature (ICZN 1999).

Neither the type locality nor the number of specimens examined were provided by Fitch for *Argyromiges pseudacaciella*. The same is true for the other two species of Gracillariidae Fitch proposed in 1859, *A. morrisella*, and *A. uhlerella*. Because it is believed that most of Fitch's collecting occurred within the vicinity of his "bug house" (still standing and now a historical site) in Salem, New York, it is likely that the type locality for all three species may be from this general area (McCabe, in litt.).

***Macrosaccus morrisella* (Fitch), comb. n.**

http://species-id.net/wiki/Macrosaccus_morrisella

Figs 1, 5, 41–44, 18–22, Tables 1, 2.

Argyromiges morrisella Fitch 1859: 838, No. 336.

Lithocolletis morrisella (Fitch).- Chambers 1871: 183.- Walsingham 1889: 52.- Riley 1891: 109, No. 5874.- Dyar 1902 [1903]: 551, No. 6269.- Braun 1908: 291.- Meyrick 1912a: 7; 1912b: 33.- Braun 1914: 110.- McDunnough 1939: 95, No. 9189.

Phyllonorycter morrisella (Fitch).- Ely 1918: 58.- Davis 1983: 10.- Maier and Davis 1989: 15.- De Prins and De Prins 2005: 323.- De Prins and De Prins 2011.

Lithocolletis texanella Zeller, 1875: 349.- Frey and Boll, 1878: 275.- Walsingham, 1889: 52 (synonym of *Phyllonorycter morrisella* (Fitch))- Riley 1891: 109, No. 5874.- Dyar 1902 [1903]: 551, No. 6269.- Braun 1908: 291.- Meyrick 1912a: 7; 1912b: 33.- Braun 1914: 110.- Ely 1918: 59.- Forbes 1923: 192.- McDunnough 1939: 95, No. 9189.- Davis 1983: 10.- Maier and Davis 1989: 15.- De Prins and De Prins 2005: 323.- De Prins and De Prins 2011.

Lithocolletis texana (Chambers 1877: 137) [misspelling].- Davis 1983: 10.

Lithocolletis amphicarpeaeella Chambers 1877: 137.- Riley 1891: 109, No. 5874 (synonym of *Phyllonorycter morrisella* (Fitch))- Dyar 1902 [1903]: 551, No. 6269.- Braun 1908: 291.- Meyrick 1912a: 7; 1912b: 33.- Ely 1918: 59.- McDunnough 1939: 95, No. 9189.- Davis 1983: 10.- De Prins and De Prins 2005: 323.- De Prins and De Prins 2011.

Lithocolletis amphicarpeaeella Riley 1891: 109, no. 5874 [misspelling].- Braun 1908: 291.- Davis 1983: 10.

Diagnosis. The forewing pattern of this species differs from that of *M. robiniella* and *M. neomexicanus* in possessing a more distinct basal white streak, in having the dorsal strigulae oriented less obliquely, and with the basal white dorsal stigula more pronounced, and from *M. gliricidius* by the darker ground colour. The forewing pattern most resembles that of *M. uhlerella* but differs in the more pronounced basal white streak which is absent or barely evident in *M. uhlerella*. The male genitalia are most similar to that of *M. robiniella*, particularly with regard to the more abruptly constricted apical third of the valva. The female genitalia differ from the latter in lacking the minute longitudinally oriented striae and spicules in the walls of the corpus bursae.

Adult (Fig. 5). Forewing length 2.3–2.8 mm.

Head: Vestiture of head and antenna similar to *M. robiniella*.

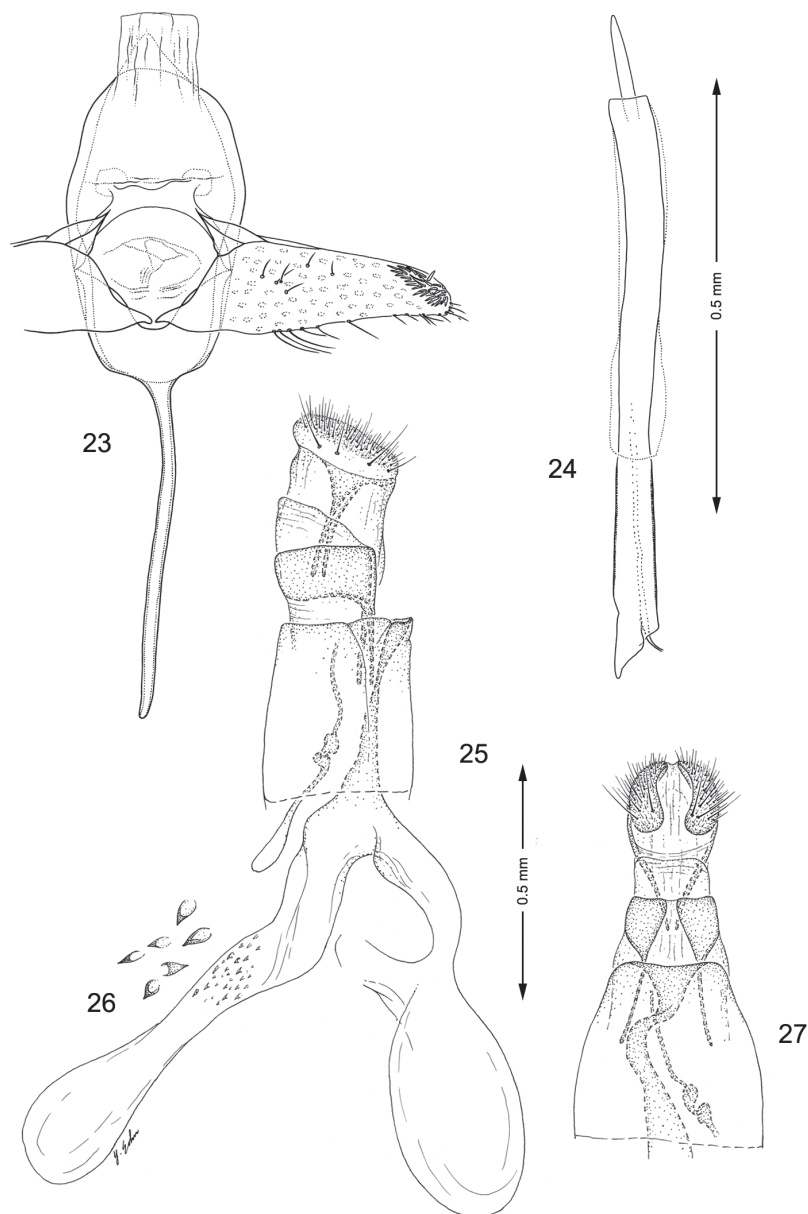
Thorax: Dark brown to fuscous dorsally, sometimes with a coppery to purplish luster; shiny white ventrally; tegula dark brown, with white suffusion anteriorly. Forewing pattern similar to *M. robiniella* except basal two costal strigulae less oblique; a slender white, slightly oblique streak usually well developed extending distad from tegula at base of wing to sometimes as far as first dorsal strigula; 3 white dorsal strigulae usually present, but these oriented less obliquely than in *M. robiniella*; basal strigula white, but sometimes obscure; median strigula connected to second costal strigula to form a narrow white fascia; black apical spot present as in *M. robiniella*; cilia light grey to white. Hindwing, including fringe, uniformly grey. Legs similar to *M. robiniella* in colour pattern.

Abdomen: Similar to *M. robiniella*, dark fuscous dorsally and white ventrally with greyish suffusion on anterior portion of segments 2–7 laterally and sometimes ventrally on A8.

Male genitalia (Figs 18, 19): Similar to *M. robiniella*, with valva gradually constricting before apex. Saccus a long, slender rod ~ 1.75× length of valva. Aedeagus long and slender, ~ 3.0× length of valva, with phallobase slightly more enlarged than in *M. robiniella*.

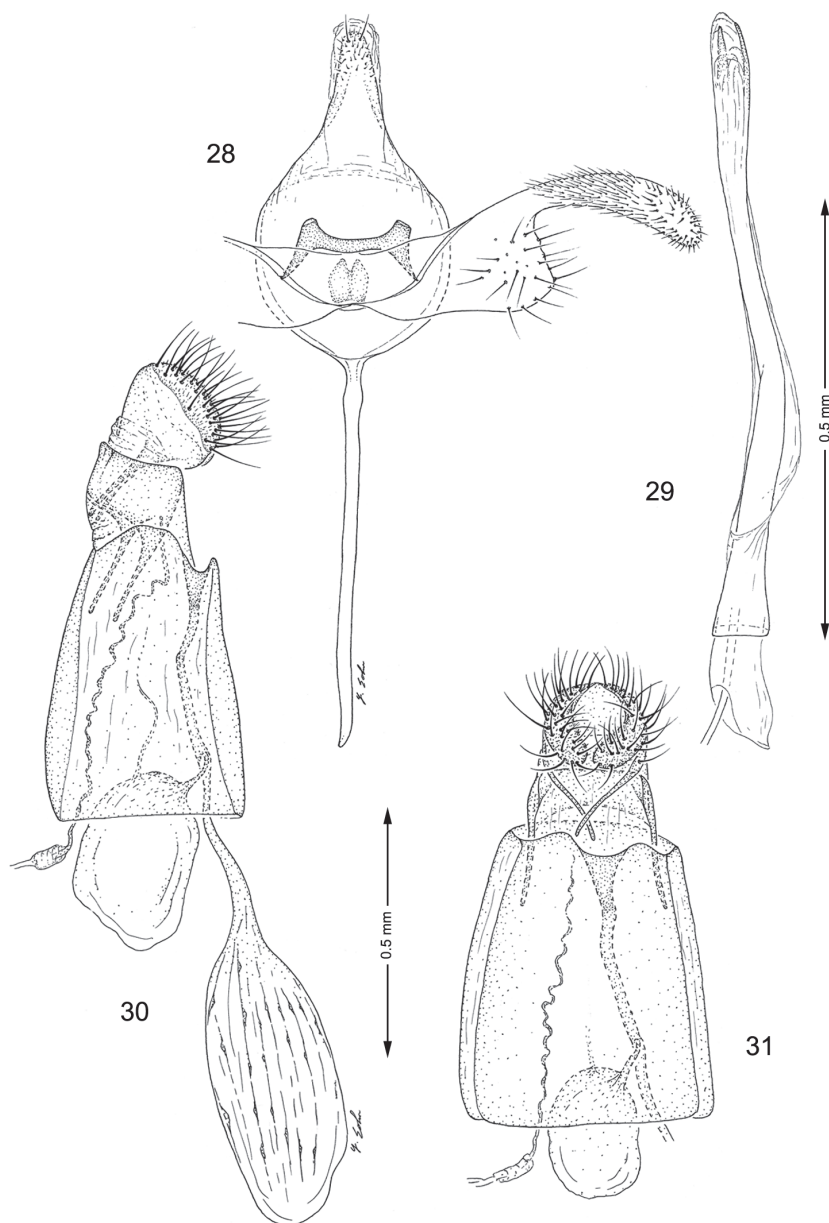
Female genitalia (Figs 20–22): Ductus bursae long and slender, nearly equal to length of elongate corpus bursae. Accessory bursae ~ 2/3 the length of corpus bursae, arising from near anterior 1/3 of ductus bursae. Corpus bursae elliptical, with series of small, scattered dentate spicules concentrated over caudal 2/3; longitudinal folds or striae not evident along walls; walls of anterior end (distal 1/3) of corpus bursae entirely membranous.

Larva and pupa. Similar to that of *Macrosaccus robiniella*.



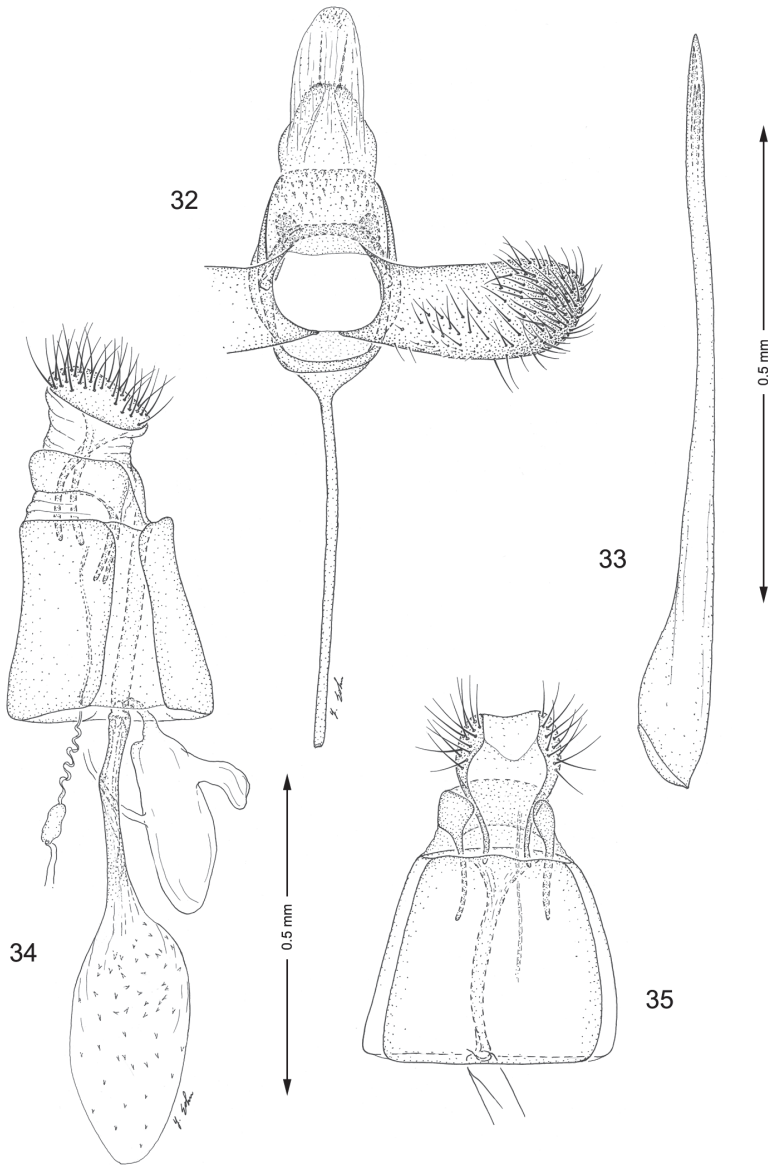
Figures 23–27. Genitalia, *Macrosaccus neomexicanus*. **23–24** Male. **23** Genital capsule, ventral view **24** Aedeagus **25–27** Female. **25** Lateral view **26** Detail of signa within corpus bursae **27** Segments 7–10, ventral view.

Larval mine. (Figs 41–44) The mine begins as an elongate serpentine track on the under (abaxial) side of the leaflet. This enlarges to an elongate-oval, whitish blotch which eventually becomes strongly tentiform (Fig. 43).



Figures 28–31. Genitalia, *Macrosaccus uhlerella*. **28–29** Male. **28** Genital capsule, ventral view **29** Aedeagus **30–31** Female. **30** Lateral view **31** Segments 7–10, ventral view.

Hosts. (Table 1). Fabaceae: *Amphicarpa bracteata* (L.) Fernald, (= *Amphicarpa monoica* (L.) Nutt., = *Falcata comosa* (L.) Kuntze, = *Amphicarpa comosa* (L.) Loudon), (Chambers 1878: 111; Walsingham 1889: 119; Ely 1917: 59). *Strophostyles*



Figures 32–35. Genitalia, *Macrosaccus gliricidius*. **32–33** Male. **32** Genital capsule, ventral view **33** Aedeagus **34–35** Female. **34** Lateral view **35** Segments 7–10, ventral view.

leiosperma (Torrey and A. Gray), (= *Strophostyles pauciflorus* (Bentham) S. Watson), new record. The primary host, *Amphicarpa bracteata*, is a low growing, trifoliate vine which occurs in damp woodlands widely from southern Canada and Montana to Texas and Florida. *Strophostyles leiosperma* is a climbing, trifoliate vine which occurs in drier habitats through the central United States from Arizona to Pennsylvania and Florida.

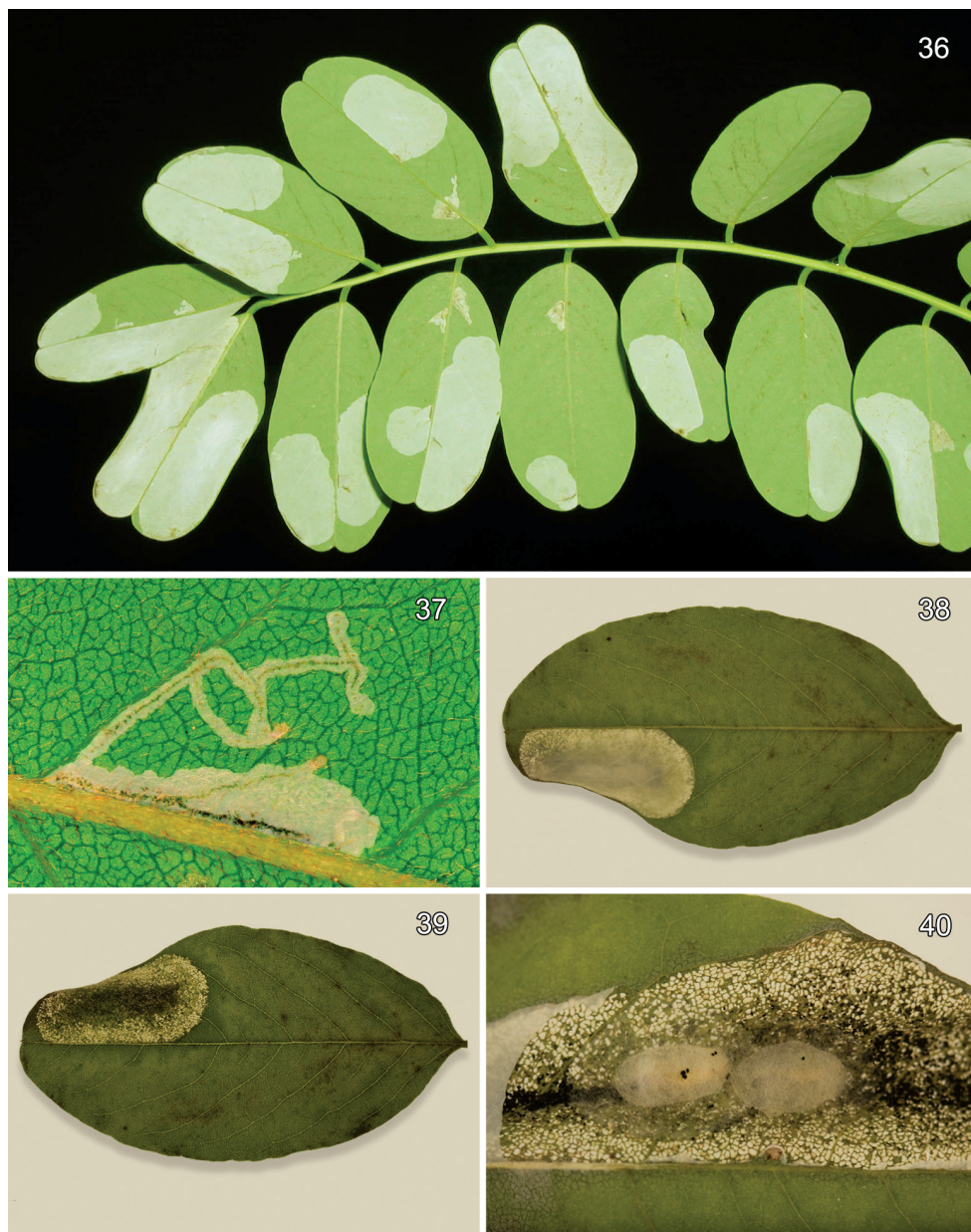
Types. *Argyromiges morrisella* Fitch: Lectotype ♂, (present designation): "Type; *Argyromiges morrisella* Ft.; Figured by Miss A. Braun, Feb. 1908; Lectotype ♂, *Macrosaccus morrisella* (Fitch) by D. R. Davis." (USNM). [Abdomen is missing].

Lithocolletis texanella Zeller: Holotype ♂, "Type 1336"; "Dallas, Texas", (MCZ). Paratype ♂, "Type", "*Lithoc. Texanella* Z. B1/77", "Dallas, Texas", "Zeller Coll., Walsingham Collection 1910–427", "*Lithocolletis morrisella* Fitch", (BMNH).

Lithocolletis amphicarpeaeella Chambers: Lectotype ♂, (present designation): "Type, 1326"; "Kentucky [crossed out], Chambers"; "*Lithocolletis amphicarpeaeella* Cham."; "Lectotype ♂, *Lithocolletis amphicarpeaeella* Chambers, by D. R. Davis", (MCZ); Paralectotype ♂, "N J, Chambers 1/77" "*Lith. Amphicarpeaeella* Nr. 3, Syntype, select KRT", (BMNH).

Note: In the lower right corner of drawer Mi 4423, a label with the following handwritten text is present: "Nb. Chambers' syntypes. The specimens bearing the serial numbers 1–68, and the specimens of *G. hermannella* var. *lingulacella* immediately following, were received by Stainton from Chambers. The numbers refer to a list made by Chambers; many of the specimens are likely to be syntypes. See Stainton foreign correspondence, letters nos. 94, 97 and 111 (by Chambers) and Stainton's "translations" of Chambers' awful handwriting, nos. 95, 99 and 96 respectively (the letters are out of chronological sequence). – KRT, 1980".

Material examined. CANADA: MANITOBA: 1 ♀, Aweme: 31 Aug 1931, Host: *Strophostyles pauciflora* (= *Strophostyles leiosperma*), R. M. White, (CNC). ONTARIO: Pt. Pelee: 1 ♀, 10 Oct 1967, T. N. Freeman, Host: Hog Ranot 63–46, (CNC). Simcoe: 1 ♂, 15 Sep 1955, T. N. Freeman, Host: *Amphicarpa monoica* (= *Amphicarpa bracteata*) 65–85, (CNC). Toronto: 2 ♂, 2 ♀, 5.22, Parish; 1 ♂, 6.22, Parish, (BMNH). QUEBEC: Fairy Lake: 1 ♂, 28 Aug 1955, Host: *Amphicarpa* 55–178, G. G. Lewis, (CNC). UNITED STATES: COLORADO [no specific locality provided]: 1 ♂, Type 1326, [Kentucky crossed out] Chambers, Lectotype *Lithocolletis amphicarpeaeella* Cham. ♂, (MCZ); 1 ♂, 1 ♀, Type 1326, [Kentucky crossed out] Chambers, Paralectotype *Lithocolletis amphicarpeaeella* Cham., (MCZ). CONNECTICUT: Hartford Co: Southington: 1 ♂, 3 Sep 1981, C. T. Meier, Host: *Amphicarpa bracteata*, Leaflet, (USNM). KENTUCKY: 1 ♀, Chamb., 132, (MCZ). ILLINOIS: Adams Co: Quincy: 1 ♀, 15 Feb 1948; 2 ♂, 3 ♀, 6–20 Apr 1947; J. P. Nielson, (INHS). Coles Co: Fox Ridge State Park: 1 ♀, 1 Jun 1991, em. 9 Jun 1991; 1 ♂, 1 ♀, 7 Jun 1991, em. 10 Jun 1991; 2 ♂, 3 ♀, 17 Jun 1991, em. 18–25 Jun 1991; 14 Jul 1991, em. 15 July 1991; 1 ♂, 2 ♀, 2 Aug 1992, em. 6–9 Aug 1992, T. Harrison, Host: *Amphicarpa bracteata*, (INHS). Putnam Co: 2 ♂, 1 ♀, 15 Jan 1941; 1 ♀, 8 Oct 1964; 2 ♂, 3 ♀, 13–30 Sep 1967; 4 ♂, 1 ♀, 2–8 Oct 1969, underside tentiform mine *Amphicarpa monoica*, M. O. Glenn, (INHS). MARYLAND: Montgomery Co: 2 mi. S. Laytonsville: 1 ♂, DOA 8 Oct 2009, D.R. Davis, Host: *Amphicarpa bracteata*, (USNM). Little Bennett Regional. Park: 3 ♂, 3 Aug 2002, em. 14 Aug 2002, D. R. and S. R. Davis, 3 ♂, 5 ♀, 6 Aug 2006, em. 10–16 Aug 2006 DNA/BOLD ID RDOPO081-09, GenBank GU669599, DNA/BOLD ID RDOPO083-09, GenBank GU669598 ; 2 ♂, 7 Aug 2010, em. 16–18 Aug 2010, D. R. and M. M. Davis, DRD slide 2664, Host: *Amphicarpa bracteata*, slides USNM 34180, 34181, 34182, DNA/



Figures 36–40. Leaf mines of *Macrosaccus robiniella* on *Robinia pseudoacacia*. **36** Abaxial blotch mines, with kind permission of György Csóka **37** Early instar, abaxial serpentine mines, with kind permission of György Csóka **38** Abaxial blotch mine **39** Adaxial view of Fig. 38 **40** Opened mine with 2 cocoons.

BOLD ID 00715473, DNA/R50BOLD ID 00715475, (USNM). Plummers Island: 1 ♂, 5 Nov 1914, Shannon, (USNM). Prince Georges Co: Seton Belt Woods: 1 ♂, 11 Jul 1977, E. Jäckh, (USNM). MICHIGAN: Calhoun Co: 4 ♂, T1S-R6W Sec 15: 31 Aug

1996, em. 7–11 Sep 1996, lot RJP654.17-18, Host: *Amphicarpa bracteata*. Clinton Co: T05N-R01 R01W S24: 28 Aug 1991, em. 7–11 Sep 1996, R. J. Priest, lot RJP 932.6-7, Host: *Amphicarpa bracteata*, (USNM). NORTH CAROLINA: Macon Co: Highlands, 3865': 1 ♂, 31 Jul 1958, R. W. Hodges, (USNM). NEW YORK: Thompkins Co: Ithaca, Six Mile Creek: 3 ♂, 1 ♀, 8 Apr 1945, (CU); 1 ♂, 10 Jul 1960, 1 ♂, 10 Jul 1960, R. W. Hodges, Host: *A. monoica* (L.), (USNM). OHIO: Hamilton Co: Cincinnati: 1 ♂, em. 23 Aug 1908, Annette F. Braun, B361, (MCZ); 1 ♀, em. 16 Jul 1908, 1 ♂, em. 2 Aug 1908, 1 ♂, em. 23 Aug 1908, 1 ♂, em. 24 Aug 1908, 1 ♂, em. 25 Aug 1908, 1 ♂, 1 ♀, em. 2 Sep 1908, 1 ♂, 5 Sep 1918, slides USNM 30891, 30892, 97446, 97447, (USNM). TEXAS: 3 ♂, 1 ♀, Boll, (BMNH). Dallas Co: Dallas: 2 ♂, (holotype and paratype of *L. texanella* Z.), type 1336, Boll, (MCZ); "*Lithoc Texanella* Z, B 1/77, type", (BMNH); 2 ♀, (*L. texanella* Z.), (BMNH); 3♂, 3♀ (*L. texanella* Z.) in coll. Stainton (BMNH).

Distribution. *Macrosaccus morrisella* occurs widespread across eastern North America from Manitoba and Ontario, Canada, south and west to Texas and Colorado (Chambers 1877).

Remarks. Chambers in his 1877 description of *Lithocolletis amphicarpeaeella* expressed doubt if this was a new species or new variety (as he did on the same page and line for "*Lithocolletis amorphaeella* n.sp.? or var.?"). Their descriptions included long, detailed comparisons of the forewing patterns of these two new moths as well of *robiniella* and "*texana*" (misspelled). No locality for either name was mentioned except for Colorado in the title of the publication (Chambers 1877). Each of the three "type" specimens of *amphicarpeaeella* in the collections of the MCZ have the name "Kentucky" crossed out on the specimen label "Kentucky, Chambers", and no mention of Colorado appears. A male specimen in best condition has been selected as lectotype.

The holotype specimen of *Lithocolletis texanella* Zeller upon examination was found to be a male and not a female as stated originally by Zeller (1875).

Macrosaccus neomexicanus Davis, sp. n.

urn:lsid:zoobank.org:act:3FD42A3B-6E1B-4788-82F7-D9B2AF3D3354

http://species-id.net/wiki/Macrosaccus_neomexicanus

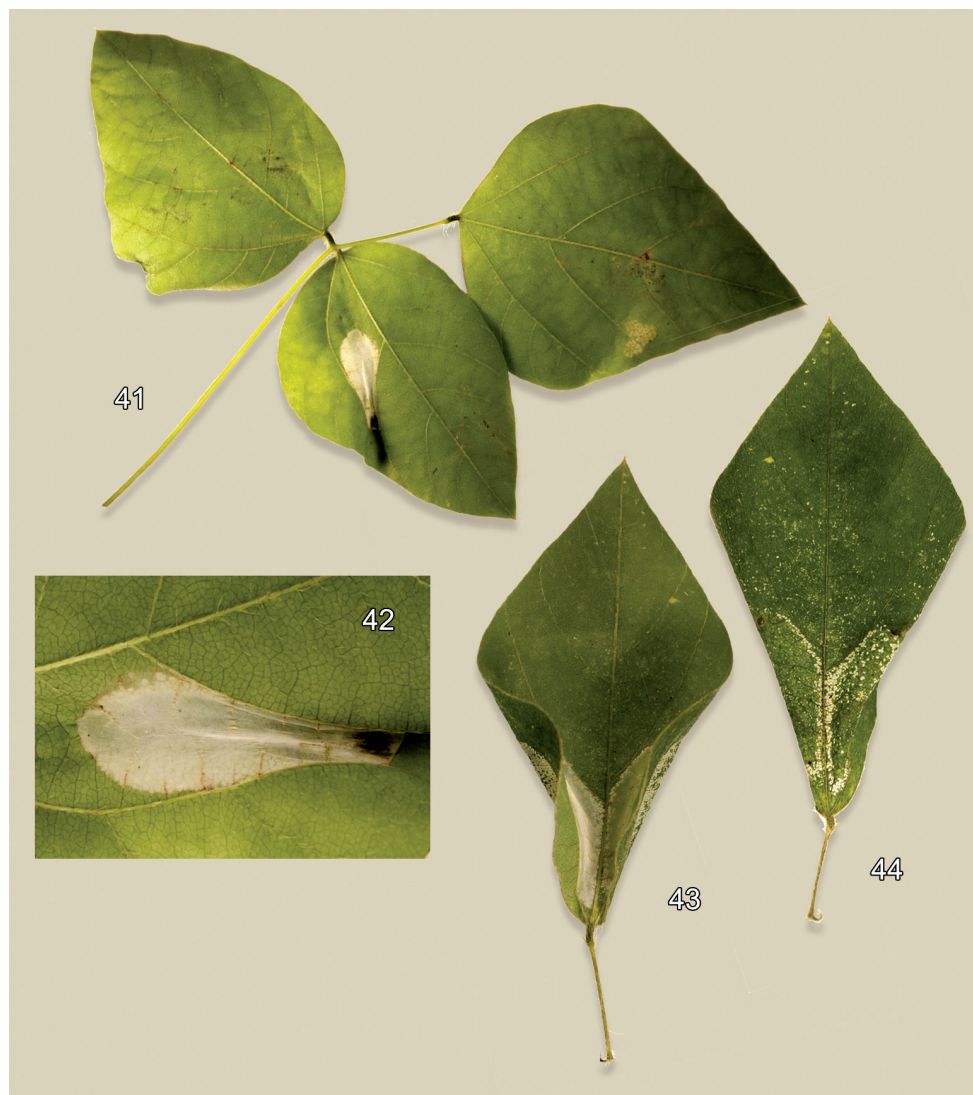
Figs 1–6, 23–27, 45–50, Tables 1, 2.

Diagnosis. As discussed in the diagnosis of *M. robiniella*, this species most resembles the former in general appearance. They differ in distribution, host preference, in genital morphology (see diagnoses of *M. robiniella*), and possibly overall size, with the wingspan of *neomexicanus* being slightly larger.

Adult (Fig. 6). Forewing length 2.7–3.5 mm.

Head: Vestiture of head and antenna similar to *M. robiniella*; apical segment of antenna white to grey.

Thorax: Dark brown dorsally, with whitish suffusion anteriorly and laterally; white ventrally; tegula dark brown, with pale grey to white suffusion anteriorly. Forewing and hindwing patterns very similar to *M. robiniella*. Vestiture of legs similar to *robiniella*.



Figures 41–44. Leaf mines of *Macrosaccus morrisella* on *Amphicarpa bracteata*. **41** Abaxial tentiform blotch mine **42** Detail of abaxial tentiform blotch mine **43** Two abaxial blotch mines at leaf base **44** Adaxial view of Fig. 43.

Abdomen: Similar to *M. robiniella*, dark fuscous dorsally and white ventrally with greyish suffusion on anterior portion of segments 2–7 laterally and sometimes ventrally on A8.

Male genitalia (Figs 23, 24): Valva relatively simple, gradually narrowing before apex without abrupt constriction; apex narrowly rounded, densely setose, particularly along costal margin. Saccus a slender, elongate rod $\sim 1.3\times$ length of valva. Aedeagus very long and uniformly slender, $\sim 2.5\times$ length of valva.



Figures 45–50. Habitat and leaf mines of *Macrosaccus neomexicanus* on *Robinia neomexicana*. **45** Mixed pine-juniper habitat of *Robinia neomexicana*, Kaibab National Forest, Coconino Co., Arizona, ~2130 m **46** Multiple early instar serpentine and blotch mines on abaxial leaf surface **47** Later stage abaxial mines after multiple blotch mines begin to coalesce **48** Late stage tentiform blotch mine, adaxial view **49** Completely folded leaf resulting from double tentiform mines, adaxial view **50** Opened (with ventral leaf epidermis removed) aggregate blotch mines with 8 pupal cocoons, abaxial view.

Female genitalia (Figs 25–27): Ductus bursae moderately long and slender, $\sim 1/3$ the length of elongate corpus bursae. Accessory bursae nearly as long as corpus bursae, arising from junction of ductus bursae and corpus bursae; with a smaller lateral pouch arising \sim midway along side of accessory bursae. Corpus bursae relatively slender, anterior end only slightly broader; a dense scattering of minute spicules encircling middle; remaining walls of corpus bursae entirely membranous.

Larva and pupa. Similar to that of *Macrosaccus robiniella*.

Larval mine (Figs 46–50). The mine begins as a relatively short, serpentine track which enlarges to an elongate-oval, whitish blotch located on the under (abaxial) side of the leaflet. As the larva develops and begins laying down silk, the mine becomes strongly tentiform, causing the upper (adaxial) surface to roll over (Figs 48, 49).

Host. (Table 1). Fabaceae: *Robinia neomexicana* Gray. The host is a moderately small, spiny shrub growing to as high as 5 meters and usually forming dense thickets (Fig. 45). It occurs from California to Texas and north to Wyoming.

Life history (Figs 46–50). Some collections of this species from southern Arizona have been from dense infestations. In such populations, oviposition tends to be concentrated on fewer available leaflets with as many as 45 short, initial serpentine mines observed on a single leaflet. These soon coalesce resulting in a single large blotch covering nearly the entire lower side of the leaflet (Fig. 47). Larval mortality is probably high under these conditions. One large composite mine opened contained 14 live and 11 dead, late instar larvae and no pupae. A maximum of 11 cocoons with pupae (5 on one side of the midrib and 6 on the other side) were found in one leaflet (DRD rearing lots 541, 541.1, Fig. 50).

Holotype. ♂: UNITED STATES: ARIZONA: Cochise Co: Carr Canyon: Huachuca Mts: 20 Sep 1985, em. 27 Sep 1985, HOST: *Robinia neomexicana*, R. S. Wielgus, digital image captured, (USNM).

Paratypes. UNITED STATES: ARIZONA: Coconino Co: North Rim Grand Canyon: 1 ♀, 15–16 Aug 1978, em. 17 Aug – 6 Sep 1978, G. Deschka, HOST: *Robinia neomexicana*, (BMNH). Cochise Co: Carr Canyon: Huachuca Mts: 70 ♂, 57 ♀, 20 Sep 1985, em. 21 Sep - 2 Oct 1985, R.S.Wielgus, DRD541, HOST: *Robinia neomexicana*, slides USNM 28416, 30890, 34267, (USNM). NEW MEXICO: Catron Co: Rocky Canyon., Gila Nat. Forest: 1 ♂, 1969, em. 6 Aug 1969, D. & M. Davis, DRD642.2, Host: *Robinia neomexicana*, (USNM). Otero Co: Deerhead Campground, ca. 2 mi. S. Cloudcroft: 1 ♂, 1 ♀, 18–19 Jul 1969, em. 2 Aug 1969, D. & M. Davis, DRD 642, Host: *Robinia neomexicana*, DNA/BOLD ID RDOPO084-09, GenBank GU669596, DNA/BOLD ID RDOPO085-09, GenBank GU669597, (CCDB, USNM). Sandoval Co: Pakitza Campground, 4 mi. E. Ponderosa, Santa. Fe Nat. Forest: 7 ♂, 9 ♀, em. 4–11 Aug 1969, D. & M. Davis, DRD 642.1, Host: *Robinia neomexicana*, slides USNM 34183, 34184, (USNM).

Distribution. Known only from the southwestern United States from Arizona and New Mexico.

Etymology. The specific name is derived from the specific name of its plant host. The specific epithet is an adjective in the nominative singular.

***Macrosaccus uhlerella* (Fitch), comb. n.**

http://species-id.net/wiki/Macrosaccus_uhlerella

Figs 7, 8, 28, 29–31, 51–53, Tables 1, 2.

Argyromiges uhlerella Fitch, 1859:838, No. 337.

Lithocolletis uhlerella (Fitch).- Chambers 1871: 183.- Walsingham 1889: 53.- Riley 1891: 109, No. 5900.- Dyar 1902 [1903]: 551, No. 6268.- Braun 1908: 291.- Forbes 1923: 192.- Meyrick 1912a: 7; 1912b: 33.- Braun 1914: 114.- McDunnough 1939: 95, No. 9190.

Phyllonorycter uhlerella (Fitch).- Ely 1918: 59.- Davis 1983: 10.- De Prins and De Prins 2005: 360.- De Prins and De Prins 2011.

Lithocolletis amorphaeella Chambers 1877: 132, 137.- Walsingham 1889: 53 (synonym of *Lithocolletis uhlerella*).- Riley 1891: 109, No. 5900.- Braun 1908: 292.- Dyar 1902 [1903]: 551, No. 6268.- Braun 1908: 291.- Meyrick 1912a: 7; 1912b: 33.- Braun, 1914: 114.- McDunnough 1939: 95, No. 9190.

Lithocolletis amorphae Frey and Boll 1878: 275.- Walsingham 1889: 53 (synonym of *Lithocolletis uhlerella*).- Riley 1891: 109, No. 5900.- Dyar 1902 [1903]: 551, No. 6268.- Braun 1908: 292.- McDunnough 1939: 95, No. 9190.

Diagnosis. The forewing pattern of this species is most similar to that of *M. morrisella* in having the basal strigulae less oblique than those present in *M. robiniella* and *M. neomexicanus*, but it differs from *M. morrisella* in lacking the distinct basal white streak typical of the latter. The male genitalia of *M. uhlerella* are distinct in possessing the most modified, slender valvae (Fig. 28) of any member of *Macrosaccus*.

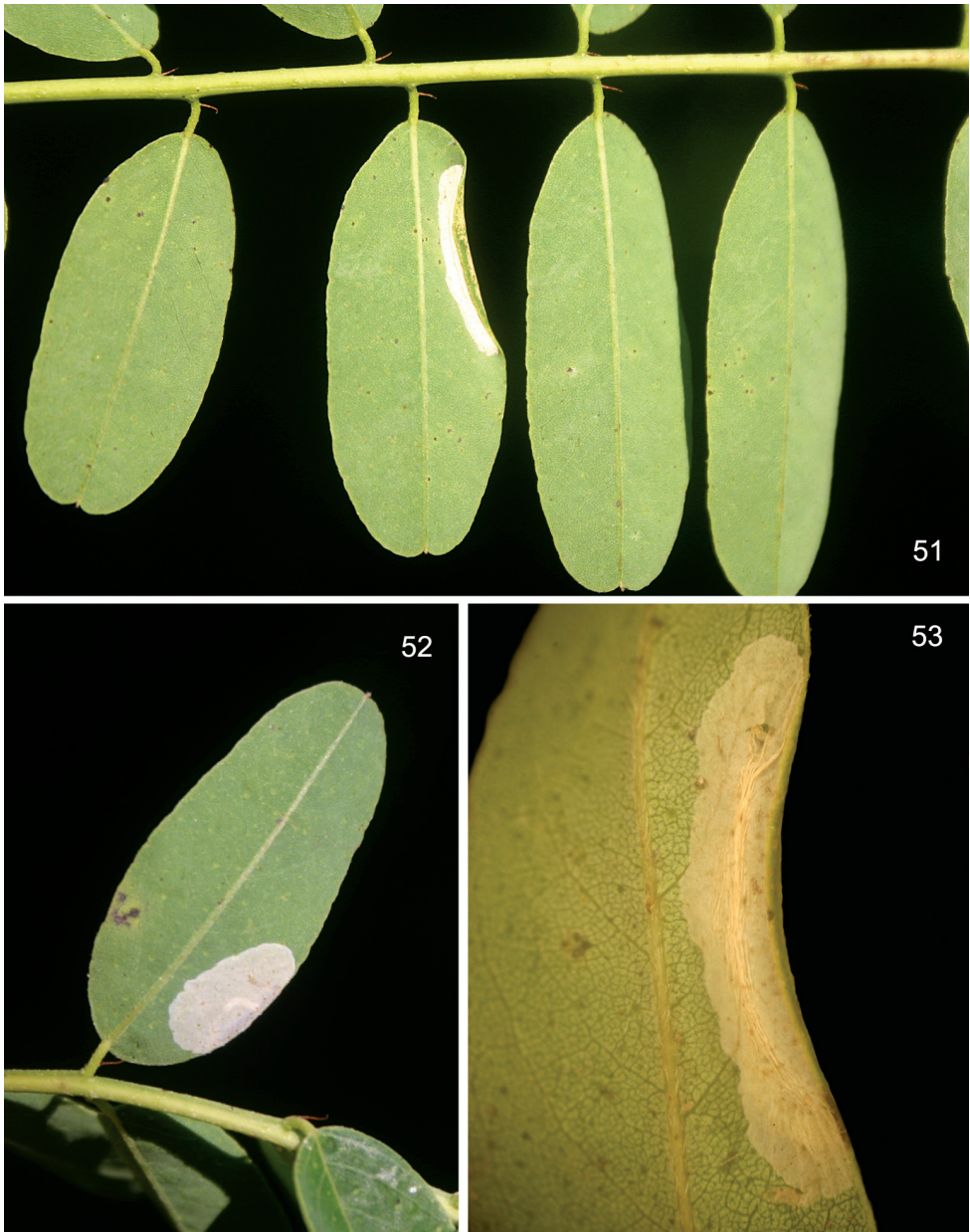
Adult (Figs 7, 8). Forewing length 2.2–2.8 mm.

Head: Vestiture of head and antenna similar to *M. robiniella* and *M. morrisella*.

Thorax: Light to dark brown to fuscous dorsally, sometimes with a slight orange luster and a suffusion of fuscous posteriorly; shiny white ventrally; tegula usually orange brown, occasionally with fuscous suffusion posteriorly. Forewing mostly light brownish orange with 4 white costal strigulae, each usually with pale to dark fuscous borders; pattern similar to *M. morrisella* except without a distinct slender, oblique, white streak from tegula at base of wing; 3 white dorsal strigulae usually present, but these oriented less obliquely than in *M. robiniella*; basal strigula white, but sometimes obscure; median strigula connected to second costal strigula to form a narrow white fascia as in *M. morrisella*; dorsal half of wing with black scaling variably present between strigulae; a large black apical spot present similar to that of *M. robiniella* and *M. morrisella*; cilia light grey to white. Hindwing, including fringe, uniformly grey. Legs similar to *M. robiniella* in colour pattern.

Abdomen: Similar to *M. robiniella*, dark fuscous dorsally and white ventrally with greyish suffusion laterally on anterior portion of segments 2–7 and sometimes ventrally on A8.

Male genitalia (Figs 28, 29): Distal half of valva abruptly constricted to ~ 1/3 the width of basal half; saccular lobe broadly produced, truncate. Saccus a long, slender rod ~ 1.3× length of valva. Aedeagus long and slender, ~ 3.0× length of valva, with phallobase only slightly more enlarged than aedeagus.



Figures 51–53. Leaf mines of *Macrosaccus uhlerella* on *Amorpha fruticosa*. **51** Abaxial tentiform blotch mine **52** Flat blotch mine **53** Detail of abaxial tentiform blotch mine. Photographs by T. Harrison.

Female genitalia (Figs 30, 31): Ductus bursae long and slender, slightly longer ($\sim 1.2\times$) than length of elongate corpus bursae. Accessory bursae spherical, \sim half the length of corpus bursae, arising from approximately midway along ductus bursae. Corpus bursae elliptical, with series of small, dentate spicules arranged in

faint longitudinal folds or striae; walls of anterior end (distal 1/6) of corpus bursae membranous.

Larva and pupa. Not examined.

Larval mine (Figs 51–53). The mature mine is an elongate-oval, whitish blotch located on the under (abaxial) side of the leaf usually near the edge of the leaflet. Eventually, as the mine becomes tentiform, the leaf edge is slightly curled (Fig. 51).

Hosts. (Table 1). *Amorpha fruticosa* L., (Chambers 1878: 58; Frey and Boll 1878: 276; Walsingham 1889: 119; Braun 1908: 292). *Amorpha* sp., *Robinia* sp. (Robinson et al. 2002: 357). The primary host, *Amorpha fruticosa*, is a shrub up to 4 meters high which occurs naturally from Louisiana to Florida and north to Wisconsin and Pennsylvania. Because no adults reared from *Robinia* are known or have been examined, the host record reported in Robinson et al. (2002) is questionable.

Types. *Argyromiges uhlerella* Fitch [type material and deposition not stated, believed lost]: [New York]. *Lithocolletis amorphaeella* Chambers: Lectotype (present designation), ♀: “Type 1327; Chambers, Colorado; *Lithocolletis amorphaeella* Cham.; Lectotype ♀, *Lithocolletis amorphaeella* Chambers, by D. Davis; ♀ genitalia on slide 4530, D.R. Davis”, (MCZ), [head, right wings missing]. *Lithocolletis amorphae* Frey and Boll: Type material not stated, deposition unknown; [Texas].

Material examined. UNITED STATES: COLORADO: Specific locality unknown: 1 ♀, lectotype, *Lithocolletis amorphaeella* Cham., DRD slide 4530, (MCZ). ILLINOIS: McDunnough Co: 3 mi. East of Good Hope, Short Fork Seep, Ti7N-R2W, Section 27–28: 2 ♂, 2 ♀, 7 Aug 2010, emerged 11–17 Aug 2010, leaf mine on *Amorpha fruticosa*, J. Wiker and T. Harrison, slide USNM 33918, (USNM). Putnam Co: 1 ♂, 1 ♀, 29 Mar 1938, DRD slide 4508; 1 ♂, 18 Aug 1939; 1 ♂, 8 Sep 1940, DRD slide 4507; 2 ♂, 20 Sep 1967, reared from underside leafmine *Amorpha fruticosa*; 2 ♂, 25 Sep 1940; 1 ♂, 5 Oct 1946, DRD slide 4506, reared from leafmine, *Amorpha fruticosa*, M. O. Glenn, (INHS). Vermilion Co: Kickapoo State Recreation Area: 1 ♀, 13 Jun 1991, moth iss. 24 Jun 1991, T. Harrison, (INHS). MISSOURI: Boone Co: Colombia: 1 ♀, 14 Dec 1969, W. S. Craig, under bark of sycamore, (USNM). TEXAS: Specific locality unknown: 4 ♀, from *Amorpha fruticosa*, (BMNH). Dallas Co: Dallas: 2 ♂, 3 ♀, Boll, slide BM 4003, (BMNH); Dallas, Boll. 1876, 1 ♂, 4 ♀, bred from *Amorpha fruticosa*, Stainton collection 1893-134, (BMNH).

Distribution. *Macrosaccus uhlerella* is known to occur from Colorado, Illinois, Missouri, New York, and Texas.

Remarks. For over 120 years *Argyromiges uhlerella* Fitch has been regarded as the senior synonym of *amorphaeella* Chambers. The inadequacy of the original description of *Argyromiges uhlerella* (quoted below), together with the disappearance of any type material, has caused some uncertainty regarding this insect's identity. In his review of the insects feeding on *Robinia pseudoacacia*, Fitch (1859) proposed two names now assigned to *Macrosaccus* which he believed to be related to the *Robinia* leafminer: *Argyromiges pseudacaciella* (now considered a synonym of *M. robiniella*) and *Argyromiges uhlerella*. Fitch stated that he did not know the hosts for these two moths (i.e., neither had not been reared). Walsingham (1889) concluded that Fitch's description of *uhlerella*

agreed with that of *M. amorphaeella*, proposed 18 years later by Chambers (1877), and he consequently synonymized the latter name. All later workers treating this complex accepted Walsingham's decision. Closer examination of wing pattern variation within large series of reared *M. robiniella*, however, suggests that Fitch's description more approximates the greyish forewing colour of some specimens of *M. robiniella* than it does the non-greyish, more brownish forewing colour prevalent in the smaller sample of adult *Macrosaccus* reared from *Amorpha fruticosa* examined. Fitch's description also contains such abnormalities as the "five white spots along their outer sides" and "the tip of the wings is here replaced by a short black stripe thrice as long as it is wide", both of which may possibly reflect the poor condition of his specimen(s). Worn specimens of *M. robiniella* have been observed with one or two strigulae indistinct or missing, as well as some with reduced apical spots. Similar variation might also be found to occur within moths reared from *Amorpha*, once more specimens become available for examination.

No type material of "*Argyromiges uhlerella*" is believed to exist. In 1977, during a search for Fitch's Lepidoptera types deposited in the USNM, Tim McCabe found a pin bearing Fitch's label 8158 (the type number for *uhlerella*) in the main collection. The moth was missing and was presumed destroyed. The pin with that number has since disappeared. Because the name *uhlerella* has been used consistently as the valid name for this taxon since before 1899, we believe that this usage should continue even though some doubt now exists regarding the correct application of the name.

Original description of *Argyromiges uhlerella* Fitch:

"337. Uhler's leaf-miner, *Argyromiges Uhlerella*, new species."

"This resembles *Pseudacaciella*, but is throughout of paler color, the fore wings being golden gray, with five white spots along their outer sides, of which the hindmost ones are small, the others quite large and bordered with blackish upon their anterior sides; and the black dot on the tip of the wings is here replaced by a short black stripe thrice as long as it is wide; whilst the hind wings and their fringes are pale silvery gray. These marks will suffice to distinguish this from the two preceding species."

***Macrosaccus gliricidius* Davis, sp. n.**

urn:lsid:zoobank.org:act:19A1403C-D313-42BE-AE90-588AF6876F0D

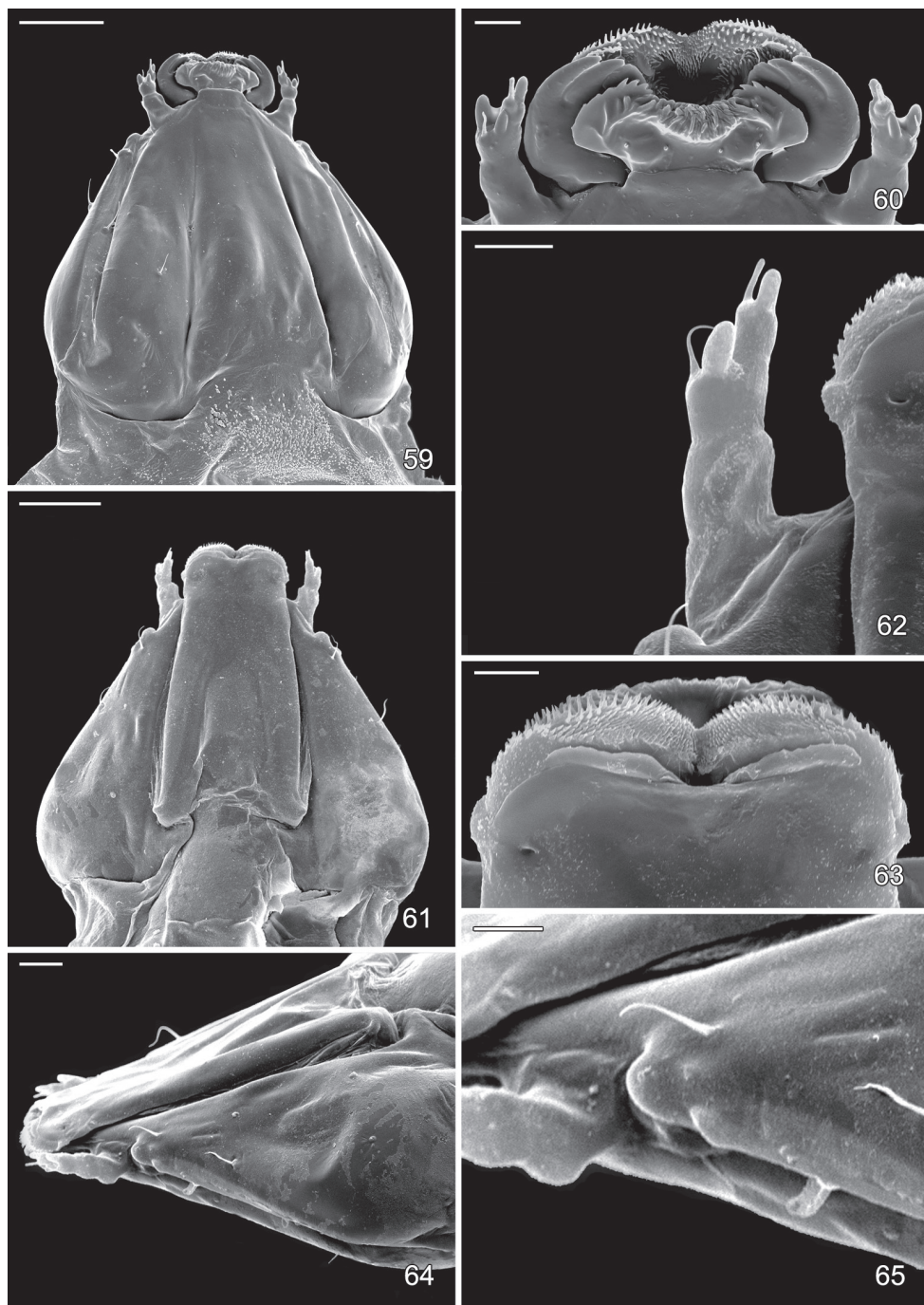
http://species-id.net/wiki/Macrosaccus_gliricidius

Figs 1, 9, 32–35, 54–58, Tables 1, 2.

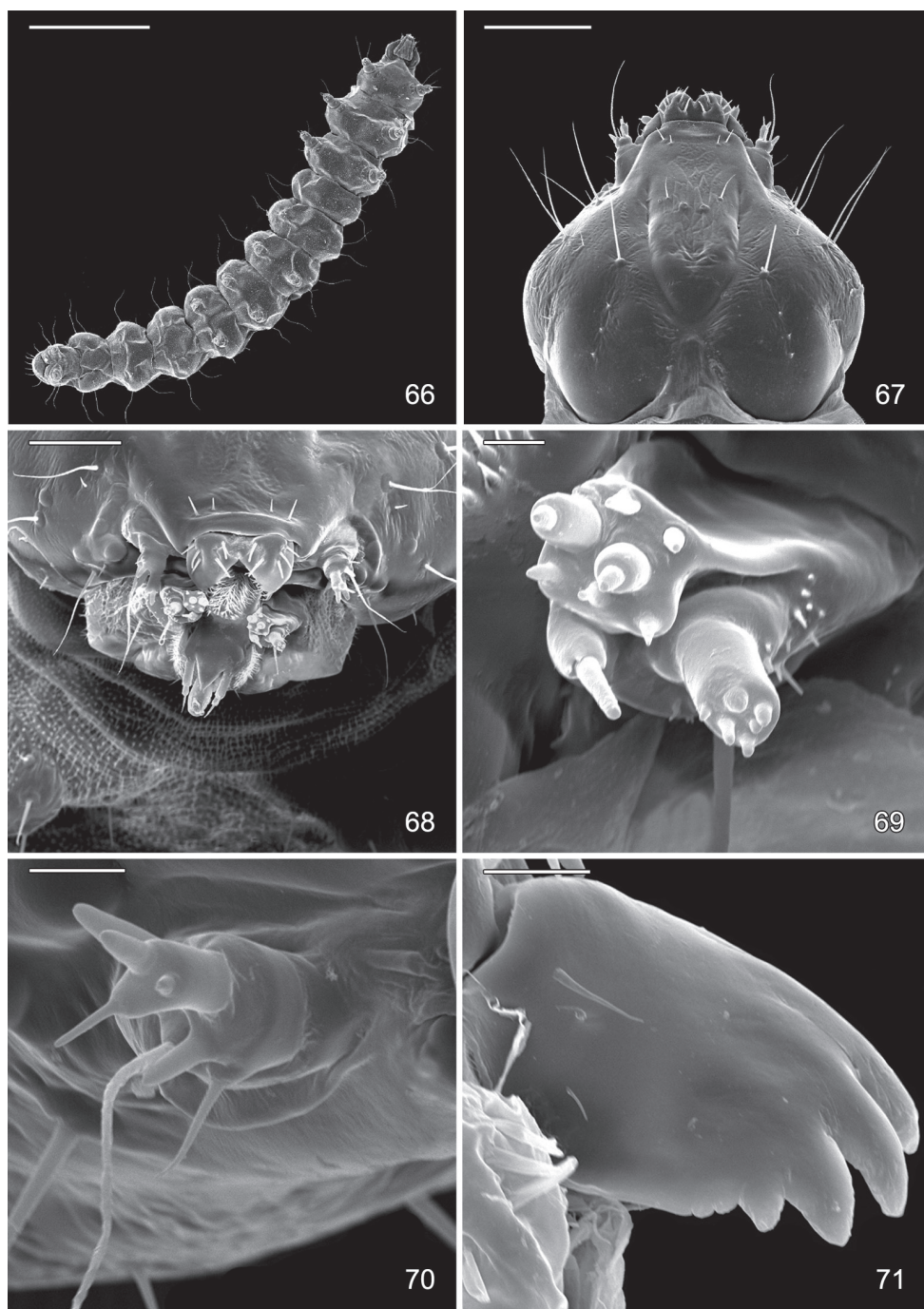
Diagnosis. The forewing pattern of this species is similar to *M. robiniella* and *M. neomexicanus* in possessing 4 white costal and 3 dorsal, mostly sharply oblique strigulae, with a median fascia often formed by the junction of the 2nd costal and median dorsal strigulae. The pale golden brown ground colour of *M. gliricidius* is distinctly paler than that of the other species. The forewing of *M. gliricidius* also differs from other *Macrosaccus* in possessing a small, elongate white subapical spot and a more reduced dark fuscous apical spot. The male valva of *M. gliricidius* is distinct in having the distal half more broadly rounded than that of other *Macrosaccus*.



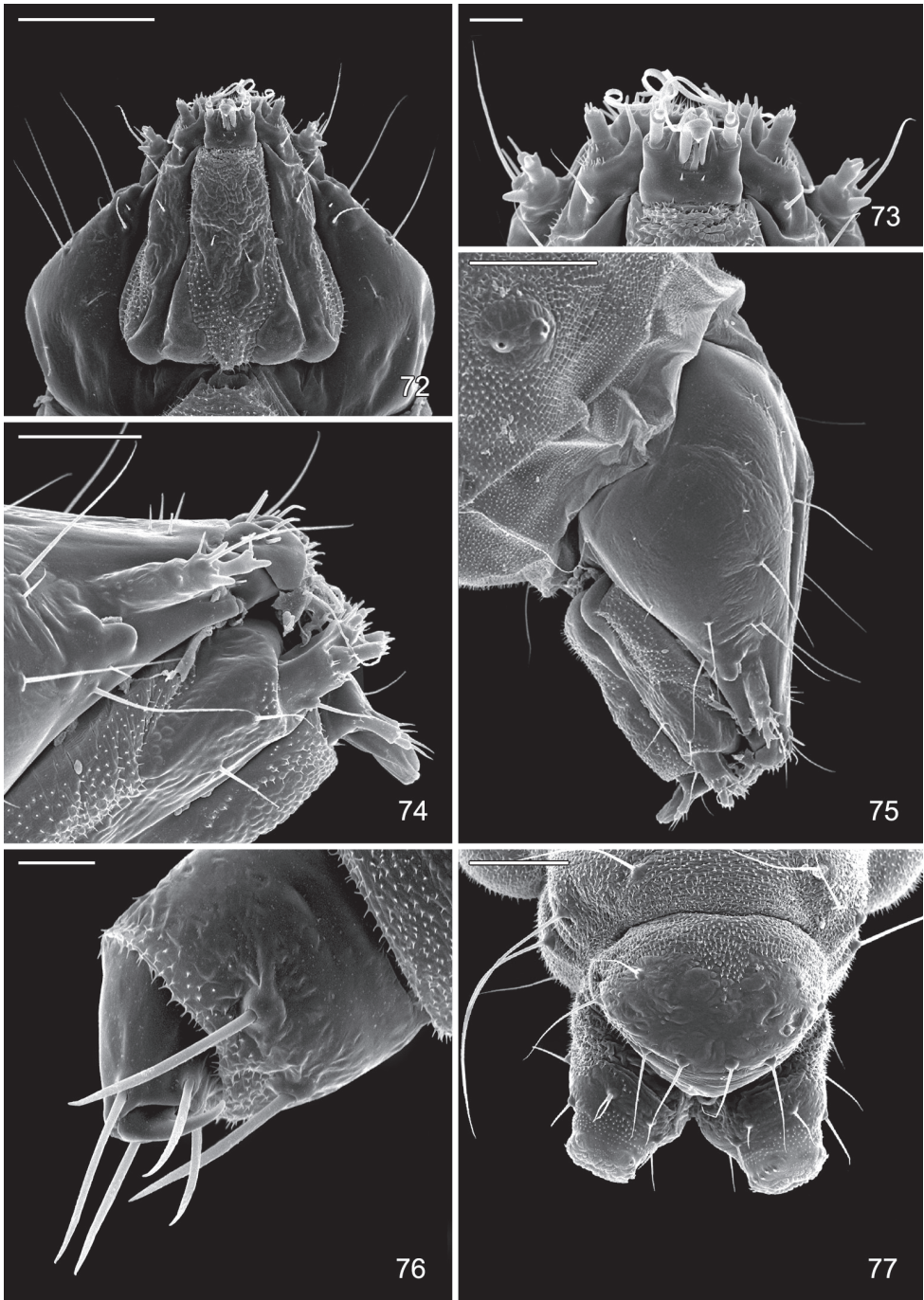
Figures 54–58. Leaf mines of *Macrosaccus gliricidius* on *Gliricidia sepium*. **54** General damage to host **55** Adaxial blotch mine **56** Late instar tissue feeding larva **57** Open blotch mine with single cocoon **58** Pupa with cocoon removed. Photographs by R. Cave.



Figures 59–65. Sap feeding larval instar of *Macrosaccus robiniella*. **59** Head, dorsal view (50 μ m) **60** Detail of mouthparts, antenna, dorsal view (10 μ m) **61** Head, ventral view (50 μ m) **62** Antenna dorsal view (10 μ m) **63** Detail of mouthparts, ventral view (10 μ m) **64** Head, lateral view (20 μ m) **65** Detail of stem-matal area, lateral view (20 μ m). (Scale lengths in parentheses).



Figures 66–71. Late tissue feeding instar larva of *Macrosaccus robiniella*. **66** Ventral view (1 mm) **67** Head, dorsal view (100 μ m) **68** Mouthparts, dorsal view (50 μ m) **69** Maxilla, anterior view (5 μ m) **70** Antenna, lateral view (10 μ m) **71** Mandible, dorsal view (10 μ m). (Scale lengths in parentheses).



Figures 72–77. Late tissue feeding instar larva of *Macrosaccus robiniella*. **72** Head, ventral view (100 μ m) **73** Detail of mouthparts, ventral view (20 μ m) **74** Lateral view of mouthparts (50 μ m) **75** Lateral view of head (100 μ m) **76** Thoracic leg (20 μ m) **77** Abdominal segments 9, 10, dorsal view (100 μ m). (Scale lengths in parentheses).

Adult (Fig. 9). Forewing length 2.2–2.6 mm.

Head: Vestiture of head and antenna similar to *M. robiniella* except vertex generally paler and with more white scales concentrated toward occiput.

Thorax: Dorsum with a narrow, median, longitudinal band of light golden brown bounded laterally with white; tegula light golden brown; venter white. Forewing pale golden brown with 4 equally spaced, oblique, white costal strigulae and 3 white, dorsal strigulae, each bordered by dark brown scales; 2nd costal strigula connected to median dorsal strigula; subapical dorsal strigula directed inward toward small, white subapical spot; dark fuscous apical spot poorly developed, with a more elongate subapical spot immediately basad to rudimentary apical spot; fringe mostly pale greyish white, with narrow, dark brown median band and broad, grey inner band. Hindwing, including fringe, uniformly grey. Foreleg mostly dark fuscous dorsally, white ventrally, with 2 white annuli around basal tarsomeres; midleg mostly white with oblique bands of white extending dorsally over tibia; tarsomeres more broadly banded with white dorsally; hindleg mostly white with much of tibia fuscous dorsally, and with 3 broad fuscous annuli dorsally over tarsomeres.

Abdomen: dark brown dorsally and laterally along anterior margins of A3–7; white ventrally.

Male genitalia (Figs 32, 33): Valva simple, becoming slightly broader near apex; apex broadly rounded, setose; saccus a slender, elongate rod ~ 1.6× length of valva. Aedeagus very long and slender, ~ 3.5× length of valva; phallobase moderately enlarged.

Female genitalia (Figs 34, 35): Ductus bursae long and slender, ~ 1.25× the length of corpus bursae. Accessory bursae ~ 0.8× the length of corpus bursae, arising from near middle of ductus bursae at a point where the ductus is slightly constricted; a smaller lateral pouch arising near caudal end of accessory bursae. Corpus bursae elliptical, with numerous acute spicules somewhat evenly scattered over much of inner surface but less dense near anterior end.

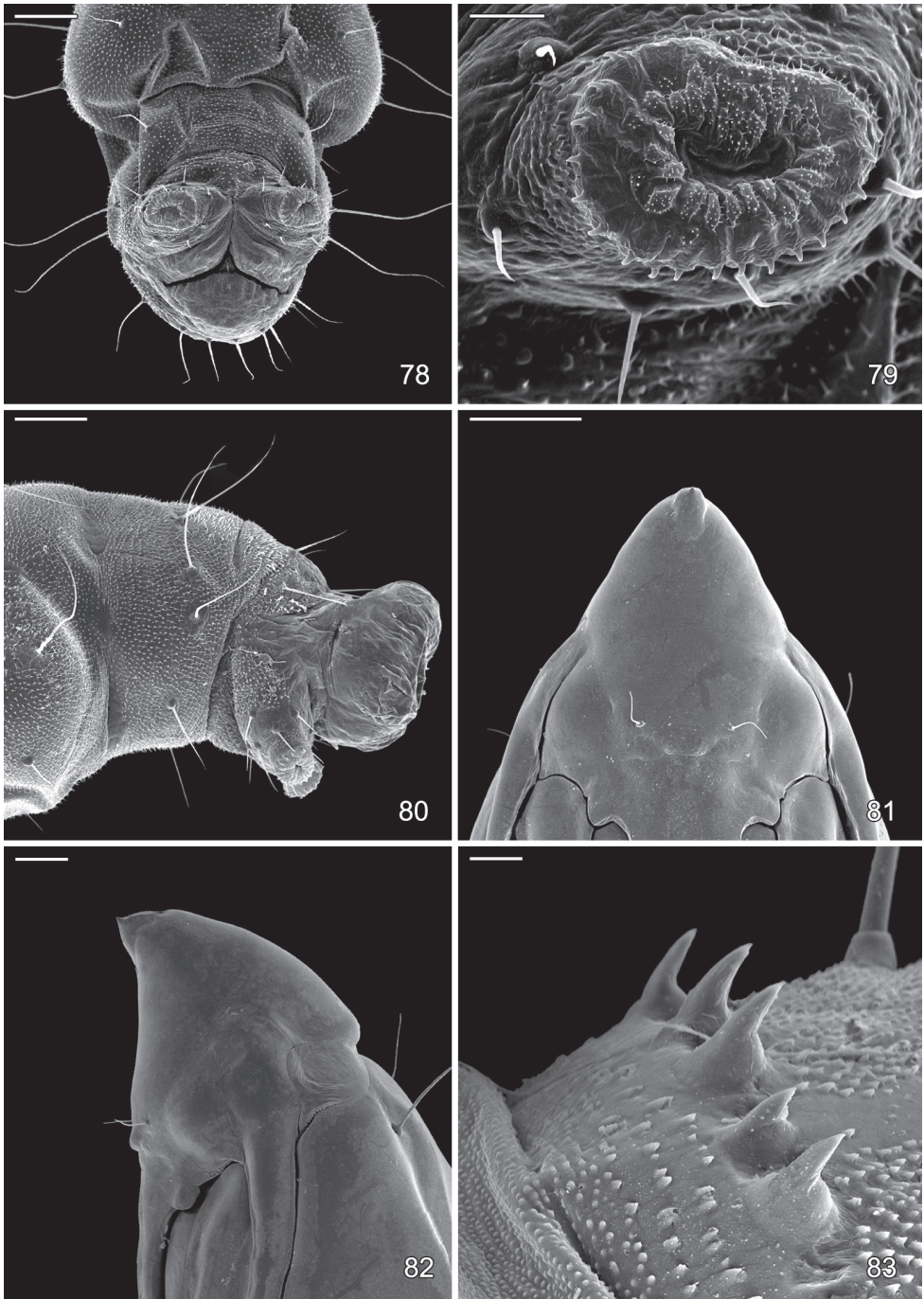
Larva and pupa. (Figs 56, 58). Similar to that of *Macrosaccus robiniella*.

Larval mine (Figs 54–58). The mine begins as an elongate serpentine track which abruptly enlarges to an elongate-oval, whitish blotch located on either the upper (adaxial) or lower (abaxial) side of the leaflet. When present on the under side, the blotch mines usually develop along the midrib. Only the upper side blotch mines occurred directly on top of the midrib (Fig. 55, Cave, *in litt.*).

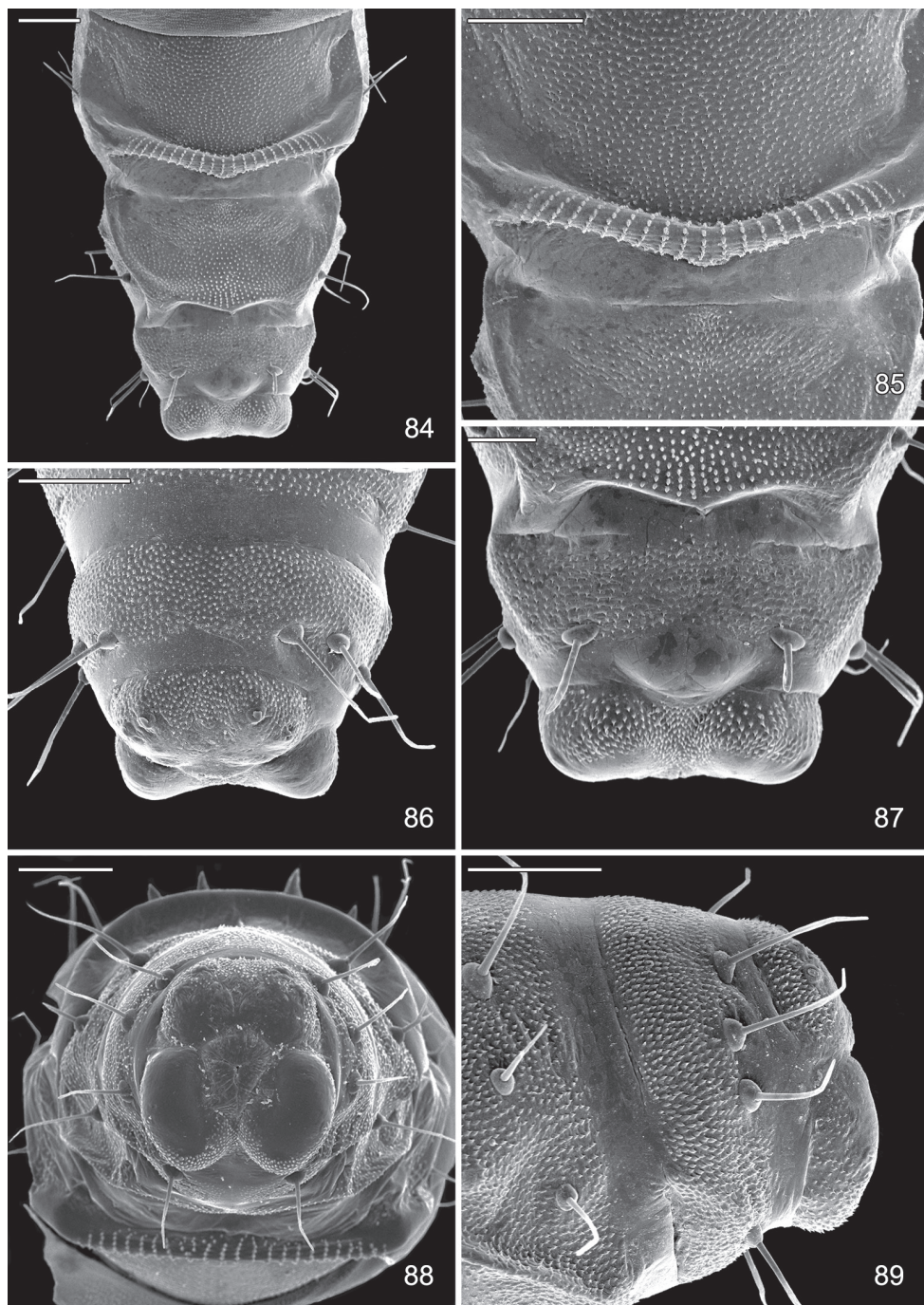
Host. (Table 1). Fabaceae: *Gliricidia sepium* (Jacq.). *Gliricidia sepium* is a small to medium-sized, thornless tree growing to a height of 10–12 meters. It is believed to have originated in Central America and has been introduced into many tropical countries around the world. It can be grown as dense hedges and is frequently used as “living fences”.

Parasitoids. Eulophidae: *Zagrammosoma multilineatum* (Hansson and Cave, 1993).

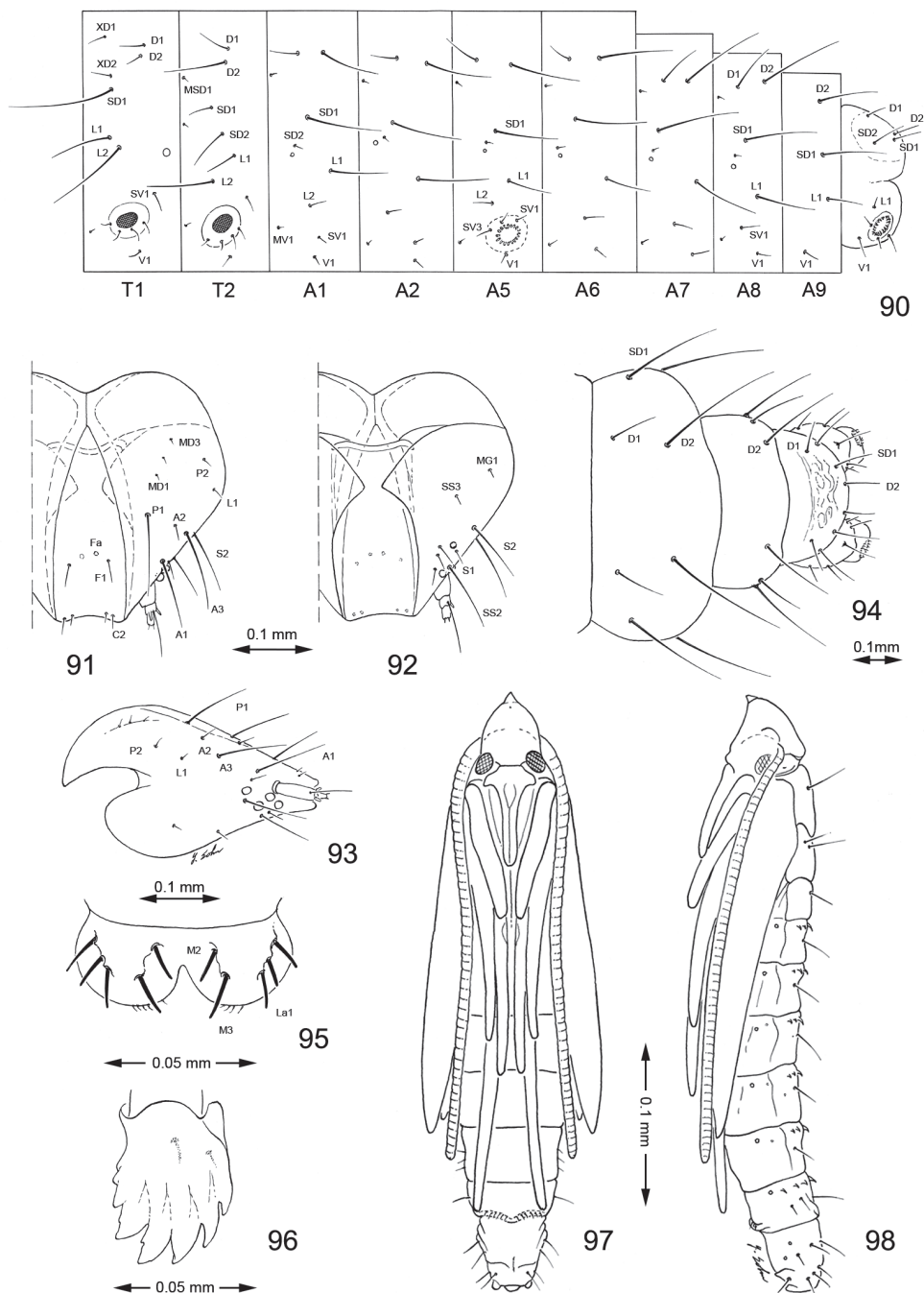
Holotype. ♂: HONDURAS: Dept. Francisco Morazán: Guaimaca, Rio Morazán, 14°32'N, 86°51'W: 26 Jul 1992, em. 5 Aug 1992, R. D. Cave, DRD1165, Host: *Gliricidia sepium*, digital image captured, (USNM).



Figures 78–83. Late tissue feeding instar larva and pupa of *Macrosaccus robiniella*. **78–80** Larva **78** Abdominal segments 9, 10, ventral view **79** Anal proleg **80** Abdominal segments 9, 10, lateral view. **81–83** Pupa **81** Head, ventral view **82** Lateral view **83** Anterior row of dorsal abdominal spines. (Scale lengths in parentheses).



Figures 84–89. Pupa of *Macrosaccus robinella*. **83** Abdominal segments 7, 8, 9+10, ventral view (100 μ m) **85** Detail of accessory cremaster, abdominal sternum 7 (100 μ m) **86** Abdominal segments 8, 9+10, dorsal view (100 μ m) **87** Abdominal segments 8, 9+10, ventral view (50 μ m) **88** Caudal view of abdomen (100 μ m) **89** Abdominal segments 8, 9+10, lateral view (100 μ m). (Scale lengths in parentheses).



Figures 90–98. Late tissue feeding instar larva and pupa of *Macrosaccus robiniella*. **90–96** Larval chaetotaxy. **90** Lateral schematic of prothorax, mesothorax, and abdominal segments 1, 2, 5–10 **91** dorsal view of head **92** Ventral view **93** Lateral view **94** Dorsal view of abdominal segments 8–10 **95** Labrum, dorsal view **96** Mandible. **97–98** Pupa. **97** Ventral view **98** lateral view. (Bar scale for figures as indicated).

Paratypes. HONDURAS: Dept. Francisco Morazán: Guaimaca, Rio Morazán, 14°32'N, 86°51'W: 2 ♂, 4 ♀, 26 Jul 1992, em. 5 Aug 1992, R. D. Cave, DRD1165, Host: *Gliricidia sepium*, slides USNM 34118–34121, BOLD ID RDOPO086-09, GenBank GU669594, BOLD ID RDOPO087-09, GenBank GU669595, (USNM). San Antonio de Oriente, El Zamorano: 1 ♀, 21 Jul 1988, R. Cave, Host: *Gliricidia sepium*, (USNM). Tegucigalpa: Steven Passoa, (USNM). Dept. Olancho: Juticalpa, Sta. Cruz: 2 ♂, 1 ♀, 5 Aug 1988, R. Cave, Host: *Gliricidia sepium*, slides USNM 30888, 30889, 30893, (USNM). FRENCH WEST INDIES: GUADELOUPE: Lamentin, Chaude Ravine: 1 ♂, 10 ♀, 10 May 2004, Jean Etienne, Host: *Gliricidia sepium*, slides USNM 34186, 34187, 34265, DNA/BOLD ID RDOPO366-10, GenBank HM382079, DNA/BOLD ID HM382080, GenBank HM382080, (USNM).

Distribution. Known from Central America (Honduras) and the West Indies (Guadeloupe).

Etymology. The species name is derived from the generic name of its host, *Gliricidia*. The specific epithet is a noun in the nominative singular.

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References

- Antyukhova OV (2007) A review of mining Lepidoptera in the parks of the Pridnestrovje region. [Антохова, О. В. Обзор минеров парковой зоны в Приднестровском регионе]. Вестник Приднестровского университета 2: 62–67.
- Barnes W, McDunnough JH (1917) Check List of the Lepidoptera of Boreal America. Herald Press, Decatur, Illinois, 392 pp.
- Bidzylia OV, Budashkin YI (2004) New records of Lepidoptera from Ukraine. Proceedings of Zoological Museum of Kiev Taras Shevchenko National University 2: 59–68.
- Bolchi Serini G (1990) Parassitoidi di *Parectopa robiniella* Clemens e di *Phyllonorycter robinellus* (Clemens) (Lepidoptera Gracillariidae). Bollettino di Zoologia agrariae Bachicoltura 22: 139–149.

- Bolchi Serini G, Trematerra P (1989) Comparsa del neartico *Phyllonorycter robiniellus* (Clemens) (Lepidoptera Gracillariidae) in Italia. Bollettino di Zoologia agrariae Bachicoltura 21: 193–198.
- Braun AF (1908) Revision of the North American species of the genus *Lithocolletis* Hübner. Transactions of the American Entomological Society 34: 269–357, pls. xx–xxiv.
- Braun AF (1914) Evolution of the color pattern in the microlepidopterous genus *Lithocolletis*. Journal of the Academy of Natural Sciences, Philadelphia 16: 103–168, pls. iii–iv.
- Braun AF (1925) Microlepidoptera of Northern Utah. Transactions of the American Entomological Society 51: 183–226.
- Buhl P, Falck P, Jorgensen B, Karsholt O, Larsen K, Vilhelmsen F (2005) Records of Microlepidoptera from Denmark in 2004 (Lepidoptera). Entomologiske Meddelelser 73: 73–86.
- Busck A (1903) Notes on Brackenridge Clemens' types of Tineina. Proceedings of the Entomological Society of Washington 5: 181–220.
- Busck A (1909) Notes on Microlepidoptera, with descriptions of new North American species. Proceedings of the Entomological Society of Washington 11: 87–103.
- Buszko J (1996) Gracillariidae. In: Karsholt O, Razowski J (Eds) The Lepidoptera of Europe. A Distributional Checklist. Apollo Books, Stenstrup, 48–54.
- Buszko J, Nowacki J (2000) The Lepidoptera of Poland. A Distributional Checklist. Polish Entomological Monographs Vol. 1. Polskie towarzystwo entomologiczne, Poznan, Toruń, 178 pp.
- Chambers VT (1871) Micro-Lepidoptera. Canadian Entomologist 3: 54–58, 84–88, 108–112, 127–130, 146–149, 161–166, 182–185, 205–209, 221–224. doi:10.4039/Ent354-3
- Chambers VT (1872) Micro-Lepidoptera. Canadian Entomologist 4: 7–12, 25–29, 41–44, 65–69, 88–92, 106–108. doi:10.4039/Ent47-1
- Chambers VT (1875) Tineina of the United States. Cincinnati Quarterly Journal of Science 2: 226–259.
- Chambers VT (1877) Art. VI. The Tineina of Colorado. Bulletin of the United States Geological Survey 3: 121–145.
- Chambers VT (1878) Art. IV. Tineina and their foodplants. Bulletin of the United States Geological and Geographical Survey of the Territories 4: 107–124.
- Chapman TA (1902) The classification of *Gracilaria* [sic] and allied genera. Entomologist, an Illustrated Journal of British Entomology 35: 81–88, 138–142, 159–164.
- Clemens B (1859) Contribution to American Lepidopterology. No. 2, Proceedings of the Academy of Natural Sciences of Philadelphia [1859]: 317–328.
- Clemens B (1872) Micro-Lepidopterous Larvae. In: Stainton HT (Ed) The Tineina of North America. John van Voorst, London, 161–178.
- Csóka G, Péntes Z, Hirka A, Mikó I, Matosevic D, George D (2009) Parasitoid assemblages of two invading black locust leaf miners, *Phyllonorycter robiniella* and *Parectopa robiniella* in Hungary. Periodicum biologorum 111: 405–411.
- Davis DR (1983) Gracillariidae. In: Hodges RW, Dominick T, Davis DR, Ferguson DC, Franclemont JG, Munroe EG, Powell JA (Eds) Check List of the Lepidoptera of North America North of Mexico. E.W. Classey Ltd. and the Wedge Entomological Research Foundation, London, 9–11.

- Davis DR (1987) The Gracillariidae, blotch leaf miners. In: Stehr FW (Ed) Immature Insects. Kendall / Hunt Publishing Company, Dubuque, Iowa, 372–376.
- Davis DR, Deschka G (2001) Biology and systematics of the North American *Phyllonorycter* leafminers on Salicaceae, with a synoptic catalogue of the Palearctic species (Lepidoptera: Gracillariidae). Smithsonian Contribution to Zoology 614: 1–89, Figs 1–451, 6 maps, 5 tables.
- Davis DR, Robinson GS (1998) The Tineoidea and Gracillarioidea. In: Kristensen NP (Ed) Lepidoptera, moths and butterflies. Volume 1: Evolution, systematics, and biogeography. Handbook of Zoology IV (35). Walter de Gruyter, Berlin, New York, 91–117.
- Deschka G (1993) Die Miniermotte *Cameraria ohridella* Deschka & Dimic eine Gefahr für die Roßkastanie *Aesculus hippocastanum* L. (Insecta, Lepidoptera, Lithocolletidae). Linzer biologische Beiträge 25: 141–148.
- De Prins J, De Prins W (2011) Global Taxonomic Database of Gracillariidae (Lepidoptera). <http://www.gracillariidae.net> [accessed 11 March 2011]
- De Prins J, Mozūraitis R, Lopez-Vaamonde C, Rougerie R (2009) Sex attractant, distribution and DNA barcodes for the Afrotropical leaf-mining moth *Phyllonorycter melanosparta* (Lepidoptera: Gracillariidae). Zootaxa 2281: 53–67.
- De Prins W, De Prins J (2005) Gracillariidae (Lepidoptera). In: Landry B (Ed) World Catalogue of Insects, vol. 6. Apollo Books, Stenstrup, 1–502.
- De Prins W, Groenen F (2001) *Phyllonorycter robiniella*, een nieuwe soort voor de Belgische fauna (Lepidoptera: Gracillariidae). Phegea 29: 159–160.
- Dimić N, Graora D, Magud B, Perić P (1999) Opet jedna nova vrsta minera lista u entomofauni Jugoslavije. Biljni lecar, Novi Sad 27: 34–37.
- Dimić N, Dautbasić M, Magud B (2000) *Phyllonorycter robiniella* Clemens, nowa vrsta minera lista u entomofauni Bosne i Hercegovine. Works of the Faculty of Forestry of the University of Sarajevo 1: 7–15.
- Dyar HG (1903) A list of North American Lepidoptera. United States National Museum Bulletin 52 (1902): xix + 723.
- Ely CR (1918) A revision of the North American Gracillariidae [sic] from the standpoint of venation. Proceedings of the Entomological Society of Washington 19: 29–77.
- Fitch A (1859) Report on the noxious, beneficial and other insects of the state of New York. Fifth report. Transactions of the New York State Agricultural Society 18 (1858): 781–854, 9 Figs Also published separately with different pagination (p. 1–74) and with an index to parts 3–5, New York.
- Fologne E (1962) Notes d'une excursion à Fonduleffe, près de Dinant. Annales de la Société entomologique belge 6: 23–25.
- Forbes WTM (1923) The Lepidoptera of New York and neighboring states, Part 1, Primitive forms, Microlepidoptera, Pyraloids, Bombyces. Cornell University Agriculture Experiment Station. Memoir 68: 1–729.
- Frey H, Boll J (1878) Tineen aus Texas. Entomologische Zeitung, Stettin, 39: 249–279.
- Gibogini B, Alma A, Arzone A (1996) Ricerche bio-etologiche su Imenotteri della biocenosi di *Phyllonorycter robiniellus* (Clemens) (Lepidoptera Gracillariidae). Bollettino di Zoologia agrariae Bachicoltura 28: 13–22.

- Girardoz S, Volter L, Tomov R, Quicke DLJ, Kenis M (2007) Variations in parasitism in sympatric populations of three invasive leaf miners. *Journal of Applied Entomology* 131: 603–612. doi:10.1111/j.1439-0418.2007.01146.x
- Hajibabaei M, Janzen DH, Burns JM, Hallwachs W, Hebert PDN (2006) DNA Barcodes distinguish species of tropical Lepidoptera. *Proceedings of the National Academy of Sciences of the United States of America* 103: 968–971. doi:10.1073/pnas.0510466103
- Hansson C, Cave RD (1993) First record of *Kratoysma* (Hymenoptera: Eulophidae) from the New World, including the description of two new species. *Proceedings of the Entomological Society of Washington* 95: 253–257.
- Hansson C, Shevtsova E (2010) Three new species of *Achrysocharoides* Girault (Hymenoptera: Eulophidae) parasitoids of *Phyllonorycter* spp. (Lepidoptera: Gracillariidae) on *Acer platanoides* and *Robinia pseudoacacia*. *Zootaxa* 2388: 23–43.
- Herbert PDN, Penton EH, Burns JM, Janzen DH, Hallwachs, H (2004) Ten species in one: DNA Barcoding reveals cryptic species in the Neotropical skipper butterfly *Astrartes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America*. 101: 14812–14817. doi:10.1073/pnas.0406166101
- Hering M (1927) Die Minenfauna der Canarischen Inseln. *Zoologische Jahrbücher, Abteilung für allgemeine Zoologie und Physiologie* 53: 405–486.
- Hoare RJB (2000) A new genus of primitive Nepticulidae (Lepidoptera) from eastern Australia, with a revised diagnosis of nepticulid subfamilies. *Zoological Journal of the Linnean Society* 128: 289–317. doi:10.1111/j.1096-3642.2000.tb00165.x
- Huemer P, Deutsch H, Habeler H, Lichtenberger F (1992) Neue und bemerkenswerte Funde von Kleinschmetterlingen in Österreich. *Bericht des naturwissenschaftlich-medizinischen Vereins in Innsbruck* 79: 199–202.
- ICZN International Commission on Zoological Nomenclature (1999) International code of zoological nomenclature. Fourth Edition. London: The International Trust for Zoological Nomenclature., c/o The Natural History Museum, London, UK, xxix+306 pp.
- Kasch K, Nicolai V (2002) *Phyllonorycter robiniella* (Clemens) (Lepidoptera, Gracillariidae) – ein nordamerikanischer Schmetterling neu in Berlin. In: Kowarik I, Starfinger U (Hrsg.): *Biologische Invasionen. Herausforderung zum Handeln?* Neobiota 1: 193–202.
- Kawahara AY (2010) Phylogenomics. Life-history, evolution and taxonomy of leaf mining moths (Lepidoptera: Gracillarioidea). Ph.D. Dissertation. University of Maryland, College Park, 170 pp.
- Klots AB (1970) Lepidoptera. In: Tuxen SL (Ed) *Taxonomist's glossary of genitalia in insects*. Munksgaard, Copenhagen, 115–130.
- Kristensen NP (2003) Skeleton and muscles: adults. In: Kristensen NP (Ed) *Lepidoptera, moths and butterflies. Volume 2: Evolution, systematics, and biogeography. Handbook of Zoology IV* (35). Walter de Gruyter, Berlin, New York, 39–131.
- Kuchlein JH, Kuchlein-Nijsten C, De Prins W (2002) *Phyllonorycter medicaginella*, nieuw voor de Belgische fauna (Lepidoptera: Gracillariidae). *Phegea* 30: 89–94.
- Kumata T (1961) Descriptions of a new genus and a new species of Gracillariidae from Japan (Lepidoptera). *Insecta Matsumurana* 24: 52–56.

- Kumata T (1963) Taxonomic studies on the Lithocolletinae of Japan (Lepidoptera: Gracillariidae) Part I. *Insecta Matsumurana* 25: 53–90.
- Kumata T (1993) A contribution to the knowledge of the Malaysian Lithocolletinae (Gracillariidae, Lepidoptera), with a revision of Indian *Cameraria* associated with Leguminosae. *Insecta Matsumurana*, N.S. 48: 1–85.
- Kumata T (1995) Some species of the subfamily Lithocolletinae (Gracillariidae, Lepidoptera) collected in the Philippines. *Insecta Matsumurana*, N.S. 52: 105–131.
- Kuznetsov VI (1981) Fam. Gracillariidae (Lithocolletiidae) – leaf blotch miners. In: Medvedev GS (Ed) A guide to the insects of the European part of the USSR. Lepidoptera. Vol. 4. Lepidoptera. Part 2. Nauka, Leningrad, 149–311.
- Kuznetsov VI, Baryshnikova SV (2001) Review of Palearctic genera of the gracillariid moths (Lepidoptera, Gracillariidae), with description of a new subfamily Ornixolinae Kuznetsov et Baryshnikova, subfam. n. *Entomologicheskoe Obozrenie* 80: 96–120.
- Kuznetsov VI, Stekol'nikov AA (1987) Functional morphology of the male genitalia and notes on the classification and phylogenetic relationships of mining moths of superfamily Gracillarioidea (Lepidoptera). *Entomologicheskoe Obozrenie* 66: 52–65.
- Kuznetsov VI, Stekol'nikov AA (2001) New approaches to the system of Lepidoptera of world fauna. Nauka, St. Petersburg, 462 pp.
- Laštůvka Z (1993) Katalog von Faltern der Mährisch-Schlesischen Region (Lepidoptera). Landwirtschaftliche und Orstliche Universität, Brno, 130 pp.
- Leraut P (1997) Liste systématique et synonymique des lépidoptères de France, Belgique et Corse (deuxième édition). *Alexanor Supplement*: 1–526.
- Liblikas I, Mozūraitis R, Santangelo EM, Noreika R, Borg-Karlson A-K (2009) Syntheses, characterizations, and biological activities of tetradeca-4,8-dien-1-yl acetates as sex attractants of leaf-mining moth of the genus *Phyllonorycter* (Lepidoptera: Gracillariidae). *Chemistry & Biodiversity* 6: 1388–1403. doi:10.1002/cbdv.200800210
- Lopez-Vaamonde C, Agassiz D, Augustin S, De Prins J, De Prins W, Gomboc S, Ivinskis P, Karsholt O, Koutroumpas A, Koutroumpa F, Laštůvka Z, Marabuto E, Olivella E, Przybyłowicz L, Roques A, Ryrholm N, Šefrová H, Šima P, Sims I, Sinev S, Skulev B, Tomov R, Zilli A, Lees D (2010) Lepidoptera. In: Roques A, Kenis M, Lees D, Lopez-Vaamonde C, Rabitsch W, Rasplus J-Y, Roy DB (Eds) Alien terrestrial arthropods of Europe. *BioRisk* 4: 603–668.
- Maier CT (1988) Gracillariid hosts of *Sympiesis marylandensis* (Hymenoptera: Eulophidae) in New England. *Annals of the Entomological Society of America* 81: 728–732.
- Maier CT, Davis DR (1989) Southern New England host and distributional records of Lithocolletine Gracillariidae (Lepidoptera) with comparison of host specificity in temperate regions. *Entomological Society of America, Miscellaneous Publications*, No. 70: 1–23.
- McDunnough JH (1939) Check List of the Lepidoptera of Canada and the United States of America. Part II. Microlepidoptera. *Memoirs of the Southern California Academy of Sciences* 2: 1–171.
- Meyrick E (1912a) Lepidoptera Heterocera (Tineae). Fam. Gracillariidae [sic]. In: Wytzman P (Ed) *Genera Insectorum*. Fascicule 128. V. Verteneuil & L. Desmet, Imprimeurs-Éditeurs, 1–36.

- Meyrick E (1912b) Adelidae, Micropterigidae, Gracilariidae [sic]. In: Wagner H (Ed) *Lepidopterorum Catalogus*, Pars 6, W. Junk, Berlin, 25–68.
- Navone P (2003) Reperimento in Italia di una specie nearctica del genere *Achrysocharoides* (Hymenoptera Eulophidae), parassitoide di *Phyllonorycter robiniella* (Clemens). *Bollettino di Zoologia agraria e Bachicoltura* 35: 79–82.
- Needham JG, Frost SW, Tothill BH (1928) *Leaf-mining Insects*. The Williams and Wilkins Co., Baltimore, viii+351 pp.
- Nețoiu C (2003) O nouă molie minieră la salcâmul din România- *Phyllonorycter robiniella* Clemens 1859 (Lepidoptera: Gracillariidae). *Muzeul Olteniei Craiova, Studii și comunicări, Științele Naturii* 19: 154–156.
- Nicolai V (2005) The invasive leaf miner *Phyllonorycter robiniella* feeding on black locust, *Robinia pseudoacacia*, in Central Europe (Lepidoptera: Gracillariidae). *Entomologia Generalis* 28: 193–200.
- Noreika R (2008) *Phyllonorycter robiniella* (Clemens, 1859) (Lepidoptera: Gracillariidae) – a new species for the Lithuanian fauna. *Naujos ir retos Lietuvos vabzdžių rūšys* 19 (2007): 35–38.
- Noyes JS (2010) *Universal Chalcidoidea Database*, The Natural History Museum, London. <http://www.nhm.ac.uk/research-curation/research/projects/chalcidoids> [accessed 27 December 2010]
- Olivella E (2002) *Phyllonorycter robiniella* (Clemens, 1859) arriba a la península Ibèrica (Lepidoptera: Gracillariidae). *Butlletí de la Societat catalana de Lepidopterologia* 87 (2001): 35–38.
- Opler PA, Davis DR (1981) The leafmining moths of the genus *Cameraria* associated with Fagaceae in California (Lepidoptera: Gracillariidae). *Smithsonian Contributions to Zoology* 333: i–iii, 1–58.
- Packard AS (1890) *Insects injurious to forest and shade trees*. Fifth Report of the U.S. Entomological Commission. House of Representatives Miscellaneous Document 269: 361–373.
- Peck O (1985) The taxonomy of the Nearctic species of *Pediobius* (Hymenoptera: Eulophidae), especially Canadian and Alaskan forms. *Canadian Entomologist* 117: 647–704. doi:10.4039/Ent117647-6
- Powell JA, Opler PA (2009) *Moths of Western North America*. University of California Press, Berkeley, Los Angeles, London, xiii+369 pp.
- Ratnasingham S, Hebert PD (2007) Bold: The Barcode of Life Data System. *Molecular Ecology Notes* 7: 355–364. <http://www.barcodinglife.org>. doi:10.1111/j.1471-8286.2007.01678.x
- Riley CV (1891) Tineina. In: Smith JB. *List of the Lepidoptera of Boreal America*. American Entomological Society, Philadelphia, 94–114.
- Robinson GS (1976) The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. *Entomologist's Gazette* 27: 127–132.
- Robinson GS, Ackery PR, Kitching IJ, Beccaloni GW, Hernández LM (2002) Hostplants of the moth and butterfly caterpillars of America North of Mexico. *Memoirs of the American Entomological Institute* 69: 1–824.
- Robinson GS, Ackery PR, Kitching IJ, Beccaloni GW, Hernández LM (2007) HOSTS – a Database of the World's Lepidopteran Hostplants. <http://www.nhm.ac.uk/research-curation/research/projects/hostplants> [accessed 31 May 2010]

- Šefrová H (2002) *Phyllonorycter robiniella* (Clemens, 1859) – egg, larva, bionomics and its spread in Europe (Lepidoptera, Gracillariidae). Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis 50: 7–12.
- Seljak G (1995) *Phyllonorycter robiniella* (Clemens), še en nov listni zavrtac robinije v Sloveniji. Gozdarski vestnik 53: 78–82.
- Stone KR (2009) *Robinia pseudoacacia*. In: Fire effects information system. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Services Laboratory. <http://www.fs.fed.us/database/feis/>
- Szabóky C, Csóka G (1997) A *Phyllonorycter robiniella* Clemens 1859 akáclevél aknázómoly megtelepedése Magyarországon. Növényvédelem 33: 569–571.
- Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA 4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Molecular Biology and Evolution 24: 1596–1599. <http://www.kumarlab.net/publications>. doi:10.1093/molbev/msm092
- Tomov R (2003) *Phyllonorycter robiniella* (Clemens, 1859) (Lepidoptera, Gracillariidae), a new pest on black locust *Robinia pseudoacacia* L. in Bulgaria. Proceedings, scientific papers. The 50th anniversary of University of Forestry Sofia, 105–107.
- Vári L (1961) South African Lepidoptera. Vol. I. Lithocolletidae. Transvaal Museum Memoir 12: xix+238 pp., 112 pls.
- Walsingham Lord (de Grey T) (1889). Steps toward a revision of Chambers' Index, with notes and descriptions of new species (cont.). Insect Life 2: 23–26, 51–54, 77–81, 116–120.
- Walsingham Lord (de Grey T) (1908) Microlepidoptera of Tenerife. Proceedings of the Zoological Society of London (1907): 911–1034, pls. 51–53.
- Watkinson IA (1985) Gracillariidae. Lithocolletinae. In: Heath J, Emmet AM (Eds) The moths and butterflies of Great Britain and Ireland. Volume 2. Cossidae-Heliodinidae. Harley Books, Colchester, Essex, 294–362.
- Weaver JE, Dorsey CK (1965) Parasites and predators associated with five species of leaf-mining insects in black locust. Annals of the Entomological Society of America 58: 933–934.
- Weaver JE, Dorsey CK (1967) Larval mine characteristics of five species of leaf-mining insects in black locust, *Robinia pseudoacacia*. Annals of the Entomological Society of America 60: 172–186.
- Whitebread SE (1990) *Phyllonorycter robiniella* (Clemens, 1859) in Europe (Lepidoptera, Gracillariidae). Nota lepidopterologica 12 (1989): 344–353.
- Whitebread SE, Joos R (1986) Nachtfalter und Kleinschmetterlinge. In: Blattner M, Ritter M, Ewald KC (Eds) Basler Natur-Atlas I. Basler Naturschutz, Basle, 116–121.
- Zeller PC (1875) Beiträge zur Kenntniss der nordamericanischen Nachtfalter, besonders der Microlepidopteren. Dritte Abheilung. Verhandlungen der zoologisch-botanischen Gesellschaft in Wien 25: 205–360, pls. 8–10.
- Zhu C-D, Huang D-W (2001) A Study of Chinese *Elachertus spinola* (Hymenoptera: Eulophidae). Zoological Studies 40: 317–354.