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Mr. Darwin's mysterious spider: on the type species of the genus *Leucauge* White, 1841 (Tetragnathidae, Araneae)

DIMITAR DIMITROV[1,3] & GUSTAVO HORMIGA[2]

[1]*Postdoctoral Fellow, Department of Biological Sciences, The George Washington University, Washington, D.C. 20052, USA*
[2]*Ruth Weintraub Professor of Biology, Department of Biological Sciences, The George Washington University, Washington, D.C. 20052, USA. E-mail: hormiga@gwu.edu*
[3]*current address: Zoological Museum, University of Copenhagen, Department of Entomology, Universitetsparken 15, DK-2100, Copenhagen, Denmark. E-mail: dimitard.gwu@gmail.com*

Abstract

For more than a century and a half the identity of *Linyphia* (*Leucauge) argyrobapta* White, 1841, the type species of the spider genus *Leucauge*, has been a mystery and an obstacle for revisionary work on this orb weaving genus. The only known specimen of *argyrobapta*, the type, was collected by Charles Darwin in Rio de Janeiro during the voyage of the H.M.S. Beagle and was lost after White's description was published. We designate a neotype for *Linyphia argyrobapta* (White, 1841) based on specimens collected in the type locality. The common and widespread American species *Leucauge venusta* (Walckenaer, 1841) is a senior synonym of *L. argyrobapta*.

Key words: Taxonomy, systematics, orb weavers, morphology, spider webs

Introduction

In May 1832, during the voyage of the H.M.S. Beagle, Charles Darwin collected near Rio de Janeiro (Brazil) an orb weaving spider with a brilliantly colored oblong abdomen. His detailed field notes on the specimen include a description of the web architecture and conclude with a remark about an abdominal red mark that was "like a ruby with a bright light behind." He thought that this orb weaving species was "closely allied to *Epeira*" and proposed for it the new name *Leucauge*. Darwin's specimen, a female, was studied by White (1841) who formally described it as *Linyphia (Leucauge) argyrobapta* White, 1841. Adam White's description, based on the single specimen available, lacked illustrations and has proved insufficient to ascertain the identity of *L. argyrobapta* (e.g., Cambridge, 1903; Levi, 1980). Furthermore, the type specimen is lost (Levi, 1980) and this has been confirmed during the course of our study by the curators of the Natural History Museum (London) and the Oxford University Museum of Natural History (Oxford). With 185 described species, *Leucauge* White, 1841 is one of the most species rich araneoid spider genera (Platnick, 2009). The genus is most diverse in the tropics but several species live in temperate zones in the southern and the northern hemisphere. There are no *Leucauge* species known from Europe, Northern Asia or North Africa. Many *Leucauge* species have bright coloration with shiny abdominal guanine patches. They spin horizontal to vertical orb webs which are built every morning (Eberhard, 1988). If the web is damaged during the day it is repaired or completely replaced. Their webs are often built in open sunny spots, such as patches of secondary growth along roads and forest gaps, and gardens and orchards. Some species prefer habitats along the shores of fresh water bodies while other species are found in pristine primary forests. Some *Leucauge* species are so common and well known, even to non-specialists, that they have been granted common names such as the "orchard spider" [*Leucauge venusta* (Walckenaer, 1841)]. Numerous studies have been published on a diversity of aspects of the biology of a few *Leucauge* species, to the extent that these spiders can be referred as model organisms for spider biology (e.g., Bishop and Connolly, 1992; Buckles, 1999; Craig and Freeman,

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1991; Eberhard, 1987, 1988; Eberhard and Huber, 1998; Hénaut *et al.*, 2001, 2006; Kato *et al.*, 2008; Moya-Laraño *et al.* 2007, 2009; Opell, 1997; Opell *et al.*, 2006; Tso *et al.*, 2006, 2007; Yoshida, 2000; Zschokke *et al.* 2006). Despite the high number of species and their importance as model organisms, the systematics and phylogenetic relationships of *Leucauge* species are very poorly understood, including the alpha-taxonomy of the group. In fact, it is neither rare nor surprising to see studies on various biological aspects of *Leucauge* species in which the study subjects are only identified to the genus, and not to the species (e.g., Craig and Freeman, 1991; Baldissera *et al.* 2004; Grostal and Walter, 1999; Hoffmaster, 1985; Schoener and Spiller, 2006; Takada *et al.* 2008).

Although the genus *Leucauge* has never been the subject of a taxonomic revision, new species continue to be described outside a revisionary context (e.g., Zhu *et al.*, 2003), often based only on one sex. At present 115 *Leucauge* species (62%) are known from just one sex or even juveniles (Platnick, 2009) and often from just a single or a very few specimens. Furthermore, an extraordinarily high number of new species remain to be described (F. Álvarez-Padilla, pers. comm., Hormiga and Dimitrov, unpublished). Along with the high number of species, revisionary work in *Leucauge* has been difficult due to the loss of the only known specimen of the type species, *L. argyrobapta*. In order to facilitate future monographic work we designate a neotype and re-describe the type species of *Leucauge* based on newly collected specimens in and around the type locality of *L. argyrobapta*. It seems particularly fit and timely, that in celebrating the bicentennial anniversary of Darwin's birth and the publication of *On the origin of species* one century and a half ago, we clarify the nature of "the only spider name which can be attributed to Charles Darwin" (Cameron, 2005:302).

Material and methods

All specimens for this study were collected in various localities in Rio de Janeiro by Abel Pérez-González, Adriano B. Kury and Thiago S. Moreira accompanied by the two authors in 2007. The morphological methods follow those previously described in Dimitrov and Hormiga (2009) and Hormiga (2002). Specimens were examined and illustrated using Leica MZ16 or Leica MZ16A stereo microscopes with a camera lucida and a Leica DMRM compound microscope with a drawing tube. Drawings were prepared with graphite pencils on acid-free cotton paper. Hairs and macrosetae are not depicted in the final drawings. For male palp illustrations the left palp was used. Epigyna were treated with SIGMA Pancreatin LP 1750 enzyme complex (Álvarez-Padilla and Hormiga, 2008) and transferred to methyl salicylate solution for examination and illustration. Digital images of the specimens in alcohol were taken with a Leica DC500 digital camera mounted on a Leica MZ16A stereoscopic microscope. Scanning electron microscope (SEM) observations and photographs were done in a LEO 1430VP scanning electron microscope. For SEM study abdomen, legs, cephalothorax and left male palp were dissected, cleaned ultrasonically and dehydrated in 100% ethanol (for 24 hours). Preparations were critically point dried, mounted as described in Álvarez-Padilla and Hormiga (2008) and Au-Pd coated for observation. The female internal genitalia and the tracheal system were cleaned by digestion (no ultrasonic cleaning was carried out for these digested preparations). Pencil drawings were scanned and edited using Gimp 2.6.4 and Adobe Photoshop CS2. Final plate layout and editing was done with Adobe Illustrator CS2. All measurements are in millimeters.

Abbreviations Used in Text and Figures

AC	aciniform gland spigots
AG	aggregate gland spigots
ALE	anterior lateral eyes
ALS	anterior lateral spinnerets
BH	basal hematodocha
C	conductor
CB	cymbium

CD	copulatory duct
CY	cylindrical gland spigots
E	embolus
F	fundus
FD	fertilization duct
FL	flagelliform spigot
M	membrane
MAP	major ampullate gland spigot
mAP	minor ampullate gland spigot
P	paracymbium
PI	piriform gland spigots
PLE	posterior lateral eyes
PLS	posterior lateral spinnerets
PME	posterior median eyes
PMS	posterior median spinnerets
S	spermatheca
ST	subtegulum
T	tegulum

Museum Collections

MNRJ Museu Nacional do Rio de Janeiro, Brazil.

Comments. In May 1832, during his stay in Rio de Janeiro, Darwin collected the specimen that was later studied and described by Adam White. Most likely the specimen was collected in or near the Tijuca area. The original Tijuca forest was greatly altered to plant coffee but in the second half of the 19th century this area was reforested as part of a program to protect Rio de Janeiro's water supply. Similar habitats are also found in various patches of Atlantic forest in and around Rio's urban area such as the park surrounding the Pão de Açúcar and Morro da Urca, and the Rio de Janeiro Botanical Garden. Access to the Tijuca forest is nowadays restricted because of its status as a National Park. Poor neighborhoods suffering high rates of endemic crime (favelas) surround the park and pose an additional obstacle to fieldwork in the area. However, Tijuca and other remnants of Atlantic forest in the Rio area are just a few kilometers apart and share very similar climatic conditions and vegetation. Furthermore, since the Tijuca forest has undergone a process of deforestation and subsequent reforestation after Darwin visited the area, potential differences with similar nearby habitats are even less significant. Therefore we focused our search for specimens matching the original description of *L. argyrobapta* on areas in Rio de Janeiro near Tijuca but with easier access. We also examined specimens from Tijuca and nearby areas deposited at the Museu Nacional do Rio de Janeiro.

We examined all specimens of *Leucauge* housed in the Museu Nacional collection. Once sorted to morphospecies, these *Leucauge* specimens were compared to the description of *L. argyrobapta*. Although White's (1841) publication is not illustrated, it provides a fairly detailed description of the somatic morphology of the type specimen. Additionally, the notes that Darwin took in the field (see Keynes, 2000) give very detailed description of the web and of the coloration of the live specimen. Based on these descriptions we were able to select specimens that match Darwin and White's description of *Leucauge argyrobapta*. The description of the live spider was of upmost importance for matching the specimens in the field, particularly the red marks on the abdomen. Of all morphospecies collected in the area just one had coloration which matched Darwin' and White's descriptions (Fig. 1A–G). Close examination of these specimens matching the description of *L. argyrobapta* showed that they are conspecific with the widespread and common species *L. venusta*. We document in this paper that *L. venusta* is a senior synonym of *L. argyrobapta*.

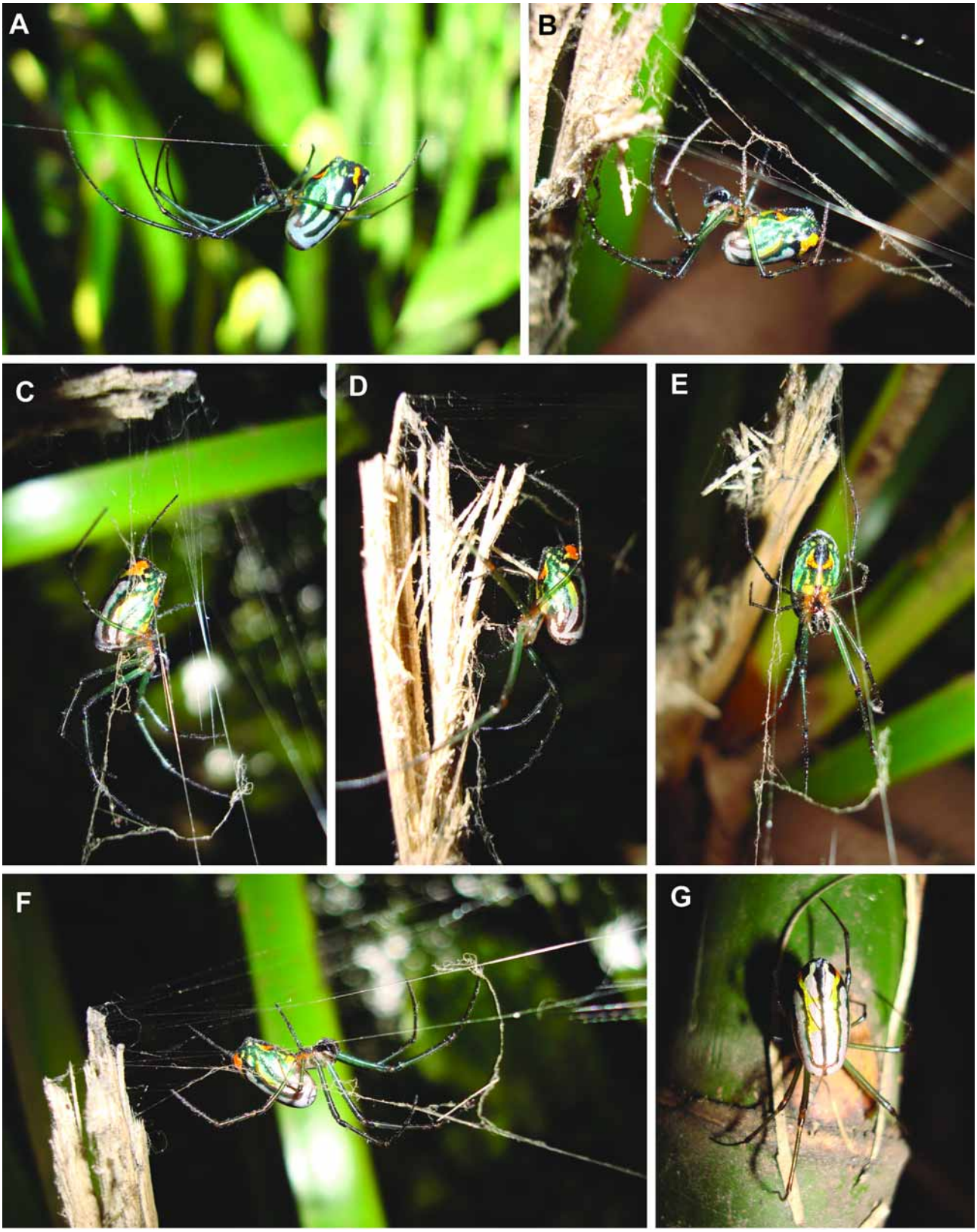

FIGURE 1. *Leucauge venusta* live female from Rio de Janeiro (Brazil): lateral A–D, F; ventral E; dorsal G.

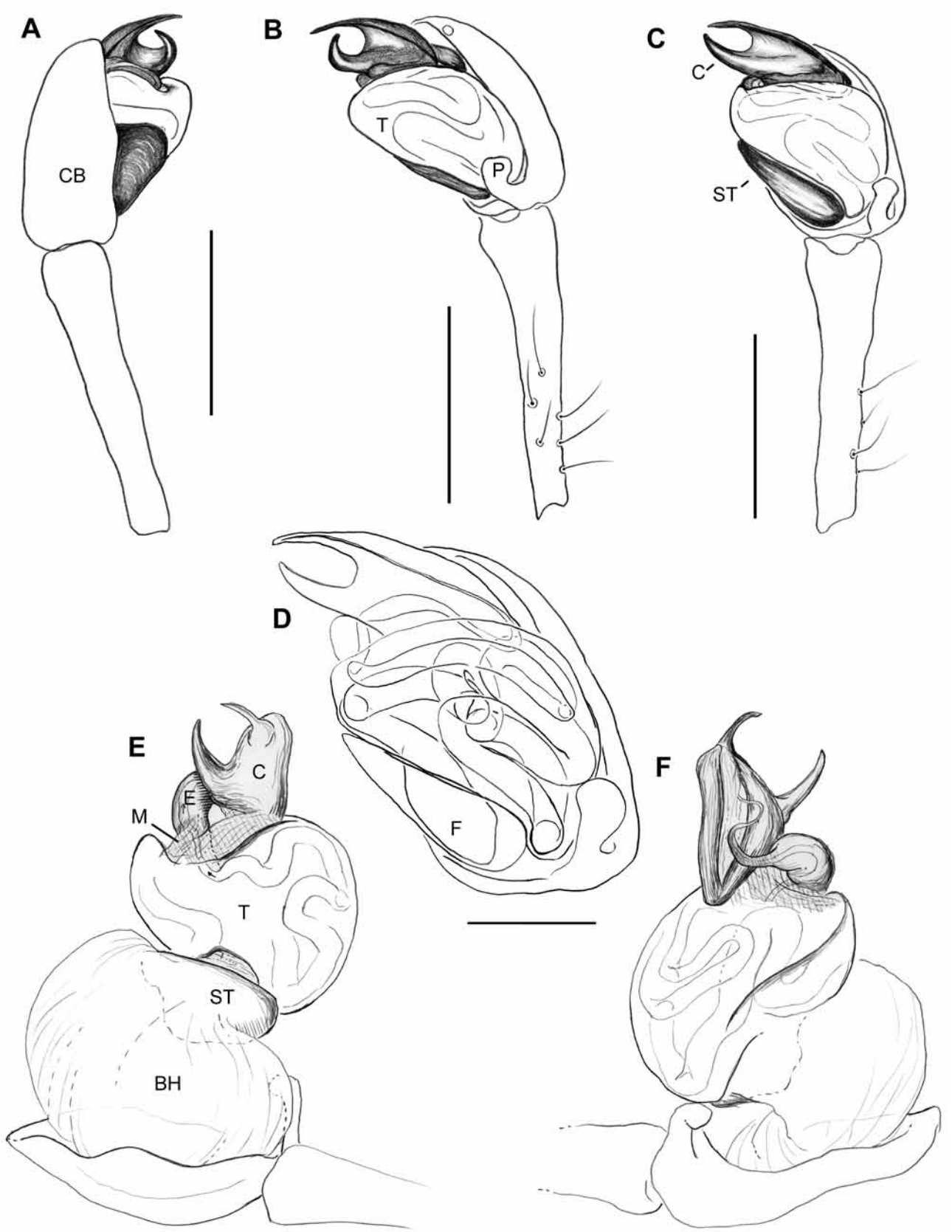

FIGURE 2. *Leucauge venusta* male (from Rio de Janeiro), palp: prolateral A; retrolateral B; ventral C; sperm duct path D; artificially expanded palp prolateral E; expanded palp retrolateral F. Scale bars: A–C 0.5 mm, D 0.2 mm.

Taxonomy

Family Tetragnathidae Menge, 1866

Genus *Leucauge* White, 1841

Type species (by monotypy) *Linyphia (Leucauge) argyrobapta* White, 1841, a junior synonym of *Epeira venusta* Walckenaer, 1841

In his field notes Darwin suggested the new genus name *Leucauge* for *argyrobapta* (see Keynes, 2000), but nevertheless White (1841) described *argyrobapta* as a species of *Linyphia* and treated *Leucauge* as a subgenus, not as a new genus. This should be hardly surprising given that in his paper White (1841: 471) explicitly expressed reluctance to erect new genera:

> *"I describe them without any systematic order, but having necessarily numbered each species, intend afterwards giving a classified index: the descriptions are in many instances prolix, and I have in most cases given the* generic *character of each species. I have done this because, at present, I am unwilling to propose new names if I can possibly refer the species I describe to any of ties established genera."*

There is no hint in Darwin's field book suggesting that *argyrobapta* had close affinities with *Linyphia*. In fact, Darwin's entry (page 38 of this particular field book, as transcribed in Keynes, 2000) starts with the following text: "Spider, orbilates [orbitéles]; closely allied to Epeira (Leucauge. *[illeg.]*)". Thus the generic placement in *Linyphia* must be entirely attributed to White. Although Waterhouse's (1902:198) *Index Zoologicus* provides the first use of *Leucauge* as a genus name, the first arachnologists to use Darwin's name at the genus rank were F. O. P.-Cambridge (1902a, 1903) and E. Simon (1903). In one of his papers on the type species of the genera of Araneae, Cambridge (1902b: 16) explicitly discusses the rank of *Leucauge* and quite openly expresses his dislike for Darwin's new name:

> *"No one that has ever been in a tropical Brazilian forest will hesitate one moment in recognizing this as a species of the* Argyroepeira *group of Emerton.*
> *One feels sorry at the necessity of sacrificing so beautiful a name for the ugly one* Leucauge *proposed by Darwin, but priority lies with the latter."*

Cameron (2005:302) deciphered the etymology of *Leucauge* (which means "with a bright gleam", in reference to the characteristic silvery guanine abdominal marks) and pointed out how Bonnet (1957) also grumbled about the replacement of the more recent genus name *Argyroepeira* Emerton, 1884 by the older one *Leucauge* after having been forgotten for sixty years. We join Professor Cameron (2005:302) in rejoicing the preservation of "the only spider name which can be attributed to Charles Darwin."

Leucauge venusta (Walckenaer, 1841)

Figures 1–12

Epeira venusta Walckenaer, 1841: 90 (see comments below about types).
Linyphia (Leucauge) argyrobapta White, 1841*:* 473. Type lost (Levi, 1980:23), Male neotype designated herein, deposited in MNRJ col. number MNRJ 9038 (see comments below about types), from Rio de Janeiro, Brazil. NEW SYNONYMY.
Epeira hortorum Hentz, 1847: 477.
Tetragnatha 5-lineata Keyserling, 1864: 145.
Argyroepeira hortorum Emerton, 1884: 332; Keyserling, 1893: 333; Emerton, 1902: 192.
Argyroepeira venusta McCook, 1894: 242.
Leucauge argyrobapta Cambridge, 1902b: 16, 1903: 438; Petrunkevitch, 1911: 355.

Leucauge venusta (Walckenaer, 1841) F. O. P.-Cambridge, 1903: 441; Petrunkevitch, 1930: 266; Saito, 1933: 48; Kaston, 1948: 265; Archer, 1951: 6; Wiehle, 1967: 193; Levi, 1980: 25; Coddington, 1990: 17; Hormiga, Eberhard & Coddington, 1995: 324; Dondale *et al.*, 2003: 51; Álvarez-Padilla, 2007: 291; Álvarez-Padilla & Hormiga, 2008: 540; Kuntner, Coddington & Hormiga, 2008: 177.
Leucauge hortorum Banks, 1909: 163; Franganillo, 1936: 85.
Leucauge mabelae Archer, 1951: 6.

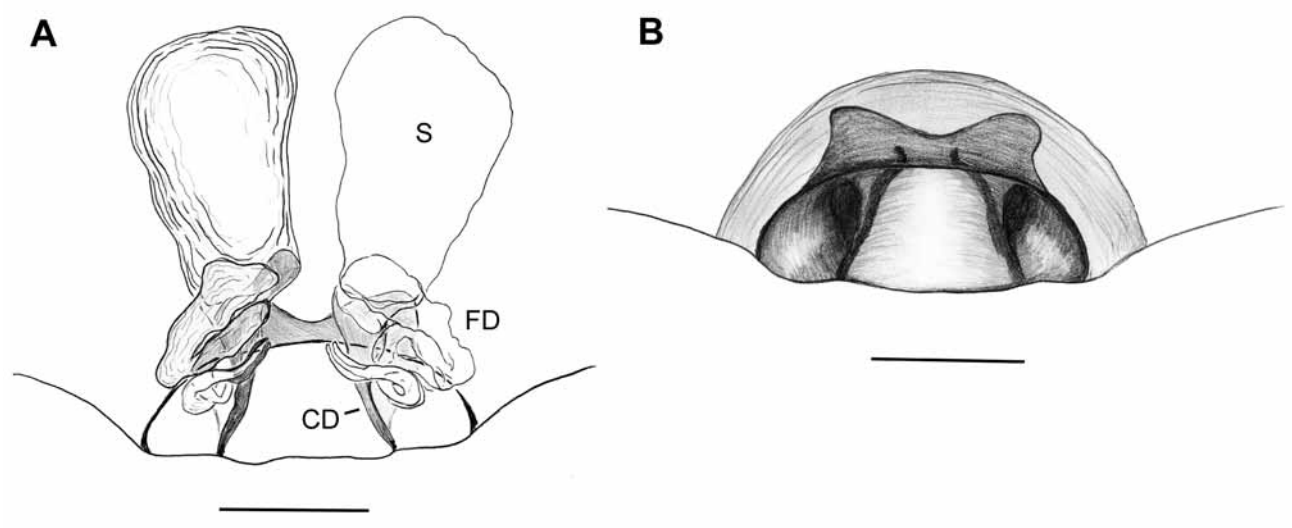

FIGURE 3. *Leucauge venusta* epigynum (from Rio de Janeiro): dorsal A; ventral B. Scale bars 0.2 mm.

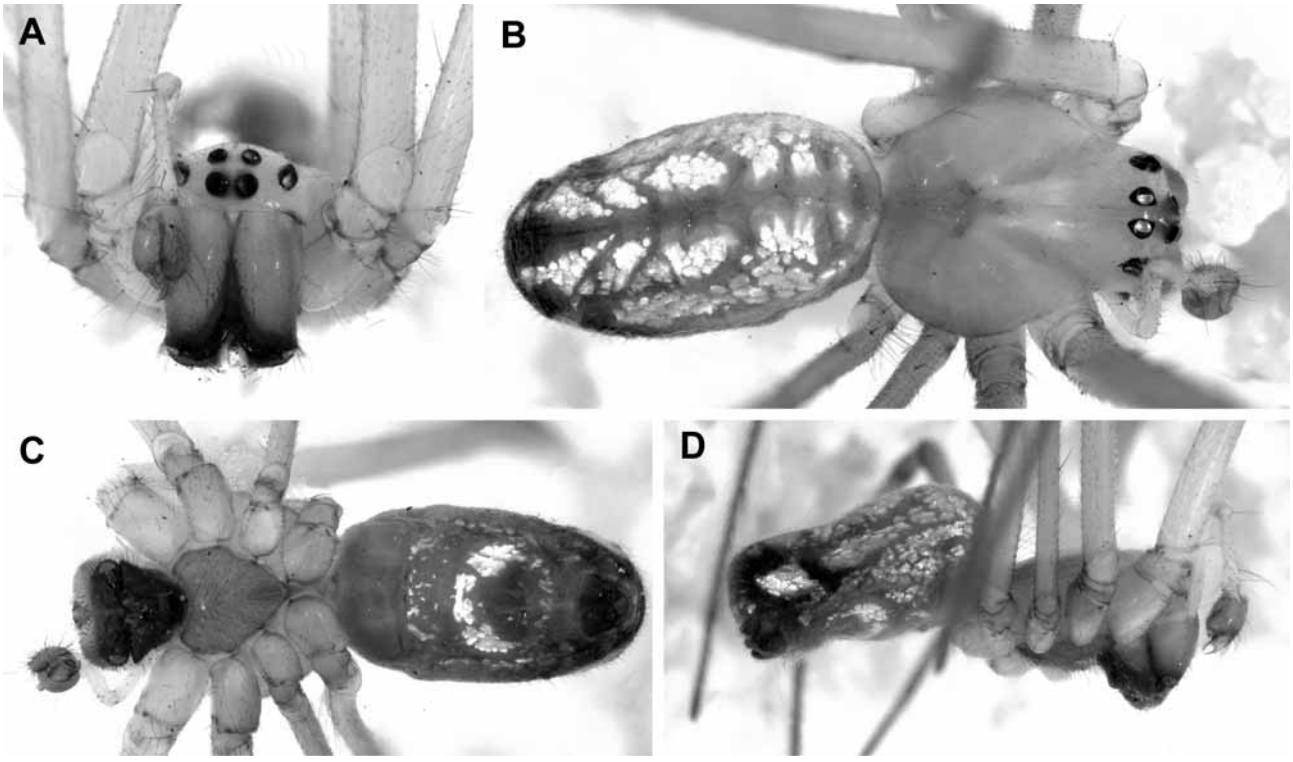

FIGURE 4. *Leucauge venusta* male from Rio de Janeiro (in alcohol): frontal A; dorsal B; ventral C; lateral D.

Notes on types: Cambridge (1903: 438), in pointing out that it was not possible to settle the identity of *Leucauge argyrobapta* "with absolute certainty" suggested that "there is a strong probability" that *argyrobapta* is a synonym of *Leucauge formosa* (Blackwall, 1863), the latter also collected in Rio de Janeiro. He also noted that the specimens of *Leucauge formosa* that he examined (which were part of the Keyserling collection) were "specifically distinct" from *Argyroepeira hortorum* (= *L. venusta*). Despite the noted

uncertainty, Cambridge did explicitly equate *argyrobapta* with *formosa* (op. cit., p. 538). Fortunately, such synonymy was not followed by subsequent authors. Illustrations of the epigynum and male palp of *Leucauge formosa* done by H.W. Levi (and available on line at http://www.oeb.harvard.edu/faculty/levi/leucauge.html) clearly show that this latter species is different from *argyrobapta* (Levi's excellent illustrations are based on specimens from Rio de Janeiro, housed in the Keyserling Collection at the Natural History Museum in London, which according to Levi were probably borrowed from John Blackwall). Under these circumstances, the only way to settle the question of the taxonomic identity of *Linyphia argyrobapta* is to designate a neotype collected in the type locality (Rio de Janeiro), in fulfillment of the qualifying conditions for neotype designation stated in the ICZN (Art. 75.3). As it turns, *Linyphia argyrobapta* is a junior synonym of *Epeira*

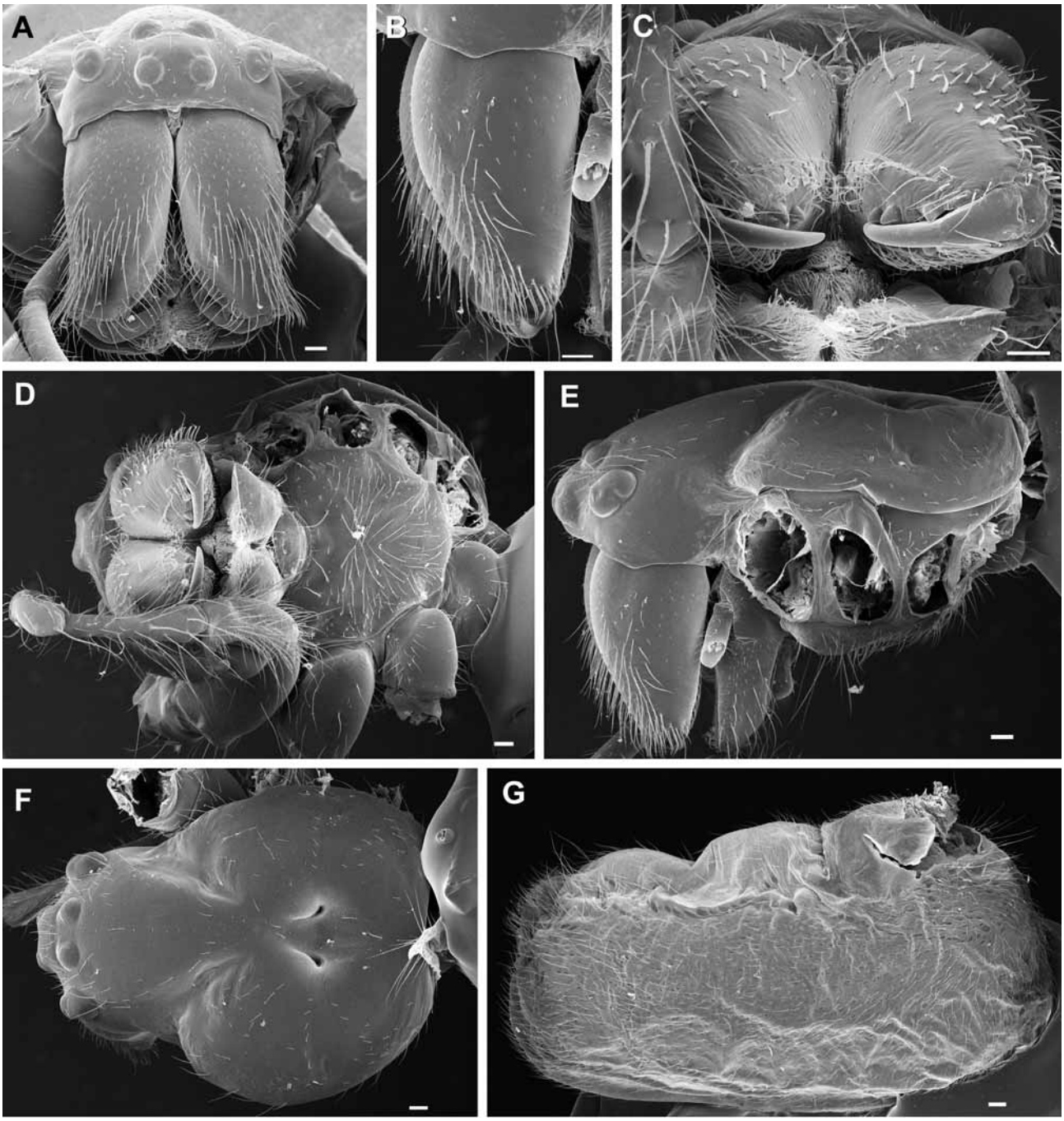

FIGURE 5. *Leucauge venusta* male (from Rio de Janeiro). Chelicerae: frontal A; lateral B; ventral C. Cephalothorax: ventral D; lateral E; dorsal F. Abdomen leteral G. Scale bars: 100 µm.

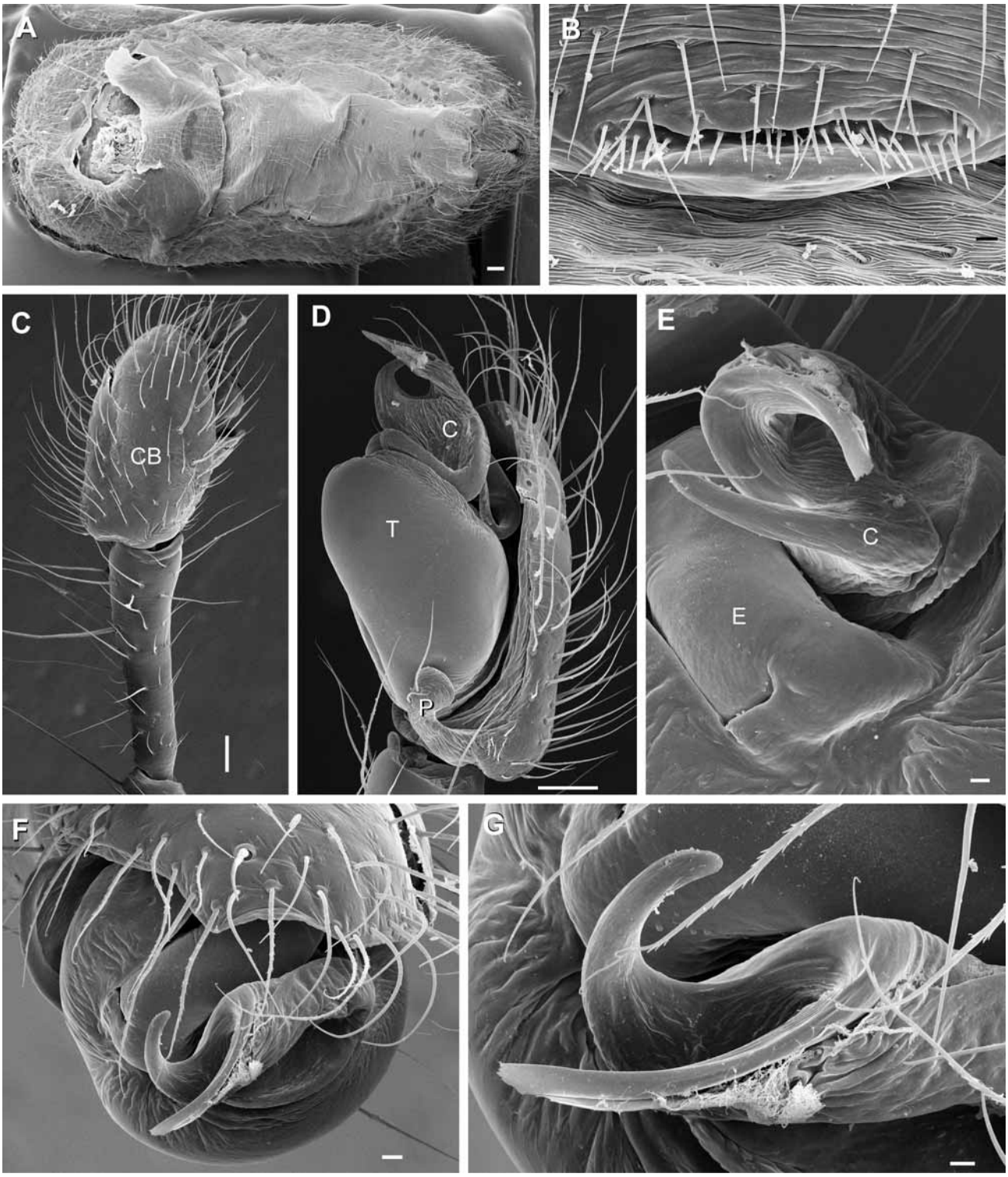

FIGURE 6. *Leucauge venusta* male (from Rio de Janeiro). Abdomen ventral A. Epiandrous fusules B. Palp: dorsal C; prolateral D; apical F; apical details E, G. Scale bars: 100 µm A, C, D; 10 µm B, G, E; 20 µm F.

venusta. The type of *Epeira venusta* is an illustration by John Abbot from his unpublished manuscript on the spiders of Georgia (USA). Abbot's original illustration is in the library of the Natural History Museum in London. Walckenaer (1841) used Abbot's manuscript (p. 13, fig. 113) to describe *Epeira venusta*. A photocopy of Abbot's illustration, in the Museum of Comparative Zoology, was examined by Levi (1980) for his redescription of *Leucauge venusta*. That the name *venusta* was published in 1841, and before Whites's *argyrobapta*, is clear from White's (1841: 473) footnote about Walckenaer's work: "July 2. Since this paper

was written the 2nd volume of Walckenaer's work has been published." It is in this second volume where the description of *Epeira venusta* was first published. Levi and Levi (1961: 54) also provide additional compelling evidence that Walckenaer's description was published in 1841, and not in 1842 as stated in Bonnet (1945: 625).

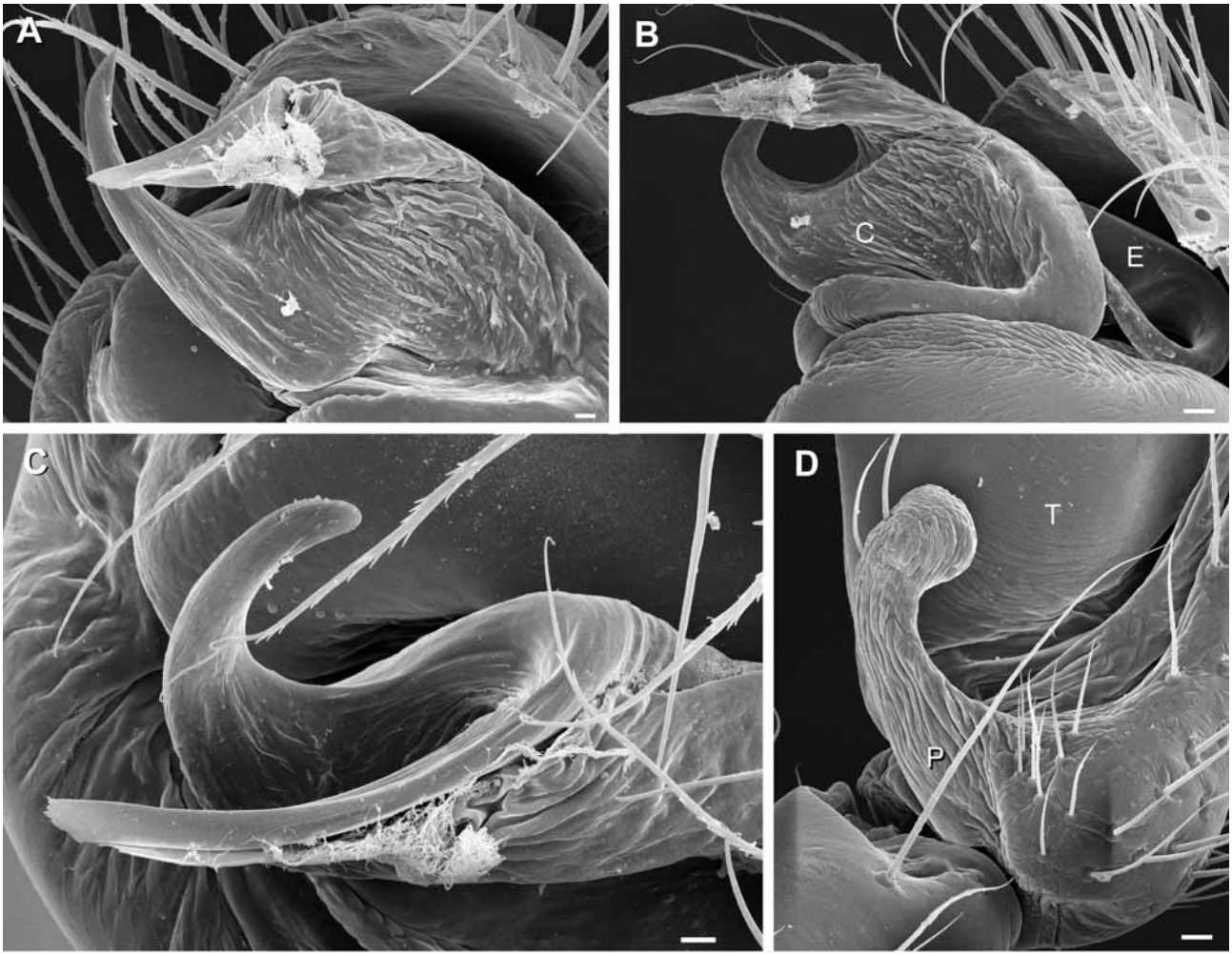

FIGURE 7. *Leucauge venusta* male (from Rio de Janeiro). Palp details: conductor and embolus A–C; paracymbium D. Scale bars: 10 µm A, C; 20 µm B, D.

Neotypes: *Neotype* by present designation, male from Brazil, Rio de Janeiro, Botanical garden of the Museu Nacional do Rio de Janeiro, lat. -22.90842, long. -43.223547 21 VIII 2007, leg. Abel Pérez-González, Adriano B. Kury, Thiago S. Moreira, Dimitar Dimitrov and Gustavo Hormiga (deposited in MNRJ).

Diagnosis: Many *Leucauge* species are very similar and identification can be difficult. Males of *L. venusta* can be distinguished from similar species [e.g., *L. formosa* (Blackwall, 1863)] by the orientation of the conductor, which is more parallel to the tegulum (Fig. 2B–C) than in other similar species. The shape of the apical processes of the conductor is also characteristic (Fig. 2A–F). Other male genitalic characters which are useful to distinguish *L. venusta* from similar congeners are: the size and position of the subtegulum with relation to the tegulum and the shape and size of the paracymbium. The epigynum (Fig. 3B) is quite similar to that of *L. formosa*, however, size and shape of spermathecae in *L. venusta* is unique to this latter species (Fig. 3A). Coloration and color pattern in both males and females of *Leucauge* are important and diagnostic. They often vary considerably among species with similar genitalic morphology, hence, facilitating the correct identification. In live specimens, the abdomen of *L. venusta* has four distinct red-orange markings (silvery when in alcohol) (Fig. 1A–G). Two are ventral and two are dorso-lateral. The ventral markings are parallel and placed laterally on distal third of the abdomen. They join proximally to form a U shaped pattern. The dorsal markings start around the middle of the abdomen and extend parallel to each other.

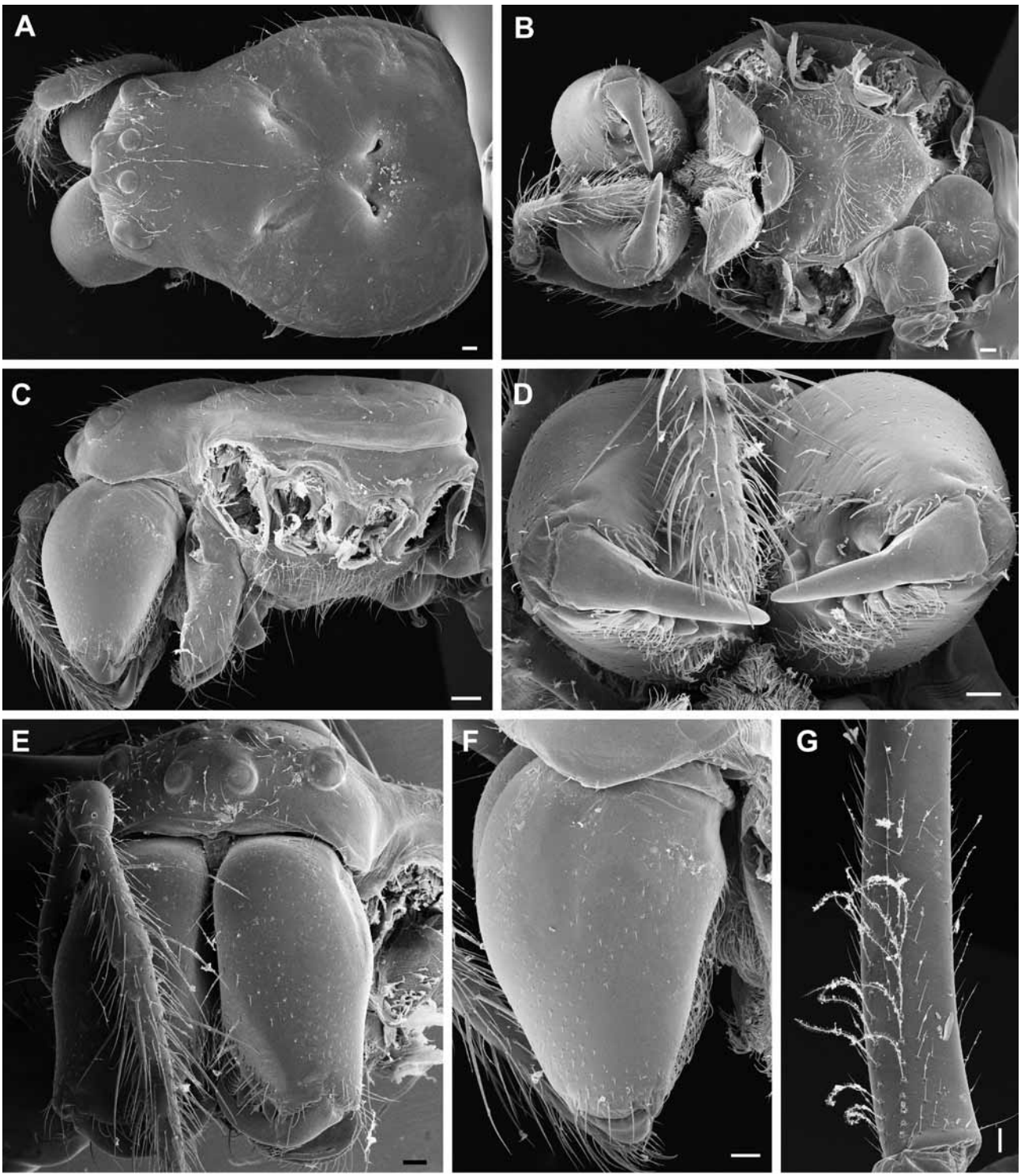

FIGURE 8. *Leucauge venusta* female (from Rio de Janeiro). Cephalothorax: dorsal (cleared) A; ventral B; lateral C. Chelicerae: ventral D; frontal E; lateral F. Leg IV femur G. Scale bars: 100 µm.

Description: *Male* (neotype of *Linyphia argyrobapta*, from Rio de Janeiro) Habitus as in Figure 4A–D. When live, carapace (Fig. 5D–F) yellowish with green markings along edges and center dorsally. Fovea well marked (Fig. 5F). Leg coxae with yellowish bases, rest of legs bright green. Abdomen (Figs. 4B–D; 5G; 6A) elongated, proximally with shiny silvery guanine bands and three thinner black lines dorsally – one in center, two more lateral. Two lateral dorsal lines change to red-orange coloration close to middle of abdomen and widen distally. Lateral sides of abdomen with thick shiny silver line close to its dorsal side followed by black

line and another silvery line with some yellowish tones followed by bright green. Ventral side of abdomen proximally green with yellowish central mark proximally and thin yellow lateral lines. Distally with a central black area and two lateral red-orange markings forming a U-shaped pattern. Two shiny rounded spots placed just lateral to spinnerets – light yellow when alive, silvery white in alcohol. All colored lines meet on distal tip of the abdomen which is black. Total length 5.50. Cephalothorax 2.35 long, 1.95 wide, 1.16 high. Abdomen 3.15 long, 1.54 wide, 1.47 high. Clypeus height 0.7 times an AME diameter. Sternum (Fig. 5D) dark brown; 1.05 long, 0.98 wide. Eyes almost the same size. Lateral eyes juxtaposed on short elevations (Fig. 5A, F). Distance between PME 1.5 times their diameter. AME-ALE distance about three AME diameters. Distance between AME almost twice their diameter. PLE-PME distance three times one PME diameter. Chelicerae (Figs. 4A; 5A–C) yellowish, darker brown distally. Distal edge of paturon with three anterior and four posterior teeth. Femur I 1.2 times the length of cephalothorax. Pedipalp as in Figures 2A–F; 6C–G; 7A–D. Palpal tibia length 0.78; cymbium length 0.58. Epiandrous fusules as in Figure 6B. Femur of leg IV dorsally with two parallel rows of branched trichobothria extending over more than two thirds of its length. Palp as in Figures 2A–E; 6C–G; 7A–D. Conductor and embolus connect to tegulum with common membrane (Fig. 2E, F).

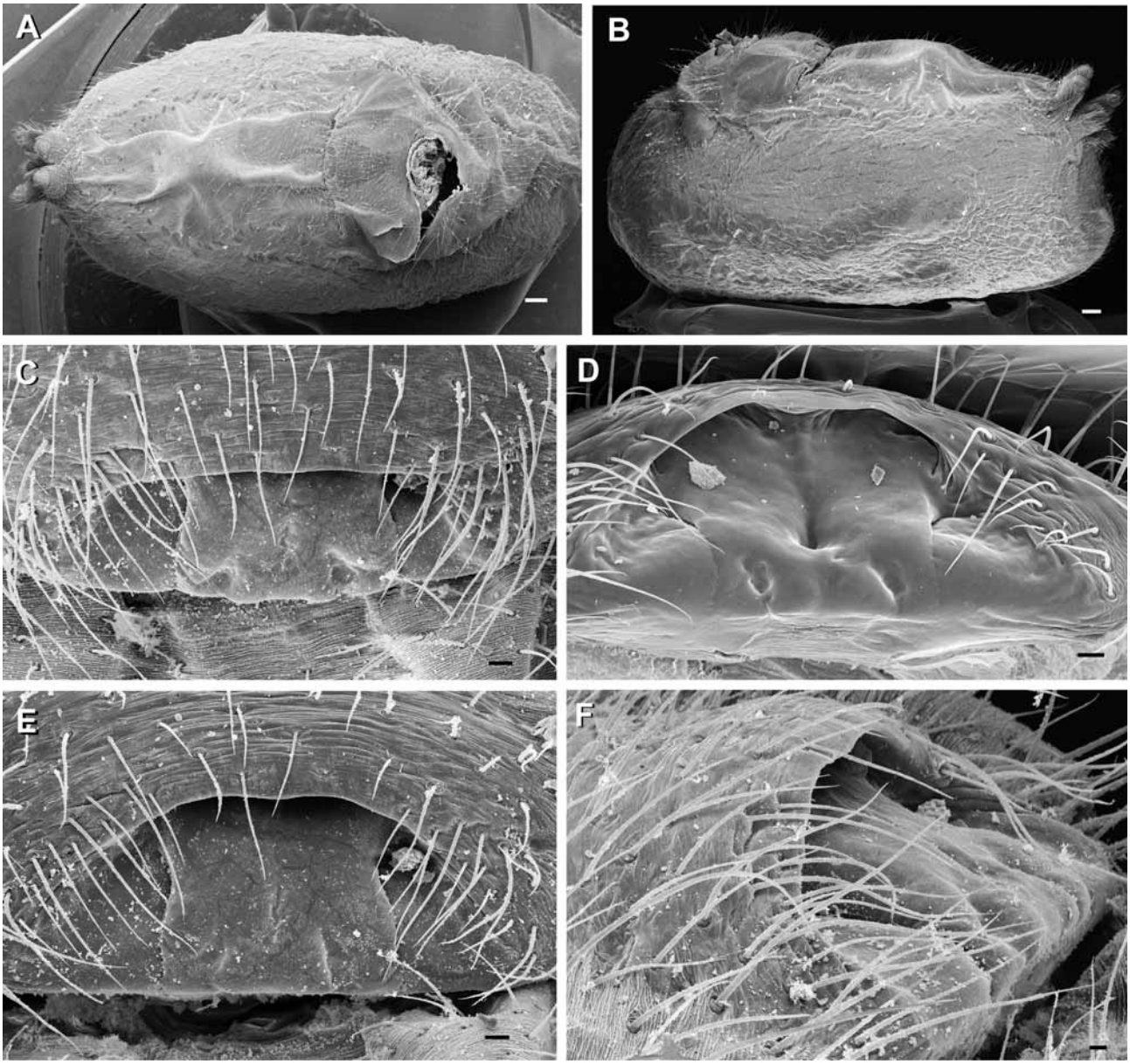

FIGURE 9. *Leucauge venusta* female (from Rio de Janeiro). Abdomen: ventral A; lateral B. Epigynum: dorsal C; caudal D; dorso-caudal E; lateral F. Scale bars: 200 µm A–B; 20 µm C–E; 10 µm F.

Female (same locality and date as male neotype). Habitus and coloration as in male (Fig. 1A–G), slightly larger than male (female total length ca. 1.3 times that of male). Total length 7.45. Cephalothorax (Fig. 8A–C) 2.88 long, 2.06 wide, 1.32 high. Abdomen (Fig. 9A–B) 4.57 long, 2.40 wide, 2.19 high. Clypeus height 0.5 times an AME diameter. Sternum (Fig. 9B) dark brown; 1.39 long, 1.16 wide. Eyes sizes and distribution as in male (Fig. 9A, E). Chelicerae as in male (Fig. 9C–F). Tracheal system haplotracheate (Fig. 10F–G), with median tracheal trunks shorter than lateral, neither of them entering the prosoma. Tracheal atrium with numerous accessory glands (Fig. 11A). Tracheal spiracle immediately anterior to spinnerets. Spinnerets as in Figure 10A–D. Femur IV dorsally with two rows of branched trichobothria as in male (Fig. 10E). Epigynum as in Figures 2A–B; 9C–F; 11B–G. Spermathecae (Figs. 3A; 11B, B) membranous and elongated. Fertilization ducts also membranous with numerous accessory glands (Fig. 11C, E, F).

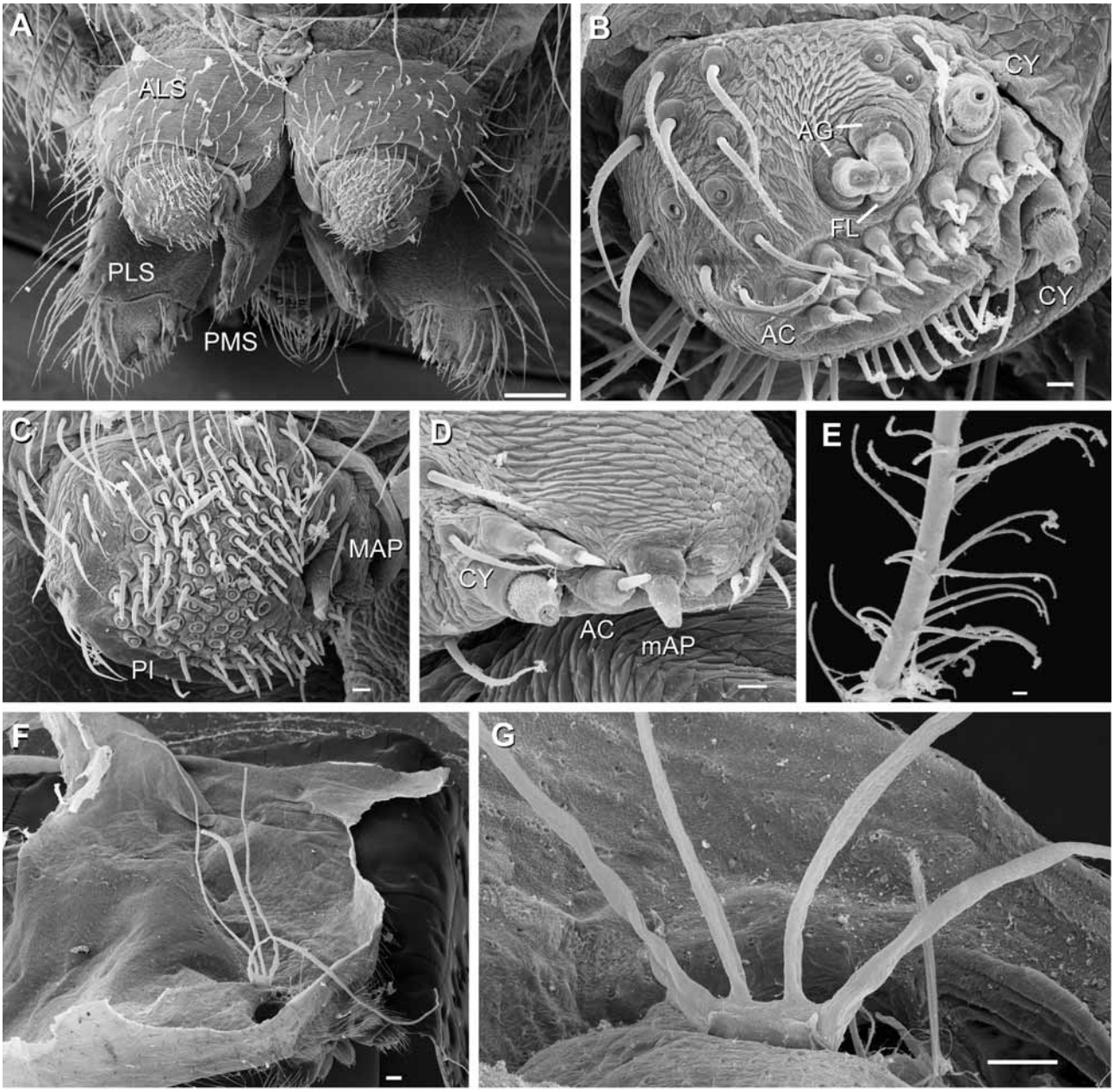

FIGURE 10. *Leucauge venusta* female (from Rio de Janeiro). Spinnerets: ventral A; PLS B; ALS C; PMS D. Leg IV trichobothria E. Tracheae: tracheal system F; tracheal base anteriorly G. Scale bars: 100 µm A, G; 10 µm B, C, D; 2 µm E; 200 µm F.

Variation: Male cephalothorax length varies between 2.24 and 2.35 (n = 4). Females cephalothorax length varies between 2.30 and 3.00 (n = 117). Total body length in males varies between 5.11 and 5.50 (n = 4) and in females between 5.88 and 9.66 (n = 117).

Distribution: *Leucauge venusta* is very widely distributed in the New World. Although, common in temperate areas of USA (Levi, 1980) this species has been already found in the neotropics (Panama, Colombia, see Cambridge, 1903) and its presence in Brazil extends further south its known distribution range. *Leucauge venusta* distribution spans from southern Canada to southern Brazil.

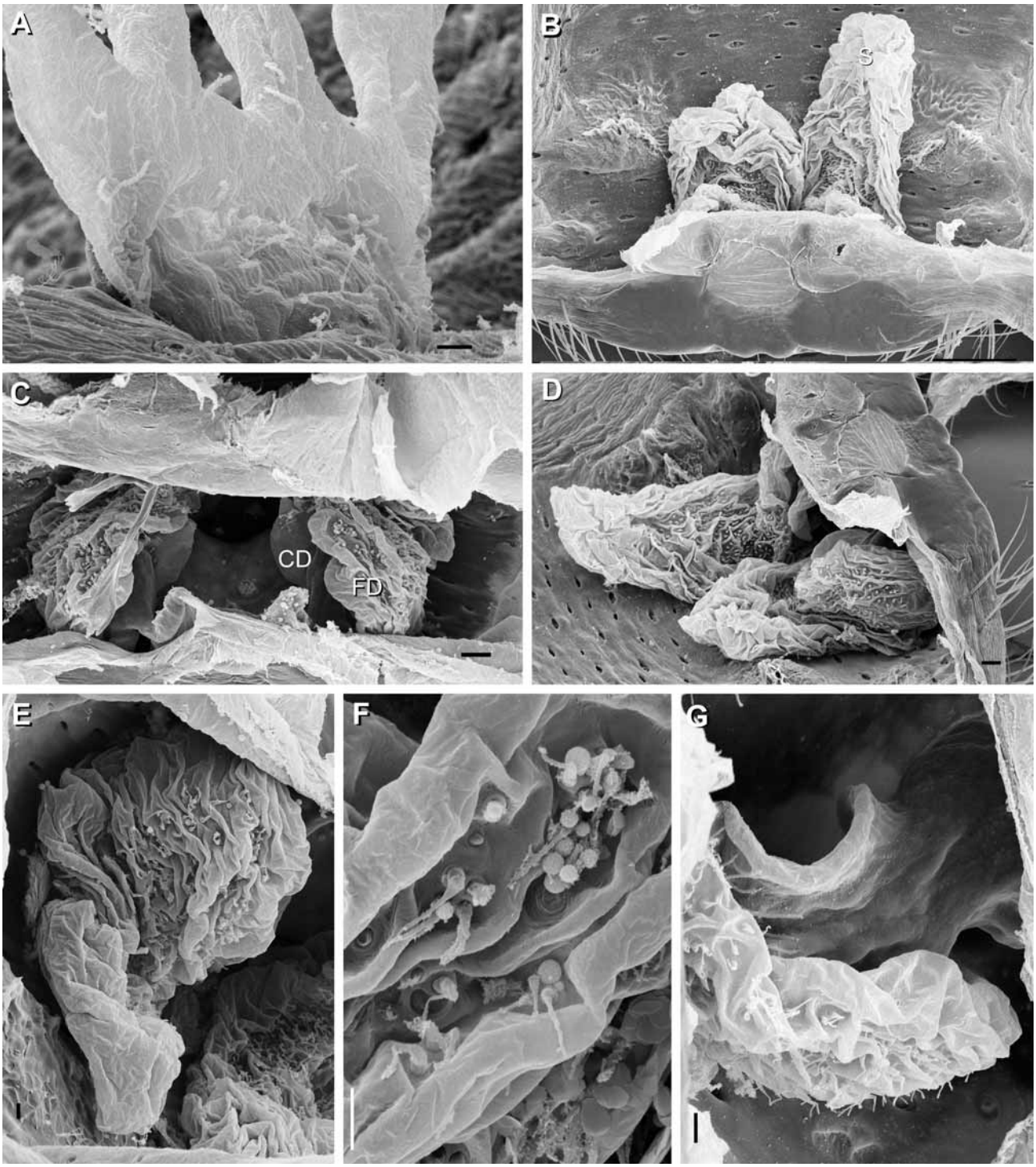

FIGURE 11. *Leucauge venusta* female (from Rio de Janeiro). Tracheal atrium caudal view A. Epigynum: dorsal B; anterior view C; lateral D. Spermathecae E. Fertilization ducts F. Spermathecae base G. Scale bars: 10 µm A, E–G ; 100 µm B; 30 µm C; 20 µm D.

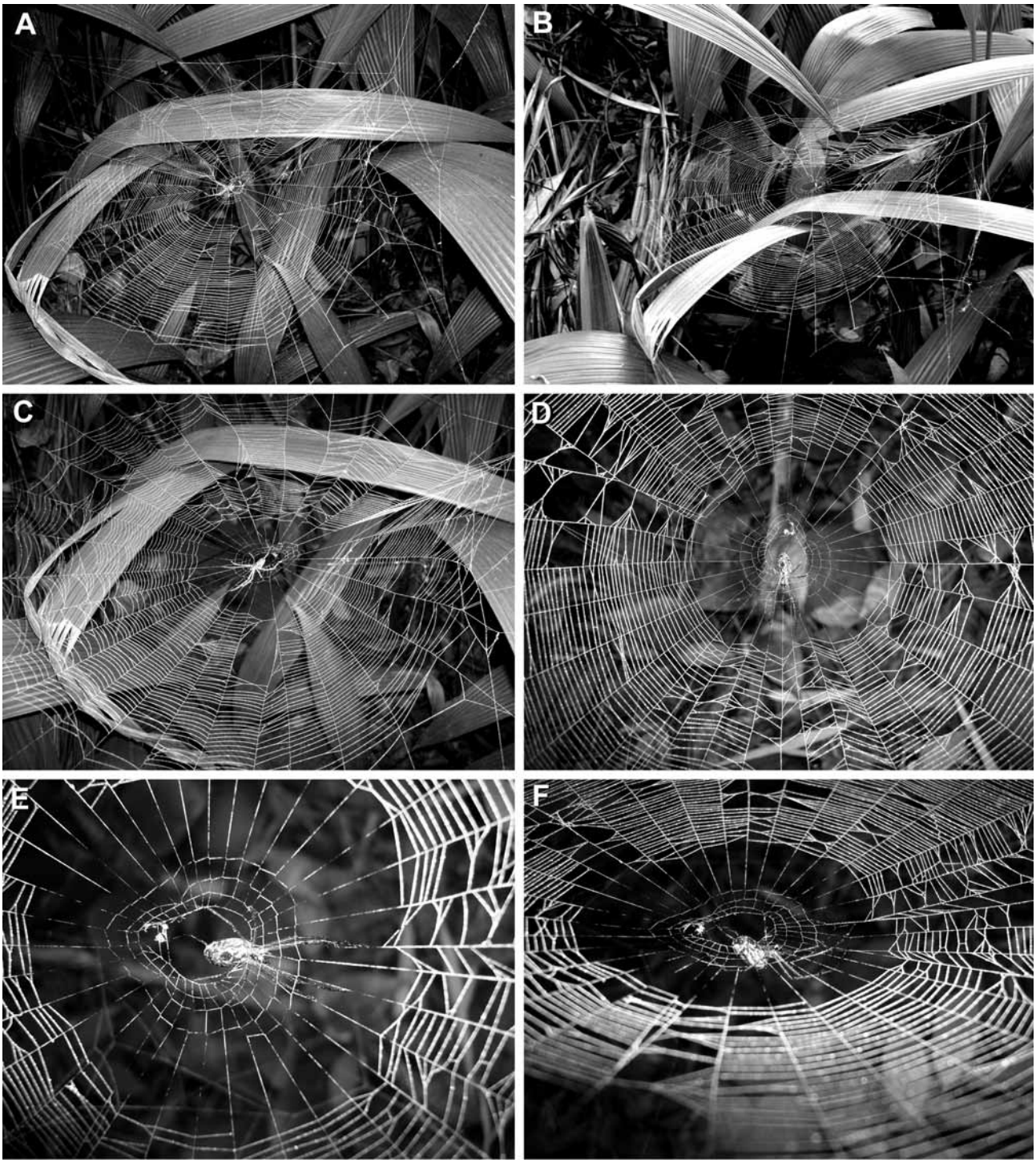

FIGURE 12. *Leucauge venusta* (from Rio de Janeiro) female web architecture A–F.

Natural history: The natural history of *L. venusta* is relatively well known. *Leucauge venusta* spins its horizontal orb web (Fig. 12A–F) in vegetation in humid tropical and temperate areas. Emerton (1902), Comstock (1913), Kaston (1947), Levi (1980) and Hénaut *et al*. (2006) describe their webs. In more temperate areas it is commonly found in irrigated orchards, gardens or vegetation along river banks. The spider usually rests in the center of the web but when disturbed it hides in an off-web retreat. *Leucauge venusta* webs may vary considerably and in some cases they have a mesh above the orb plane. The variability in web architecture in this species was first noted by Darwin (as quoted in White, 1841: 474): "*...but sometimes above, the concentric web, there is an irregular or thin tissue of network*". The web and foraging

biology of *L. venusta* was also studied in detail by Hénaut *et al.* (2001). The courtship behavior is described in detail by Castro (1995). Eberhard and Huber (1998) give further details and discuss the differences in the courtship among several *Leucauge* species.

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