

A New Genus and Species of Urodidae (Lepidoptera: Urodoidea) from Argentina with the First Report of Asymmetric Male Genitalia in the Superfamily

Author: Sohn, Jae-Cheon

Source: Florida Entomologist, 96(2) : 469-476

Published By: Florida Entomological Society

URL: <https://doi.org/10.1653/024.096.0212>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A NEW GENUS AND SPECIES OF URODIDAE (LEPIDOPTERA: URODOIDEA) FROM ARGENTINA WITH THE FIRST REPORT OF ASYMMETRIC MALE GENITALIA IN THE SUPERFAMILY

JAE-CHEON SOHN

Department of Entomology, 4112 Plant Sciences Building, University of Maryland, College Park, Maryland 20742, USA
E-mail: jsohn@umd.edu

ABSTRACT

A new genus of Urodidae, *Anomalomeuta* **gen. nov.**, is described from Argentina, with the type species, *Anomalomeuta dondavisii* **sp. nov.** The new genus is superficially similar to *Spiladarcha* Meyrick in having scattered small black spots comprised of raised scales along the forewing veins on the upper surface, but it lacks the 2 autapomorphies of the latter genus: a pair of spiniform setal zones on the ventroapical area of the tegumen, and a zone of longitudinal pleats on the ductus bursae. *Anomalomeuta* also differs from all known urodid genera by the asymmetric valvae in the male genitalia. This characteristic is reported for the first time from Urodoidea and is compared with examples of other Lepidoptera. Keys to all known urodid genera based on the external and male genital features are provided.

Key Words: *Anomalomeuta* **gen. nov.**, *Anomalomeuta dondavisii* **sp. nov.**, Argentina, Lepidoptera, taxonomy, Urodidae

RESUMEN

Se describe un nuevo género de Urodidae, *Anomalomeuta* **gen. nov.** con la especie tipo, *Anomalomeuta dondavisii* **sp. nov.**, de Argentina. El nuevo género es similar a *Spiladarcha* Meyrick en tener pequeños puntos negros dispersos que consisten de escamas elevadas sobre la nervadura de la superficie superior de las alas anteriores, pero carece de los 2 autapomorfías del género *Spiladarcha*, un par de zonas espiniformes de setas en la zona ventroapical del tegumento, y una zona de pliegues longitudinales en el ductus bursae. El género *Anomalomeuta* también difiere de todos los géneros urodidos conocidos por la valva asimétrica de los genitales masculinos. Esta característica se informó por primera vez de la superfamilia de Urodoidea, y se compara con ejemplos de otros lepidópteros. Se provee una clave para todos los géneros conocidos de urodidos, basado en las características genitales externas masculinas.

Palabras Clave: *Anomalomeuta* **gen. nov.**, *Anomalomeuta dondavisii* **sp. nov.**, Argentina, Lepidoptera, taxonomía, Urodidae

Urodidae, the sole family of the superfamily Urodoidea, belongs to the apoditrysan Lepidoptera. The group currently includes 66 species (Nieukerken et al. 2011), occurring predominantly in the Neotropics. The species constituting the family historically have been placed in Yponomeutidae or Plutellidae. Kyrki (1988) found that urodids are distinct from typical yponomeutoids in having 'tortricid' type abdominal/thoracic articulation and 3 acanthi in the frenulum of the female. Based on these features, he proposed the family Urodidae to accommodate them. Urodidae can be characterized by 5 possible autapomorphies: the lamellate male antennae, a hair-pencil on the base of the male hindwing costa; the larval prothorax without seta MXD1; the larval abdominal segment VIII with L3 ventroanterior to L1 and L2 and SV1 almost as high as L3; the larval prolegs elongate, medially constricted, with mesoseries of crochets (Kyrki 1988; Dugdale et al. 1998). Kyrki (1988)

originally included 3 genera in the family: *Urodus* Herrich-Schäffer, 1854, *Wockia* Heinemann, 1870, and *Spiladarcha* Meyrick, 1913. Heppner (1984) resurrected *Anchimacheta* Walsingham, 1914, which had been synonymized with *Spiladarcha*. More recently, Heppner (2010) described *Inca-wockia* for a unique species from Peru. To date, a total of 5 genera have been assigned to Urodidae. However, this generic diversity appears to be underestimated, as novel lineages continue to be found in the Oriental and Neotropical regions (Sohn 2012, unpublished).

The purpose of this article is to describe a new species of Urodidae from Argentina. Because this species cannot be assigned to any known genus, a new generic name is proposed. The male genitalia of this new species possess asymmetric valvae, a characteristic that is previously unreported from Urodoidea. The possible function of this feature is discussed.

MATERIALS AND METHODS

Dried specimens were obtained from the United States Museum of Natural History, Washington DC (USNM). Genitalia slides were prepared following Clarke (1941), except that chlorazol black was used for staining and Euparal resin for permanent slide mounting. The wings were slide-mounted following Hodges (2005).

Pinned specimens were examined with a Leica MZ APO stereoscope. Slide-mounted specimens were examined with a Leica LETTZ-DMRX microscope. Images were captured using the VDBK digital imaging systems, adopted by the United States Department of Agriculture and installed in the Department of Entomology, USNM.

Verbatim label data are given only for holotype. Terms for genitalia follow Klots (1970). In the description, abdominal segments are given as abbreviations: A7, A8 and A9 for the seventh, eighth, and ninth segments. Terms for wing venation follow Wootton (1979).

TAXONOMIC ACCOUNT

Anomalomeuta **gen. nov.**

Type species: *Anomalomeuta dondavisi* **sp. nov.**, by monotypy.

Diagnosis. The new genus can be associated with Urodidae by the forewing Rs_4 vein terminating above the apex and the male genitalia possessing a digitate costal process. It is distinguished from all other urodid genera in having asymmetric valvae in the male genitalia and 4 signa in the female genitalia. Within the family, it is closest to *Spiladarcha* Meyrick, 1913, sharing 2 characteristics: the forewing upper surface with small black spots of raised scales along the veins and the absence of hair pencils on the hindwings. *Anomalomeuta*, however, lacks 2 genitalic autapomorphies of *Spiladarcha* proposed by Sohn (2012); i.e., a pair of spiniform setal zones on the ventroapical area of the tegumen in males and a zone of longitudinal pleats on the ductus bursae in females.

Description

Head: Vestiture of vertex appressed, scales piliform, directed toward frons; ocelli and chaetosemata absent; antennae filiform, without pecten; flagellomeres without scales ventrally, lamination not as clear as in *Urodus*; labial palpus 1st segment $\frac{1}{2}$ as long as 2nd; 2nd segment with ventral scale tufts, denser distad; 3rd segment with obtuse apex, as long as 2nd; maxillary palpus very short, 1-segmented; haustellum naked, $2 \times$ longer than labial palpus. Thorax: Foretibial epiphysis arising from distal $\frac{1}{3}$ of tibia; hindtibia

with hairs dorsally in both sexes, denser in males; hindwing without hair pencil in both sexes. Forewing venation (Fig. 6) with Sc reaching margin at the basal $\frac{1}{3}$ of costa; Rs_1 curved to R; Rs_{2-4} reaching wing margin above apex, diverging from each other; Rs_3 closer to Rs_4 than to Rs_2 at base; M_1 nearly parallel to Rs_4 in basal half, slightly diverging from Rs_4 in distal half; M with 3 branches equidistant at base; M_2 curving to M_1 ; CuA_1 and CuA_2 short; CuA_1 curved downward, approaching CuA_2 over distal half; CuP fold close to lower margin of discal cell; accessory cell present; $1A+2A$ with small fork at base. Hindwing venation (Fig. 6) with $Sc+R_1$ reaching margin at $\frac{1}{3}$ length; Rs reaching margin at $\frac{1}{4}$ length above apex, nearly parallel to M_1 ; M_1 terminating just above apex; M_2 diverging from M_1 in distal half; M_3 parallel to M_2 , twice as far apart as M_1 and M_2 ; CuA_1 slightly diverging from M_3 ; CuA_2 arising from distal $\frac{1}{3}$ of lower margin of discal cell, curved to CuA_1 in distal half, twice as far apart as M_3 and CuA_1 at base; CuP close to $1A+2A$ over basal $\frac{1}{3}$ and then to CuA_2 over distal $\frac{1}{3}$. Abdomen: Sternum II (Fig. 3) with apodeme $\frac{1}{2}$ as long as anterolateral process, continuing to a sclerotized zone $3 \times$ longer than anterolateral process; a Y-shaped sclerotized zone behind the posterior margin. Male genitalia (Figs. 7-9) with uncus continuous from tegumen; tuba analis extending beyond uncus, connected with uncus process dorsally to form scaphium; subscaphium present; valvae asymmetrical, a costal process present only on one valva; phallus without coecum; ductus ejaculatorius arising dorsally; cornuti present. Female genitalia (Fig. 10) with ovipositor as a complex of A8, A9, papillae anales and an intersegmental membrane between A8 and A9, telescopic; posterior margin of A7 with emargination at ostium bursae; most of ductus bursae sclerotized; antrum present; ductus seminalis originating near corpus bursae; 4 signa present.

Etymology

The generic name is derived from the ermine moth genus *Yponomeuta* with the Greek prefix 'anomalo' meaning "irregular" or "abnormal" and refers to its superficial similarity to some yponomeutines. The gender is feminine, agreeing with *Yponomeuta*.

Remarks

Kyrki (1988) indicated that *Spiladarcha* is characterized by asymmetry in the male genitalia. Furthermore, the wing venation illustrated by Kyrki (1988) for *Spiladarcha* is remarkably similar to that of *Anomalomeuta*. Hence, it is very likely that Kyrki (1988) misidentified *Anomalomeuta* as *Spiladarcha*. This speculation, how-

ever, remains unverifiable because Kyrki (1988) did not provide any illustration of the external or genital features. I recently (Sohn 2012) redefined *Spiladarcha*. Based on this redefinition, *Spiladarcha* unambiguously differs from *Anomalomeuta*.

Anomalomeuta dondavisii **sp. nov.** (Figs. 1, 3–10)

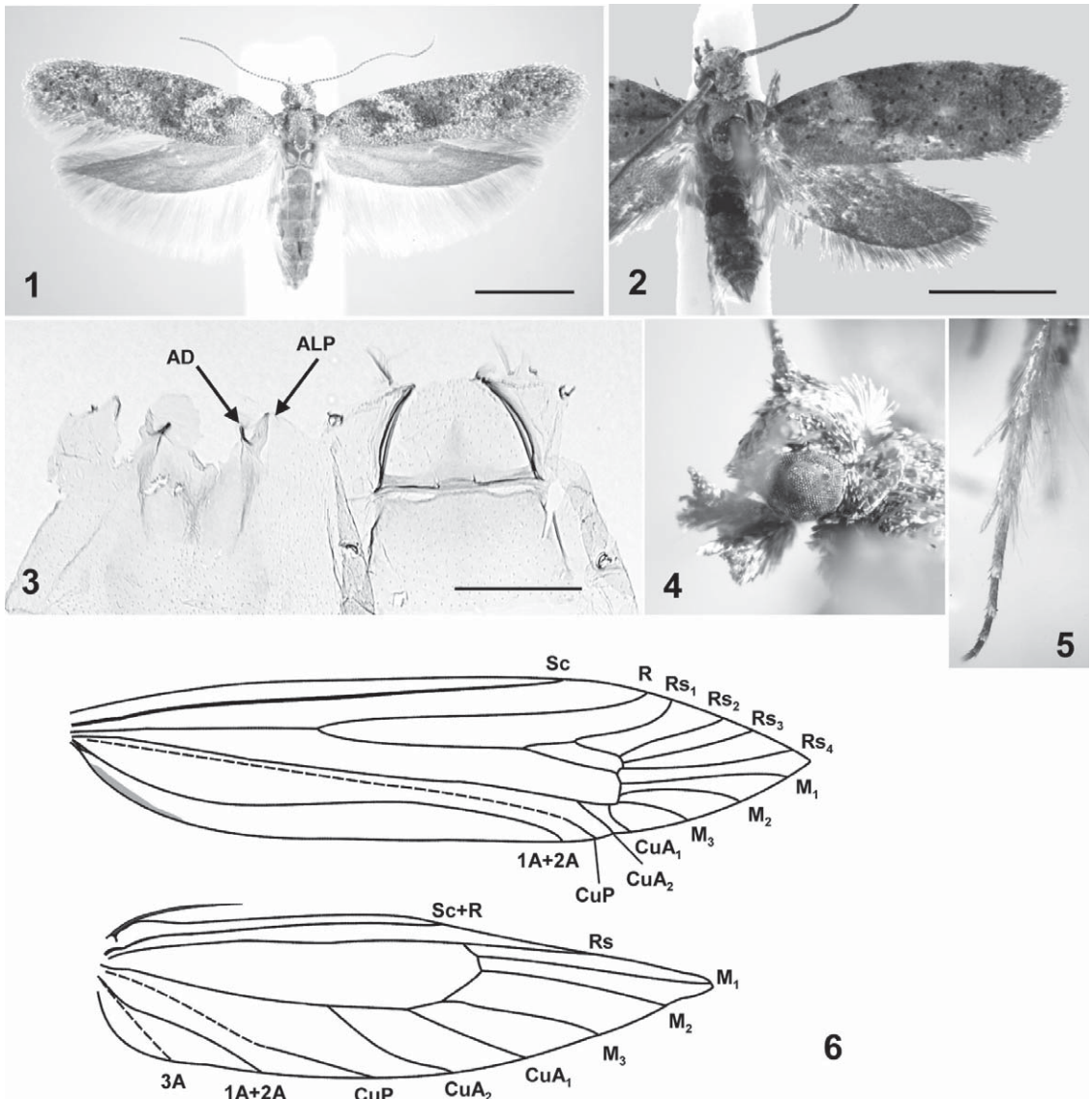
Diagnosis

The new species has grayish fuscous forewings similar to species of *Wockia* and *Spiladarcha*, but

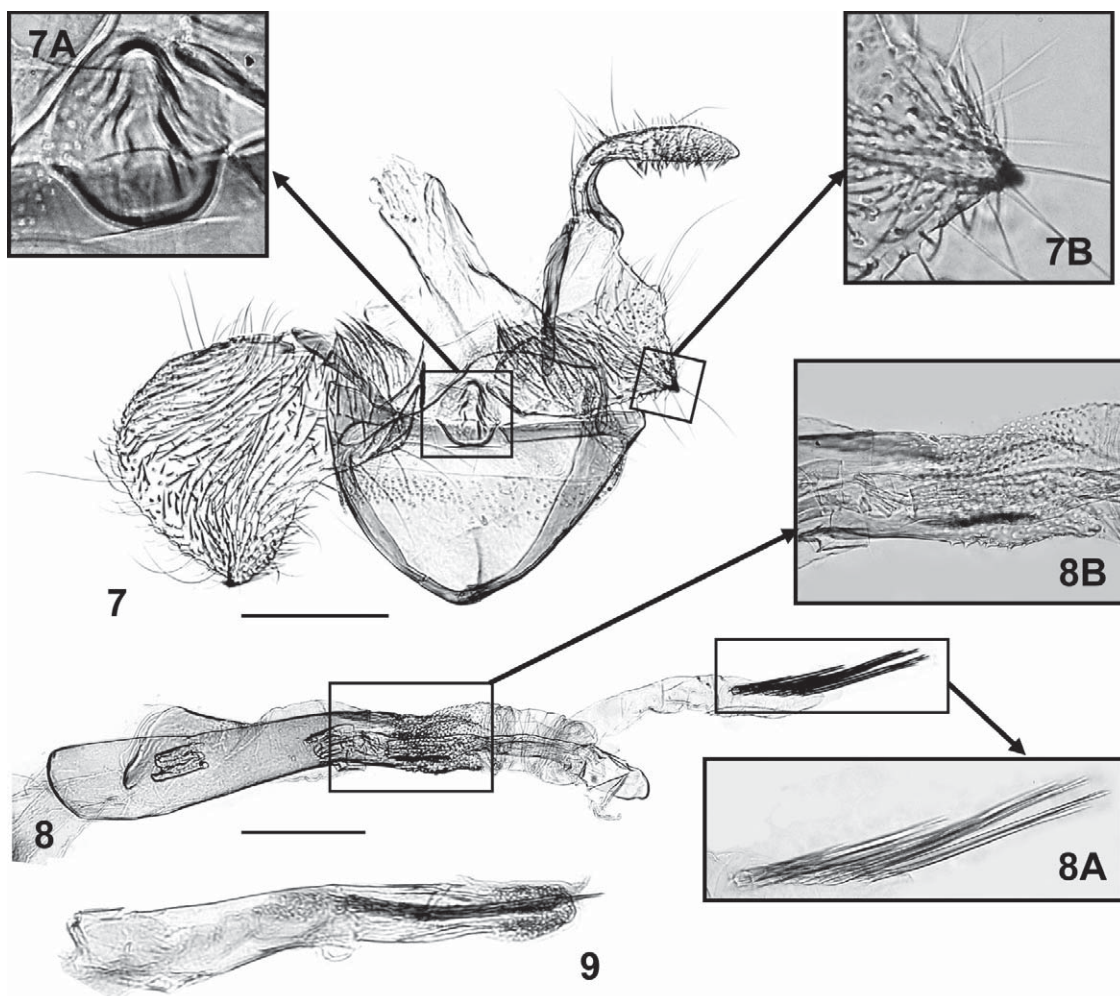
the forewings are narrower than in the latter two genera. *Anomalomeuta dondavisii* is very close to *Spiladarcha adamskii* Sohn, 2012 described from Venezuela (Fig. 2), but it differs in the presence of a fuscous subbasal line on the forewings (present as fuscous shade in *S. adamskii*) and in the presence of asymmetric valvae in the male genitalia.

Description

Head: Scales of vertex and frons dark grayish brown with brownish white tips, paler medially. Antennae 3/5 as long as forewing costa; scape



Figs. 1-6. *Anomalomeuta dondavisii* **sp. nov.** (1, 3-6) and *Spiladarcha adamskii* Sohn (2); 1-2. adult habitus, scale bars = 2mm; 3. abdominal segment II (AD = apodeme; ALP = anterolateral process), scale bar = 0.5mm; 4. head; 5. hindleg; 6. wing venation.



Figs. 7-9. Male genitalia of *Anomalomeuta dondavisi* **sp. nov.**; 7. genital capsule (insets: A. juxta; B. saccular process), scale bar = 0.25mm; 8. phallus (insets: A. cornuti; B. basal region of vesica), scale bar = 0.25mm; 9. phallus with vesica and cornuti concealed inside.

dark brown; basal 13 flagellomeres brownish white over proximal half, dark brown over distal half, with a dark brown basal and a brownish white terminal ring; the remaining flagellomeres dark gray. Labial palpus slightly ascending, becoming straight after 1st segment; 1st dark brown over basal half, brownish white over distal half; 2nd segment dark brown intermixed with brownish white, with dense, triangular scale tufts ventrally; 3rd segment scales dark brown, with white tips.

Thorax: Patagia, tegulae, and mesonotal scales dark grayish brown, with brownish white tips. Foreleg dark brown, speckled with brownish white; tibia and tarsomeres with brownish white ring at distal end. Midleg with coxa brownish gray; femur dark brown with brownish white specks denser over proximal and distal areas;

tibia dark brown, with brownish white band dorsally at basal $\frac{1}{5}$, distal $\frac{3}{5}$ densely speckled with brownish white, scales denser to distal end; tarsomeres dark brown, speckled with brownish white, with brownish white ring on distal end. Hindleg with coxa to tibia lustrous, pale yellowish gray, sparsely speckled with pale grayish brown; tarsomeres dark brown, with brownish white ring on distal end. Forewing length 5.2-7.2 mm (average = 6.4 mm, $n = 12$), elongate, brownish gray, termen sharply oblique, apex obtuse; subbasal line fuscous, notched medially; medial area of costa broadly fuscous, narrowed posteriorly, forming triangular patch; a patch of raised, dark brown scales at the apex of the inverted-triangular, fuscous, medial area; subterminal line fuscous, notched medially; erect scales of small dark brown dots scattered along wing veins on the up-

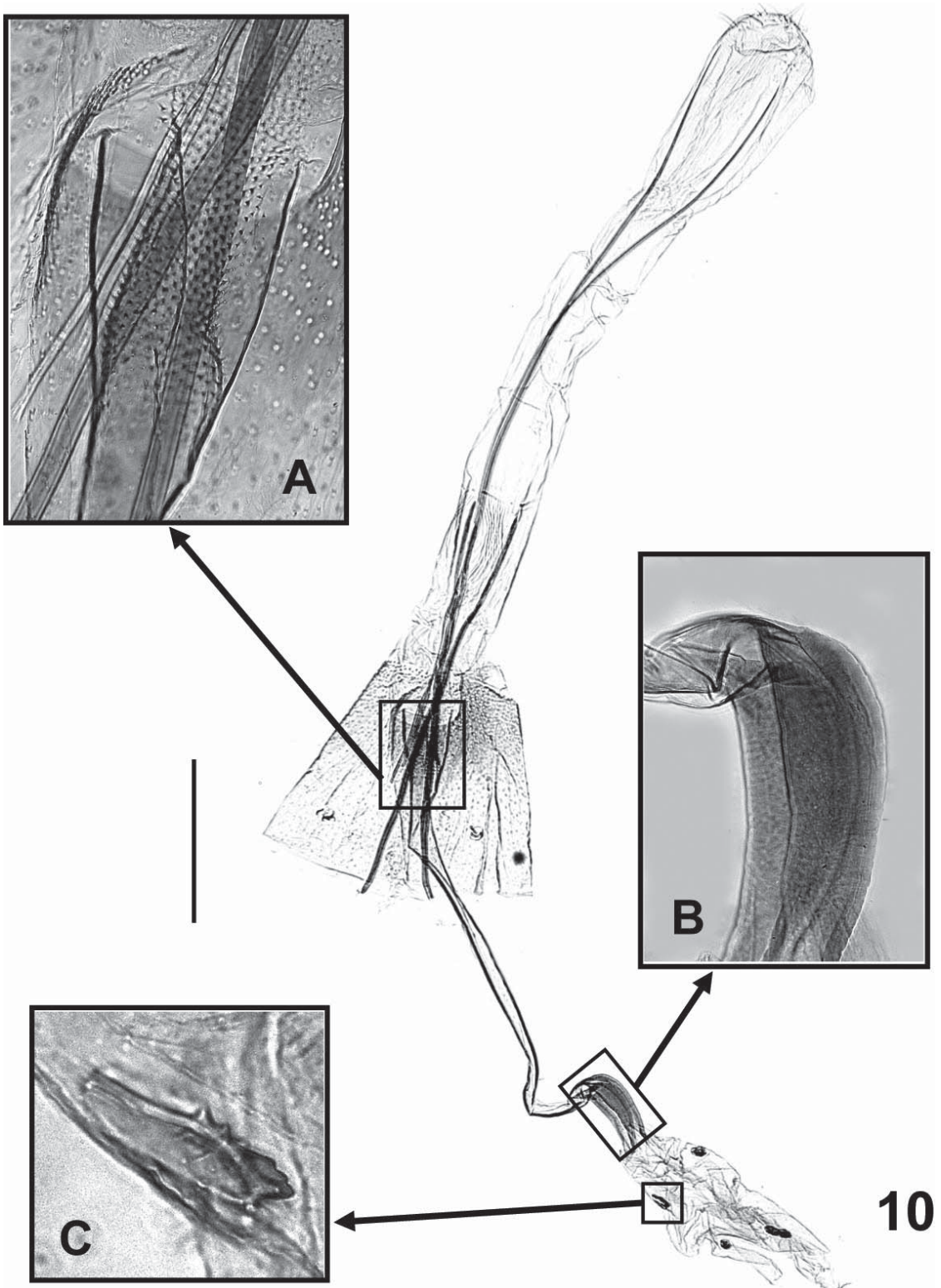


Fig. 10. Female genitalia of *Anomalomeuta dondavisi* **sp. nov.** (insets: A. antrum; B. sclerotized part of ductus bursae near to corpus bursae; C. signum), scale bar = 0.5mm.

per side; fringes dark yellowish gray. Hindwing dark yellowish gray, paler basally; fringes dark yellowish gray.

Abdomen: Tergites dark brownish gray dorsally, pale brownish gray at distal end; sternites brownish white.

Male genitalia: Uncus subtriangular, with a needle-like apical process. Tegumen semicircular, as long as saccus; subscaphium narrow. Valvae asymmetrical, left valva spatulate, densely setose on inner surface, terminal part of ventral margin slightly extended, with a dentiform, short process; right valva triangular, $\frac{2}{3}$ as long as left valva, densely setose on ventral half of inner surface, with a dentiform, short process apically, costa convex at basal $\frac{1}{3}$; costal process stout, bent at basal $\frac{1}{3}$, broadened to apex, terminal $\frac{2}{3}$ round dorsally, straight ventrally, obtuse apically. Juxta linguiform, ventral margin round, dorsal margin with V-shape projection. Vinculum as broad as tegumen, broadly extended and linguiform distally, slightly protruding apically. Phallus straight, slightly broadened to base, spinulate in terminal $\frac{1}{5}$; dorsal carina sagittate, spinulate; a narrow, strongly sclerotized zone in terminal $\frac{1}{4}$ of ventral area; vesica tubular, with a cornutal zone comprised of 9 to 11, long spines near the distal end.

Female genitalia: Ovipositor 3x longer than A7; apophyses posteriores very slender, 2x as long as apophyses anteriores; apophyses anteriores needle-like, basal $\frac{1}{4}$ very slender. Ductus bursae slender, sclerotized except for anterior $\frac{1}{6}$, posterior $\frac{2}{5}$ broadened to ostium bursae (antrum), anterior $\frac{1}{6}$ as broad as ostium bursae, flattened, concave medially, with a band-like sclerite continuous from sclerotized part of ductus bursae. Corpus bursae elliptical with four short, dentiform signa with sparsely spinulate, oval basal plates.

Types

HOLOTYPE – ♂, “A.MAHUIDA-EL CRUCE | (55) 600m, | NEUQUEN ARGENT[INA] | 9-X-82 [9 Oct. 1982] | LEG. M.Y P. GENTILI”, “Genitalia slide ♂ | By JC SOHN | USNM 96485” [a green label]. PARATYPES (19♂, 11♀) – ARGENTINA [Catamarca] 1♀, Andalgala, 4-II-1972 (WD Duckworth), USNM-96406. [Neuquén] 1♂, Rio Limay, Arroyito, 16-XI-1978 (Mision Cientifica Danesa), USNM 22681; 1♀, ditto,

16-XII-1978 (Mision Cientifica Danesa); 1♂, ditto, 18-XII-1978 (Mision Cientifica Danesa), USNM 22477 [in capsule]; 1♀, ditto, 22-III-1979 (Mision Cientifica Danesa), USNM 22479 [whole body dissection, in capsule]; 1♀, A. Mahuida-El Cruce, 600 m, 9-X-82 (MYP Gentili); 1♂, 2♀, La Pintada Roth, 650m, 21-I-1983 (MYP Gentili), USNM-96413 (female); 3♂, Neuquen, Aguada Florencio, 870m, 6-I-86 (MYP Gentili); 2♀, Neuquen, Bajada Marucho, 870m, 21-XII-86 (MYP Gentili), USNM-96405; 3♂, 2♀, Neuquen, Chorriaca, 1100m, 14-II-87 (MYP Gentili), wing venation slide SJC-W025; 2♂, 1♀, El Chocon, 400m, 6-XII-1987 (MYP Gentili). [Mendoza] 1♀, Va. El Salto, 12km. SW., Potrerillos, 20-XII-1973 (CM & OS Flint); 1♂, 1♀, 4km. East, Potrerillos, 20-22-XII-1973 (CM & OS Flint); 5♂, Bardas Blancas, 1450m, 13-II-87 (MYP Gentili), one male dissected & unmounted. [Rio Negro] 1♀, S.C. de Bariloche, Colonia Suiza, 800m, 18-X-1981 (Nielsen & Karsholt), USNM 22478.

Distribution

Argentina (Catamarca, Neuquén, Mendoza, Rio Negro).

Etymology

The species is named after Dr. Donald (“Don”) Davis (U.S. National Museum of Natural History, Smithsonian Institution, Washington DC) who has assisted my research.

DISCUSSION

Comparisons among Urodid Genera

Urodidae are comprised of 6 genera including *Anomalomeuta*. These genera can be distinguished by external and male genital features. The female genitalia of Urodidae possess features useful for species-level identifications but show no diagnostic differences among the genera. The female genitalia even of congeners are usually too divergent to provide any common feature. Therefore, the keys to distinguish the urodid genera below are based only on external features and structures of the male genitalia.

KEY TO THE GENERA OF URODIDAE BASED ON EXTERNAL CHARACTERISTICS

- 1. No antemedial patches of raised scales on forewing 2
- One or two antemedial patches of raised scales on forewing 4
- 2. Hair-pencil present on anterior margin of hindwing 3
- Hair-pencil absent on anterior margin of hindwing *Anchimacheta*

- 3. Male antennae filiform *Incawockia*
- Male antennae lamellate *Urodus*
- 4. Small black spots of raised scales present on dorsal surface of forewing along veins 5
- No small black spots of raised scales on forewing *Wockia*
- 5. Two patches of raised scales in the forewing antemedial line *Spiladarcha*
- One patch of raised scales in the forewing antemedial line *Anomalomeuta* **gen. nov.**

KEY TO THE GENERA OF URODIDAE BASED ON MALE GENITALIA

- 1. Costal process present on both valvae 2
- No costal process on the valva 5
- 2. Valvae symmetrical 3
- Valvae asymmetrical *Anomalomeuta* **gen. nov.**
- 3. Phallus with coecum 4
- Phallus without coecum *Wockia*
- 4. Tegumen above gnathos articulated, with a pair of digitate projections *Anchimacheta*
- Tegumen above gnathos unarticulated or, if articulated, with an elongate process *Urodus*
- 5. Ventral surface of tegumen above gnathos with a pair of spinose areas *Spiladarcha*
- Ventral surface of tegumen above gnathos without spinose area. *Incawockia*

Asymmetric Male Genitalia of *Anomalomeuta*

Asymmetric genitalia can be found at least ten animal phyla (Schilthuizen 2013) and widespread among insects, including Lepidoptera (Ludwig 1932). It is known that asymmetric genitalia have evolved at least 30 times independently in 11 superfamilies and 18 families of lepidopterans (Huber et al. 2007). Such a characteristic, however, has never been reported from Urodoidea, which currently includes 66 species (Nieukerken et al. 2011). *Anomalomeuta* as described in this study is the only genus of the superfamily that has asymmetric genitalia.

Huber et al. (2007) found that genital asymmetry is predominantly limited to the males in insects. *Anomalomeuta* also has asymmetric components only in the male genitalia, involving 2 structures, i.e. the vesica of the phallus and the valvae. In fact, asymmetry of the eversible vesica is nearly universal in Lepidoptera (Chapman 1902) and appears associated with asymmetry in the female internal genitalia (Huber et al. 2007). In contrast, asymmetry of the ‘accessory’ components sensu Huber et al. (2007) occurs in relatively limited numbers of Lepidoptera and appears to be unrelated to female genital structures (Huber et al. 2007). The latter case can be observed in

Anomalomeuta that has the left valva larger than the right one and also lacks a costal process.

At least seven hypotheses have demonstrated the origin and functional advantages of the genital asymmetry (reviewed in Schilthuizen 2013). Asymmetry in the valvae or other clasping devices of the lepidopteran male genitalia very likely involves the copulation position (Huber et al. 2007). It is known that most of the lower lepidopterans engage in common mating postures (Kozlov 1985). The male first approaches the female side by side, then bends his abdomen 180° towards the tip of female abdomen and grasps the female genitalia using his valvae. Shortly thereafter, the male moves his body 180° away from the female and assumes an end-to-end position sensu Huber et al. (2007). To facilitate this change in position, the male has to twist his abdomen. Otherwise it would result in an inverted contact with the female genitalia. The asymmetric valvae of *Anomalomeuta* may provide the male with an advantage by allowing effective grasping the female genitalia in the side-by-side position. However, the copulatory behavior of *Anomalomeuta* remains unknown. Another possibility is functional segregation between the left and right valvae, with the gracillariid *Phyllonorycter* (subgenus *Asymmetrivalva*) representing a good example

(Kuznetsov & Baryshnikova 2004). Interestingly, similar to *Anomalomeuta*, the male genitalia of *Phyllonorycter*, if asymmetric, usually have one valva larger than the other. *Anomalomeuta* possesses a narrower body and wings than other urodids that have symmetrical male genitalia. It would be interesting to test whether such differences affect copulation position and hence male genitalia symmetry.

ACKNOWLEDGMENTS

I would like to thank Dr. Erik J. van Nieuwerkerken (Naturalis Biodiversity Center, Leiden, Netherlands) and two anonymous reviewers for critically editing the manuscript and Dr. Donald Davis (United States National Museum of Natural History, Smithsonian Institution, Washington, DC) for allowing me to examine specimens under his care and for reviewing an early draft of the manuscript. Financial support was provided by the U.S. National Science Foundation's *Assembling the Tree of Life* program, award number 0531769.

REFERENCES CITED

- CHAPMAN, T. A. 1902. On asymmetry in the males of hemarine and other sphinges. *Trans. Entomol. Soc. London* 1902: 679-692.
- CLARKE, J. F. G. 1941. The preparation of slides of the genitalia of Lepidoptera. *Bull. Brooklyn Entomol. Soc.* 36: 149-161.
- DUGDALE, J. S., KRISTENSEN, N. P., ROBINSON, G. S., AND SCOBLE, M. J. 1998. The smaller Microlepidoptera-grade superfamilies, pp. 217-232 *In* N. P. Kristensen [ed.], *Lepidoptera, Moths and Butterflies, Vol. 1: Evolution, Systematics, and Biogeography. Handbook of Zoology Vol. IV Arthropoda: Insecta, Part 35*. Berlin: Walter de Gruyter GmbH & Co.
- HEPPNER, J. B. 1984. *Atlas of Neotropical Lepidoptera. Checklist: Part 1. Micropterigoidea – Immoidea*. Hague: Dr. W. Junk Publishers.
- HEPPNER, J. B. 2010. *Incawockia*, a new genus and species from Peru (Lepidoptera: Urodidae: Galactiinae). *Lepid. Novae* 3: 154-158.
- HODGES, R. W. 2005. Chapter 30. Order Lepidoptera, pp. 571-647 *In* C. A. Triplehorn and N. F. Johnson [eds.], Borror and DeLong's Introduction to the Study of Insects. 7th edn., Belmont: Thomson Books/Cole.
- HUBER, B. A., SINCLAIR, B. J., AND SCHMITT, M. 2007. The evolution of asymmetric genitalia in spiders and insects. *Biol. Rev.* 82: 647-698.
- KLOTS, A. B. 1970. Lepidoptera, pp. 115-130 *In* S. L. Tuxen [ed.], *Taxonomist's Glossary of Genitalia in Insects*. Munksgaard, Copenhagen.
- KOZLOV, M. V. 1985. Precopulatory behavior of lower Lepidoptera. *Entomol. Rev.* 83: 469-473.
- KUZNETSOV, V. I., AND BARYSHNIKOVA, S. V. 2004. Evolutionary-morphological approach to the systematics of leafmining moths of the genus *Phyllonorycter* Hbn. (Lepidoptera, Gracillariidae) with account of species feeding specialization. *Entomol. Rev.* 84: 588-599.
- KYRKI, J. 1988. The systematic position of *Wockia* Heinemann, 1870, and related genera (Lepidoptera: Ditrysia: Yponomeutidae auct.). *Nota Lepid.* 11: 45-69.
- LUDWIG, W. 1932. *Das Recht-Links-Problem in Tierreich und beim Menschen*. Berlin: Springer Verlag.
- NIEUEKERKEN, E. J. VAN, KAILA, L., KITCHING, I. J., KRISTENSEN, N. P., LEES, D. C., MINET J., MITTER C., MUTANEN M., REGIER, J. C., SIMONSEN, T. J., WAHLBERG, N., YEN, S.-H., ZAHIRI, R., ADAMSKI, D., BAIXERAS, J., BARTSCH, D., BENGTSSON, B. A., BROWN, J. W., BUCHELI, S. R., DAVIS, D. R., DE PRINS, J., DE PRINS, W., EPSTEIN, M. E., GENTILI-POOLE, P., GIELIS, C., HATTENSCHWILER, P., HAUSMANN, A., HOLLOWAY, J. D., KALLIES, A., KARSHOLT, O., KAWAHARA, A., KOSTER, J. C., KOZLOV, M., LAFONTAINE, J. D., LAMAS, G., LANDRY, J.-F., LEE, S., NUSS, M., PARK, K.-T., PENZ, C., ROTA, J., SCHMIDT, B. C., SCHINTLMEISTER, A., SOHN, J.-C., SOLIS, M. A., TARMANN, G. M., WARREN, A. D., WELLER, S., YAKOVLEV, R. V., ZOLOTUHN, V. V., AND ZWICK, A. 2011. Order Lepidoptera Linnaeus, 1758 *In* Z.-Q. Zhang [ed.], *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa* 3148: 212-221.
- SCHILTHUIZEN, M. 2013. Something gone awry: unsolved mysteries in the evolution of asymmetric animal genitalia. *Animal Biology* 63: 1-20.
- SOHN, J.-C. 2012. Taxonomic review of *Spiladarcha* Meyrick (Lepidoptera: Urodoidea: Urodidae) with a new species from Venezuela. *Entomol. Sci.* 15: 303-308.
- WOOTTON, R. J. 1979. Function, homology and terminology in insect wings. *Syst. Entomol.* 4: 81-93.