AN ENIGMATIC NEW POTAMANAXAS (HESPERIIDAE: PYRGINAE: ERYNNINI) IS A VISUAL MOSAIC OF CHARACTERS FROM DISTANTLY RELATED SPECIES

Nick V. Grishin

Howard Hughes Medical Institute and Departments of Biophysics and Biochemistry, University of Texas Southwestern Medical Center, 5323 Harry Hines Blvd, Dallas, TX, USA 75390-9050; Research Associate, McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL, USA 32611-2710; email: grishin@chop.swmed.edu

Abstract — A new species of Potamanaxas is described from the Chocó region in northern Ecuador. P. zagadka, sp. nov., stands out from other members of the genus both in the structure of male genitalia not being very similar to any other Potamanaxas, and unusual wing patterns that combine characters of several species. While its exact phylogenetic affinities remain puzzling, this new species is likely to be important for better understanding of this genus’ evolution and may be a prototype for its own species group. Additionally, significant differences in male genitalia and wing patterns and sympathy with P. laoma (Hewitson, 1870) in Ecuador suggest that P. trex Evans, 1953 new status is a species-level taxon and not a subspecies of P. laoma.

Resumen—Se describe una nueva especie de Potamanaxas de la región del Chocó en el norte de Ecuador. P. zagadka, sp. nov., se destaca de los otros miembros del género porque la estructura de los genitales masculinos es poco similar a las otras Potamanaxas, y además los patrones inusuales de las alas combinan características de varias especies. Aunque sus afinidades exactas filogenéticas siguen siendo poco claras, es probable que esta especie nueva sea importante para una mejor comprensión de la evolución de este género, y que pueda ser un prototipo de su propio grupo de especies. Además, las diferencias significativas de los genitales masculinos y los patrones de las alas y la simpatría con P. laoma (Hewitson, 1870) en Ecuador indican que P. trex Evans, 1953 nuevo estatus es un taxón de nivel de especie y no una subespecie de P. laoma.

Key words: taxonomy, skipper butterfly, Neotropics, parallel evolution, cucullus.

While assignment of some butterflies to a genus is straightforward, their phylogenetic affinities within a genus are far from clear. For some taxa, different characters suggest different phylogenetic relatives and species appears to look like a mixture of the characters of several, not likely closely related species. This phenomenon has been mentioned by Nicolay & Robbins (2005). For instance, Strymon jacqueline Nicolay & Robbins, 2005 exhibits dorsal wing pattern of S. dindus (Fabricius, 1793), but ventral wing pattern is similar to S. megarus (Godart, [1824]); S. giffordi Nicolay & Robbins, 2005 shares dorsal wing pattern with S. venterator (H. Druce, 1907) and ventral wing pattern with S. megarus. Such conflicting affinities present challenges when new species are discovered and analyzed in the context of described taxa. However, it is always exciting to find an unusual butterfly that looks like a chimera of other species.

One of such species is described here. Its visual chimerism is even more convoluted - hindwings look like species from one group, forewings suggest another species group and male genitalia remind of a third group. Nevertheless, two points are clear. First, the species belongs to Potamanaxas Lindsey, 1925. Second, it is new and quite distinct from all described species of this genus. A hypothesis that its closest relatives are in the P. laoma (Hewitson, 1870) group is presented, which agrees with the forewing characters and mostly with the author with Nikon D200 or D800 cameras through a 105 mm f2.8G AF-S VR Micro-Nikkor lens; dissected genitalia were photographed in glycerol with Nikon D200 camera without lens through microscopes. Images were assembled and edited in Photoshop CS5.1. Dissected genitalia photographs were taken in several focus planes and stacked in Photoshop to increase apparent depth of field.

RESULTS

Browsing through Potamanaxas specimens at the MGCL collection, I stumbled upon an unusually looking small specimen, which not only caused problems with immediate identification to species, but also in figuring out its potential closest relatives. This specimen had dark brown wings with a discal cream band, long on both wings and irregular, thus reminding of a tiny P. paralus (Godman & Salvin, 1895). However, the dorsal forewing pattern of spots in Cu₁₋₂A and 2A cells and distal half of the discal cell spot crossed by a diagonal dark band indicated that it is instead closer to the P. laoma group. Genitalia prepared by S. R. Steinhauser were not particularly similar to any known species and in lack of style from sacculus, almost smooth and only very finely granular ventral surface of gnatoh and general shape of cucullus were reminiscent of P. cranda Evans, 1953. This enigmatic species is named here.

MATERIALS AND METHODS

Potamanaxas specimens were examined in the following collections: McGuire Center for Lepidoptera and Biodiversity, Gainesville, FL (MGCL); American Museum of Natural History, New York, NY (AMNH); Natural History Museum, London, UK (BMNH); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); Museum für Naturkunde, Berlin, Germany (ZMHB); Carnegie Museum of Natural History, Pittsburgh, PA (CMNH); Academy of Natural Sciences Philadelphia Collection, Philadelphia, PA (ANSP); Senckenberg Museum für Tierkunde, Dresden, Germany (MTD); Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (DEI); and Texas A&M University Insect Collection, College Station, TX (TAMU). Standard entomological techniques were used for dissection (Robbins 1991), i.e. adult abdomen was broken off, soaked for 40 minutes (or until ready) in 10% KOH at 60°C (or overnight at room temperature), dissected and subsequently stored in a small glycerol-filled vial on the pin under the specimen. Genitalic and wing venation terminology follows Steinhauser (1981). Length measurements are in metric units and were made from photographs of specimens taken with a scale and magnified on a computer screen. Photographs of specimens and dry genitalia were taken by

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**Potamanaxas zagadka** Grishin, new species (Plate VIII, Figs. 1–2; Plate IX, Fig. 11; Plate X, Figs. 15, 22)

Description.—Male (Plate VIII, Figs. 1–2): right forewing length = 13.5 mm in holotype. Forewing twice as long as wide, rounded at apex and tornus, costa convex, margin convex from apex to Cu₁ vein, nearly straight from Cu₁ to 2A. Dorsal forewing dark brown, cream discal band from costa to 2A vein separated into spots by brown scales along the veins and central crease of discal cell, diagonal (directed along the vein R₁) brown bar in distal half of the posterior spot in discal cell and brown bar (perpendicular to costa) in anterior half from between the origin of R₁ and R veins, cream spot in Cu₁₋₂A half the length of the spot in Cu₁₋₂Cu₁, cell, band pale brown anteriad of discal cell, detached from the band cream spot at the base of M₁₋₂Cu₁, cell, distal third of 2A cell cream-yellow, vague pale yellowish spot near 2A vein at the base of Cu₁₋₂A cell based of the discal spot and a doublet of vague yellowish areas distal of the discal spot, a hint of paler brown spots in cells from apex to the base of M₁ vein and submarginal row of poorly defined very diffuse yellowish spots. Ventral forewing brown, cream discal band widening from distal third of costal cell to
anal margin, cell 2A mostly cream, band distal margin almost straight, spot at the base on M₃-Cu₁ cell extends distad beyond the band margin, basal band margin diffuse overscaled with slate and fused with the brown basal area, dorsal pattern vaguely showing inside the band, diffuse cream-yellow spots subapically in cells between R₈ and M₂ veins, near costa in R₁-R₂ cell, hint of paler spots in each cell along the wing margin and postdiscally near the distal end of discal cell. **Hindwing** nearly triangular, slightly longer than wide, rounded at apex and tornus, margin convex from apex to Cu₁ vein, nearly straight from Cu₁ to 2A. Dorsal hindwing dark brown, cream discal band about 1/4 of the wing width from costa to vein 2A, veins inside the band scaled with dark brown, paler band at costa, overscaled with brown near 2A vein, band margins irregular, band widest by the costa, constricted from Rs to M₂, widening in cell M₂-M₁, and narrowing towards 2A, paler brown areas inside brown background distad the band, a hint of paler brown spots along the wing margin. **Ventral hindwing** mostly pale, slate-yellowish, distal third brown, basal margin of brown area irregular, offset based between veins Rs and M₁, and near the vein Cu₁ in Cu₁-2A cell, brown area constricted to the margin from the middle of cell Cu₁-2A to anal margin, diffuse pale-yellow spots in cells along the inner margin and a hint of brown spots slightly paler than the background by the wing margin in the brown area, basal third of the wing darker than discal area, less yellow, more slate and with brown scales, wing slat from vein 2A to anal margin, brown along the margin. **Fringes** brown, the same color as wing margins above and below, with pale scales at pale discal bands. **Head** and palpi brown above slate below, antennae brown with slate scales at joints beneath and on the sides. **Thorax** dark-brown above, slate below; legs mostly slate and cream with brown scales. Abdomen used for genitalic preparation prior to examination, no scales remain. **Male genitalia** (Plate IX, Fig. 11; Plate X, Figs. 15, 22): tegumen slightly wider than long, half-circular at anterior margin in dorsal view, construed caudad of vinculum, small medial bulge in lateral view; uncus divided with arms about the width of tegumen at constriction; gnathos divided caudad, almost smooth, not granular on its surfaces caudad, separated from uncus; saccus long and narrow, longer than tegumen; penis about twice the saccus length, juxta rounded; valva narrow, its "height" (dorso-ventral) about half of its length (anterior-posterior) from the base to beginning of cucullus, cucullus about as long as valva, not separated from the valva, narrowing caudad towards the middle and rounded at the tip in lateral view, dorsal margin irregularly serrated, with a broad and short tooth-like process at the base, the process directed inwards and dorsad, its caudal edge with a smaller and wider tooth near the base and even smaller serrations caudad; saccus without a style-like projection at the base.

**Female:** unknown or unrecognized.

**Types.**– Holotype male, with the following labels: white, handwritten: || ECUADOR-ESM | LITA 650 M | IX-02 || ; white, printed: || Allyn Museum | Acc. 2003-9 || ; white, printed: || Genit. Vial No. | SRS-5745 || ; red, printed: || HOLOTYPE | Potamanaxas | zagadka GRISHIN || . The holotype is in the collection of the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, FL.

**Type locality.**– Ecuador: Esmeraldas Province, near Lita, elevation 650 m.

**Etymology.**– “zagadka” (Russian, Ukrainian and Bulgarian: загадка, Polish: zagadka, pronounced as “zah-gut-kah” with the stress on the second syllable, or /za’gatka/ in International Phonetic Alphabet) is a Slavic word for riddle, puzzle, conundrum, or enigma and refers to the unusual “mosaic” appearance of this species that makes it difficult to find its close relatives within *Potamanaxas*. The name is a non-latinized noun in apposition.

**Distribution and phenology.**– The species is known only from the holotype collected in the Chocó region of northern Ecuador in September.

**Diagnosis:** The new species belongs to *Potamanaxas* because it possesses the characters listed for the genus by Evans (1953). Namely, the forewing costa is convex, apex rounded, not truncate, outer margin (=termen) convex, inner margin (=dorsum) not concave. The forewing cell is shorter than the inner margin and the posterior branch of vein M₃ is invisible. Forewing Sc vein (=vein 12) is short, ending basad of the end of discal cell, and the R₁ vein (=vein 11) ends over the end of the discal cell. Hindwing costa and inner margin are about equal in length. Dorsally, white-banded, no hyalinity is present in pale areas on wings. Mid-tibiae lack spines. The third segment of palpi is porrect (i.e. “in line with the body”, Evans (1949), p. xviii). Antennae are about half of the costa in length, with the club arcuate about its center, apicalcely sharply pointed, nearly equal in length to the unbtent portion of the club, and the nudum (scaleless portion of antennal club) consists of around 17 segments. Costal fold, thoracic pouch and tibial tufs are absent.

Using Evans’s (1953) *Potamanaxas* key, the new species keys out to *P. frenda* Evans, 1953, which is apparently wrong, because *P. frenda* possesses short cucullus, about the same length as the basal process of cucullus, and much shorter than the rest of the valva, and a thumb-like process off saccus (Plate X, Fig. 16). The new species has a very long cucullus, almost as long as the rest of the valva, and a saccus without a process, barely with a hint of a bulge (Plate IX, Fig. 11; Plate X, Fig. 15). Wing patterns, especially those of the hindwing, which has broader pale areas in *P. frenda*, also differ (Plate VIII, Figs. 1–4).

No described *Potamanaxas* species comes very close to *P. zagadka* n. sp.

In facies, it may be immediately recognized by *P. laoma*-like dorsal forewing with almost square but rounded at angles Cu₁-2A cell cream spot being smaller than the cream spot above it (in cell Cu₁-Cu₂), cream streak in 2A cell positioned near tornus rather than directly under the Cu₁-2A cell, and a small pale spot at the base of M₁-Cu₁ cell; but very different from *P. laoma* hindwing, which is mostly brown, without prominent spotting in distal third, and with a discal cream band from costa to vein 2A; this band does not contain brown spots, is rather narrow (less than a third of wing’s length) and its constituent spot in cell Cu₁-Cu₂ is well defined at edges and is larger than the spot at the base of M₁-Cu₁ cell.

More precisely, the following characters (a combination of the first four of which is diagnostic), set the new species apart from all other *Potamanaxas*:

1. Cucullus extended and narrow, as long as the rest of the valva, terminally rounded in lateral projection; (2) basal process of cucullus strongly developed, clav-like, slightly more than twice longer than wide at the base, terminates with a sharp point, directed partly inwards and posteriorwards, with an additional shallow "tooth" on its caudal margin; (3) ampulla-costa only slightly convex, not extending further dorsal than the process of cucullus, a portion of valva that does not include cucullus is almost rectangular, twice longer (cephalocaudal direction) than "tall" (dorsoventral direction), dorsal edge of ampulla is at close right angle with the process of cucullus, a gap between them is broad and L-shaped; (4) saccus lacks a process at the base and only with a vaguely defined bulge; (5) dorsal hindwing dark-brown with a discal cream band, crossed by brown veins, from costa to vein 2A, width of the band is about a quarter of wing’s length, no brown spots inside the band, cream spot in this band at the base of Cu₁-Cu₂ cell is strongly developed with sharply defined edges, and is larger than the spot at the base of M₁-Cu₁ cell; hindwing largely brown without clearly defined pattern basad and distad of the cream band; (6) ventral hindwing with a broad (1/3 of the wing length) brown band at the margin not separated into spots; (7) dorsal forewing discal cream spot in Cu₁-2A cell is about half in length of the triangular pale spot in Cu₁-Cu₂ cell, cream streak in 2A cell is close to tornus, distinctly distad of the Cu₁-2A spot and not just below it; (8) dorsal forewing with a cream spot at the base of M₁-Cu₂ cell, detached from the discal band; (9) dorsal forewing discal cream spot posterior of the central crease with diagonal band of brown scales in distal third, distal third of cream spot anterior of the crease with a similar brown band perpendicular to costa.

**DISCUSSION.**

At the first glance, this dark *Potamanaxas* species reminds of a small *P. parulus* - dorsally dark brown wings with discal cream bands (compare Plate VIII, Figs. 1 and 7). However, on a more detailed look the differences are notable: relative size of the forewing cream spots in Cu₁-Cu₂ and Cu₁-2A cells - these spots being about equal length in *P. parulus*, and the lower spot being half the length of the upper spot in the new species; positioning of the cream streak in cell 2A on the dorsal forewing - this streak being right under the Cu₁-Cu₂ discal spot in *P. parulus*, and the streak being closer to the tornus in the new species; and the discal cell cream spot is divided by brown scales along central crease and both halves are crossed by bands of brown scales in the new species, but these scales are absent in *P. parulus* except near the distal margin by the central crest.

These characters of the new species were attributed by Evans (1953) to the *P. laoma*, *P. frenda* and *P. andraemon* (Mabille, 1898) groups. It is likely that the new species is closely related to them. While it keys to *P. frenda* due to the absence of postdiscal spots on the forewing (Evans 1953: 143), facies of the two species are very different (compare Plate VIII, Figs. 1 and 3). In the *P. laoma* group, the darkest species is *P. trex* Evans, 1953 **new status** (Plate VIII, Fig. 5), but its facies do not match well either, especially the hindwing pattern. I treat *P. trex* as a species-level taxon and not a subspecies of *P. laoma*.
because: 1) male genitalia valvae are shaped very differently, more elongated, without a “neck”-like narrow base of cucullus separating it from the rest of the valva in *P. laoma* (see *P. laoma* syntype valva Plate VII, Fig. 42 in Grishin 2013b); its cucullus points posterior, is not bulbous near its distal end, and the basal process of cucullus is shorter and broader (Plate X, Fig. 17); vs. cucullus bending postdorsadors, bulbous near the distal end and with a longer and thinner basal process in *P. laoma*; 2) it is generally smaller and darker than *P. laoma*, e.g. distal half of dorsal forewing cell Cu₂-2A is violet-brown, without cream-colored spots of *P. laoma*; and its discal cream-colored spot in cell Cu₂-2A is elongated and fully separated into two segments by a belt of dark scales along ventigial vein 1A; this spot in *P. laoma* is narrower especially by the vein Cu₂, mostly entire and broad-L shaped, but may be partly interrupted by dark scales on the sides; 3) both taxa have been collected in or near Sangay National Park, Ecuador (Pettit 2013).

In contrast to *P. zagadka* n. sp., no known *P. laoma* or *P. andraemon* group species possesses a single discal hindwing band clearly reaching posterior of discal cell with dark brown essentially unspotted background elsewhere. In described species, pale areas are largely by costa and apex and are divided by a brown central row of partly fused postdiscal brown spots. These spots are defined even in *P. tress*, which has mostly dark hindwing (Plate VIII, Fig. 5). Ventrally, described *Potamanaxas* species from the *P. frenda*, *P. laoma* or *P. andraemon* groups exhibit brown spots on a largely pale hindwing (Plate VIII, Figs. 4, 6). The new species is characterized by an entire marginal band more similar to the one seen in *P. paralus*.

With hopes to clarify position of the new species within *Potamanaxas*, male genitalia of all *Potamanaxas* species with extended cuculli were compared. Genitalia for representative taxa, assembled from those long cuculli in Evans sketches (Evans 1953) with inclusion of *P. quira* E. Bell, 1956, which was described after the Evans book was published, are shown in Plate X, Figs. 16–21 & 23–36; many genitalia are of the primary type specimens. These and many other *Potamanaxas* specimens are shown in Warren et al. (2013). A comprehensive compilation of references about all taxa is given by Mielke (2005) with additional studies done by Grishin (2012, 2013a,b). Compared to *P. zagadka* n. sp. (Plate IX, Fig. 11; Plate X, Figs. 15) none gives a very close match. In some, cucullus is too short, although it may appear long on a rough Evans sketch, and those are: *P. frenda* (Plate X, Fig. 16), *P. tress* (Plate X, Fig. 17), *P. flavofasciata* (Hewitson, 1870) (Plate X, Fig. 21), and *P. paphos* Evans, 1953 (Plate X, Fig. 31). *P. effusa* (Dr audit, 1922) has the process of cucullus with a bulbous tip (Plate X, Fig. 26) and in the new species the process narrows to a point instead (Plate X, Fig. 15). The new species lacks the basal process of sacculus, which is prominently developed in many *Potamanaxas* species, i.e. *P. paralus* (Plate X, Fig. 18), *P. latrea* (Hewitson, 1875) subspecies (Plate X, Figs. 27–29), *P. thestia* (Hewitson, 1870) (Plate X, Fig. 30), *P. lamasi* Grishin, 2013 (Plate X, Fig. 34), *P. fuma* Evans, 1953 (Plate X, Fig. 35) and *P. forum* Evans, 1953 (Plate X, Fig. 36). While the cucullus of the *P. thorius* (Hewitson, 1870) type specimen is broken off (Plate X, Fig. 24), its tegumen is armed with a prominent, head-shaped bulge at the distal end (Plate X, Fig. 23). This bulge is barely defined in *P. zagadka* n. sp. Complete genital capsule of a *P. thorius* specimen is shown in Plate X, Fig. 25 for comparison. *P. quira* (Plate X, Fig. 32) and *P. perornatus* (Plate X, Fig. 33) can be excluded due to their angled costa, thinner basal process of cucullus and cucullus narrowing to a point. Interestingly, this leaves us with *P. cranda* Evans, 1953 (Plate X, Figs. 19–20), whose cucullus and valva body are somewhat similar in shape to those of *P. zagadka* n. sp., but their wing patterns are quite different (compare Plate VIII, Figs. 1–2 and 9–10), and *P. cranda* lacks a claw-like process at the base of cucullus. Apparently, none of the described species is very genitalically close to *P. zagadka* n. sp.

Currently, *P. zagadka* n. sp. is known from a single specimen from Ecuador. However, with requests for identification I was shown photographs of live individuals from West Andes in Colombia (Plate X, Figs. 12–14). While not completely agreeing with the facies of *P. zagadka* n. sp. and being paler and more patterned on the forewing, these individuals appear to be close to *P. zagadka* n. sp., and are either this species or yet another unnamed species very close to it. Among all *Potamanaxas* species, dorsal hindwing pattern is uniquely shared between these individuals and *P. zagadka* n. sp. It is possible that *P. zagadka* n. sp. is the first representative of yet another species group in a large and complex genus *Potamanaxas* and future studies will address these questions.

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Figs. 1–10. *Potamanaxas* primary type specimens, males. 1–2. *P. zagadka* n. sp. holotype, Ecuador: Esmeraldas Province, “Lita”, 650 m, Sep-2002, Allyn Museum Acc. 2003-9, genitalia vial No. SRS-5745 (genitalia Plate IX, Fig. 11); 3–4. *P. frenda*, [holo]type, Peru, ex. de Mathan, R. Oberthür Coll., Brit. Mus. 1931-136, specimen No. BMNH(E) #1054200 (genitalia Plate X, Fig. 16); 5–6. *P. trex*, [holotype], Ecuador, Hewitson collection, specimen No. BMNH(E) #1054195 (left valva Plate X, Figs. 17); 7–8. *P. paralus* syntype, Peru: Cosnipata Valley, leg. H. Whitely, Godman-Salvin Collection 1912-23, type H 772, specimen No. BMNH(E) #1054005; 9–10. *P. cranda* holotype, Costa Rica, J. J. Joicey Collection B.M. 1925-451, specimen BMNH(E) #1054194 (valva Plate X, Figs. 19-20). Dorsal and ventral surfaces are shown on odd- and even-numbered figures, respectively. Labels are shown between the views of a specimen, and for *P. paralus* also above and below the specimen. Round white type label are shown in dorsal and ventral views, except the one placed near the abdomen of *P. paralus*, because it does not contain text below. Labels are reduced 2.5 times compared to specimens: small scale bar below the lectotype labels refers to labels, and larger scale bars refer to specimens. 1–2 is in MGCL collection, others are in BMNH collection and photos are copyright (©) Trustees of the Natural History Museum, London; used with permission.
Fig. 11. *Potamanaxas zagadka* n. sp., male genitalia, holotype. Prepared by S. R. Steinhauser, valvae and penis with juxta separated from the genital ring, vial No. SRS-5745. For each image, genital part is specified on top and shown view is listed at the bottom: a. - left valva, lateral interior; b. - right valva, lateral interior; c. - right valva, lateral exterior; d. - left valva, lateral exterior; e. - right valva, posteriorlateral interior; f. - right valva, dorsal; g. - right valva, ventral; h. - valvae, ventrolateral, interior; i. - genital ring (tegumen, uncus, gnathos, vinculum & saccus), ventral; j. - genital ring, dorsal; k. - genital ring, posterior; l. - genital ring, anteriorlateral; m. - genital ring, left lateral; n. - genital ring, right dorsolateral; o. - genital ring, right lateral; p. - penis & juxta, anterior; q. - penis & juxta, left lateral; r. - penis & juxta, ventral; s. - penis & juxta, dorsal. All images are to scale, except h, which was reduced to fit the space.
Figs. 12–14. *Potamanaxas* sp. live individuals. Colombia: West Andes, Risaralda Dpt., Pueblo Rico, road to Monteriza Peak. These individuals are either *P. zagadka* n. sp. or a yet unnamed sibling species. 12–13. 1500 m, 1-Sep-2012, by Kim Garwood; 14. 12-Sep-2010, by Shirley Sekarajasingham.


All images are to scale. "F" indicates mirror image (left-right inverted).