New Genera of Western Hemisphere Pseudomorphini (Insecta, Coleoptera, Carabidae) with notes on their distributions, ways of life, and hypothesized relationships

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SUMMARY

The Western Hemisphere Pseudomorphini was last revised by Notman in 1925 based on only a few known species (22) and paltry few specimens (73). A recent study of collections from throughout the Americas (1360 specimens) has revealed numerous new species contained in four new genera plus the nominate genus, and a change in status of a previously described subgenus. *Manumorpha* *n. gen.* (Type species – *Manumorpha biolat* Erwin & Geraci, new species, Ecuador, Perú), *Samiriamorpha* *n. gen.* (Type species – *Samiriamorpha grace* Erwin & Geraci, new species, Perú), *Yasunimorpha* *n. gen.* (Type species – *Yasunimorpha piranha* Erwin & Geraci, new species, Ecuador), and *Tuxtlamorpha* *n. gen.* (Type species – *Pseudomorpha tuxtla* Liebeher & Will, México) are described and their respective type species designated. *Notopseudomorpha* Baehr 1997, **new status**, is accorded generic rank with *P. laevissima* Chaudoir as type species. A summary of the contained species in each higher-level taxon and their overall distributions are provided. A genus level phylogeny for Western Pseudomorphini is inferred using maximum parsimony based on 33 adult morphology characters.

**Keywords:** Carabidae, Pseudomorphini, Western Hemisphere, taxonomy, phylogeny, way of life
RESUMEN

Los Pseudomorphini del Hemisferio Occidental fueron revisados por última vez por Notman en 1925 en base a solo unas pocas especies (22) y especímenes (73). Un estudio reciente de colecciones a lo largo de las Américas (1360 especímenes) a revelado numerosas especies nuevas contenidas en cuatro géneros nuevos además del género nominal, y un cambio en el estado de un género previamente descrito. Manumorpha n. gen. (Especie tipo - Manumorpha biolat Erwin & Geraci, nueva especie, Ecuador, Perú), Samiriamorpha n. gen. (Especie tipo - Samiriamorpha gracil Erwin & Geraci, nueva especie, Perú), Yasunimorpha n. gen. (Especie tipo - Yasunimorpha piranha Erwin & Geraci, nueva especie, Ecuador), and Tuxtulamorpha n. gen. (Especie tipo - Pseudomorpha tuxtula Liebheer & Will, México) se describen y se designa respectivamente su especie tipo. Notopseudomorpha Baehr 1997, nuevo estado, se decide como rango genérico con P. laevissima Chaudoir como especie tipo. Un resumen de las especies contenidas en cada taxa de nivel superior y su distribución general son provistos. La filogenia a nivel de género para los Pseudomorphini Occidentales es inferida usando máxima parsimonia basada en 33 caracteres morfológicos de los adultos.

INTRODUCTION

Pseudomorphini Newman 1842 is a Western Hemisphere – Australasian – Afroaustral Tribe of the beetle family Carabidae. Western Hemisphere members of this markedly unusual Tribe, in physical and behavioral attributes, were previously placed in a single genus, Pseudomorpha Kirby 1825. Their collective species' distributions encompass both the Nearctic, Neotropical, and northern parts of the Neaustral Realms. In this paper, in preparation for a complete revision of Pseudomorphini of the Western Hemisphere, we describe four new genera and elevate a subgenus status taxon to genus level.

George Horn (1867) wrote of these beetles: “These insects are not easy to obtain, as they are provokingly agile.” E.A. Schwarz studied specimens of this Tribe in the early 20th Century and turned his notes over to Howard Notman of the Brooklyn Entomological Society; therein, Schwarz wrote, “... Pseudomorphas are numerous in their habitat, but are difficult to capture. They live in dead leaves and move with great agility, assisted by the numerous setae with which they are provided.” We now know that pseudomorpheine members are generally found in and around ant or termite nests and their immature stages in the Western Hemisphere are apparently obligatory myrmecophiles (Lenko, 1972, Erwin, 1981), perhaps even isopterophiles, as well (cf. label on a N. laevissima specimen). Adults are mostly collected at lights (UV, MV, and White) and while there on the collecting sheet, they scurry about rapidly much like tiny cockroaches, and are often very hard to grab. Notman (1925), in the only revision of the group for the Western Hemisphere, had 73 specimens at hand representing 22 species. Subsequently, Darlington (1935), Van Dyke (1943, 1953), Ogueta (1967), and Liebherr and Will (1997) accounted for six more species represented by 53 additional specimens. Thus, until now, only 126
specimens have been studied and documented in the literature. Currently, we now have 
borrowed at hand that total 1360 specimens, and that fact alone accounts for the extraor-
dinary discoveries noted below under “Accounts of Taxa.” Given the state of Carabid 
taxonomy intensively pursued by our mentors and colleagues over the past century for 
North America with in-depth knowledge, keys, descriptions, and natural histories of 
all the Tribes, this discovery of species richness in the Pseudomorphini surely must be 
regarded as the last “taxonomic goldmine” left in North America. Of course, we can 
expect many more such taxonomic gold mines in Middle and South America. 

At least two Western Hemisphere species, reportedly P. hubbardi Notman and P. 
augusta/a Horn are known to be ovoviviparous (Liebherr & Kavanaugh, 1985). All spe-
cies included in the genera of the Western Hemisphere, as far as known, are fully winged 
and male adults of many of them and some females as well have been recorded at lights 
(UV, MV, and White), thus it is likely that they are very good dispersers. However, most 
species have fairly restricted known ranges. Whether this has to do with host fidelity to 
particular ant or termite species, or simply it is a matter of difficulty in collecting them 
is unknown, however host fidelity could be tested with intensive fieldwork by digging 
up ant nests to find adults and larvae, rather than merely collecting adults at lights. In 
his study of N. laevissima (Chaudoir), Lenko (1972) reported that 7 out of 32 nests of 
the ant Camponotus rufipes (Fab.) were home to N. laevissima larvae.

MATERIALS AND METHODS

Length and width measurements follow the conventions suggested by Ball (1972) and 
Kavanaugh (1979). Apparent body length (ABL) is measured from apex of labrum to 
apex of longer elytron. Standardized body length (SBL) is given herein for the Holotype 
of each type species and is the sum of the lengths of the head (measured from the apex 
of the Clypeus to a point on midline at level of the posterior edge of the compound eyes), 
pronotum (measured from apical to basal margin along midline), and elytron (measured 
from apex of scutellum to apex of the longer elytron). In the case of species in the genus 
Notopseudomorpha and Samiriamorpha, in which members have hidden mouthparts in 
dorsal aspect, the measure is taken from the front margin of the head (frons). Total width 
(TW) is measured across both elytra at their widest point (usually this is a measure of 
the left elytron doubled because pinned specimens often do not have both elytra contigu-
ous). Pronotum length to width ratios and elytra length to width ratios are given as such 
following the TW report for each species description below. The habitus images of the 
adult beetles were made with a Leica M420 microscope and an EntoVision™ system. 
Precise measures were taken using the Archimed software embedded in the EntoVi-
sion™ system. Male genitalia were illustrated using standard pen and ink techniques; 
an image of one female reproductive system, that of P. tenebroides Notman, is provided 
here and females of an exemplar of each genus will be illustrated and described in the 
forthcoming monograph of the subtribe mentioned above (Erwin, in prep).
Maximum parsimony analyses of unordered equally weighted multistate morphology characters were performed in PAUP 4.0b10 (Swofford, 1999). A heuristic search was done using TBR branch swapping and a random addition sequence (10 reps). A bootstrap analysis was performed using a full heuristic search algorithm (10,000 replicates) and a random addition sequence (10 reps), retaining groups compatible with the 50 percent majority rule consensus. Characters were mapped onto the most parsimonious topologies recovered by the heuristic search using the “trace all changes” tool in MacClade v.4.08 (Maddison & Maddison, 2000). The genera Orthogonius and Spallomorpha were chosen a priori as outgroups.

ACCOUNTS OF TAXA

Western Hemisphere genera of Pseudomorphini Newman 1842

- Manumorpha Erwin & Geraci, n. gen. Ecuador, Perú
- Notopseudomorpha Bachr 1997, new status Middle and South America
- Pseudomorpha (s. str.) Kirby 1825 USA south to Argentina
- Samiriamorpha Erwin & Geraci, n. gen. Perú
- Tuxtlamorpha Erwin & Geraci, n. gen. México, Honduras
- Yasunimorpha Erwin & Geraci, n. gen. Ecuador

Key to the Western Hemisphere Genera of Pseudomorphini

1 Mouthparts not visible in dorsal aspect. Preocular lobe absent ........................................... 2
1' Mouthparts visible in dorsal aspect. Preocular lobe present ........................................ 3

2(1) Dorsal surface glabrous, markedly shiny.................. Notopseudomorpha Bachr 1997
2' Dorsal surface finely setiferous, not shiny

3(1) Elytra multisetiferous; body form rather broad and subdepressed with elytra not or barely tapered to broadly round apex ......................... 4
3' Elytra with only scutellar and umbilicate setae; body form narrow, somewhat cylindrical with elytra markedly tapered to apex

4(3) Dorsal surface with dense vestiture, of very long thick erect setae equal in length at least to basal 4 antennomeres, but no pubescence; body form subconvex, elytra tapered posteriorly.......................... Manumorpha Erwin & Geraci new genus
4' Dorsal surface with sparse or no long vestiture, longer setae equal in length only to at most basal 3 antennomeres, also usually with short pubescence; body form subconvex, elytra slightly tapered posteriorly or not ......................... 5

5(4') Major setae of dorsal surface erect or slightly curved posteriorly

................................................. Pseudomorpha Kirby 1825
5' Major setae of elytra posteriorly and markedly decumbent

................................................. Tuxtlamorpha Erwin & Geraci new genus
Pseudomorphini Newman 1842


PROPOSED ENGLISH VERNACULAR NAME. False-form beetles.

DIAGNOSIS: Head ventrally with deeply recess grooves for receiving antennal bases; mandibular scrobe nearly effaced, delimited by row of short setae; mentum and submentum fused; antennal scape partially visible in dorsal aspect. Anterior coxal cavities closed, median coxal cavities conjunct, metepimeron visible. Abdomen with 6 visible sterna, sternum II with medial emargination on posterior edge. Male parameres long, nearly of same length (more or less symmetrical, or not), glabrous or setose, not balteate; phallobase bonnet-shaped.

CLASSIFICATION: According to the Maddison Lab at Tucson (Ober, 2002), Pseudomorphini occupies a position in the higher Carabidae, within the Harpalinae. The male genitalic median lobe has a bonnet-like base as in the lebiomorphs, yet their accompanying parameres are large and nearly symmetrical, as in basal carabid lineages. Although most pseudomorphine lineages are without setae on the parameres, as in the more derived carabids, members of several genera in both the Western and Eastern Hemispheres have one to several short setae, as in some primitive lineages of the family. This is also true for some members of other more derived lineages such as Orthogonius, Graphipterus, and some Panagaeini. Both DNA sequences and way of life suggest that the orthogonines and pseudomorphines are related; orthogonines are termitophilous. However, all known lineages of Pseudomorphini have been so highly selected for life with ants (and possibly termites) that external structures do not help in finding more normal carabid relatives. Erwin (2007) suggested that the Tribe Xenaroswellianini might be in some way be related to Pseudomorphini; see also Notman (1925) and Baehr (1992, 1997).

*Pseudomorpha* Kirby 1825

(Figs 1, 7, 13, 15, 16)

_Pseudomorpha_ Kirby, 1825: 98. **Type species:** _Pseudomorpha excrucians_ Kirby 1825:101. Original monotypy.


_Axinophorus_ Dejean, 1829:174. **Type species:** _Aixinophorus lecontei_ Dejean & Boisduval 1829, synonym of _Pseudomorpha excrucians_ Kirby 1825:101.

_Drepanus_ Dejean, 1831:434. **Type species:** _Aixinophorus lecontei_ Dejean & Boisduval 1829, synonym of _Pseudomorpha excrucians_ Kirby 1825:101.


PROPOSED ENGLISH VERNACULAR NAME.—Western False-form beetles.

DIAGNOSIS.—Baehr (1997) adequately diagnosed members of this genus as follows: “Body fairly wide to almost cylindrical, elytra posteriorly gently convex; head prognathous; eyes situated laterally, without ventral border, ventral part more or less triangular;
clypeus partly or completely fused to frons; labrum separated from clypeus by a sulcus; supraorbital, clypeal, suborbital, and gular setae present, preorbital seta absent; antennal grooves deep; lateral plate of maxilla not enlarged; antenna elongate, basal antennomere simple; mental tooth elongate, triangular; glossa fused with paraglossae to a wide plate, bisetose but sometimes with additional elongate setae; labial palpi very large, markedly

Fig. 1. Habitus, dorsal aspect of *Pseudomorpha (Pseudomorpha) excrucians* Kirby, Covington, LA.
Fig. 2. Habitus, dorsal aspect of *Tuxtalamorpha tuxtla* (Liebherr & Will), Veracruz, México.
Fig. 3. Habitus, dorsal aspect of *Notopseudomorpha laevissima* (Chaudoir), Brazil.
Fig. 4. Habitus, dorsal aspect of *Manumorpha biolat* Erwin & Geraci, Pakitza, Perú.
Fig. 5. Habitus, dorsal aspect of *Yasunimorpha piranhna* Erwin & Geraci, Yasuni, Ecuador.
Fig. 6. Habitus, dorsal aspect of *Samiriamorpha grace* Erwin & Geraci, Rio Samiria, Perú.
Fig. 7. Aedeagus and parameres of *Pseudomorpha excrucians* Kirby, Georgia, USA.
Fig. 8. Aedeagus and parameres of *Tuxtlamorpha* sp. Guatemala.
Fig. 9. Aedeagus and parameres of *Notopseudomorpha laevisima* (Chaudoir), Brazil.
Fig. 10. Aedeagus and parameres of *Manumorpha biola* Erwin & Geraci, Pakitza, Perú.
Fig. 11. Aedeagus and parameres of *Yasunimorpha pirambna* Erwin & Geraci, Yasuni, Ecuador.
Fig. 12. Aedeagus and parameres of *Samiriamorpha grace* Erwin & Geraci, Rio Samiria, Perú.
securiform; ventral surface of head large, not concealed by the mouth parts; prosternal process straight, rather short, depressed between coxae; number of umbilical pores of elytra variable; femora moderately or strongly compressed, with deep grooves; tibiae and tarsi not compressed, elongate; 6 protarsus biseriately clothed at 1st and 2nd tarsomere, mesotarsus uniseriately clothed at 1st and 2nd tarsomere or not clothed; S sternum VII not excised; 6 sternum VIII apically divided, highly asymmetric; aedeagus with simply folded internal sac; parameres fairly similar, though left paramere always considerably larger; 2 stylomer 1 and 2 separated, though shape very variable; no distinct dorsal and ventral ensiform setae present, but nematiform setae present though sometimes very short and not always arising from a pit."

The following is additional information not found in Baehr (1997).

Size small to medium for tribe and family, ABL: 7.0 to 11.1 mm, TW = 2.0 to 5.8 mm.

Male genitalia (Fig. 7): Phallus normal; in ventral aspect (Fig. 7) narrow, basal bulb swollen, crested or not; dorsal surface with short membranous ostium; apex more or less subtruncated, rounded, or acute; in lateral aspect (Fig. 7), with shaft curved ventrad, apical portion narrowed and somewhat acute. Endophallus with or without patches of microtrichia. Parameres (Fig. 7) glabrous or setiferous, left wider than right, both broad and long, equal or subequal in length. Female genitalia: As in Fig. 15.

Geographic distribution.—The geographical range of this genus extends from Oregon, Utah, and Colorado, USA in the north, through México and Central America to Catamarca Province, Argentina in the south (Fig. 16). South American species also occur in Brazil and Peru and undoubtedly elsewhere, as well.

Notes.—Ten informal species groups are now recognized (Erwin, in prep) based on sets of shared attributes. In these group, 114 species are currently recognized, 86 of which are new to science. In addition, there are still a few unresolved groups at present and their resolution will add to the list of known species. Whether the ten species groups are truly monophyletic, or not, must await a species level phylogenetic analysis, which is outside the scope of the present paper. In addition, the status of the subgenus Austropseudomorpha Baehr 1997 must await further study of the Western Hemisphere fauna.

**Pseudomorpha (s. str.) excrucians** Kirby 1825
(Figs 1, 7)

*Pseudomorpha excrucians* Kirby, 1825:101.
*Axinophorus lecontei* Dejean, 1837:176.
*Pseudomorpha ruficollis* Casey, 1924:148.


Derivation of specific epithet.—The word “excruciatus” is from the Latin, *excrucio*, meaning torture or torment, and likely in reference to the false form of these beetles, i.e. many character states are of the Carabidae, but the general form is not.
**PROPOSED ENGLISH VERNACULAR NAME.**—Excruciating False-form beetle.

**DIAGNOSIS.**—With the attributes of the genus as diagnosed above and color pecious, elytra much darker than rufous pronotum and head; and it is the only bicolored species in North America; pronotum (Fig. 1) wider at base than elytra, disk evenly and finely punctate, each puncture with a long seta although the central disc is rubbed in most specimens; elytral interneurs 1-7 well-defined, each with moderately impressed setigerous punctae; elytral intervals (Fig. 1) randomly punctate with setigerous punctae wide spread, mostly close to adjacent interneurs.

**DESCRIPTION.**—(Fig. 1). Size: Large. ABL = 8.0 to 9.5 mm; SBL (Holotype) = 7.94 mm; TW = 3.8 to 4.0 mm. Holotype pronotum ratio: 2.50; Holotype elytron ratio: 1.55. Color: Head and pronotum rufous, elytra rufopiceous, venter and appendages rufotestaceous. Luster: Dorsal surface shiny. Microsculpture: Head with very fine isodiametric sculpticells; effaced from pronotal disk; elytra with nearly effaced very fine flat transverse sculpticells. Head: Clypeal suture effaced at middle. Frons sparsely and moderately coarsely punctulate in paramedial patches at eye level, setigerous pores with moderately long setae. Prothorax: Pronotum (Fig. 1) moderately convex, much wider than long, with fringe of long stout setae along lateral margin, fringe of shorter setae along anterior and medial posterior margins; anterior margin beaded, posterior margin not beaded. Disk with longitudinal shallowly impressed and discontinuous line and with sparse moderately coarse setigerous punctae, each with a long erect seta; median disc glabrous. Pterothorax: Elytral interneurs moderately coarsely punctate, all interneurs more or less equally impressed, setigerous pores wide-spaced, intervals randomly sparsely punctate. Metepisternum longer than wide, surface sparsely setiferous, setae short. Metasternum sparsely setiferous. Metathoracic wings fully developed. Abdomen: Sternum broadly and shallowly incised medially. All sterna moderately setiferous, IV broadly and densely so, medially; male with dense patch of setae medially on sterna V and VI, their patch width about two-fifths length of posterior trochanter (Fig. 13). Male genitalia: (Fig. 7) Phal- lus slightly arcuate to the left in dorsal aspect, apex broadly rounded, ventral margin nearly straight in apical third. Parameres (Fig. 7): in ventral aspect left shorter than right and slightly narrower, distal margin rounded; distal margin of right acute. Phallobase not crested.

**WAY OF LIFE.**—Macrohabitat: Lowlands, 3 – 397 meters altitude in Eastern Deciduous Forest/Pine barrens zones. Microhabitat: On sandy substrates likely near ant nests and in the surrounding vicinity. Dispersal abilities: Macropterous, capable of flight; swift runner. Seasonal occurrence: Adults found active in July (Louisiana), and June – July (South Carolina). Behavior: See under genus above.

**GEOGRAPHIC DISTRIBUTION.**—This species occurs in southeastern USA – AL, GA, LA, MS, SC.

**Tuxtlamorpha** Erwin & Geraci, new genus
(Figs 2, 8, 16)

*Type species:* *Pseudomorpha tuxtla* Liebherr & Will, 1997:54, here designated.

**PROPOSED ENGLISH VERNACULAR NAME.**—Combed False-form beetles.

**DIAGNOSIS.**—With the attributes of the Tribe as described above and dorsal surface with numerous long decumbent and markedly course setae scattered on head and pronotum, and in 9 perfect rows on the elytra (excluding the interrupted omblicate series). Clypeus and labrum deflected at about 45° angle, frons slightly convex; preocular lobe present produced anteriorly, confluent with eye posteriorly. Antenna short, extended to level of mid-procoxae; antennomeres of equal width distally, each slightly compressed. Gena below eye markedly angulate, sharply beaded. Elytra proportionally smaller in comparison with pronotum and head, and evenly tapered to moderately narrow rounded apex. Male with broad setal patch on sterna VI and VII, set in shallow transverse excavation, this groove posteriorly with a row of long setae that are angulate dorsally at their tips, the setae sigmoid in shape from lateral aspect.

**NOTES.**—Two species are now recognized (Erwin, in prep) based on sets of shared attributes. One of these is new to science.

**GEOGRAPHIC DISTRIBUTION.**—The geographical range of this genus extends from Vera Cruz, México to Honduras (Fig. 16).


**DERIVATION OF SPECIFIC EPITHET.**—The word “tuxtla” is derived from the name of the biodiversity station in Vera Cruz.

**PROPOSED ENGLISH VERNACULAR NAME.**—Tuxtla False-form beetle.

**DIAGNOSIS.**—See under genus above.

**DESCRIPTION.**—(Fig. 2). *Size:* Large. ABL = 10.6 to 12.0 mm; SBL (Holotype) = 9.04 mm; TW = 6.0 to 6.2 mm. Holotype pronotum ratio: 2.61; Holotype elytron ratio: 1.19. *Color:* Head, pronotum and elytra dark brown, venter and appendages piceous. *Luster:* Dorsal surface moderately shiny. *Microsculpture:* Dorsal surface of pronotum with very fine slightly stretched sculpticells; that of head and elytra very fine isodiametric sculpticells. *Head:* Clypeus glabrous; frons irregularly and sparsely micropunctulate, setigerous pores with short setae; vertex glabrous. Occiput medial to hind margin of eye without small isolated group of coarse setiferous pores. *Prothorax:* Pronotum (Fig. 2) markedly convex, not depressed along midline, wider than long, without fringe of long stout setae along lat-
eral and anterior margins; with such setae in a group of five at hind angle and with sparse marginal setae on posterior margin; entire disk with sparse vestiture of stout decumbent setae; anterior and lateral margins beaded, bead of lateral margin efface at posterior angle, posterior margin somewhat discolored but not beaded; disk without longitudinal shallowly impressed midline. *Pterothorax*: Elytral interneurs finely punctate, not striate, each with long posteriorly decumbent seta; intervals with occasional setigerous pores adjacent to interneurs. Metepisternum longer than wide, surface not setiferous. Metasternum markedly convex medially, surface not setiferous. Metathoracic wing fully developed. *Abdomen*: Sternum III broadly and shallowly arcuate medially. All sterna sparsely setiferous, IV broadly and more densely so medially; male unknown. *Male genitalia*: Unknown (see note below). The male genitalia of an undescribed species from Guatemala is illustrated (Fig. 8)

**WAY OF LIFE.** — **MACROHABITAT**: Lowlands, 150 meters altitude. **MICROHABITAT**: Unknown. **DISPERAL ABILITIES**: Macropterous, capable of flight; swift runner. **SEASONAL OCCURRENCE**: Adults found in July. **BEHAVIOR**: See under genus above. Adults found at lights at night.


**GEOGRAPHIC DISTRIBUTION.** — (Fig. 16). This species is known from southeastern México — VC.

**NOTES.** — Both known specimens of *T. tuxtla* are females, however the single specimen of an undescribed species from Honduras is a male (Erwin, in prep). An illustration of that male’s aedeagus is presented here, as the likelihood of similarity is great, as exemplified in the other species groups of pseudomorphines. *Male genitalia*: (Fig. 8) Phallus very slightly arcuate to the right in dorsal aspect, apex recurved to the left and narrowly rounded, ventral margin markedly arcuate throughout its length, apex broad, truncate. Parameres (Fig. 8): in ventral aspect left slightly shorter, right paramere somewhat broader than left and somewhat broader distally, distal margins of both acute, rounded at tip.

*Notopseudomorpha* Baehr 1997, new status
(Figs 3, 9, 14, 16)

**Type species.** *Pseudomorpha laevissima* Chaudoir 1852:63, Brazil, designated by Baehr (1997:42).

**PROPOSED ENGLISH VERNACULAR NAME.** — False False-form beetles.

**DIAGNOSIS.** — With the attributes of the Tribe as described above and dorsal surface devoid of setae except umbilicate series of elytron. Mouthparts mostly hidden in dorsal aspect; clypeus very small, deflected at about 45° angle, frons slightly convex; preocular lobes absent. Antenna short, extended to middle of procoxae; antennomeres of uniform width throughout, each slightly compressed. Gena below eye markedly angulate; beaded. Elytra proportionally small in comparison with pronotum and moderately tapered to narrowly rounded apex. Male with dense and divided setal patches on sterna V and VI,
set in two shallow excavations. Posterior-most setae of each patch shallowly elbowed ventrally.

**NOTES.**—Nine species are now recognized (Erwin, in prep) based on specimens ranging from Argentina north to Costa Rica. Of these nine species, six are new to science.

**GEOGRAPHIC DISTRIBUTION.**—The geographical range of this genus extends from Costa Rica to Argentina (Fig. 16).

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**Notopseudomorpha laevissima** (Chaudoir) 1852

(Figs 3, 9)

*Pseudomorpha laevissima* Chaudoir 1852:63.


**DERIVATION OF SPECIFIC EPITHET.**—The word “laevissima” is a Latin adjective, meaning smooth, and refers to the entire dorsal surface which is devoid of setae or any type of blemish.

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**Fig. 13.** Abdominal segments of male *Pseudomorpha excrucians* Kirby, Covington, LA; V and VI with modified setae.

**Fig. 14.** Abdominal segments of male *Notopseudomorpha* sp. Costa Rica; V and VI with modified setae.

**Fig. 15.** Female genitalia of *Pseudomorpha tenebroides* Notman, Florida Canyon, AZ.
PROPOSED ENGLISH VERNACULAR NAME.— Smooth False-form beetle.

DIAGNOSIS.— See under genus above.

DESCRIPTION.— (Fig. 3). Size: Medium. ABL = 9.1 to 9.5 mm; SBL (Holotype) = 7.41 mm, TW = 5.1 to 5.2 mm. Holotype pronotum ratio: 2.55; Holotype elytron ratio: 1.39. Color: Head, pronotum and elytra dark rufous brown, venter and appendages dark yellowish-brown. Luster: Dorsal surface very shiny. Microsculpture: Dorsal surface with very fine isodiametric and slightly stretched sculpticells, these nearly effaced on some individuals. Head: Frons and vertex finely micropunctulate. Occiput medial to hind margin of eye without small isolated group of coarse setiferous pores; outer angle of gena at corner of eye 4-setose. Prothorax: Pronotum (Fig. 3) markedly convex, not depressed along midline, wider than long, without fringes of setae along margins, some individuals with one or two marginal setae at hind angle; anterior and lateral margins beaded, bead of lateral margin efficac at posterior angle, posterior margin somewhat discolored but not beaded; disk with longitudinal shallowly impressed midline. Pterothorax: Elytral disc featureless; ombilicate setal series present; margin with fringe of stout setae. Metepisternum longer than wide, surface not setiferous. Metasternum markedly convex medially, sparsely setiferous throughout. Metathoracic wing fully developed. Abdomen: Sternum III broadly and shallowly incised medially. All sterna at least sparsely setiferous, IV broadly and more densely so medially; male see above under genus. Male genitalia: (Fig. 9) Phallus straight in dorsal aspect, apex acutely rounded, ventral margin markedly tapered through its length; basal bonnet relatively quite large. Parameres (Fig. 9): in ventral aspect left and right coequal in length, left slightly smaller and somewhat narrower distally, distal margins of both narrowly rounded.

WAY OF LIFE.— Macrohabitat: Lowlands to midlands, 150 – 1000 meters altitude, in the Cerrado vegetation zone in Brazil and the Chaco and Yungas zones in Argentina. Microhabitat: Adults are found in nests of the ant Camponotus rufipes (Fab.) in Brazil. Dispersal abilities: Macropterous, capable of flight (Lenko, 1972); swift runner. Seasonal occurrence: Adults found in January – February, and December. Behavior: See under genus above. Adults found at lights at night. Larvae eat larvae of the ant host in the core of the nest, then retreat to the nest periphery at the time for pupation. Lenko (1972) did not discover the food of adults.

OTHER SPECIMENS EXAMINED.— Female, BRAZIL, Chapada, (CMNH:ADP109125); male, São Paulo, January (Parker) (NMNH:ADP110380); female, Minas Gerais, Viçosa, Corrego da Paraiso (Mata do Prefeitura) (Mata do Paraiso), 703 m, 20.768° S, 42.877° W, February (T.J. Henry) (NMNH:ADP110357).

ADDITIONAL SPECIMENS.— Ogueta (1967) lists the following localities: BRAZIL: Pirassunga, Edo. São Paulo, Nova Teutonia, Novo Friburgo. ARGENTINA: Misiones (Puerto Bemberg), Tucumán (Las Cuchillas), Catamarca.

GEOGRAPHIC DISTRIBUTION.— (Fig. 16). This species occurs in eastern and southeastern Brazil and northern Argentina.

NOTES.— The larval description and some notes on life history were published by Lenko (1972). A second species assigned by Baehr (1992) to this genus (P. glabra Ogueta, now N. glabra (Ogueta)) is found in the Argentine province of Santiago del Estero.
Manumorpha Erwin & Geraci, n. gen.
(Figs 4, 10, 16)

Type species: Manumorpha biolat Erwin & Geraci, sp. n., Perú, present designation.

Proposed English vernacular name.—Hairy False-form beetles.

Diagnosis.—With the attributes of the Tribe as described above and dorsal surface with numerous long and erect markedly course setae densely located on head and pronotum, and in 9 perfect rows on the elytra (excluding the interrupted omblilicate series). Clypeus deflected at about 45° angle, frons slightly bulbous; preocular lobes present, hind angles not flush with eye. Antenna long, extended beyond prosternal process; middle antennomeres broad, decreasing in size proximally and distally, each moderately compressed. Gena below eye markedly angulate; suboptical ridge beaded. Elytra proportionally not small in comparison with pronotum and markedly tapered to narrowly rounded apex. Male with slightly denser setal patch on sternum VI, but this not set in shallow excavation; no denser setal patch on sternum V.

Behavior.—Many species of ants nest in suspended dried palm fronds where members of this genus are found and given the known life history of members of other genera in Pseudomorphini, it is like that M. biolat adults frequent these ant nest and the larvae are myrmecophilus there.

Notes.—The genus at present contains three species, all of which are new to science.

Geographic distribution.—The geographical range of this genus extends from Ecuador to Perú (Fig. 16).

Manumorpha biolat Erwin & Geraci, sp. n.
(Figs 4, 10)


Derivation of specific epithet.—The word “biolat” is an acronym for the program “Biodiversity in Latin America” run by the Smithsonian Institution in the 1980/90’s and under which this species was discovered on sponsored expeditions.

Proposed English vernacular name.—Biolat False-form beetle.

Diagnosis.—With the attributes of the genus as described above and color rufous brown (Fig. 4), elytra darker than pronotum; pronotum (Fig. 4) wider at base than elytra across humeri; elytral intervals 1–9 well-defined, each with markedly coarse setigerous punctulae; elytral (Fig. 4) interneurs without, or rarely with a single random setigerous puncture.

Description.—(Fig. 4). Size: Medium. ABL = 7.1 to 8.2 mm; SBL (Holotype) = 6.26 mm; TW = 2.4 to 4.2 mm. Holotype pronotum ratio: 1.54; Holotype elytron ratio: 1.39. Color: Head, pronotum, elytra and venter rufous brown, appendages somewhat testa-
ceous. *Luster*: Dorsal surface moderately shiny. *Microsculpture*: Dorsal surface with very fine slightly stretched sculpticells. *Head*: Frons micropunctulate, setigerous pores with short and long setae scattered except on vertex where they form more or less an uneven transverse line. Occiput medial to hind margin of eye without small isolated group of coarse setiferous pores. *Prothorax*: Pronotum (Fig. 4) moderately convex, depressed along midline, wider than long, with fringe of long stout setae along lateral and anterior margins, and over entire disk; anterior and lateral margins beaded, bead of lateral margin efface at posterior angle, posterior margin somewhat discolored but not beaded; disk with longitudinal shallowly impressed midline. *Pterothorax*: Elytral interneurs impunctate, striae barely traceable, intervals with setigerous pores closely spaced, each slightly raised, coarsely impressed. Metepisternum longer than wide, surface sparsely setiferous. Metasternum markedly convex medially, sparsely setiferous throughout. Metathoracic wing fully developed. *Abdomen*: Sternum III broadly and shallowly incised medially. All sterna sparsely setiferous, IV broadly and more densely so medially; male with small denser patch of setae medially on sternum VI, the patch width less than half that of the length of posterior basitarsus. *Male genitalia*: (Fig. 10) Phallus slightly arcuate to the right in dorsal aspect, apex narrowly rounded, ventral margin markedly arcuate throughout its length. Parameres (Fig. 10): in ventral aspect left shorter and slightly smaller than right and somewhat narrower distally, distal margins of both narrowly rounded.

**WAY OF LIFE.**—**MACROHABITAT**: Lowlands, 356 meters altitude, in tropical rain forest. **MICROHABITAT**: Adults are found in dry attending fronds of palm trees (*Astrocaryum chonta* Mart.). **DISPERSAL ABILITIES**: Macropterous, capable of flight; swift runner. **SEASONAL OCCURRENCE**: Adults found in October – November. **BEHAVIOR**: See under genus above.


**GEOGRAPHIC DISTRIBUTION.**—(Fig. 16). This species occurs in southeastern Perú.

**Yasunimorpha** Erwin & Geraci, n. gen.

(Figs 5, 11, 15)

**Type species**: *Yasunimorpha piranha* Erwin & Geraci, sp. n. ECUADOR. Present designation.

**PROPOSED ENGLISH VERNACULAR NAME.**—Narrow False-form beetles.

**DIAGNOSIS.**—With the attributes of the Tribe as described above, form subcylindrical, and dorsal surface of head and pronotum devoid of setae and pubescence, elytra with only two setae (excluding the interrupted umbilicate series). Clypeus continuous with frons, not deflected at an angle, frons flat; preocular lobes defined but not produced. Antenna very short, not extended to level of procoxal process; antennomeres
3-10 quadrate, flattened, increasing in size distally. Gena below eye not produced, edge barely visible in dorsal aspect. Elytra proportionally small in comparison with length of pronotum and somewhat tapered to narrowly rounded apex. Abdomen of both sexes devoid of pubescence except in male with dense double setal patches on sternum V and VI; these not set in shallow excavation and with very small separation between patches.

**BEHAVIOR.**—Many species of ants build nests in the rain forest canopy and given the known life history of members of other genera in Pseudomorphini, it is likely that *Y. piranha* adults frequent these ant nest and the larvae are myrmecophilus there.

**NOTES.**—The genus at present is monotypic.

**GEOGRAPHIC DISTRIBUTION.**—The presently known location of this genus is eastern Ecuador (Fig. 16).

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**Yasunimorpha piranha** Erwin & Geraci, sp. n.

(Figs 5, 11)

**Holotype.**—**ECUADOR:** Orellana Province, nr. Yasuni National Park, Onkone Gare Station, 0.657° S, 076.452° W, 236m, 16 January 1994 (T.L. Erwin, et al.) (NMNH:ADP110379, male). One paratype is listed below under other specimens examined.

**DERIVATION OF SPECIFIC EPITHET.**—The word “piranha” is in reference to the general area in which the holotype and paratype were collected at Onkone Gare Station. Onkone Gare are the Huoarani words for *Piraña* (piranha) and is the name of the stream near the fogging plot from which specimens were collected.

**PROPOSED ENGLISH VERNACULAR NAME.**—*Yasuni False-form beetle.*

**DIAGNOSIS.**—With the attributes of the genus as described above and color black with rufinistic highlights (Fig. 5), elytra two-toned, basally black, apex rufous; pronotum (Fig. 5) at base subequal to width of elytra across middle; neither elytral interneurs nor intervals evident, disk with only two moderately coarse setigerous punctulae, one near scutellum and the other at basal third midway between suture and lateral side, ombilicate series present.

**DESCRIPTION.**—(Fig. 5). **Size:** Small. **ABL** = 5.8 to 6.0 mm; **SBL** (Holotype) = 4.37 mm; **TW** = 1.9 to 2.0 mm. **Holotype pronotum ratio:** 1.67; **Holotype elytron ratio:** 1.25. **Color:** Head, pronotum and elytra black with rufinistic highlights, elytra two-toned, basally black, apex rufous, venter rufous, appendages testaceous. **Luster:** Dorsal surface moderately alutaceous. **Microsculpture:** Sculpticells effaced from dorsal surface. **Head:** Frons densely micropunctulate, setae, including clypeal and supraorbital setae, and pubescence absent. Occiput medial to hind margin of eye without small group of coarse setiferous pores. Eyes flat, asetiferous. **Prothorax:** Pronotum (Fig. 5) markedly convex, longer than wide, devoid or setae and pubescence, surface densely micropunctate; only lateral margin beaded, that not complete basally, posterior margin discolored but not beaded; disk with longitudinal impressed line nearly effaced. **Pterothorax:** Elytra markedly convex, surface densely micropunctate, interneurs and intervals effaced, two setigerous pores, one near
scutellum, the other at middle at basal third of elytron. Metepisternum longer than wide, surface sparsely setiferous. Metasternum short, markedly convex medially, without vestiture. Metathoracic wing fully developed. \textit{Abdomen}: Sternum III broadly and shallowly incised medially. All sterna devoid of vestiture except VII with one pair of wide-spaced setigerous pores near apical margin and male with dense double patch of setae medially on sterna V and VI, their patch width slightly less that length of posterior trochanter and narrowly separated medially. \textit{Male genitalia}: (Fig. 11) Phallus slightly arcuate to the right in dorsal aspect, apex narrowly pointed and thick, ventral margin slightly arcuate throughout its length. Parameres (Fig. 11): in ventral aspect left shorter than right and somewhat narrower, its distal margin pointed, that of the left rounded.

\textbf{Way of Life. — Macrohabitat:} Lowlands, 236 meters altitude, in tropical rain forest. \textbf{Microhabitat:} Mixed rain forest canopy crowns of the following tree species: \textit{Astrocaryum chambira} Burret, \textit{Pouteria reticulata} (Engl.) Eyma, \textit{Inga capitata} Desv., \textit{Ceropia ficifolia} Warb. ex Snethl.). \textbf{Dispersal Abilities:} Macropterous, probably capable of flight. \textbf{Seasonal Occurrence:} Adults found in January, the dry season. \textbf{Behavior:} See under genus above.

\textbf{Other Specimen Examined. — Ecuador: Orellana Province, nr. Yasuni National Park, Onkone Gare Station, 0.657° S, 076.452° W, 236m, 24 January 1994 (T.L. Erwin, et al.)(NMNH:ADP110292, paratype female). The holotype will be deposited in the National Natural History Museum in Quito, Ecuador.}

\textbf{Geographic Distribution. —} (Fig. 16). This species is known presently from eastern Ecuador.

\textit{Samiriamorpha Erwin & Geraci, n. gen.}  
(Figs 6, 12, 16)

\textbf{Type species:} \textit{Samiriamorpha grace} Erwin & Geraci, \textit{sp. n.} Perú, present designation.  
\textbf{Proposed English Vernacular Name. —} Flat False-form beetles.

\textbf{Diagnosis. —} With the attributes of the Tribe as described above and dorsal surface with numerous moderately short and markedly fine setae scattered on head and pronotum, and in both interneurs and intervals on the elytra. Form somewhat depressed. Mouthparts not visible from above; clypeus vertical, frons subtly convex; preocular lobes absent. Antenna very short, extended only to level of middle of prosternal process; antennomeres very broad decreasing in size distally from antennomere 9, each moderately compressed. Gena below eye markedly angulate; subocular ridge beaded. Elytra not proportionally small in comparison with pronotum and moderately tapered to narrowly rounded apex. Male with two dense setal patches on sternum V and VI, these divided by a narrow space.

\textbf{Notes.} This genus is at present monotypic.

\textbf{Geographic Distribution. —} The presently known location of this genus is north-central Perú (Fig. 16).
**Fig. 16.** General distribution patterns of overall ranges of the taxa included.

*Samiriamorpha grace* Erwin & Geraci, *sp. n.*

(Figs 6, 12)

**Holotype.** — *Perú*: Loreto Department, nr. Pacaya-Samiria National Reserve, Cocha Shinguito, nr. Rio Samiria, 05.179° S, 074.654° W, 119 m, 13 June 1990 (T.L.)
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Erwin, G.P. Servat, et al. (NMNH:ADP110418, male). Paratypes are listed below under other specimens examined.

**Derivation of specific epithet.** — The word "grace" is an eponym and used in reference to the first name of one of the collectors of the type series, Grace P. Servat.

**Proposed English vernacular name.** — Grace’s False-form beetle.

**Diagnosis.** — With the attributes of the genus as described above and color rufopiceous, the head and pronotum more rufous that elytra, venter and appendages rufotestaceous; pronotum (Fig. 6) at base broader than width of elytra across humeri; neither elytral interneurs nor intervals evident although setae appear in lines likely marking the interneurs, and therefore intervals with some scattered setae; ombilicate series present.

**Description.** — (Fig. 6). **Size:** Medium (all four studied specimens are the same size). ABL = 8.0 mm; SBL (Holotype) = 6.32 mm; TW = 4.3 mm. Holotype pronotum ratio: 2.65; Holotype elytron ratio: 1.13. **Color:** Head, pronotum and elytra rufopiceous, elytra darker in tone, venter and appendages rufotestaceous. **Luster:** Dorsal surface shiny. **Microsculpture:** Dorsal surface with finely impressed and transverse sculpticells; these partially effaced from disc of pronotum. **Head:** Frons sparsely micropunctulate, setae moderately long and very fine; vertex glabrous. Occiput medial to hind margin of eye without small group of coarse setiferous pores. Eyes nearly flat, asetiferous. **Prothorax:** Pronotal disc (Fig. 6) nearly flat, wider than long, surface densely micropunctate, setae moderately long and very fine, all margins with a fringe of moderately coarse setae; anterior and lateral margins beaded, the lateral margin not complete basally; posterior margin discolored but not beaded; disk with longitudinal impressed line shallowly impressed. **Pterothorax:** Elytral disc nearly flat, surface densely micropunctate, interneurs and intervals effaced, traceable only by following rows of setae. Metepisternum longer than wide, surface without vestiture. Metasternum short, markedly convex medially, with patch of vestiture on the convexity. Metathoracic wing fully developed. **Abdomen:** Sternum III and IV fused medially. All sterna with scattered vestiture, no central patch on III; male with dense double patch of setae medially on sterna V and VI, their total patch width subequal to length of posterior trochanter. **Male genitalia:** (Fig. 12) Phalbus robust, very slightly arcuate to the right in dorsal aspect, apex broadly rounded and thick, ventral margin slightly almost straight throughout its length. Parameres (Fig. 12): in ventral aspect both nearly of same length, left somewhat narrower, its apex narrowly rounded, that of the left truncate.

**Way of life.** — **Macrohabitat:** Lowlands, 119 meters altitude, in rainforest surrounded by black water swamps and rivers. **Microhabitat:** The series of 4 specimens were found by insecticidal fogging a big tree with vines, epiphytes and Azteca ant nests. **Dispersal abilities:** Macropterous, probably capable of flight; swift runner. **Seasonal occurrence:** Adults found in June. **Behavior:** See under genus above.

**Other specimens examined.** — Two females, one male with same data as Holotype, above. The holotype will be deposited at Museo de Historia Natural, Lima, Peru.

**Geographic distribution.** — (Fig. 16). This species occurs in north-central Perú.
PHYLOGENY

Bootstrap analysis of 33 morphology characters for Pseudomorphini genera produced only moderate support for relationships among genera (Fig. 17a). A heuristic search recovered one most parsimonious tree topology with Orthogonius and Spallomorpha at the base (tree length = 78, consistency index = 0.667, retention index = 0.518, rescaled consistency index = 0.346). Two synapomorphies support the clade defined at Node A (Fig. 17b): these genera all possess elytra with setose lateral margins and pubescent abdominal sterna. Node B has a moderately strong bootstrap value and is supported by seven characters. Only one of those characters is an unreversed synapomorphy, however (Fig. 17b, Appendix I). The recovery of Tuxtlamorpha and Samiriamorpha as sister taxa is supported by a uniquely shared apically blunt phallicus, but the placement of Xenaroswelliana in relation to Manumorpha and Pseudomorpha is unclear. Character traces revealed six autapomorphic character states for Xenaroswelliana (Fig. 17b) that give the genus a noticeably different gross appearance than other Pseudomorphini (Fig. 17a). This supports Erwin's interpretation of this genus as a separate tribe (Erwin, 2007) that is perhaps related in some way to the Pseudomorphini proper because of the shared and completely unique carabid character, that of a ventral sulcus into which the antennal base is tucked away. In Xenaroswelliana members, the sulcus is only partially developed indicating that this taxon should be basal to all the Pseudomorphini, if the character system is evolving toward its sophisticated appearance in the pseudomorphines. Molecular data from multiple gene fragments are needed to confirm the placement of Xenaroswelliana in relation to other Western Hemisphere Pseudomorphini genera.

DISCUSSION

The Western Hemisphere Pseudomorphini ranks as one of the poorest known carabid Tribes. Although the North American species have been well collected, they have not been integrated into a synthetic taxonomic treatment and numerous species remain undescribed. Middle and South America are woefully under-collected for members of this Tribe. The lack of tropical specimens collected at lights may mean that adults are not attracted and therefore must be dug from ant nests or hand-collected in the vicinity of nests. Our canopy fogging program has found them, but not commonly, and only so when we actually targeted ant nests. Many ants nest in trees in the tropics, so focused fogging will surely garner specimens. We predict our Neotropical fauna will rival the diversity found in Australia (cf. Baehr, 1992, 1997). A species level revision of the Tribe in the Western Hemisphere is presently underway (TLE) based on 1360 specimens borrowed from many institutions. In this material, more than 120 species and 5 genera are represented.
Fig. 17. a. Topology recovered from a bootstrap analysis of 33 structural attributes (bootstrap values presented at appropriate nodes). b. Structural attributes traced on to the most parsimonious tree recovered from a heuristic search: state transitions for corresponding characters are indicated by arrows (see Appendix 1).
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