Zootaxa 2218: 1–34 (2009)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Cladistic analysis of the subfamily Arsenurinae (Lepidoptera, Saturniidae) based on adult morphology

AMABÍLIO J. A. DE CAMARGO[1], OLAF H. H. MIELKE[2] & MIRNA M. CASAGRANDE[2]

[1] *Embrapa Cerrados. Rodovia BR 020, Km 18, Caixa Postal 08223, 73310-970 Planaltina, DF, Brazil.*
E-mail: amabilio@cpac.embrapa.br
[2] *Departamento de Zoologia, Universidade Federal do Paraná. Caixa Postal 19020,*
81531-980 Curitiba, Paraná, Brazil. E-mail: omhesp@ufpr.br, mibras@ufpr.br

Abstract

The family Saturniidae is distributed on all continents except polar areas, and includes about 1528 species in 162 genera, being the group with the largest diversity among Bombycoidea. Approximately 970 species are known from the New World. However, recent molecular studies indicate 1861 species in 162 genera and nine subfamilies. The family Arsenurinae consists of 63 species distributed exclusively in ten Neotropical genera, with phylogenetic relationships poorly understood. The goal of this study was to test the monophyly of the subfamily, tribes and genera using cladistic analysis of adult morphological characters. The subfamily, tribes and genera were all recovered as monophyletic groups with the following relationships among genera: (*Almeidaia* ((*Loxolomia*, *Copiopteryx*) ((*Rhescyntis*) ((*Grammopelta*, *Arsenura*) ((*Caio*) ((*Dysdaemonia*, *Titaea*) *Paradaemonia*)))))). Both tribes, Arsenurini and Almeidaiini, share several characters, but morphological study of Almeidaiini demonstrates that it also presents significant differences.

Key words: Lepidoptera, Saturniidae, Arsenurinae, cladistic analysis

Introduction

Among the Bombycoidea, the family Saturniidae presents the largest diversity. Based on data from material deposited in Brazilian institutions and bibliographic records, 1528 species of Saturniidae are known worldwide. Of those, 966 occur in the New World, at least 382 of them in Brazil (Camargo 2007). However, Regier *et al.* (2008), based on molecular studies, presented 1861 species in 162 genera and nine subfamilies. There are seven subfamilies recognized by Ferguson (1971): Arsenurinae, Ceratocampinae, Hemileucinae, Agliinae, Ludiinae, Salassinae and Saturniinae. Recently, some authors (Minet 1994; Lemaire & Minet 1998; Balcázar-Lara & Beutelspacher 2000) also included the subfamilies Oxyteninae and Cercophaninae, totaling nine subfamilies. Lemaire (1971, 1978, 1980, 1988, 1996, 2002) has published widely on Saturniidae, notably the New World subfamilies, with studies covering morphology, distribution and classification.

Arsenurinae is an exclusively Neotropical group treated as a subfamily for the first time by Jordan (1922). Bouvier (1930) named the group Rhescyntinae and some subsequent authors continued using this name (Schüssler 1936; Michener 1952; Ferguson 1971). Other taxonomic combinations have also been proposed: Travassos & Noronha (1968) described a new family Dysdaemoniidae, including the genera *Caio*, *Dysdaemonia*, *Titaea* and *Paradaemonia* based on the median spurs of the hind legs, but this family is currently not used by most authors.

The most evident external morphological characteristics of Arsenurinae are: brown or gray color (except in *Almeidaia*); hind wings with extensions in the form of a tail, especially on males; and presence of a hair tuft on both sides of the first abdominal segment, at the spiracular line. The antennae, wing venation and genitalia are variable within the group. For example, the uncus of the male genitalia may vary from simple to trifid, and

Accepted by L. Gall: 26 Jun. 2009; published: 2 Sep. 2009

the valvae from simple in *Grammopelta* to lobate in other genera. The gnathos may be present only as short lateral arms, narrow and slightly sclerotized, or even connected by a plate in a few species of *Caio*. The cornuti on the vesica of the aedeagus may be absent or present with varying aspects.

Many important studies on the subfamily Arsenurinae have been published in recent years, including Michener (1952), Ferguson (1971), and Peigler (1993) who made phylogenetic studies of the group. D'Abrera (1995) has presented excellent illustrations of the majority of the species, and Regier *et al.* (2008) estimate relationship across Saturniidae. The most complete taxonomic revision of the group was published by Lemaire (1980), which presented details about classification, morphology and geographic distribution of the 57 species known at the time. More recently the inclusion of *Almeidaia aidae* has raised the number of species to 58 and the number of subspecies to 26 (Lemaire 1996). In the past few years, four Brazilian species of Arsenurinae were described: *Dysdaemonia concisa*; *Rhescyntis reducta*; *Paradaemonia balsasensis* and *Paradaemonia meridionalis*. Presently, with the revised status of *Paradaemonia castanea* by Racheli (2006), a total of 63 species are known and distributed in ten genera divided in two tribes: Arsenurini with nine genera and Almeidaiini with one (Camargo & Becker 1999; Becker & Camargo 2001; Mielke & Furtado 2005; Camargo *et al.* 2007).

The phylogeny of the group was briefly treated by Michener (1952) and Lemaire (1980), who observed that some apomorphies separate the genus *Almeidaia* into a distinct tribe. The most significant study on the relationship among the Arsenurinae was made by Peigler (1993), the only work to have applied cladistic methodology. The purpose of the present study was to test the monophyly of the subfamily Arsenurinae and its tribes, as well as to propose a hypothesis about the phylogenetic relationships among the genera using adult morphological characters.

Although the species of Arsenurinae are distributed throughout the Neotropical region, they usually do not occur in altitudes higher than 1,500 m. The largest diversity occurs in lowland humid forests. However, there are many species that are specialized and endemic to xeric areas e.g., Cerrados of central Brazil and Caatinga (Lemaire 1980; Camargo & Becker 1999). The immature stages of few Arsenurinae species have been described. The eggs are round, flattened, opaque and brownish. The caterpillars possess scoli in the form of a horn during their first instars, being a dorsal scolus of the eighth segment and a subdorsal pair on the third thoracic segment(Lemaire 1980; Peigler 1993). Although there is little information about the host plants of Arsenurinae, the group seems to be polyphagous. Some *Arsenura*, *Almeidaia*, *Caio*, *Dysdaemonia* and *Titaea* feed on Bombacaceae; *Rhescyntis* on Myristicaceae and Annonaceae; *Copiopteryx* on Sapotaceae and Santalaceae; *Paradaemonia* on Lythraceae; and *Loxolomia* on Lecythidaceae. There are some records of *Arsenura* also feeding on Annonaceae, Tiliaceae, Sterculiaceae, Myrsinaceae, Euphorbiaceae, Asteraceae (Compositae) and Melastomataceae (Travassos & D'Almeida 1937; D'Araujo e Silva *et al.* 1968; Dias 1978; Janzen 1982; Stone 1991; Peigler 1993; Furtado 1998, 2001a, 2001b; Diniz *et al.* 2001).

Materials and Methods

Sixty one species of the subfamily Arsenurinae (ingroup) were included in the analyses, while females of *Arsenura thomsoni*, *Paradaemonia berlai* and *Almeidaia romualdoi* were not available for this study. Literature data were also included in the analyses, these species include: male and female of *Arsenura delormei* and *Rhescyntis descimoni*; female of *Copiopteryx jehovah* and the male of *Caio harrietae*. The two included outgroups were *Eacles imperialis* (Ceratocampinae) and *Oxytenis modestia* (Oxyteninae). Some authors (e.g., Michener 1952; Minet 1994; Aiello & Balcázar-Lara 1997) have considered the subfamily Oxyteninae to be ancestral to Arsenurinae. Although the subfamily Ceratocampinae is considered an ancestral group among the Saturniidae, its position is more apical in relation to Arsenurinae (Michener 1952; Lemaire 1988; Balcázar-Lara & Wolfe 1997).

The majority of the examined specimens came from the Collection Pe. Jesus Santiago Moure, Federal University of the Paraná, Brazil (DZUP). Other material came from the National Museum of the Rio de

Janeiro, Brazil (MNRJ); Instituto Osvaldo Cruz, Rio de Janeiro, Brazil (IOC); private collection pf Olaf H. H. Mielke, Curitiba, Brazil (OM); private collection of Carlos Guilherme Costa Mielke, Curitiba, Brazil (CGCM); Instituto Nacional de Biodiversidad, Costa Rica (INBio); and the entomological collection of EMBRAPA Cerrados, Brasília, Brazil (CPAC).

Species Examined

Saturniidae Boisduval, 1837

Arsenurinae Jordan, 1922
Arsenurini (Jordan, 1922) Lemaire, 1980
Arsenura Duncan, 1841
- *albopicta* Jordan, 1922
- *archianassa* Draudt,1930
- *armida* (Cramer,1779)
- *aspasia* (Herrich-Schäffer, [1853])
- *batesii* (R. Felder & Rogenhofer, 1874)
- *beebei* (Fleming, 1945)
- *biundulata* Schaus, 1906
- *ciocolatina* Draudt,1930
- *cymonia* (W. Rothschild, 1907)
- *delormei* Bouvier, 1929
- *drucei* Schaus, 1906
- *meander* (Walker, 1855)
- *mossi* Jordan, 1922
- *orbignyana* (Guérin-Ménevile, [1884])
- *pandora* (Klug, 1836)
- *polyodonta* (Jordan, 1911)
- *ponderosa* W. Rothschild, 1895
- *rebeli* Gschwandner, 1920
- *sylla* (Cramer, 1779)
- *thomsoni* Schaus, 1906
- *xanthopus* (Walker, 1855)

Caio Travassos & Noronha, 1968
- *romulus* (Maassen, 1869)
- *championi* (H. Druce, 1886)
- *richardsoni* (H. Druce, 1890)
- *harrietae* (Forbes, 1944)

Copiopteryx Duncan, 1841
- *derceto* (Maassen, [1872])
- *jehovah* (Strecker, 1874)
- *semiramis* (Cramer, 1775)
- *sonthonnaxi* É. André, 1905
- *virgo* Zikán, 1929

Dysdaemonia Hübner, [1819]

boreas (Cramer, 1775)
brasiliensis W. Rothschild, 1906
concisa Becker, 2001
fosteri W. Rothschild, 1906
Grammopelta W. Rothschild, 1907
lineata (Schaus, 1906)
Loxolomia Maassen, 1869
serpentina Maassen, 1869
johnsoni Schaus, 1932
Paradaemonia Bouvier, 1925
andensis (W. Rothschild, 1907)
berlai Oiticica, 1946
gravis (Jordan, 1922)
mayi (Jordan, 1922)
nycteris (Jordan, 1922)
meridionalis Camargo, O. Mielke & Casagrande, 2007
orsilochus (Maassen, 1869)
platydesmia (W. Rothschild, 1907)
pluto (Westwood, [1854])
ruschii May & Oiticica, 1943
samba (Schaus, 1906)
terrena (Jordan, 1922)
thelia (Jordan, 1822)
Rhescyntis Hübner, [1819]
descimoni Lemaire, 1975
hermes (W. Rothschild, 1907)
hippodamia (Cramer, 1777)
pseudomartii Lemaire, 1976
reducta Camargo & Becker, 2001
Titaea Hübner, [1823]
lemoulti (Schaus, 1905)
orsinome Hübner, [1823]
tamerlan (Maassen, 1869)
timur (Fassl, 1915)

Ameidaiini Lemaire, 1980
Almeidaia Travassos, 1937
aidae Mielke & Casagrande, 1981
romualdoi Travassos, 1937

Eacles imperialis (Drury, 1773) (Ceratocampinae): OUTGROUP
Oxytenis modestia (Cramer, 1780) (Oxyteninae): OUTGROUP

Character Analysis

Matrices were built based on morphological characters of adults: antennae, wings, legs, thorax, abdomen and genitalia. Matrices were constructed in NEXUS format using NDE (Page 2002), and analyzed in NONA (Goloboff 1993) implementing a heuristic search and 1000 replications. The commands used were: *hold*=10000, *multi**N=1000, multiple TBR (*multi*max**). Topologies were visualized in Winclada (Nixon 1999) and characters were examined on the trees using ACCTRAN optimization (accelerated transformation). The ingroup and outgroup were analyzed together following Nixon & Carpenter (1993), and characters were not ordered or weighted. The Jackknife test has been used with these kinds of data, and was used here to verify the reliability of clade support (Müller 2005).

Wing nomenclature follows Comstock (1918) and Nielsen & Common (1991); band denomination (wing pattern) follows Lemaire (1971), Nijhout (1991) and Heppner (1998). Scale bars on the images of characters: legs, antennae and genitalia = 1.0 mm; wings = 1.0 cm.

The data matrix included 40 characters, with 23 of these being binary and 17 multistate. The characters and states included in the analyses are as follows.

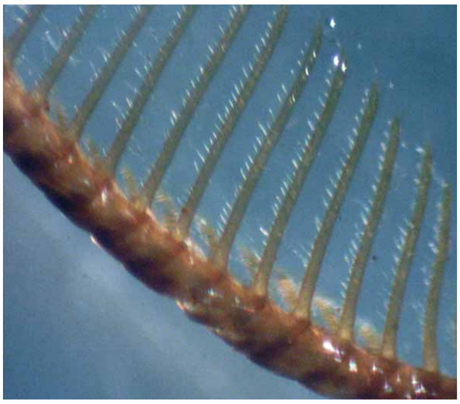
1. Antennae—insertion of pectins:
0. Lateroventral position
1. Laterodorsal position

Terms used for this character refer to the position of origin (insertion) of the pectins, being equivalent to the dorsolateral and lateral terms used by Michener (1952). The lateroventral orientation of the pectins (1:0) appears only on the bipectinated antenna of *Oxytenis*. According to Michener (1952) this kind of pectin orientation is an apomorphic character in Saturniidae because it is also found in *Periga* Walker, 1855 (Hemileucinae), but the plesiomorphy of the character is assumed by Minet (1994), accepting the presence in *Periga* as a case of reversion. The ancestral position of *Oxytenis* has been defended for many reasons, including the bipectinate antennae, which are also present in the most primitive members of the family e.g., Cercophaninae. According to Ferguson (1971), in some cases there is a possibility of reversion from the quadripectinate to the bipectinate state, as in the diurnal species of *Hemileuca* Walker, 1855 and the females of *Saturnia* Schrank, 1802. Peigler (1993) treated the quadripectinate condition as primitive (or plesiomorphic). The laterodorsal orientation (1:1) in quadripectinate antennae is the most frequent state in Saturniidae.

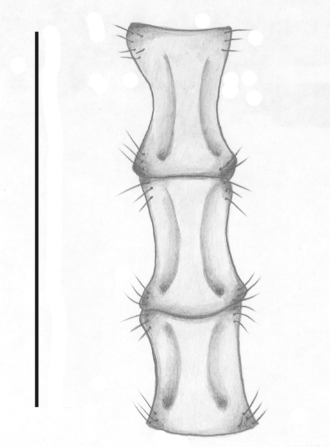

1:0
Oxytenis modestia (dorsal view-20x)
1:1
Copiopteryx semiramis (dorsal view-10x)

2. Antenna—sensilla on male antennomer:
0. Long and straight (exclusive of pectins)
1. Short and straight
2. Curved forming a ring
3. Curved forming a ring in the basal one-third of the antenna and straight in the apical third

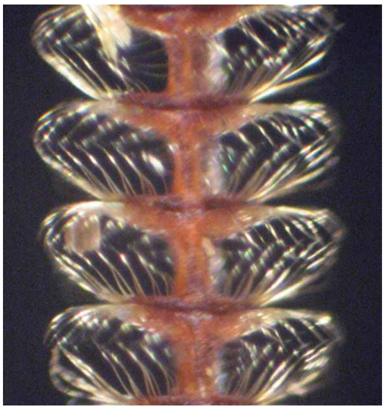
Although the dentate antennae do not present pectins they show sensilla, so this character was analyzed in general for all antennomers. Two states were found: straight and curved sensilla. These states were subdivided to refer to the length or location of the sensilla, which permits a better characterization. There is no information about this character in the literature.



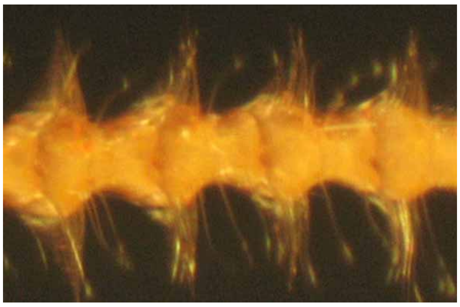
2:0
O. modestia (dorsal view-40x)



2:1
G. lineata (dorsal view)



2:2
L. serpentina (dorsal view-30x)



(2:3)
E. imperialis (apical part-40x)

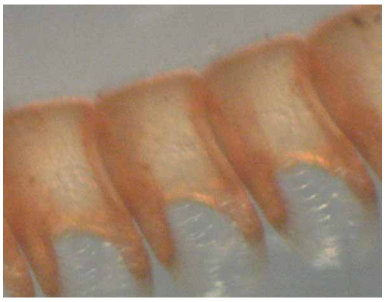
(2:3)
E. imperialis (dorsal view-10x)

3. Antenna—scales:

0. Absent

1. Present

A scaled antenna was only found in *Oxytenis* (outgroup). According to Michener (1952) it is a primitive character among the Saturniidae.



3:0
L. serpentina (lateral view-40x)

3:1
O. modestia (lateral view-40x)

4. Male antenna—basal and median thirds modified (pectinated) in comparison with the apical third (dentated):

0. Absent
1. Present

This kind of antenna is typical of Ceratocampinae except for *Procitheronia* Michener, 1949 and *Bathyphlebia* R. Felder & Rogenhofer, 1874 (Balcázar-Lara & Wolfe 1997). Michener (1952) considered the antennae with modified apical third to be plesiomorphic.

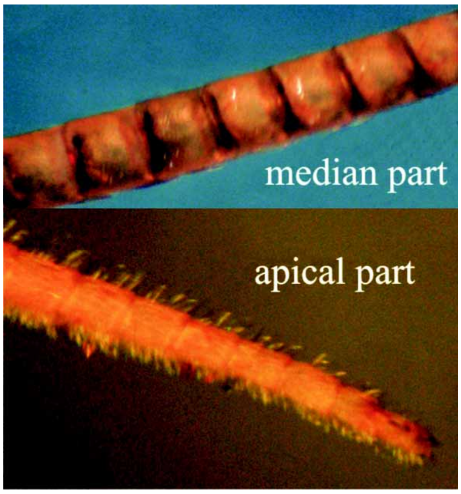
4:0
O. modestia (dorsal view)

4:1
E. imperialis (dorsal view)

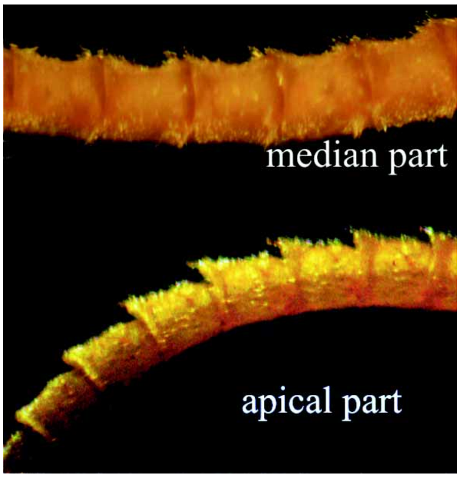
5. Female antenna—basal and median thirds modified (simple) in comparison with the apical third (dentate):

0. Absent
1. Present

Simple antennae are commonly found in Saturniidae females although pectinate and dentate antennae also occur in many Arsenurinae. Modified antennae occur in Ceratocampinae where the final portion is dentate.



5:0
A. pandora (lateral view-40x)



5:1
E. imperialis (lateral view-40x)

6. Forewings—form:

0. Short and rounded with narrow apex in both sexes
1. Short and rounded on females and semi-elongated on males (broad apex in both)
2. Long and rounded and in some cases with curved apex
3. Elongated with linear apex (straight)
4. Elongated with narrow apex

Wing shape is used to separate groups within Saturniidae. Large and wide wings have been considered primitive, with the smaller sphingiform ones more specialized (Michener 1952). The first two states (6:0 and 6:1) are found in *Oxytenis* and *Eacles*, respectively (outgroups). The other three states (6:2, 6:3 and 6:4) are the more general forms present in Arsenurinae.

6:0
O. modestia (dorsal view)

6:1
E. imperialis (dorsal view)

6:2
A. sylla (dorsal view)

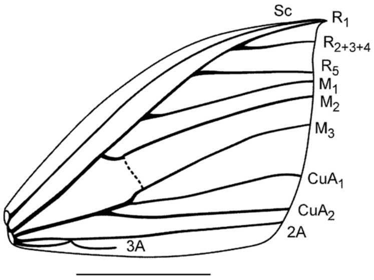
6:3
C. semiramis (dorsal view)

6:4
A. aidae (dorsal view)

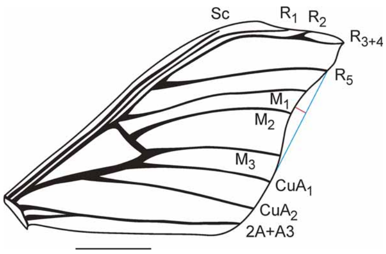
7. Male forewing—subapical concavity of outer edge between R_5 and CuA_1:

0. Absent
1. Present and little prominent
2. Present and very prominent

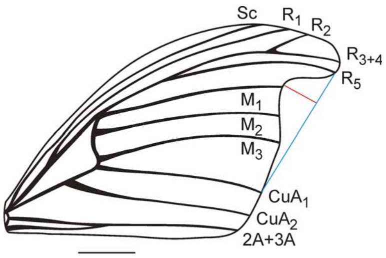
A straight line between R_5 and CuA_1 was traced to encode this character. The distance between this line and the outer edge of the wing was used as follows: distance less than 0.5 cm, concavity is weakly prominent; greater than or equal to 0.5 cm very prominent. Three basic forms were found in the concavity of forewings. In *Oxytenis* the concavity of the outer edge is completely absent (7:0) with the state 7:1 the most predominant in Arsenurinae, especially in the genus *Arsenura*. The most prominent concavity is observed in *Caio* and *Rhescyntis* (7:2).



7:0
O. modestia



7:1
G. lineata



7:2
C. romulus

8. Forewing—sub-marginal band:

0. Absent

1. Present

One of the most significant features of Arsenurinae is the ground color of the wings, which is usually gray or brown. The ornamentation usually involves lines and bands of various shades (Lemaire 1980) that can be used as taxonomic characters. The bands are absent only in the tribe Almeidaiini and in the outgroup (8:0) but present in all Arsenurini (8:1).

8:0
O. modestia (dorsal view)

8:1
A. sylla (dorsal view)

9. Forewing—two marginal dark spots between both M_3 and CuA_1 and CuA_1 and CuA_2:

0. Absent

1. Present

These contrasting dark spots are typical and exclusive to the genus *Rhescyntis*, in which species generally show a lighter color on the marginal band. This lighter shade is particularly evident in *R. pseudomartii*, *R. hippodamia* and *R. reducta*.

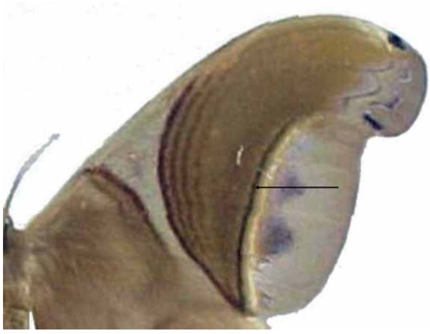
9:0
A. sylla (dorsal view)

9:1
R. hippodamia (dorsal view)

10. Forewing—form of the marginal line:

0. Concave
1. Wavy, not in the form of an “S”
2. Straight
3. Regularly convex at least until M_1
4. Wavy in the form of an “S”
5. Irregular (dentated)

Six different states were defined for this character from smooth to dentate or from concave to convex. In general these states remain constant within the genera with little variation.

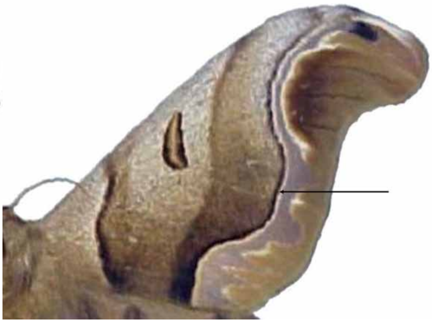


10:0
R. pseudomartii (dorsal view)

10:1
A. xanthopus (dorsal view)

10:2
D. fosteri (dorsal view)

10:3
P. thelia (dorsal view)



10:4
C. romulus (dorsal view)

10:5
L. serpentina (dorsal view)

11. Forewing—dilatations (prominences or lobes) of marginal line:

0. Absent
1. Present

The marginal band lines in *Arsenura* species usually presents dilatations or thickenings that Lemaire (1980) called outer line lobes, and this is present in either more or less prominent ways within the group. This thickening is discrete and variable in some species like *A. sylla* and constant and prominent in others like *A. meander*. Since this character is absent in all other analyzed taxa, it is considered an autapomorphy of *Arsenura*.

11:0
O. modestia (dorsal view)

11:1
A. polyodonta (dorsal view)

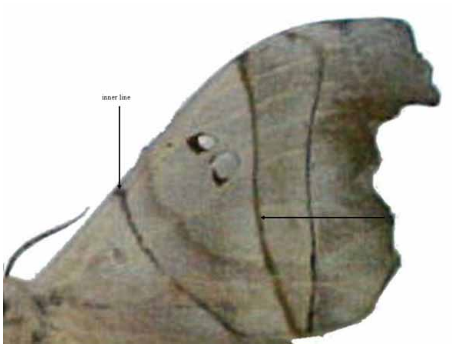
12. Forewing—dark line on median band bordering the inner line:

0. Absent

1. Present

This is one of the synapomorphic characters of *Dysdaemonia* and *Titaea*, being absent in the rest of the analyzed taxa. It appears more discrete in *Dysdaemonia* species, especially in *D. brasiliensis* and *D. concisa*, and is more evident in *T. lemoulti*. These two genera share several characters and are phylogenetically close.

12:0
O. modestia (dorsal view)



12:1
D. brasiliensis (dorsal view)

13. Forewing—costal margin:

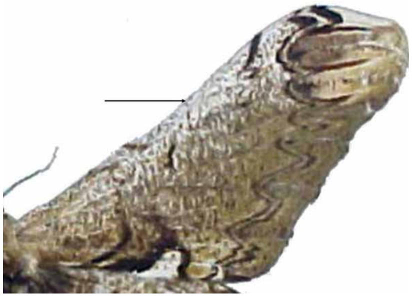
0. Convex

1. Concave all over the margin

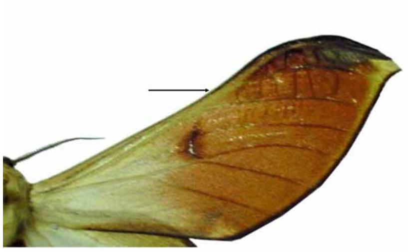
2. Accented concavity in the median region

The form of the costal margin of forewings is usually convex (13:0). The differentiated concave states occur only in *Loxolomia* (13:1) and *Almeidaia* (13:2) that also have narrow and elongate wings.

13:0
O. modestia (dorsal view)



13:1
L. serpentina (dorsal view)



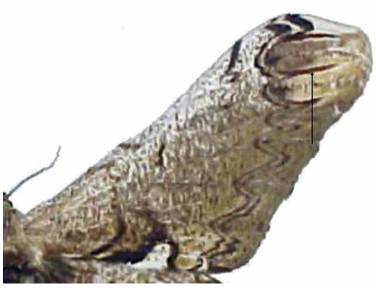
13:2
A. aidae (dorsal view)

14. Forewing—apical teeth spots form:

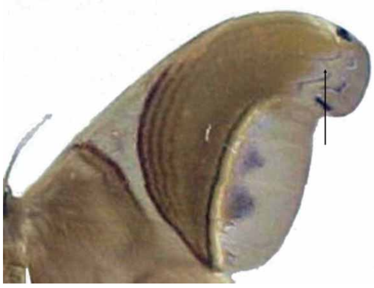
0. Absent
1. Present and with the base closed
2. Present and with the base open

This is an important species group character at the generic level because it is present in two of the ten genera in Arsenurinae and it is absent in the outgroup (14:0). These spots are evident in *Loxolomia* (14:1) and appear as two inverted teeth (with a closed base) whereas in *Rhescyntis* (14:2) the spot is more conspicuous in the form of three apical teeth with an open base. According to Becker & Camargo (2001) the variation in form or shape of these spots is an important character that separates *Rhescyntis* species.

14:0
O. modestia (dorsal view)



14:1
L. serpentina (dorsal view)



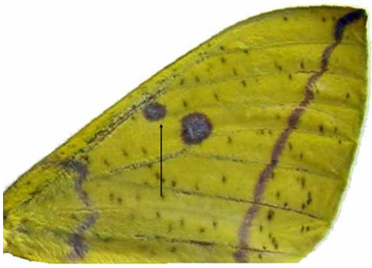
14:2
R. pseudomartii (dorsal view)

15. Forewings – cellular spots:

0. Absent
1. Present with a dark circular spot
2. Present with a discrete irregular dark spot
3. Present with an evident irregular dark spot
4. Present in the form of a trace or kidney-shaped
5. Present, irregular and interrupted by a discal spot (fenestrate)

This character is represented by any spot occurring in the discal cell or in the limit of the superior disc-cellular veins (sdc), median disc-cellular (mdc), inferior disc-cellular (idc) or the median cubital vein (m-cu). As the cellular spots may be absent or present in various forms in Arsenurinae, six states were encoded.

15:0
O. modestia (dorsal view)

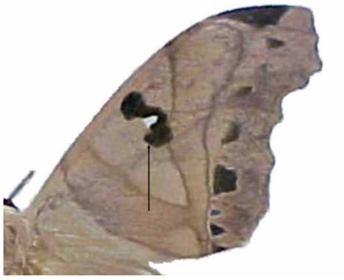


15:1
E. imperialis (dorsal view)

15:2
D. brasiliensis (dorsal view)

15:3
C. jehovah (dorsal view)

15:4
C. romulus (dorsal view)



15:5
T. lemoulti (dorsal view)

16. Forewings – diffuse oblique lines in median area (between inner and costal edges):

0. Absent
1. Present

The majority of *Paradaemonia* species present forewings with a dark ground color mixed with diffuse oblique lines between inner and costal edges. This character is a synapomorphy for the genus, although the lines seem to be less evident in some species.

16:0
O. modestia (dorsal view)

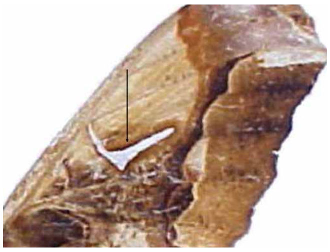
16:1
P. meridionalis (dorsal view)

17. Forewings – fenestrated spots:

0. Absent
1. Present (one or two semi triangular or elongate hyaline spots)
2. Present (circular spots)
3. Present (not so circular spots)

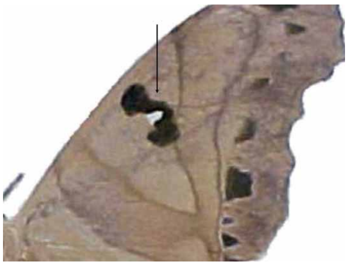
Forewings with fenestrated spots appear in three of the ten genera: in *Copiopteryx* (17:1) they are usually bigger on females and present various shapes with the semi triangular or elongate hyaline spots being the predominant form; in *Dysdaemonia* and *Titaea* (except in *T. orsinome*) it appears as one or two circular or semi circular spots (17:2 and 17:3).

17:0
R. pseudomartii (dorsal view)



17:1
C. derceto (dorsal view)

17:2
D. brasiliensis (dorsal view)



17:3
T. lemoulti (dorsal view)

18. Hindwings – sub-marginal lines:

0. Absent or merely diffuse spots
1. Characteristic curved line

Dysdaemonia species show a characteristic curved line in the hindwings. It could appear as a spot or thick line in some specimens, with origin in the outer margin at the end of 2A, reaching the extension in the form of a tail just in the line of M_2 (18:1). The extension and intensity of this line are autapomorphic characters for the species in the genus. In all other examined taxa this line is absent or appears as diffuse spots in the marginal area.

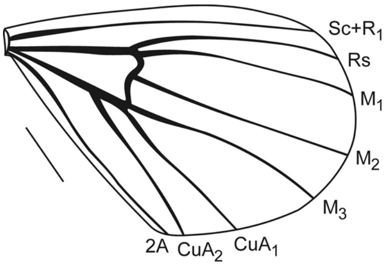
18:0
A. rebeli (dorsal view)

18:1
D. brasiliensis (dorsal view)

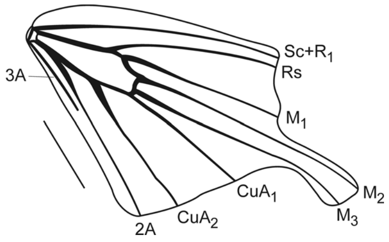
19. Hindwings – males with extension in the form of a tail:

0. Absent
1. Present and short with expansion of M_2 and M_3
2. Present and long with expansion of M_2, M_3 and CuA_1

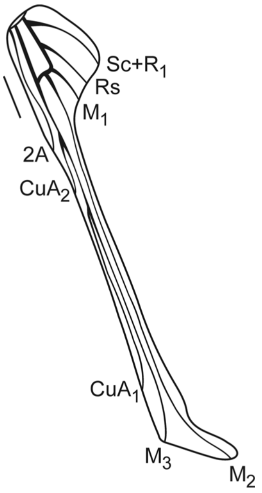
Two principal types of hindwing extension were found. In the first (19:1), an expansion of M_2 and M_3 makes them longer than usual in species without the hindwing tail. In the second (19:2), besides the elongation of M_2, M_3 and $CuA_{1,}$ there is an anastomosis of the M_3 with CuA_1 and CuA_2.



19:0
C. romulus



19:1
D. concisa



19:2
C. semiramis

20. Hindwings – fenestrate spot:

0. Absent
1. Present and circular
2. Present, elongated or semi triangular

Fenestrate hindwings are shown in *Dysdaemonia* (20:1) and in *Copiopteryx* species (20:2). In both genera the female fenestrate spots are bigger and more evident than in males except, for *D. fosteri* where both sexes show similar spots. In *Copiopteryx* species the fenestrate spots vary from little and imperceptible to large and evident. For example, in *C. semiramis* they are almost imperceptible depending on the geographic origin of the specimen.

20:0
A. rebeli (dorsal view)

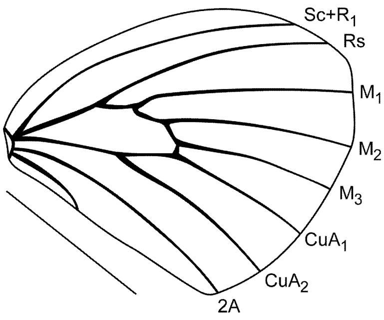
20:1
D. fosteri (dorsal view)

20:2
C. derceto (dorsal view)

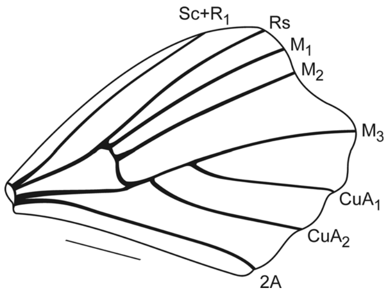
21. Hindwings – origin of CuA$_2$:

0. Far from CuA$_1$ and M$_3$
1. Anastomosed in the base with CuA$_1$ and M$_3$

CuA$_2$ has its origin far from CuA$_1$ and M$_3$ in most analyzed taxa in this study (21:0). The anastomosis of CuA$_2$ with CuA$_1$ and M$_3$ is one of the synapomorphies of the genera *Copiopteryx* and *Loxolomia*, supporting the clade established in the cladistic analysis (Fig. 1).



21:0
E. imperialis



21:1
L. serpentina

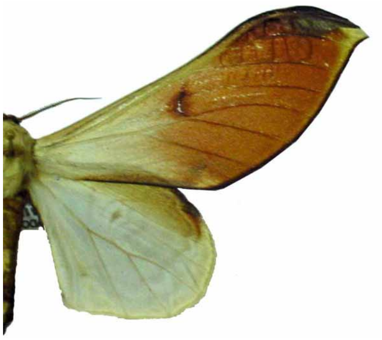
22. Fore and hind wings – upper side with lines or stripes (forming bands):

0. Absent or merely spots without lines or definite bands formed

1. Present merely as small evident lines

2. Present with very evident lines

The constant presence of bands of various shapes of ground colors in the wings is one of the distinguishing characteristics of the tribe Arsenurini. In the tribe Almeidaini the spots do not form lines or definite bands.



22:0
A. aidae (dorsal view)

22:1
O. modestia (dorsal view)

22:2
A. rebeli (dorsal view)

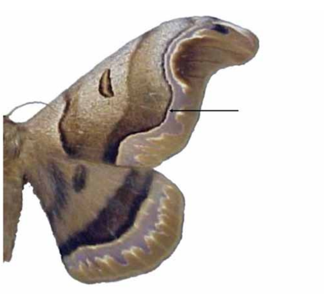
23. Fore and hind-wing – marginal band with clear sigmoidal area (characteristic):

0. Absent or present in another shape

1. Present

The presence of a lighter sigmoidal line in the marginal band is an autapomorphic character of the genus *Caio* that also shows other apomorphies that make it unique, although close to *Arsenura*.

23:0
A. rebeli (dorsal view)



23:1
C. romulus (dorsal view)

24. Fore and hind wings – dark veins:

0. Absent
1. Present

The veins of Arsenurinae are visualized only after the diafanization process (24:0). The genus *Grammopelta* is an exception which presents darker scales on the veins that contrast with the ground color, giving a checkered aspect to the wings (24:1).

24:0
C. romulus (dorsal view)

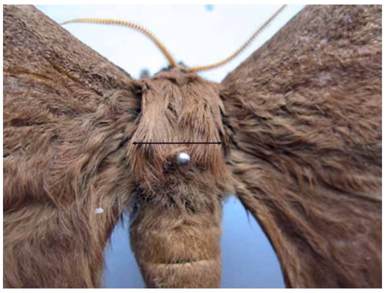
24:1
G. lineata (dorsal view)

25. Thorax:

0. Fragile
1. Moderately robust
2. Very robust (flight adapted)

In general, saturniid moths are poor fliers, although the males of some species are capable of long distance reproductive dispersal. This flight capacity may be related to strength and form of the thorax. *Oxytenis* and *Almeidaia* (25:0) and Arsenurinae (25:1) in general show a weaker thorax in relation to Ceratocampinae (25:2). The Ceratocampinae are among the best fliers in Saturniidae, with a robust thorax. According to Janzen (1984), a prominent example is *Syssphinx molina* (Cramer, 1780). Since flight capacity certainly has nothing to do with wingspan (several species of *Rhescyntis* have wide wings and a moderately robust thorax (25:1) and are still poor fliers) it is impossible to establish a relationship between the size and strength of the thorax and wingspan. For a better definition of this character some measures of the thorax width were taken: the median thorax width of 15 males of *Oxytenis modestia* (25:0) was 5.82 ± 0.75 mm; of *Arsenura armida* (25:1) was 11.19 ± 0.92 mm and of *Eacles imperialis* (25:2) was 13.70 ± 0.83 mm.

25:0
O. modestia (dorsal view)



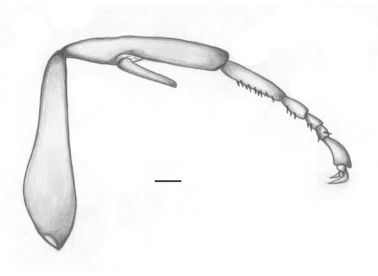
25:1
A. armida (dorsal view)

25:2
E. imperialis (dorsal view)

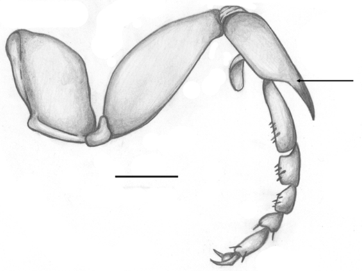
26. Legs—dorsal projection in the form of an apical spine in the fore tibiae:

0. Absent
1. Present

Lemaire (1971) referred to this apical projection in the fore tibiae as a “tibial tip”, being one of the apomorphic characters that supports the tribe Almeidaiini. However Michener (1952) argued that it is a phylogenetic character of minor importance because it appears in unrelated groups within the family. In fact, these spines are present in some species of Ceratocampinae and Hemileucinae but are always more discrete and less sclerotized when compared to *Almeidaia*. This character was considered plesiomorphic by Peigler (1993) and appears only in the tribe Almeidaiini within the subfamily Arsenurinae.



26:0
C. romulus

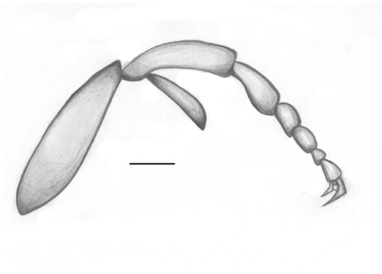


26:1
A. aidae

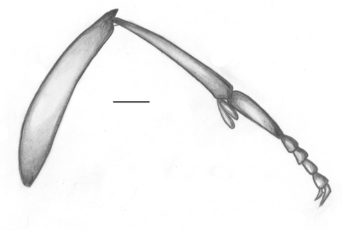
27. Legs—tibial spurs formula:

0. 0-2-4 without apical spine
1. 0-2-4 with apical spine
2. 0-2-2

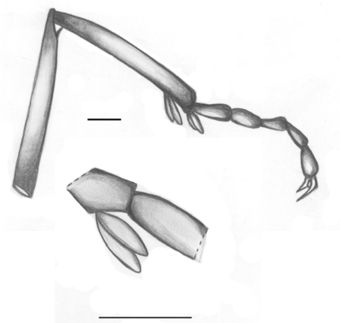
To encode this character, the number of tibial spurs was expressed as a formula as mentioned by Scoble (1995). The fore tibiae do not present spurs, only an epiphysis near their base that according to Michener (1952) is probably a modified spur (27:0). The median (27:1) and hind tibiae always present at least one pair of apical spurs. However, many saturnids also present an additional pair of median spurs in their median legs (27:2). According to Michener (1952), the presence of this extra pair of spurs is a primitive character in Saturniidae. Two basic forms of the spurs were observed: with or without an apical spine. The outgroup taxon *Oxytenis modestia* presents spurs with a cylindrical apex and without a sclerotized terminal spine, unlike all the other taxa.



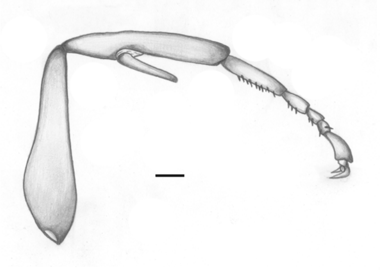
27:0
O. modestia (fore leg)



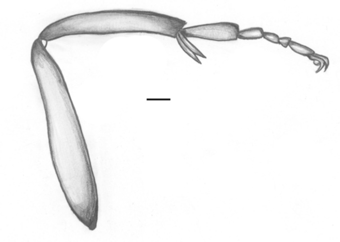
27:0
O. modestia (median leg)



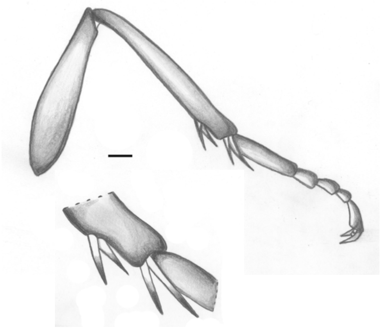
27:0
O. modestia (hind leg)



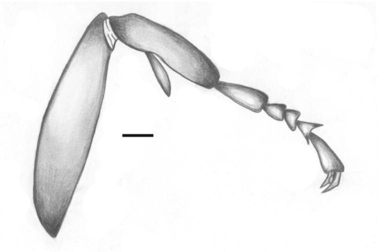
27:1
C. romulus (fore leg)



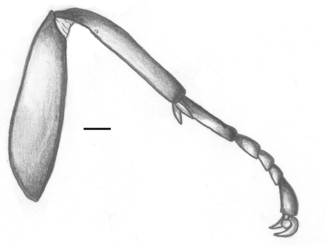
27:1
C. romulus (median leg)



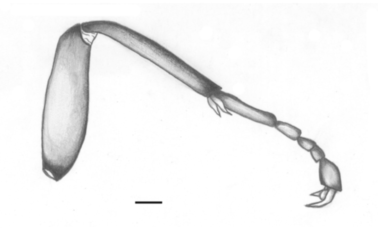
27:1
C. romulus (hind leg)



27:2
A. armida (fore leg)



27:2
A. armida (median leg)



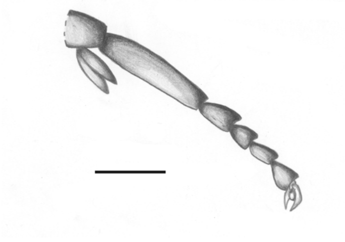
27:2
A. armida (hind leg)

28. Legs—tarsomere spines:

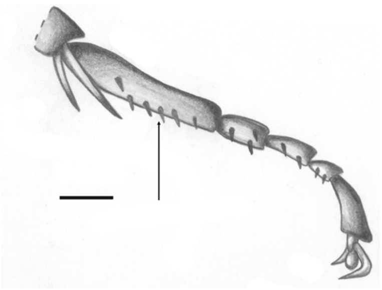
0. Absent

1. Present

According to Michener (1952), the presence of numerous tarsal spines is a primitive character. Tarsal spines are absent in the outgroups *Eacles imperialis* and *Oxytenis modestia*, but they are present in all Arsenurinae except *Grammopelta lineata*.



28:0
O. modestia (mesothoracic)



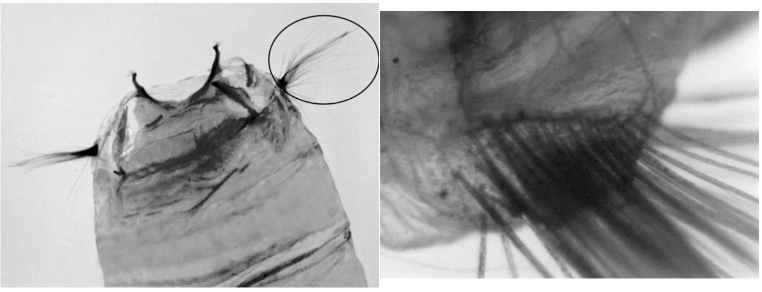
28:1
C. romulus (mesothoracic)

29. Abdomen—first abdominal segment of the males with a cerdae tuft at the spiracle line:

0. Absent

1. Present

All males of Arsenurinae present a cerdae tuft on the first abdominal segment at the spiracle line. This tuft may serve a sexual attraction function, but this is not clear. It is a synapomorphic character of the subfamlily. These cerdae are substantial and evident in many species, especially the ones of the tribe Arsenurini. In the tribe Almeidaiini, the cerdae are shorter, thinner and less visible than in Arsenurini. They are also easily lost in the dissection process.



10x

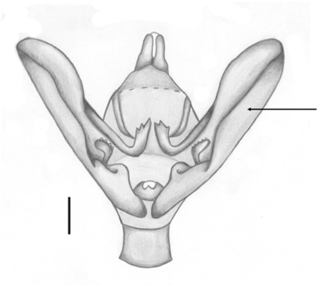
32x

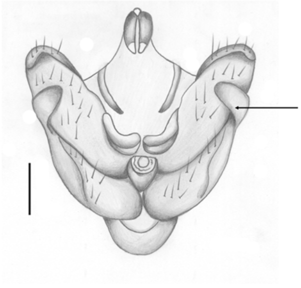
29:1
A. aidae (dorsal and lateral view)

30. Male genitalia – form of the valvae:

0. Simple
1. Lobate

The genus *Grammopelta* presents simple valvae with the ventral margin being smooth (30:0), while all other Arsenurinae present an apical or subapical process that appears more or less evident in the ventral margin of the valvae. It is an autapomorphic character of the monotypic genus *Grammopelta* that has an exclusively South American distribution. According to the relationship hypothesis presented in Fig. 1 this genus is phylogenetically close to the genus *Arsenura*.

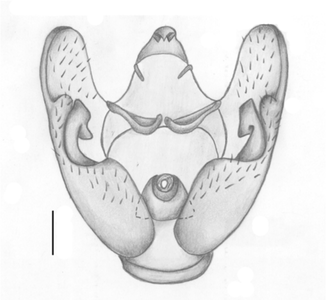

30:0
G. lineata (ventral view)

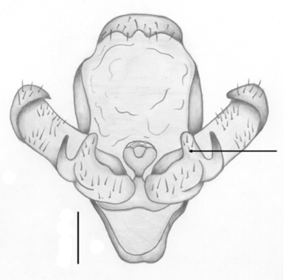

30:1
P. mayi (ventral view)

31. Male genitalia – dentate process in dorsal edge of the sacculus:

0. Absent
1. Present

Modifications in the outer edge of the valvae are observed in Oxyteninae (31:1) and in the other primitive members of each subfamily within Saturniidae (Michener 1952). Various forms of these modifications have been recorded, but the homology of the structures is often difficult to establish. Since there is no previous mention of discrepancies in the structures, it has been encoded separately.

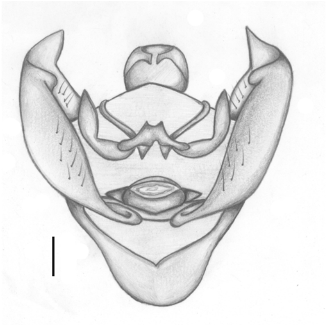

31:0
A. armida (ventral view)


31:1
O. modestia (ventral view)

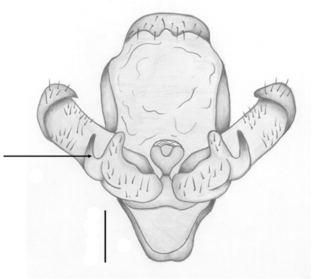
32. Male genitalia – projection (lobe) in the form of a spine in the valvae:

0. Absent
1. Present in the ventral face of the sacculus
2. Present in the dorsal face of the sacculus (harp)

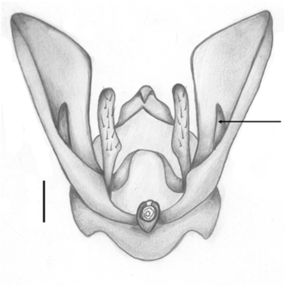
As mentioned in the previous character, the homology of the structures can be difficult to characterize. For this reason the structures that appear in the form of a spine were encoded and separated from the form with other modifications of the valva. Balcázar-Lara & Wolfe (1997) also mentioned this discrepancy or difficulty in establishing the homology of the male genitalia structures. Most Arsenurinae species do not present this character (32:0), that have been observed only in *Oxytenis* (32:1) and in *Almeidaia* (32:2).



32:0
E. imperialis (ventral view)



32:1
O. modestia (ventral view)

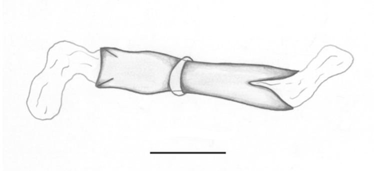


32:2
A. romualdoi (ventral view)

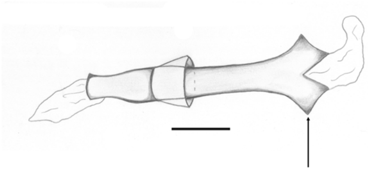
33. Male genitalia – aedeagus with symmetrical lateral subapical projections (teeth):

0. Absent
1. Present

Some particularities of the aedeagus may serve as important phylogenetic characters. The presence of lateral projections (33:1) in the aedeagus of *Titaea* species is an autapomorphy that strengthens the monophyletic genus hypothesis (Fig. 1).



33:0
P. mayi (ventral view)

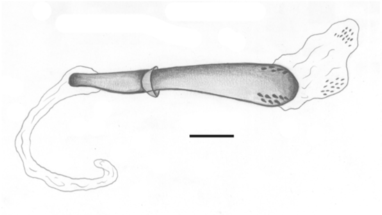


33:1
T. tamerlan (ventral view)

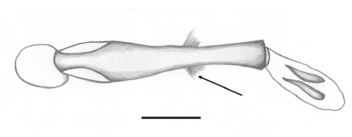
34. Male genitalia – spines in the median portion of the aedeagus:

0. Absent
1. Present

The presence of spines in the median portion of the aedeagus, in association with other characters, is an autapomorphy of *Grammopelta lineata* that confirms this as a well established monotypic genus.



34:0
L. serpentina (ventral view)

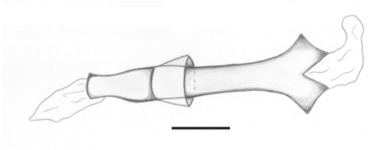


34:1
G. lineata (ventral view)

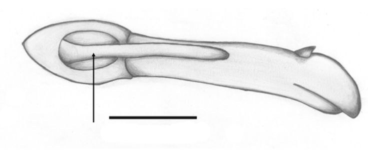
35. Male genitalia – elongated projection in the ventral side of the aedeagus:

0. Absent
1. Present

The presence of an elongated projection in the ventral face of the aedeagus (35:1) is an autapomorphic character in *Oxyteninae* that shows a completely different form in relation to the other examined taxa.



35:0
T. tamerlan (ventral view)

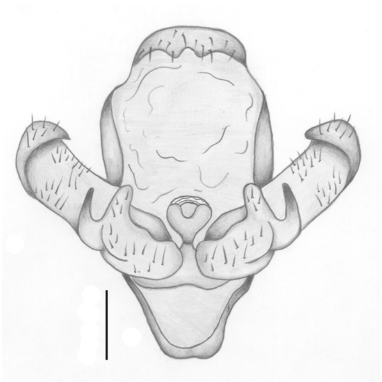


35:1
O. modestia (ventral view)

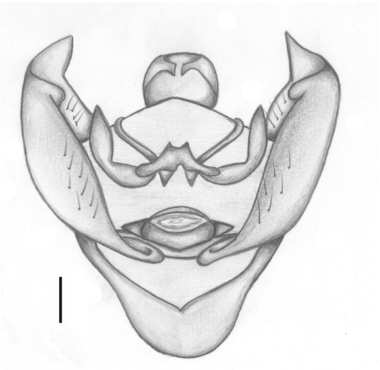
36. Male genitalia – transtilla:

0. Absent
1. Present and smooth with lateral arms fused to a sclerotized plate
2. Present and smooth without fused lateral arms
3. Present with a prominent apical spine
4. Present with cerdae
5. Present with last third marginally serrated
6. Present with rugose papillae
7. Present with semicircular apical portion or in the form of a half moon
8. Present with apical portion that unites with the juxta
9. Present with robust apical portion

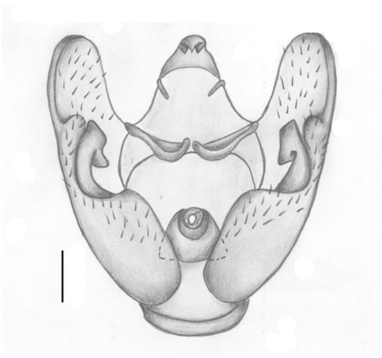
The great variation observed makes this character difficult to encode. Ten states of the basic form of the transtilla were recognized. However, there are particularities for each species. It is absent in *Oxytenis* (36:0) and according to Balcázar-Lara & Wolfe (1997) it is also absent in some genera of Ceratocampinae. The other nine observed states (36:1-36:9) are quite characteristic, following a basic pattern with little variation for each genus. The transtilla of *Eacles imperialis* (outgroup) presents robust lateral arms that are fused to a sclerotized plate (36:1); the basic pattern of *Arsenura* species is the absence of this plate (36:2); in *Dysdaemonia* species there is an accented sclerotization of the apical portion that is tapered for most species (36:3); *Loxolomia* species present the apical portion covered by cerdae, and wide and curved lateral arms (36:4); *Grammopelta lineata* presents a serrated apex (36:5); and *Rhescyntis* species present rugose papillae. The transtilla of *Titaea* species is variable and the basic pattern observed was encoded as semicircular or in the form of a half moon (36:7). According to Lemaire (1980), the diagnostic characteristic of *Paradaemonia* species is a transtilla ventrally united by a membranous zone that connects with the juxta in the anterior portion, being very evident in some species (36:8). The last encoded state (36:9) is found in *Copiopteryx* species that presents a robust transtilla with wide arms and an apical portion, especially in *C. jehovah* and *C. sonthonnaxi*.



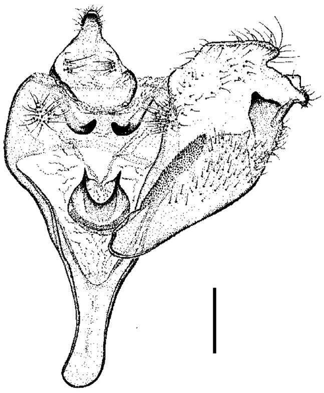
36:0
O. modestia (ventral view)



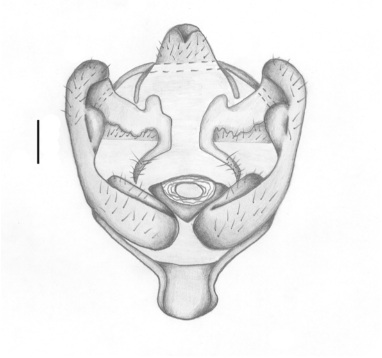
36:1
E. imperialis (ventral view)



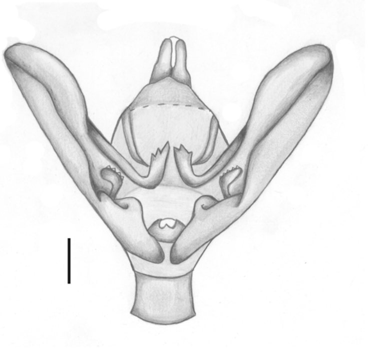
36:2
A. armida (ventral view)



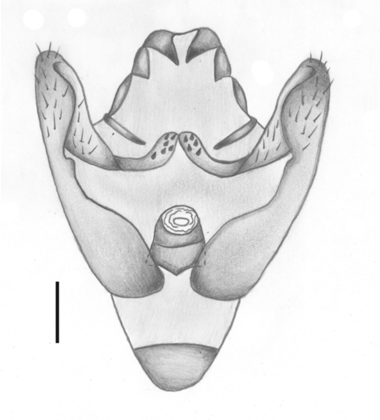
36:3
D. concisa (ventral view)



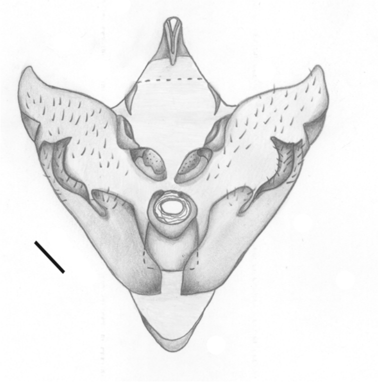
36:4
L. serpentina (ventral view)



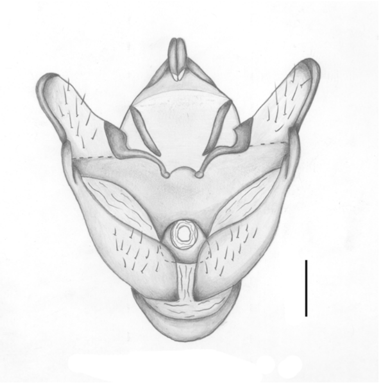
36:5
G. lineata (ventral view)



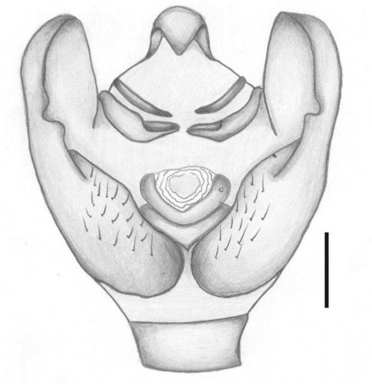
36:6
R. pseudomartii (ventral view)



36:7
T. tamerlan (ventral view)



36:8
P. meridionalis (ventral view)



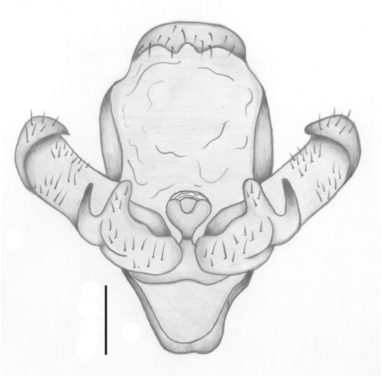
36:9
C. sonthonnaxi (ventral view)

37. Male genitalia – gnathos:

0. Absent

1. Present

The absence of gnathos is an autapomorphy of *Oxytenis modestia* (outgroup). Within the Arsenurinae this character is important only to strengthen the monophyly of the ingroup and is not taxonomically informative.



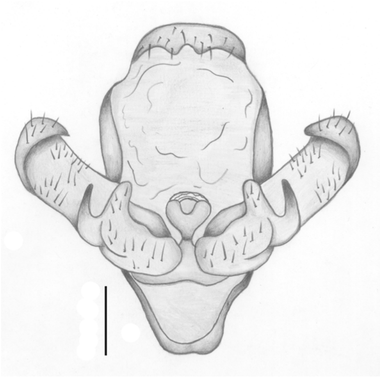
37:0
O. modestia (ventral view)

37:1
C. sonthonnaxi (ventral view)

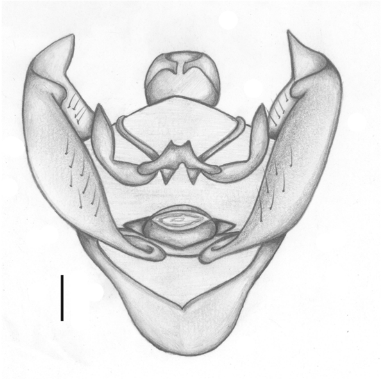
38. Male genitalia – lateral arms of the gnathos:

0. Absent
1. Present, long and strongly sclerotized
2. Present, generally short and weakly sclerotized

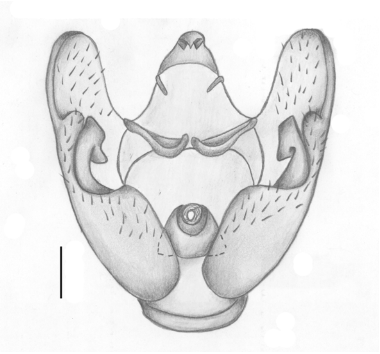
The gnathos may be absent in some Saturniidae (38:0). In some cases e.g., *Eacles imperialis* this structure is long, wide and strongly sclerotized (38:1). In general, the Arsenurinae present a weakly sclerotized gnathos that is discrete in many cases (38:2). There is some variation in sclerotization and interspecific forms within each group.



38.0
O. modestia (ventral view)



38.1
E. imperialis (ventral view)

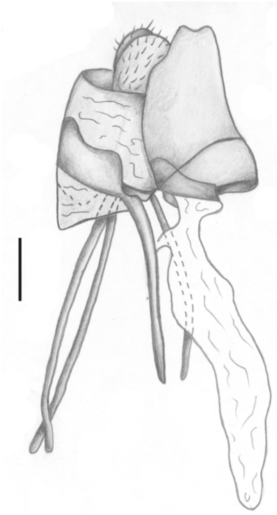


38.2
A. armida (ventral view)

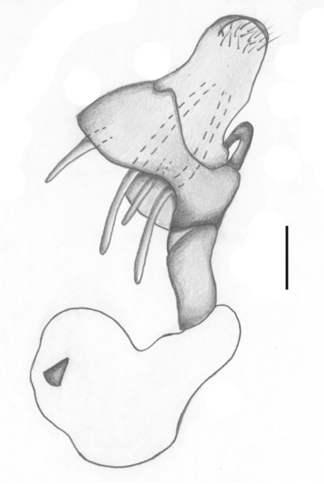
39. Female genitalia – signum in the bursa:

0. Absent
1. Present and discrete in the proximal portion
2. Present and discrete in the median portion
3. Present and evident (occupying large part of the bursa)

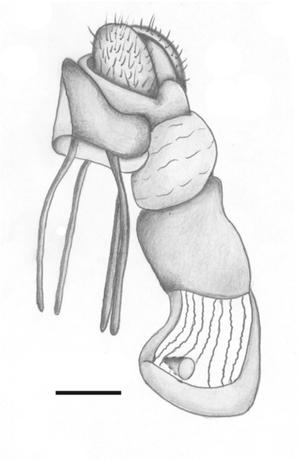
The majority of the species analyzed lack the signum in the bursa (39:0). Its absence is observed independently in different clades, in distant branches of the phylogenetic tree. Three possible states were found where the signum is present: in *Almeidaia* it appears in the form of a drop in the proximal area of the bursa (39:1); in *Copiopteryx* (except *C. derceto*) it occupies the median portion of the bursa and differs from other groups by being more or less streaked (39:2); in *Oxytenis modestia* it is evident and appears as two sclerotized plates that occupy most of the bursa (39:3).



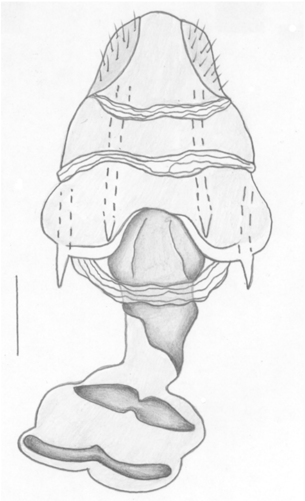
39:0
C. romulus (lateral view)



39:1
A. aidae (lateral view)



39:2
C. sonthonnaxi (lateral view)

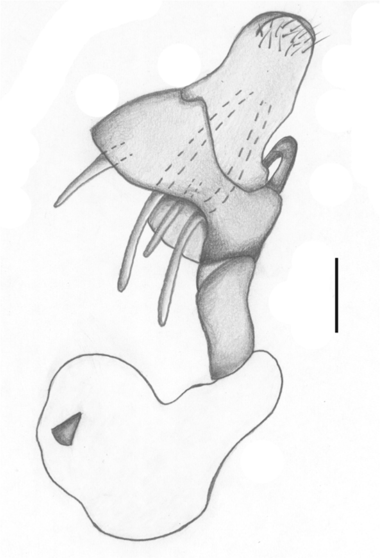


39.3
O. modestia (ventral view)

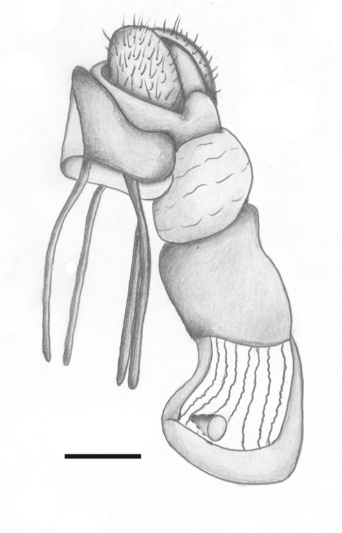
40. Female genitalia – grooves in the bursa:

0. Absent
1. Present

Streaked tissue in the bursa appears only in *Copiopteryx* species, with *C. derceto* the sole exception.



40:0
A. aidae (lateral view)



40:1
C. sonthonnaxi (lateral view)

Results and Discussion

Subfamily Arsenurinae as a monophyletic group

The analysis resulted in a single cladogram (L=76; Ci=98; Ri=99), with previously published taxonomic groupings in the subfamily Arsenurinae (tribes and genera) appearing as monophyletic, corroborating Lemaire (1980). Arsenurinae is therefore reconfirmed as monophyletic, with few homoplasies and several strong synapomorphies for included groupings (Figs. 1-2): long and rounded forewings that show a curved, linear or tapered apex (character 6); cellular spots that appears within the subfamily as irregular and discrete dark spots (e.g., *Dysdaemonia*), more evident (e.g., *Copiopteryx*), like a trace (e.g., *Arsenura* and *Caio*) or even a dark macula circling the hyaline spot (e.g., *Titaea*) (character 15); the presence of tarsal spines (character 29); transtilla with varied states (character 36); and lateral arms of the gnathos generally slightly sclerotized and of reduced size (character 38).

Jackknife analysis resulted in 102 equally parsimonious trees presenting different topologies (L=79; Ci=94; Ri=98). The strict consensus tree of 100 Jackknife replications is given in Fig. 3. When Jackknife or Bootstrap values are low, it generally indicates the clade is supported by few characters, by homoplasies or a combination of both. According to Regier *et al.* (2002) a clade that presents a value higher than 80% is a strongly supported clade. The results show that the subfamily presents a 90% supported clade.

Tribes as monophyletic groups

Corroborating Lemaire (1980), the tribes are recovered as monophyletic groups: Almeidaiini is supported by six synapomorhies and Arsenurini by two. Tribe Almeidaiini is supported by the following characters: elongated forewings with tapered apex (character 6); costal margin of the forewings with an accented concavity in the median region (character 13); lines or bands absent in fore and hindwings (character 22); presence of a characteristic prolongation in the form of an apical spine in the forelegs called “tibial tip” by Lemaire (1971) (character 26); male genitalia presenting a spine-like projection (harp) in the valves beginning in the dorsal face of the sacculus (character 32); and bursa with a signum in the proximal area (character 39). Arsenurini species present brown or grayish ground color and the formation of lines and bands that supports the group (character 8). Another synapomorphy is the slightly robust thorax that indicates the lack of flight adaptation (character 25).

Jackknife results indicate a 96% clade support for Almeidaiini and 80% for Arsenurini, justifying the taxonomic hierarchy established by Lemaire (1980). Both tribes share several characters, but a morphological study of *A. aidae* (Almeidaiini) demonstrates that it also presents significant differences, like the pilifer absence and fore tibia with a strong and prominent apical spine (Camargo *et al.* 2005a, 2005b, 2006).

Monophyletic genera

All defined genera (Lemaire 1980) are monophyletic with solid support given by several synapomorphies (Figs. 1–2). The percentage of clade support is shown in Fig. 3. Following the position of each genus given in Fig. 1, the characters that support each clade are presented as follows. The characters of each genus are also listed following their position in the cladogram. The genus *Almeidaia* presents the same apomorphies that support the tribe Almeidaiini.

Loxolomia: dentate marginal band line in the forewing (character 10:5); costal margin of the forewings concave in all its extension (character 13:1); characteristic spot in form of the teeth in the apex of the forewings (character 14:1).

Copiopteryx: dark and irregular cellular spots in the forewings (character 15:3); forewings with elongated or semi-triangular hyaline spots (character 17:1); hypertrophy of the tails in both sexes, showing an expansion of M_2, M_3 and CuA_1 veins (character 19:2); non circular fenestrate spots in the hindwings, being the basic form of all other fenestrated Arsenurinae (character 20:2); robust transtilla with broad apical portion, especially in *C. jehovah* and *C. sonthonnaxi* (character 36:9); signum occupying the median portion of the streaked bursa, unlike other taxa (characters 39:2 and 40:1).

Rhescyntis: presence of two characteristic marginal spots in the forewings, between the CuA_1 and CuA_2 (character 9:1); dentiform spots in the apex of the forewings (character 14:2), and transtilla with rugose papillae (character 36:6).

Grammopelta: supported by five synapomorphies and one homoplasy: male antennae with short and straight sensilla (character 2:1); veins presenting dark scales in all wings (character 24:1); tarsi spines are present in all Arsenurinae, except in *G. lineata* which constitute a homoplasic character (character 28:0); simple valvae are exclusive (character 30:0); spines in the median portion of aedeagus (character 34:1) and transtilla with serrated apex (character 36:5).

Arsenura: forewing with sinuous line separating the outer from the median lines (character 10:1) and presence of lobes or dilatation in the marginal line (character 11:1).

Caio: forewing with sigmoidal marginal band line and adjacent area (characters 10:4 and 23:1).

Dysdaemonia: circular fenestrate spot in the forewings (character 17:2); hindwings presenting a characteristic curved line with its origin at the line of 2A vein and reaching the tail like prolongation at the line of M_2 vein (character 18:1); and circular fenestrate spot in the hindwings (character 20:1).

Titaea: genus with the least support from the Jackknife analysis but with four synapomorphies: forewings with cellular spot in the form of an arch usually around the fenestrate spot (character 15:5); lateral projections in aedeagus (character 33:1); transtilla circular or in the form of a half moon apical portion (character 36:7); and forewings with semi-elongated and not perfectly circular fenestrae (character 17:3).

Paradaemonia: forewing with the marginal band line regularly convex (character 10:3); median area of all wings with diffuse oblique lines characteristic of this group (character 16:1); and transtilla ventrally united by a membranous zone (character 36:8).

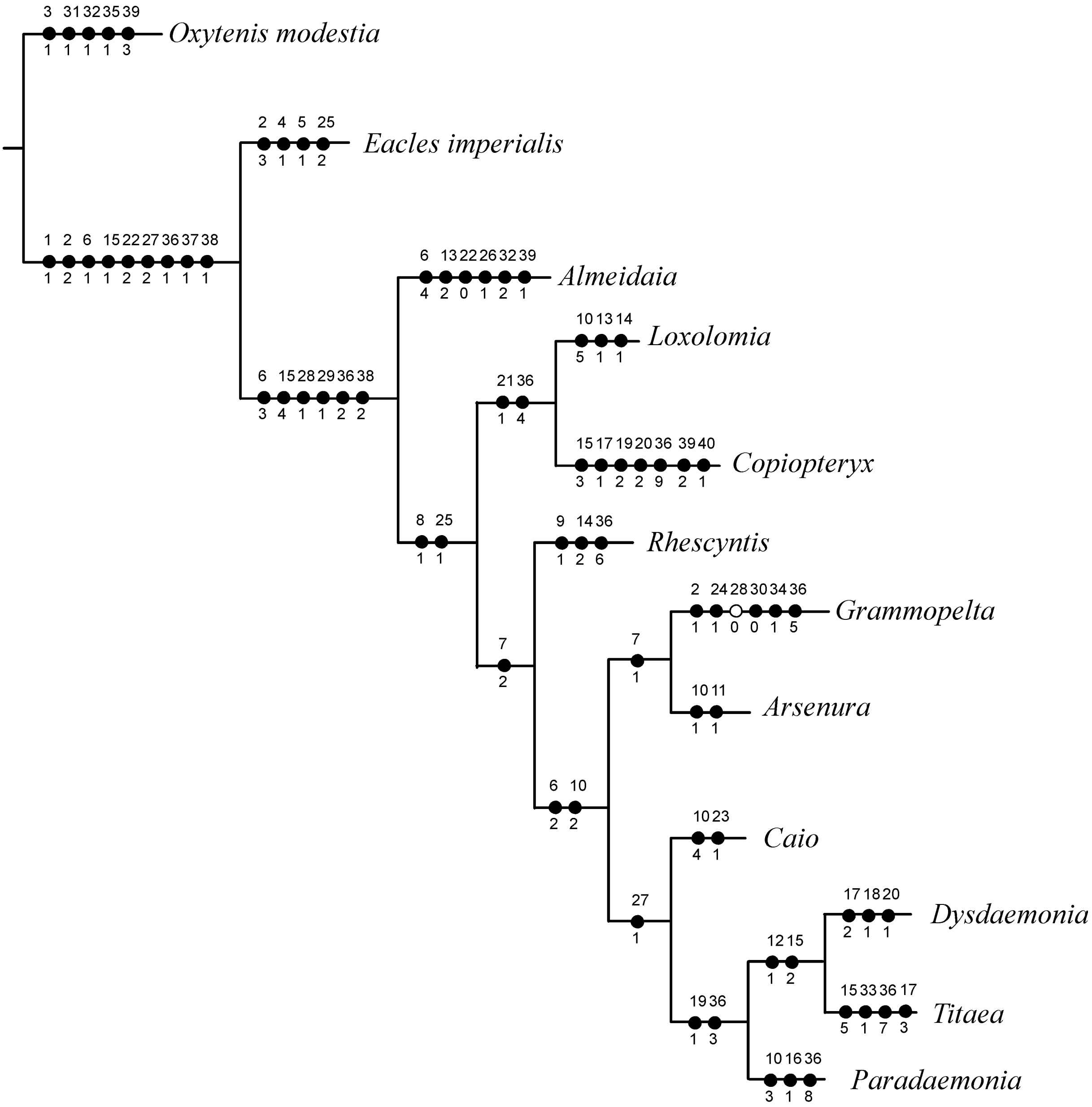


FIGURE 1. Cladogram showing proposed relationship of genera of Arsenurinae and Acctran optimization (L=76; Ci=98; Ri=99). Filled circles are synapomorphies, open circles homoplasies. Numbers above the branches indicate the character, numbers below are the states for each.

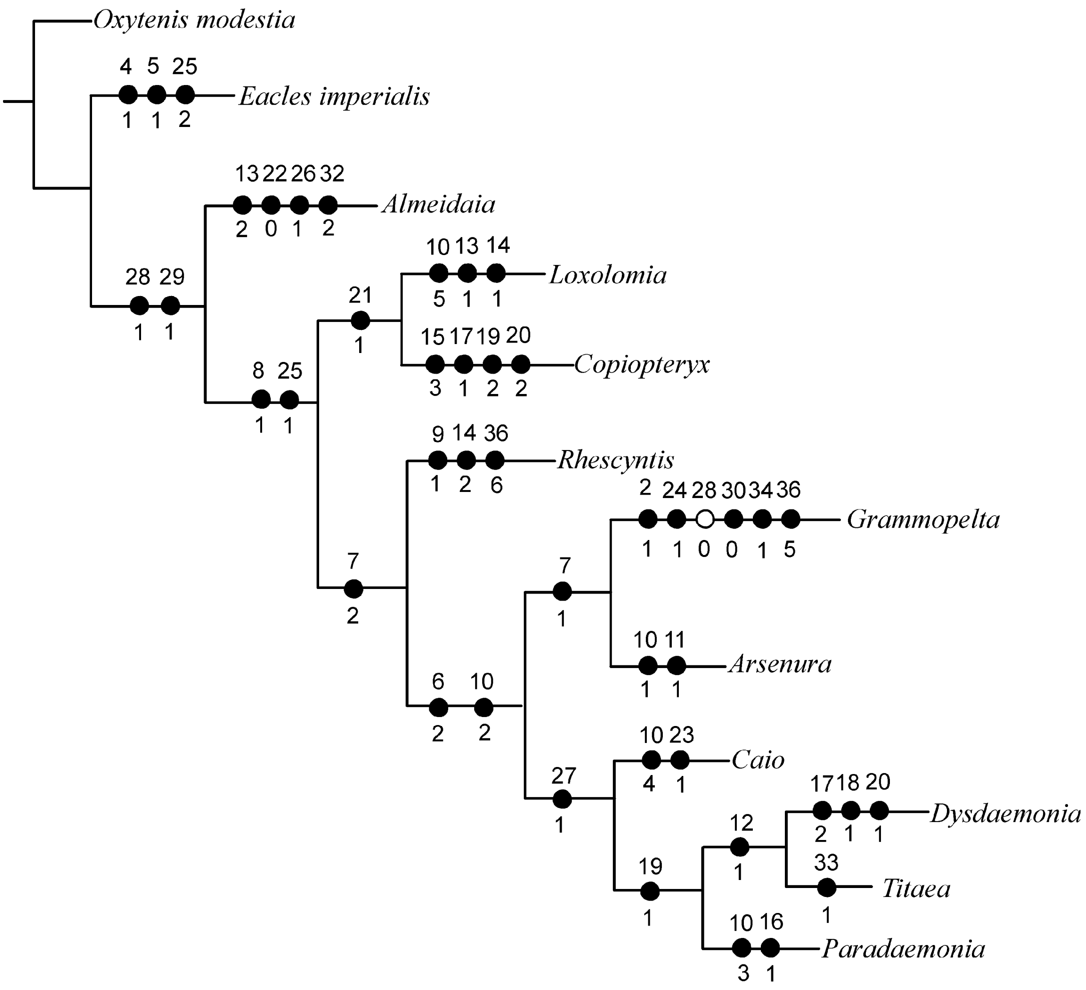


FIGURE 2. Relationship of genera of Arsenurinae with unambiguous optimization (L=76; Ci=98; Ri=99). Filled circles are synapomorphies, open circles homoplasies. Numbers above the branches indicate the character, numbers below are the states for each.

Relationshipss between Arsenurinae genera

Except for brief proposals by Michener (1952), the tribal separation (Almeidaiini and Arsenurini) presented by Lemaire (1980) and work by Peigler (1993), the relationship among the ten genera within Arsenurinae have been incompletely presented and discussed. The results of this study corroborate Peigler (1993) only partially, with different topologies for some clades, possibly given the characters used and sample universe. The analysis resulted in the following relationship hypothesis among the genera: (*Almeidaia* ((*Loxolomia*, *Copiopteryx*) (*Rhescyntis* ((*Grammopelta*, *Arsenura*) (*Caio* (*Paradaemonia* (*Dysdaemonia*, *Titaea*))))))).

It is perhaps not surprising that the genus *Almeidaia* forms a separate clade, given the distinct morphological aspects compared to other Arsenurinae. This result is in agreement with Lemaire (1980), who included the group in a separate tribe. According to Lemaire (1980) and Peigler (1993), *Almeidaia* shares affinities with Ceratocampinae, and could be designated as a separate subfamily, being apparently a primitive group.

The relationship between *Loxolomia* and *Copiopteryx* is supported by the common origin of $M_{3,}$ CuA_1 and CuA_2 (character 21:1). Similar to Peigler (1993), *Rhescyntis* appears neighboring this clade, although belonging to another large clade formed by the other genera.

Grammopelta and *Almeidaia* have been considered as the most primitive genera among the Arsenurinae (Michener 1952; Lemaire 1980), so the less basal position of *Grammopelta* and its status of sister group of

Arsenura was not expected. These two genera present several distinct characters and the support of this clade is only 51% according to Jackknife analysis. However, the basic form of the wings, more evident on males and especially with less accented subapical concavity, had some influence on the final result of the analysis. According to Peigler (1993), the relationship between *Grammopelta* and *Loxolomia* is even less supported (17%), and he indicated this is probably a false sister-group.

The relationship between *Caio*, *Dysdaemonia*, *Titaea* and *Paradaemonia* is supported basically by the tibial spur formula (character 27:1). This result was expected given the general appearance of the adults, especially between *Titaea* and *Dysdaemonia*. Except for *Paradaemonia*, whose larvae feed on Lythraceae, there are records that larvae of the species of these genera are specialized in Bombacaceae (Travassos & D'Almeida 1937; D'Araujo e Silva *et al*. 1968; Dias 1978; Janzen 1982; Stone 1991; Peigler 1993). The relationship hypothesis among these genera is in agreement with the results presented by Peigler (1993).

The relationship proposed by Michener (1952), where the genera *Arsenura*, *Dysdaemonia*, *Titaea* and *Paradaemonia* are presented as subgenera of *Rhescyntis*, and also the association between *Loxolomia* and *Grammopelta* proposed by Peigler (1993), were not corroborated by the cladistic analysis.

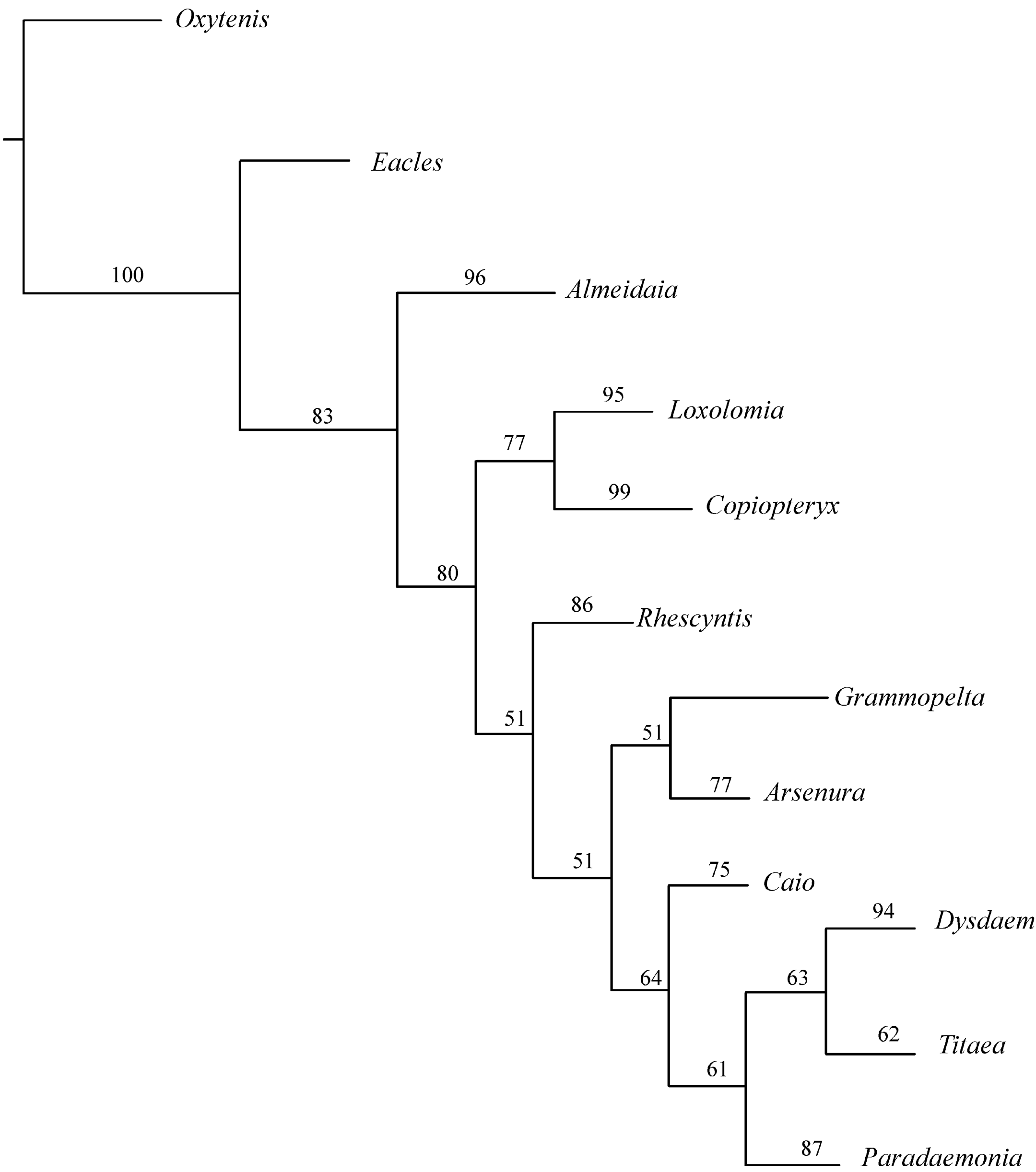


FIGURE 3. Strict consensus tree of 100 Jackknife replications based on 40 adult morphological characters. Values represent the frequency (%) that a clade was found in the replications.

Acknowledgments

The authors are grateful to Embrapa Cerrados and technicians Wellington Cavalcanti for help with line drawings and Jânio Fonseca Silva for help with specimen preparation. We thank Karen Schmidt and Adewale Okeowo Adeniyi for correcting grammar and Nícholas F. Camargo for final art for the figures. We also thank Embrapa for financial support, curators of the entomological collections listed herein for access to material, and reviews from Richard Peigler, Manoel M. Dias Filho and Akito Y. Kawahara.

References

Aiello, A. & Balcázar-Lara, M. (1997) The immature stages of *Oxytenis modestia*, with comments on the larvae of *Asthenidia* and *Homoeopteryx* (Saturniidae: Oxyteninae). *Journal of the Lepidopterists Society*, 51 (2), 105-118.

Balcázar-Lara, M. & Wolfe, K.L. (1997) Cladistics of the Ceratocampinae (Lepidoptera: Saturniidae). *Tropical Lepidoptera*, 8, Suppl. 2, 1-53.

Balcázar-Lara, M. & Beutelspacher, C.R. (2000) Saturniidae. *In*: Llorente, J.E., González, E. & Papavero, N. (Eds.), *Biodiversidad, Taxonomia y Biogeografia de Artropodos de México: Hacia una síntesis de su conocimiento*. CONABIO, UNAM, México, pp. 501-513.

Becker, V.O. & Camargo, A.J.A. (2001) Three new species of Saturniidae (Lepidoptera) from central Brazil. *Revista Brasileira de Zoologia*, 18 (1), 163-170.

Bouvier, E.L. (1930) Seconde contribution à la connaissance dês Saturnioides du Hill Museum. *Bulletin of the Hill Museum*, 4, 1-116.

Camargo, A.J.A. (2007) A new species of *Hylesia* Hübner (Lepidoptera, Saturniidae, Hemileucinae) from Brazilian Cerrado. *Revista Brasileira de Zooogia*, 24 (1), 199-202.

Camargo, A.J.A., Casagrande, M.M., Mielke, O.H.H. & Furtado, E. (2005a) Morfologia externa do adulto de *Almeidaia aidae* Mielke & Casagrande (Lepidoptera, Saturniidae, Arsenurinae, Almeidaiini). I. Cabeça, apêndices e região cervical. *Revista Brasileira de Zoologia*, 22(3), 619-622.

Camargo A. J. A., Casagrande, M. M., Mielke, O. H. H. & Furtado, E. (2005b) Morfologia externa do adulto de *Almeidaia aidae* Mielke & Casagrande (Lepidoptera, Saturniidae, Arsenurinae, Almeidaiini). II. Tórax e apêndices. *Revista Brasileira de Zoologia*, 22 (4), 1152-1158.

Camargo A.J.A., Casagrande, M.M., Mielke, O.H.H. & Furtado, E. (2006) Morfologia externa do adulto de *Almeidaia aidae* Mielke & Casagrande (Lepidoptera, Saturniidae, Arsenurinae, Almeidaiini). III. Abdome. *Revista Brasileira de Zoologia*, 23 (1), 157-161.

Camargo, A.J.A. & Becker, V.O. (1999) Saturniidae (Lepidoptera) from the Brazilian Cerrado: Composition and Biogeographic Relationships. *Biotropica*, 31 (4), 696-705.

Camargo A.J.A., Mielke, O.H.H., Casagrande, M.M. (2007) Nova espécie de *Paradaemonia* Bouvier (Lepidoptera, Saturniidae, Arsenurinae) do centro-sul do Brasil. *Revista Brasileira de Zoologia*, 24 (4), 1131-1138.

Comstock, J.H. (1918) The wings of Lepidoptera. *In*: Comstock, J.H. (Ed.), *The wings of insects*, Publishing Company**,** Ithaca, New York, 319-346.

D´Abrera, B. (1995) Saturniidae Mundi: *Saturniidae Moths of the World*. Part 1. Automeris Press, Keltern, Germany, 177 pp.

D'Araujo e Silva, A.G., Gonçalves, C.R., Galvão, D.M., Gonçalves, A.J.B., Gomes, J.;, Silva, M.N. & Simoni, L. (1968) Quarto catálogo dos insetos que vivem nas plantas do Brasil. Parte II, 1º Tomo - Insetos, hospedeiros e inimigos naturais. Ministério da Agricultura, Rio de Janeiro, 622 pp.

Dias, M.M. (1978) Morfolofia [sic] e biologia de *Dysdaemonia boreas* (Cramer, 1775) (Lepidoptera, Adelocephalidae). *Revista Brasileira de Entomologia*, 22, 83-90.

Diniz, I.R., Morais, H.C. & Camargo, A.J.A. (2001) Host plants of lepidopteran caterpillars in the Cerrado of Distrito Federal, Brazil. *Revista Brasileira de Entomologia*, 45 (2), 107-122.

Ferguson, D. C. (1971) *Bombycoidea, Saturniidae (Part). The Moths of North America*, E. W. Classey and R. B. D. Publications, London. Fascicle 20, 2A, 153 pp.

Furtado, E. (1998) Estágios imaturos de *Loxolomia johnsoni* Schaus (Lepidoptera, Saturniidae, Arsenurinae). *Revista Brasileira de Zoologia*, 15 (4), 847-852.

Furtado, E. (2001a) *Copiopteryx semiramis* (Cramer): notas suplementares à sua biologia (Lepidoptera, Saturniidae, Arsenurinae). *Revista Brasileira de Zoologia*, 18 (2), 637-640.

Furtado, E. (2001b) *Arsenura orbignyana* (Guérin-Méneville, [1844]) e seus estágios imaturos (Lepidoptera: Saturniidae, Arsenurinae). *SHILAP, Revista de Lepidopterologia*, 29 (116), 385-389.

Goloboff, P.A. (1993) NoName (NONA), version 1.5.1. Program and documentation. Fundación y Instituto Miguel Lillo, Tucúman, Argentina.

Heppner, J.B. (1998) *Classification of Lepidoptera. Part 1. Introduction. Holartic Lepidoptera*, Florida, 5, Suppl.,148 pp.

Janzen, D.H. (1982) Guia para la identificacion de mariposas nocturnas de la familia Saturniidae del Parque Nacional Santa Rosa, Guanacaste, Costa Rica. *Brenesia*, 19/20, 255-299.

Janzen, D.H. (1984) Two ways to be a tropical big moth: Santa Rosa saturniids and sphingids. *Oxford Surveys in Evolutionary Biology*, 1, 85-140.

Jordan, K. (1922) A monograph of the Saturnian subfamily Ludiinae. *Novitates Zoologicae*, 29, 249-326.

Lemaire, C. (1971) Révision du genre *Automeris* Hübner et dês genres voisins. Biogéographie, éthologie, morphologie, taxonomie (Lep. Attacidae). *Mémoires du Muséum National D'Histoire Naturelle*, 68 (fascicule unique), 1-576.

Lemaire, C. (1978) *Les Attacidae Américains (=Saturniidae). Attacinae*. Édition C. Lemaire, Neuilly-sur-Seine, 238 pp.

Lemaire, C. (1980) *Les Attacidae Américains (=Saturniidae). Arsenurinae*. Édition C. Lemaire, Neuilly-sur-Seine, 199 pp.

Lemaire, C. (1988) *Les Attacidae Américains (=Attacidae). Ceratocampinae*. Museo Nacional de Costa Rica. San José, Costa Rica, 480 pp.

Lemaire, C. (1996) Saturniidae, pp. 28-49. *In:* Heppner, J.B. (ed). *Checklist: Part 4B. Drepanoidea – Bombycoidea – Sphingoidea. Atlas of Neotropical Lepidoptera 5B*. Gainesville, Association for Tropical Lepidoptera, L + 87pp.

Lemaire, C. (2002) The *Attacidae of America. Hemileucinae. Part A*. Goecke & Evers, Keltern, Germany, 688 pp.

Lemaire, C & Minet, J. (1998) The Bombycoidea and their relatives. *In*: Kristensen, N.P. (Ed.). *Handbook of Zoology*. New York, De Gruyter, pp. 321-353.

Michener, C.D. (1952) The Saturniidae (Lepidoptera) of the Western Hemisphere, morphology, phylogeny, and classification. *Bulletin of the American Museum of Natural History*, 98 (5), 335-502.

Mielke, C.G.C. & Furtado, E. (2005) *Paradaemonia balsasensis* sp. nov. da Serra do Penitente, Balsas, Maranhão, Brasil (Lepidoptera, Saturniidae, Arsenurinae). *Revista Brasileira de Zoologia*, 22 (3), 653-655.

Minet, J. (1994) The Bombycoidea: phylogeny and higher classification (Lepidoptera: Glossata). *Entomologica Scandinavica*, 25 (1), 63-88.

Müller K, F. (2005) The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. *BMC Evolutionary Biology*, 5:(58). Available from: http://www.biomedcentral.com/1471-2148/5/58 (accessed 2 April 2009).

Nielsen, E.S & Common, F.B. (1991) Lepidoptera (Moths and butterflies), *In*: CSIRO (Ed.). *The Insects of Australia*. Cornell University Press, Ithaca, New York, pp. 817-915.

Nijhout, H.F. (1991) *The development and evolution of butterfly wing patterns*. Washington and London, Smithsonian Institution Press, 297 pp.

Nixon, K.C. & Carpenter, J.M. (1993) On outgroups. *Cladistics*, 9, 413-426.

Nixon, K.C. (1999) WINCLADA, version 1.00.08. Program and documentation. Cornell University, Ithaca, New York.

Page, R.D.M. (2002) NDE (NEXUS Data Editor for windows) versão 0.5.0. Available from http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html (accessed 30 December 2002)

Peigler, R.S. (1993) Cladistic analysis of the genera of the subfamily Arsenurinae (Saturniidae). *Journal of the Lepidopterists' Society*, 47 (3), 211-228.

Racheli, L (2006) List of the Arsenurinae of Peru with taxonomic notes on *Titaea raveni* (Johnson & Michener, 1948) stat. rev. and *Paradaemonia castanea* (Rothschild, 1907) stat. rev. (Lepidoptera, Saturniidae). *Galathea*, 22 (1), 41-47.

Regier, J.C., Grant, M.C., Mitter, C., Cook C.P., Peigler, R.S. & Rougerie, R. (2008) Phylogenetic relationships of wild silkmoths (Lepidoptera: Saturniidae) inferred from four protein-coding nuclear genes. *Systematic Entomology*, 33 (2), 219-228.

Regier, J.C., Mitter, C., Peigler, R.S. & Friedlander, T.P. (2002) Monophyly, composition, and relationships within Saturniidae (Lepidoptera: Saturniidae): evidence from two nuclear genes. *Insect Systematics & Evolution*, 33, 9-21.

Schüssler, H. (1936) Syssphingidae. *In*: Strand, E. (Ed.). *Lepidopterorum Catalogus*, Pars 70, Neubrandenburg, 230 pp.

Scoble, M.J. (1995) *The Lepidoptera: form, function, and diversity*. Oxford University Press Inc, New York, 404 pp.

Stone, S.E. (1991) Foodplants of world Saturniidae. *Memoir of the Lepidopterists' Society*, 4,1-186.

Travassos, L. & Noronha, D. (1968) Nota sobre Rhescyntinae de Michener, 1949 (Lepidoptera) II. *Atas da Sociedade de Biologia do Rio de Janeiro*, 12 (3), 153-154.

Travassos, L. & D´Almeida, R. F. (1937) Contribuição para o conhecimento da bionomia de alguns lepidópteros brasileiros. *Memórias do Instituto Oswaldo Cruz*, 32, 499–516.

Appendix

Matrix of 40 characters used to analyze the phylogeny of the Arsenurinae subfamily (ingroup) and outgroups (bold). ? = data missing; - = character not applicable.

Appendix 1.

.

Taxa \ characters	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**
Oxytenis modestia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0
Eacles imperialis	1	3	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	2	0	2	0	0	1	0	0	0	0
Arsenura albopicta	-	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura archianassa	-	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura armida	-	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura aspásia	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura batesii	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura beebei	-	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura biundulata	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura ciocolatina	-	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura cymonia	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura delormei	?	?	?	?	?	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	?	2	0	0	1	0	2	?	1	1	?	0	0	0
Arsenura drucei	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura meander	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura mossi	-	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura orbignyana	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura pandora	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura polyodonta	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura ponderosa	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura rebeli	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura sylla	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura thomsoni	1	2	0	0	?	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Arsenura xanthopus	1	2	0	0	0	2	1	1	0	1	1	0	0	0	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Caio championi	-	2	0	0	0	2	2	1	0	4	0	0	0	0	4	0	0	0	0	0	0	2	1	0	1	0	1	1	1	1	0	0	0	0
Caio harrietai	?	?	?	?	0	2	2	1	0	4	0	0	0	0	4	0	0	0	0	0	0	2	1	0	1	0	1	1	1	1	0	0	0	0
Caio richardsoni	-	2	0	0	0	2	2	1	0	4	0	0	0	0	4	0	0	0	0	0	0	2	1	0	1	0	1	1	1	1	0	0	0	0
Caio romulus	-	2	0	0	0	2	2	1	0	4	0	0	0	0	4	0	0	0	0	0	0	2	1	0	1	0	1	1	1	1	0	0	0	0

Appendix 1.

.

Taxa \ caracteres	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**
Copiopteryx derceto	1	2	0	0	0	3	0	1	0	0	0	0	0	0	3	0	1	0	2	2	1	2	0	0	1	0	2	1	1	1	0	0	0	0
Copiopteryx jehovah	1	2	0	0	?	3	0	1	0	0	0	0	0	0	3	0	1	0	2	2	1	2	0	0	1	0	2	1	1	1	0	0	0	0
Copiopteryx semiramis	1	2	0	0	0	3	0	1	0	0	0	0	0	0	3	0	1	0	2	2	1	2	0	0	1	0	2	1	1	1	0	0	0	0
Copiopteryx sonthonnaxi	1	2	0	0	0	3	0	1	0	0	0	0	0	0	3	0	1	0	2	2	1	2	0	0	1	0	2	1	1	1	0	0	0	0
Copiopteryx virgo	1	2	0	0	0	3	0	1	0	0	0	0	0	0	3	0	1	0	2	2	1	2	0	0	1	0	2	1	1	1	0	0	0	0
Dysdaemonia boreas	-	2	0	0	0	2	2	1	0	2	0	1	0	0	2	0	2	1	1	1	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Dysdaemonia brasiliensis	-	2	0	0	0	2	2	1	0	2	0	1	0	0	2	0	2	1	1	1	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Dysdaemonia concisa	1	2	0	0	0	2	2	1	0	2	0	1	0	0	2	0	2	1	1	1	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Dysdaemonia fosteri	-	2	0	0	0	2	2	1	0	2	0	1	0	0	2	0	2	1	1	1	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Grammopelta lineata	-	1	0	0	0	2	1	1	0	2	0	0	0	0	4	0	0	0	0	0	0	2	0	1	1	0	2	0	1	0	0	0	0	1
Loxolomia johnsoni	-	2	0	0	0	3	0	1	0	5	0	0	1	1	4	0	0	0	0	0	1	2	0	0	1	0	2	1	1	1	0	0	0	0
Loxolomia serpentina	-	2	0	0	0	3	0	1	0	5	0	0	1	1	4	0	0	0	0	0	1	2	0	0	1	0	2	1	1	1	0	0	0	0
Paradaemonia andensis	1	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia berlai	1	2	0	0	?	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia gravis	1	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia meridionalis	-	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia mayi	1	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia nycteris	-	2	0	0	?	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia orsilochus	1	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia platydesmia	-	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia pluto	-	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia ruschii	-	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia samba	-	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia terrena	-	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Paradaemonia thelia	1	2	0	0	0	2	2	1	0	3	0	0	0	0	4	1	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	0	0
Rhescyntis descimoni	?	?	?	?	?	3	2	1	1	0	0	0	0	2	4	0	0	0	0	0	?	2	0	0	1	0	2	?	1	1	0	0	0	0
Rhescyntis Hermes	1	2	0	0	0	3	2	1	1	0	0	0	0	2	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0

Appendix 1.

.

Taxa \ caracteres	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**
Rhescyntis hippodamia	1	2	0	0	0	3	2	1	1	0	0	0	0	2	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Rhescyntis pseudomartii	1	2	0	0	0	3	2	1	1	0	0	0	0	2	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Rhescyntis reducta	1	2	0	0	0	3	2	1	1	0	0	0	0	2	4	0	0	0	0	0	0	2	0	0	1	0	2	1	1	1	0	0	0	0
Titaea lemoulti	1	2	0	0	0	2	2	1	0	2	0	1	0	0	5	0	3	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	1	0
Titaea orsinome	1	2	0	0	0	2	2	1	0	2	0	1	0	0	5	0	0	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	1	0
Titaea tamerlan	1	2	0	0	0	2	2	1	0	2	0	1	0	0	5	0	3	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	1	0
Titaea timur	1	2	0	0	0	2	2	1	0	2	0	1	0	0	5	0	3	0	1	0	0	2	0	0	1	0	1	1	1	1	0	0	1	0
Almeidaia aidae	1	2	0	0	0	4	0	0	0	-	0	0	2	0	4	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	0	2	0	0
Almeidaia romualdoi	1	2	0	0	?	4	0	0	0	-	0	0	2	0	4	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	0	2	0	0