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# CLADISTIC ANALYSIS OF THE GENERA OF THE SUBFAMILY ARSENURINAE (SATURNIIDAE)

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**ABSTRACT.** The Neotropical saturniid subfamily Arsenurinae contains about 60 species in ten genera. Hypothetical phylogenies of the ten genera were constructed using cladistic methodology to analyze morphological characters of adults and larvae. Based on the resultant cladograms, *Titaea* and *Dysdaemonia* are sister-groups, and this pair may be the sister-group of *Paradaemonia*. These three are probably the sister-group to *Caio* and possibly to *Arsenura*. *Copiopteryx* and *Rhescyntis* are sister-groups based on the suite of characters used. Other relationships are less certain from the available data; larvae of three genera are not known. At least four genera are specialists on Bombacaceae as larval hostplants, but several other plant families are used by species in the other genera evaluated. Arsenurinae appears to be a relict group represented by relatively few species and genera.

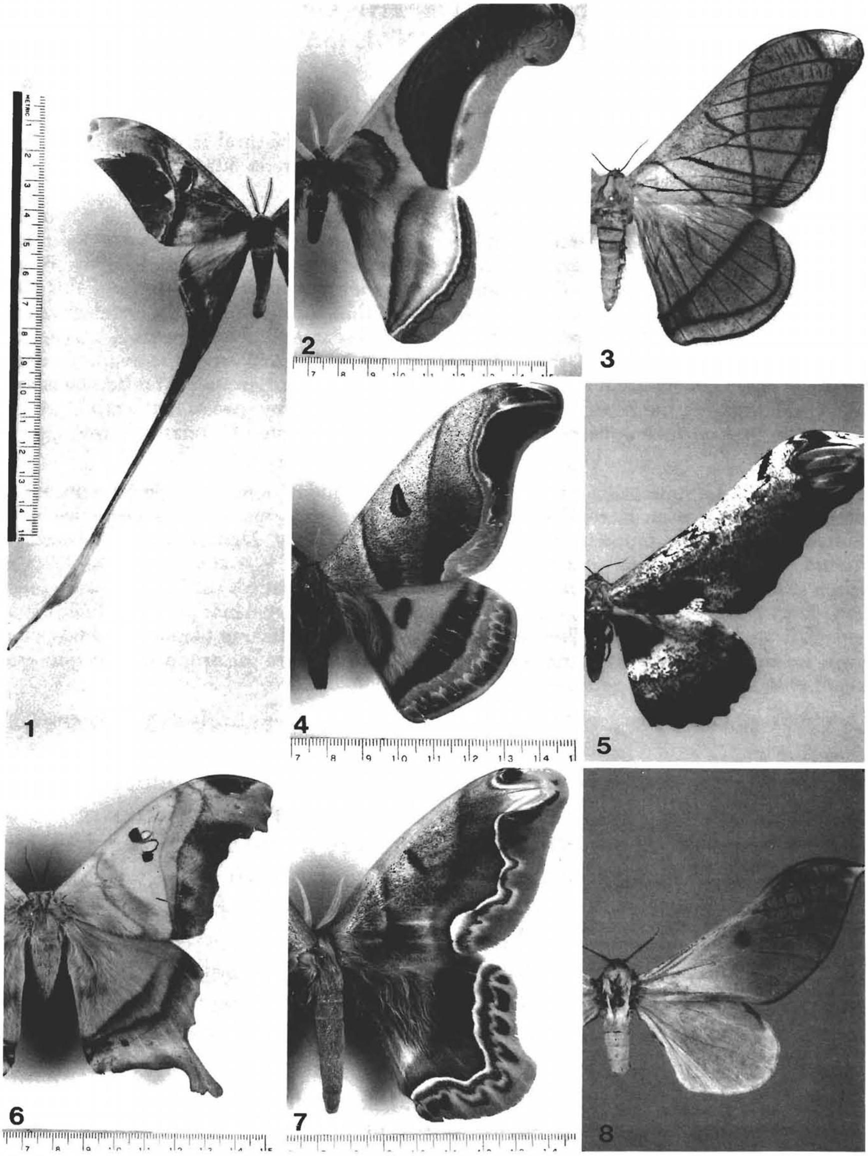
**RESUMEN.** La subfamilia Arsenurinae de las Saturniidae tiene cerca de 60 especies en diez géneros, todos en la región neotropical. Se empleó la metodología cladística para ilustrar las filogenías hipotéticas de los diez géneros. *Titaea, Dysdaemonia,* y *Paradaemonia* son grupos afines, juntos probablamente con *Caio* y *Arsenura*. *Copiopteryx* y *Rhescyntis* son grupos afines basado en el juego de características usado. Otras relaciones son menos ciertas con los datos existentes. Las orugas de cuatro o más géneros son fitófagas especialistas sobre la familia Bombacaceae, pero otras familias de plantas son huéspedes para los demás géneros de Arsenurinae. Esta subfamilia es un grupo relicto que está representado para pocos especies y géneros.

**Additional key words:** systematics, phylogeny, morphology, early stages, Neotropical.

The Neotropical saturniid subfamily Arsenurinae includes approximately 60 species ranging from northern Mexico to northern Argentina (Lemaire 1980). The moths are large to very large, and their coloration is restricted to earth tones, mainly shades of brown, gray, cream, and dull orange (Figs. 1–8). In the revisionary works of Michener (1952) and Ferguson (1971–72), the name Rhescyntinae was used for this group. Lemaire (1980) published a definitive treatment of the subfamily, providing details on classification, synonymy, morphological characters, and distribution of each species. Relationships between the ten genera have not been proposed except for a superficial "tree" in Michener's (1952) work, and the fact that Lemaire (1980) separated the genus *Almeidaia* into a separate tribe. Strecker (1875:101) also offered some brief, yet insightful, comments on relationships within this group.

## MATERIALS AND METHODS

This cladistic analysis presupposes that all ten genera of the subfamily were correctly defined by Lemaire (1980) (see Table 1). Michener (1952) classified the species of *Caio* under *Arsenura*, and grouped *Arsenura* along with *Rhescyntis, Dysdaemonia, Titaea,* and *Paradae-*



FIGS. 1–8. **1**, *Copiopteryx semiramis* (Cramer), Rancho Grande, Aragua, Venezuela; **2**, *Rhescyntis pseudomartii* Lemaire, Itatiaia, Santa Catarina, Brazil; **3**, *Grammopelta lineata* (Schaus), Anchicaya, Valle, Colombia; **4**, *Caio romulus* (Maassen), Itatiaia, Santa Catarina, Brazil; **5**, *Loxolomia johnsoni* Schaus, Sinop, Mato Grosso, Brazil; **6**, *Titaea tamerlan* (Maassen), Colombia; **7**, *Arsenura biundulata* Schaus, Rio Vermelho, Santa Catarina, Brazil; **8**, *Almeidaia romualdoi* Travassos, Rio Verde, Mato Grosso, Brazil.

TABLE 1. Genera of Arsenurinae.

| Genus | Type-species | No. of known species |
|---|---|---|
| *Arsenura* Duncan | *armida* (Cramer) | ca. 23 |
| *Caio* Travassos & Noronha | *romulus* (Maassen) | 4 |
| *Dysdaemonia* Hübner | *boreas* (Cramer) | 3 |
| *Titaea* Hübner | *orsinome* Hübner | 4 |
| *Paradaemonia* Bouvier | *pluto* (Westwood) | 12 |
| *Rhescyntis* Hübner | *hippodamia* (Cramer) | 4 |
| *Copiopteryx* Duncan | *semiramis* (Cramer) | 5 |
| *Loxolomia* Maassen | *serpentina* Maassen | 2 |
| *Grammopelta* Rothschild | *lineata* (Schaus) | 1 |
| *Almeidaia* Travassos | *romualdoi* Travassos | 2 |

*monia* as five subgenera of *Rhescyntis*. Subgeneric usage is well established in Hymenoptera taxonomy where the majority of Michener's contributions are found, but subgenera receive much less usage in Lepidoptera taxonomy. With the exception of *Caio*, the generic groupings of Lemaire and Michener are in agreement and I accept them as monophyletic groups. The purpose of this paper is to propose hypotheses of the phylogeny of these genera through the construction of cladograms. The works of Michener and Lemaire provide ample data on the morphology of the adults of each genus, and the present study incorporates available information on the immature stages, using published life histories (Schreiter 1925, Travassos & d'Almeida 1937, Travassos 1946, Lordello & Mariconi 1953, Otero 1965, d'Almeida 1975, Dias 1978, Brenner & Lampe 1987) and larvae preserved in alcohol. Preserved material of 1st instar larvae available to this study were: *Arsenura armida* (Cramer), *A. ponderosa* Rothschild, *A. polyodonta* (Jordan), *A. rebeli* Gschwandner, *Caio richardsoni* (Druce), *C. championi* (Druce), *Dysdaemonia boreas* (Cramer), *Titaea tamerlan* (Maassen), *Paradaemonia andensis* (Rothschild), *Rhescyntis* sp., and *Copiopteryx semiramis* (Cramer). Preserved mature caterpillars of several of these also were available.

Numbers of species listed in Table 1 differ from the revision of Lemaire (1980) for three genera as follows: 1) some of the so-called subspecies within *Arsenura* are considered by me to be full species; 2) what has been cited as *Caio undilinea* (Schaus) is apparently a form of the variable *C. championi* (Druce) (C. Lemaire, pers. comm.); 3) a second species of *Almeidaia* was described as *A. aidae* by Mielke and Casagrande (1981).

Although American taxonomists and evolutionary biologists neither understood nor utilized cladistic theory and methodology until the 1960's and 1970's, the work of Michener (1952) actually employed

TABLE 2. Matrix of the 23 characters used to analyze the phylogeny for the ten genera. See text for explanation.

| *Arsenura* | *Caio* | *Dysdaemonia* | *Titaea* | *Paradaemonia* | *Rhescyntis* | *Copiopteryx* | *Loxolomia* | *Grammopelta* | *Almeidaia* |
|---|---|---|---|---|---|---|---|---|---|
| A | A | A | A′ | A | A′ | A′ | A | A | A |
| B | B′ | B′ | B | B′ | B | B | B′ | B′ | B |
| C″ | C′ | C′ | C′ | C′ | C | C | C′ | C′ | C″ |
| D | D | D | D | D | D′ | D′ | D | D | D |
| E | E | E′ | E′ | E′ | E | E′ | E | E | E |
| F′ | F′ | F′ | F′ | F′ | F | F″ | F | F | F |
| G′ | G | G′ | G′ | G | G′ | G | G | G | G |
| H | H | H′ | H′ | H | H | H′ | H | H | H |
| I′ | I′ | I′ | I′ | I′ | I′ | I′ | I′ | I | I″ |
| J′ | J′ | J″ | J″ | J″ | J″ | J″ | J″ | J | J |
| K′ | K′ | K′ | K′ | K′ | K′ | K′ | K′ | K′ | K |
| L′ | L | L | L | L | L′ | L′ | L′ | L′ | L′ |
| M″ | M″ | M″ | M″ | M | M | M′ | M′ | M″ | M |
| N″ | N′ | N″ | N″ | N″ | N″ | N | — | — | — |
| O | O″ | O′ | O′ | O′ | O′ | O | — | — | — |
| P | P | P | P | P′ | P′ | P′ | — | — | — |
| Q′ | Q′ | Q′ | Q′ | Q′ | Q′ | Q | — | — | — |
| R | R′ | R | R | R | R | R | — | — | — |
| S | S | S | S | S′ | S | S′ | — | — | — |
| T | T′ | T″ | T″ | T″ | T″ | T″ | — | — | — |
| U | U′ | U′ | U′ | U′ | U′ | U′ | — | — | — |
| V | V′ | V′ | V′ | V′ | V′ | V′ | — | — | — |
| W′ | W′ | W′ | W′ | W | W | W | — | — | — |

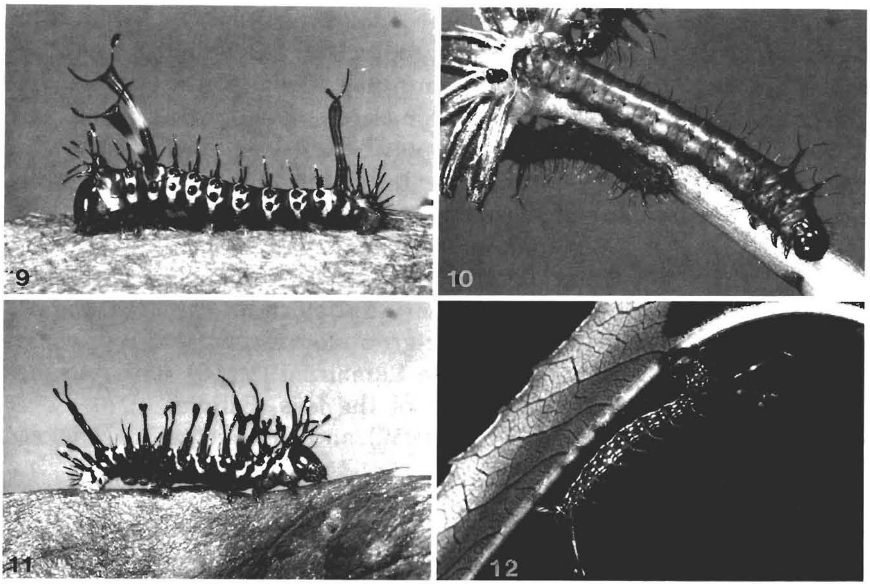
cladistic theory. This is clear from his discussions of out-group comparison in determining which characters were apomorphic (i.e., derived, advanced) and which plesiomorphic (i.e., ancestral, primitive). Methods in the present study are the same as those explained in detail in another cladistic analysis of the nine genera of the saturniid tribe Attacini (Peigler 1989); the reader is also referred to a succinct overview of cladistic methodology by Andersen (1978). The branching pattern is determined by the greatest number of shared apomorphies between each possible pair. The characters used in this analysis are discussed below and their distribution among taxa is shown in Table 2. A second cladistic method was applied to the data in Table 2 by the computer program PAUP (Phylogenetic Analysis Using Parsimony) (Swofford 1990), using the branch-and-bound search option. Characters E, F, H, O, P, S, and V were judged to have greater value and therefore counted twice in the PAUP analysis, and *Almeidaia* was designated as the outgroup.

All authors agree that the Arsenurinae and Ceratocampinae (=Citheroniinae) are the most plesiomorphic subfamilies of Saturniidae (Michener 1952, Lemaire 1980, 1988), and some Brazilian authors have combined the two under the family name Adelocephalidae. Although these two subfamilies are possibly sister-groups, the following shared characters probably include symplesiomorphies in the context of Saturniidae: female antennae simple, abdomen elongated, wing colors and patterns simple yet cryptic, discal spots better developed on forewing than on hindwing, larvae with elongated horns on meso- and metathoracic and 8th abdominal segments, pupation below ground without cocoon. Some of these characters are apomorphic in the context of the other Bombycoidea (Minet 1991), but a careful comparison with other bombycoid groups would be necessary to determine whether Ceratocampinae and Arsenurinae are sister-groups or simply two groups sharing several primitive characters (see Lemaire 1988:16). The two subfamilies differ in several characters of the legs (Oiticica 1940), wing venation, male antennae (Michener 1952), and larval structure (Packard 1905).

The two families that are possibly most closely allied to the Saturniidae are Cercophanidae and Oxytenidae (Michener 1952, Jordan 1924). In this study these two Neotropical families were used for out-group comparison with Arsenurinae, as well as the subfamily Ceratocampinae, other saturniid subfamilies, and other families in Bombycoidea. Minet (1986) proposed that the Cercophanidae as defined by Jordan and accepted by subsequent authors, may be a paraphyletic group and probably should be included in the Saturniidae. The saturniid subfamily Agliinae also possesses some plesiomorphic characters (Michener 1952), as seen in figures of the immature stages given by Kuroko (1976) and Gómez de Aizpúrua (1988). This study also uses concise morphological summaries of several families of Bombycoidea that were provided by Common (1990). The large, brown, Australian bombycoid moth *Chelepteryx collesi* Gray (Anthelidae) (Common 1990) bears a remarkable convergent resemblance in size, wing pattern, and color to some *Arsenura*. In light traps, *Arsenura* also closely resemble large Noctuidae (*Ascalapha* Hübner and *Thysania* Dalman) (C. Lemaire pers. comm.).

## Immature Stages

Although little has been published on the immature stages of Arsenurinae, certain conclusions and sets of characters can be stated. It is particularly unfortunate that the 1st instar larvae of several groups remain unknown. These include Oxytenidae, *Loxolomia*, *Grammopelta*, and *Almeidaia*, the latter two of which are considered to be the most primitive arsenurine genera based on adult characters (Michener 1952, Lemaire 1980). When these larvae become known, their characters will either strengthen or modify the hypotheses of the phylogeny

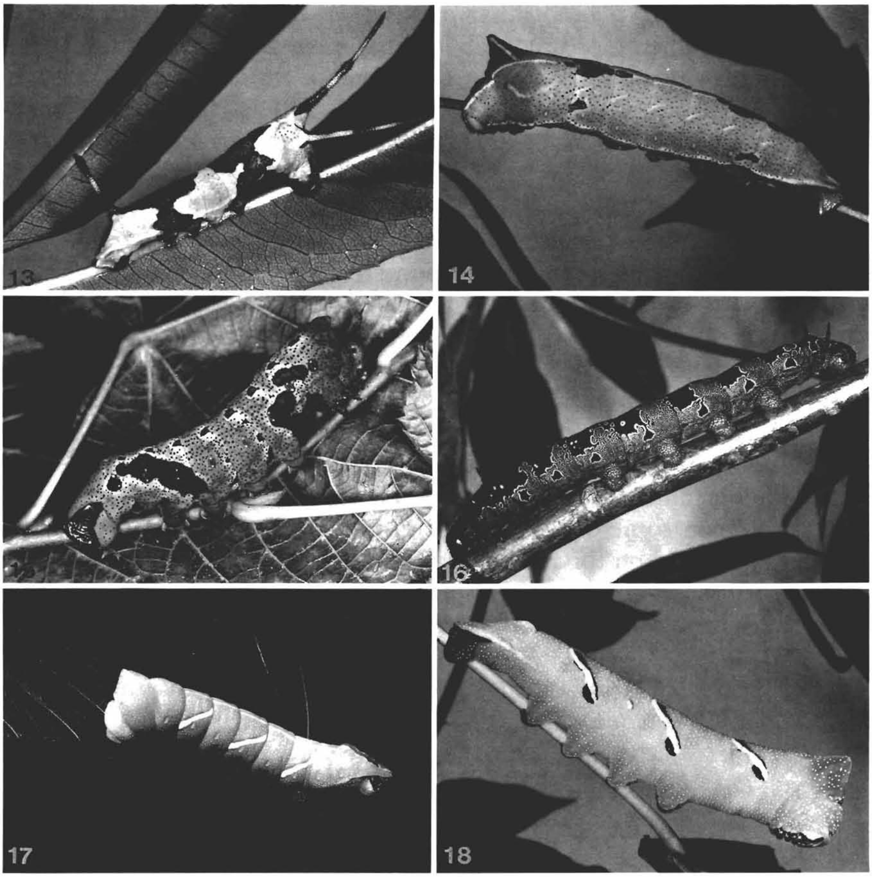


FIGS. 9–12. First instar larvae of Arsenurinae. **9,** *Rhescyntis hippodamia* (Cramer), French Guiana; **10,** *Arsenura polyodonta* (Jordan), Lake Chapala, Jalisco, Mexico; **11,** *Paradaemonia* sp., French Guiana; **12,** *Dysdaemonia boreas* (Cramer), Santa Rosa de Puriscal, Costa Rica.

proposed in the present paper. For example, *Loxolomia* and *Grammopelta* are probably not true sister-groups, but in the absence of larval characters, the four synapomorphies of the adults could not be ignored. Representative examples of larvae are presented in Figs. 9–18.

*Form of larvae:* Within the genera of the subfamily for which the mature larvae are known, there are two main forms: (1) gracile, weakly hirsute, with smooth integument (*Rhescyntis,* most *Arsenura*) (Fig. 16), and (2) stout, glabrous, with granulose integument (*Caio, Dysdaemonia, Copiopteryx*) (Figs. 14, 15, 17, 18). The latter form is considered plesiomorphic based on the presence of these characters in larvae of Cercophanidae (Packard 1914), Oxytenidae (Jordan 1924, Nentwig 1985), Agliinae (Kuroko 1976, Gómez de Aizpúrua 1988), and most Ceratocampinae (Lemaire 1988). Form of larvae was not used in the present analysis because it cannot be discretely quantified nor qualified.

Larvae of certain arsenurines bear a striking but convergent resemblance to notodontid larvae such as the Palearctic *Cerura vinula* (L.) and the Nearctic *Cerura scitiscripta* Walker (see Gómez de Aizpúrua 1988, Nässig 1988). The tentacles and the peculiar brown and green pattern shared by these Arsenurinae and Notodontidae evidently impart the same protective function, probably simulating a rolled or twisted



FIGS. 13–18. Larvae of Arsenurinae. **13, 14,** *Dysdaemonia boreas* (Cramer), third and fifth instars, Santa Rosa de Puriscal, Costa Rica; **15,** *Titaea tamerlan* (Maassen), fifth instar, State of Rio de Janeiro, Brazil; **16,** *Arsenura polyodonta* (Jordan), fifth instar, Lake Chapala, Jalisco, Mexico; **17,** *Caio championi* (Druce), fifth instar, Santa Rosa National Park, Guanacaste, Costa Rica; **18,** *Caio richardsoni* (Druce), fifth instar, Sonora, Mexico.

leaf (see also Nentwig 1985). This category includes the full-grown larva of *Rhescyntis* (Travassos & d'Almeida 1937) which lacks tentacles, although its laterally flattened form may also mimic a legume seed pod. The mature larvae of *Cercophana frauenfeldi* Felder (Cercophanidae) (Packard 1914, pl. 31) also resembles a seed pod and the larva of *Rhescyntis*. In contrast to these examples of camouflaged forms, larvae of several *Arsenura* are aposematic, colored black and orange. These probably derive and sequester toxic substances from their hostplants.

*Structure of 1st instar larvae:* In all 11 species in seven genera of Arsenurinae for which 1st instar larvae were examined, the crochets are in the form of a uniordinal mesoseries. In all mature larvae examined, these form biordinal or triordinal mesoseries. The same is true in the genus *Aglia* Ochsenheimer for larvae of the 1st and 4th (the last in *A. tau* (L.) according to Packard 1914, and R. Oberprieler pers. comm.) or 5th (the last in *A. microtau* Inoue according to Kuroko 1976) instars. These observations verify the prediction by Pease (1961:101) that older larvae would be found to have more crochets.

All species have enlarged bifid dorsal scoli on the metathorax. Likewise, no useful characters were found on the abdominal segments. However, the dorsal and subdorsal scoli on the prothorax and mesothorax vary widely and appear to be valuable in phylogenetic analysis. Again, the Palearctic *Aglia* agrees in having very large dorsal scoli on the prothorax and metathorax, and greatly reduced mesothoracic ones. In the Brahmaeidae, the prothoracic scoli are reduced (Packard 1914, pl. 34). In 1st instar Ceratocampinae, some genera have hypertrophic dorsal scoli on all three thoracic segments (e.g., *Citheronia* Hübner and *Eacles* Hübner, some of the most primitive genera according to Michener 1952), others on the mesothorax and metathorax only, others (e.g., *Anisota* Hübner) only on the mesothorax (Packard 1905). The structure of prothoracic scoli provides strong support for the separation of *Caio* from *Arsenura*.

*Hostplants:* No hostplants have been reported for *Loxolomia, Grammopelta,* or *Almeidaia*. For the other seven genera, *Rhescyntis* uses nutmeg (*Virola*, Myristicaceae); *Copiopteryx* uses Sapotaceae and Santalaceae; *Paradaemonia* uses Lythraceae; and *Caio, Dysdaemonia,* and *Titaea* apparently specialize on Bombacaceae. The large genus *Arsenura* uses several families in addition to Bombacaceae. Specific hostplant records are tabulated in Table 3. Bombacaceae, Tiliaceae, Malvaceae, and Sterculiaceae belong to the order Malvales (Lawrence 1951). Utilization of this plant group may be plesiomorphic for Arsenurinae since some Cercophanidae feed on Tiliaceae (Jordan 1924), but the phylogeny proposed below suggests that specialization on Bombacaceae is more likely apomorphic. If so, it is unlikely that *Loxolomia, Grammopelta,* and *Almeidaia* will be found to feed on Bombacaceae. Oxytenidae are specialists on Rubiaceae (Jordan 1924, Nentwig 1985), whereas Ceratocampinae utilize several plant groups, not including Bombacaceae (d'Araújo e Silva et al. 1968, Lemaire 1988). The families Myristicaceae, Sapotaceae, Santalaceae, Bombacaceae, Rubiaceae, and Lythraceae are all in different orders (Lawrence 1951).

## Analysis of Characters

Characters used in the present cladistic analysis are detailed below. In each case, out-group comparison was used as far as possible to determine character polarity in Arsenurinae. Under each one, my reasons are given to reduce chances of misinterpretation of my methods. The results are tabulated in Table 2. Letters without a prime mark represent the plesiomorphic condition, letters with one prime mark the apomorphic condition, and with two prime marks the most apomorphic condition in a transformation series.

A. Antennal cones. A = simple; A′ = multiple. The multiple cones are the apomorphic condition according to Michener (1952). This is evidently a character that is easily reversed and thus not very useful in the present phylogenetic analysis.

B. Antennae in male. B = quadripectinate; B′ = quadridentate; B″ = simple. Longer projections, the longest ones called rami, are plesiomorphic within the Saturniidae and most other Bombycoidea.

C. Antennae in female. C = quadripectinate; C′ = quadridentate; C″ = simple. Presumed polarity is based on same reasoning as in character B above.

D. Shape of antennal rami. D = flattened, straight rami; D′ = longer, curved rami. Outgroup comparison is based on other saturniid groups, since the groundplan bombycoid antenna is bipectinate and therefore of no relevance here (R. Oberprieler pers. comm.).

E. Forewing apex and outer margin. E = smooth edge; E′ = scalloped. The undulating edges of wings as seen in the few genera of Arsenurinae are very rare in Saturniidae and all Bombycoidea in general but are common in several groups of Geometridae (not considered here to be an out-group). Scalloped margins occur in the hindwings but not the forewings of the long-tailed *Antistathmoptera* Tams (Saturniinae: Pseudapheliini), a genus of African moths superficially resembling *Copiopteryx*. Scalloped outer margins are regarded as apomorphic in Arsenurinae.

F. Hindwing with tail. F = untailed (normal); F′ = short tail; F″ = long tail. This character is known to occur in unrelated saturniid groups (Peigler 1989:104).

G. Uncus. G = simple; G′ = bifid. Although both situations occur in several saturniid subfamilies, it appears that the simple condition is plesiomorphic within Arsenurinae because it exists in *Almeidaia* and *Grammopelta*, genera that Michener (1952) and Lemaire (1980) considered to be the most primitive arsenurines based on other evidence.

H. Fenestrae in wings. H = absent; H′ = present. These are absent in all Ceratocampinae except *Neorcarnegia* Draudt (Lemaire 1988) and rare in the other bombycoid families, so their presence in Arsenurinae is considered to be apomorphic.

I. Labial palpi. I = three-segmented, with large third segment; I′ = three-segmented, with reduced third segment; I″ = two-segmented. Michener (1952:356) and Lemaire (1988:12) indicated that the three-segmented condition is plesiomorphic. The condition varies between one and three segments in Ceratocampinae, Hemileucinae, and Saturniinae.

J. Radial veins in forewing. J = four-branched; J′ = three-branched or four-branched (both cases exist within a single genus); J″ = three-branched. Reduction in branches is apomorphic based on out-group comparison.

K. Prothoracic tibial spur. K = present; K′ = absent. The presence of this prominent spur in *Almeidaia* is considered plesiomorphic on the basis of the outgroup comparison (e.g., *Eacles*).

L. Metathoracic tibial spurs. L = present; L′ = absent. A pair of spurs is present in certain Oxytenidae (Jordan 1924, pl. 12), Eupterotidae, Lasiocampidae, Anthelidae, Sphingidae, and Bombycidae (Common 1990). Loss of these is considered to be apomorphic. It is not clear if those present in the Arsenurinae are homologous to those present in other groups. Hence the interpretation of their presence as plesiomorphic is not certain.

M. Lateral spiny protuberances on aedeagus. M = absent; M′ = present but weak; M″ = present and prominent. Although comparable structures occur in certain species of *Eacles* (Ceratocampinae) (Lemaire 1988) and Cercophanidae (Jordan 1924, pl. 21), the occurrence of these in Arsenurinae is considered apomorphic. These are absent in most species of all out-groups. Their occasional presence in diverse groups is clearly the result of homoplasy.

N. Size of prothoracic dorsal scoli in 1st instar larva. N = large; N′ = medium; N″ = tiny. The large condition is plesiomorphic. Large scoli occur in Ceratocampinae, Agliinae, and Hemileucinae (Kuroko 1976, Packard 1905).

O. Setae of prothoracic dorsal scoli in 1st instar larva. O = two setae; O′ = three setae; O″ = 5 or 10 setae. The condition of two setae is apparently the plesiomorphic state because it occurs in Ceratocampinae and Hemileucinae. In other groups, such as Bombycidae and Saturniinae, clusters of numerous setae are found in this position (Nässig 1989). There are five setae per scolus in *Caio richardsoni* and ten in *C. championi*.

P. Shape of prothoracic dorsal scoli in 1st instar larva. P = normal, with setae; P′ = flattened apex. Whether the flattened portion is a seta, or the seta is lost and the apex itself is flattened is not clear. Here the flattened apex is regarded as the apomorphic condition. The flattened swollen tips of some Ceratocampinae appear to be very different from this condition and are almost certainly not homologous.

Q. Size of prothoracic subdorsal scoli in 1st instar larva. Q = large, bifid; Q′ = small to tiny. The large and bifid condition is the plesiomorphic one as it occurs in Ceratocampinae and Agliinae.

R. Setae of prothoracic subdorsal scoli in 1st instar larva. R = 2 setae; R′ = 3 setae. The condition of two setae is normal (plesiomorphic) in Ceratocampinae, Brahmaeidae, and other out-groups. Three species of *Arsenura* examined possess two such setae, whereas these scoli in *A. armida* have none. According to Lordello and Mariconi (1953), two setae are present in *A. xanthopus* (Walker).

S. Shape of prothoracic subdorsal scoli in 1st instar larva. S = small, bulbous or slightly elongated; S′ = elongated and flattened. The long flattened scoli are judged to be apomorphic.

T. Mesothoracic dorsal scoli in 1st instar larva. T = large, bifid; T′ = small, bifid; T″ = tiny, simple. Judging from out-groups such as Ceratocampinae, Brahmaeidae, and Hemileucinae, larger and bifid scoli represent the plesiomorphic condition. In all larvae of Arsenurinae examined, two setae are present on each scolus.

U. Mesothoracic subdorsal scoli in 1st instar larva. U = bifid; U′ = simple. Judging from out-groups, the bifid condition is plesiomorphic. In all larvae of Arsenurinae examined, two setae are present on each scolus.

V. Bases of dorsal and subdorsal prothoracic scoli. V = not fused; V′ = fused. These scoli are relatively large in Ceratocampinae, but the bases are not fused. Fusion occurs in all known arsenurine larvae except in *Arsenura*. In the latter genus, all four scoli may be set within a large prothoracic sclerite, suggesting the beginning of fusion.

W. Hostplants. W = feeding on plants besides Bombacaceae; W′ = specializing on Bombacaceae. This character is included to reinforce the clade of three or four genera that specializes on Bombacaceae.

## RESULTS AND DISCUSSION

The two cladistic methods (tabulating synapomorphies and the PAUP analysis) resulted in different hypotheses of the phylogeny as shown in Figs. 19 and 20. Both trees suffer from the lack of data as shown in Table 2, i.e., larvae not known for three genera. The set of data based on adult structure of pinned specimens could be improved by adding characters derived from scanning electron microscopy. Based on the adult and larval characters used, the two cladograms (Figs. 19, 20) represent the most likely hypotheses of the phylogeny of the subfamily. These two phylogenetic trees actually agree in four of the nine branching sequences. The alliance of *Titaea, Dysdaemonia, Paradaemonia,* and *Caio* is not surprising in view of the appearance of the adult moths. The position of *Almeidaia* as the out-group to all others is likewise expected, and agrees with Lemaire's (1980) placement of this genus into a separate tribe. Lemaire (1980 and pers. comm.) said that *Almeidaia* also shares affinities with Ceratocampinae, and that perhaps this genus should be assigned to its own subfamily. It is apparently an ancient relict like we see in *Aglia*, *Polythysana* Walker, and *Salassa* Moore, genera which Michener (1952) discussed as having mixtures of subfamily characters. The association between *Copiopteryx* and *Rhescyntis* is unexpected because of the superficially very different wing shapes, yet closer examination of the wing patterns of these two genera as compared to other genera suggests that a true alliance exists.

The PAUP analysis found 12 equally parsimonious trees requiring 60 character state changes. None of the 12 trees generated by the analysis agree closely with the one shown in Fig. 19. The majority rule consensus cladogram is shown in Fig. 20. Rohlf's consistency index (CI) for this cladogram was 0.76.

Regarding hostplant preferences (see Table 3), certain hypotheses may now be formulated. Specialization on Bombacaceae is plesiomorphic for the clade *Titaea* + *Dysdaemonia* + *Paradaemonia* + *Caio*. The one record of *Paradaemonia* feeding on Lythraceae indicates an apomorphic change (i.e., secondary loss of feeding specialization on Bombacaceae, indicated by a W in Fig. 19), supported by additional observations that other species of *Paradaemonia* do not accept Bombacaceae in captivity (K. Wolfe pers. comm.). Release from dependence on Bombacaceae could be related to the fact that *Paradaemonia* has three times the number of species as each of the other genera in its clade, and a relatively wide distribution. If we accept Fig. 19, Bombacaceae are secondarily exploited by *Arsenura*, yet Fig. 20 suggests that this character may be plesiomorphic for the clade of *Arsenura* plus the above four genera. More hostplant records are needed, but they are difficult to obtain for most of the species living in the primary rainforest of the tropics.

The Arsenurinae are not rich in species, as compared to many moth groups, and thus appear to be a relict group with comparatively few surviving representatives. Another reason for the low numbers of species could be that these moths do not speciate rapidly. Except for *Arsenura cymonia* (W. Rothschild), the group is limited to low elevations, and speciation in other Saturniidae has apparently been facilitated in montane habitats (C. Lemaire pers. comm.). Michener (1952) considered Arsenurinae to be the most primitive saturniids. The hypothetical ancestor must have been a large species that did not have a genetic capacity for bright wing coloration (shades of yellow, green, pink, and orange),

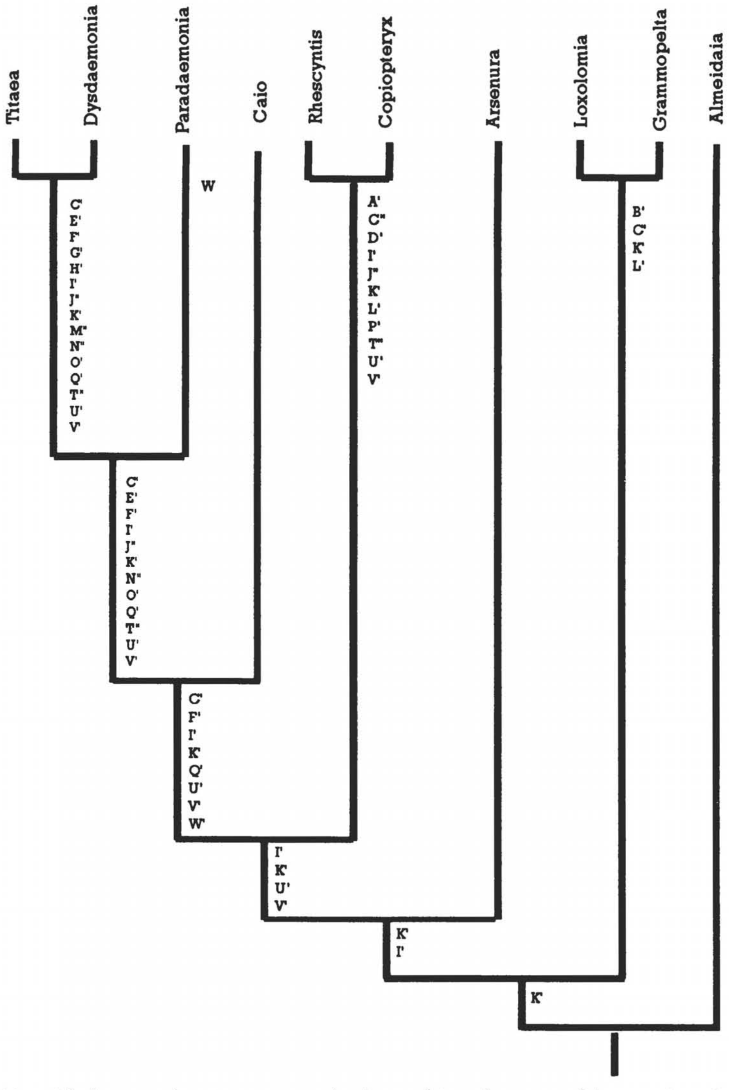


FIG. 19. Cladogram showing proposed relationships of genera of Arsenurinae in which synapomorphies are tabulated.

which is common in other saturniid groups. Most genera in the group have only about five species, and the two genera considered most primitive have only one or two species. It is possible that many lineages have died out, leaving several genera with no individual extant sister-groups. The resulting cladograms yield clades in which some genera are considered to be the sister-group of a large aggregate of genera.

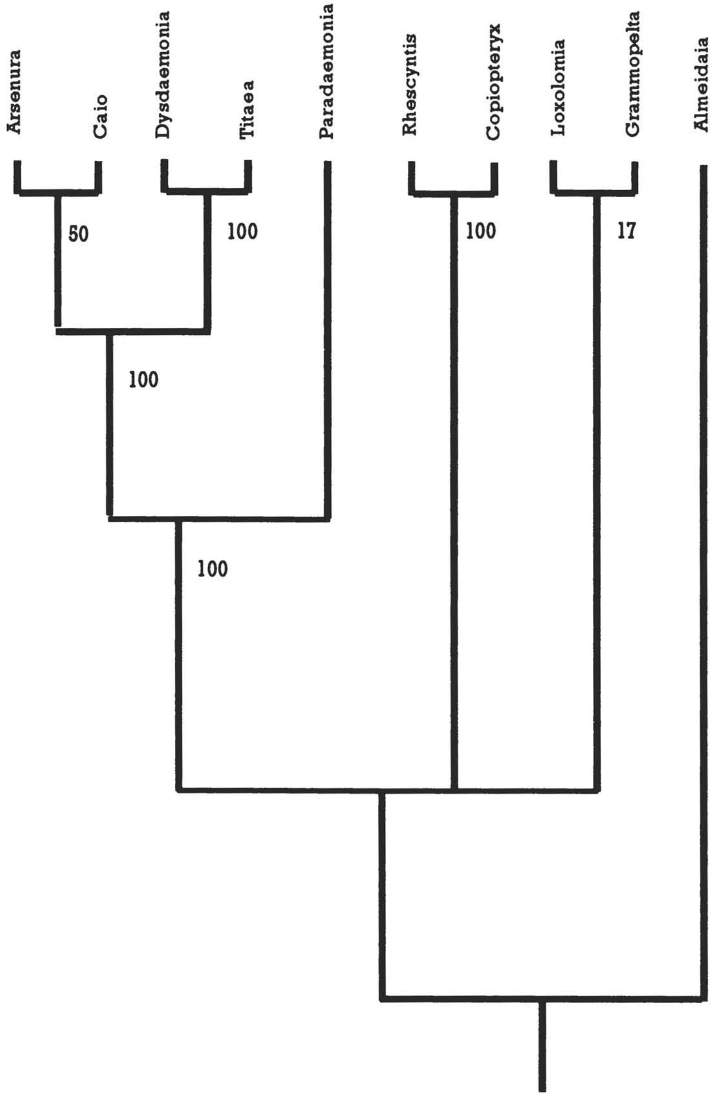


FIG. 20. Majority rule consensus tree showing proposed relationships of genera of Arsenurinae using PAUP analysis. Numbers represent percent of equally parsimonious trees having the respective branching sequence.

Below the generic level, it is clear that *Caio romulus* represents the extant sister-group of the other more northern representatives of its genus. *Caio* was evidently separated into the Mexican (or possibly Guiano-Amazonian) and southern Brazilian components at a time in the past, the former speciating and dispersing (see Halffter 1976, Le-

TABLE 3. Known hostplants of Arsenurinae.

| Moth | Hostplant and plant family | References |
|---|---|---|
| *Arsenura armida* (Cramer) | *Bombacopsis quinata* (Jacq.) Dugand, Bombacaceae; *Luehea* sp.,* Tiliaceae | Janzen (1982) |
| *Arsenura batesi arcaei* Druce | *Tilia platyphyllos* Scop.,* Tiliaceae | Brenner & Lampe (1987) |
| *Arsenura polyodonta* (Jordan) | *Chorisia insignis* H.B.&K., Bombacaceae | Schreiter (1943) |
| *Arsenura rebeli* Gschwandner | *Tilia* sp.,* Tiliaceae | Stone (1991) |
| *Arsenura xanthopus* (Walker) | *Urena lobata* L., Malvaceae<br>*Luehea divaricata* Mart., *L. grandiflora* Mart., *L. ocrophylla* Mart., *L. paniculata* Mart., Tiliaceae | Packard (1914)<br>Lordello & Mariconi 1953 |
| *Arsenura* sp. (Costa Rica) | *Curatella americana* L., Dilleniaceae | K. L. Wolfe (pers. comm.) |
| *Arsenura* spp. (Brazil) | *Anona* sp., *Rollinia longifolia* A.St.Hil., Anonaceae; *Ceiba pentandra* (L.) Gaertn., *Chorisia speciosa* St.Hil., Bombacaceae; *Luehea divaricata* Mart., Tiliaceae; *Sterculia excelsa* Mart., *Theobroma cacao* L., *Guazuma ulmifolia* Lam., Sterculiaceae; *Myrsine umbellata* Mart., Myrsinaceae; H.B.&K., Euphorbiaceae; *Vernonia cinerea* Less. (=*diffusa*), Compositae; *Tibouchina* sp., Melastomataceae | d'Araújo e Silva et al. (1968) |
| *Caio championi* (Druce) | *Bombacopsis quinata* (Jacq.) Dugand, Bombacaceae<br>*Tilia silvestris* Desfontaines,* Tiliaceae | Janzen (1982)<br>C. Lemaire (pers. comm.) |
| *Caio richardsoni* (Druce) | *Chorisia* sp.,* *Ceiba acuminata* Rose, Bombacaceae | Stone (1991) |
| *Dysdaemonia boreas* (Cramer) | *Ceiba pentandra* (L.) Gaertn., Bombacaceae<br>*Chorisia speciosa* St.Hil., Bombacaceae | D. H. Janzen (pers. comm.)<br>Dias (1978) |
| *Dysdaemonia fosteri* W. Rothschild | *Chorisia insignis* H.B.&K., Bombacaceae | Schreiter (1925) |
| *Titaea tamerlan* (Maassen) | *Chorisia* sp., Bombacaceae<br>*Bombacopsis quinata* (Jacq.) Dugand, Bombacaceae<br>*Tilia platyphyllos* Scop.,* Tiliaceae | Travassos (1946)<br>Janzen (1982)<br>Stone (1991) |
| *Paradaemonia pluto* (Westwood) | *Cuphea carthagenensis* (Jacq.) Macbride (=*balsamonea*), Lythraceae | d'Araújo e Silva et al. (1968) |
| *Rhescyntis pseudomartii* Lemaire | *Virola bicuhyba* (Schott.) Warb., Myristicaceae | Travassos & d'Almeida (1937) |

TABLE 3. Continued.

| Moth | Hostplant and plant family | References |
|---|---|---|
| *Rhescyntis hippodamia norax* Druce | *Virola quatemalensis* (Hemsl.) Warb. probably, Myristicaceae | Vázquez (1965) |
| *Copiopteryx semiramis* (Cramer) | *Lucuma caimito* Roem., Sapotaceae | Travassos (1946) |
| | *Manilkara chicle* (Pittier) Gilly, Sapotaceae | Janzen (1982) |
| *Copiopteryx semiramis phoenix* (Deyrolle) | *Acanthosyris spinescens* (Mart. & Eichl.) Griseb., Santalaceae | d'Araújo e Silva et al. (1968) |
| *Copiopteryx sonthonnaxi* André | *Mimusops* sp., Sapotaceae | d'Araújo e Silva et al. (1968) |

* Hostplant in captivity.

maire 1977). The same north vs. south vicariance appears to apply to the two groupings within *Copiopteryx* as defined by Lemaire (1980). Whether the divergent wing pattern and coloration of *Titaea orsinome* is the result of phylogenetic divergence, or is an ecological adaptation to the plateaus of central Brazil is unknown, but I suspect the latter to be the case. The other genera are quite homogenous in the wing fascia among their species. Possible interpretations of why the genus *Arsenura* is much more species-rich include the following. It is able to speciate more rapidly, or is more adaptable and therefore declining less rapidly. The proposed hypotheses of the phylogeny do not support the idea that this group has more species because it is an older lineage.

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