

CLADISTICS OF THE CERATOCAMPINAE (LEPIDOPTERA: SATURNIIDAE)

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Contemporary insect systematists must face two distinct challenges. One is the provision of descriptive and analytical taxonomic reports on the insects, producing the cladistic patterns that serve as the general frame of reference for comparative entomology and the source of evolutionary patterns in need of causal explanations. The other is to inventory effectively a fauna that may be 2 to 60 times as diverse as all insects described during the past 200 years (Wheeler, 1990).

The Ceratocampinae is the second most numerous subfamily of the New World Saturniidae. With 170 known species, distributed in 27 genera, it includes some of the largest and smallest taxa of the family. The subfamily is distributed from southern Canada to northern Argentina, with a high percentage of species associated with deciduous or partially deciduous dry forests (Lemaire, 1988). In general, the peculiar male antennae (quadripectinate basally and simple distally), the sphingid-like shape of the male, and the very ornate armature of the early instar larvae, characterize the Ceratocampinae (Michener, 1952; Lemaire, 1988).

The Ceratocampinae have been the subject of three outstanding modern works. Michener (1952) published a morphological treatment of the Saturniidae, which dealt with genera and higher taxa of the New World, plus subfamilies of the Old World. The classification proposed by Michener (1952) has been widely used since by researchers in the field. In his study, Michener included all the genera of Ceratocampinae (under Citheroniinae) known at the time and proposed several new genera and subgenera for the subfamily. Ferguson (1971-72) provided an excellent revision for the group in North America. Lemaire (1988) published a revision for the whole subfamily for the first time.

There are several aspects of Ceratocampinae that make it an interesting group for a cladistic analysis. It has been considered a "primitive" group among Saturniidae (Michener, 1952; Lemaire, 1988), a condition for considering the subfamily as an outgroup candidate in future cladistic analyses of other subfamilies. Due to the extensive revision of Lemaire (1988), there is a sound taxonomic knowledge of the group, an essential requirement for any cladistic analysis. Although it is usually easy to define genera by apomorphic characters, the determination of relationships between genera is far more difficult (Lemaire, 1988), and in general the higher classification of Saturniidae is still far from stable (Minet, 1986; Holloway, 1987). Recently, Peigler (1989, 1993) published the first two papers in which cladistic methodolo-

gies are used to study the relationships among Saturniidae taxa, and Minet (1994) rehabilitated Draudt's (1927) concept of the Saturniidae. This conception treats the "Oxyteninae" and "Cercophanidae," two "aberrant families" as originally described by Jordan (1924), as two saturniid subfamilies. Further, Minet (1994) stated that the Oxyteninae are likely to represent the most "primitive" lineage of the Saturniidae, based on antennal characters.

Lemaire (1988) and Michener (1952) studied the morphology of the adults. Although there is a lack of technical descriptions of Saturniidae larvae (e.g., Heppner and Wang, 1987), the immatures of some Ceratocampinae have been reared in recent times. The present study incorporates available information on the immature stages, both from the literature and from preserved larvae.

The objectives of the present study were as follows:

1. Identify monophyletic groups within the Ceratocampinae, using both adult and larval characters.
2. Provide a comprehensive analysis of the adult and larval morphology of Ceratocampinae.

MATERIAL AND METHODS

Taxa

All the genera of the Ceratocampinae were considered as the ingroup for the study. Those taxa for which subgenera or "species groups" have been proposed, were considered as independent entities and coded for accordingly (i.e., *Psilopygida* (P.) and *P. (Psigida)* and the six species groups of *Syssphinx* proposed by Lemaire, 1987). These taxa made a total of 33 taxa for the ingroup (27 genera, two subgenera and six species groups) (Table 1). For all the taxa included in the ingroup, at least one species was thoroughly studied, and literature characters were always compared against actual specimens (with the exception of *Mielkesia*, for which we had no specimens).

Michener (1952) and Lemaire (1987) concluded that Arsenurinae is phylogenetically nearer to Ceratocampinae than to any other subfamily of Saturniidae. And some authors, such as Jordan (1922) even united Ceratocampinae and Arsenurinae into "Arsenuridae", distinct from Saturniidae, but conforming the superfamily Saturnioidea together. Minet (1994) showed that *Oxytenis* Hübner, *Asthenidia* Westwood and *Homoeopterys* Jordan form a monophyletic group and, because he concluded that they represent the most "primitive" lineage of the Saturniidae, he

TABLE 1. Taxa included in the cladistic analysis (ingroup and outgroup), number of species known, their geographical distribution, references to immature illustrations or descriptions and food plants reported (based mainly on Stone, 1991).

Taxa		Geographical distribution	Larval illustrations or descriptions	Hostplants
INGROUP				
<i>Eacles</i>	17	s. Canada to n. Argentina	Crocomo & Parra, 1979; Feige, 1971; Gage, 1976; Lampe, 1986; Lemaire, 1987; Packard, 1905	Aceraceae, Anacardiaceae, Betulaceae, Cornaceae, Cupressaceae, Ebenaceae, Fabaceae, Fagaceae, Hamamelidaceae, Juglandaceae, Malvaceae, Melastomataceae, Oleaceae, Pinaceae, Platanaceae, Rosaceae, Ulmaceae
<i>Bathyphebia</i>	5	sw. Venezuela to se. Peru (Andean)		
<i>Citheronia</i>	21	n. USA to n. Argentina	Bourquin, 1945; Burmeister, 1879; Dias, 1978a, 1981, 1982; Janzen, 1982; Lampe, 1985; Lemaire, 1987; Packard, 1905; Tuskes, 1987; Vázquez, 1944	Anacardiaceae, Aquifoliaceae, Cayocaraceae, Combretaceae, Euphorbiaceae, Hamamelidaceae, Juglandaceae, Lorantheae, Malvaceae, Myrtaceae, Oleaceae, Salicaceae
<i>Procitheronia</i>	3	French Guiana to Bolivia and se. Brazil	Dias, 1991	<i>Croton floribundus</i> (Euphorbiaceae)
<i>Schausiella</i>	11	Costa Rica to Bolivia and se. Brazil	Lemaire, 1987; Travassos, 1958	<i>Hymenaea</i> (Fabaceae: Caesalpinioideae)
<i>Othorene</i>	4	Mexico to se. Brazil	Lemaire, 1987; Travassos & Noronha, 1967b	<i>Terminalia</i> (Combretaceae), <i>Gleditsia</i> (Fabaceae: Caesalpinioideae), <i>Quercus</i> (Fagaceae), <i>Psidium</i> (Myrtaceae), <i>Manilkara</i> (Sapotaceae)
<i>Cicia</i>	5	Guiano-Amazonian region and c.-se. Brazil		<i>Gleditsia</i> (Fabaceae: Caesalpinioideae)
<i>Dacunju</i>	1	c.-se. Brazil		
<i>Giacomellia</i>	2	Bolivia and n. Argentina (sub-Andean areas)		
<i>Almeidella</i>	3	se. Brazil	Otero, 1971	
<i>Psilopygoides</i>	1	Guianan-Amazonian		
<i>Ceropoda</i>	1	Mato Grosso (Brazil) and Paraguay		
<i>Mielkesia</i>	1	Curitiba (Paraná, Brazil)		
<i>Psilopygida</i>	1	Argentina and e. Bolivia (Andes)	Bourquin, 1945	<i>Gleditsia</i> (Caesalpinioideae), <i>Acacia</i> (Fabaceae: Mimosoideae)
<i>Psilopygida</i> (<i>Psigida</i>)	2	Tropical South America		
<i>Syssphinx molina</i> gp.	1	Mexico to Argentina	Packard, 1905; Travassos & Ferreira d'Almeida, 1937	<i>Cassia</i> , <i>Gleditsia</i> (Caesalpinioideae), <i>Robinia</i> (Faboideae), <i>Acacia</i> , <i>Albizia</i> , <i>Pithecellobium</i> (Fabaceae: Mimosoideae), <i>Salix</i> (Salicaceae)
<i>Syssphinx quad-rilineata</i> gp.	7	Mexico to Ecuador	Heitzman, 1961; Tuskes, 1986	<i>Cassia</i> , <i>Gleditsia</i> , <i>Haematoxylum</i> , <i>Parkinsonia</i> (Caesalpinioideae), <i>Robinia</i> (Faboideae), <i>Acacia</i> , <i>Albizia</i> , <i>Pithecellobium</i> , <i>Prosopis</i> (Fabaceae: Mimosoideae)
<i>Syssphinx bisecta</i> gp.	16	Mexico to Ecuador	Comstock, 1947; Tuskes, 1986	<i>Cercidium</i> , <i>Gleditsia</i> , <i>Gymnocladus</i> , <i>Parkinsonia</i> (Caesalpinioideae), <i>Robinia</i> (Faboideae), <i>Acacia</i> , <i>Pithecellobium</i> , <i>Prosopis</i> (Fabaceae: Mimosoideae)
<i>Syssphinx bicolor</i> gp.	1	se. Canada to ne. Mexico		<i>Gleditsia</i> , <i>Gymnocladus</i> , <i>Hymenaea</i> (Caesalpinioideae), <i>Robinia</i> (Fabaceae: Faboideae), <i>Quercus</i> (Fagaceae)
<i>Syssphinx amena</i> gp.	1	Amazonian		
<i>Syssphinx ocellata</i> gp.	3	e. slopes of Andes, n. Venezuela to Bolivia		
<i>Anisota</i>	13	Canada to Guatemala	Riotte & Peigler, 1980; Wolfe & Peigler, 1993	<i>Acer</i> (Aceraceae), <i>Corylus</i> (Betulaceae), <i>Castanea</i> , <i>Fagus</i> , <i>Quercus</i> (Fagaceae), <i>Carya</i> (Juglandaceae), <i>Rubus</i> (Rosaceae)
<i>Dryocampa</i>	1	se. Canada to Florida and e. Texas	Allen, 1976	<i>Acer</i> (Aceraceae), <i>Fagus</i> , <i>Quercus</i> (Fagaceae), <i>Juglans</i> (Juglandaceae)
<i>Adeloneivaia</i>	15	Mexico to n. Argentina	Janzen, 1982; Lampe, 1987; Lemaire, 1987; Packard, 1905	<i>Acacia</i> , <i>Inga</i> , <i>Lysiloma</i> (Fabaceae: Mimosoideae), <i>Quercus</i> (Fagaceae), <i>Salix</i> (Salicaceae)
<i>Adelowalkeria</i>	6	Tropical South America	Dias, 1986; Lemaire, 1987	<i>Machaerium</i> (Fabaceae: Faboideae)
<i>Megaceresa</i>	1	c. Brazil		
<i>Rachesa</i>	4	Colombia to Bolivia (Andes)		
<i>Ceratesa</i>	1	e. Bolivia and nw. Argentina		
<i>Scolesa</i>	6	c.-e. and se. Brazil, nw. Argentina and se. Peru		
<i>Citioica</i>	2	Mexico to Bolivia	Lemaire, 1987	<i>Robinia</i> (Fabaceae: Faboideae), <i>Salix</i> (Salicaceae)
<i>Oiticella</i>	3	Venezuela to se. Brazil and Argentina		<i>Mimosa</i> (?) (Fabaceae: Mimosoideae)
<i>Ptiloscola</i>	9	Mexico to Bolivia and se. Brazil	Janzen, 1982; Lemaire, 1987	<i>Acacia</i> (Fabaceae: Mimosoideae)
<i>Neorcarnegia</i>	1	c.-se. Brazil to e. Bolivia		
OUTGROUP				
<i>Arsenura</i>	20	Mexico to Bolivia and s. Brazil	Brenner & Lampe, 1987	<i>Annona</i> (Annonaceae), <i>Bombacopsis</i> , <i>Bombax</i> , <i>Chorisia</i> (Bombacaceae), <i>Urena</i> (Malvaceae), <i>Tilia</i> (Tiliaceae)
<i>Dysdaemonia</i>	3	Mexico to Bolivia and n. Argentina	Dias, 1978b	<i>Bombax</i> , <i>Ceiba</i> , <i>Chorisia</i> (Bombacaceae), Malvaceae, Tiliaceae
<i>Oxytenis</i>	17	Mexico to Bolivia and se. Brazil	Aiello & Balcázar, 1997	<i>Alibertia</i> , <i>Genipa</i> (Rubiaceae)

reassigned them to that family as the subfamily Oxyteninae. We only had the opportunity to study first instar larvae of 10 genera: *Oxytenis*, *Arsenura*, *Dysdaemonia* (outgroup), and *Eacles*, *Citheronia*, *Schausiella*, *Othorene*, *Syssphinx*, *Anisota*, *Dryocampa*, *Citioica*, *Adelowalkeria* (ingroup). Because of this information, and the available immature stages, we decided to consider *Oxytenis* (Oxyteninae), *Arsenura* and *Dysdaemonia* (Arsenurinae) as the outgroups in our study.

Collections

The bases for the study were the collections of the Florida State Collection of Arthropods (FSCA, Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL), and the collection of the American Museum of Natural History (AMNH, New York, NY) which houses the original preparations and most material studied by Michener in 1952.

Preparation of Material

We dissected the whole body of male and female adults for at least one species of each of the selected taxa under study (the only exception was *Mielkesia*, for which sufficient material was lacking for this study). After the wings were removed, the rest of the body was soaked in cold potassium hydroxide (KOH) for 24 hours, or boiled for a few minutes and then placed in 70% ethanol. Genitalic preparations, legs and antennae were stained with chlorazol black (1% in 70% ethanol) and preserved in 70% ethanol. Wings were bleached in 4.5% sodium hypochlorite and mounted on slides in Euparal for study of venation.

Structures of systematic importance of both adult and larvae were drawn using a camera lucida. Some characters were examined with a scanning electron microscope (SEM). For the SEM studies, larval specimens were sonicated with an ultrasonic cleaner (Mettler Electronics) for 3 minutes in a 70% solution of ethanol, then dehydrated in a graded series of ethanols (70, 80, 90, 100%). Drying was accomplished with a critical point dryer (DCP-1 Denton Vacuum) using carbon dioxide. Dried larval specimens and adult parts were mounted on stubs with electrical tape (Scotch 3M 1182) or on insect points. Thereafter they were coated with a sputter coater (Denton Vacuum Desk II) using a gold target for 6 minutes (15 mA). The specimens were observed with a Hitachi 570s SEM (15kV), and photographed (4x5 Polaroid 55 P/N and 35 mm Ilford 50 B&W).

Morphological Terms

Larval morphological nomenclature follows Dethier (1941) for antennae, Grimes and Neunzig (1986a, b) for maxillary terminology, and Stehr (1987) for chaetotaxy and general morphology. Morphological terms for the pupae are from Mosher (1914, 1916a, b).

Nomenclature for general adult morphology follows Michener (1952), Lemaire (1973, 1978, 1988), Common (1990), Nielsen and Common (1991), and Scoble (1992). Genitalic terminology follows Klots (1970) and Lemaire (1978).

Characters

Data from 99 characters (APPENDIX 2) were derived from adult external morphology (60 characters) and immature morphology (39 characters).

Unfortunately, we only had the opportunity to study first instar larvae of 10 genera. In most cases only one larva was available for study, and critical-point drying for SEM study sometimes produced inconsistent results; this was also noted by Miller (1991). We found that those specimens that were better preserved (i.e., boiled or distended before fixation), are more likely to result in good material for study. Due to these limitations, we were not able to study all specimens and/or structures with SEM. When more larvae are available, we are sure that further characters and a finer partitioning of character states will be found. Some of the characters that we used in the analysis may prove inconsistent, but we had to extrapolate them. Only after larger series of specimens, and more species representing genera of all major clades are studied, will a better picture emerge.

Because of the incompleteness of immature characters, and to compare the information from adult and immature characters (APPENDIX 2), the data matrix was analyzed in four steps: all taxa, adult characters only (36 by 99); 14 taxa (genera with immatures known or available to us), immature characters (14 by 39); the same 14 taxa, and all characters (14 by 99); and finally all taxa and all characters (36 by 99, coding the missing information with "?", see below).

Cladistic Methodology

The ultimate goal of systematics is a classification that reflects phylogenetic hypotheses and that is a maximally informative reference system for comparative biology (Farris, 1979; Wheeler, 1990). Phylogenetic systematics or cladistics attempts to identify and recognize the pattern of relationships among the organisms under study (Funk, 1986; Wiley, 1981; Wiley *et al.*, 1991). In this study, we used the principles of phylogenetic systematics as developed by Hennig (1966). He stated that only monophyletic taxa should be regarded as historical entities. The only logical basis for inferring monophyly, Hennig also asserted, is to show that the component taxa of a group share derived character states, or synapomorphies. The taxa under study are ordered in hierarchical branching diagrams on the basis of synapomorphies and the application of the parsimony criterion, that is, the simplest explanation which requires the least number of character changes, and thus the minimum number of extra assumptions. Experimental studies have demonstrated that grouping by synapomorphy produces the most stable classifications (Mickevich, 1978, 1980; Miller, 1987; Schuh and Farris, 1981; Schuh and Polhemus, 1980).

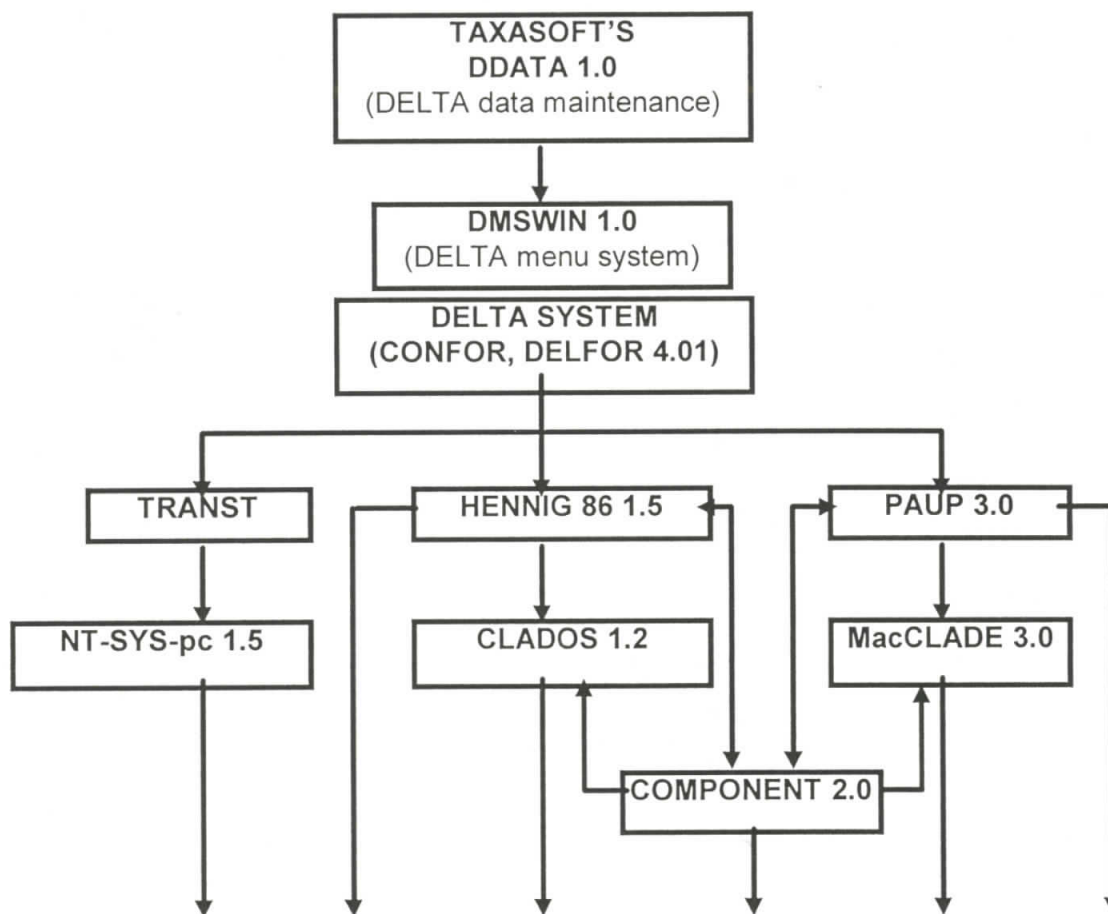


Fig. 1. Software and pathways used in the present study.

The main advantage of cladistics over other methods is that the hypotheses (classifications) generated are capable of being re-analyzed, or falsified (Funk, 1986; Wiley, 1981; Wiley *et al.*, 1991). This confers credibility to the method. This is of special importance, since according to Wheeler (1990), without credible phylogenetic hypotheses and classifications, it is not possible to make intelligent choices about conserving insect diversity or studying it. Until cladistic relationships are understood, biological studies will lack a well-founded historical component (Miller, 1987; Wheeler, 1990).

Character Coding

No *a priori* determination of character polarities was made. Cladistic parsimony dealt with the problem of polarity by rooting the cladograms with the outgroup (Nixon and Carpenter, 1993). No multistate characters were treated as ordered (= additive), so the 99 characters were treated as unordered (= non-additive). A missing data code was used when the information was not available for a character or for variable character states. The matrices used in the analysis are in APPENDIX 2.

Tree Building

The data matrices for adult and larval characters were analyzed based on the principle of maximum parsimony. The 14 taxa (including the outgroup) in the data matrix derived from larval morphology and the combined (adult and larval) data matrix, permitted the search of trees by exact algorithms. But for the

adult matrix, with 36 taxa, the use of exact algorithms with the phylogenetic software available was extremely time-consuming and not feasible, thus, heuristic (approximate) methods were used.

For the exact methods in Hennig86 (Farris, 1989a), we used the *ie** option which generates trees by implicit enumeration and retains all trees found (where computer memory permits). In PAUP, we used the *branch and bound* command, an algorithm guaranteed to find all minimum-length trees (Hendy and Penny, 1982; Swofford, 1991). In the case of heuristic methods in Hennig86, we first used the *mhennig** option, which constructs several trees, each by a single pass through the data, adding the terminals in different order and then applying branch-swapping to each of the initial trees. Then, we used the *bb** option that applies extended branch-swapping to the trees previously generated by the *mhennig** option, retaining all the trees found (Farris, 1989a). The heuristic algorithm in PAUP includes the stepwise addition of taxa to a developing tree and then the rearrangement of these trees via branch-swapping techniques (Swofford, 1991; Swofford and Olsen, 1990).

Several indices have been proposed in the literature that measure the "fit" of characters to particular trees. We calculated the consistency index (c) (Kluge & Farris, 1969), retention index (r) (Farris, 1989b), and the rescaled consistency index (rc) (Farris, 1989b).

When more than one equally parsimonious tree was found, we performed Farris' "successive weighting" (Farris, 1989b) for the

When more than one equally parsimonious tree was found, we performed Farris' "successive weighting" (Farris, 1989b) for the set of trees.

Consensus Trees

Consensus trees are a convenient way to summarize the agreement between two or more trees (Page, 1993). We computed a strict consensus tree (Sokal and Rohlf, 1981) when more than one most parsimonious tree was found. The strict consensus tree of a set of trees contains only those clusters found in all the trees under study. The consensus trees were obtained with COMPONENT (Page, 1993) using Day's algorithm (Day, 1985).

Bootstrap

The bootstrap technique is a "resampling technique" because it estimates the form of the sample distribution by repeatedly resampling data from the original data set (matrix) (Efron, 1982; Efron and Gong, 1983). Felsenstein (1985) discussed the potential application of the technique for the first time in estimating statistical confidence of phylogenetic hypotheses.

Phenetic Methods

For comparison purposes, we performed a phenetic analysis of the Ceratocampinae taxa. A similarity matrix (*sensu* Sneath and Sokal, 1973) was calculated using a modified version of Gower's similarity coefficient (Dallwitz *et al.* 1993; Gower, 1971) with DELTA's program CONFOR (Dallwitz *et al.*, 1993). It was then translated into a matrix suitable for the program NTSYSpc (Rohlf, 1989) using the program TRANSNT supplied with DELTA.

A cluster analysis (unweighted pair-group method using arithmetic averages, UPGMA) (Sneath and Sokal, 1973) was performed on the similarity matrix, and the results were summarized in phenograms. The FIND option of NTSYS was used to identify tied values for the closest pair of objects, so that the program tries each of the alternative clusterings. To be considered a "tie," two values must differ by less than 10^{-10} . A matrix of cophenetic values was generated from the phenograms and then compared (correlated) to the original matrix. This way, the index of cophenetic correlation was calculated. The index is a measure of the goodness of fit of the cluster analysis: a close value of the cophenetic correlation to 1.0 indicates a good fit. When more than one phenogram was found, we calculated a strict consensus tree.

Software

To have the data for our analysis in a flexible, data-coding format, we used DELTA (Descriptive Language for Taxonomy) (Askevold and O'Brien, 1994; Dallwitz *et al.*, 1993; Partridge *et al.*, 1993). The data, coded in a combination of numerical and text data, is stored mainly in three normal text (ASCII) files, which in turn, with the help of a computer and associated software, can produce different files as output. The output files of more interest for our study were natural language descriptions that enable an easy checking of the data itself and converted files to formats required for phylogenetic and phenetic analysis. To speed up the process of coding and writing the essential three ASCII files needed by the DELTA software, we used Taxasoft's DDATA (Gouda, 1994). In order to bring together the DELTA and other software, under an easily operated shell in Microsoft's

Windows™, we used the DELTA Menu System (Lander, 1994). With DELTA's CONFOR, character state matrices were generated as input files for cladistic analysis to be performed by HENNIG-86 v. 1.5 (Farris, 1989A) and PAUP 3.0 (Swofford, 1991). The programs CLADOS v. 1.2 (Nixon, 1992) and MacCLADE v.3.0 (Maddison and Maddison, 1992) were used to examine character distributions. COMPONENT v.2.0 (Page, 1993) was used to compare and make consensus trees. The similarity matrix calculated with DELTA, was then translated by TRANSNT (a program supplied with DELTA), and phenograms were calculated with NT-SYSPc v.1.5 (Rohlf, 1989) (Fig. 1).

RESULTS

CLADISTIC ANALYSIS

Adults

The Ceratocampinae form a monophyletic group that is distinguished from other saturniid subfamilies by three apomorphies: (a) sphingid-like body shape (character 59), (b) with some D scoli distinct and conspicuously projecting in the last instar larva (character 95), and (c) pupa with a projecting and bifid cremaster.

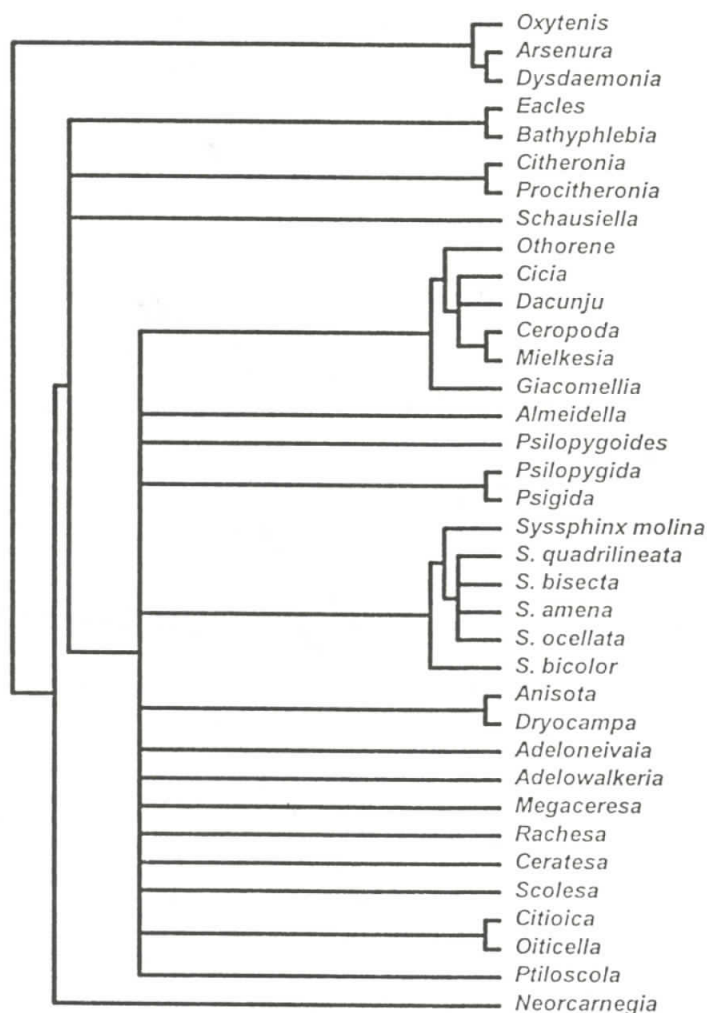


Fig. 2. Strict consensus cladogram of the 182 most parsimonious cladograms (length = 193; CI = 41; RI = 70), resulting after analyzing 60 unweighted adult characters.

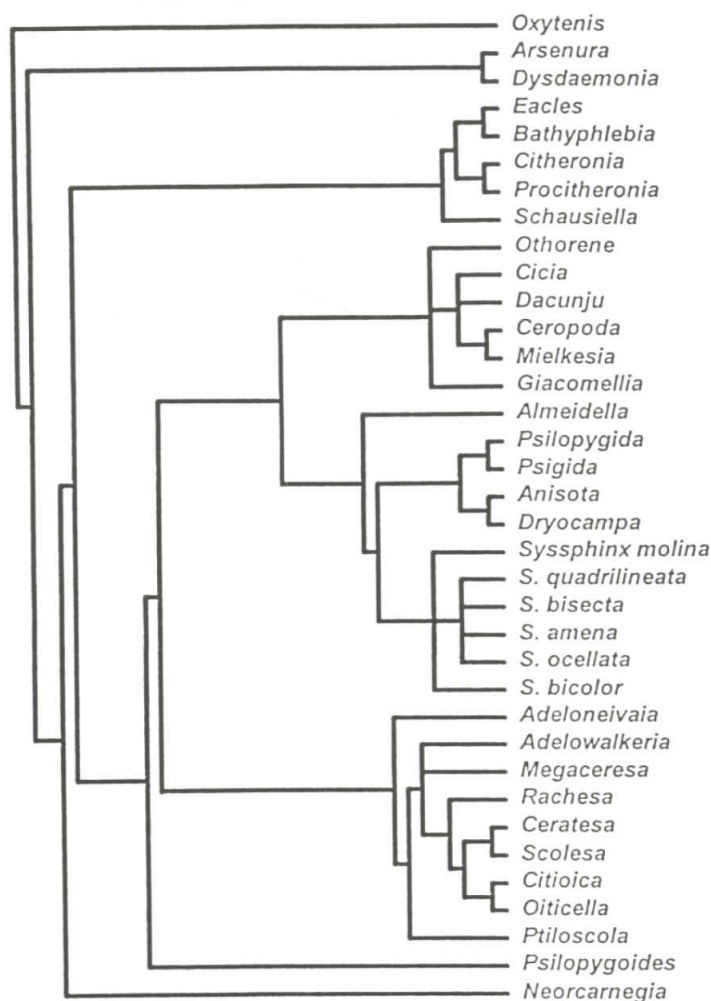


Fig. 3. Strict consensus tree of 54 equally parsimonious trees found after the successive weighting procedure from 60 adult characters.

The analysis of the 60 adult character data matrix, using equal weights with Hennig86, produced 182 equally parsimonious cladograms, each with a length of 193 steps, a consistency index (CI) of 0.41, and a retention index (RI) of 0.70 (their strict consensus tree is in Fig. 2). When successive weighting was applied, 54 minimum-length cladograms were retained after the fifth round of weighting, with a length of 496 steps, a CI of 0.66 and a RI of 0.84. A strict consensus of those 54 trees is shown in Figure 3. Values for the CI, RI and weight (RI X CI X 100) after the successive weighting are shown in APPENDIX 3.

The results indicate that *Neorcarnegia* is the most plesiomorphic genus (bottom of Fig. 2 and Fig. 3), and thus the sister group to the rest of the taxa. A clade formed by ((*Eacles*, *Bathyphebia*) (*Citheronia*, *Procitheronia*) *Schausiella*) (**Eac-Sch**) is the most plesiomorphic group after *Neorcarnegia* and before *Psilopygoides*. *Adeloneivaia* and *Adelowalkeria* s. l. —(*Adelowalkeria*, *Megaceresa* (*Rachesa* ((*Ceratesa* *Scolesa*) (*Citioica*, *Oiticella*)))) *Ptiloscola*—, would then constitute the sister group to the remaining taxa. *Othorene* s. l. (*Othorene*, *Giacomellia* (*Cicia*, *Dacunju* (*Ceropoda*, *Mielkesia*))) and the clade (*Almeidella* ((*Psilopygida* (*Anisota*, *Dryocampa*)) *Syssphinx*)) are adelpho-taxa.

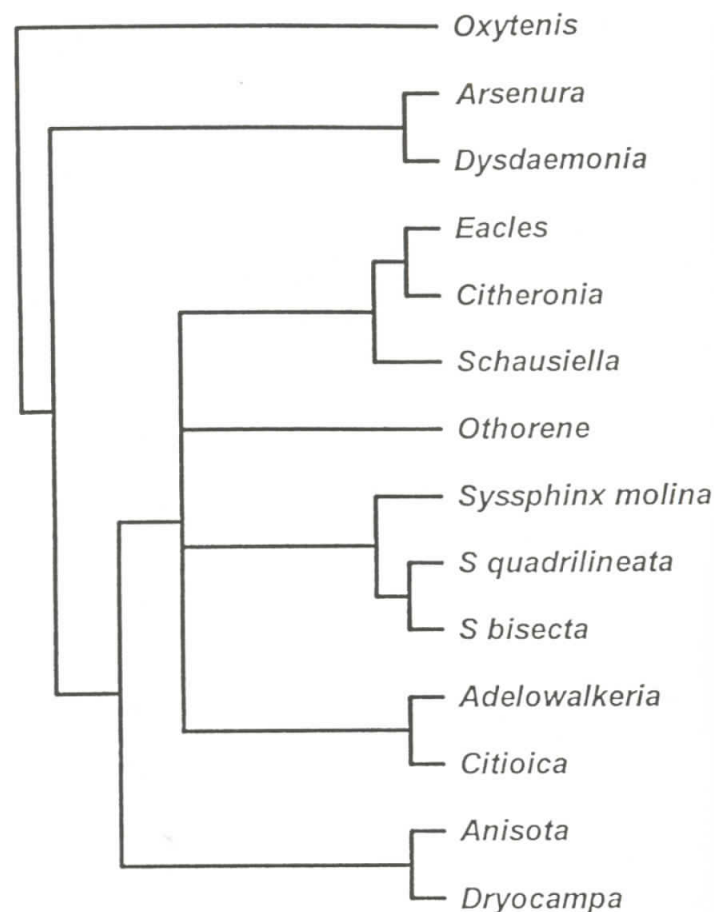


Fig. 4. Strict consensus of the three most parsimonious trees (length = 86, CI = 0.77, RI = 0.78), found after analyzing 39 immature characters.

The size of the matrix and the high levels of homoplasy caused PAUP to spend 11:45 hr to run 11 replications of the bootstrap procedure and causing a tree-buffer overflow. Hence, the procedure was prohibitively time consuming in order to have enough replicates to be statistically significant, according to Felsenstein (1985).

Immature Stages

The analysis of 39 unweighted larval and pupal characters of eleven Ceratocampinae taxa by implicit enumeration produced three equally parsimonious trees with a length of 86 steps, CI = 0.77 and RI = 0.78. The same three cladograms remained after successive weighting; therefore this procedure had no effect on our analysis. The strict consensus is in Fig. 4.

The *Anisota*-*Dryocampa* clade always occurs as the most plesiomorphic, then four constant clades are found: (a) *Eacles*-*Citheronia*-*Schausiella*, (b) *Othorene*, (c) *Syssphinx*, and (d) *Adelowalkeria*-*Citioica*, but their relationships are completely unresolved in the consensus tree. A majority-rule consensus tree resulting of 100 bootstrap replications is shown in Fig. 5. Only three clades lay at or above the 95% confidence limit: (*Eacles*, *Citheronia*), (*Citioica*, *Adelowalkeria*), and (*Anisota*, *Dryocampa*).

Adult and Immature Stages

The analyses of the adult and immature data matrices combined for the eleven genera or species-groups representatives for which

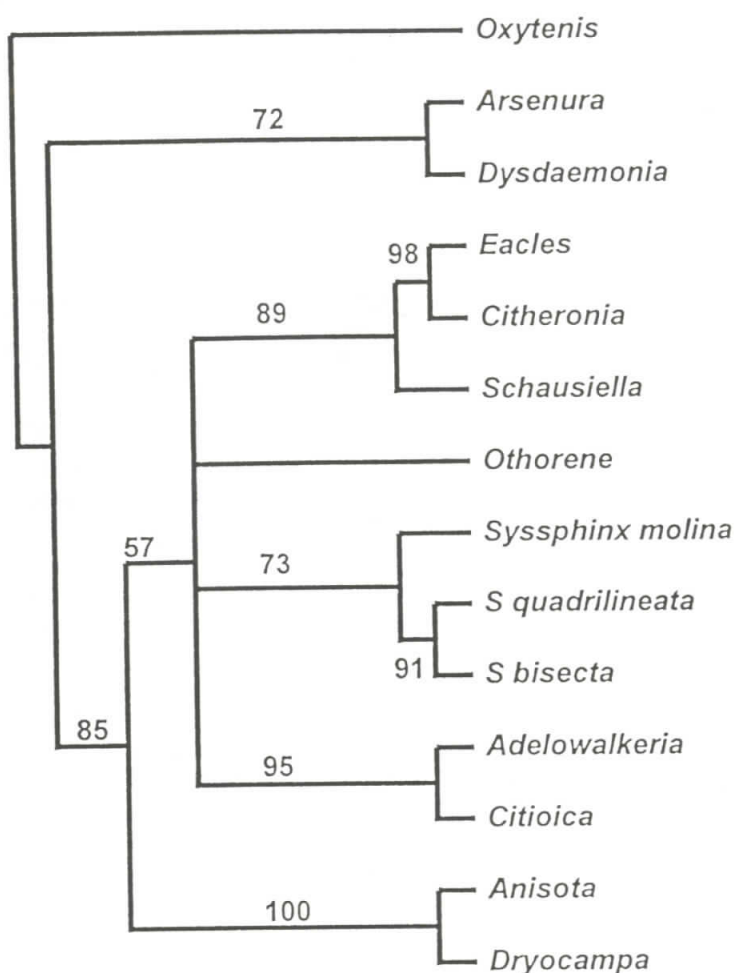


Fig. 5. Majority-rule consensus tree of 100 bootstrap replications based on 39 immature characters. Values represent the frequency (%) a clade was found in the bootstrap replications.

immatures were available in our study produced two cladograms when the implicit enumeration algorithm was used. These minimum-length trees had 193 steps, CI = 0.69, and RI = 0.73; their strict consensus tree is shown in Fig. 6. One tree was retained after the successive weighting procedure after the first round (length = 1044, CI = 0.85, RI = 0.87, Fig. 68). Values for the CI, RI and weight (RI X CI X 100) after the successive weighting are shown in APPENDIX 3.

Four constant clades were found in the two minimum-length trees: (a) *Eacles*-*Citheronia*-*Schausiella*, (b) *Othorene*-*Syssphinx*, (c) *Anisota*-*Dryocampa*, and (d) *Adelowalkeria*-*Citioica*. Although these four clades are unresolved in the consensus cladogram, in the tree retained after successive weighting the relationships among them are fully resolved.

The results of 100 bootstrap replications are summarized in a majority rule consensus (Fig. 7). Four clades are at or above the 95% confidence interval: the ingroup, (*Eacles*, *Citheronia*), (*Anisota*, *Dryocampa*), and (*Adelowalkeria*, *Citioica*). Slightly behind this interval, the three representatives of *Syssphinx* were found in 94% of the replications.

The simultaneous analyses of 99 adult and immature charac-

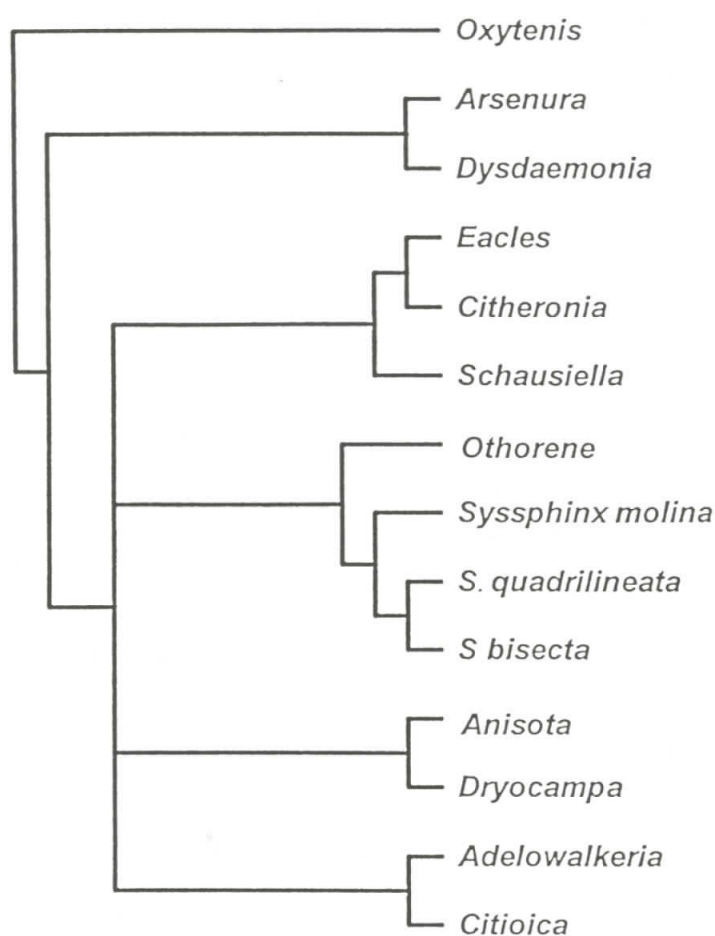


Fig. 6. Strict consensus cladogram of the two most parsimonious trees (L = 193, CI = 69, RI = 73) resulting after analyzing 99 unweighted adult and immature characters for the 14 taxa with known immatures.

ters for the 36 taxa with the heuristic search, produced 22 trees with 282 steps, CI = 0.52 and RI = 0.71. Their strict consensus tree is shown in Fig. 8. Again, *Neorcarnegia*, appears as the most plesiomorphic genus, and the clades **Ea-Sch**, (*Adeloneivaia*, *Adelowalkeria* s.l.), *Othorene* s.l., *Syssphinx*, and the clade (*Psylopigida* (*Anisota*, *Dryocampa*)) were found on all these cladograms. When compared to the cladograms generated from adult characters alone, few differences can be observed. The (*Adeloneivaia*, *Adelowalkeria* s.l.) clade is the most plesiomorphic group after *Neorcarnegia* and **Ea-Sch**. *Psilopygoides* is placed between (*Adeloneivaia*, *Adelowalkeria* s.l.) and the remaining taxa. *Syssphinx* appears as the sister group of *Othorene*, instead of being the sister group of (*Psylopigida* (*Anisota*, *Dryocampa*)). The consensus cladogram generated from the 22 most parsimonious trees found (Fig. 8) shows a better resolution than the consensus cladogram obtained from the adult data alone. We attempted to apply the bootstrap technique for all data and all characters, but it took 88 hours to make only two replicates.

PHENETIC ANALYSIS

Adults

The analysis of the Gower's similarity coefficient matrix, derived from 60 adult characters, using the UPGMA method, result-

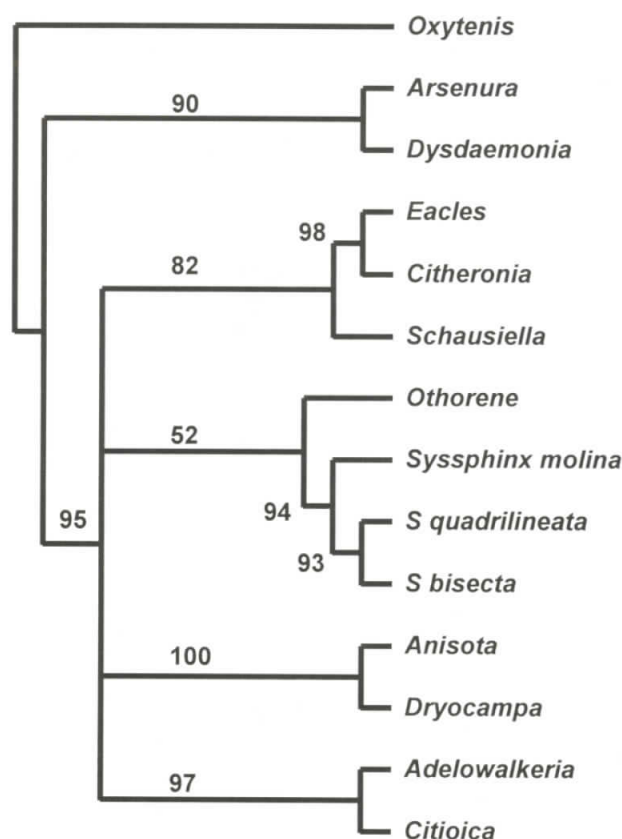


Fig. 7. Majority-rule consensus tree based on the bootstrap samples for the adult and immature data for the 14 taxa with known immatures. Values represent the frequency (%) a clade was found in the bootstrap replications.

ed in four "tied" phenograms. The "ties" are due to the very close values of *Othorene* and *Giacomellia*, and the *Syssphinx* groups of species. The cophenetic correlation coefficient was good ($r = 0.89523$). Six general clusters were found: (a) **Ea-Sch** + *Neorcarnegia*, (b) *Adeloneivaia* + **Ade-Oit**, (c) *Psilopygoides*, (d) *Psilopygida* + *Syssphinx*, (e) **Oth-Mie**, and (f) as the most basal clade *Anisota-Dryocampa* (Fig. 9). The strict consensus phenogram is presented in Fig. 10.

Immature Stages

For the larvae, the UPGMA clustering of the similarity matrix yielded one phenogram with a very good fit ($r = 0.90673$) (Fig. 11). The phenogram shows two main clusters: first, *Othorene-Syssphinx* clusters distantly to *Citioica-Adelowalkeria*; second, *Eacles-Citheronia-Schausiella* clusters even farther to *Anisota-Dryocampa*.

Adult and Immature Stages

The UPGMA cluster analysis of the Ceratocampinae OTU's with known immature stages (11 taxa), using 99 characters and Gower's coefficient of similarity produced only one phenogram (Fig. 12) with a very good matrix correlation ($r = 0.90673$). The phenogram agrees with the larval character based phenogram, with the exception that *Anisota-Dryocampa* arises basally and does not cluster with *Eacles-Citheronia-Schausiella*.

CHARACTER ANALYSIS

In the following list, all the characters used in the study are briefly discussed. The characters are arranged according to life stage and tagma. The observed variation, character states and distribution of characters are discussed. Lists of characters are found in APPENDIX 1, and the data matrices in APPENDIX 2. Characters are numbered beginning at "0" to conform to Hennig86 format.

Adults

The best morphological treatment for the Saturniidae is that of Michener (1952). He made a thorough morphological description of *Eacles imperialis* (Drury) to provide the basis for the terminology used in his work. We followed his terminology except that we followed Klots' terminology for the genitalia (Klots, 1970). Ferguson (1971) and Lemaire (1988) noted that Michener confused the gnathos with the transtilla and referred to the valvae as harpes. From Michener's paper, we were able to select 102 adult and 2 immature characters to use in our cladistic analysis. We found Michener's observations extremely accurate, but after comparing the characters against actual specimens, we dropped 42 characters because they were not informative or because we found them very difficult to score. Also, Michener (1952) presented a table showing what he considered the primitive (plesiomorphic) and specialized (apomorphic) states for characters of systematic interest; this summary provided very useful comparisons with our findings. The final data matrix used for the cladistic analysis herein included 60 characters from the adult morphology.

HEAD

Character 0. Frontal protuberance.

Michener (1952) used this term to refer to the dorsoventrally flattened projection of the lower end of the frons. Several frontal projections have been described from members of the Noctuidae, Notodontidae, Geometridae (see Miller, 1991), but the frontal protuberance in most groups of saturnids seems unique. In most Ceratocampinae it is very strong and received a score of "0" (Fig. 14). The Arsenurinae have a distinct but blunt and transverse protuberance ("1"), *Anisota* and *Dryocampa* have a low and transverse frontal protuberance ("1"). *Oxytenis*, on the other hand, only has a small projection which seems to be very different from that of other saturnids (Fig. 13). According to Michener (1952), it is often absent in Oxyteninae and Cercophaninae. It has been proposed that the frontal protuberance assists the adult moth to break through hard soil (Miller, 1991). Michener (1952) considered the character state elongated frontal protuberance "specialized," as opposed to broad and transverse.

Character 1. Upper ends of eyes extending above lower margins of antennal sockets.

Only in *Anisota* and *Dryocampa* do the upper ends of the eyes not reach the lower margins of the antennal sockets. In *Adeloneivaia*, the eyes extend up to the lower margins of the antennal sockets (Riotte and Peigler, 1981: fig. 1a,b), but do not really extend beyond them. Michener (1952) considered the latter condition as "specialized."

Character 2. Antennal length.

The Oxyteninae and Arsenurinae have many-segmented antennae, clearly longer than the thorax. Five genera, *Bathyphebia*, *Psilopygoides*, *Ceropoda*, *Megaceresa*, and *Rachesa*, have antennae that are about as long as thorax. But the majority of Ceratocampinae have antennae two-thirds as long as the thorax. This latter character state was considered by Michener (1952) as the most "specialized."

Character 3. Pectination of male antennae.

All Ceratocampinae have quadripectinate antennae ("0"), but the outgroups show two different characters states (Fig. 16): *Dysdaemonia*

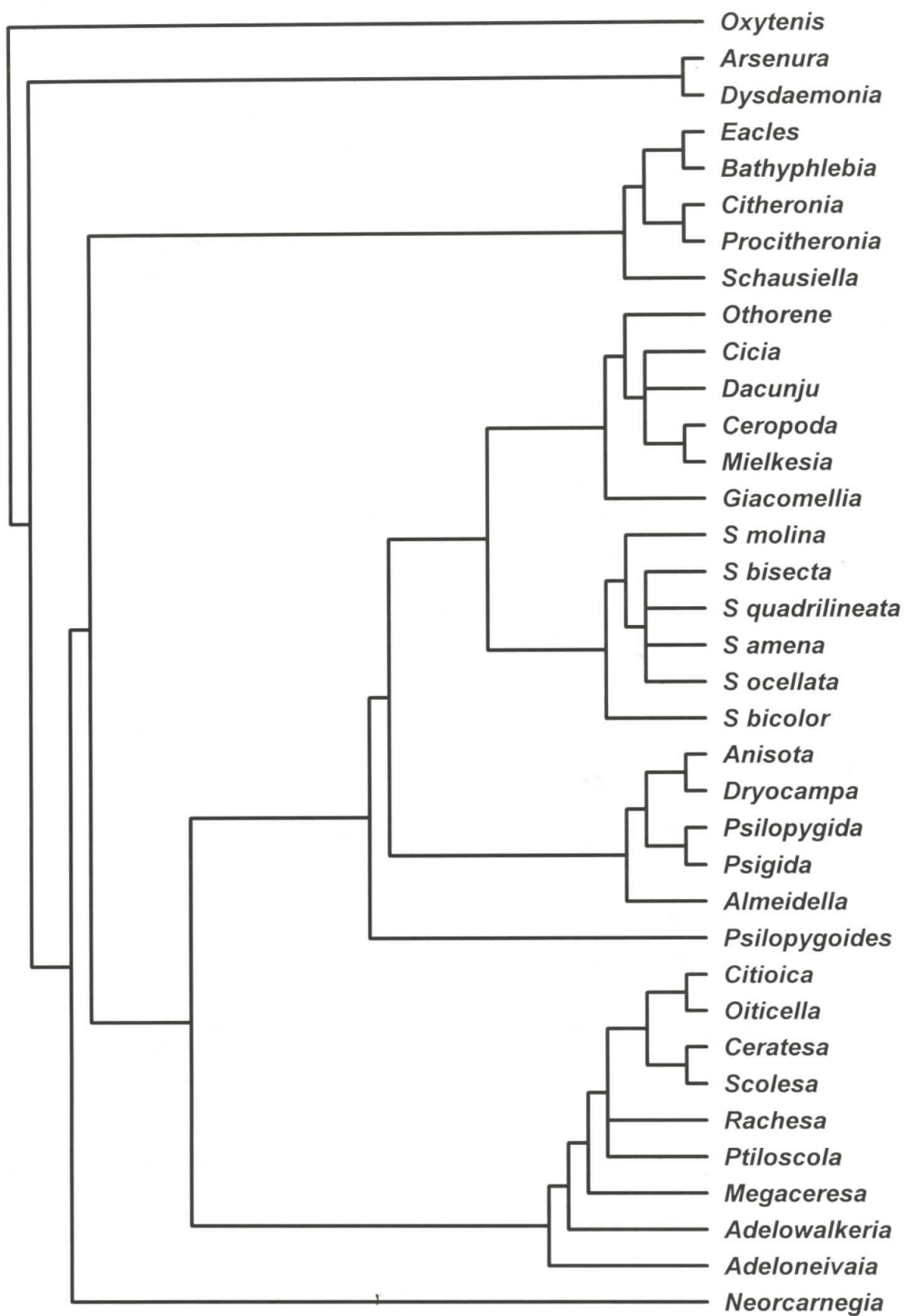


Fig. 8. Strict consensus cladogram of the 22 most parsimonious trees ($L = 282$, $CI = 52$, $RI = 71$) resulting after analyzing 99 unweighted adult and immature characters for all the taxa.

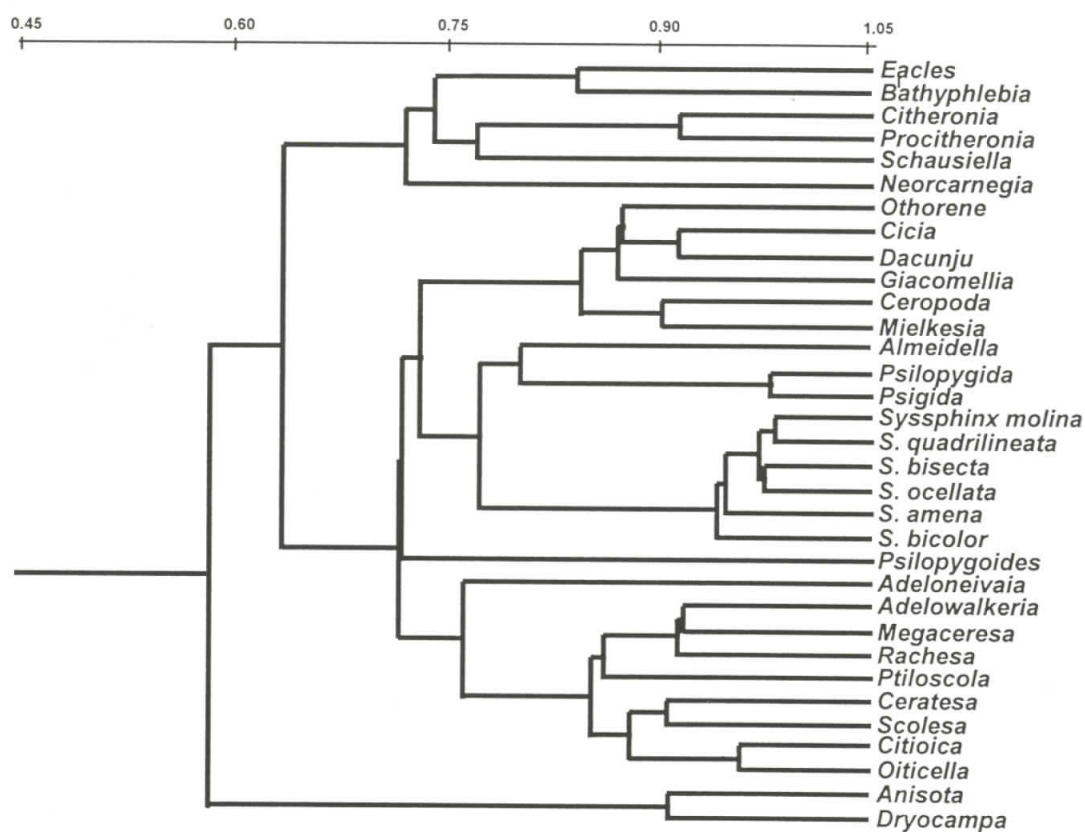


Fig. 9. First of four "tied" phenograms derived from 60 adult characters, using Gower's similarity coefficient and UPGMA method ($r = 0.89523$).

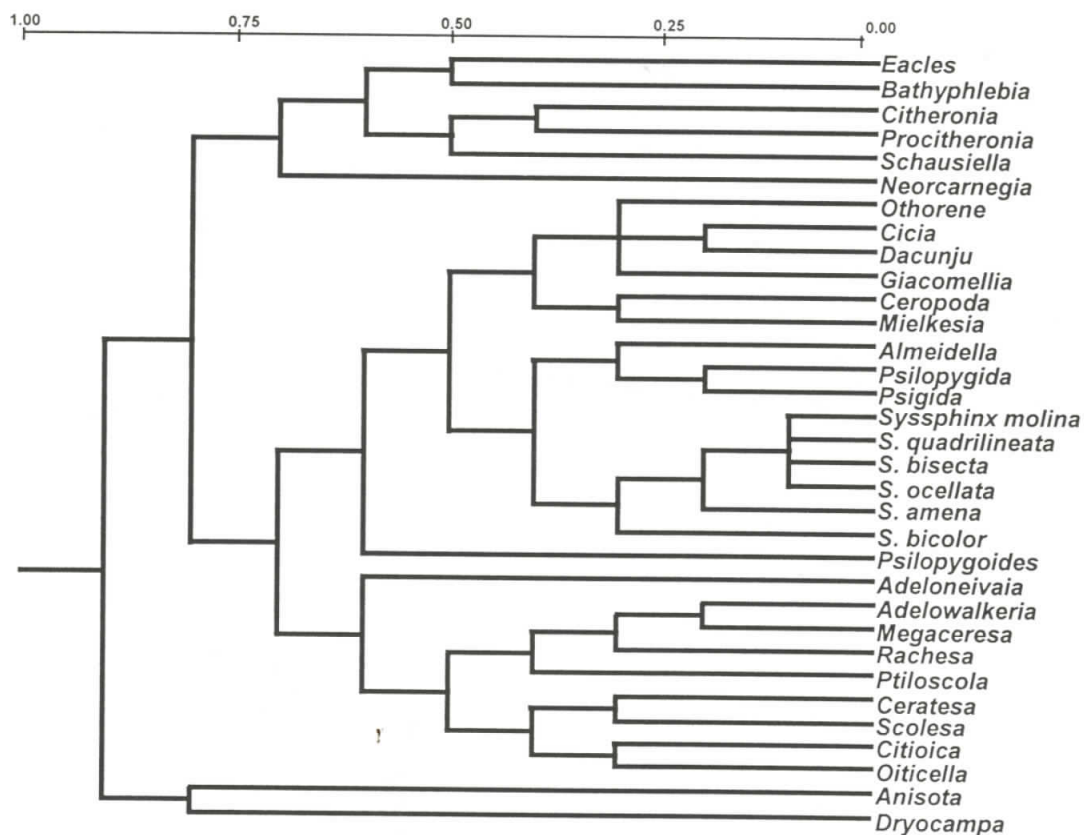


Fig. 10. Strict consensus tree from four tied phenograms calculated from 60 adult characters.

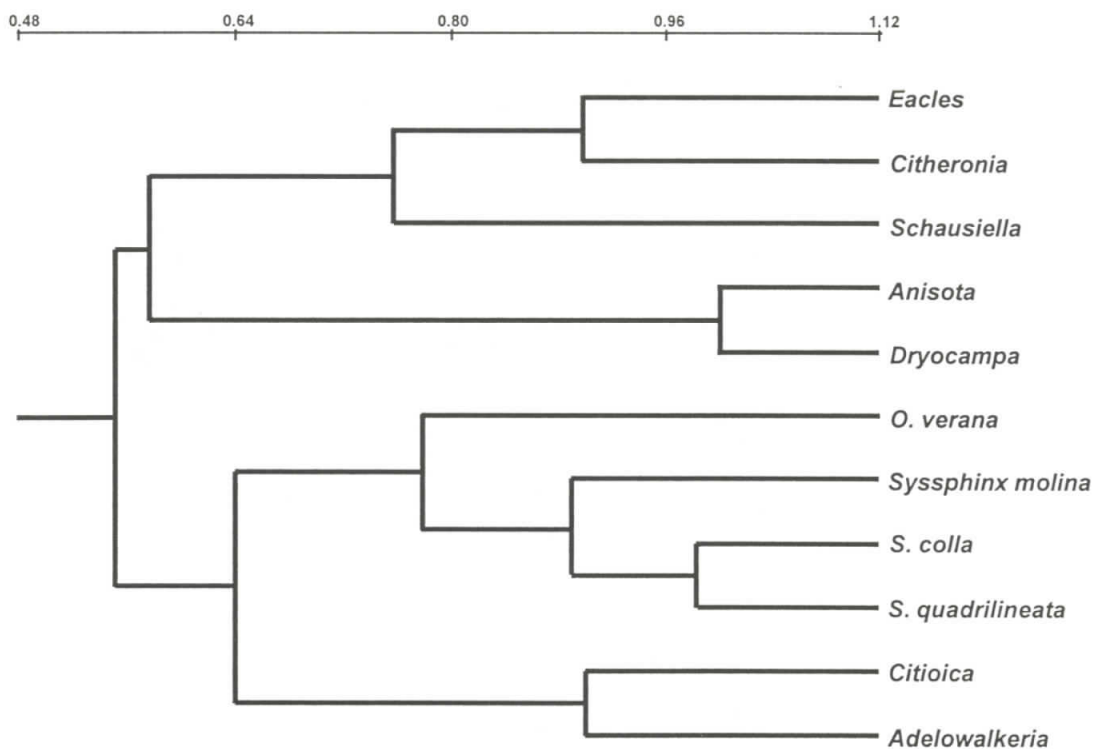


Fig. 11. Phenogram produced by UPGMA cluster analysis of 11 Ceratocampinae OTU's using 39 immature characters and Gower's coefficient of similarity ($r = 0.90673$).

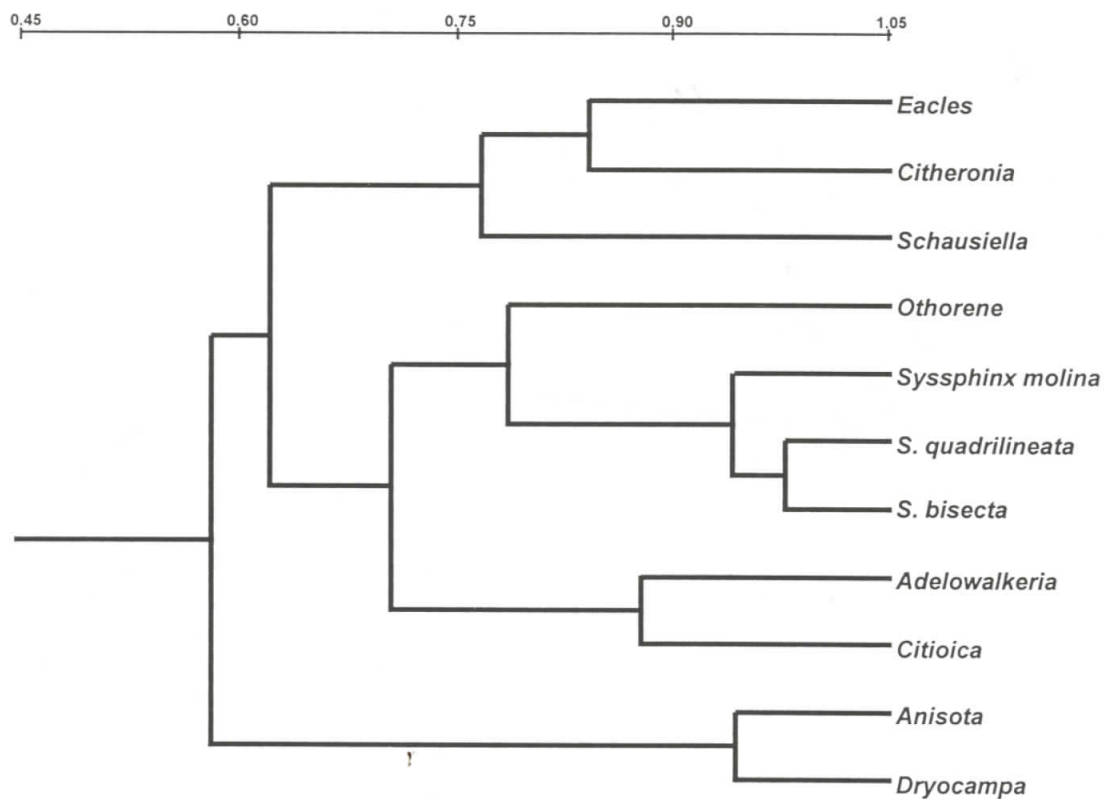
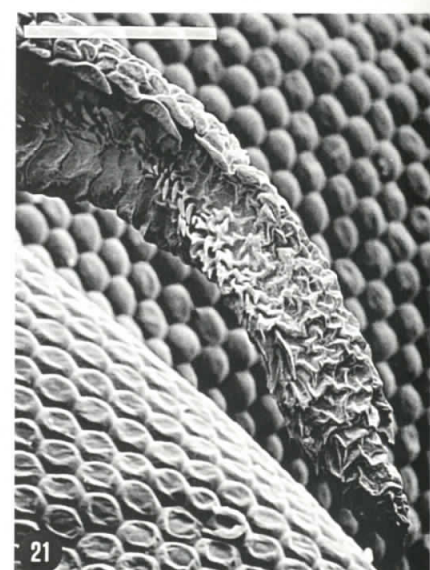
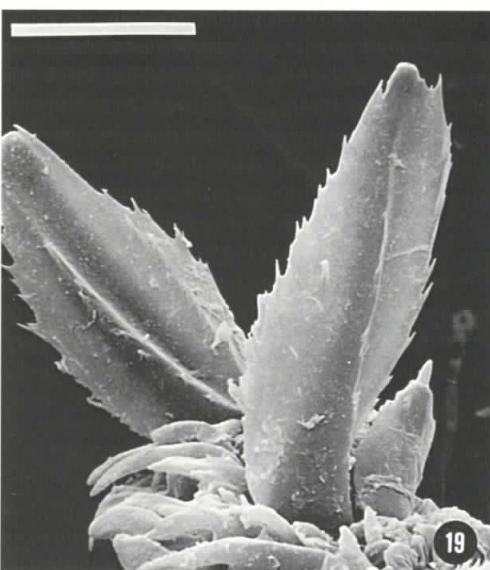
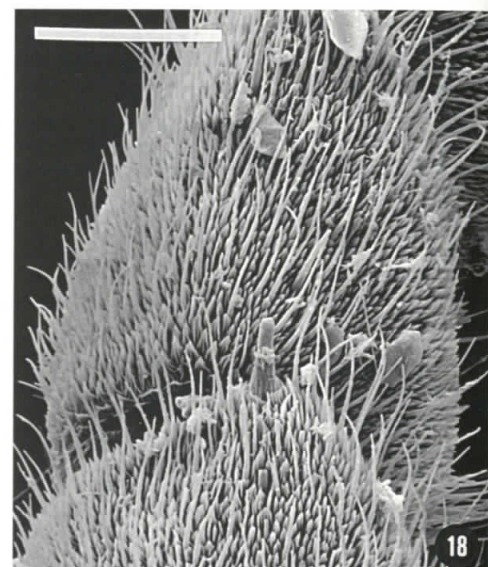
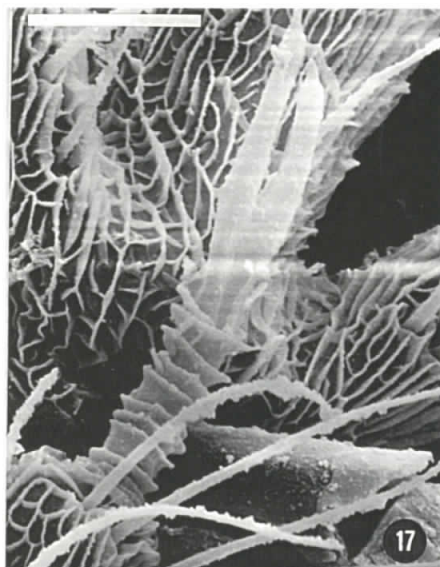
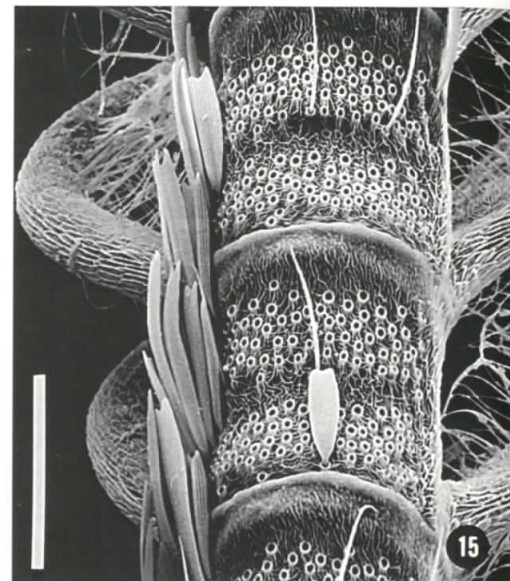


Fig. 12. UPGMA phenogram of 11 Ceratocampinae OTU's for 99 characters based on adult and larval morphology and Gower's similarity coefficient of similarity ($r = 0.90673$).



has quadridentate antennae ("0"), a common state found in Arsenurinae, but *Arsenura* shows both states ("0", "1"). Finally, the Oxyteninae have bipectinate antennae ("2") (Fig. 15).

Character 4. Pectination reach in male antennae.

In the outgroup the antennae are pectinate to the apex ("0"). But typically, the Ceratocampinae have antennae with proximal half to three-fifths of flagellum pectinate ("1") (Fig. 16). The only exceptions are *Bathyphebia* and *Procitheronia*. In *Bathyphebia*, the antennae of the male are quadripectinate to the apex, while in *Procitheronia* the antennae are quadripectinate on the basal three-fifths of the flagellum, then successively quadridentate and simple to the apex. Michener (1952) considered "flagellum of male narrowly quadripectinate to apex" as the plesiomorphic character and "flagellum broadly quadripectinate to apex" as the apomorphic state.

Character 5. Rami size of male.

We recognized three character states: (a) short (largest rami 1 to 2.5 times longer than segment length ["0"]), (b) medium sized (largest rami from 2.6 to 3 times longer than segment length ["1"]) and (c) large (3.1 or more times longer than segment length ["2"]). The Arsenurinae show the first character state, as well as *Eacles*, *Bathyphebia*, *Citheronia*, *Procitheronia* and *Neorcanegia*. Most of the rest of Ceratocampinae have medium sized rami, and only *Cicia*, *Almeidella*, *Psilopygida*, *Dryocampa* and the *Syssphinx bicolor* and *S. amena* groups have large rami.

Character 6. Basal rami distinctly longer than apical rami.

Only in *Bathyphebia*, *Othorene*, *Cicia*, *Dacunju* and *Ceropoda*, are the basal rami clearly longer than the apical rami ("0"). In the rest of the subfamily, the basal rami and apical rami are subequal ("1").

Character 7. Antennal cones simple.

All the taxa studied possess simple antennal cones, that is single, laterally compressed projections at the apices of the ventral surfaces of the antennal segments (Fig. 18). At least in *Oxytenis modestia* Cramer, we found a different type of antennal cone, which is forked at its apex (Fig. 17). Regardless of this different shape, we scored this state as "0". The alternative state is found in some Arsenurinae, Saturniinae and the genus *Goodia* of the Ludiinae which have multiple separate projections arising from a more or less broadly produced region at the lower apex of the antennal segments referred as to multiple antennal cones ("1") (Michener, 1952). Michener (1952) considered as specialized the multiple antennal cones condition.

Character 8. Antennal cones absent on the pectinate portion of antennae.

This is the common state in the Ceratocampinae ("0"), with the only exception in *Adeloneivaia*. In this genus, there is almost always a ventral cone on each segment. In the Arsenurinae, the cones are present only in the distal half of the antenna, but as in this subfamily the antennae are pectinate to the apices ("1"). Michener (1952) considered the state "cones recognizable to base of flagellum" as apomorphic.

Character 9. Non-pectinate portion of shaft of antenna compressed to strongly compressed.

In all the ingroup taxa, the antennae are somewhat compressed at the level of the non-pectinate region of the antennae. We scored as "1" the

condition found in *Othorene*, *Cicia*, *Dacunju*, and *Giacomellia*, where this region of the antennae is only slightly compressed. A score of "0" was given to the rest of the taxa, showing a strong compression.

Character 10. Pectination of female antennae.

While the majority of the female Ceratocampinae exhibit simple antennae (scored as "0"), three other character states are found. *Bathyphebia* and *Procitheronia*, and some Arsenurinae show a quadridentate state ("1"). The quadripectinate condition is found in *Othorene*, *Cicia*, *Dacunju*, *Ceropoda*, and *Adeloneivaia* ("2"). Finally, the females of *Oxytenis* have bipectinate antennae ("3").

Character 11. Dorsal bristles of non-pectinate region of antennae.

Although conspicuous in many cases, the dorsal bristles of this region of the antennae are sometimes inconspicuous but present. We decided to score this character states in the following way: (a) conspicuous, or with one or more inconspicuous but definitively present ("0"), and (b) apparently absent ("1").

Character 12. Size of clypeus.

The outgroup and the ingroup have a clypeus that is three to five times as wide as long ("0"). Only *Anisota* and *Dryocampa* have a clypeus represented by a mere rim beneath the frontal protuberance ("1").

Character 13. Scales of clypeus.

Following Michener (1952), we recognized two different states regarding the scales on the clypeus. Many taxa in the ingroup present characteristic "erect" scales on the clypeus (Michener, 1952) ("0"). The outgroup and many taxa of the ingroup lack such scales, thus the absence is considered as the plesiomorphic state ("1").

Character 14. Clypeus projection.

In the genera *Almeidella* and *Adeloneivaia*, the clypeus is produced medially as the frontal protuberance ("0"). According to our findings, this state has evolved separately.

Character 15. Separation of clypeus from frons.

We coded three states for this character: (a) clypeus separated from frons by a distinct line ("0") (Fig. 14), (b) separated from frons by a scant line ("1") (Fig. 13), and (c) separated from frons by a strong groove ("2"). Only *Psilopygoides* was coded as having a strong groove. The state in which the clypeus is indistinguishably fused to the frons is the apomorphic one (Michener, 1952).

Character 16. Clypeofrons convex laterally.

In the subfamily Ceratocampinae, the frons is strongly convex laterally, adjacent to the eyes ("0"). A similar condition is found in the tribe Attacini (Saturniinae) (Arora and Gupta, 1979; Peigler, 1989; Michener, 1952: fig. 2). A frons convex at sides, next to eyes, is apomorphic according to Michener (1952) ("1").

Character 17. Pilifers with setae.

The pilifers are a pair of lateral lobes of the labrum that usually bear setae. They are found in several groups of Lepidoptera. According to Michener (1952), setae on the pilifers are present in *Janioides* (Cercophaninae), but are absent in the other Cercophaninae and Oxyteninae. They are present in all the members of the Arsenurinae ("0"), and completely absent in Ceratocampinae and the rest of the Saturniidae ("1"). According to Michener (1952), in its "primitive" state the pilifers are conspicuous and bear bristles.

Character 18. Pilifers convex.

The outgroup and the genera *Eacles*, *Bathyphebia*, *Citheronia* and *Procitheronia* exhibit pilifers that range from little to distinctly convex ("0"). The remaining genera have pilifers that are not projecting ("1").

Character 19. Mandibular rudiments large and protuberant.

This state is found in the outgroup and *Eacles*, *Bathyphebia*, *Citheronia*, *Procitheronia*, *Schausiella* and *Neorcanegia* ("0") (Fig. 14); in other taxa they are low and inconspicuous ("1"). A special state was found in *Almeidella* which shows small but strongly convex and high mandibular rudiments ("2").

Fig. 13-21. Head morphology (line lengths after each figure description): 13) Head of adult male *Oxytenis modestia* (Cramer) in ventral view. Left galea and labial palpus removed (0.5mm). 14) Head of adult male *Eacles imperialis* (Drury) in ventral view. Left galea and labial palpus removed (0.75mm). 15) Male antenna of *Oxytenis modestia* (Cramer), dorsal view near antennal midpoint (86µm). 16) Male antenna of *Adeloneivaia flavosignata* (Walker), dorsal view near antennal midpoint (0.75mm). 17) Male antenna of *Oxytenis modestia* (Cramer), ventral view showing antennal cone (30µm). 18) Male antenna of *Adeloneivaia flavosignata* (Walker), ventral view of terminal segments showing antennal cone (0.86µm). 19) Sensilla on the distal portion of the adult proboscis of *Oxytenis modestia* (Cramer) (43µm). 20) Sensilla on the distal portion of the adult proboscis of *Eacles imperialis* (Drury) (60µm). 21) Sensilla on the distal portion of the adult proboscis of *Adeloneivaia flavosignata* (Walker) (120µm).

Character 20. Proboscical fossa longer than broad.

There is a lot of variation in the shape and depth of the proboscical fossa, but we found it very difficult to code the variation. A finer study with SEM should prove very useful to find new characters. A clearly different character state was found in the *Anisota* and *Dryocampa*: fossa wider than long ("1").

Character 21. Walls of proboscical fossa.

Three character states were observed regarding the walls of the fossa: (a) walls subvertical ("0"), *Eacles*, *Bathyphebia*, *Psilopygoides*, *Psilopygida*, and *Adeloneivaia*, exhibit the state; (b) walls vertical ("1"), shared by the majority of the taxa in the outgroup and ingroup; and (c) walls slanting ("2"), found only in *Anisota* and *Dryocampa*. A deep fossa with vertical walls was considered by Michener (1952) the "primitive" character state.

Character 22. Relation of the maxillary stipites to the walls of fossa.

The stipites can be free from or in contact with the walls of fossa. Sometimes it is very difficult to separate the two conditions so we decided to code them as "0" (Michener, 1952: fig. 3). The other character state is stipites included in the walls ("1"). The latter state is found in *Othorene*, *Cicia*, *Dacunju*, *Giacomellia*, *Ceropoda* and *Syssphinx*.

Character 23. Maxillary stipites extending backward to posterior margins of sockets of labial palpi.

This character state is found exclusively in *Psilopygida*, *Anisota* and *Dryocampa* ("2"). A different state was coded for *Schausiella* ("1"): posterior ends of stipites not reaching palpal sockets. The most common condition in the taxa studied was that of stipites extending backward to or slightly behind anterior margins of palpal sockets ("0") (Michener, 1952: fig. 3).

Character 24. Galea size.

The galea in the Oxyteninae is large (Jordan, 1924; Michener, 1952) (Fig. 13). In the Arsenurinae, some taxa have large galea, but even in the same genus some taxa have it reduced: the same is found in *Eacles* (Fig. 14). Taxa having galea as long as the fossa or longer were scored as "1" and those with a shorter galea as "0". A rather long and curled galea was considered by Michener (1952) as the plesiomorphic state.

Character 25. Galeae curled.

In most moths, the elongated galeae are coiled when not in use ("0"). In Oxyteninae (Fig. 13), in the Arsenurinae with large galeae and most Ceratocampinae, the galeae are curled which could be interpreted as if these two characters (large galea and curling) were correlated ("1"). In *Syssphinx*, the galea are not curled although they are large.

Character 26. Sensillae of galeae.

Oxyteninae and the Arsenurinae with long galeae bear conspicuous sensillae on the galeae ("1") (Fig. 19). The Ceratocampinae, on the other hand, lack any conspicuous sensillae ("0") (Fig. 20 and Fig. 21). Michener (1952) considered a "galea without papillae" as the apomorphic state.

Character 27. Size of labial sclerite.

Anisota and *Dryocampa* exhibit a very small labial sclerite. No such reduction was found in any other taxa studied.

Character 28. Labial palpi arising very close to one another.

This character is found only in *Anisota* and *Dryocampa*. In these genera, the labial palpi originated very close. We scored this state as "0".

Character 29. Labial palpi extending well in front of frontal protuberance.

This state is considered as plesiomorphic, because it is found in the outgroup. *Eacles*, *Bathyphebia*, *Citheronia*, *Procitheronia* and *Schausiella*, bear palps that extend well in front of the frontal protuberance ("0") (Fig. 14). In *Anisota* and *Dryocampa*, the palps reach a point slightly in front of the frontal protuberance ("0"). All other taxa have labial palpi reaching forward to clypeus, or very short ("1"). The long condition was scored as the primitive state by Michener (1952).

Character 30. Labial palpi segmentation.

The outgroups have three-segmented labial palpi; this is regarded as the plesiomorphic state (Fig. 22). A reduction in the number of segments is found in most taxa. Genera having two-segmented palpi constitute the majority ("1") (Fig. 23). A third character state is present in *Cicia*, *Dacunju*, *Ceropoda*, *Scolesa* and *Neorcarnegia*, that have only one segment. The reduction in number of palpal segments is apomorphic (Michener, 1952).

THORAX**Character 31. Shape of the anepisternal suture.**

Michener (1952) stated that the size of the anepisternum and the direction of the anepisternal suture provide characters of considerable importance in Saturniidae. In a great many moths, the anepisternal suture is directed somewhat downward posteriorly, reaching the pleural suture at or below the lower end of the deeply impressed portion of the latter so that the anepisternum is large. In the Oxyteninae and Arsenurinae, the anepisternal suture reaches the pleural suture at a very short distance below the lower end of the deeply impressed portion of the latter. In the Ceratocampinae this state is found only in *Schausiella*, *Psilopygoides* and *Neorcarnegia* ("1") (Michener, 1952: fig. 33). The second state, anepisternal suture reaching the pleural suture well below the lower end of the deeply impressed portion of the latter, is shared by the rest of the ingroup ("0") (Michener, 1952: fig. 8).

Character 32. Deeply impressed portion of pleural suture at an angle of about 160 degrees to straight lower portion.

This condition is found in *Eacles*, *Bathyphebia*, *Neorcarnegia*, *Anisota* and *Dryocampa* ("1") (Michener, 1952: fig. 8). The state of deeply impressed portion of pleural suture directed in about the same direction as lower straight ("0") (Michener, 1952: fig. 33).

Character 33. Curved portion intervening between deeply impressed portion and lower portion of pleural suture inconspicuous.

Only *Bathyphebia* and *Neorcarnegia* exhibit this trait ("0"). In the rest of the taxa the portion intervening between the two regions of the pleural suture is conspicuous ("1").

Character 34. Epiphysis of male very large, reaching to apical third of tibia or beyond.

This is the common state for most Ceratocampinae, and for the two Arsenurinae used as outgroups ("1"). *Oxytenis*, *Eacles*, *Bathyphebia*, *Schausiella*, and *Neorcarnegia* always bear epiphysis that reach slightly beyond the middle of the tibia ("0"): this character is variable in *Anisota*.

Character 35. Fore tibia without an apical spine.

Although ordinarily without apical spines ("0"), the fore tibiae in some taxa are provided with one or more long apical spines ("1"). The latter is the case in *Giacomellia*, *Ceropoda*, and *Ceratesa*. In *Anisota* they may be present or absent. Michener (1952) argued that this character is of little or no phylogenetic significance, as it occurs in unrelated groups of the family. He hypothesized that the presence of spines could be related to some habit of the adults such as digging out of the ground in those groups that pupate beneath the surface (*i.e.* in Ceratocampinae).

Character 36. Tibial spurs.

In the Lepidoptera, the midtibia usually carries an apical pair of spurs, and the hind tibia a median and an apical pair of similar spurs (Common, 1990). In the Saturniidae these spurs have bare apices which are ordinarily flat or concave on one side, the resulting margins being toothed or serrated in most cases (Michener, 1952). In the Ceratocampinae the spurs are short, the subapical ones of the posterior tibiae are absent, and the serrated portion is usually short. Two states involving this trait can be differentiated in this subfamily and in the outgroup: (a) with apical halves concave on one side ("0") and (b) only apical third or less hooked and concave on one side ("1"). Michener (1952) suggested that the first state is the apomorphic one.

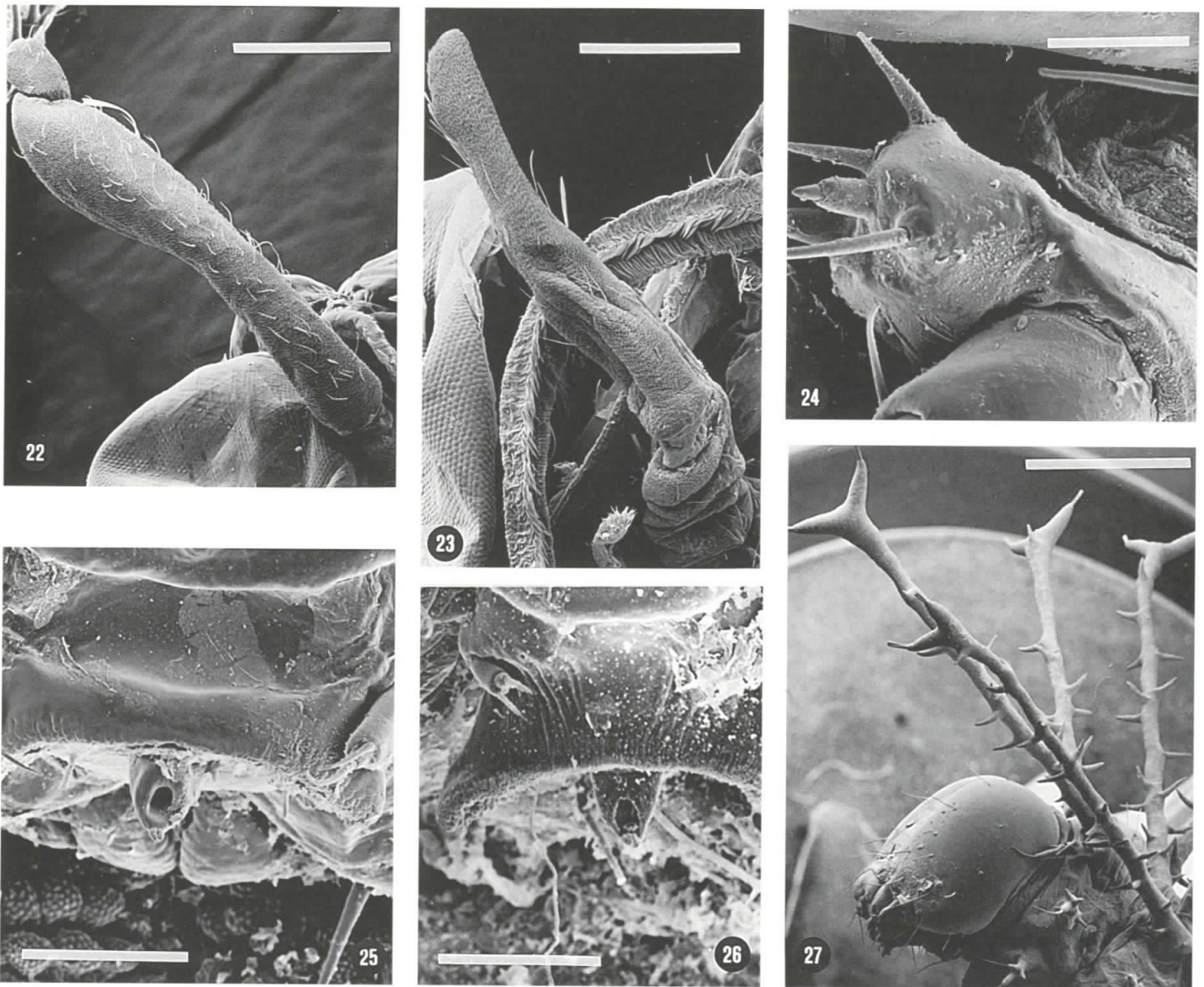


Fig. 22-27. Adult and larval head morphology (line lengths after each figure description): 22) Labial palpus of adult *Oxytenis modestia* (Cramer) (0.75mm). 23) Labial palpus of adult *Eacles imperialis* (Drury) (0.75mm). 24) Left maxillary palpus of first instar larva of *Eacles ormondei* Scha. Dorsoposterior view (20µm). 25) Labial complex of *Eacles ormondei* Scha (80µm). 26) Labial complex of *Othorene hodeva* (Druce) ? (80µm). 27) Head and first thoracic segments of first instar larva of *Eacles ormondei* Scha (1.4mm).

Character 37. Forewing torni shape.

We recognized three states concerning the shape of the torni. In the outgroups and *Syssphinx*, *Cicia*, *Dacunju*, *Giacomellia*, and *Ceropoda* the torni are only somewhat conspicuous ("1") (Lemaire, 1987: fig. 143, 157), while in genera such as *Eacles*, *Neorcarnegia*, and *Citheronia* among others, the torni are clearly defined ("0") (Lemaire, 1987: fig. 3); furthermore, in some other taxa, the torni are quasi-elliptical ("2") (Lemaire, 1987: fig. 185).

Character 38. Eye spots absent.

Many Saturniidae are easily recognized by the presence of characteristic eye-spots on the wings. Blest (1957a, b) and more recently, Qberprieler and Nässig (1994) have discussed the significance of these color patterns in the family. Michener (1952) and Lemaire (1988) showed that in most species of Ceratocampinae, the habitus is reduced to the ante- and postmedian lines and discal spots, and that the eye-spots are normally absent ("0"). Only *Eacles* and *Bathyphebia* have eye-spots

("1"). This type of eye-spot is found only in these genera and is thus considered a synapomorphy.

Character 39. Shape of the torni of the hind wings.

In most Arsenurinae, and in *Neorcarnegia*, the hind wing torni are clearly produced ("2") (Lemaire, 1987: fig. 376). *Anisota*, *Dryocampa*, *Adelowalkeria*, *Megaceresa*, *Rachesa* and *Ptiloscola*, exhibit hindwings provided with somewhat produced torni ("1") (Lemaire, 1987: fig. 299). The most common state is torni rounded, not produced ("0") (Lemaire, 1987: fig. 332).

Character 40. Antemedial line present on the forewings.

There are different degrees in the reduction of the habitus in the Ceratocampinae, with no reduction as ("0"). In many taxa the reduction of the wing pattern involves the absence or the extreme reduction of the antemedial line ("1").

Character 41. Postmedial line on the forewings.

In the Saturniidae, there is typically a postmedial line on the fore-

wings: presence of the line ("0") is the most widespread condition in the taxa studied. In *Citheronia*, the postmedial line is replaced by a series of internervular dots, an autapomorphy for the genus ("1"). According to our cladograms, the postmedial line has disappeared independently several times ("2"). A special case is *Giacomellia*, in which there is a contrasting wide line that runs from the apex to the base ("3") (Lemaire, 1987: Plate 40, fig. 19-22): it is not clear whether this line is homologous with the postmedial in other Ceratocampinae.

Character 42. Vein R1.

The origin and relationship of R1 to the other radials is variable in Ceratocampinae. In a few cases, the R1 is stalked with the other radials ("0"), as in *Oxytenis* (Michener, 1952: fig. 38). More often, it arises from the apex of the discal cell ("1") (Michener, 1952: fig. 17), but in a few cases, such as in Arsenurinae, R1 arises before the apex of discal cell ("2") (Michener, 1952: fig. 43).

Character 43. V1 cell in the forewing open.

This small cell at the base of the forewing between the bases of veins 1V and 2V is present in most saturniids, but in the Ceratocampinae the prevailing situation is V1 cell open ("1") (Michener, 1952: Fig. 56-57). In our analysis, a closed V1 cell is plesiomorphic ("0") (Michener, 1952: Fig. 17).

ABDOMEN

Generic grouping in the Ceratocampinae has been largely based on genitalic characters (Michener, 1952; Lemaire, 1988). While the genitalia provide excellent characters to separate and diagnose genera, they are usually so specialized that it is very difficult to homologize the different regions and structures in them. It has been claimed by several authors that with few exceptions, they are of little help in establishing relationships at the suprageneric level (Holloway *et al.*, 1987; Nassig and Holloway, 1988; Nässig and Oberprieler, 1994; Oberprieler and Duke, 1994). Nevertheless, we used 13 characters from the male genitalia (44-56).

As in the case of the male genitalia, the problem with the different genitalic structures in the female involves determining homology (Klots, 1970; Miller, 1991). Although external genitalic characters are invaluable to distinguish taxa at the specific level, they are of little help at higher taxonomic levels. In view of these problems, we only used two characters of the female genitalia (characters 57-58).

Character 44. Ninth tergum of male much longer than uncus.

The ninth tergum of the male is very variable in size in the Ceratocampinae, but in a few cases it is clearly longer than the uncus ("1") (Michener, 1952: fig. 172, 174). In both subgenera of *Psilopygida* the ninth tergum is the longest for the subfamily. *Ceratesa* has a long ninth tergum ("0") (Michener, 1952: fig. 195), but not as long as that found in *Psilopygida*.

Character 45. Uncus shape.

In the Ceratocampinae the uncus is either simple ("1") or bilobed ("0"). We found it very difficult to code this character, and we are not really sure that the states are always homologous. At least for some of the genera, the condition appeared independently, according to our cladograms.

Character 46. Gnathos absent.

The gnathos is completely absent in *Dacunju* ("0") (Lemaire, 1987: fig. 159). This is an autapomorphy for the genus in the context of the subfamily, but in various other Lepidoptera the gnathos has also disappeared.

Character 47. Gnathos forming a plate.

According to our findings, the gnathos is represented only by lateral arms in its plesiomorphic state ("2") (Michener, 1952: fig. 140). In many

taxa, the gnathos forms a ventral plate ("0") (Michener, 1952: fig. 155). Few taxa (*Ceropoda-Mielkesia* and *Citioica-Oiticella*) have a more or less intermediate state in which the gnathos is formed by two lobes not fused ("1") (Michener, 1952: fig. 169).

Character 48. Gnathos fused to transtilla.

In the literature, it is noted that the gnathos is fused to the transtilla in *Schausiella* and *Almeidella* (Lemaire, 1988) ("1") (Michener, 1952: fig. 148). We consider that although of a different nature, the "ventral plate" in *Psilopygida*, *Syssphinx*, *Anisota* and *Dryocampa* represent the fused gnathos and transtilla (Michener, 1952: fig. 155).

Character 49. Gnathos connected to the internal face of valvae by a membrane.

The genitalia of *Psilopygida*, *Syssphinx*, *Anisota* and *Dryocampa* present the peculiarity of having a gnathos connected to the internal face of the valvae by a membrane ("1") (Michener, 1952: fig. 155): this character was not found in any other taxa.

Character 50. Transtilla (Michener's gnathos) absent.

The transtilla is absent in *Ceropoda* and *Mielkesia*, and in *Adeloneivaia* and *Adelowalkeria s.l.* ("1") (Michener, 1952: fig. 169). In *Oxytenis*, the transtilla is absent too. The transtilla has disappeared independently in different clades.

Character 51. Transtilla shape.

We recognized four different states involving the shape of the transtilla. In most Ceratocampinae, the transtilla forms a plate (state "0"). Usually, the transtilla of *Othorene*, *Cicia*, *Dacunju*, and *Giacomellia* consists of a divided plate (Michener, 1952: fig. 167). In some species of *Othorene*, the transtilla is fused into a ventral plate, but there is an evident cleft followed by a groove ("1") (Michener, 1952: fig. 162). In *Arsenura*, *Dysdaemonia*, *Bathyphebia* and *Neorcarnegia*, the transtilla is represented only by lateral arms ("2") (Michener, 1952: fig. 137). We considered as a fourth state the condition found in *Psilopygida* where the transtilla forms a plate connected to the tegumen by lateral arms ("3") (Michener, 1952: fig. 172).

Character 52. Juxta absent.

Only in *Ptiloscota* is the juxta absent ("1") (Michener, 1952: fig. 204). In the context of the Ceratocampinae, the absence of the juxta is an autapomorphy for *Ptiloscota*. In other taxa of the Ceratocampinae the juxta is either free from the valvae, or partially fused to the valvae. We could not find a satisfactory way to separate the two conditions, so we considered both as state ("0") (Michener, 1952: fig. 162, 169).

Character 53. Valvae with a cleft or depressed line in the outer margin.

Michener (1952), noted that in the Oxyteninae and the more primitive members of each of the subfamilies of Saturniidae, the valvae bear a distinct notch in the outer margin which is often prolonged as a membranous line across the valvae. This condition is found in *Oxytenis*, the Arsenurinae used as the outgroup, and the basal clades of Ceratocampinae ("0") (Michener, 1952: fig. 100). In *Adelowalkeria s.l.*, there are various types of processes that may represent a modified lower lobe of the valvae ("1" should be applied, if correct) (Michener, 1952: fig. 206). However, we coded these genera with a "0", because we considered this condition not to be homologous with the condition previously mentioned. Further studies are needed to assess the real homologies of the genitalia of the Ceratocampinae and in general of all the Lepidoptera (Klots, 1970). To deal with the status of the valvae of *Adelowalkeria s.l.*, we used the character 55.

Character 54. Valvae asymmetrical.

Taxa as distantly related as *Citioica-Scolesa-Ptiloscota*, and *Schausiella* and *Cicia*, have evolved asymmetrical male genitalia ("1") (Michener, 1952: fig. 190). The asymmetry normally involves the valvae, but in *Schausiella* the uncus shows asymmetry due to the presence of a spine on one side of the uncus (Michener, 1952: fig. 148).

Character 55. Valvae with a long process arising from the middle of inner margin.

Michener (1952) hypothesized that the portion below the cleft of the valvae in some Ceratocampinae has been bent upward to form a large inner spine ("1"). In *Adelowalkeria s.l.*, this projection bends towards the base of the valvae and emerges as a free spine-like process from the base of the upper portion of the valvae (Michener, 1952: fig. 206). In our cladograms, this character is a synapomorphy for this clade.

Character 56. Valvae harpes.

Two different types of harpes are found in the Ceratocampinae: (a) long harpes are found in the *Syssphinx bisecta*, *S. quadrilineata*, *S. amena*, and *S. ocellata* groups ("2") (Michener, 1952: fig. 151); (b) small harpes are present only in *Ceropoda* and *Mielkesia* ("1") (Michener, 1952: fig. 169). Harpes are lacking in the remainder of the Ceratocampinae.

Character 57. Eighth tergum in the female.

We used four character states associated with the eighth tergum in the female: (a) scarcely bilobed ("0") (Lemaire, 1987: fig. 50), (b) with sublateral sclerotic lobes ("1") (Lemaire, 1987: fig. 64), (c) bilobed ("2") (Lemaire, 1987: fig. 136), (d) not bilobed ("3") (Lemaire, 1987: fig. 180).

Character 58. Ostium bursae opening shape.

Citheronia and *Procitheronia* are the only taxa in which the ostium bursae opening is a transverse slit ("1") (Lemaire, 1987: fig. 73). The typical shape of the ostium opening is a round hole or a longitudinal slit ("0") (Lemaire, 1987: fig. 49).

Character 59. General body shape sphingid-like.

The Ceratocampinae have long and narrow wings and a comparatively long and stout body, and the males are among the fastest-flying saturniids (Janzen, 1984).

Immature Stages

There have been relatively few studies on the larval morphology of Saturniidae. Most papers deal with non-technical descriptions. Packard (1905) illustrated several larvae of Ceratocampinae; he used numbers to identify the setae. The color plates in this paper are very helpful to identify larvae, and the line drawings are useful to compare setal positions, although sometimes abdominal segments 8-10 are confused and some setae are missing. Pease (1961) published the most comprehensive study of the first instar larvae for the family. He used Hinton's setal nomenclature (Hinton, 1946), presented a key for the taxa he studied, and illustrated the chaetotaxy and the prolegs. The only difference between his nomenclature and the one we follow (Stehr, 1987) lies in the use of the term chalaza. Pease's "scolus" and "chalaza" both correspond to "scolus" as defined by Stehr (see Oberprieler and Duke, 1994). More recently, there has been an interest in describing life cycles of Saturniidae and excellent descriptions of Ceratocampinae larvae have been published (Brenner and Lampe, 1987; Dias, 1978a, 1978b, 1981, 1982, 1986, 1991; Janzen, 1982; Riotte and Peigler, 1980; Wolfe and Peigler, 1993; Wolfe and Pescador, 1994).

Setal maps of all the genera studied are presented (Fig. 56-65). For the sake of clarity, in the setal maps the boxes representing segments were drawn separated and segment A9 contour especially was oversimplified. For the same reason, in the last abdominal segment we only indicated the setae on the anal and proleg shields.

The characters and coding used were based on the information available from the literature, and from the first instar larvae

available to us: *Oxytenis modestia* Cramer, *Eacles imperialis* (Drury), *E. ormondei* Schaus, *Citheronia regalis* (Fabricius), *C. splendens* (Druce), *Schausiella carabaya* (W. Rothschild), *Othorene verana* Schaus, *O. hodeva* (Druce) (?), *Syssphinx molina* (Cramer), *S. quadrilineata* (Grote & Robinson), *S. colla* Dyar, *Anisota virginensis* (Drury), *Dryocampa rubicunda* (Fabricius), *Adelowalkeria plateada* (Schaus) and *Citioica anthoniis* (Herrich-Schäffer). We consider all the following characters and their states tentative, and inevitably we had to extrapolate our findings based on the available larvae to the whole genus. When information suggesting variability within genera was available, we incorporated this information in the data matrix.

LARVAL HEAD

We found clues that some head characters may provide significant phylogenetic information. Relative sizes of the setae on the epicranium, relative sizes of sensilla on the maxillary palpus, and antennae deserve further study, but longer series of larvae from more taxa are necessary.

Character 60. Sensilla trichodea III (STIII) below STII dorsoposterior wall of maxillary lobe.

Grimes and Neunzig (1986b) found that the sensilla trichodea II (STII) and STIII in the maxillary lobe are morphologically related to each other, and as a rule they have the same size and shape and are very close to each other. Also, they showed that STII and STIII usually occur side by side along the dorsoposterior edge of the distal surface of the mesal lobes. As they pointed out, a curious exception to this occurs in *Anisota virginensis* (Drury) where STIII is auriculate and is located below STII on the dorsoposterior wall of the lobe ("1"). We found this state in all the ingroup (Fig. 24). In the outgroup, STIII had the normal position side by side with STII on dorsoposterior edge of the distal surface ("0").

Character 61. Spinneret compressed dorsoventrally.

This character pertains only to the outgroup. In *Oxytenis*, *Arsenura* and *Dysdaemonia* the spinneret is compressed dorsoventrally ("1"). The ingroup has the spinneret not compressed dorsoventrally ("0") (Fig. 25).

Character 62. Spinneret triangular in shape.

We noticed that only in *Othorene* (including the larva questionably identified as *O. hodeva*) is the spinneret triangular ("1") (Fig. 26). We found that other Ceratocampinae have a rounded spinneret ("0") (Fig. 25). This structure may eventually provide more characters and states as in Noctuidae (Godfrey, 1987) and Notodontidae (Miller, 1991).

Character 63. Labial palpus the same size as the first segment of the maxillary palpus.

Most taxa examined bear a labial palpus that is shorter than the first segment of the maxillary palpus ("0"). An exception to this situation was found in *Oxytenis* and *Citioica* ("1").

LARVAL THORAX**Character 64. XD almost as or as large as D and SD on T2-3.**

In *Oxytenis*, *Eacles*, *Citheronia*, *Schausiella* and *Adelowalkeria*, the scolus XD on the cervical shield is very long and rivals in size the D and SD scoli on T2-3 ("0") (Fig. 27). In the Arsenurinae of the outgroup and the remainder of Ceratocampinae, XD is shorter than D and SD on T3 ("1") (Fig. 31).

Character 65. Relative sizes of XD and SD on prothoracic shield.

Eacles, *Citheronia*, *Schausiella*, *Adelowalkeria* and *Citioica* show an XD scolus that is several times as long as SD ("0") (Fig. 27). The rest of the taxa have an XD that is subequal to SD, in *Dysdaemonia* being short ("2"); larger in the remaining genera ("1") (Fig. 28-29, 31).

Character 66. Primary setae present on D and SD scoli.

In all first instar larvae of the taxa studied, the primary setae are conspicuous on the D and SD scoli ("0") (Fig. 33). Only in *Oxytenis* are the primary setae absent on D and SD ("1").

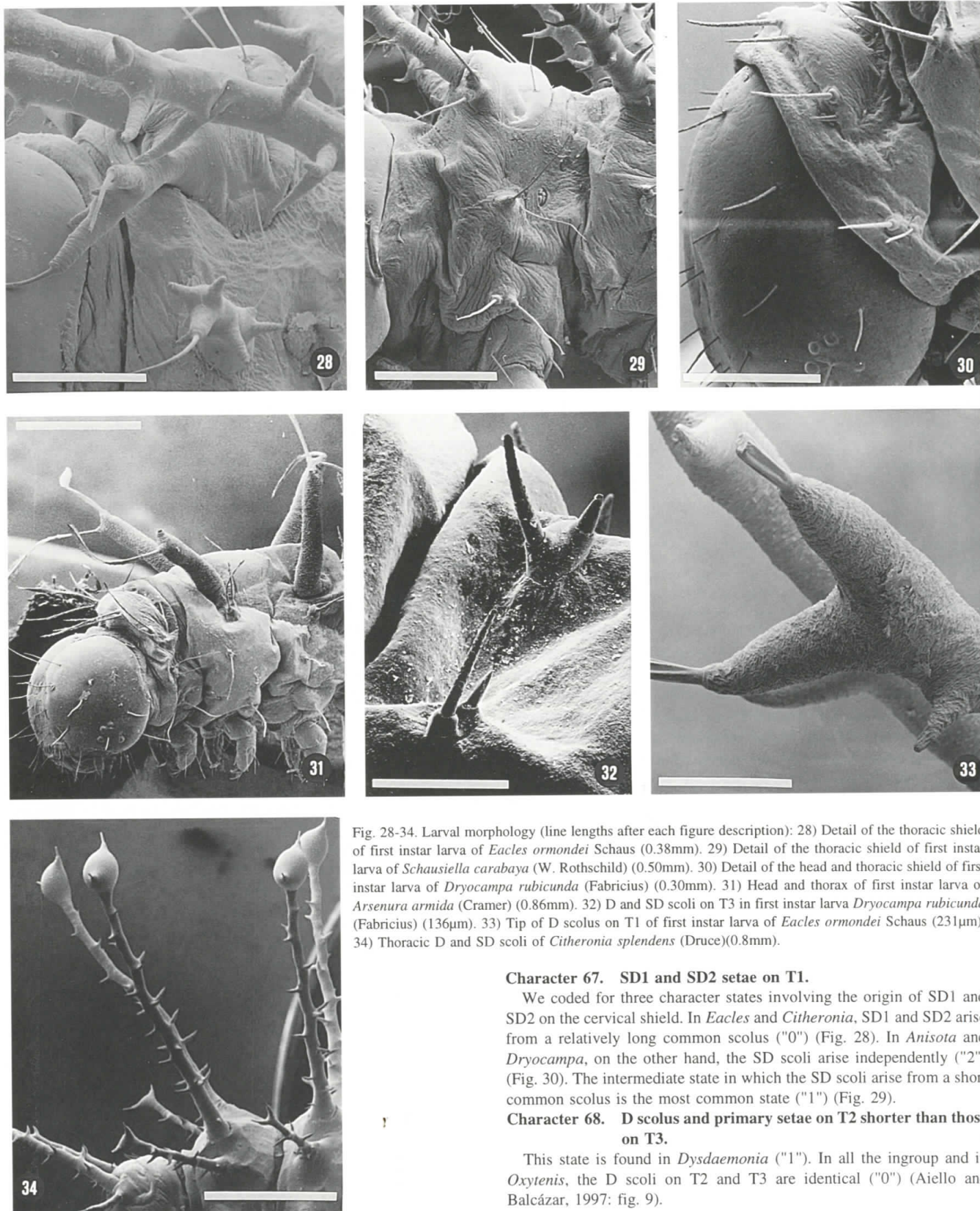


Fig. 28-34. Larval morphology (line lengths after each figure description): 28) Detail of the thoracic shield of first instar larva of *Eacles ormondei* Schaus (0.38mm). 29) Detail of the thoracic shield of first instar larva of *Schausiella carabaya* (W. Rothschild) (0.50mm). 30) Detail of the head and thoracic shield of first instar larva of *Dryocampa rubicunda* (Fabricius) (0.30mm). 31) Head and thorax of first instar larva of *Arsenura armida* (Cramer) (0.86mm). 32) D and SD scoli on T3 in first instar larva *Dryocampa rubicunda* (Fabricius) (136µm). 33) Tip of D scolus on T1 of first instar larva of *Eacles ormondei* Schaus (231µm). 34) Thoracic D and SD scoli of *Citheronia splendens* (Druce) (0.8mm).

Character 67. SD1 and SD2 setae on T1.

We coded for three character states involving the origin of SD1 and SD2 on the cervical shield. In *Eacles* and *Citheronia*, SD1 and SD2 arise from a relatively long common scolus ("0") (Fig. 28). In *Anisota* and *Dryocampa*, on the other hand, the SD scoli arise independently ("2") (Fig. 30). The intermediate state in which the SD scoli arise from a short common scolus is the most common state ("1") (Fig. 29).

Character 68. D scolus and primary setae on T2 shorter than those on T3.

This state is found in *Dysdaemonia* ("1"). In all the ingroup and in *Oxytenis*, the D scoli on T2 and T3 are identical ("0") (Aiello and Balcázar, 1997: fig. 9).

Character 69. L scolus on T1 with 1 to 3 secondary setae.

Pease (1961) noted that in *Eacles*, the L scolus on T1 bears secondary setae ("0") (Fig. 56). This condition was not found anywhere else.

Character 70. D1 and SD scoli and setae on T3 different.

In *Anisota* and *Dryocampa*, these scoli are different in shape ("1") (Fig. 32), while the widespread situation in other taxa studied is that D1 and SD are identical on T3 ("0") (Fig. 31). The condition in *Arsenura*, with scoli with different shapes, was not considered homologous with that of *Anisota-Dryocampa*.

Character 71. D and SD scoli on T3 with spines.

This state is missing in *Anisota-Dryocampa*, and *Adelowalkeria-Citioica* of the ingroup, and in the outgroup ("1") (Fig. 32). Other taxa have strong spines on most D and SD scoli ("0") (Fig. 29, 34).

Character 72. Shape of tip of D scolus on T3.

There are several obvious variations of the shape of the apical region of the D and usually SD scoli on T3, but the coding of this character posed many difficulties due to the lack of larger series of larvae to examine. We were hesitant to code 9 states for only 14 taxa. All the taxa in the outgroup were scored with different values. The first instar larva of *Oxytenis modestia* (Aiello and Balcázar, 1997) has very peculiar D and SD scoli, and could represent an autapomorphy for the subfamily. These scoli are long with a smooth spherical tip (even at very high magnifications), and bear no trace of the primary setae ("0") (Aiello and Balcázar, 1997: fig. 14). In *Arsenura armida* the D scolus on T3 is a mid-sized projection not clearly tapering to its tip, and is only very slightly bifurcated with two serrated setae at each tip ("7") (Fig. 31). The D scolus of *Dysdaemonia boreas* is very long and bears at its tip two globose structures covered with small spines ("4") (Fig. 40). *Eacles* has long D and SD scoli on T3 with bifid tips that are not swollen at all ("5") (Fig. 33). In *Schausiella* the tip of these scoli are not swollen either, but they are slightly bifid and closely associated with long spines ("8") (Fig. 35). *Citheronia*, *Procitheronia* (Dias, 1991) and *Othorene* have long scoli swollen at the tip ("3") (Fig. 34, 36), but this region is not really rounded as it is in *Syssphinx* ("1") (Fig. 37). We scored these tips of the D scolus as two states. In *Citioica* and *Adelowalkeria* the D scolus is little swollen, and more triangular in profile than in any of the other taxa studied ("2") (Fig. 39). Finally, in *Anisota* and *Dryocampa* the D scolus of this segment is very short, and bears two strong spines one of which is longer than the scolus itself ("6") (Fig. 38).

Character 73. Shape of primary setae on largest D and SD scoli on T2-3.

In general, the dominant largest scoli all carry the same type of primary setae on all segments where they are present but we restricted this state to the largest scoli on T2-3. These setae are absent in *Oxytenis*; in *Arsenura*, they are flattened and serrate ("3") (Fig. 31), and in the other outgroup, *Dysdaemonia*, they are flattened but not serrate ("2"). Two character states were identified in the ingroup: peg-like ("0") (Fig. 36-37, 39), the most widespread state; and bristlelike ("1") found in *Schausiella*, *Anisota* and *Dryocampa* (Fig. 35).

Character 74. Primary setae on D and SD scoli on T3 parallel to each other.

In *Syssphinx*, the peg-like primary setae on the D and SD scoli are situated parallel to each other ("0") (Fig. 37). In the rest of the taxa studied, they are widely divergent forming acute or obtuse angles ("1") (Fig. 35-36, 38-39).

Character 75. Surface of D and SD scoli on T3.

Five different stages involving the vestiture of these scoli were recognized. In *Syssphinx quadrilineata* and *S. colla* (*S. bisecta* group), we scored this character as pubescent ("2") (Fig. 37). In the case of *Syssphinx molina* and *Othorene*, we considered that the scoli were puberulous ("3") (Fig. 36). *Adelowalkeria* and *Citioica* show pilose scoli ("1") (Fig. 39); in *Oxytenis* and *Dysdaemonia* they are muricate ("4") (Fig. 40). The rest of the taxa were scored as glabrous ("0"). It is not

clear whether the hairs and cuticular projections are homologous with the spines found in some taxa.

Character 76. Shape of tarsal setae 1 and 3.

Beck (1960) proposed a numbering system for tarsal setae in Noctuidae, and Godfrey (1980) and Miller (1991) used Beck's nomenclature to refer to tarsal setae characters in Noctuidae and Notodontidae, respectively. In *Oxytenis* and *Arsenura*, the tarsal setae (TS) 1 and 3 are lanceolate ("1") (Aiello and Balcázar, 1997: fig. 13), while in the other taxa they are aciculate ("0") (Fig. 41).

Character 77. Relative sizes of tarsal setae.

We found three states regarding the relative size of the tarsal setae. In most taxa, there are no evident differences in the size of these setae ("0"); in *Oxytenis* and *Dysdaemonia*, TS2 appears larger than TS1 and TS3 ("1") (Aiello and Balcázar, 1997: fig. 13); and in *Citioica* TS1 seems shorter than TS2 and TS3 ("2") (Fig. 42). More specimens are needed to better score this character.

LARVAL ABDOMEN**Character 78. SV on A1-2.**

In *Schausiella*, *Othorene*, *Syssphinx*, *Adelowalkeria* and *Citioica*, the subventral group has two setae ("1") (Fig. 58-65). The other taxa have only one subventral seta ("0") (Fig. 56-57, 63).

Character 79. Primary setae on D scolus on A1-8.

Four types of setae are found on the dorsal scoli on the abdomen (A1-8). We coded as aciculate the type found in *Eacles* and *Citheronia* ("0") (Fig. 43). The type found in *Anisota* and *Dryocampa* is aciculate but short and was scored as another state ("3") (Fig. 45). The most widespread is the bristle-like type ("1") (Fig. 44). A flattened, serrate type is found in some *Arsenurinae* such as *Copiopteryx* and *Arsenura* ("2").

Character 80. Setae on D scolus on abdomen barbate.

In addition to the primary setae shape, we found that the surface of the setae can be either smooth ("0") or barbate ("1"). The latter state is found in *Syssphinx*, *Adelowalkeria* and *Citioica* (Fig. 46).

Character 81. Surface of D scolus on abdomen.

Often, the surface of the D scoli on the abdomen is glabrous and does not show any special formations on the surface ("2"). In *Adelowalkeria* and *Citioica* these scoli are pilose ("1") (Fig. 47). In *Syssphinx quadrilineata* and *S. colla* these scoli are muricate ("3") (Fig. 46), while in *S. molina* they are squamose ("0") (Fig. 48). A fourth state is found in *Oxytenis* and *Dysdaemonia* where the D scolus is finely spinose ("4") (Fig. 49).

Character 82. Spines on D1, SD and L scoli of A1-7.

In most of the taxa studied the longest scoli on A1-7 lack spines ("2") (Fig. 47). *Syssphinx quadrilineata* and *S. colla* have spines, but only at the base of the scoli ("0") (Fig. 46). On the other hand, *Eacles*, *Citheronia*, *Schausiella* and *Othorene* have spines along the entire length of the scoli ("1") (Fig. 43): this character was used by Pease (1961) in his key.

Character 83. Origin of seta L2 on A8.

In the outgroup and *Eacles*, L2 projects caudad from the base of L scolus ("0") (Fig. 56) (Pease, 1961). L2 at top of the L scolus is the normal situation found in most taxa ("1") (Fig. 58), excepting *Adelowalkeria* and *Citioica*, where L2 is missing ("2") (Fig. 64-65).

Character 84. Number of crochets.

Pease (1961), considered that the number of crochets could be related to the size of the larvae. We found that while there is some correlation between these variables, it is not always so. In the taxa studied the range was from 6 in *Oxytenis* to 32 in *Schausiella* (Fig. 50). Most taxa examined had between 13 and 18 crochets. Three states were coded: (a) few crochets (only *Oxytenis*) ("0"); (b) intermediate number of crochets (13-18) ("1"), and (c) many crochets (22 or more) ("2"). The last state is found in *Eacles* (22 crochets), *Citheronia* (25) and *Schausiella* (32).

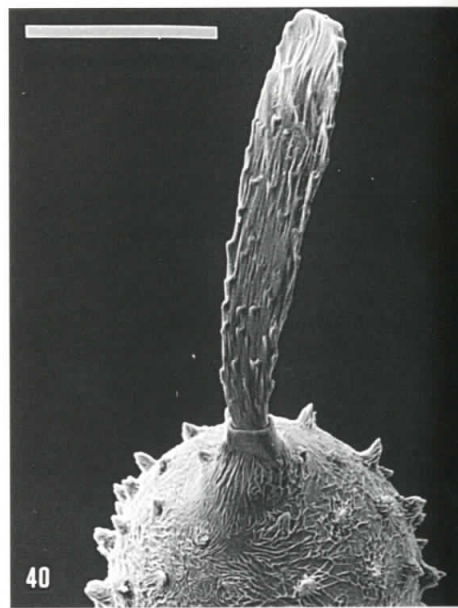
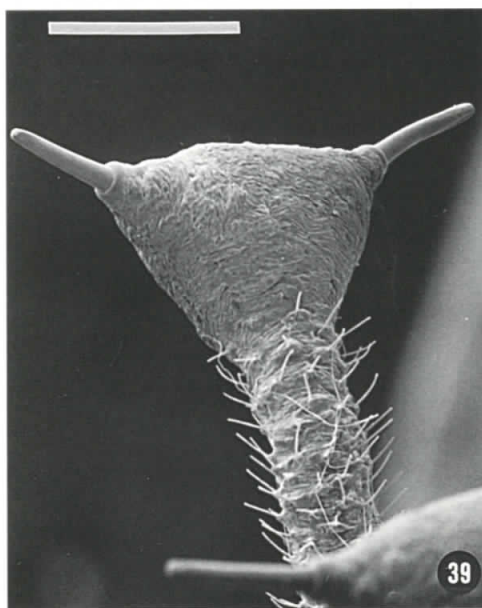
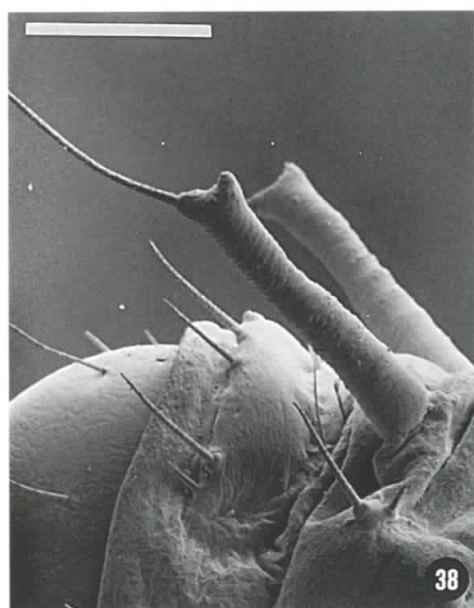
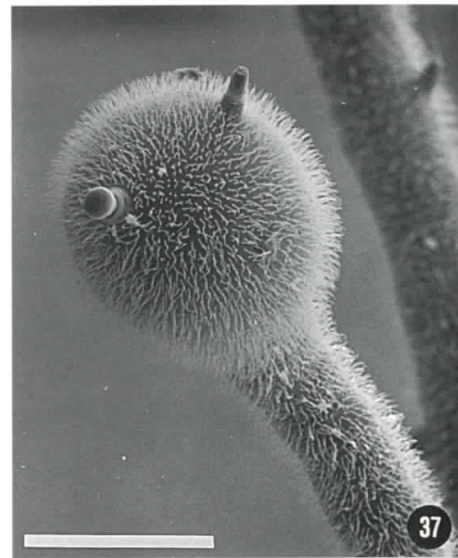
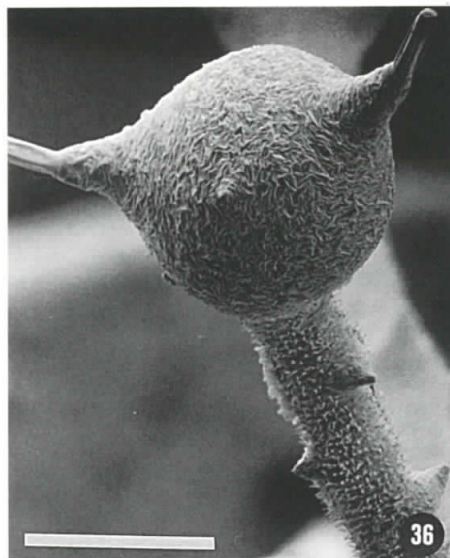


Fig. 35-43. Larval morphology (line lengths after each figure description): 35) Thoracic D and SD scoli of *Schausiella carabaya* (W. Rothschild) (0.56mm). 36) Tip of D sculus on T1 of first instar larva of *Othorene verana* Schaus (250 μ m). 37) Tip of D sculus on T1 of first instar larva of *Syssphinx colla* Dyar (190 μ m). 38) Detail of T1-2 of *Dryocampa rubicunda* (Fabricius) (0.30mm). 39) Tip of D sculus on T1 of first instar larva of *Citioica anthonilis* (Herrich-Schäffer) (250 μ m). 40) Tip of D sculus on T1 of first instar larva of *Dysdaemonia boreas* (Cramer) (150 μ m). 41) Right pretarsus of mesothoracic larval leg of *Schausiella carabaya* (W. Rothschild). 42) Right pretarsus of mesothoracic larval leg of *Citioica anthonilis* (Herrich-Schäffer). 43) D sculus on A3 of *Eacles ormondei* Schaus (0.38mm).

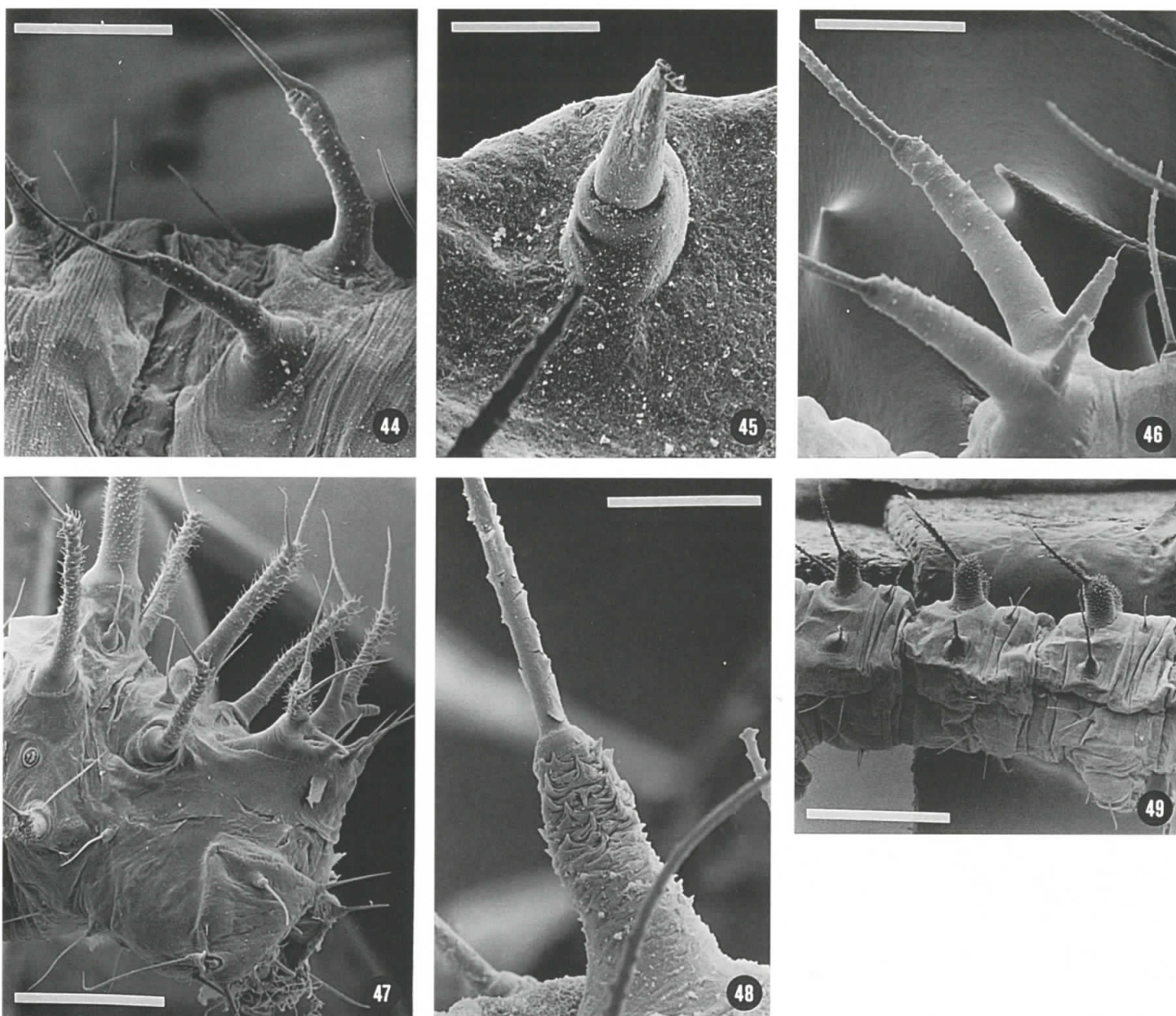


Fig. 44-49. Larval morphology (line lengths after each figure description): 44) D sculus on A3 of *Othorene hodeva* (Druce) ? (0.25mm.) 45) D sculus on A3 of first instar larva of *Dryocampa rubicunda* (Fabricius) (0.12mm). 46) D sculus on A3 of first instar larva of *Syssphinx colla* Dyar (0.26mm). 47) Lateral view of last abdominal segments of first instar larva of *Citioica anthoniis* (Herrich-Schäffer) (0.60mm). 48) D sculus on A3 of first instar larva of *Syssphinx molina* (Cramer) (0.33mm). 49) Lateral view of segments A1-3 of first instar larva of *Dysdaemonia boreas* (Cramer) (0.86mm).

Character 85. Crochets deeply set in the spatula on the proleg.

Only in the Arsenurinae of the outgroup are they deeply set in the spatula on the proleg ("0") (Fig. 52). In *Oxytenis* and the ingroup they are not deeply set in the spatula on the proleg ("1") (Fig. 50-51).

Character 86. Crochet remnants of an outer row present on some specimens.

In *Oxytenis*, *Eacles*, *Citheronia* and *Schausiella*, there is an "extra" row of small crochets ("0") (Aiello and Balcázar, 1997: fig. 15); see also Fig. 50. Pease (1961) stated that this "extra" row is not always present in *Eacles*.

Character 87. Prolegs with a fleshy lobe that gives the crochets a more or less C-shaped pattern.

This condition is found in *Oxytenis* and all the ingroup ("0"), only in *Arsenura* and *Dysdaemonia* do the prolegs lack the fleshy lobe and the middle crochets appear of similar size to those on the sides ("1").

Character 88. D scoli on A8 fused on dorsomeson.

This character has often been cited as a synapomorphy for the Saturniidae (Nässig, 1994) ("0"). In the Ceratocampinae, only *Anisota* and *Dryocampa* have the D scoli on A8 separated on the dorsomeson ("1").

Character 89. Shape of middorsal sculus on A8.

In *Eacles* and *Citheronia*, the middorsal sculus on A8 is long, with spines, and has the primary setae arising from different lobes ("0") (Fig. 53). In *Dysdaemonia*, *Schausiella*, *Othorene* and *Syssphinx*, it is long, with spines, but the primary setae do not arise from clearly different lobes ("1") (Fig. 54). A third state is shared by *Adelowalkeria* and *Citioica*, these taxa have a long sculus, but without spines ("2") (Fig. 55). A fourth state is found in *Arsenura*: short without spines ("3").

Character 90. D2 scoli on A9 fused into a middorsal sculus.

This character has been considered a synapomorphy for the American subfamilies of Saturniidae: Arsenurinae, Ceratocampinae and Hemileucinae ("0"). Only *Oxytenis* has the D2 scoli not fused on A9 ("1").

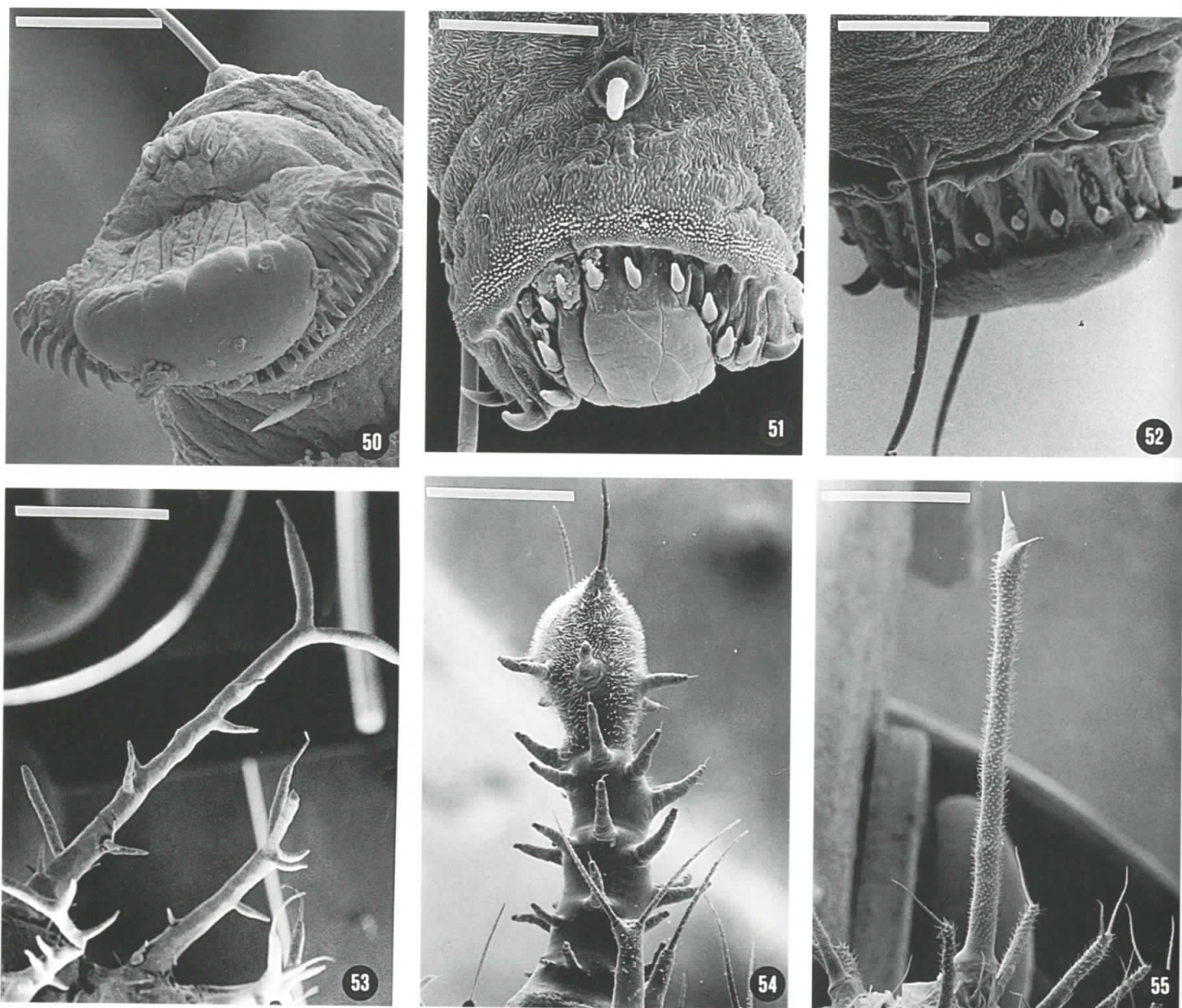


Fig. 50-55. Larval morphology (line lengths after each figure description): 50) Left proleg of *Schausiella carabaya* (W. Rothschild) (75µm). 51) Left proleg of *Syssphinx colla* Dyar (75µm). 52) Left proleg of *Dysdaemonia boreas* (Cramer) (100µm). 53) Detail of the middorsal scoli on A8 of first instar larva of *Eacles ormondei* Schaus (0.35mm). 54) Detail of the middorsal scoli on A8 of first instar larva of *Syssphinx colla* Dyar (0.30mm). 55) Detail of the middorsal scoli on A8 of first instar larva of *Citoica anthoniis* (Herrich-Schäffer) (0.30mm).

Character 91. Shape of middorsal scoli on A9.

Only in *Eacles*, *Citheronia* and *Schausiella*, do the fused scoli on A9 resemble the thoracic D scoli ("0") (Fig. 55). The remainder of the taxa have short middorsal scoli, without spines ("1").

Character 92. SV on A9 prominent.

While in most taxa the SV seta on A9 is relatively inconspicuous ("1") (Pease, 1961), it is prominent in *Eacles* and *Citheronia* ("0").

Character 93. Lateral plate of A10 shows some fusion of scoli.

We only observed this state in *Eacles*, and it is more developed in *Neorcarnegia* ("1"), according to Pease (1961). In all other taxa studied, the scoli are clearly separated ("0").

Character 94. Number of setae on lateral plate of proleg on A10.

We are using this character with some doubts, larger series of specimens are needed to make sure there is constancy. Only in *Othorene* are there six setae present ("1") (Fig. 60). *Anisota* and *Dryocampa* bear only four ("2") (Fig. 63), and the remaining taxa have five ("0") (Fig. 56-59, 61-62, 64-65).

The following three last instar characters are the only ones we found useful in our analysis. Again, not until more mature larvae are technically described, will more character complexes be available and will their certain distribution among taxa be assessed.

Character 95. Last instar larva with D "Sternwarzen" type scoli on T2 conspicuously distinct and projecting.

In our analysis, this character represents a synapomorphy for the ingroup. Nässig (1988) recognized two main types of scoli in Saturniidae: (a) scoli of "Sternwarzen" type (asterisk-like) or derived from such type, found in Saturniinae and Ludiinae; and (b) scoli not derived from the "Sternwarzen" type, found in Arsenurinae, Ceratocampinae, Hemileucinae and Agliinae. In Arsenurinae, Agliinae and Oxyteninae, the last instar larva is "hornless" ("0") (Aiello and Balcázar, 1997; Michener, 1952; Packard, 1914). In the Hemileucinae, including *Polythysana* Walker, the full grown larva retains the characteristic urticating scoli —type 7 in Nässig's arrangement (1988) — of previous

instars. But the only subfamily in which the larvae keep at least some thoracic "horns" — "Horns" type 5 according to Nässig (1988)— in the last instar is Ceratocampinae ("1").

Character 96. D and SD scoli on abdomen inconspicuous.

This is the case for the outgroup and *Schausiella*, *Othorene* and *Syssphinx molina* ("2"). In *Adelowalkeria* and *Citioica*, D and SD on T2-T3 are short, but evident ("1"). Other taxa examined have these abdominal scoli as large as those on T2-3 ("0").

Character 97. Abdominal D and SD silver or nacreous on the outside.

Some Ceratocampinae taxa such as *Syssphinx*, *Othorene*, *Adelowalkeria* and according to Lemaire (1988) *Adeloneivaia* and *Ptiloscola* present D and SD scoli on the abdomen with metallic or nacreous coloring on the outside ("0"). This peculiar pattern may have a cryptic function and as far as we know, it is not found in any other taxa outside the Ceratocampinae ("1").

PUPA

Although we used only one character from the pupa, it represents a synapomorphy for the Ceratocampinae.

Character 98. Cremaster projecting and bifid.

We consider this character a synapomorphy for the Ceratocampinae, all known pupae show a relatively long apically bifid cremaster ("0") (Riotte and Peigler, 1981: pl. 8, fig. 1-3). In Arsenurinae, the cremaster is long but from the described pupae, never bifid ("1") (Dias, 1978b: fig. 13-15). In *Oxytenis* (Aiello and Balcázar, 1997: fig. 17) and some Saturniinae, the cremaster is absent or not protruding; some other Saturniinae have a long cremaster, but again it is never bifid. Nässig (1994) characterized the pupae of *Saturnia* Schrank s.l. as having a "broad, sometimes strongly bifid cremasters with strong bristles", but they do not project. Oberprieler and Duke (1994), described a bifid cremaster in *Spiramiopsis comma* Hampson and, although projecting, from the illustrations this cremaster is not exactly as that found in Ceratocampinae.

DISCUSSION

CLADISTIC ANALYSIS

ADULTS

Some generalizations can be drawn from the consensus tree derived from the most parsimonious cladograms resulting after successive weighting. Only one adult character appears as a synapomorphy for the subfamily: the sphingid-like body shape (character 59 (Fig. 66). *Neorcarnegia* appears as the most plesiomorphic taxon in all the cladograms found. Michener placed this taxon as a relatively apomorphic genus on his phylogenetic scheme, but without stalking the branch to any other (Michener, 1952: 370). Lemaire (1988) placed *Neorcarnegia* at the end of his taxonomic arrangement, but stated that its position within the subfamily was difficult to establish due to several peculiarities shown, and that some traits are shared with *Bathyphebia*, *Citheronia* and *Procitheronia*, suggesting a plesiomorphic condition.

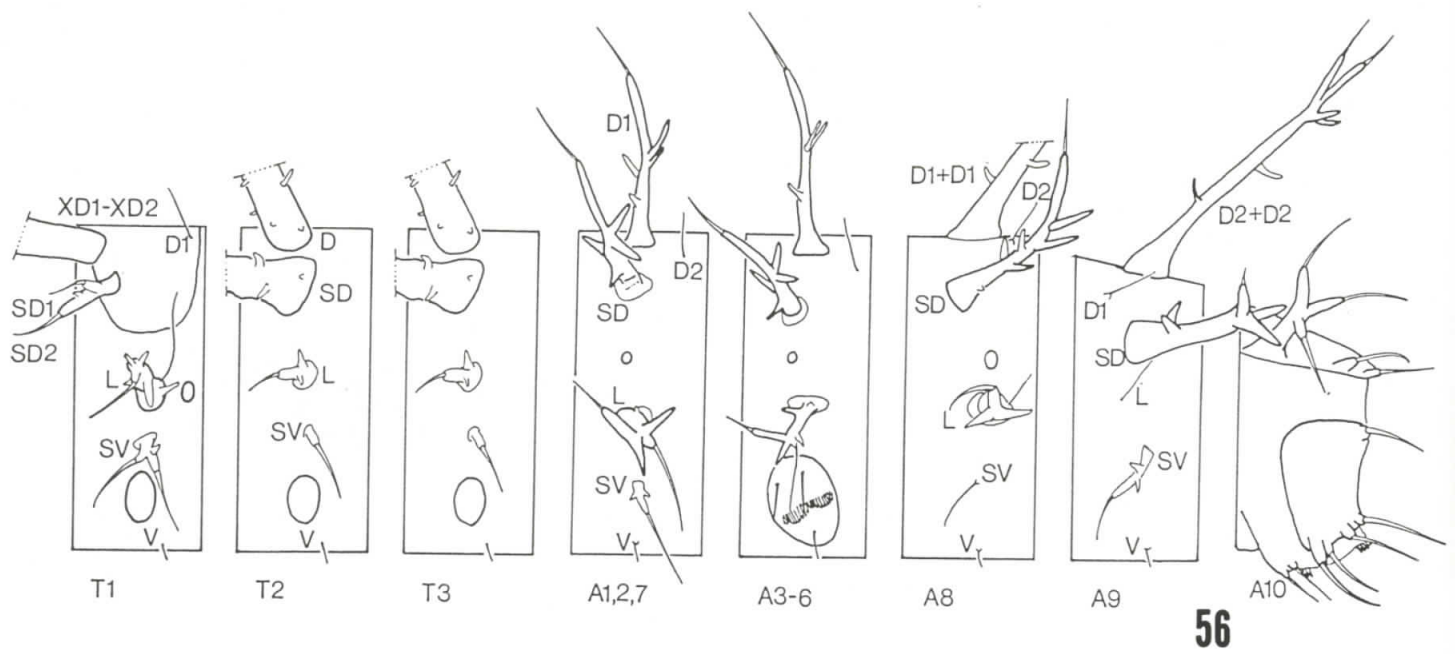
The next most plesiomorphic clade is formed by ((*Eacles*, *Bathyphebia*) (*Citheronia*, *Procitheronia*) *Schausiella*) (**Eac-Sch**), thus agreeing with Michener's (1952) conception. A plesiomorphic condition for these taxa is implicit in Lemaire's (1988) arrangement. The (*Eacles*, *Bathyphebia*) clade is supported by one synapomorphy: the peculiar wing pattern consisting of eye spots (character 38). The *Citheronia-Procitheronia* monophyletic clade is sustained by the shape of the ostium bursae opening,

consisting of a transverse slit (character 58). We did not find any synapomorphy for the clade **Eac-Sch**, and their appearance (basally in the cladogram) relies on the possession of some plesiomorphic characters shared with the outgroup and *Neorcarnegia*: mandibular rudiments large and protuberant (character 19); epiphysis of male reaching only beyond middle of tibia (character 34, this character implies a reversal in *Citheronia-Procitheronia*); and closed V1 cell in forewing (character 43, in *Procitheronia* this state is lost).

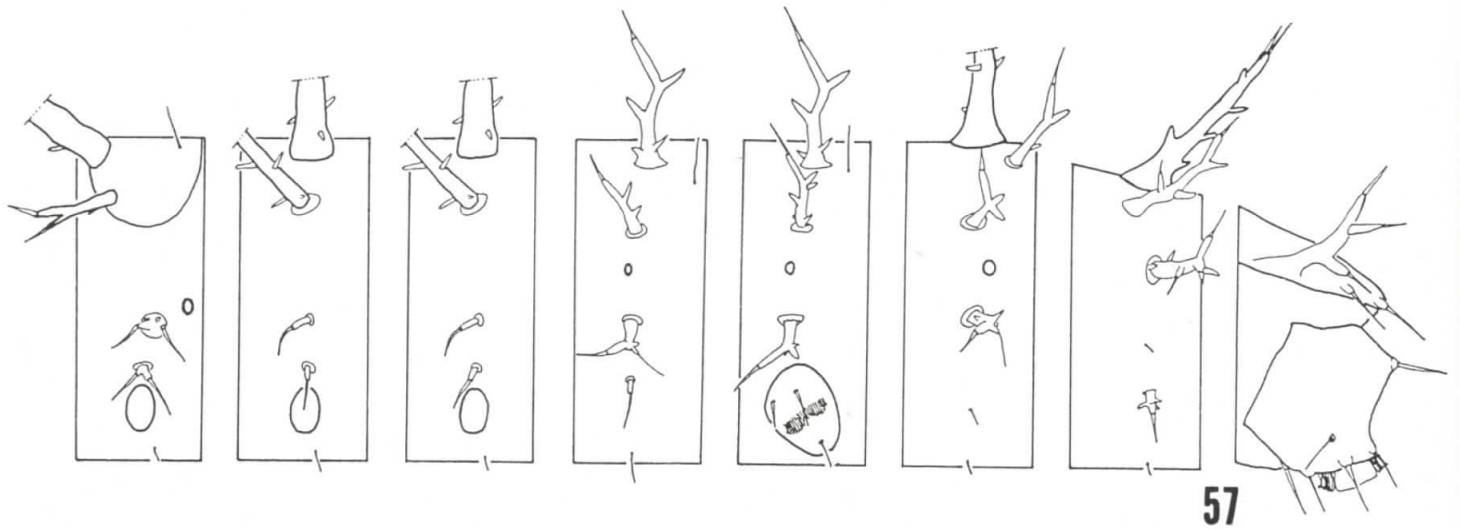
In his phylogenetic arrangement, Michener (1952) considered *Psilopygoides* as an early offshoot of the *Syssphinx* branch. Lemaire (1988) noted that the systematic position of *Psilopygoides* is very difficult to establish due to the very peculiar genitalia, and placed this genus between *Othorene* s.l. and *Almeidella*. In our cladograms, the sister group of the **Eac-Sch** is the clade formed by *Psilopygoides* and the remaining Ceratocampinae taxa. This clade is supported by the presence of an open V1 cell on the forewing, although assuming a parallelism in *Procitheronia*. The monophyly of the genera of Ceratocampinae exclusive of the previously discussed clades is supported by a reduction in the segmentation of the labial palpi (character 30). This assemblage is constituted by (*Adeloneivaia*, *Adelowalkeria* s.l.) and (*Othorene* s.l. (*Almeidella* ((*Psilopygida* (*Anisota*, *Dryocampa*)) *Syssphinx*))).

Support for the (*Adeloneivaia*, *Adelowalkeria* s.l.) branch is found in the absence of a transtilla, although a parallel disappearance of the transtilla is found in *Oxytenis* and the (*Ceropoda*, *Mielkesia*) clade (character 50). Monophyly for the eight genera included in *Adelowalkeria* s.l. is well supported by a male genitalic character: valvae with a long process arising from the middle of inner margin (character 55). Good evidence for the monophyly of *Othorene* s.l. is also found in a male genitalic character: the transtillar plate is divided by a groove or membrane (character 51). The (*Almeidella* ((*Psilopygida* (*Anisota*, *Dryocampa*)) *Syssphinx*)) clade is established by the possession of a gnathos fused to the transtilla: a similar condition is found in *Schausiella*, but after our analysis we consider that the condition in *Schausiella* is not homologous, and it is very likely that a close examination of the character will lead to the finding of differences in structure. As was pointed out for the Lepidoptera by Klots (1970), genitalic structures in the Ceratocampinae are in need of more study before homologies can be determined with confidence. Another clade supported by genitalic characters is ((*Psilopygida* (*Anisota*, *Dryocampa*)) *Syssphinx*). In these taxa, the gnathos is connected to the internal face of the valvae by a membrane (character 49).

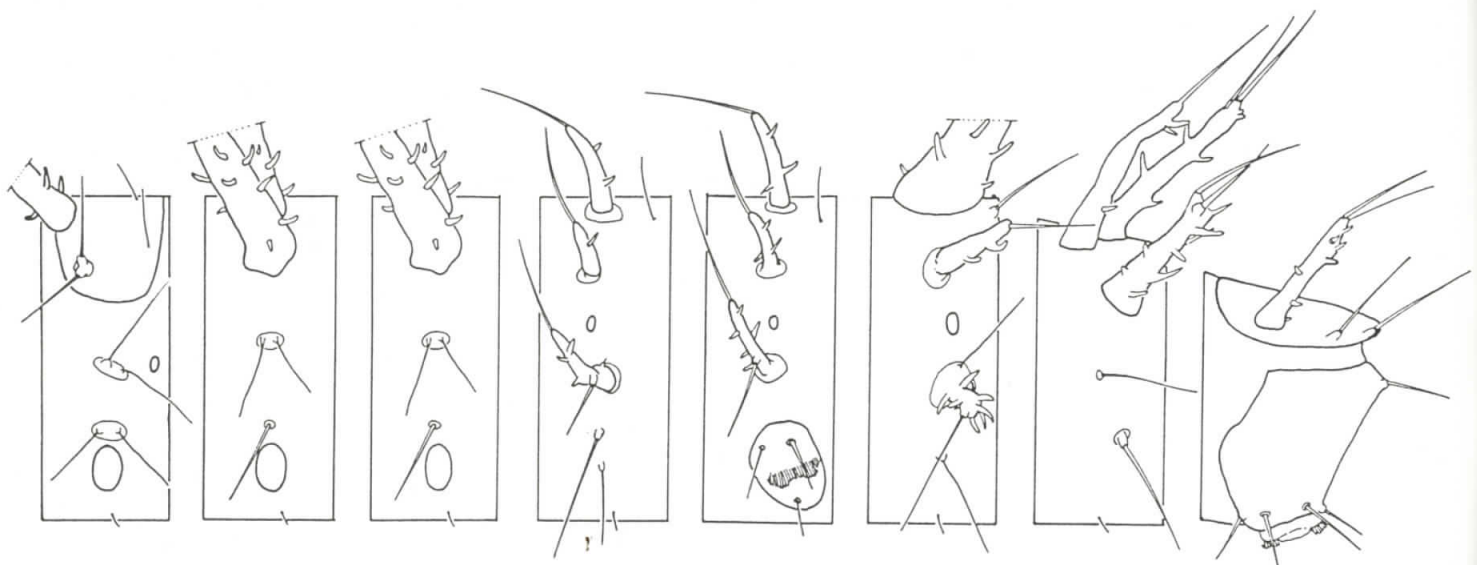
The (*Psilopygida* (*Anisota*, *Dryocampa*)) clade is supported by one synapomorphy involving mouth parts. These genera share maxillary stipites extending backward to posterior margins of the sockets of the labial palpi (character 23). The (*Anisota*, *Dryocampa*) monophylum is by far the best established, and was always found in all minimum-length cladograms. There are five synapomorphies in this clade: the clypeus is reduced to a small rim (character 12); the proboscoidal fossa is wider than long (character 20); the walls of the proboscoidal fossa are slanting (character 21); the labial sclerite is very small (character 27); and the labial palpi arise very close to each other (character 28). Not surpris-



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57



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Fig. 56-58. Larval chaetotaxy (setal maps of first instars): 56) *Eacles ormondei* Schaus (24 mi. N. of Atoyac, Guerrero, Mexico): A = abdominal segment, D = dorsal setae, L = lateral setae, SD = subdorsal setae, SV = subventral setae, V = ventral seta, XD = extradorsal setae. 57) *Citheronia splendens* (Druce) (Sonora, Mexico). 58) *Schausiella carabaya* (W. Rothschild).

ingly, the two subgenera of *Psilopygida* were found in most cladograms as a monophyletic entity. A synapomorphy for this clade is found in the transtilla, forming a plate connected to the tegumen by lateral arms (character 51).

In the cladogram used to map the character distributions, and from those explained above, it is evident that there are no true synapomorphies defining the most inclusive clades found in our analysis based on adult characters. Therefore, many clades are distinguished by features corresponding to absences of apomorphies used to recognize other such taxa (cf. Ackery and Vane-Wright, 1984). Further, some characters, such as reduction in number of palpal segments and the open V1 cell on forewings, are good synapomorphies within the ingroup, but are homoplastic in the context of the Lepidoptera. The same situation has been noted by several researchers in general for the Bombycoidea (i. e., Common, 1990; Franclemont, 1973; Holloway, 1987; Lemaire, 1988; Nässig and Holloway, 1988; Nässig and Oberprieler, 1994; Scoble, 1992). Most bombycoid taxa have been grouped mainly on characters of absence, and although recently Minet (1986, 1994) has proved that some of these taxa are true monophyletic groups based on several synapomorphies, many systematic problems remain unsolved and further studies are needed (Oberprieler and Duke, 1994).

The most inclusive groupings found in the cladograms resulting from the analysis of adult characters are thus based on the most parsimonious interpretations of groups of characters, rather than on a single "silver bullet," as Miller (1991) stated for the Notodontidae.

Sanderson and Donoghue (1989) convincingly showed that homoplasy increases as the number of taxa in a given study increases. They analyzed data from 56 cladistic analyses. Three of these papers with 35, 37 and 47 taxa are closer in number with the taxa we studied. The CI were 0.43, 0.26 and 0.39 respectively, so our results are consistent with them, and not dramatically low.

We consider that the high homoplasy level found in the adult character data matrix is the result of independent reductions or losses, in different lineages of characters involving several structures but more strikingly mouthparts. On the other hand, most of the "true" synapomorphies involve genitalic structures. This situation is consistent with a group of insects in which the adults do not feed, and most activities are restricted and oriented to mating and oviposition over a very short period of time (Janzen, 1984). Thus, we find highly modified genitalic structures in the Ceratocampinae which are very helpful to establish phylogenetic relationships at and slightly above the generic level, but most other characters are less useful. Anyway, in the case of the mouth parts, independent reductions of characters imply that the ancestor of the Ceratocampinae must have had, if not functional, at least well developed mouth parts.

IMMATURE STAGES

In our analysis, we used 39 larval characters: 35 are derived from first instar larvae, and only three from last instar larvae, and one from pupal morphology. However, two of the three characters that we assume are synapomorphies for the Ceratocampinae are found in the last instar larvae and the pupae (characters 95, 98).

In the following discussion, we refer to first instar larval characters, unless otherwise noted.

We were able to study only a very limited number of larvae (11 ingroup taxa), and although we present setal maps for the first instars of three genera, the number is still very small. However, the larvae included in the matrix are representatives of most clades found in the adult-based analysis: *Eacles*, *Citheronia* and *Schausiella* from the (**Eac-Sch**) clade; *Othorene* from *Othorene s.l.*; *Anisota* and *Dryocampa* from the same adult clade; *Syssphinx molina*, *S. colla* and *S. quadrilineata* belonging to three species groups of *Syssphinx*; and finally *Adelowalkeria* and *Citioica* from the *Adelowalkeria s.l.* lineage.

Not surprisingly, *Anisota* and *Dryocampa* appear as the most basal clade in all the minimum-length trees found. For a long time, it has been noted that the most distinctive larvae among the known Ceratocampinae are those of *Anisota* and *Dryocampa* (Lemaire, 1988; Packard, 1905; Pease, 1961; Riotte and Peigler, 1980). Pease (1961:109) wrote "there seem to be more and greater differences separating these genera from the rest of the Citheroniinae [= Ceratocampinae] than there are separating the Citheroniinae from the Rhescyrtidinae [= Arsenurinae] and the Hemileucinae." According to our findings, five characters support the monophyly of this group: SD1 and SD2 scoli arising independently on the prothoracic shield (character 67); D1 and SD setae and scoli on T3 identical (character 70); tip of D and SD scoli on T3 not swollen, blunt (character 72); the presumed primary setae on D scoli on A1-8 are short, strong, acicular (character 79); and there are four setae on the lateral plate of proleg on A10 (character 94).

In the consensus tree derived from the three most parsimonious cladograms, a polytomy of four branches is found as the sister group to the *Anisota-Dryocampa* clade (Fig. 6). Possession of 20 or more crochets (character 74) and a long, spinose, apically bifid middorsal scoli on A9 (character 61), provide support for the clade ((*Eacles*, *Citheronia*) *Schausiella*) (Fig. 67). The *Syssphinx* taxa studied share two characters involving the shape of the thoracic D and SD scoli: the tip of these scoli are globose (character 72) and the primary setae on D and SD scoli are parallel to each other (character 74). Six characters may represent synapomorphies for the *Adelowalkeria-Citioica* clade: tip of D and SD thoracic scoli globose (we coded for two "globose" states, see character 72); same scoli and abdominal D scoli pilose (characters 75, 81); seta L2 on A8 absent (character 83); long middorsal scoli on A8 without spines (character 89); and last instar larva with abdominal D and SD scoli as large as those on T2-3 (character 96).

The lowest groupings retained in the larval consensus tree are found in the adult-based cladogram, i. e., ((*Eacles*, *Citheronia*) *Schausiella*), *Syssphinx*, (*Adelowalkeria*, *Citioica*) and (*Anisota*, *Dryocampa*). It is important to note that the larvae of "critical" genera, such as *Neorcarnegia*, *Psilopygoides*, *Adeloneivaia* and *Almeidella*, have not been described. The relationships between these genera and other better supported clades are tentative and weakly defined, according to our findings based on adult morphology. To firmly establish the position of these genera, it is necessary to study and describe their life cycles.

As in the case of the adult-based cladograms, the CI of the

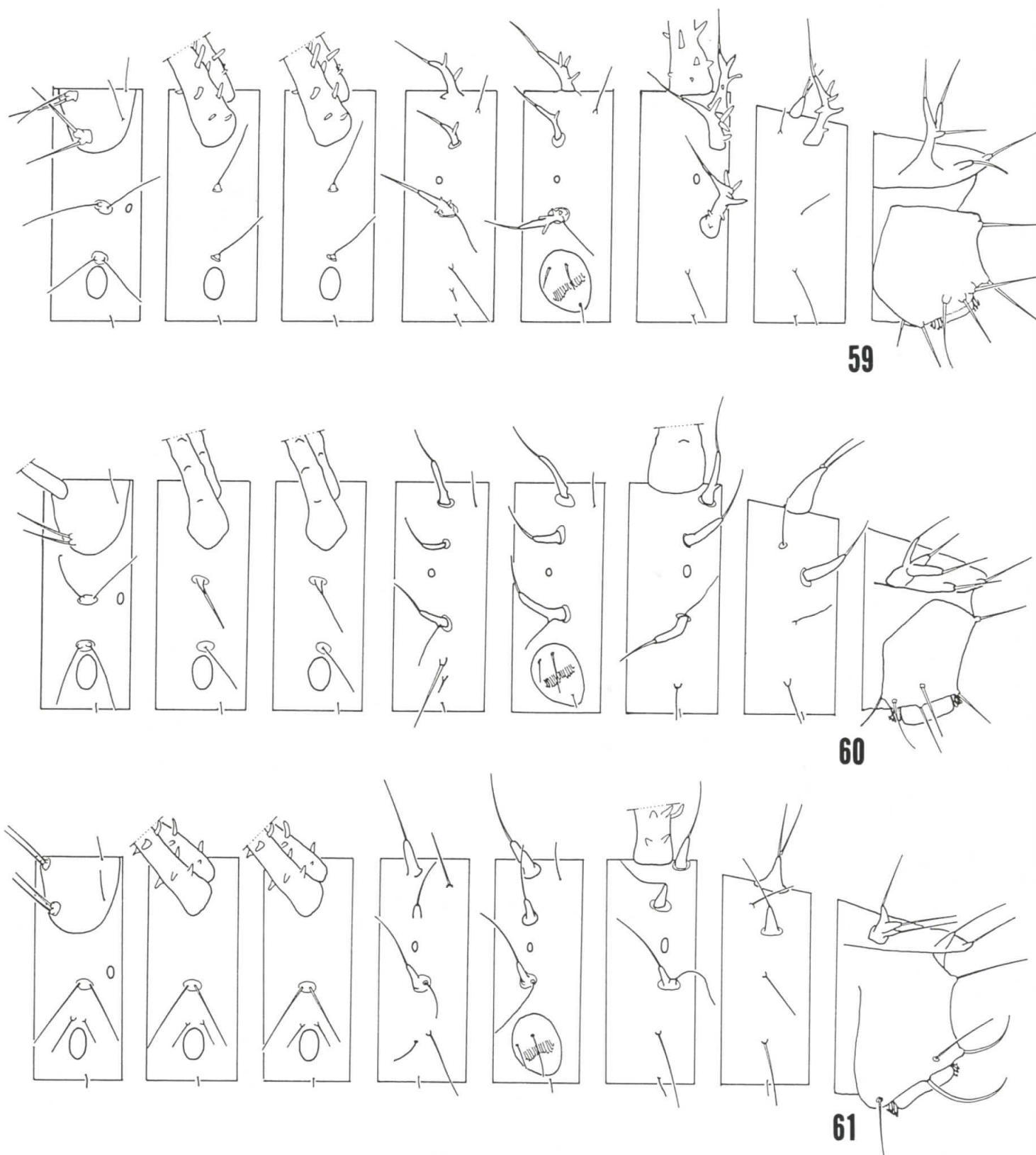


Fig. 59-61. Larval chaetotaxy (setal maps of first instars): 59) *Othorene verana* Schaus (Comitán, Chiapas, Mexico). 60) *Othorene hodeva* (Druce) ? (Apuya Oriente, Ecuador). 61) *Sysphinx molina* (Cramer) (46 km W of Soto la Marina, Tamaulipas, Mexico).

larval analysis (0.77) falls close to the values found in the papers studied by Sanderson and Donoghue (1989). Five of these papers had between 10 and 12 taxa with a CI range of 0.59 to 0.80.

The majority-rule consensus tree calculated from 100 bootstrap replications is identical to the strict consensus tree from the three most parsimonious cladograms. The clade formed by *Anisota* and *Dryocampa* is retained at a 100% level—as in the case of the adult-based analysis. *Adelowalkeria* and *Citioica* the only two representatives of *Adelowalkeria* s.l. appeared in 95% of the repetitions. *Eacles* and *Citheronia*, on the other hand appeared in 98% of the repetitions. Surprisingly, the *Syssphinx* species groups, with *S. molina* as the most plesiomorphic taxon, appeared in only 73% of the cladograms resulting from the repetitions, although *Syssphinx colla* and *S. quadrilineata* are supported in 91% of the trees found. The ingroup appeared as a monophyletic assemblage only in 85% of the times.

ADULTS AND IMMATURES

The single cladogram retained after successive weighting (Fig. 68), using all the characters for the 14 taxa with known immatures—identical to one of the original two found in the analysis of 99 unweighted characters—requires only one rearrangement to make it fully compatible with the consensus tree based on adult characters (Fig. 2). Placing (*Anisota-Dryocampa*) as the sister group of *Syssphinx* adds only two steps to this minimal length tree.

If we compute an agreement subtree of the consensus tree based on adult characters, this cladogram and any of the fully resolved cladograms resulting after the successive weighting of the adult data matrix, we only need to prune two leaves, *Anisota* and *Dryocampa*, to get the greatest agreement subtree (GAS). An agreement subtree of two trees is an identical subtree that can be obtained from both trees by pruning leaves with the same label (= common pruned trees) (Finden and Gordon, 1985; Page, 1993).

The bootstrapping results support the same monophyletic groups that are supported on the immature stages based analysis, but monophyly for the ingroup is supported in 95% of the cladograms found during the repetitions. In this case, the *Anisota-Dryocampa* group is not the most plesiomorphic clade, but forms a polytomy with the other taxa.

When adult and immature information was combined (coding all the missing information as “?” for the 19 taxa with unknown immatures), five clades found in all minimum length trees found from the adult and immature data alone were also retained: **Eac-Sch**, *Adeloneivaia-Adelowalkeria* s.l., *Anisota-Dryocampa*, *Syssphinx*, and *Othorene* s.l.

The **Eac-Sch**, *Adeloneivaia-Adelowalkeria* s.l., and *Syssphinx* clades are supported by the same synapomorphies discussed in the immature section. On the other hand, *Othorene* s.l. is supported by the adult characters previously pointed out, and the clade (*Psilopygida* (*Anisota*, *Dryocampa*)) is supported by a combination of both adult and immature characters. Support for the placement of *Syssphinx* as the sister group of *Othorene* s.l. is substantiated by one synapomorphy: maxillary stipites included in the walls of the fossa (character 22) (Fig. 69-70). The positions of *Psilopygoides* and *Almeidella*, although in the latter case it is

identical to that found in the adult based cladograms, is the result of the most parsimonious interpretation of several characters.

Even though the consensus tree derived from all characters (99) shows a better resolution than the cladogram obtained from the adult data alone, some of the clades at lower levels remain unresolved. The relationships of *Cicia* and *Dacunju* within *Othorene* s.l., and *Rachesa* and *Ptiloscota* within *Adelowalkeria* s.l. must be further studied. Larval characters may prove very useful towards resolving this polytomies and to support or falsify other clades found, specially those lacking “true” synapomorphies.

Nixon and Carpenter (1996) showed that simultaneous analysis of combined data maximizes cladistic parsimony than separate analysis, hence we consider the consensus cladogram derived from adult and immature morphology (Fig. 8) our best working hypothesis.

PHENETIC COMPARISON

The phenograms from adult, larval and combined data are compatible except for the *Syssphinx* and the *Anisota-Dryocampa* clusters. The internal branches within the *Syssphinx* cluster in two different ways in the four phenograms generated from the adult data matrix, but in the larval and overall phenograms, they are identical. More important is the fact that the *Anisota-Dryocampa* cluster appears in two different positions on the three phenograms. In the adult and overall phenograms, this cluster is basal and very distantly related to the other taxa; in the larval phenogram, *Anisota-Dryocampa* clusters with *Eacles-Citheronia-Schausiella*, but again very distantly.

Not surprisingly, the phenogram branching patterns resemble to a high degree that of the cladograms. One principle in numerical taxonomy is to use as many characters as possible. But in our case, we only used characters that could help resolve phylogenetic relationships, and consequently the “resemblance” among taxa is restricted to these characters.

The position of genera whose relationships are weakly supported on the adult character based cladograms, such as *Neorcarnegia*, *Psilopygoides*, and *Almeidella*, account for the most interesting differences between the cladograms and phenograms. In the adult phenograms, *Neorcarnegia* always clusters basally to the *Eacles-Bathyphebia-Citheronia-Procitheronia-Schausiella* grouping, while *Almeidella* clusters with *Psilopygida* and *Psilopygoides* are distantly related to the *Othorene* s.l.-*Almeidella-Psilopygida-Syssphinx* cluster.

CONCLUSIONS

The Ceratocampinae constitute a monophyletic group defined by three synapomorphies: adults with sphingid-like body shape, last instar larva with some thoracic D scoli distinct and conspicuously projecting, and pupa with a projecting and bifid cremaster. Although some clades are still too tentative, we consider the consensus cladogram derived from simultaneous adult and immature morphology (Fig. 8) our best working hypothesis. There is evidence that *Neorcarnegia* is a plesiomorphic taxon, and perhaps the sister group of the rest of the Ceratocampinae. Another plesiomorphic group is that formed by (*Eacles*, *Bathyphebia*) (*Citheronia*, *Procitheronia*) *Schausiella*, which is

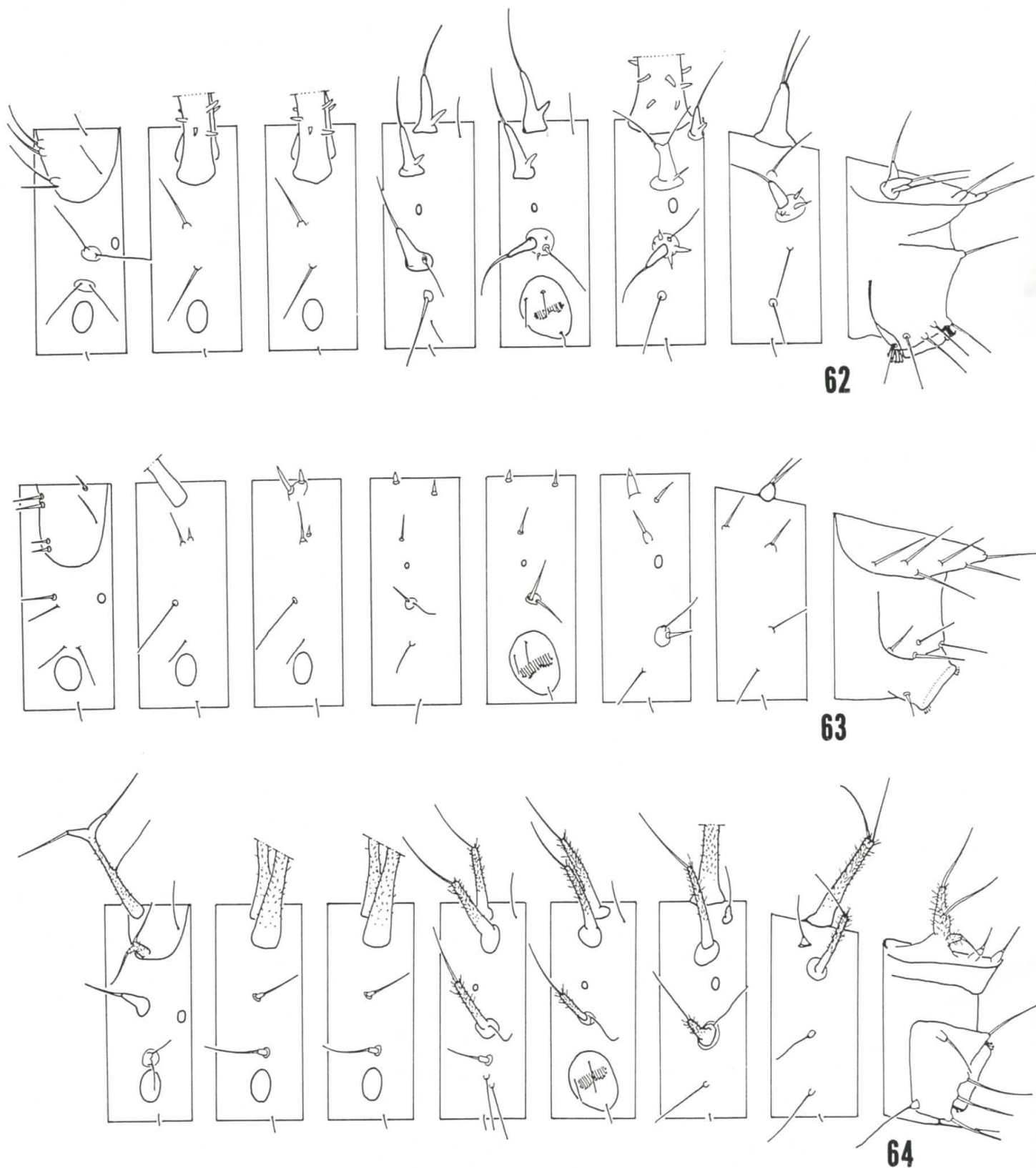


Fig. 62-64. Larval chaetotaxy (setal maps of first instars): 62) *Syssphinx quadrilineata* Dyar (46 km W of Soto la Marina, Tamaulipas, Mexico). 63) *Dryocampa rubicunda* (Fabricius) (Casselberry, Florida). 64) *Citioica anthonilis* (Herrich-Schäffer) (Lacanjá, Chiapas, Mexico).

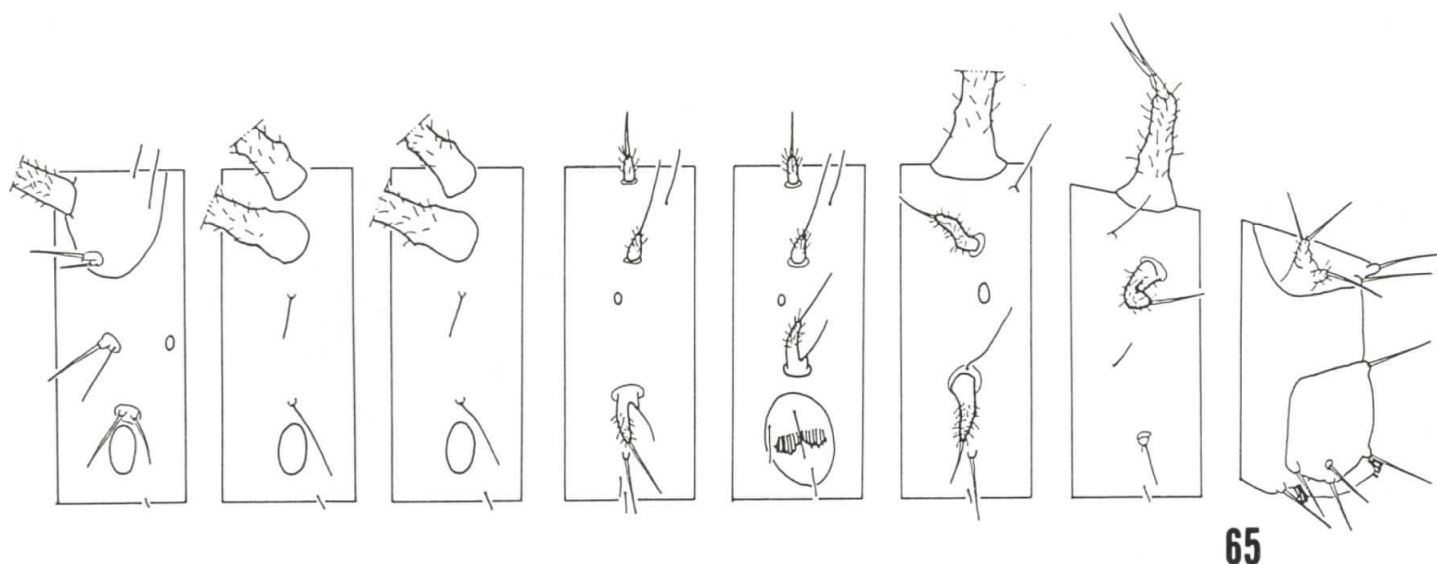


Fig. 65. Larval chaetotaxy (setal map of first instar): *Adelowalkeria plateada* (Schaus).

followed by (*Adeloneivaia*, *Adelowalkeria* s.l.). *Psilopygoides* is the adelphotaxon of the remainder of the subfamily, which is a phylogenetic sequence of (*Almeidella* ((*Anisota*, *Dryocampa*) *Psilopygida*)), (*Syssphinx*, *Othorene* s.l.).

The cladograms obtained from adult characters alone require two changes to be fully compatible with the cladograms derived from the simultaneous analysis: a switch of places between *Psilopygoides* with (*Adeloneivaia*, *Adelowalkeria* s.l.) and *Othorene* s.l. with (*Almeidella*((*Anisota*, *Dryocampa*) *Psilopygida*)).

The study of immatures of 11 taxa representatives, agrees with the hypothesis derived from adult and immature morphology at lower levels (close to the terminal taxa), but showed no resolution at higher levels (close to the root).

In some respects, results have fallen short of our expectations. Most clades are supported by only one "true" synapomorphy, and others are based exclusively on the most parsimonious interpretations of groups of characters. There are also some unsolved polytomies. The failure to find suitable characters in the present study, may explain in part both the polytomies and the lack of synapomorphies. But the absence of appropriate morphological characters of the imago has long been a major barrier to firmly establish relationships among "bombycoid" taxa.

Our results suggest that larval and pupal characters may prove very important to solve some of the unanswered questions. The fact that two of the three characters considered as synapomorphies for the subfamily are derived from immature stages is a strong incentive to study them. Data from studies of life cycles, rearing and technical descriptions of immatures may be more important to understand phylogenetic relationships in Ceratocampinae than adult characters. On the other hand, molecular data may be particularly informative. We hope this paper can provide the basis for future studies on the Saturniidae, and specifically on the Ceratocampinae, and that interest is stimulated by this work so that other researchers may test our phylogenies by studying additional characters and taxa.

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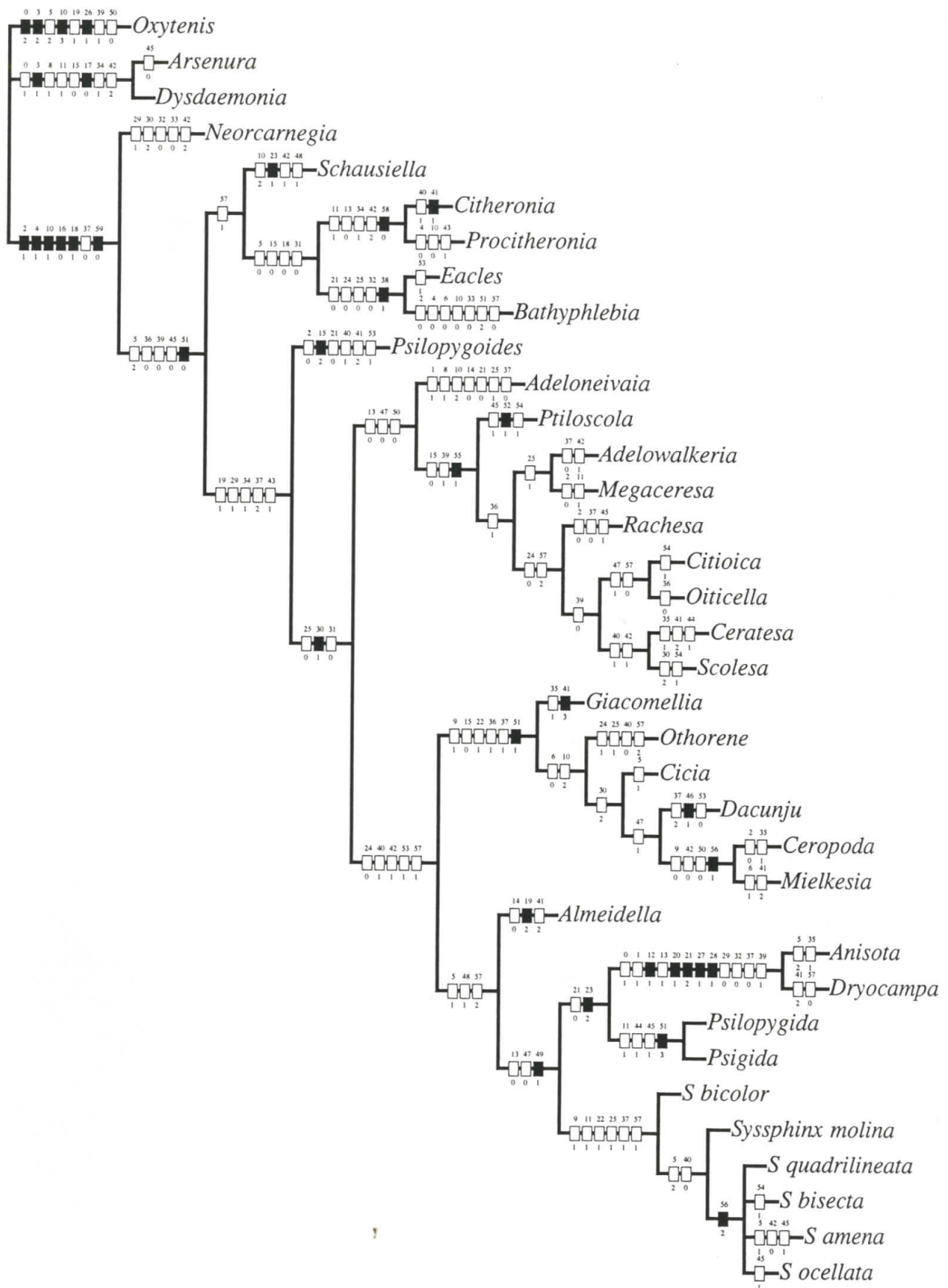


Fig. 66. One of 54 cladograms of Ceratocampinae genera (from 60 adult characters) retained after successive weighting procedure (length = 193; CI = 41; RI = 70)). Character state changes are superimposed: solid black squares = synapomorphies; open squares parallelisms. Character numbers above hashmark, state numbers below.

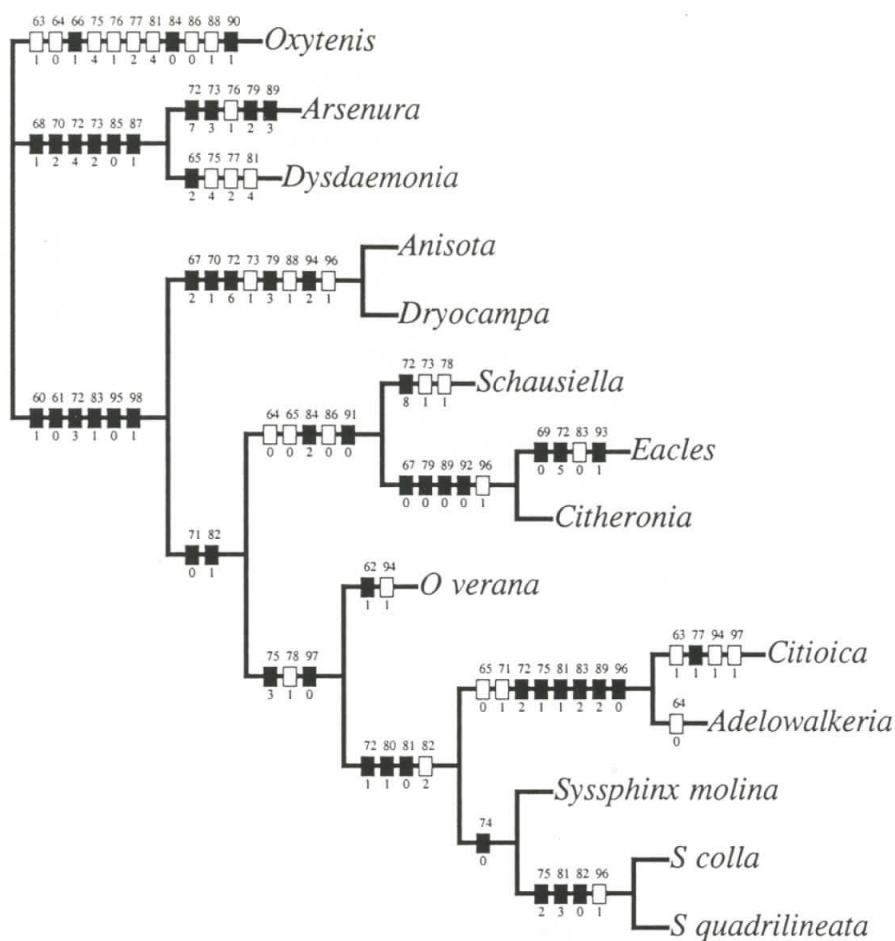


Fig. 67. One of three most parsimonious cladograms ($L = 86$, $CI = 0.77$, $RI = 0.78$) of 11 Ceratocampinae taxa based on larval characters. Character state changes are superimposed: solid black squares = synapomorphies; open squares = parallelisms. Character numbers above hashmark, state numbers below.

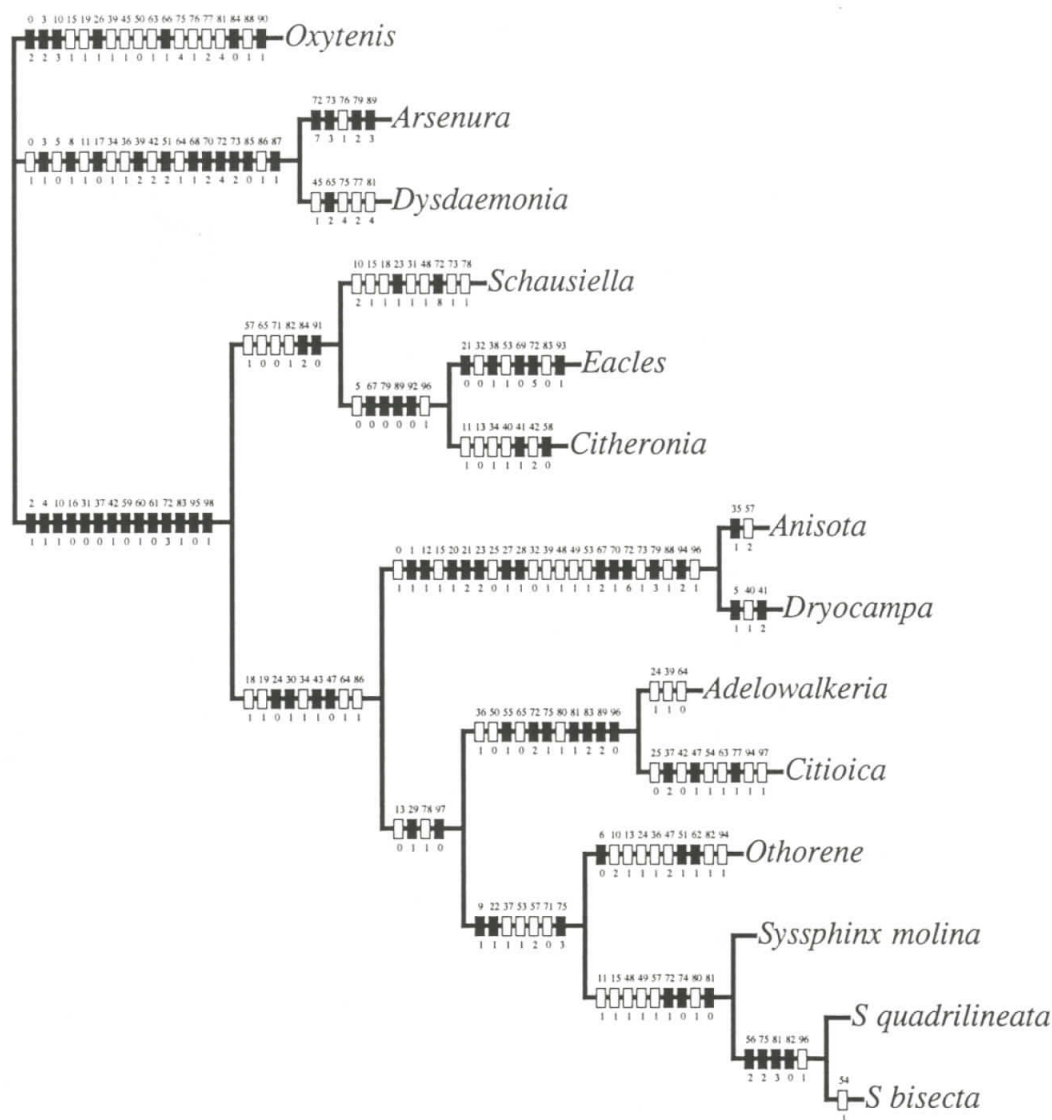


Fig. 68. One of two most parsimonious cladograms ($L = 193$, $CI = 0.69$, $RI = 0.73$) of 11 Ceratocampinae taxa based on larval and adult characters; identical to the one retained after successive weighting. Character state changes are superimposed: solid black squares = synapomorphies; open squares = parallelisms. Character numbers above hashmark, state numbers below.

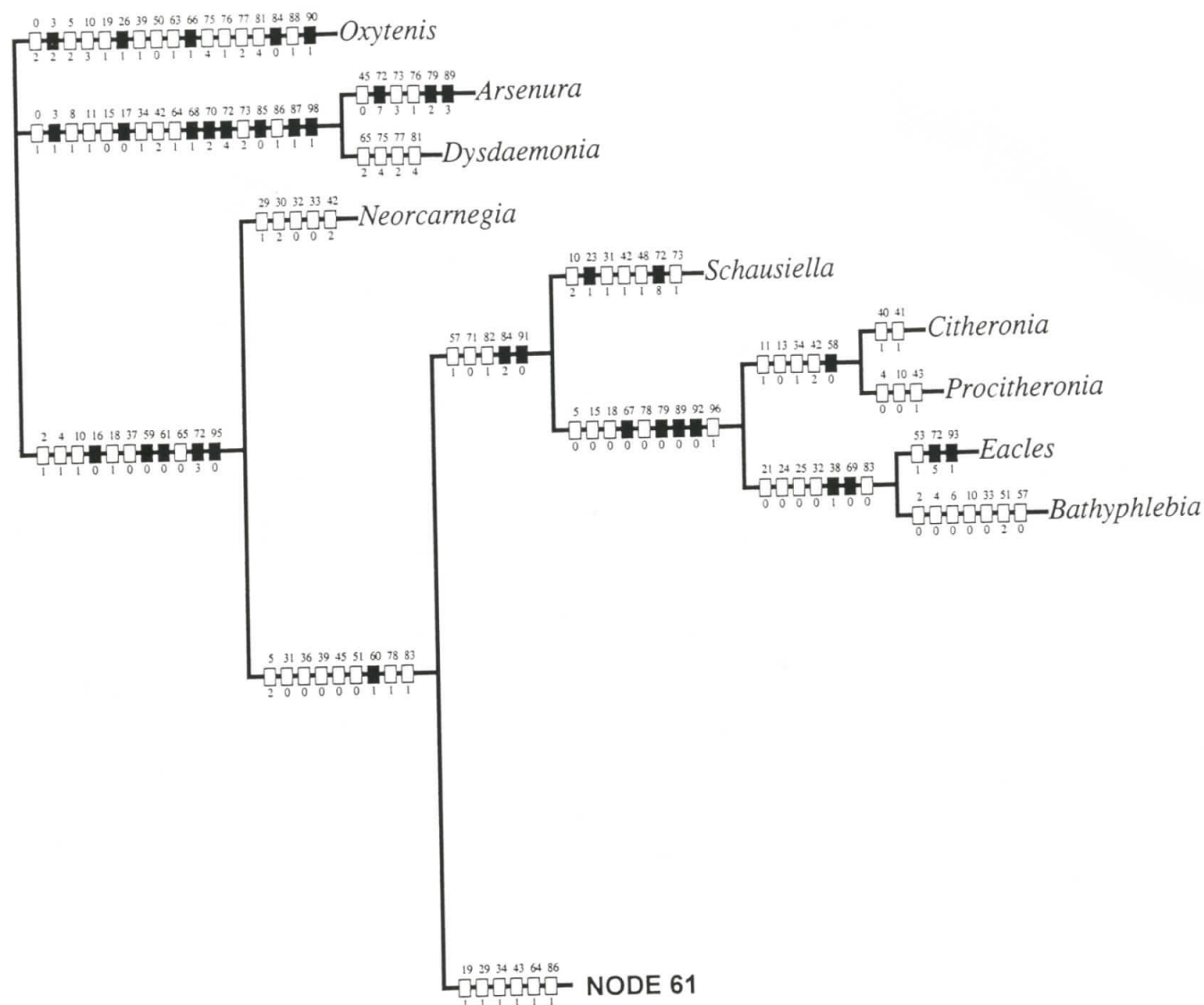


Fig. 69. One of 22 most parsimonious cladograms ($L = 282$, $CI = 0.52$, $RI = 0.71$) of 33 Ceratocampinae taxa based on 99 unweighted larval and adult characters. Character state changes are superimposed: solid black squares = synapomorphies; open squares = parallelisms. Character numbers above hashmark, state numbers below. (Node 61 continues on Fig. 70)

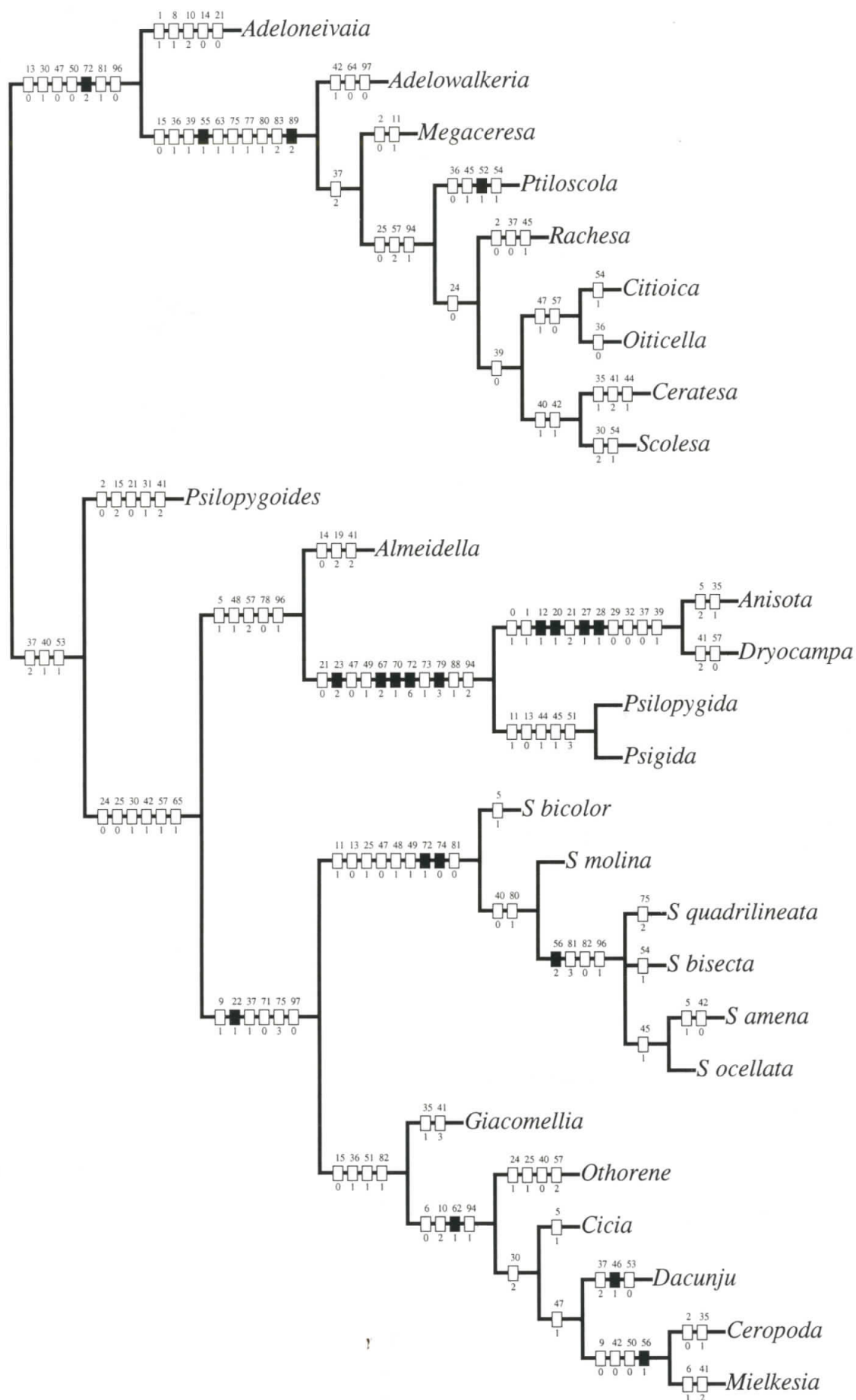


Fig. 70. Node 61 from one of 22 most parsimonious cladograms ($L = 282$, $CI = 0.52$, $RI = 0.71$) of 33 Ceratocampinae taxa based on 99 unweighted larval and adult characters. Character state changes are superimposed: solid black squares = synapomorphies; open squares = parallelisms. Character numbers above hashmark, state numbers below. (Root is on Fig. 69).

APPENDIX 1

CHARACTER LIST

Characters used in the cladistic analysis. Characters 0 to 59 refer to imaginal morphology, and 60 to 98 to larval and pupal morphology.

0. Frontal protuberance
 0. distinct
 1. low and transverse
 2. absent
1. Upper ends of eyes
 0. extending above lower margins of antennal sockets
 1. not reaching lower margins of antennal sockets
2. Antennae
 0. about as long as thorax
 1. two-thirds as long as thorax
 2. longer than thorax
3. Male antennae (Pectination)
 0. narrowly quadripectinate, or quadripectinate
 1. quadridentate
 2. bipectinate
4. Male antennae (pectination reach)
 0. pectinate to the apex
 1. with proximal half to three-fifths of flagellum pectinate
5. Rami (male, size)
 0. short (largest rami 1 to 2.5 longer than segment length)
 1. medium sized (largest rami from 2.6 to 3 times longer than segment length)
 2. large (3.1 or more times longer than segment length)
6. Rami (male antennae, basal rami-apical rami size)
 0. basal rami distinctly longer than apical rami
 1. basal rami and apical rami subequal
7. Antennal cones (whether simple or multiple)
 0. simple
 1. multiple
8. Antennal cones (pectinate portion of antennae)
 0. absent
 1. present
9. Shaft of antenna (compression, non-pectinate portion)
 0. strongly compressed, or compressed
 1. slightly compressed
10. Female antennae (pectination)
 0. narrowly quadripectinate, or quadridentate
 1. simple
 2. quadripectinate
 3. bipectinate
11. Dorsal bristles (non-pectinate region of antennae)
 0. conspicuous, or with one or more inconspicuous
 1. absent
12. Clypeus (size)
 0. four or five times as wide as long, or three times as wide as long
 1. a mere rim beneath frontal protuberance
13. Clypeus (scales)
 0. with erect scales
 1. without erect scales
14. Clypeus (produced)
 0. produced medially as the frontal protuberance
 1. not produced medially
15. Clypeus (separation from frons)
 0. separated from frons by a distinct line
 1. separated from frons by an indistinct line
 2. separated from frons by a strong groove
16. Clypeofrons
 0. convex laterally
 1. flat laterally
17. Pilifers
 0. with setae
 1. without setae
18. Pilifers (shape)
 0. distinctly convex, or little convex
 1. not projecting
19. Mandibular rudiments
 0. large and protuberant
 1. low and inconspicuous
 2. small but strongly convex and high
20. Proboscical fossa (size)
 0. longer than wide
 1. wider than long
21. Proboscical fossa (walls)
 0. walls subvertical
 1. walls vertical
 2. walls slanting
22. Maxillary stipites (relation to walls of fossa)
 0. in contact with walls of fossa, or free from walls of fossa
 1. included in the walls
23. Maxillary stipites (extension)
 0. extending backward to or slightly behind anterior margins of palpal sockets
 1. posterior ends not reaching palpal sockets
 3. extending backward to posterior margins of sockets of labial palpi
24. Galea (size)
 0. very short
 1. as long as the fossa or longer
25. Galeae (curling)
 0. not curled
 1. curled
26. Galeae (papillae)
 0. without conspicuous papillae
 1. with conspicuous papillae
27. Labial sclerite (size)
 0. large
 1. very small
28. Labial palpi (origin from one another)
 0. not very close to each other
 1. arising very close to one another
29. Labial palpi (reach)
 0. extending well in front of frontal protuberance
 1. reaching forward to clypeus, or very short
30. Labial palpi (segmentation)
 0. three-segmented
 1. two-segmented
 2. one-segmented
31. Anepisternal suture
 0. reaching pleural suture well below lower end of deeply impressed portion of latter
 1. reaching pleural suture a very short distance below lower end of deeply impressed portion of latter
32. Deeply impressed portion of pleural suture
 0. at an angle of about 160 degrees to straight lower portion
 1. parallel to lower straight portion

33. Curved portion intervening between deeply impressed portion and lower portion of pleural suture
 0. inconspicuous
 1. oblique, or conspicuous
34. Epiphysis (male, size)
 0. large, reaching beyond middle of tibia
 1. very large, reaching to apical third of tibia or beyond
35. Tibial spines
 0. absent
 1. present
36. Tibial spurs
 0. with apical halves concave on one side
 1. only apical third or less hooked and concave on one side
37. Forewings (torni)
 0. torni clearly defined
 1. torni fairly conspicuous
 2. quasi-elliptical
38. Eye spots
 0. absent
 1. present
39. Anal angles of hind wings
 0. rounded, not produced
 1. somewhat produced
 2. produced
40. Antemedial line (forewings)
 0. present
 1. absent
41. Postmedial line (forewings)
 0. normal, runs from a point close to apex to midpoint of anal margin
 1. replaced by a series of internervular dots
 2. absent
 3. runs from the apex to the base
42. R1
 0. stalked with the other radials
 1. arising from apex of discal cell
 2. arising before apex of discal cell
43. V1 (forewing)
 0. closed
 1. open
44. Ninth tergum (male)
 0. shorter than or equal to uncus, or equal to or larger than uncus
 1. much longer than uncus
45. Uncus
 0. bilobed
 1. simple
46. Gnathos (presence)
 0. present
 1. absent
47. Gnathos (plate)
 0. forming a plate
 1. formed by two lobes not fused
 2. represented only by lateral arms
48. Gnathos (fusion to transtilla)
 0. not fused to transtilla
 1. fused to transtilla
49. Gnathos (relation to valvae)
 0. free from valvae
 1. connected to the internal face of valvae by a membrane
50. Transtilla (Michener's gnathos)
 0. absent
 1. present
51. Transtilla (Ventral plate, Michener's gnathos, membranous division)
 0. forming a plate
 1. forming a plate divided by a groove
 2. represented only by lateral arms
 3. forming a plate connected to the tegumen by lateral arms
52. Juxta
 0. free from valvae, or partially fused to valvae
 1. absent
53. Valvae (cleft)
 0. with a cleft or depressed line in the outer margin
 1. without a cleft or depressed line in the outer margin
54. Valvae (symmetry)
 0. symmetrical
 1. asymmetrical
55. Valvae (middle of inner margin)
 0. normal
 1. with a long process arising from the middle of inner margin
56. Valvae (harpes)
 0. without harpes
 1. with tiny harpes
 2. with long harpes
57. Eighth tergum (female)
 0. scarcely bilobed
 1. with sublateral sclerotic lobes
 2. bilobed
 3. not bilobed
58. Ostium bursae (shape)
 0. a round hole or longitudinal slit
 1. a transverse slit
59. Body shape
 0. sphingid-like
 1. with rounded wings and relatively small body
60. Sensilla trichodea III of maxillary lobe
 0. side by side with STII on dorsoposterior edge of the distal surface
 1. below the STII on dorsoposterior wall of lobe
61. Spinneret (compression)
 0. not compressed dorsoventrally
 1. compressed dorsoventrally
62. Spinneret shape
 0. rounded
 1. triangular
63. Labial palpus (length)
 0. shorter than first segment of maxillary palpus
 1. subequal in length to first segment of maxillary palpus
64. XD (size)
 0. at least as large as D and SD on T2-3
 1. shorter than D and SD on T3
65. XD and SD on cervical plate
 0. XD several times as long as SD
 1. subequal large
 2. subequal short
66. Primary setae
 0. present on D and SD scoli
 1. absent on D and SD scoli
67. SD1 and SD2 setae on T1
 0. arising from a relatively long common scoli
 1. arising from a short common scoli
 2. arising independently
68. D scoli and primary setae on T2
 0. identical to those on T3
 1. different from those on T3 (shorter)

69. L scolus on T1
 0. with 1 to 3 secondary setae
 1. with no secondary setae
70. D1 and SD setae and scoli on T3
 0. identical
 1. different
71. D and SD scoli on T3
 0. with spines
 1. without spines
72. Tip of D and SD scoli on T3 (shape)
 0. smooth spherical tip, without primary setae
 1. swollen at the tip, rounded
 2. little swollen, triangular in profile
 3. swollen at the tip, subspherical (not really rounded)
 4. globose covered with small spines
 5. bifid tips, not swollen
 6. with two strong spines, one of which is longer than scolus, not swollen
 7. mid-sized projection not tapering to its tip, slightly bifurcated
 8. not swollen, slightly bifid, associated with long spines
73. Primary setae on largest D and SD scoli on T2-3 (shape)
 0. peg-like
 1. bristlelike
 2. flattened not serrated
 3. flattened serrated
74. Primary setae on D and SD scoli on T3 (orientation)
 0. parallel to each other
 1. widely divergent forming acute or obtuse angles
75. D and SD scoli on T3
 0. glabrous
 1. pilose
 2. pubescent
 3. puberulous
 4. muricate
76. Tarsal setae 1 and 3
 0. aciculate
 1. lanceolate
77. Tarsal setae (relative sizes)
 0. all of the same size
 1. TS1 shorter than TS2 and TS3
 2. TS2 larger than TS1 and TS3
78. SV on A1-2
 0. 1
 1. 2
79. Primary setae on D scoli on A1-8
 0. aciculate long
 1. bristlelike
 2. serrate
 3. aciculate short
80. Setae on D scoli on abdomen
 0. smooth
 1. barbate
81. D scoli on abdomen
 0. squamose
 1. pilose
 2. glabrous
 3. muricate
 4. finely spinose
82. Spines on D1, SD and L scoli of A1-7
 0. only at the base of scoli
 1. along the whole length of scoli
 2. without spines
83. Seta L2 on A8
 0. projects caudad from base of L scoli
 1. at top of L scoli
 2. missing
84. Number of crochets
 0. less than 10
 1. 10 to 20
 2. more than 20
85. Crochets
 0. deeply set in the spatula on the proleg
 1. not deeply set in the spatula on the proleg
86. Crochet remnants of an outer row
 0. present on some specimens
 1. never present
87. Prolegs (fleshy lobe)
 0. with a fleshy lobe that gives the crochets a more or less C-shaped pattern
 1. without a fleshy lobe so that middle crochets appear of similar size to those on the sides
88. D scoli on A8 (fusion)
 0. fused on dorsomeson
 1. not fused on dorsomeson
89. Middorsal scoli on A8 (shape)
 0. long, with spines, primary setae arising from different lobes
 1. long, with spines, primary setae do not arise from different lobes
 2. long, without spines
 3. short, without spines
90. D2 scoli on A9 (fusion)
 0. fused into a middorsal scoli
 1. not fused
91. Middorsal scoli on A9 (shape)
 0. shape resembling thoracic D scoli
 1. short without spines
92. SV on A9
 0. prominent
 1. relatively inconspicuous
93. Lateral plate of A10
 0. with scoli separate
 1. shows some fusion of scoli
94. Number of setae on lateral plate of proleg on A10
 0. 5
 1. 6
 2. 4
95. Last instar larva
 0. with D scoli on T2 conspicuously distinct and projecting
 1. with D scoli on T2 not projecting
96. D and SD scoli on abdomen
 0. as large as those on T2-T3
 1. short, but evident
 2. inconspicuous
97. Abdominal D and SD
 0. silver or nacreous on the outside
 1. not silver or nacreous on the outside
98. Cremaster (pupa)
 0. bifid
 1. not bifid

APPENDIX 2

DATA MATRICES

Data matrix for the outgroup (*Oxytenis*, *Arsenura*, *Dysdaemonia*) and 33 taxa of Ceratocampinae (27 genera, two subgenera and six species groups) used in the cladistic analysis. For the character state descriptions, see APPENDIX 1. Characters are numbered starting at "0" to conform with Hennig86. Missing data and variable characters were scored as "?".

Taxa	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>Oxytenis</i>	2	?	2	2	0	2	?	0	0	?	3	0	0	1	1
<i>Arsenura</i>	1	0	2	?	0	0	?	0	1	?	?	1	0	1	1
<i>Dysdaemonia</i>	1	0	2	1	0	0	?	0	1	?	0	1	0	1	1
<i>Eacles</i>	0	0	1	0	1	0	1	0	0	0	1	0	0	1	1
<i>Bathyphebia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Citheronia</i>	0	0	1	0	1	0	1	0	0	0	1	1	0	0	1
<i>Procitheronia</i>	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1
<i>Schausiella</i>	0	0	1	0	1	2	1	0	0	0	2	0	0	1	1
<i>Othorene</i>	0	0	1	0	1	2	0	0	0	1	2	?	0	1	1
<i>Cicia</i>	0	0	1	0	1	1	0	0	0	1	2	?	0	1	1
<i>Dacunju</i>	0	0	1	0	1	2	0	0	0	1	2	?	0	1	1
<i>Giacomellia</i>	0	0	1	0	1	2	1	0	0	1	1	?	0	1	1
<i>Almeidella</i>	0	0	1	0	1	1	1	0	0	0	1	0	0	1	0
<i>Psilopygoides</i>	0	0	0	0	1	2	1	0	0	0	1	?	0	1	1
<i>Ceropoda</i>	0	0	0	0	1	2	0	0	0	0	2	?	0	1	1
<i>Mielkesia</i>	0	0	1	0	1	2	1	0	0	?	?	?	0	1	1
<i>Psilopygida</i> (P.)	0	0	1	0	1	1	1	0	0	0	1	1	0	0	1
<i>Psilopygida</i> (Psigida)	0	0	1	0	1	1	1	0	0	0	1	1	0	0	1
" <i>S. molina</i> " group	0	0	1	0	1	2	1	0	0	1	1	1	0	0	1
" <i>S. quadrilineata</i> " group	0	0	1	0	1	2	1	0	0	1	1	1	0	0	1
" <i>S. bisecta</i> " group	0	0	1	0	1	2	1	0	0	1	1	1	0	0	1
" <i>S. bicolor</i> " group	0	0	1	0	1	1	1	0	0	1	1	1	0	0	1
" <i>S. amena</i> " group	0	0	1	0	1	1	1	0	0	1	1	1	0	0	1
" <i>S. ocellata</i> " group	0	0	1	0	1	2	1	0	0	1	1	1	0	0	1
<i>Anisota</i>	1	1	1	0	1	2	1	0	0	0	1	0	1	1	1
<i>Dryocampa</i>	1	1	1	0	1	1	1	0	0	0	1	0	1	1	1
<i>Adeloneivaia</i>	0	1	1	0	1	2	1	0	1	0	2	0	0	0	0
<i>Adelowalkeria</i>	0	0	1	0	1	2	1	0	0	0	1	0	0	0	1
<i>Megaceresa</i>	0	0	0	0	1	2	1	0	0	0	1	1	0	0	1
<i>Rachesa</i>	0	0	0	0	1	2	1	0	0	0	1	?	0	0	1
<i>Ceratesa</i>	0	0	1	0	1	2	1	0	0	0	1	0	0	0	1
<i>Scolesa</i>	0	0	1	0	1	2	1	0	0	0	1	0	0	0	1
<i>Citioica</i>	0	0	1	0	1	2	1	0	0	0	1	0	0	0	1
<i>Oiticella</i>	0	0	1	0	1	2	1	0	0	0	1	0	0	0	1
<i>Ptiloscota</i>	0	0	1	0	1	2	1	0	0	0	1	0	0	0	1
<i>Neorcarnegia</i>	0	0	1	0	1	0	1	0	0	0	1	0	0	1	1

Taxa	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
<i>Oxytenis</i>	1	1	1	0	1	0	1	0	0	1	1	1	0	0	0
<i>Arsenura</i>	0	1	0	0	0	0	1	0	0	?	?	?	0	0	0
<i>Dysdaemonia</i>	0	1	0	0	0	0	1	0	0	?	?	?	0	0	0
<i>Eacles</i>	0	0	1	0	0	0	0	0	0	?	?	0	0	0	0
<i>Bathyphebia</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Citheronia</i>	?	0	1	0	0	0	1	0	0	1	1	0	0	0	0
<i>Procitheronia</i>	?	0	1	0	0	0	1	0	0	1	1	0	0	0	0
<i>Schausiella</i>	1	0	1	1	0	0	1	0	1	1	1	0	0	0	0
<i>Othorene</i>	0	0	1	1	1	0	1	1	0	1	1	0	0	0	1
<i>Cicia</i>	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1
<i>Dacunju</i>	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1
<i>Giacomellia</i>	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1
<i>Almeidella</i>	1	0	1	1	2	0	1	0	0	0	0	0	0	0	1
<i>Psilopygoides</i>	2	0	1	1	1	0	0	?	0	1	1	0	0	0	1
<i>Ceropoda</i>	0	0	1	1	1	0	1	1	0	0	0	0	0	0	1
<i>Mielkesia</i>	0	0	1	1	1	0	1	?	?	?	?	0	0	0	1
<i>Psilopygida</i> (P.)	1	0	1	1	1	0	0	0	2	0	0	0	0	0	1
<i>Psilopygida</i> (Psigida)	1	0	1	1	1	0	0	0	2	0	0	0	0	0	1
"S. molina" group	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1
"S. quadrilineata" group	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1
"S. bisecta" group	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1
"S. bicolor" group	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1
"S. amena" group	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1
"S. ocellata" group	1	0	1	1	1	0	1	1	0	0	1	0	0	0	1
<i>Anisota</i>	1	0	1	1	1	1	2	0	2	0	0	0	1	1	0
<i>Dryocampa</i>	1	0	1	1	1	1	2	0	2	0	0	0	1	1	0
<i>Adeloneivaia</i>	1	0	1	1	1	0	0	0	0	1	1	0	0	0	1
<i>Adelowalkeria</i>	0	0	1	1	1	0	1	0	0	1	1	0	0	0	1
<i>Megaceresa</i>	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1
<i>Rachesa</i>	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1
<i>Ceratesa</i>	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1
<i>Scolesa</i>	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1
<i>Citioica</i>	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1
<i>Oiticella</i>	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1
<i>Ptiloscota</i>	0	0	1	1	1	0	1	0	0	1	0	0	0	0	1
<i>Neorcarnegia</i>	1	0	1	1	0	0	1	0	0	1	1	0	0	0	1

Taxa	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
<i>Oxytenis</i>	0	1	?	?	0	0	?	1	0	1	?	0	0	0	0
<i>Arsenura</i>	0	1	1	1	1	0	1	1	0	2	0	0	2	0	0
<i>Dysdaemonia</i>	0	1	1	1	1	0	1	1	0	2	0	0	2	0	0
<i>Eacles</i>	0	0	0	1	0	0	0	0	1	0	0	0	?	0	0
<i>Bathyphebia</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Citheronia</i>	0	0	1	1	1	0	0	0	0	0	1	1	2	0	0
<i>Procitheronia</i>	0	0	1	1	1	0	0	0	0	0	0	0	2	1	0
<i>Schausiella</i>	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0
<i>Othorene</i>	1	0	1	1	1	0	1	1	0	0	0	0	1	1	0
<i>Cicia</i>	2	0	1	1	1	0	1	1	0	0	1	0	?	1	0
<i>Dacunju</i>	2	0	1	1	1	0	1	2	0	0	1	0	1	1	0
<i>Giacomellia</i>	1	0	1	1	1	1	1	1	0	0	1	3	1	1	0
<i>Almeidella</i>	1	0	1	1	1	0	?	2	0	0	1	2	1	1	0
<i>Psilopygoides</i>	0	1	1	1	1	0	0	2	0	0	1	2	0	1	0
<i>Ceropoda</i>	2	0	1	1	1	1	1	1	0	0	1	0	0	1	0
<i>Mielkesia</i>	?	0	1	1	1	0	1	1	0	0	1	2	?	?	0
<i>Psilopygida</i> (P.)	1	0	1	1	1	0	0	2	0	0	?	0	1	1	1
<i>Psilopygida</i> (Psigida)	1	0	1	1	1	0	0	2	0	0	1	?	1	1	1
" <i>S. molina</i> " group	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0
" <i>S. quadrilineata</i> " group	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0
" <i>S. bisecta</i> " group	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0
" <i>S. bicolor</i> " group	1	0	1	1	1	0	0	1	0	0	1	0	1	1	0
" <i>S. amena</i> " group	1	0	1	1	1	0	0	1	0	0	0	0	0	1	0
" <i>S. ocellata</i> " group	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0
<i>Anisota</i>	1	0	0	1	?	1	?	0	0	1	?	0	1	1	0
<i>Dryocampa</i>	1	0	0	1	1	0	0	0	0	1	1	2	1	1	0
<i>Adeloneivaia</i>	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0
<i>Adelowalkeria</i>	1	0	1	1	1	0	1	0	0	1	0	0	1	1	0
<i>Megaceresa</i>	1	0	1	1	1	0	1	2	0	1	0	0	0	1	0
<i>Rachesa</i>	1	0	1	1	1	0	1	0	0	1	0	0	0	1	0
<i>Ceratesa</i>	1	0	1	1	1	1	1	2	0	0	1	2	1	1	1
<i>Scolesa</i>	2	0	1	1	1	0	1	2	0	0	1	?	1	1	0
<i>Citioica</i>	1	0	1	1	1	0	1	2	0	0	0	0	0	1	0
<i>Oiticella</i>	1	0	1	1	1	0	0	2	0	0	0	0	?	1	0
<i>Ptiloscota</i>	1	0	1	1	1	0	0	2	0	1	?	?	0	1	0
<i>Neorcarnegia</i>	2	1	0	0	0	0	1	0	0	2	0	0	2	0	0

Taxa	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
<i>Oxytenis</i>	1	0	?	0	?	0	?	0	0	0	0	0	?	1	1
<i>Arsenura</i>	0	0	2	0	0	1	2	0	0	0	0	0	?	1	1
<i>Dysdaemonia</i>	1	0	2	0	0	1	2	0	0	0	0	0	?	1	1
<i>Eacles</i>	0	0	2	0	0	1	0	0	1	0	0	0	1	1	0
<i>Bathyphebia</i>	0	0	2	0	0	1	2	0	0	0	0	0	0	1	0
<i>Citheronia</i>	0	0	2	0	0	1	0	0	0	0	0	0	1	0	0
<i>Procitheronia</i>	0	0	2	0	0	1	0	0	0	0	0	0	1	0	0
<i>Schausiella</i>	0	0	2	1	0	1	0	0	0	?	0	0	1	1	0
<i>Othorene</i>	0	0	2	0	0	1	1	0	1	0	0	0	2	1	0
<i>Cicia</i>	0	0	2	0	0	1	1	0	1	?	0	0	1	1	0
<i>Dacunju</i>	0	1	?	0	?	1	1	0	0	0	0	0	1	1	0
<i>Giacomellia</i>	0	0	2	0	0	1	1	0	1	0	0	0	1	1	0
<i>Almeidella</i>	0	0	2	1	0	1	0	0	1	0	0	0	2	1	0
<i>Psilopygoides</i>	0	0	2	0	0	1	0	0	1	0	0	0	3	1	0
<i>Ceropoda</i>	0	0	1	0	0	0	?	?	1	0	0	1	1	1	0
<i>Mielkesia</i>	0	0	1	0	0	0	?	0	1	0	0	1	1	1	0
<i>Psilopygida (P.)</i>	1	0	?	1	1	1	3	0	1	0	0	0	2	1	0
<i>Psilopygida (Psigida)</i>	1	0	?	1	1	1	3	0	1	0	0	0	2	1	0
" <i>S. molina</i> " group	0	0	0	1	1	1	0	0	1	0	0	0	1	1	0
" <i>S. quadrilineata</i> " group	0	0	0	1	1	1	0	0	1	0	0	2	1	1	0
" <i>S. bisecta</i> " group	?	0	0	1	1	1	0	0	1	1	0	2	1	1	0
" <i>S. bicolor</i> " group	0	0	0	1	1	1	0	0	1	0	0	0	1	1	0
" <i>S. amena</i> " group	1	0	0	1	1	1	0	0	1	0	0	2	1	1	0
" <i>S. ocellata</i> " group	1	0	0	1	1	1	0	0	1	0	0	2	1	1	0
<i>Anisota</i>	0	0	0	1	1	1	0	0	1	0	0	0	2	1	0
<i>Dryocampa</i>	0	0	0	1	1	1	0	0	1	0	0	0	0	1	0
<i>Adeloneivaia</i>	0	0	0	0	0	0	?	0	0	0	0	0	3	1	0
<i>Adelowalkeria</i>	?	0	0	0	0	0	?	0	0	0	1	0	?	1	0
<i>Megaceresa</i>	0	0	0	0	0	0	?	0	0	0	1	0	3	1	0
<i>Rachesa</i>	1	0	0	0	0	0	?	0	0	0	1	0	2	1	0
<i>Ceratesa</i>	0	0	0	0	0	0	?	0	0	0	1	0	2	1	0
<i>Scolesa</i>	0	0	0	0	0	0	?	0	0	1	1	0	?	1	0
<i>Citioica</i>	0	0	1	0	0	0	?	0	0	1	1	0	0	1	0
<i>Oiticella</i>	0	0	1	0	0	0	?	0	0	0	1	0	0	1	0
<i>Ptiloscola</i>	1	0	0	0	0	0	?	1	0	1	1	0	?	1	0
<i>Neorcarnegia</i>	1	0	2	0	0	1	2	0	0	0	0	0	3	1	0

[illegible]

[illegible]

[illegible]

APPENDIX 3

NUMBER OF STEPS, CI, RI AND FINAL CHARACTER WEIGHTS

Number of steps, CI, and RI for each adult character used in the analysis after the successive weighting (54 trees).

best fits

Chars	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Steps	3	2	6	2	3	8	3	0	2	3	7	5	1	4	2	5	1	1	2
ci	66	50	33	100	33	25	33	100	50	33	42	20	100	25	50	40	100	100	50
ri	66	50	33	100	50	50	50	100	50	77	42	66	100	81	0	78	100	100	83

Chars	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Steps	3	1	5	2	2	4	6	1	1	1	3	4	2	3	2	3	4	4	9
ci	66	100	40	50	100	25	16	100	100	100	33	50	50	33	50	33	25	25	22
ri	85	100	50	90	100	70	66	100	100	100	77	83	80	50	0	50	0	78	65

Chars	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Steps	1	5	6	7	9	2	2	7	1	4	2	1	3	4	1	4	4	1	2
ci	100	40	16	42	22	50	50	14	100	50	50	100	33	75	100	25	25	100	100
ri	100	62	58	0	46	85	50	25	100	86	90	100	81	85	100	82	0	100	100

Chars	57	58	59
Steps	8	1	1
ci	37	100	100
ri	58	100	100

worst fits

Chars	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Steps	3	2	6	2	3	8	4	0	2	3	8	5	1	4	2	5	1	1	2
ci	66	50	33	100	33	25	25	100	50	33	37	20	100	25	50	40	100	100	50
ri	66	50	33	100	50	50	25	100	50	77	28	66	100	81	0	78	100	100	83

Chars	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Steps	3	1	5	2	2	4	6	1	1	1	3	4	2	3	2	3	4	4	9
ci	66	100	40	50	100	25	16	100	100	100	33	50	50	33	50	33	25	25	22
ri	85	100	50	90	100	70	66	100	100	100	77	83	80	50	0	50	0	78	65

Chars	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
Steps	1	5	7	7	9	2	2	7	1	4	2	1	3	4	1	4	4	1	2
ci	100	40	14	42	22	50	50	14	100	50	50	100	33	75	100	25	25	100	100
ri	100	62	50	0	46	85	50	25	100	86	90	100	81	85	100	82	0	100	100

Chars	57	58	59
Steps	9	1	1
ci	33	100	100
ri	50	100	100

Final weights after successive weighting for the 60 characters used in the analysis of the adults.

Character	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Final weight	4	2	1	10	1	1	1	10	2	2	1	1	10	2	0
Character	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Final weight	3	10	10	4	5	10	2	4	10	1	1	10	10	10	2
Character	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Final weight	4	4	1	0	1	0	2	1	10	2	0	0	1	4	2
Character	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
Final weight	0	10	4	4	10	2	6	10	2	0	10	10	2	10	10

Number of steps, CI, and RI for each larval character used in the analysis after the successive weighting (three trees).

best fits

Chars	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Steps	1	1	1	2	3	2	1	2	1	1	2	1	8	4	1	5	2	3	2
ci	100	100	100	50	33	100	100	100	100	100	100	100	100	75	100	80	50	66	50
ri	100	100	100	0	50	100	100	100	100	100	100	100	100	50	100	75	0	0	83

Chars	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Steps	3	1	5	3	3	2	1	2	1	2	3	1	1	1	1	3	1	4	2
ci	100	100	80	66	66	100	100	50	100	50	100	100	100	100	100	66	100	50	50
ri	100	100	66	75	75	100	100	66	100	50	100	100	100	100	100	50	100	60	75

Chars	38
Steps	1
ci	100
ri	100

worst fits

Chars	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Steps	1	1	1	2	3	3	1	2	1	1	2	2	8	4	1	5	2	3	2
ci	100	100	100	50	33	66	100	100	100	100	100	50	100	75	100	80	50	66	50
ri	100	100	100	0	50	75	100	100	100	100	100	83	100	50	100	75	0	0	83

Chars	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Steps	3	2	5	3	3	2	1	2	1	2	3	1	1	1	1	3	1	4	2
ci	100	50	80	66	66	100	100	50	100	50	100	100	100	100	100	66	100	50	50
ri	100	75	66	75	75	100	100	66	100	50	100	100	100	100	100	50	100	60	75

Chars	38
Steps	1
ci	100
ri	100

Final weights after successive weighting for the 99 characters used in the analysis of the adults and larvae (one tree).

Character	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Final weight	4	10	10	10	10	4	10	10	10	10	0	2	10	2	10
Character	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Final weight	1	10	10	3	3	10	10	10	10	1	2	10	10	10	10
Character	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Final weight	10	3	2	10	0	10	1	5	10	2	0	10	1	10	10
Character	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59
Final weight	0	10	5	2	3	2	10	10	2	0	10	10	0	10	10
Character	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Final weight	10	10	10	0	1	5	10	10	10	10	10	4	10	3	10
Character	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89
Final weight	6	0	0	4	10	3	5	5	5	10	10	3	10	2	10
Character	90	91	92	93	94	95	96	97	98						
Final weight	10	10	10	10	3	10	3	3	10						