

CLADISTICS AND CLASSIFICATION
OF THE NOTODONTIDAE
(LEPIDOPTERA: NOCTUOIDEA)
BASED ON LARVAL AND
ADULT MORPHOLOGY

JAMES S. MILLER

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JAMES S. MILLER
Kalbfleisch Curatorial Fellow
Department of Entomology
American Museum of Natural History

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ABSTRACT

A phylogeny for the Notodontidae was constructed based on cladistic relationships among 52 notodontid species. The study included taxa from all previously recognized family group categories and all biogeographic regions. Twelve species, chosen from the rest of the Noctuoidea, served as an outgroup. The data set consisted of 174 morphological characters (100 from adults and 74 from final instar larvae) comprising 437 character states. Cladistic analyses using the Hennig86 parsimony program produced eight equally parsimonious trees, each with a length of 853 steps, a consistency index of 0.30, and a retention index of 0.66.

All morphological characters are described and all character states are figured using line drawings, photographs, and scanning electron micrographs. Adult and larval habitus photographs for taxa used in the analysis are also included.

The Notodontidae, as here defined, is a monophyletic group. Six adult and five larval synapomorphies support monophyly, but none occur universally. The genus *Doa* Neumoegen and Dyar (Doidae) is hypothesized to be the sister-group of the Notodontidae. *Oenosandra* Walker, an Australian genus formerly referred to the notodontid subfamily Thaumetopoeinae, is instead placed as the sister group of Doidae + Notodontidae. The Oenosandridae, new family, is proposed.

In a reclassification of the Notodontidae, nine monophyletic subfamilies are recognized: the Thaumetopoeinae, Pygaerinae, Platychasmatinae, Notodontinae, Phalerinae, Dudusinae, Heterocampinae, Nystaleinae, and Dioprinae. The Hemiceratini of previous authors is of uncertain status, and placement of the genus *Lirimiris* requires further research. The new tribe Scranciini is placed in the Dudusinae. A key to notodontid subfamilies is presented, and apomorphic character states, as well as diagnoses, are listed for each group.

General topics related to phylogeny of the Notodontidae are discussed. First, the question of whether taxon addition will affect the proposed classification is addressed. *Platychasma virgo* Butler, previously placed in its own notodontid subfamily, the Platychasmatinae, is used as a test case. When added to the analysis this species arises as a basal lineage in the Notodontidae. Topology in the rest of the cladogram is unaffected. The subfamily Platychasmatinae is retained.

The proposed hypothesis of relationships among subfamilies is roughly similar to previous concepts of notodontid phylogeny. For example, the current scheme supports placement of the Thaumetopoeinae and Pygaerinae as basal groups and placement of the Dioprinae and Nystaleinae as derived sister groups. However, in most other respects this new phylogeny differs from previous hypotheses.

Larval and adult data were also analyzed separately. Consensus trees for larvae and for adults show poor resolution compared to the tree based on all data. Monophyly of some subfamilies (e.g., the Dudusinae) is supported exclusively by adult synapomorphies, and of others (e.g., the Heterocampinae) by larval characters. These results suggest that constructing a stable classification for the Notodontidae requires data from both life stages.

As a group, the Notodontidae do not show obvious larval host association patterns. Nevertheless, cladistic analyses suggest that almost all Salicaceae-feeders belong in a monophyletic group and that, for the most part, Fagaceae specialists are restricted to the Heterocampinae. The Dioprinae, unique among Notodontidae in being diurnal and in typically feeding on toxic plants, appear to have evolved from a nocturnal ancestor that utilized nontoxic hosts.

INTRODUCTION

My interest in notodontid classification and phylogeny arose through an ongoing study of dioprine moths. Dioptrines have been accorded family status since Walker (1865), but Minet (1983, 1986) and Weller (1989) recently suggested that the group is subordinate within the Notodontidae; both authors recognized the tribe Dioptrini within the subfamily Notodontinae. My original intention was to test these hypotheses with the hopes of firmly establishing monophyly of the Dioptrini and precisely identifying their sister group in

preparation for an analysis of generic relationships. It soon became apparent, however, that our understanding of notodontid phylogeny is rudimentary and that the family classification is in disarray. I decided that firmly establishing the sister group of the Dioptrini would require a phylogenetic analysis of all major notodontid groups.

This research has three aims. The first is to provide additional synapomorphies for the Notodontidae. Only two are commonly cited: presence of two, rather than one, micro-

scopic proprioceptor (MD) setae on segment 1 of the larval abdomen (Hinton, 1946; Common, 1979), and presence of a ventrally directed metathoracic tympanum in adults (Richards, 1932). However, dioptine larvae have a single MD seta on the first abdominal segment (Weller, 1989), the condition found in all other Lepidoptera. Further, species of the genus *Doa* (Doidae) possess a ventrally directed tympanum (Richards, 1932). Thus, neither apomorphy provides conclusive evidence of membership in the Notodontidae. Godfrey et al. (1989) discussed two apomorphic larval traits that are widespread among notodontids: the presence of stipital lobes and a smooth, rather than serrate, mandibular margin. However, again neither character provides unambiguous evidence for monophyly of the family, since some notodontid larvae have serrate mandibles, and thaumetopoeines lack stipital lobes (Godfrey et al., 1989).

The second aim of this project is to provide a comprehensive analysis of notodontid adult and larval morphology. The study of immature stages, especially larvae, has played a pivotal role in notodontid systematics since Packard's (1895a) pioneering work on classification of North American species. Yet since that time, there have been no detailed comparative studies of larval morphology for the Notodontidae, even though our knowledge of lepidopteran larval structure has advanced tremendously, especially with the advent of the scanning electron microscope. Similarly, recent authors have discovered new adult characters in various noctuoid groups, but these have not been considered in a comprehensive study for the Notodontidae. In addition to reexamining and reanalyzing previously available character information, in this paper I describe new character systems.

Third, I propose a revised subfamilial classification for the Notodontidae. Because it is a fairly large family (approximately 3500 described species; Seitz, 1932; Weller, 1989), my approach was to analyze cladistic relationships among a selected set of taxa. Fifty-two species (table 1) were chosen to represent previously recognized subfamilies and tribes in the Notodontidae, including the Thaumetopoeinae (or Thaumetopoeidae of some authors) and Dioptini. Among the few exist-

ing studies of notodontid phylogeny and classification, none have treated the world fauna; I attempted to include taxa from every biogeographic region. I performed parsimony analyses of the morphological data set, and the resulting cladograms are used as justification for a revised classification. My classification is not intended to be definitive, but it does represent an advance over previous ones. I hope it can provide a stable framework for a classification of the world notodontid fauna.

In addition to the three main goals outlined above, I address four questions of general interest. First, I examine the effects on my classification of taxon addition using the species *Platychasma virgo* Butler, which became available late in my study, as an example. Next, I discuss hypotheses of relationship among notodontid subfamilies. Third, I compare the topology of cladograms produced by data on larvae with those produced by data on adults and discuss the implications for classification of the Notodontidae. Finally, I examine host associations in the Notodontidae in light of my cladistic hypotheses to see whether clear patterns emerge.

MONOPHYLY OF THE NOCTUOIDEA

I follow most authors (e.g., Forbes, 1923, 1948; Richards, 1932; Bourgogne, 1951; Brock, 1971; Watson et al., 1980; Franclemont, 1983; Minet, 1983, 1986; Kristensen, 1985; Weller, 1989) in recognizing the superfamily Noctuoidea to include the Noctuidae, Arctiidae, and Lymantriidae, plus the Notodontidae and their relatives. Some workers (e.g., d'Almeida, 1932; Kiriakoff, 1970a, 1970b; Pinhey, 1975; Common, 1979; Tikhomirov, 1981; Barlow, 1982) have placed the notodontids in a separate superfamily, the Notodontioidea. Presence of the metathoracic tympanal organ shows that these families, including the Notodontidae, form a monophyletic group (Nielsen, 1989). There is little doubt that the noctuoid tympanum is apomorphic within the Lepidoptera, and at present I see no reason to question the hypothesis that the structure is homologous in all these groups.

Richards (1932) divided the noctuoid families into two categories: those with "trifid"

forewing venation and those with "quadrid" venation. These terms refer to whether the cubital vein system appears either three-branched, with vein M2 approximately halfway between M1 and M3, or four-branched, with M2 arising close to the base of M3 (see Character 35). I follow Richards's terminology. The trifold Noctuoidea have historically included the family group categories Notodontidae, Thaumetopoeidae (Thaumetopoeinae), and Dioptidae (Dioptini). The quadrid families thus include the rest of the Noctuoidea and constitute the outgroup for this study. These group names should not be confused with the terminology that has been applied to two major divisions of the Noctuidae (see discussion in Kitching, 1984a). In noctuids, "Trifidae" and "Quadridae" are sometimes used to refer to a similar condition of the cubital and medial veins in the hind wing (see Character 42).

The only published branching diagrams of noctuid higher group relationships are those of Forbes (1923) and Richards (1932). Both authors argued that the trifold Noctuoidea are more primitive than the quadrids. Brock claimed that the Notodontidae "show the least modification in the superfamily [Noctuoidea]" (1971: 78). Subsequent workers have followed this suggestion (e.g., Holloway et al., 1987; Weller, 1989), and it is now generally regarded that the notodontid lineage is the sister group to the rest of the Noctuoidea. I will discuss these hypotheses as they relate to my results in the section entitled Classification of the Notodontidae.

THE TRIFID NOCTUOIDEA

Four family level groups have been placed in the trifold Noctuoidea (Notodontidae of authors): the Thyretidae, the Thaumetopoeidae, the Dioptidae, and the Notodontidae. As discussed above, proposed synapomorphies for these taxa include a tympanal membrane that faces ventrally and two MD setae rather than one on segment A1 of the larva. A third potential synapomorphy is the presence of socii in the male genitalia (Pierce and Beirne, 1941; Tikhomirov, 1981). Each of these characters is discussed in detail in the section entitled Character Analysis, and synapomorphies are summarized in the section

entitled Monophyly of the Notodontidae. Below I give a brief overview for each of the four groups.

The Thyretidae, first recognized by Kiriakoff (1949), is a fairly small family comprising approximately 200 species restricted to Africa (Kiriakoff, 1953, 1960). Kiriakoff (1949, 1953) proposed that they are related to notodontids, arguing that both groups have similar tympanal morphologies. He was followed by Pinhey (1975) and Common (1979). Minet (1983, 1986), with some reservations, considered thyretids to be a subfamily of the Notodontidae. However, even though Pinhey (1975) and Kiriakoff (1949) noted that thyretids have quadrid rather than trifold forewing venation, neither questioned their relationship to notodontids. Recent study has shown that thyretid adults possess a metepisternal tymbal organ (see Character 29), indicating membership in the Arctiidae (Holloway et al., 1987; Weller, 1989). Therefore, the family will not be discussed further in this paper.

The processionary moths, an Old World group, have been recognized as either a notodontid subfamily (Aurivillius, 1889; Turner, 1903, 1922; Sick, 1940; Börner, 1944; Bourgogne, 1951; Common, 1979; Minet, 1983) or a separate family, the Thaumetopoeidae (e.g., Staudinger and Rebel, 1901; Forbes, 1948; Kiriakoff, 1970b; Pinhey, 1975; Watson et al., 1980). The caterpillars spend the day communally in a silk nest of up to 600 individuals and leave the nest at night to feed (Holland, 1893a; Pinhey, 1975; Common, 1979). Larvae travel end-to-end in a continuous "procession" (Bourgogne, 1951; Pinhey, 1975; Carter, 1982), giving the group its common name. The caterpillars bear dorsal tufts of deciduous setae that can cause skin irritations (Common, 1979; Carter, 1982; see Character 157).

The family name Dioptidae was first proposed by Walker (1865), but the group's phylogenetic position has been controversial. There are approximately 400 described diopline species (Bryk, 1930), and all (with the exception of one North American endemic; see Miller, 1987a) are Neotropical in distribution. Most are relatively small, diurnal, and brightly colored (Hering, 1925), but the group as a whole is extremely diverse in both ap-

pearance and habit (Köhler, 1930). Dioptine species are involved in numerous, widely disparate mimicry complexes. Dioptines bear little resemblance to other Notodontidae (Jordan, 1923b) and early workers were unsure of the group's placement in lepidopteran classification; according to Hering, "There is probably no family that posed such great difficulties to the specialists of former times, as the Dioptidae did" (1925: 501). Seitz claimed that "mimicry chiefly caused this confusion, because even expert specialists confounded mimetic resemblance with phyletic resemblance" (1925: 499). Most early lepidopterists relied entirely on superficial adult characters, such as wing pattern, wing venation, and shape of the labial palpi, in their attempts to place species in natural groupings. The study of lepidopteran genitalic morphology, an important source of character information, did not become common until the 1940s. Dioptines were first considered to be close relatives of the Geometridae (Packard, 1895a) or Arctiidae (Dyar, 1896). Early workers, such as Druce (1907) and Dognin (1916), described many species in the geometrid subfamily Cyllopodinae, but dioptines have also been described in groups as far removed as the Psychidae (see Miller, 1987a).

Interestingly, one of the first researchers to notice a morphological similarity between the Dioptidae and Notodontidae was Bodine (1896) in his comparative study of lepidopteran antennae. Later, morphology of immatures provided convincing evidence of a close relationship between the two groups (Fracker, 1915; Mosher, 1916). Forbes (1922a) originally thought that the metathoracic tympanum was absent in adult dioptines, and he therefore placed them at the base of the Noctuoidea. A short time later Forbes acknowledged that a tympanum does occur and revised his assessment of the group's phylogenetic position, stating that "at present the family is not really distinguished from the Notodontidae in any very tangible

way" (1922b: 71). This view has subsequently prevailed, and in fact, when the details of adult and larval morphology are compared, the similarities between dioptines and other notodontids are clear (Köhler, 1930; Franclemont, 1970; Minet, 1983, 1986; Miller, 1987a, 1988a; Weller, 1989).

The family name Notodontidae was first proposed by Stephens (1829), whose familial concept was remarkably accurate given the rudimentary state of morphological knowledge at that time. He provided a family diagnosis based on superficial adult and larval characters, and placed 14 British genera in the group. The taxonomic history of the Notodontidae was recently reviewed by Weller (1989), who estimated the group to include 3500 species. It is worldwide in distribution, but over half the species occur in the Neotropics (Seitz, 1932; Weller, 1989). It was Dyar (1897) who first placed the family in the Noctuoidea.

Among recent workers, the concept of the family Notodontidae has broadened. The Thaumetopoeidae are now often regarded as being a subfamily and, a more controversial issue, the Dioptidae are considered a tribe (Diopitini) of the subfamily Notodontinae. Brock may have been the first to suggest that the Dioptidae should not be accorded family status, briefly noting (without further explanation) that dioptids "probably [belong] in the Notodontidae" (1971: 33). Minet noted that, like specialized notodontids, the larval anal prolegs of dioptids are reduced or absent (1983: 368), and he therefore gave them tribal status in the subfamily Notodontinae. Weller (1989) regarded the Diopitini and Hemiceratini, the latter a Neotropical tribe (Forbes, 1939a), as sister groups. Further, those two tribes together were considered to be the sister group of the Nystaleini. The hypotheses of Minet and Weller will be discussed in detail in my discussion of notodontid classification.

PREVIOUS WORKS ON THE NOTODONTIDAE

This section is intended to familiarize the reader with important taxonomic studies on the Notodontidae. I leave detailed discussion of previous classifications for a later section

(see Classification of the Notodontidae) where I compare them with my own.

Dyar (1897) remains the only previous author to revise and classify the Notodontidae

on a world level, treating the species of North America, Europe, and India, the only faunas adequately known at the time. He discussed 65 genera, giving generic keys and lists of included species. He divided the Notodontidae of Packard (1895a) into three families: the Ptilodontidae, the Melalophidae (= Pygaerinae), and the Eupterotidae (= Apatelodidae). The last, placed by most early workers in the Notodontidae, is now considered a family in the Bombycoidea (Forbes, 1939a; Franclemont, 1983). Dyar based his generic classification on superficial external adult and larval characters. Gaede's (1934) catalog is the only existing species list for the world fauna. Although an extremely useful work, it is outdated and badly in need of revision. Almost all other studies on the family have taken a regional approach. The vast majority are essentially faunal lists with descriptions of new taxa, and few authors have proposed supergeneric classifications.

The North American notodontid fauna, comprising 138 species (Franclemont, 1983), has been examined in reasonable detail. Packard's (1895a) volume is the most comprehensive study ever published on the Notodontidae. Packard gave diagnoses and keys for 69 species in 21 genera, providing adult and larval descriptions, host-plant records, drawings of pupae, color figures of many larvae, and photographs of adults. His classification remains one of the most detailed yet proposed. Neumoegen and Dyar's (1894a, 1894b) work complements that of Packard, but it is less comprehensive. They recognized 79 North American species in 23 genera. Their classification differs little from Packard's.

Forbes (1948) and Franclemont, in *Lepidoptera of New York and Neighboring States*, gave keys and diagnoses for 58 notodontid species in 20 genera. Where known, larval diagnoses and host-plant records were presented. Their work is particularly valuable in that most of the species they discussed occur throughout eastern North America. The family classification proposed, based largely on Packard (1895a), Dyar (1897), and Neumoegen and Dyar (1894a, 1894b), is the one most widely used today.

Godfrey and Appleby (1987) listed general larval characters for the family and provided diagnoses and photographs for caterpillars of

21 North American species in 16 genera. Their work is a guide to larval identification and does not address family classification.

Compared with the Notodontidae of America north of Mexico, the fauna southward is much larger (Seitz, 1932; Weller, 1989) and is poorly understood (Forbes, 1948). The Neotropical literature was reviewed by Weller (1989), so below I describe only the major papers.

An important early work is that of Schaus (1901). His key treated 113 genera, of which 40 were described as new. Although some of these genera are North American, Schaus deferred to Packard's (1895a) work concerning those and instead concentrated on the Neotropical taxa. Schaus described 75 Neotropical notodontid species, as well as the larvae of several taxa. No family level categories were discussed.

Druce (1887) listed 154 species (in 40 genera) of Notodontidae, 32 of which were newly described. However, some of the genera were incorrectly placed; an example is the large genus *Gonodonta* Hübner, now in the Noctuidae. For each species, Druce gave reference to the original description and provided detailed locality information. In 1898, Druce provided additional locality data for some taxa and described 14 more species.

Dyar (1908) described 5 genera and 32 species from the collections of the United States National Museum. Sixteen of these new species were in the large and taxonomically difficult genus *Hemiceras* Guenée, for which Dyar presented a key to the 97 species known at that time.

Draudt's (1932) study of the Neotropical notodontid fauna treated close to 1500 species, 67 newly described. He did not write a generic key, but did outline diagnostic features for 157 genera based largely on wing venation. This remains the single most important work on Central and South American Notodontidae and, because adults of many taxa are figured, it provides the only means for identifying species aside from reading the original descriptions. Like Dyar (1908), Draudt presented a key to the species of *Hemiceras*, which by 1932 numbered over 150. Draudt's classification was rudimentary. He placed three genera (*Datana*, *Ichthyura*, and *Rosema*) in the subfamily Melalophinae (= Pygaerinae), diagnosed by having "hairy

larvae," and the other 154 genera in the Notodontinae, with no distinguishing subfamilial characters given.

Another extremely important study is that of Forbes (1939a; see also Forbes, 1942). Although the fauna of Barro Colorado Island, Panama, is relatively small for the Neotropics (144 species in 46 genera), this remains one of the few papers to address the classification of Neotropical Notodontidae. When taken together, Forbes's 1939a and 1948 works provide a fairly complete classification for New World Notodontidae. Forbes acknowledged, however, that this classification was "very largely artificial" (1942: 277). In addition to giving keys, diagnoses, and flight times for all taxa, Forbes (1939a) figured the male genitalia of newly described species in *Tachuda* Schaus and *Apela* Walker and the wing venation of representative species in 38 genera. In another paper, Forbes (1930) gave keys and diagnoses for five notodontid species occurring in Puerto Rico.

The Notodontidae of Cuba were revised by Torre and Alayo (1959). They treated 25 species, two newly described, the majority of these belonging in the Nystaleini. For each species, Torre and Alayo discussed general external morphology of adults and gave detailed distribution data. They figured male genitalia of all species and female genitalia of many.

Weller (1989) focused on understanding generic boundaries and generic interrelationships among members of the Neotropical tribe Nystaleini (Notodontinae), first proposed by Forbes (1948). Weller's paper was the first study on Notodontidae to take a rigorous cladistic approach. It is also the most detailed study to date concerning systematics of the Neotropical fauna. After identifying apomorphic characters to support monophyly of the Nystaleini, Weller placed 18 genera (approximately 250 species) in the tribe. Her study was based on examination of adult morphology, including legs, antennae, labial palpi, the thoracic tympanum, and abdominal sterna and terga, as well as the male and female genitalia. Weller provided morphological illustrations, keys to the genera (including diagnostic genitalic features), and a checklist for the species of Nystaleini.

The Old World notodontid fauna does not

include as many species as that in the New World. Several regions have received rather complete treatment, thanks largely to the various catalogs of Kiriakoff (1964, 1967, 1968, 1970a, 1970b). Unfortunately, few workers on Old World Notodontidae have addressed higher classification, and none of them have attempted to combine their findings with what is known concerning the New World. The result is that not even a rudimentary world classification exists. Below, I briefly review the most significant works on Old World Notodontidae.

An important early paper on South African species (Janse, 1920) described adult morphology in detail, although genitalia were not studied at that time. Janse provided keys to 38 genera and 89 species (many newly described) and figured wing venation, legs, antennae, and heads of many taxa. He recognized eight generic groups (numbered I–VIII). Janse presented a branching diagram showing a "phylogeny of the Notodontidae," but his scheme is not interpretable in a cladistic sense.

Gaede (1928) treated the entire African notodontid fauna, approximately 325 species at that time. Each species was briefly discussed, and adults of most taxa were figured in color.

Kiriakoff, by far the most productive notodontid worker in terms of number of papers published, revised the African fauna (1964, 1970a), including Madagascar (1969a), and described new taxa in smaller papers (e.g., Kiriakoff, 1962a, 1962b, 1963c). Kiriakoff is best known for erecting hundreds of new genera. For example, of the 174 genera he listed for the African fauna (1964), Kiriakoff described 97. However, Kiriakoff's generic concepts have rarely been examined rigorously. His works are valuable, first, because they bring together the taxonomic literature for these little-known moth groups, and, second, because they provide keys. Although Kiriakoff was one of the few researchers to propose family group names for the Notodontidae (e.g., 1950c, 1969b), his views on classification have frequently been criticized, and his conclusions seem to vary from paper to paper (Weller, 1989).

Pinhey (1975) gave a brief discussion of notodontid adults and larvae, as well as short diagnoses for the 59 species occurring in

Southern Africa, with color photographs of adults. Synonymies, distribution data, and larval host plants (where available) were also listed.

The Indo-Australian fauna was given comprehensive treatment by Gaede (1930), who recognized approximately 400 species in 100 genera. Gaede gave a short diagnosis for each species and figured adults of most taxa. The only other complete treatment of the Indo-Australian fauna was by Kiriakoff (1968). Although few species had been described since Gaede (1930), Kiriakoff recognized 228 rather than 100 genera. Again, most of those new generic names are attributable to Kiriakoff himself.

An early work on the fauna of India and surrounding regions was Moore's (1882). He treated only 10 species (in 10 genera), but was among the first to classify the Notodontidae of that region. Moore recognized two subfamilies: the Dicranurinae (= Cerurinae) and the Notodontinae. Hampson (1892) presented a broader and more detailed treatment. He covered 114 species (20 newly described) in 37 genera and provided a short definition of the Notodontidae, but did not attempt to subdivide the family. In addition to presenting a generic key based on wing venation, Hampson gave a short synopsis for each species. Bryk (1949) gave diagnoses and distribution data for 51 species of Notodontidae, 23 of which were newly described, occurring in India and Burma.

Gardner's papers (1943, 1946), describing larvae of 19 Indian genera, detail notodontid larval morphology. Gardner provided keys, as well as descriptions and figures of numerous morphological structures, many of which he discovered. He did not address classification, nor did he combine his findings with what Hampson (1892) had found concerning adults. Regardless, these are extremely important works.

The Australian Notodontidae, a relatively small fauna (Holloway, 1983), were discussed by Turner (1903), who recognized 31 species in 19 genera. Ten species were newly described. In the next two decades, the number of taxa increased to 64 species in 33 genera, divided between two subfamilies: the Cnethocampinae (= Thaumetopoeinae) with nine genera and the Notodontinae with 24 (Tur-

ner, 1922). Turner gave diagnostic features for both subfamilies.

The notodontid fauna of Borneo was treated by Holloway (1976, 1983). He provided a useful general introduction to the family, including brief discussions of adult and larval morphology, host-plant relationships, and biogeography (Holloway, 1983), and gave diagnostic features for the 122 species of Notodontidae occurring in Borneo. Male genitalia of all taxa were figured, and black-and-white (1976) or color (1983) photographs of adults were provided. Holloway discussed everything known concerning the larvae of each species. The works of van Eecke (1930) and Bender (1985), covering the Sumatran Notodontidae, supplement Holloway's. In the first of these, 32 species in 15 genera were recognized, while Bender, who followed the generic nomenclature of Kiriakoff (1968), recognized 176 species in 86 genera. Bender (1985) figured male and female genitalia for a few species, but adults of all taxa were shown in color.

Smaller papers discussing Indo-Australian Notodontidae include Kiriakoff (1970d, 1974), Dierl (1976a, 1976b), Schintlmeister (1981, 1987), Holloway and Bender (1985), and Bänziger (1988a). Barlow (1982) presented brief discussions for 23 Southeast Asian species.

The Notodontidae of the eastern Palearctic region were treated by Leech (1889, 1898). Leech listed 69 notodontid species in 33 genera from China, Japan, and Korea. Eleven species were newly described. In a more recent work, Chistyakov (1977) discussed the 74 species of Notodontidae occurring in the Maritime Territory of the eastern Palearctic.

An impressive early work on the Notodontidae of Japan, Korea, and Taiwan was published by Marumo (1920). He treated 115 species in 45 genera, with five new species and five new genera. His paper gives a key to the genera (for adults) based largely on wing venation, palpi, and legs. In addition, Marumo presented a detailed diagnosis for each genus with a list of included species. For each species he summarized the taxonomic literature, discussed distribution, and described the immature stages (larval and pupal) where these were known. Adult structures, including labial palpi, antennae,

epiphyses, and wing venation, were beautifully figured, and color illustrations of most adults and some larvae were presented. Unfortunately, Marumo did not address classification of the Notodontidae above the generic level.

Matsumura described notodontid species, genera, and subfamilies from Japan, Korea, and Taiwan. Sugi (1979) cataloged Matsumura's types (over 100 species), designated lectotypes, and provided photographs. The majority of Matsumura's papers described species and genera without reference to notodontid classification or morphology. However, in two papers (Matsumura, 1925, 1929b) he classified the Palearctic Notodontidae into 11 subfamilies, six of which were new, and provided a subfamilial key. For three of these—the Dudusinae, Stauropinae, and Cerurinae (= Dicranurinae)—Matsumura listed generic keys and diagnoses, as well as species checklists for Japan and Taiwan. The diagnoses were based largely on wing venation, as well as on antenna, proboscis, and leg morphology.

More recently, Sugi (1982) cataloged the Japanese Notodontidae, providing color photographs and distribution data. He has also described new species from Japan (e.g., Sugi, 1977, 1980). Color photographs of adults and larvae for Japanese species, as well as host-plant records, can be found in Issiki et al. (1969) and Sugi (1987a).

Nam (1985) revised the same notodontid subfamilies detailed by Matsumura (1929b)—the Dudusinae, Stauropinae, and Cerurinae—for the fauna of Korea. His paper (in Korean) also gives a key to the 11 subfamilies recognized by Matsumura (1929b). Schintlmeister (1989) listed the entire Korean fauna, a total of 82 species.

The fauna of China was studied by Cai (1979a, 1979b). Although 144 species in 50 genera were discussed, the larger of the two papers (1979a) is in Chinese, making it inaccessible to most workers. Cai also (1979a) presented known host-plant records.

The western Palearctic notodontid fauna has been studied extensively by Schintlmeister (1979, 1982, 1985). In the 1985 paper, Schintlmeister analyzed 50 characters for 47 European species. Overall similarities between taxa were measured, and phenograms

were generated. Schintlmeister claimed that “clearly the ranks of genera and subfamilies are shown in the dendograms” (1985: 43). In my section entitled Classification of the Notodontidae, I reanalyze Schintlmeister's data using parsimony methods and discuss the results. Schintlmeister et al. (1987) listed the 128 species of Notodontidae known to occur in the USSR. The authors made several taxonomic changes, including synonymizing one of Kiriakoff's genera and reducing another to subgeneric status.

The most recent treatment of the Western Palearctic fauna is by de Freina and Witt (1987), who covered 46 species in 24 genera. Although they did not present keys, they discussed habitat and geographical distribution and gave diagnoses. They included drawings of male and female genitalia for almost all species and color photographs of adults. Their contribution also summarizes the literature on notodontid larvae. Carter (1982) treated 14 species of Notodontidae. For each species he showed a color photograph of the adult and presented a short discussion of distribution and life history, including known larval hosts.

Two works have treated the Palearctic notodontid fauna in its entirety. The first work was by Grünberg (1912). At that time, the fauna comprised 167 species in 45 genera. In the style typical of Seitz volumes, there were no keys, but each genus and species was diagnosed and color illustrations of adults were included. For diagnostic features, Grünberg employed the character systems (all based on adults) traditionally used by early notodontid workers: wing venation, shape of the labial palpi, antenna morphology, number of pairs of metatibial spurs, and whether the eyes are “naked” or “hairy.” He also discussed known immature stages in some detail.

The second complete treatment of Palearctic Notodontidae was by Kiriakoff (1967). He presented a key to the genera and then listed each with a diagnosis and included species. Kiriakoff figured male genitalia for at least one species in each genus and presented photographs of adults representing 54 taxa. The number of recognized species had almost doubled, from 167 in Grünberg (1912) to 331 in Kiriakoff (1967). The number of genera more than tripled, from 45 in Grünberg to

169, with 46 new generic names attributable to Kiriakoff and 22 to Matsumura. Many of these newer genera are monobasic.

In most of the studies cited above, the Thaumetopoeinae were not placed in a separate category. For example, Gaede (1930) listed thaumetopoeine genera in the Notodontidae without giving them special status. Turner (1922), on the other hand, separated them into the subfamily Cnethocampinae. The family group name (as Thaumetopoeinae) dates back to Aurivillius (1889). The entire group was revised and catalogued by Kiriakoff (1970b), who argued that it should be accorded family status.

The Neotropical tribe Dioptini has received relatively little attention from taxonomists. Prout (1918) and Hering (1925) listed

known species and revised the genera on the basis of wing venation. The only available catalog was written by Bryk (1930), while the figures and diagnoses in Hering (1925) provide the best means for species identification. Forbes (1931) gave preliminary keys to the difficult genera *Dioptis* Hübner and *Josia* Hübner. He later discussed the six species (in four genera) collected on Barro Colorado Island (Forbes, 1939a). Weller (1989), who used two dioptine species, *Scotura nervosa* Schaus and *Erbessa celata* Warren (= *unimacula*), as outgroup exemplars in her study of the Nystaleini, figured wing venation and tympanal structure for these. Additional discussions of dioptine taxonomy and anatomy can be found in Miller (1987a, 1988a, 1989) and Godfrey et al. (1989).

METHODS

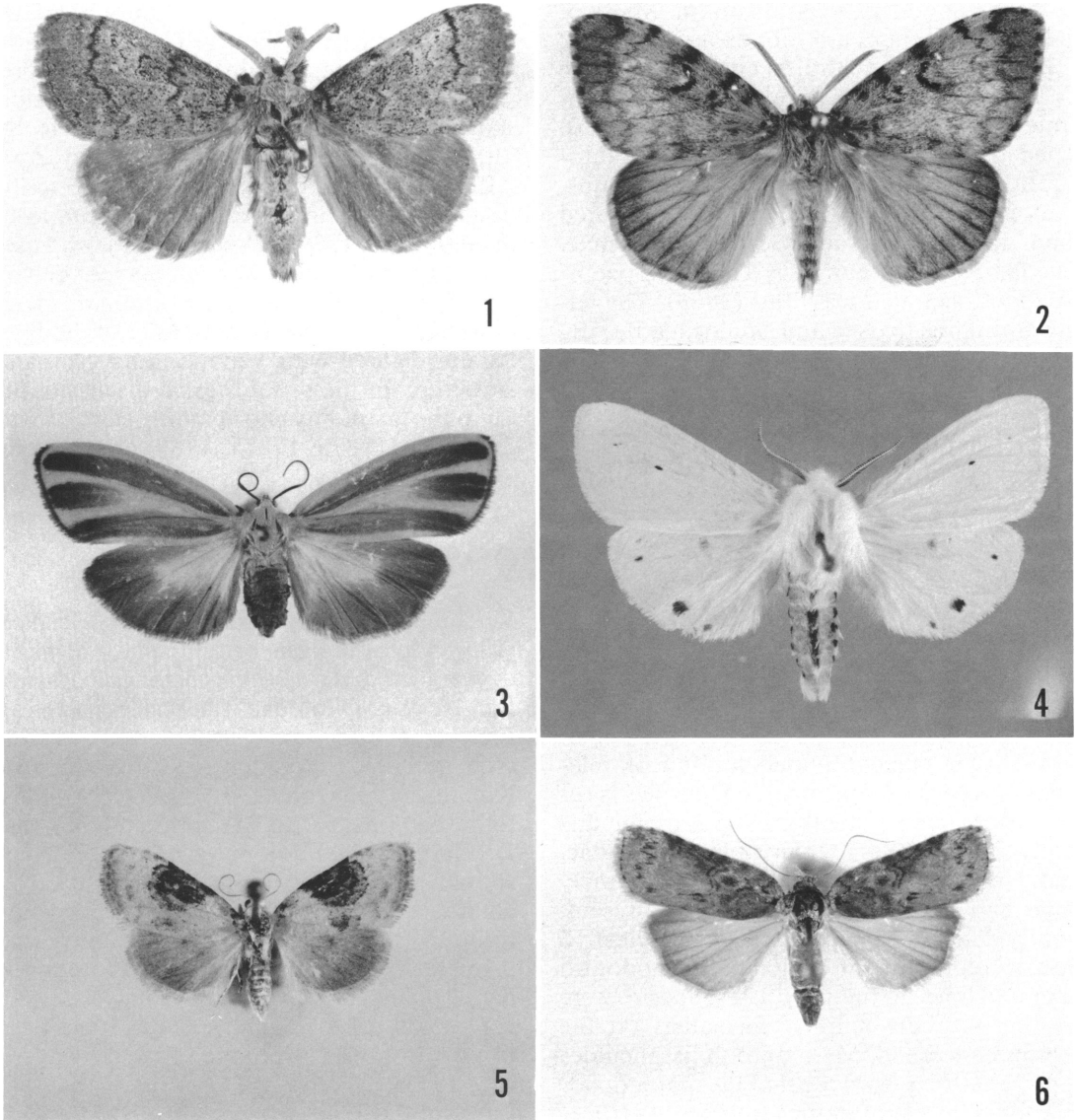
SPECIES EXAMINED (OUTGROUP)

The Noctuoidea is the largest lepidopteran superfamily (Turner, 1946), with estimates of over 50,000 described species (Weller, 1989). Our current understanding of relationships between the included families is rudimentary. The potential outgroups for this study include the Lymantriidae, Arctiidae, and Noctuidae. Each of these is extremely large and diverse, and each is, at present, poorly defined. My approach was to select 12 taxa to represent the major non-notodontid noctuoid lineages (table 1). These species were chosen with the help of specialists on the groups concerned. My outgroup list includes representatives from most of the major quadrid noctuoid subfamilies (see figs. 1–10).

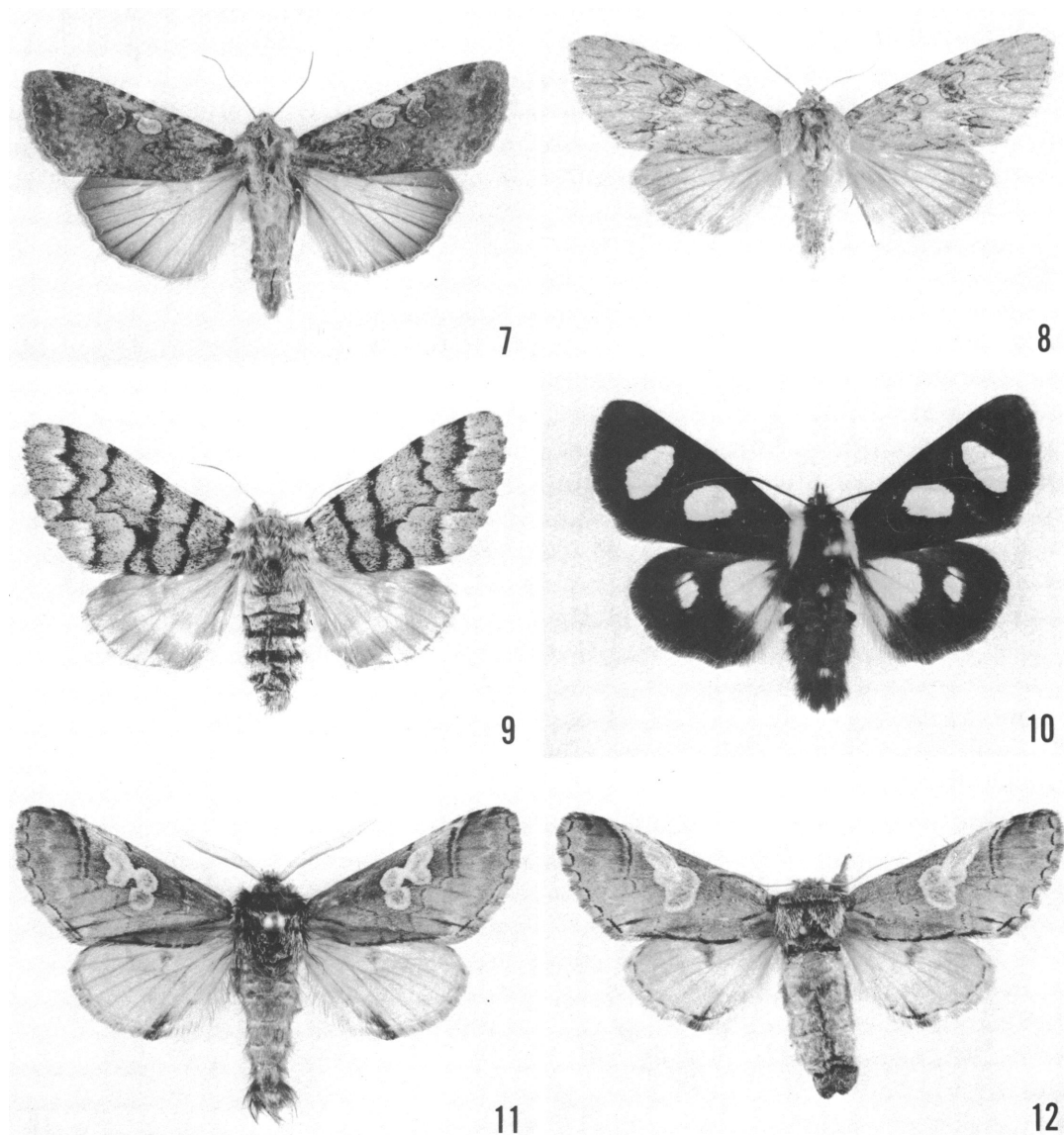
The list also includes two genera, *Diloba* Boisduval and *Doa* Neumoegen and Dyar, that have historically been difficult to place in any existing family or subfamily. Both have, at one time or another, been referred to the Notodontidae. *Diloba* contains a single species, *D. caeruleocephala* Linnaeus (figs. 11, 12). Various authors have placed it in the Notodontidae, Lymantriidae, Arctiidae, or Thyatiridae, as well as in the noctuid subfamilies Acronictinae, Plusiinae, Pantheinae, and Cuculliinae (Richards, 1932; Sick, 1935; Pierce and Beirne, 1941; Watson et al., 1980;

Kitching, 1984a; Kristensen, 1985). Kiriakoff (1970c), on the basis of tympanal morphology, argued that the species belongs in its own family, the Dilobidae. Duponchel (1845), Fletcher (1972), and Carter (1982) considered it to be a notodontid. Most recently, Kitching (1984a) and Kristensen (1985) have followed Minet's (1983) recommendation that *D. caeruleocephala* is not a notodontid, but should (tentatively) be included in the Cuculliinae. Because of the controversy surrounding this species and the possibility that it might have affinities with the Notodontidae, I included *Diloba* in my analysis.

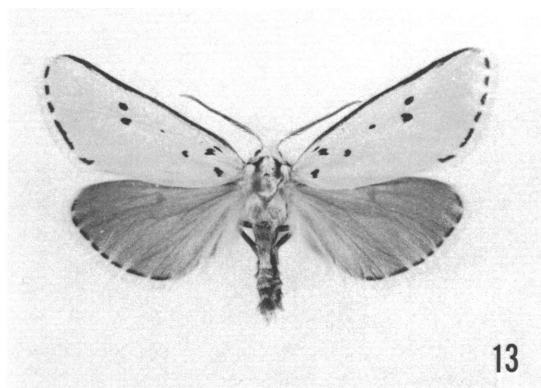
Doa is another enigmatic genus. It has been moved from the Arctiidae to the Lymantriidae to the Pericopinae (Arctiidae), back to the Lymantriidae, and back again to the Pericopinae (Watson et al., 1980; Brown, 1990). Franclemont (1983) placed it, along with the genus *Leuculodes* Dyar, in a separate tribe of the Pericopinae. After examining the larva of *D. ampla*, Donahue and Brown (1987) argued that the genus does not belong in any of these groups and, as an interim solution, recognized the family Doidae for *Doa* and *Leuculodes*. *Doa* contains five species (Bryk, 1934; Brown, 1990), with *D. ampla* (fig. 13) occurring in North America and the others ranging from Mexico south to Venezuela and Colombia. Forbes (1923) first placed *Doa* as



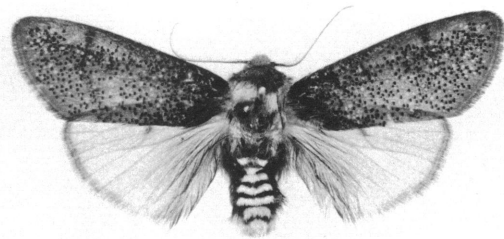
Figs. 1–6. Dorsal views of adult moths used in the study (outgroup species); FW = forewing. 1. *Dasychira dorsipennata* Barnes and McDunnough, male (Maine, AMNH; FW length = 18 mm). 2. *Lymantria dispar* (Linnaeus), male (New York, AMNH; FW length = 19 mm). 3. *Hypoprepia miniata* (Kirby), female (New Jersey, AMNH; FW length = 14 mm). 4. *Spilosoma virginica* (Fabricius), male (Illinois, AMNH; FW length = 18 mm). 5. *Nycteola frigidana* (Walker), female (Missouri, AMNH; FW length = 12 mm). 6. *Nola pustulata* (Walker), female (New Jersey, AMNH; FW length = 10 mm).



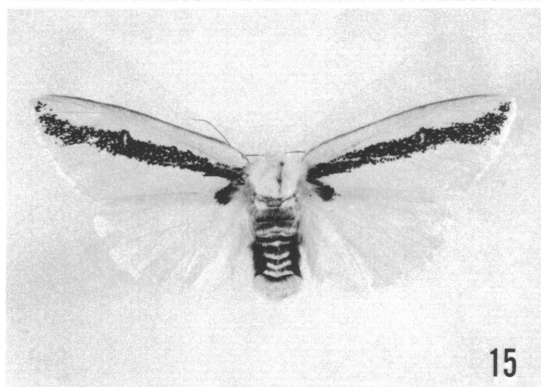
Figs. 7–12. Dorsal views of adult moths used in the study (outgroup species). 7. *Peridroma saucia* (Hübner), male (Georgia, AMNH; FW length = 22 mm). 8. *Acronicta americana* (Harris), male (New Jersey, AMNH; FW length = 25 mm). 9. *Panthea furcilla* (Packard), female (Connecticut, AMNH; FW length = 18 mm). 10. *Alypia octomaculata* Fabricius, male (New York, AMNH; FW length = 14 mm). 11. *Diloba caeruleocephala* (Linnaeus), male (West Germany, BMNH; FW length = 17 mm). 12. *Diloba caeruleocephala* (Linnaeus), female (Greece, BMNH; FW length = 18 mm).



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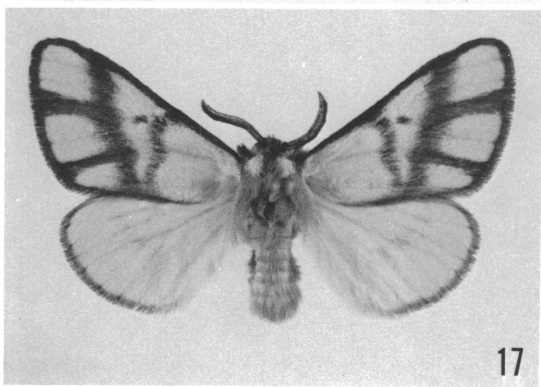
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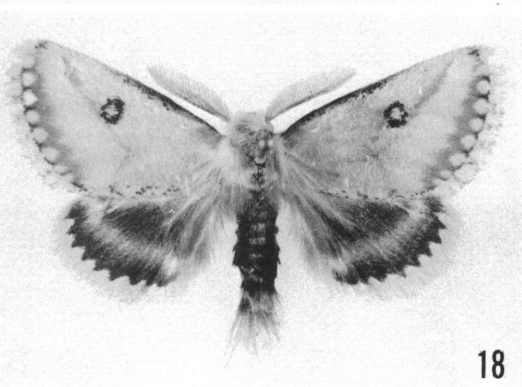
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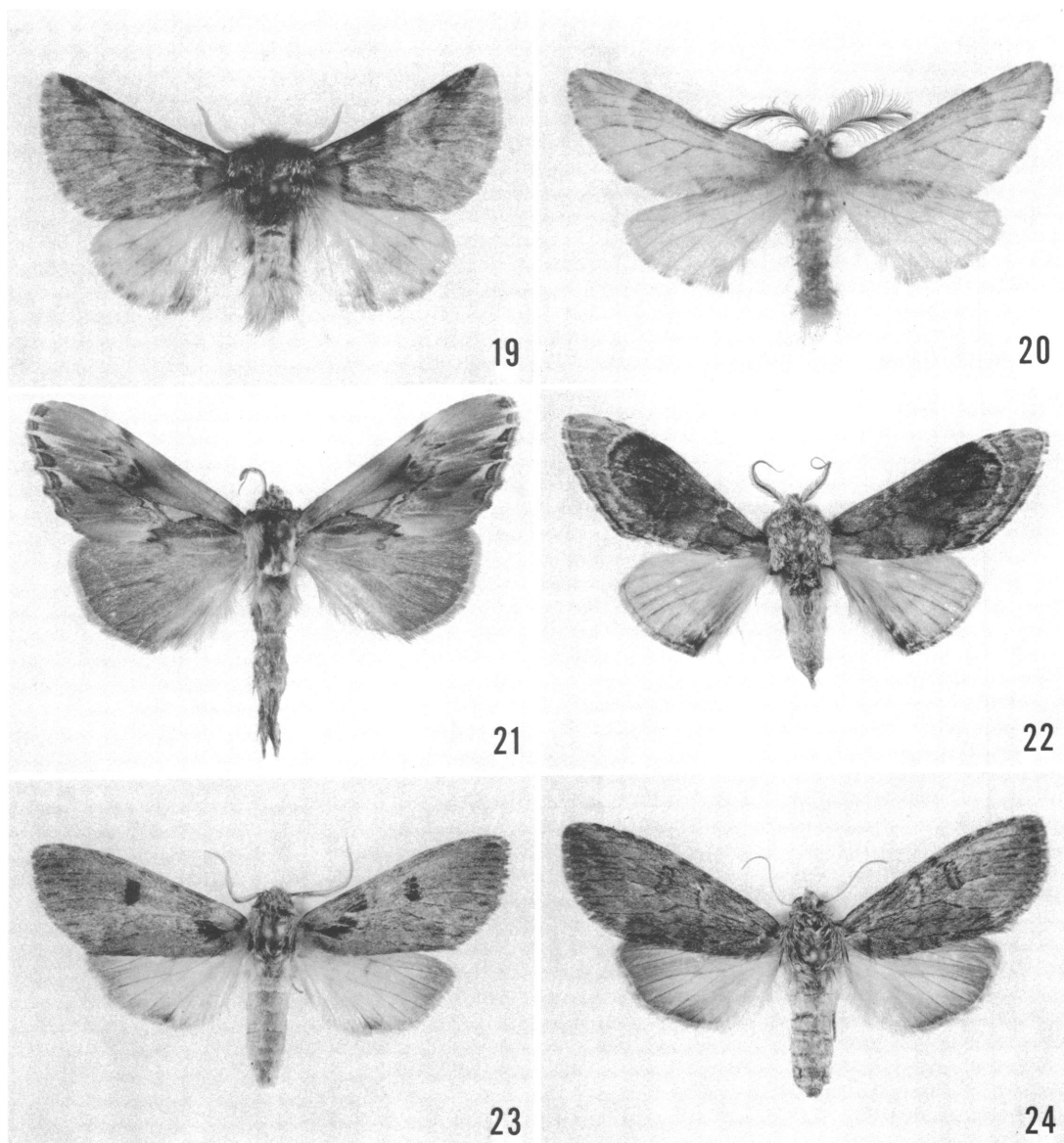


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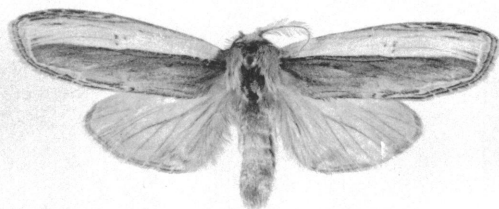
Figs. 13–18. Dorsal views of adult moths used in the study. 13. *Doa ampla* Grote, male (Arizona, AMNH; FW length = 15 mm). 14. *Oenosandra boisduvalii* (Newman), male (Australia, BMNH; FW length = 23 mm). 15. *Oenosandra boisduvalii* (Newman), female (Australia, BMNH; FW length = 26 mm). 16. *Traumatocampa pityocampa* (Denis and Schiffermüller), male (Spain, AMNH; FW length = 16 mm). 17. *Anaphe panda* (Boisduval), male (W. Africa, USNM; FW length = 20 mm). 18. *Epicoma melanosticta* (Donovan), male (Australia, AMNH; FW length = 17 mm).



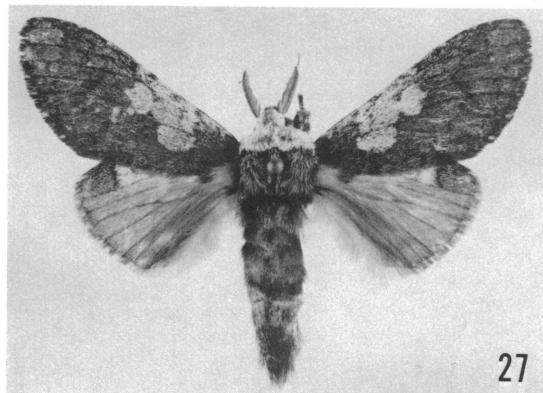
Figs. 19–24. Dorsal views of adult moths used in the study (ingroup species). 19. *Thaumetopoea processionea* (Linnaeus), male (Austria, AMNH; FW length = 13 mm). 20. *Ptilophora plumigera* (Denis and Schiffermüller), male (Germany, AMNH; FW length = 18 mm). 21. *Spatalia jezoensis* Wileman and South, male (Japan, CU; FW length = 19 mm). 22. *Fentonia ocypete* Bremer, male (Japan, AMNH; FW length = 21 mm). 23. *Goacampa variabilis* Schaus, male (Mexico, AMNH; FW length = 16 mm). 24. *G. variabilis* Schaus, female (Mexico, AMNH; FW length = 17 mm).



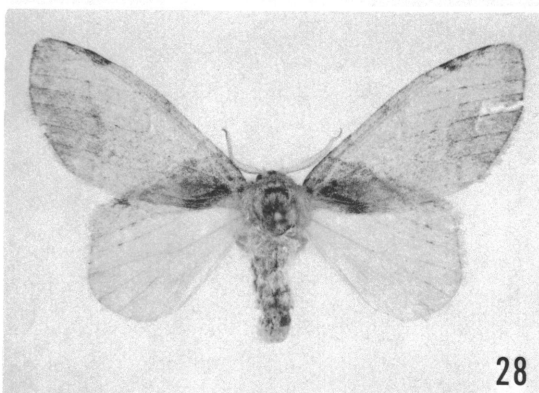
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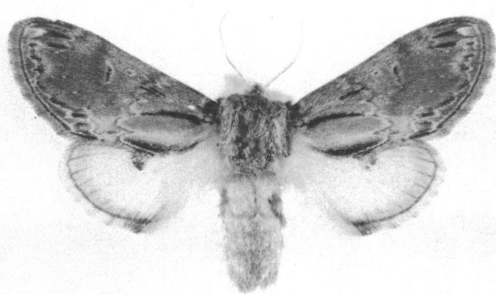
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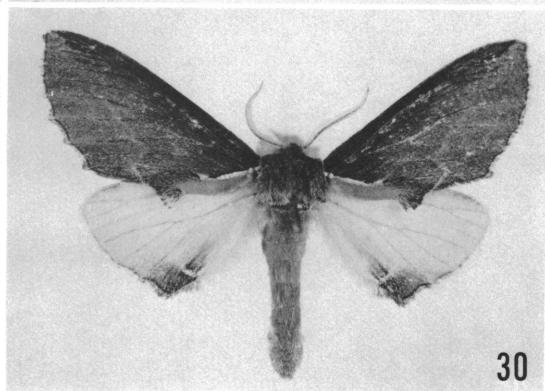
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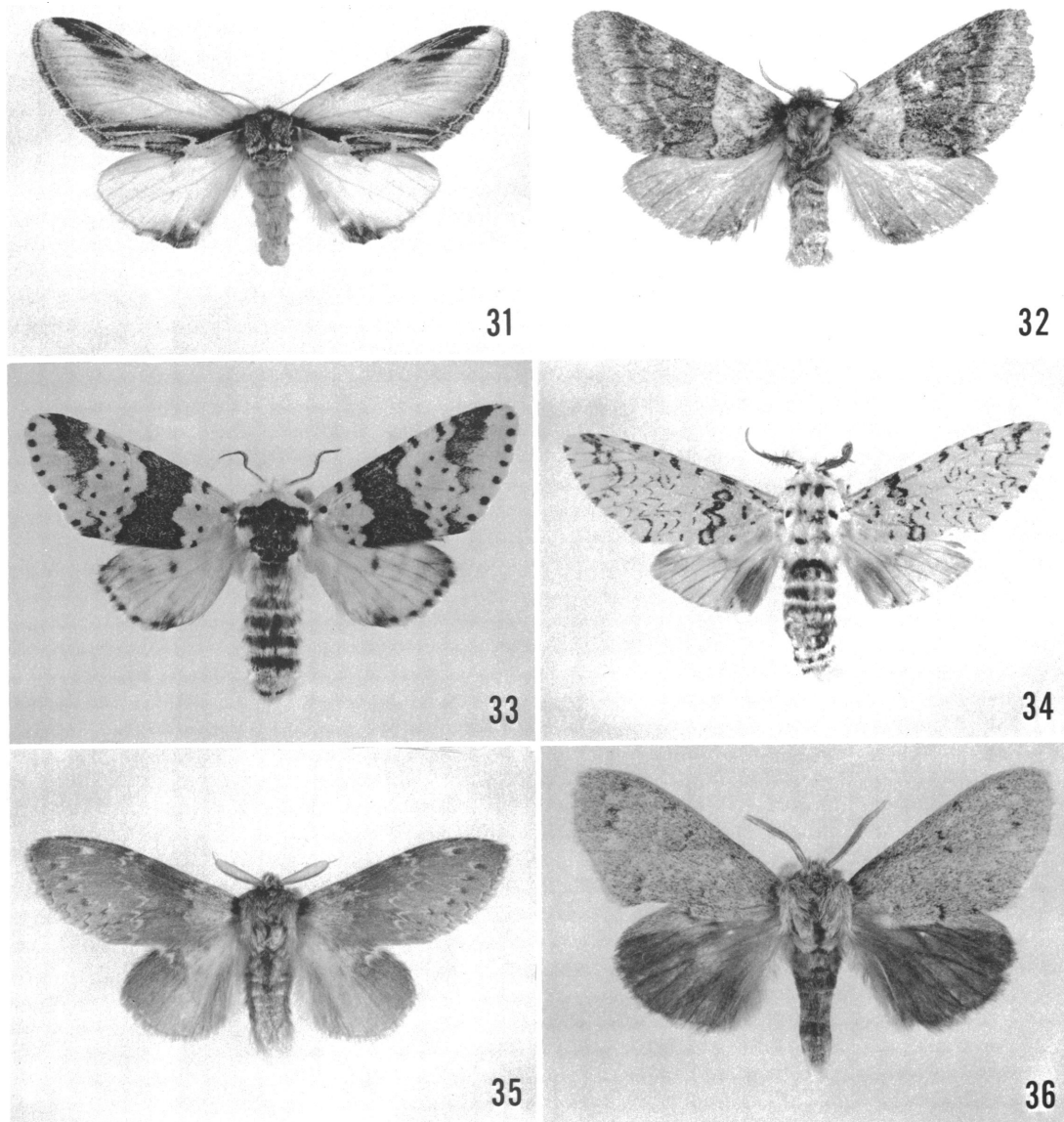


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Figs. 25–30. Dorsal views of adult moths used in the study (ingroup species). 25. *Clostera albosigma* Fitch, male (Massachusetts, AMNH; FW length = 15 mm). 26. *Lirimiris truncata* Herrich-Schäffer, male (Arizona, AMNH; FW length = 26 mm). 27. *Quadricalcarifera viridimaculata* Matsumura, male (Taiwan, USNM; FW length = 24 mm). 28. *Liparopsis postalbida* Hampson, female (Taiwan, CMNH; FW length = 19 mm). 29. *Notodonta scitipennis* Walker, male (New Jersey, AMNH; FW length = 17 mm). 30. *Odontosia elegans* Strecker, male (Wisconsin, AMNH; FW length = 25 mm).



Figs. 31–36. Dorsal views of adult moths used in the study (ingroup species). 31. *Pheosia rimosa* Packard, female (Utah, AMNH; FW length = 28 mm). 32. *Gluphisia septentrionis* Walker, female (Ontario, AMNH; FW length = 14 mm). 33. *Furcula borealis* Guérin-Ménéville, female (New Jersey, AMNH; FW length = 21 mm). 34. *Cerura liturata* Walker, male (Philippines, USNM; FW length = 30 mm). 35. *Stauropus fagi* (Linnaeus), male (Germany, AMNH; FW length = 26 mm). 36. *Cnethodonta griseascens* Staudinger, male (Japan, AMNH; FW length = 18 mm).



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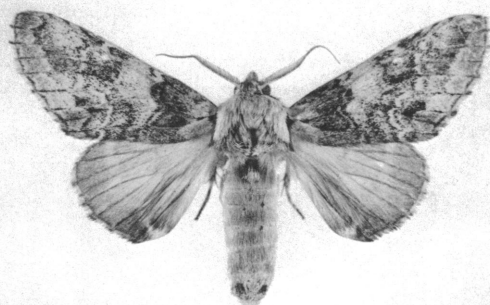
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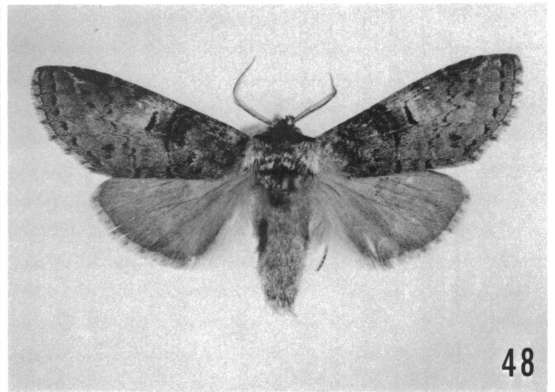
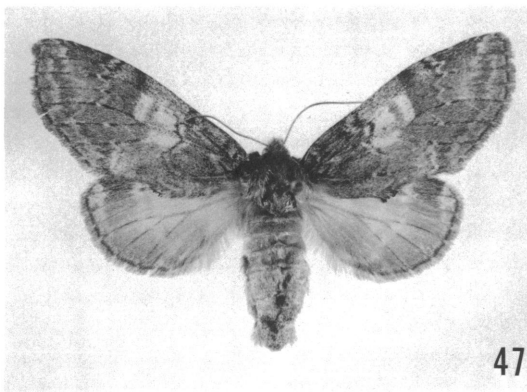
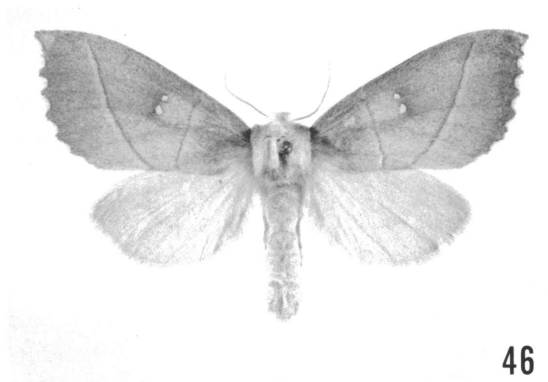
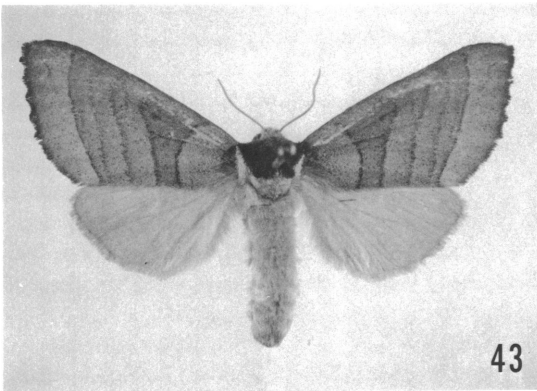


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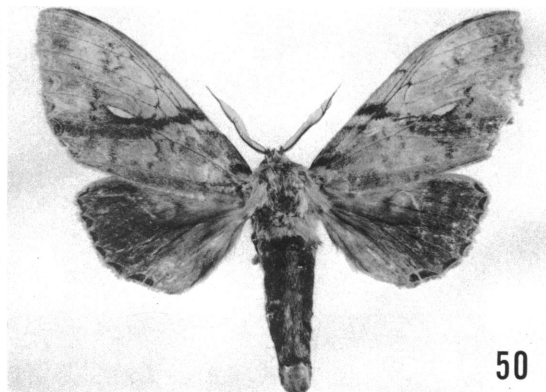
Figs. 37–42. Dorsal views of adult moths used in the study (ingroup species). 37. *Harpyia microsticta* (Hampson), male (Malaysia, AMNH; FW length = 25 mm). 38. *Heterocampa averna* Barnes and McDunnough, male (Arizona, AMNH; FW length = 20 mm). 39. *Schizura biedermani* Barnes and McDunnough, male (Texas, AMNH; FW length = 25 mm). 40. *Schizura unicornis* (J. E. Smith), male (Pennsylvania, AMNH; FW length = 14 mm). 41. *Macrurocampa marthesia* (Cramer), male (New Jersey, AMNH; FW length = 22 mm). 42. *Lochmaeus bilineata* Packard, male (New Jersey, AMNH; FW length = 18 mm).



Figs. 43–48. Dorsal views of adult moths used in the study (ingroup species). 43. *Datana ministra* (Drury), female (New Jersey, AMNH; FW length = 20 mm). 44. *Phalera bucephala* (Linnaeus), male (Germany, AMNH; FW length = 23 mm). 45. *Antheua simplex* Walker, male (Cameroun, CMNH; FW length = 25 mm). 46. *Nadata gibbosa* (J. E. Smith), female (Ontario, AMNH; FW length = 25 mm). 47. *Peridea angulosa* (J. E. Smith), female (Connecticut, AMNH; FW length = 24 mm). 48. *Ellida caniplaga* Walker, male (New Jersey, AMNH; FW length = 18 mm).



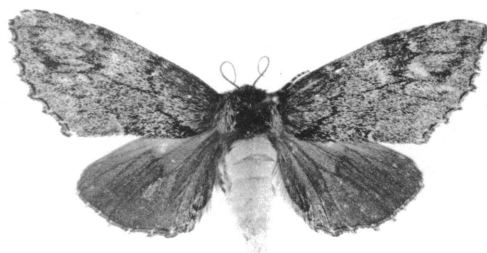
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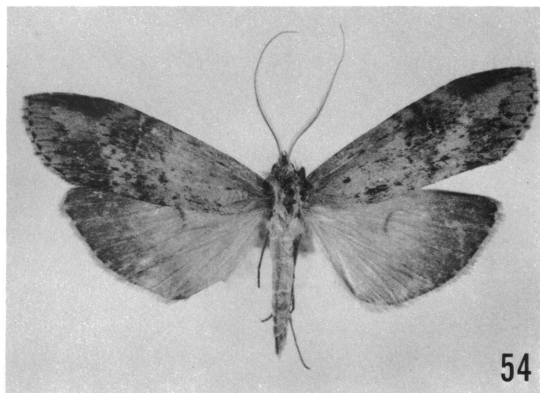
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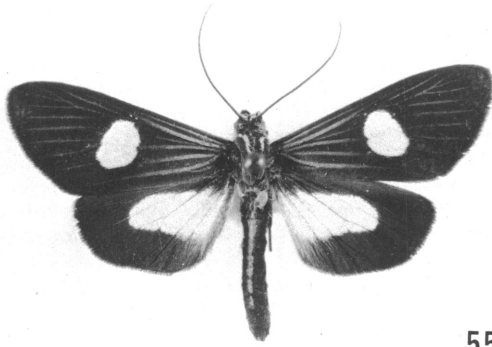


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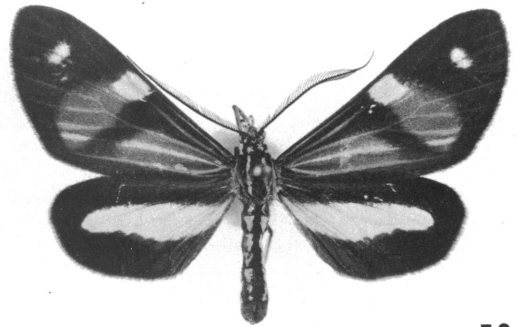


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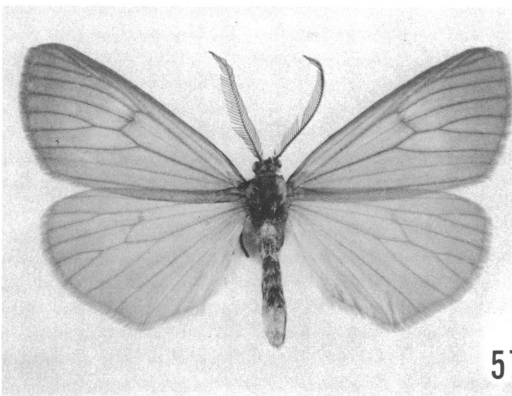
Figs. 49–54. Dorsal views of adult moths used in the study (ingroup species). 49. *Crinodes besckei* (Hübner), male (Peru, AMNH; FW length = 34 mm). 50. *Dudusa synopla* Swinhoe, male (Taiwan, CMNH; FW length = 51 mm). 51. *Tarsolepis japonica* Wileman and South, female (Taiwan, CMNH; FW length = 35 mm). 52. *Cargida pyrrha* (Druce), female (Arizona, AMNH; FW length = 21 mm). 53. *Gargetta costigera* Walker, male (Assam, USNM; FW length = 20 mm). 54. *Scrancia stictica* Hampson, female (South Africa, BMNH; FW length = 23 mm).



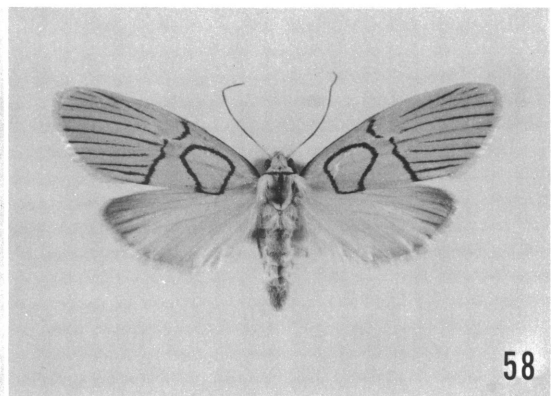
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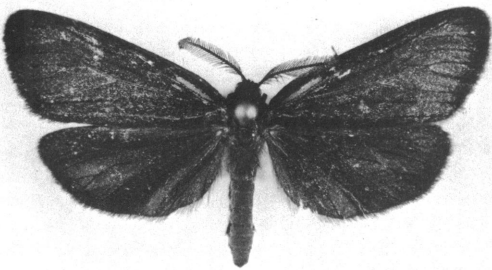
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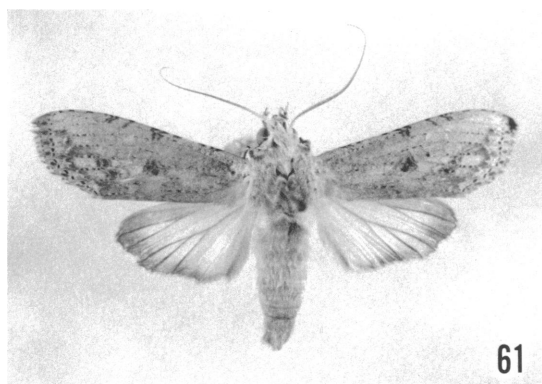


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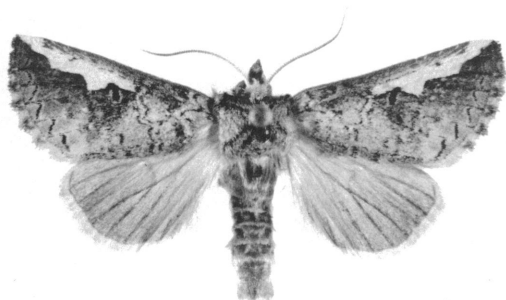
Figs. 55–60. Dorsal views of adult moths used in the study (ingroup species). **55.** *Erbesia glaucaspis* (Walker), male (Ecuador, BMNH; FW length = 16 mm). **56.** *Phaeochlaena gyon* (Fabricius), male (Brazil, CMNH; FW length = 17 mm). **57.** *Phryganidia californica* Packard, male (California, AMNH; FW length = 18 mm). **58.** *Zunacetha annulata* (Guérin-Ménéville), male (Panama, USNM; FW length = 14 mm). **59.** *Cyanotricha necyria* (Felder), male (Ecuador, USNM; FW length = 16 mm). **60.** *Josia ligata* Walker, female (Honduras, CMNH; FW length = 18 mm).



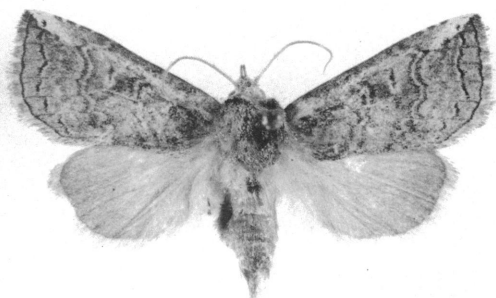
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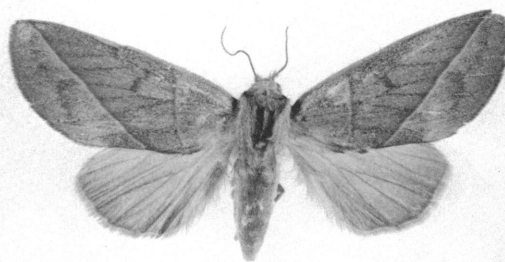
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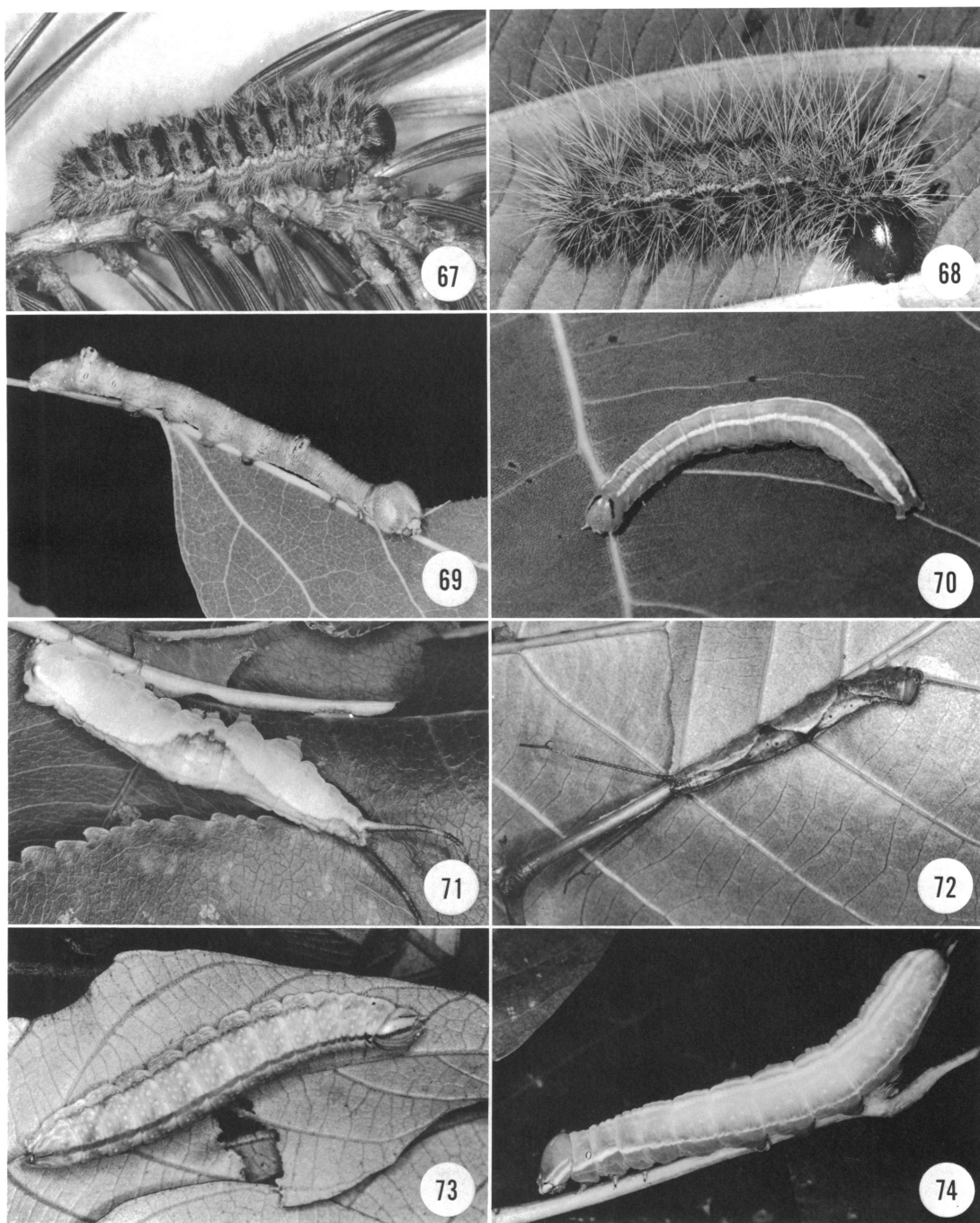


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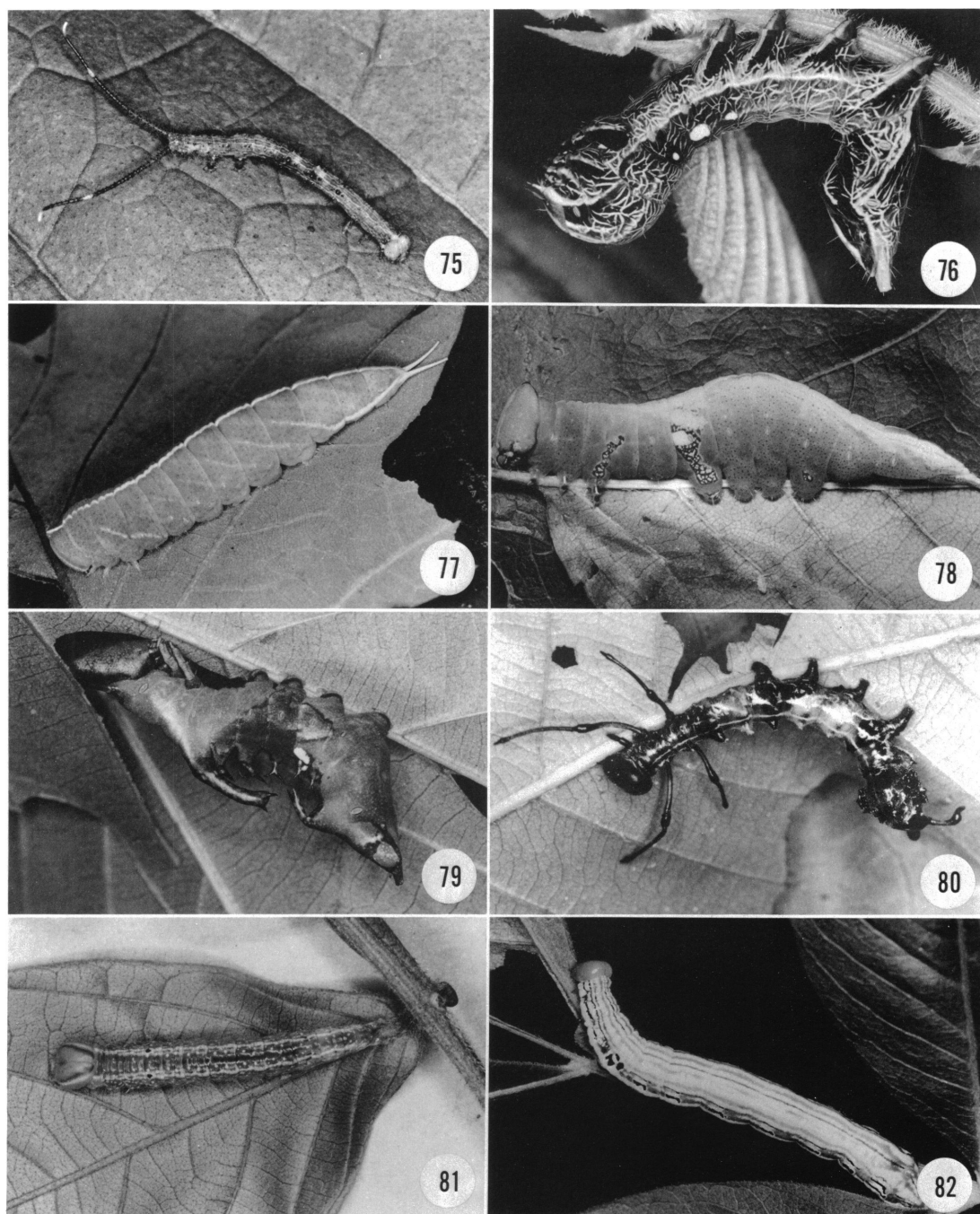


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Figs. 61–66. Dorsal views of adult moths used in the study (ingroup species). **61.** *Nystalea nyseus* (Cramer), male (Guyana, AMNH; FW length = 22 mm). **62.** *Dasylophia anguina* (J. E. Smith), male (New Jersey, AMNH; FW length = 17 mm). **63.** *Symmerista albifrons* (J. E. Smith), male (Florida, AMNH; FW length = 16 mm). **64.** *Hippia packardii* Morrison, male (Arizona, AMNH; FW length = 14 mm). **65.** *Didugia argentilinea* Druce (Texas, AMNH; FW length = 15 mm). **66.** *Hemiceras bilinea* Schaus, female (Mexico, AMNH; FW length = 21 mm).



Figs. 67–74. Last instar larvae of Notodontidae. 67. *Traumatocampa pityocampa* (Italy). 68. *Anaphe panda* (Cameroun). 69. *Odontotia elegans* (Pennsylvania). 70. *Gluphisia septentrionis* (New York). 71. *Furcula borealis* (Pennsylvania). 72. *Liparopsis postalbida* (Taiwan). 73. *Quadricalcarifera viridimaculata* (Taiwan). 74. *Peridea angulosa* (Pennsylvania). Figure 67 (photographed by R. Lewington) courtesy of David Carter (BMNH). All other photographs by John E. Rawlins (CMNH).



Figs. 75–82. Larvae of Notodontidae (final instar except where noted). 75. *Scrancia stictica* (penultimate instar, Cameroun). 76. *Crinodes besckei* (penultimate instar, Costa Rica). 77. *Macrurocampa marthesia* (Pennsylvania). 78. *Heterocampa biundata* (Pennsylvania). 79. *Harpyia microsticta* (Taiwan). 80. *Stauropus fagi* (Taiwan). 81. *Hemiceras bilinea* (penultimate instar, Costa Rica). 82. *Hippia packardii* (Texas). Figures 76 and 81 photographed by George L. Godfrey (INHS). All other photographs by John E. Rawlins (CMNH).



Figs. 83–90. Last instar larvae of Notodontidae. 83. *Pheosia rimosa* (New York). 84. *Notodonta simplaria* (New York). 85. *Cerura tattakana* (Taiwan). 86. *Antheua simplex* (Cameroun). 87. *Ellida caniplaga* (Pennsylvania). 88. *Nadata gibbosa* (Pennsylvania). 89. *Dudusa synopla* (Taiwan). 90. *Tarsolepis japonica* (Taiwan). All photographs by John E. Rawlins (CMNH).



Figs. 91–98. Last instar larvae of Notodontidae. 91. *Goacampa variabilis* (Costa Rica). 92. *Cnethodonta grisescens* (Taiwan). 93. *Schizura unicornis* (Texas). 94. *Lochmaeus bilineata* (Pennsylvania). 95. *Dasylophia anguina* (Pennsylvania). 96. *Symmerista albifrons* (Pennsylvania). 97. *Phryganidia californica* (California). 98. *Josia ligata* (Ecuador). Figure 91 photographed by George L. Godfrey (INHS). All other photographs by John E. Rawlins (CMNH).

part of an unresolved polytomy involving the quadrid Noctuoidea (see fig. 521), but later stated, "It now appears that *Doa* is more closely related to the Dioptidae than I showed it" (1948: 203). On the basis of this suggestion, I included *Doa* in my list.

This outgroup sample was intended to represent a wide range of morphological diversity for the quadrid Noctuoidea. However, the Noctuidae is such a large family that its representation in my analysis is, of necessity, incomplete; 18 subfamilies are currently recognized for the North American fauna alone (Franclemont and Todd, 1983). My approach to selecting an outgroup can only be considered an approximation, but I believe it was the only reasonable course to take (see discussions in Scoble, 1986, 1988; Weintraub and Miller, 1987; Miller, 1988b). Furthermore, experimentation with cladogram rooting indicated that ingroup topology was largely unaffected by composition of the outgroup (see Cladistic Results).

SPECIES EXAMINED (INGROUP)

I selected 52 species to represent the Notodontidae in my analyses. These are listed in table 1 according to the classification I propose. Adults of each are shown in figures 14–66, and representative larvae are illustrated in figures 67–98. The species were chosen on the basis of two criteria. First, I wanted to include representatives of the major groups. Again, species were chosen with the help of specialists on systematics of the family. I have not focused on resolving placement of unusual and taxonomically troublesome species, but instead I studied taxa that would potentially represent major species radiations and would provide a broad coverage of morphological diversity and biogeographic distribution.

The second criterion for choosing species was availability of larval material. Because earlier notodontid taxonomists relied heavily on morphology of the caterpillars, it was essential that I include larval as well as adult characters in my analysis. I therefore selected only those taxa for which I could obtain last instar larval specimens. This introduced lim-

itations. For example, larvae are unknown for some of the largest and most important dioptine genera, including the type genus of the group, *Dioptis* Walker. The Neotropical notodontid tribe Hemiceratini is poorly represented in my sample because immatures are largely unknown. For the rest of the Notodontidae, however, I was able to procure a fairly good representation (see table 1). Unfortunately, I was unable to obtain earlier instars or pupae for all the exemplar species. These will perhaps provide fruitful ground for future study (see Congruence Between Adult and Larval Data).

Adults of many of the ingroup species I used, as well as closely related species from the same genera, have been figured (often in color) in the works of Packard (1895a), Okagaki (1958), Pinhey (1975), Holloway (1983), and Bender (1985). Adults of species representing 15 of the genera used in this study were figured by Sugi (1982). He treated the following genera: *Dudusa*, *Tarsolepis*, *Stauropus*, *Quadricalcarifera*, *Cnethodonta*, *Cerura*, *Furcula*, *Harpyia*, *Phalera*, *Pheosia*, *Notodonta*, *Peridea*, *Odontosia*, *Gluphisia*, and *Clostera*. Habitus figures of larvae for many of my exemplar species appear in Packard (1895a), Kalshoven (1981), and Godfrey and Appleby (1987). Issiki et al. (1969) figured the larvae of species in the following genera represented in my study sample: *Stauropus*, *Cnethodonta*, *Tarsolepis*, *Fentonia*, *Cerura*, *Peridea*, *Ptilophora*, *Harpyia*, *Phalera*, and *Clostera*.

PREPARATION OF MATERIAL

For each species, I dissected the whole body of male and female adults. Usually only a single specimen of each sex was examined. Wings were first removed, and the rest of the body was soaked either in cold potassium hydroxide for 24 hours or in hot potassium hydroxide for 10 minutes. Scales and soft tissues were then removed with a brush. Genitalia were left attached to the body except where preparations were required for photographs, in which case they were mounted on slides. Genitalic slides for North American Notodontidae, mounted in Canada balsam, were kindly lent by J. G. Franclemont.

TABLE 1
Species Included in the Cladistic Analysis
(Ingroup species arranged according to the proposed classification)

	Larval localities ^a
Notodontidae	
Thaumetopoeinae	
<i>Anaphe</i> Walker	
<i>panda</i> (Boisduval)	S. Africa (BMNH)
<i>Epicoma</i> Hübner	
<i>melanosticta</i> (Donovan)	S. Australia (BMNH)
<i>Traumatocampa</i> Wallengren	
<i>pityocampa</i> (Denis and Schiffermüller)	Spain (BMNH)
<i>Thaumetopoea</i> Hübner	
<i>processionea</i> (Linnaeus)	“Europe” (CU)
Pygaerinae	
<i>Clostera</i> Samouelle	
<i>albosigma</i> Fitch	Montana (CU)
Platychasmatinae	
<i>Platychasma</i> Butler	
<i>virgo</i> Butler	Japan (S. Sugi)
Notodontinae	
Notodontini	
<i>Notodonta</i> Ochsenheimer	
<i>scitipennis</i> Walker	New York (CU)
<i>Odontosia</i> Hübner	
<i>elegans</i> (Strecker)	New York (CU)
<i>Pheosia</i> Hübner	
<i>rimosa</i> Packard	Arizona (CU)
Dicranurini	
<i>Ptilophora</i> Stephens	
<i>plumigera</i> (Denis and Schiffermüller)	Switzerland (BMNH)
<i>Gluphisia</i> Boisduval	
<i>septentrionis</i> Walker	New York (CU)
<i>Furcula</i> Lamarck	
<i>borealis</i> (Guérin-Ménéville)	New York (CU)
<i>Cerura</i> Schrank	
<i>tattakana</i> Matsumura ^b	Taiwan (CMNH)
<i>Liparopsis</i> Hampson	
<i>postalbida</i> Hampson	Taiwan (CMNH)
<i>Quadricalcarifera</i> Strand	
<i>viridimaculata</i> Matsumura	Taiwan (CMNH)
Phalerinae	
<i>Phalera</i> Hübner	
<i>bucephala</i> (Linnaeus)	England (BMNH)
<i>Datana</i> Walker	
<i>ministra</i> (Drury)	Illinois (INHS)
<i>Antheua</i> Walker	
<i>simplex</i> Walker	Cameroun (CMNH)
<i>Peridea</i> Stephens	
<i>angulosa</i> (J. E. Smith)	New York (CU)
<i>Nadata</i> Walker	
<i>gibbosa</i> (J. E. Smith)	New York (CU)

TABLE 1—(Continued)

	Larval localities ^a
<i>Ellida</i> Grote <i>caniplaga</i> (Walker)	New York (CU)
Dudusinae	
Dudusini	
<i>Tarsolepis</i> Butler <i>japonica</i> Wileman and South	Taiwan (CMNH)
<i>Dudusa</i> Walker <i>nobilis</i> Walker	Taiwan (CMNH)
<i>Crinodes</i> Herrich-Schäffer <i>bescke</i> (Hübner)	Costa Rica (INHS)
<i>Cargida</i> Schaus <i>pyrrha</i> (Druce)	Arizona (CU)
<i>Goacampa</i> Schaus <i>variabilis</i> Schaus	Costa Rica (INHS)
Scranciini	
<i>Scrancia</i> Holland <i>stictica</i> Hampson	Cameroon (CMNH)
<i>Gargetta</i> Walker <i>costigera</i> Walker	Thailand (BMNH)
Heterocampinae	
<i>Spatalia</i> Hübner <i>jezoensis</i> Wileman and South	Japan (BMNH)
<i>Fentonia</i> Butler <i>ocypete</i> Bremer	Japan (BMNH)
Heterocampini	
<i>Lochmaeus</i> Doubleday <i>bilineata</i> (Packard)	Illinois (INHS)
<i>Schizura</i> Doubleday <i>biedermani</i> Barnes and McDunnough	Arizona (CU)
<i>Heterocampa</i> Doubleday <i>obliqua</i> Packard	Illinois (INHS)
<i>Macrurocampa</i> Dyar <i>marthesia</i> (Cramer)	New York (CU)
Stauropini	
<i>Schizura</i> Doubleday <i>unicornis</i> (J. E. Smith)	New York (CU)
<i>Cnethodonta</i> Staudinger <i>grisescens</i> Staudinger	Japan (BMNH)
<i>Harpyia</i> Ochsenheimer <i>microsticta</i> (Hampson)	Taiwan (CMNH)
<i>Stauropus</i> Germar <i>fagi</i> (Linnaeus)	Japan (BMNH)
Diopinae	
<i>Erbessa</i> Walker <i>glauca</i> (Walker)	Venezuela (BMNH)
<i>Phaeochlaena</i> Hübner <i>gyon</i> (Fabricius)	Brazil (BMNH)
<i>Phryganidia</i> Packard <i>californica</i> Packard	California (USNM)

TABLE 1—(Continued)

	Larval localities ^a
<i>Zunacetha</i> Walker	
<i>annulata</i> (Guérin-Ménéville)	Panama (AMNH)
<i>Josia</i> Hübner	
<i>ligata</i> Walker	Ecuador (SJW)
<i>Cyanotricha</i> Prout	
<i>necyria</i> (Felder)	Colombia (AMNH)
Nystaleinae	
<i>Symmerista</i> Hübner	
<i>albifrons</i> (J. E. Smith)	Florida (CU)
<i>Didugua</i> Druce	
<i>argentina</i> Druce	Texas (USNM)
<i>Hippia</i> Möschler	
<i>packardii</i> (Morrison)	Arizona (CU)
<i>Nystalea</i> Guenée	
<i>nyseus</i> (Cramer)	Venezuela (BMNH)
<i>Dasylophia</i> Packard	
<i>anguina</i> (J. E. Smith)	Virginia (CU)
Incertae Sedis	
<i>Lirimiris</i> Walker	
<i>truncata</i> (Herrich-Schäffer)	Ecuador (SJW)
<i>Hemiceras</i> Guenée	
<i>bilinea</i> Schaus	Costa Rica (INHS)
Doidae	
<i>Doa</i> Neumoegen and Dyar	
<i>ampla</i> Grote	Arizona (CU)
Oenosandridae	
<i>Oenosandra</i> Walker	
<i>boisduvalii</i> (Newman)	S. Australia (BMNH)
Lymantriidae	
<i>Lymantria</i> Hübner	
<i>dispar</i> (Linnaeus)	New York (CU)
<i>Dasychira</i> Hübner	
<i>dorsipennata</i> Barnes and McDunnough	Pennsylvania (ELQ)
Arctiidae	
<i>Spilosoma</i> Curtis (Arctiinae)	
<i>virginica</i> (Fabricius)	New York (CU)
<i>Hypoprepia</i> Hübner (Lithosiinae)	
<i>miniata</i> (Kirby)	Pennsylvania (ELQ)
Noctuidae ^c	
<i>Panthea</i> Hübner (Panthinae)	
<i>furcilla</i> (Packard)	Pennsylvania (ELQ)
<i>Diloba</i> Boisduval (Cuculliinae)	
<i>caeruleocephala</i> (Linnaeus)	England (BMNH)
<i>Alypia</i> Hübner (Agaristinae)	
<i>octomaculata</i> (Fabricius)	Pennsylvania (ELQ)
<i>Peridroma</i> Hübner (Noctuinae)	
<i>saucia</i> (Hübner)	New York (CU)
<i>Acronicta</i> Ochseneimer (Acronictinae)	
<i>americana</i> (Harris)	New York (CU)

TABLE 1—(Continued)

	Larval localities ^a
<i>Nycteola</i> Hübner (Sarrothripinae)	
<i>frigidana</i> (Walker)	Virginia (CU)
<i>Nola</i> Leach (Nolinae)	
<i>pustulata</i> (Walker)	Massachusetts (TLM)

^a Abbreviations for museums and collections are as follows: American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), Carnegie Museum of Natural History (CMNH), J. G. Franclemont Collection, Cornell University (CU), Illinois Natural History Survey (INHS), Timothy L. McCabe Collection (TLM), Eric L. Quinter Collection (ELQ), United States National Museum (USNM), Susan J. Weller Collection (SJW).

^b Adult male characters based on *Cerura liturata* Walker.

^c Subfamily assignments according to Franclemont and Todd (1983) and Kitching (1984a, 1987).

My own slide preparations were mounted using previously described techniques (Miller, 1987a). Photographs from slide mounts were made using a Zeiss MC63 Polaroid camera attached to a Zeiss SV8 stereomicroscope.

The following adult characters were examined with scanning electron microscopy (SEM): features of the proboscis, the female frenulum, tibial spurs, and the pretarsus. Larval characters examined with SEM included abdominal MD setae, tarsal claws and setae, head microsculpture, cuticle microsculpture, and mouthparts, especially the maxillary complex. For adults, structures from dried specimens were mounted on stubs in colloidal graphite or silver paint. Proboscises were removed with forceps and the two galeae separated. These were then rinsed and lightly agitated in 70% ethanol and mounted on stubs. For species with an extremely short proboscis, the labial palpi were removed and the entire head mounted. Two scanning electron microscopes (both at the AMNH) were used during the course of my research: a Cambridge Stereoscan 250 and a Ziess DSM 950. Larval parts were critical-point dried and mounted following the procedures described in Godfrey et al. (1989) and Grimes and Neunzig (1986a, 1986b).

Preparation of larval material for SEM, especially critical-point drying of soft parts, is time consuming and produced inconsistent results. The inconsistencies seem to result from differences in both age and means of preservation of the original sample. In addition, for some species I was able to obtain

only one or two larval specimens and was hesitant to destroy them by preparation for SEM. It was therefore impossible to study each species with SEM, although doing so would likely provide additional larval character data.

MORPHOLOGICAL TERMS

Nomenclature for general adult morphology follows Forbes (1923), Ehrlich (1958a), Hodges (1971), Davis (1986), and Weller (1989). Genitalic terminology follows Klots (1970), Miller (1987a, 1988a, 1989), and Weller (1989, 1990). Wing veins are named in accordance with the scheme of Common (1979). Nomenclature for larval morphology follows Gerasimov (1952), Peterson (1962), and Stehr (1987a). Terms for more specialized adult and larval structures are discussed under the appropriate character descriptions.

Of the adult and larval characters I used, some had been studied in detail by earlier workers, some had been only superficially examined, and some are described here for the first time. In all cases, I examined the characters firsthand; none of my interpretations were drawn solely from literature descriptions. For ingroup taxa I describe and/or figure all apomorphic character states except those that have been well documented in other recent papers. I also describe some characters that proved to be autapomorphic. My rationale for doing so is that, because I examined few taxa relative to the number of notodontid species and genera, states that are

autapomorphic in my study may provide future workers with characters for uniting larger inclusive groups. Autapomorphic characters were not included in my cladistic analyses. I do not discuss outgroup characters in detail, but instead treat features that bear on the ingroup.

CLADISTIC ANALYSES

The data were analyzed using the Hennig86 parsimony program written by Farris (1988, Version 1.5). Of the 174 characters used, 56 were multistates. Among these 56, the number of states recognized per character was generally small; 14 have three states and 18 have four. The largest number of states used for any character was six (see Appendix I). Thirty-seven of the multistate characters were treated as nonadditive, but reasonable transformational hypotheses could be proposed for 19 characters and those were treated as additive. Missing data, as well as cases where I was unsure concerning a character state assignment, were scored as "?".

Unfortunately, Version 1.5 of Hennig86 does not have a means for reading character state trees (see Mickevich, 1982; Mickevich and Weller, 1990). This had two consequences for my analyses. First, each multistate character had to be treated as either completely additive or completely nonadditive (see documentation for Hennig86). For particular characters (e.g., Characters 9, 37, 86) that were coded as nonadditive, I would have preferred to impose at least partial additivity. Second, inability to code character state trees made it impossible to examine character evolution hypotheses and perform transformation series analysis (Mickevich, 1982; Mickevich and Weller, 1990). My data will be studied using those methods of character analysis when future versions of either Hennig86 or PAUP become available. The results will be published in a separate paper.

I experimented with treating particular characters as additive versus nonadditive and different cladograms resulted. For example, if all 174 characters are treated as nonadditive, there is almost no resolution with regard to relationships among subfamilies. Further, changes in treatment of relatively few char-

acters often had dramatic effects on cladogram topology, especially at the more basal nodes. However, the classification I propose in this paper would be largely unaffected by these differences in results. Appendix I lists the characters and specifies which character coding was applied to each.

The complete data matrix employed 63 taxa. The cladogram was rooted using the outgroup criterion. I searched for shortest cladograms using the following method. First, the "mhennig*" option constructed several initial trees by making passes through the data. Branch-swapping was performed on each of these. The preliminary trees were then treated with the "bb*" command, which applies extended branch-swapping to the trees found by "mhennig*", generating all the cladograms it can find. The "bb*" option was employed (rather than "bb") because it utilizes all available tree memory space to store its results, although in my study relatively few trees were found.

In certain cases, autapomorphic character states appear in the data matrix. For example, Character 101 describes the surface structure of the larval head. In caterpillars of *Liparopsis postalbida* the head is covered with large spicules, a morphology unique among the species in my study sample. I therefore recognized a separate character state for the larval head surface of *L. postalbida*. Other examples of autapomorphic character states include the greatly modified spinneret of *Cnethodonta grisescens* (Character 126) and the female eighth tergum of *Phryganidia californica* (Character 53). When additional notodontid species are studied, all of these may provide evidence of relationship.

ACKNOWLEDGMENTS

At the outset of this research, my general knowledge of the Notodontidae was infinitesimal. Several colleagues were essential in guiding me through the maze of notodontid taxonomy. They helped choose exemplar species, pointed out problems regarding the family classification, helped with the literature, and provided countless discussions concerning the minutiae of adult and larval morphology. Without the aid of these people I

would have no doubt floundered and would have spent a great deal of effort studying inappropriate and unnecessary issues. For such assistance, I am extremely grateful to David Carter (The Natural History Museum [BMNH], London), J. G. Franclemont (Cornell University [CU], Ithaca), George Godfrey (Illinois Natural History Survey [INHS], Champaign), Jeremy Holloway (CAB International Institute of Entomology, London), Ian Kitching (The Natural History Museum, London), Don Lafontaine (Canadian National Collections, Ottawa), John E. Rawlins (Carnegie Museum of Natural History [CMNH], Pittsburgh), Shigero Sugi (Tokyo), and Susan Weller (Louisiana State University). Many of the larval characters I describe were first pointed out to me by David Carter.

During the course of my study, I performed several preliminary cladistic analyses as the data set grew. These were done using the mainframe PHYSYS installations at the Systematic Entomology Laboratory (Smithsonian Institution) and the Entomology Department of the Museum of Comparative Zoology (Harvard University). For help with these analyses and for the kind use of their facilities, I thank Mary Mickevich (Smithsonian) and Jim Carpenter (Harvard). Michael Schwartz (Canadian National Collections) and Steve Farris (American Museum of Natural History [AMNH]) provided helpful assistance during my final analyses using the Hennig86 program.

The photographs of notodontid caterpillars were made from slides taken by John Rawlins, George Godfrey, and David Carter. I especially want to thank John Rawlins, who loaned most of the larval pictures. Andrew Simon and Peling Fong (AMNH) provided assistance with scanning electron microscopy, and members of the AMNH photography department were extremely helpful with photographic reproduction.

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I would like to express special appreciation to two of my mentors. First, I thank John Rawlins, whose efforts rearing Lepidoptera in Asia, Africa, South America, and the U.S. provided extremely rare and invaluable material. This study would have suffered greatly without the larval specimens he collected. John also gave various forms of encouragement and criticism along the way. Second, I offer my thanks to J. G. Franclemont, who provided gracious support through all aspects of this research. In particular, he put up with me during long hours while I used his personal library; he lent numerous genitalic slides and preserved larvae from his collection; and he tirelessly provided guidance concerning notodontid taxonomy, and concerning systematics and biology of the Lepidoptera in general.

I would like to dedicate this paper to the memory of my father, Richard S. Miller, whose example inspired me to study natural history.

CLADISTIC RESULTS

Cladistic analysis of the final data set produced eight equally parsimonious cladograms, each with a length of 853 steps, a retention index (RI) of 0.66, and a consistency index (CI) of 0.30. A strict consensus of those eight trees is shown in figures 99 and 100. The data were also analyzed using the most recent version of PAUP (Version 3.0E; Swoford, 1990) and identical results were obtained. In all analyses, characters were unweighted. The consensus tree is fully resolved except for three trichotomies within otherwise well-defined clades.

Formation of major monophyletic groupings in the Notodontidae and understanding relationships among those were my primary interests. Resolving the three trichotomies was largely irrelevant to this study. However, in an attempt to select one tree from among the eight trees of equal length, I applied successive approximations character weighting (SACW; Farris, 1969; Carpenter, 1988). After five iterations the SACW procedure produced nine rather than eight trees. When corrected for increased weights, the SACW trees were also longer than the original ones. I chose to accept my initial unweighted results.

Carpenter (1988) noted that for SACW to be effective, additive binary coding should be applied to multistate characters so they do not artificially receive greater weight. My data were not coded in that manner.

The two types of analyses produced trees of slightly different topology. Importantly, these differences would require very little change in the classification I propose. First, in the SACW trees, the genus *Hemiceras* arises as the sister group of the Dudusinae (Clade 27, fig. 100) rather than as the sister group of Clade 35. However, I regard *Hemiceras* to be incertae sedis, so this result is inconsequential. The only other significant difference between the SACW and unweighted analyses involves the position of *Ellida*. As a result of the unweighted analysis I tentatively place *Ellida* in the Phalerinae; it is the basal taxon in Clade 22 (fig. 99). However, SACW suggested that the genus arises one node farther down, at Clade 21. This would remove *Ellida* from the Phalerinae, and technically a new family group category would have to be cre-

ated for it. Again, however, by all accounts the position of this genus is ambiguous. The status of both *Ellida* and *Hemiceras* is further discussed in the section entitled Classification of the Notodontidae.

In order to estimate how much of the observed homoplasy is attributable to character changes in the outgroup, I ran the data using just one of the outgroup exemplars, *Peridroma saucia* (Noctuidae), to root the cladogram. I chose that species on the rather arbitrary grounds that its larva is not covered with secondary setae (see Character 140), since presence of these often obscures important primary setal characters. Rooting the cladogram using *P. saucia* produced the same eight trees as the original analysis that employed 11 outgroup taxa. Each of those trees had a CI of 0.32, only slightly higher than when the complete outgroup was used. To further investigate this finding I performed a series of experiments. First, I found that another noctuid species, *Alypia octomaculata* (Agaristinae), produced the same result as *P. saucia*. I then eliminated all quadrifid noctuoids from the matrix and designated *Doa ampla* as the outgroup. Again the same eight ingroup trees were generated. Finally, using the four thaumetopoeine exemplars as an outgroup yielded identical results regarding the rest of the Notodontidae.

Two conclusions can be reached from these rooting experiments. First, many authors have stressed the importance of carefully choosing outgroup species for cladistic analyses (e.g., Watrous and Wheeler, 1981). My results suggest that, at least in some cases, such claims are exaggerated; I could have found the same trees for the Notodontidae using a single, quite distantly related species as an outgroup. The advantage of using a large outgroup is that one obtains a better estimate of morphological variation outside the clade of primary interest. In addition, character optimizations for basal nodes of the ingroup tree can be more accurately determined. The second conclusion I would draw is that, for the characters used, little of the observed homoplasy is attributable to character changes in the outgroup.

Before proceeding, I should comment on

what may seem to be a low overall CI (0.30). Sanderson and Donoghue noted that "low CI values are widely considered to be symptomatic of poor character analysis and dubious results" (1989: 1787). These authors recently examined the general effects on cladogram CI of the number of taxa included, the number of characters used, the type of taxa studied (animal or plant), and whether the data are morphological or molecular. Sanderson and Donoghue concluded that only the first of these, taxon number, has any effect. They showed that cladogram consistency indexes are negatively correlated with increased taxon number. According to their regression of CI on number of taxa (based on 60 plant and animal data sets), a CI of 0.30 is typical for a study, such as mine, with approximately 60 terminal taxa.

Finally, I would like to make some general points regarding my cladistic results. First, I obtained the surprising result that *Oenosandra* (figs. 14, 15), considered by previous authors to be a member of the Thaumetopoeinae, is not a member of the Notodontidae. I consider it to be the basal element of the trifold noctuoid lineage. Further, I suggest that *Doa* (fig. 13) is the sister group to the Notodontidae, perhaps solving a long-standing problem concerning the status of the Doidae. Both of these results are discussed in more detail in the section entitled Classification of the Trifold Noctuoidea. At least three synapomorphies support the monophyly of a clade comprising *Oenosandra*, *Doa*, and the Notodontidae (see p. 169). Both genera were therefore treated as ingroup taxa for the final analysis.

The cladogram shown in figures 99 and 100 will form the basis for subsequent discussion; it is the phylogeny from which I derived my classification of the Notodontidae. A complete apomorphy list for that cladogram is presented in Appendix III.

CHARACTER ANALYSIS

The following is a list of all the characters used, arranged in order of life stage (adult or larval) and tagma. For each character, I discuss observed variation, list the states recognized, and examine character state distributions. A complete list of characters is presented in Appendix I, the data matrix is shown in Appendix II, and consistency indices for each character are given in Appendix IV.

When discussing species from my study list, I do not always indicate their familial or subfamilial ranking. The reader should refer to table 1 in that regard.

ADULTS

There are few general treatments of notodontid morphology. Arru (1965) published a comprehensive examination of adult morphology, larval morphology, and life-history characteristics for *Clostera anastomosis* (L.) in Italy. Weller (1989) presented an overview of notodontid adult morphology, focusing on structural variation in the Nystaleinae. Papers covering adult morphology in the Noctuidae (e.g., Forbes, 1954; Callahan, 1969; Oseto and Helms, 1976; Ryabov, 1988)

proved helpful for my research. Studies on subgroups of the Noctuidae that present fairly general morphological descriptions include those of Lafontaine (1981, 1987) for the Noctuinae and Kitching (1987) for the Plusiinae. Ferguson gave a useful introduction to lymantriid morphology (1978), and discussed general morphology of the Arctiidae (1985).

HEAD

Tentorium: *Character 1. Shape of the Tentorial Crest.* The tentorium, an internal bridge in the head connecting the anterior and posterior tentorial pits (Snodgrass, 1935), serves as the site of attachment for the antennal and cibarial muscles (Ehrlich and Davidson, 1961; Ehrlich and Ehrlich, 1962; Oseto and Helms, 1976; Chapman, 1982). Variation in shape of the tentorium in Papilionidae was described by Ehrlich (1958b) and has subsequently played an important role in papilionid tribal classification (see discussions in Ehrlich, 1958b; Munroe, 1961; Hancock, 1983; Miller, 1987b).

The tentorium of outgroup species and most notodontids is roughly sinuate with a dorsal swelling, the tentorial crest (Ehrlich,

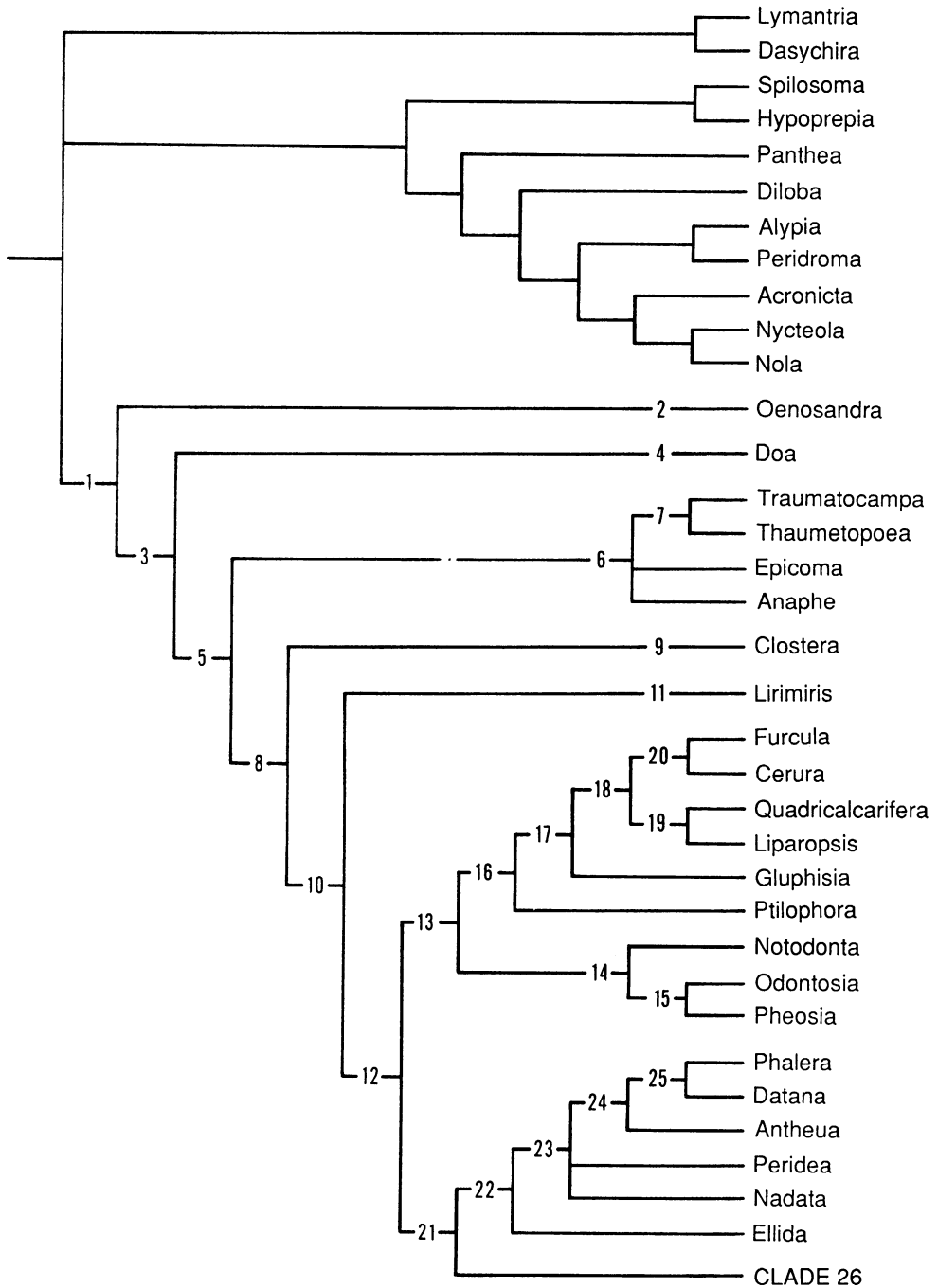


Fig. 99. Results of Hennig86 analyses of 174 unweighted characters (100 from adults and 74 from final instar larvae) for 63 species. A total of eight equally parsimonious trees were found (length = 854 steps, CI = 0.30, RI = 0.66). The strict consensus of those eight trees is shown in figure 99 (Clades 1 through 25) and figure 100 (Clades 26 through 53). *Lymantria* through *Nola* were designated as the outgroup. For species names see table 1.

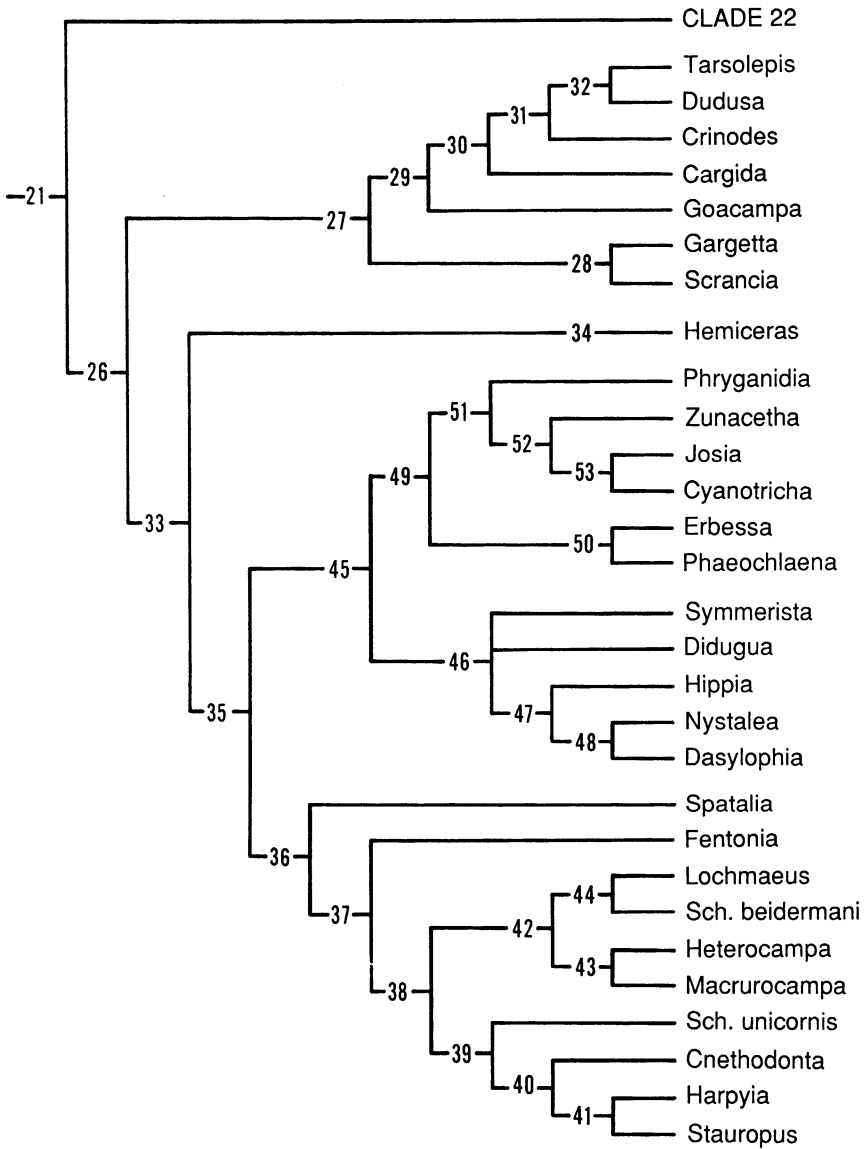
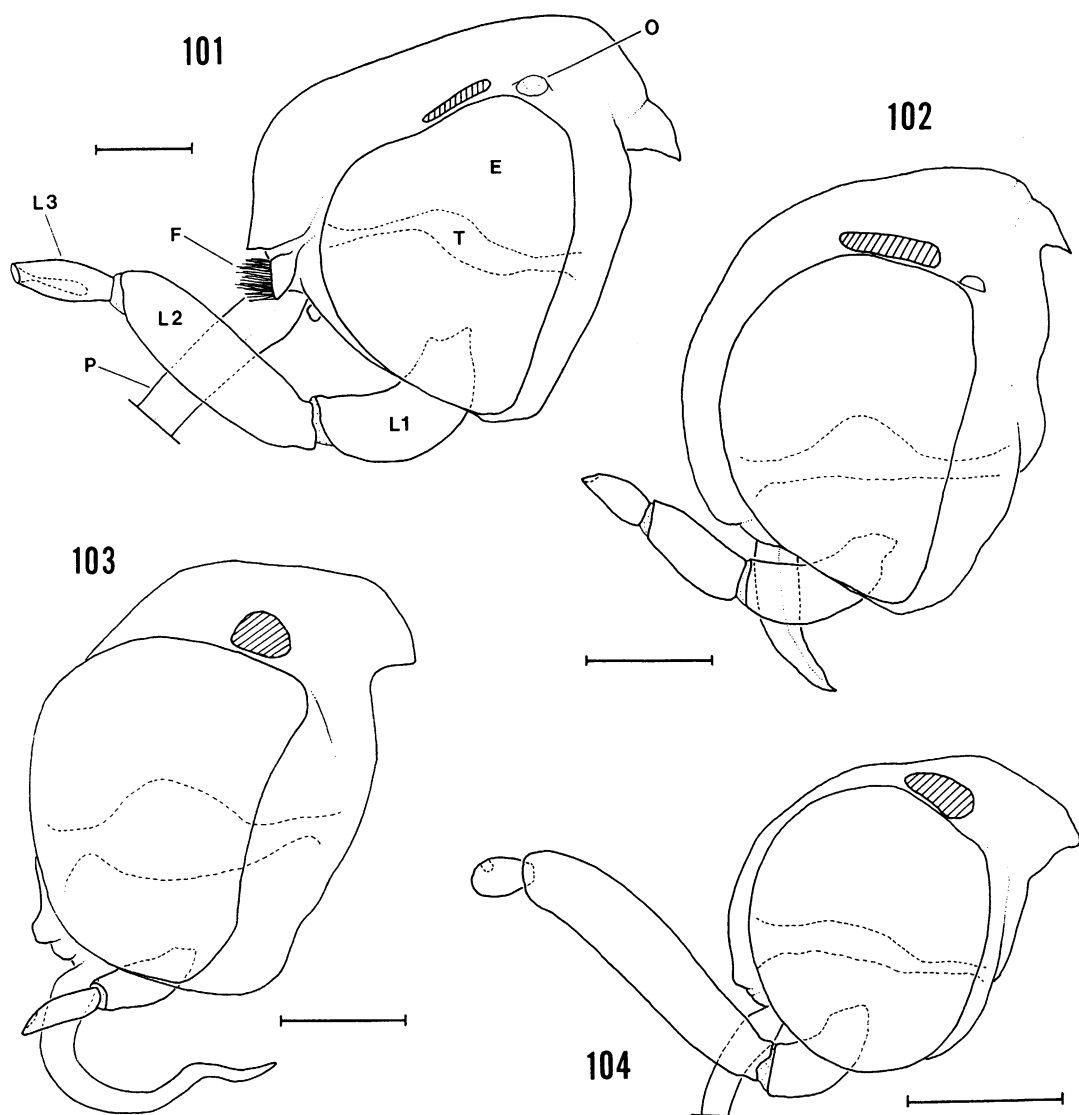


Fig. 100. Clades 26 through 53 from the analysis described in figure 99, where the remainder of the tree is shown. For species names see table 1.

1958a), at about its midpoint (e.g., figs. 101–115). Some Notodontidae lack a crest, and the tentorium is narrow with roughly parallel sides. A narrow tentorium appears to be derived. The derived state occurs in most Nystaleinae (fig. 112) and in the Dioptiinae (figs. 110, 111), as well as in the Scranciini (figs. 108, 109). There seems to be a rough corre-

lation between having a long proboscis and lacking tentorial crests.

Frons: *Character 2. Frontal Projections.* The frons of some adult Notodontidae protrudes and is heavily sclerotized, often with sharp anterior projections or teeth. This trait appears to have evolved at least two separate times within the family: in the Thaumeto-

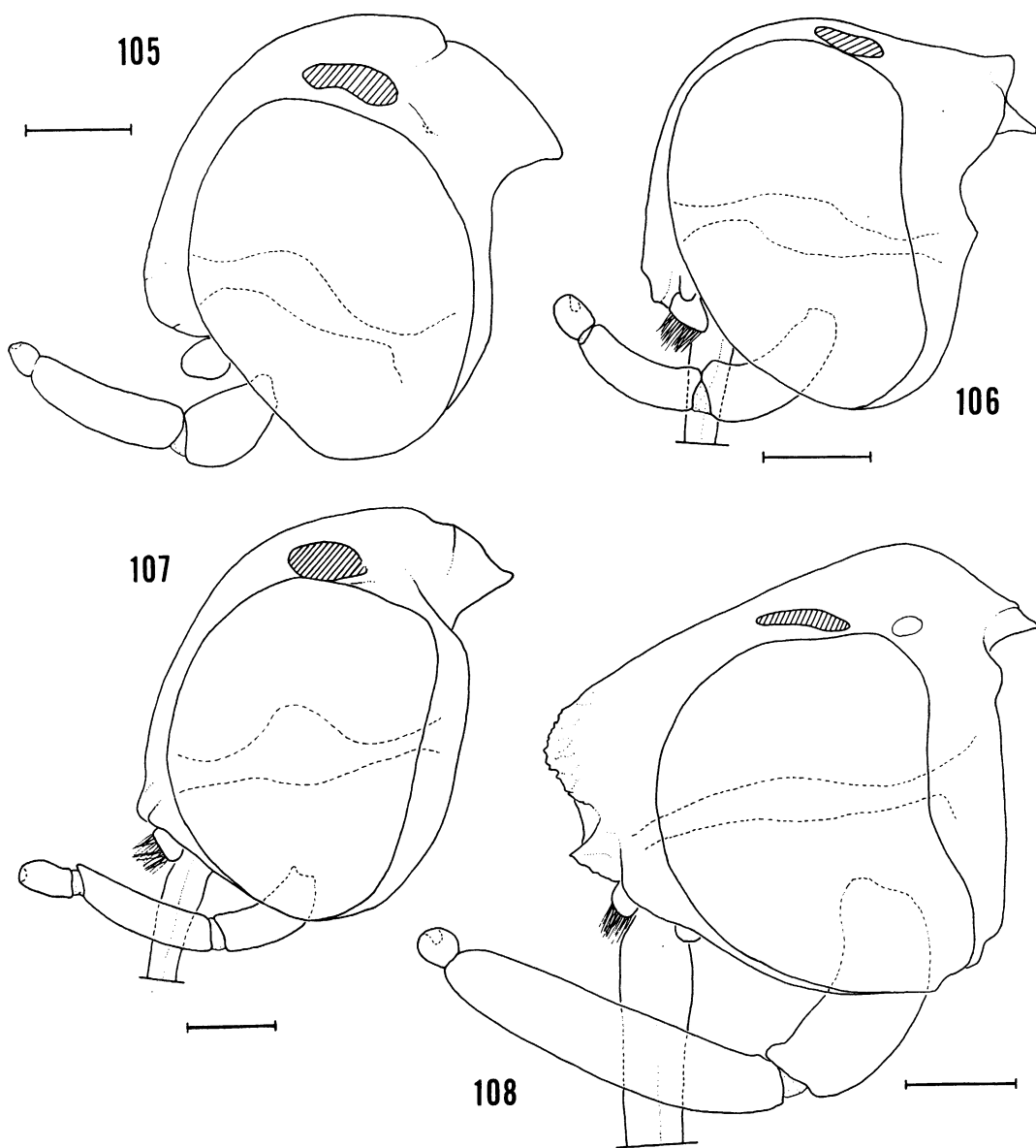


Figs. 101–104. Adult male heads in lateral view (anterior at left) with scales and antennae removed; antennal sockets indicated by cross-hatching. For long-tongued species only the base of the proboscis is shown. 101. *Peridroma saucia* (Noctuidae). 102. *Notodonta pacifica*. 103. *Furcula borealis*. 104. *Doa ampla* (Doidae). E = eye. F = pilifer. L1–L3 = labial palpus segments 1–3. O = ocellus. P = proboscis. T = tentorium. Scale lines = 0.5 mm.

poeinae and in the Dudusinae. A heavily sclerotized frons occurs in *Gargetta* (fig. 108) and *Scrancia* (fig. 109; see also Janse, 1920). The frons of *Goacampa variabilis* (Dudusini) is remarkably modified, with sclerotized wrinkles and projections (fig. 115). If my hypothesis is correct, that *Scrancia* and *Gargetta* (Scranciini) form the sister group of the

Dudusini, then there are two equally parsimonious possibilities: a sclerotized frons could be primitive for the subfamily Dudusinae but, among Dudusini, was lost in taxa above *Goacampa* (see fig. 100), or it evolved separately in both the Scranciini and Dudusini.

Traumatocampa pityocampa has a frons

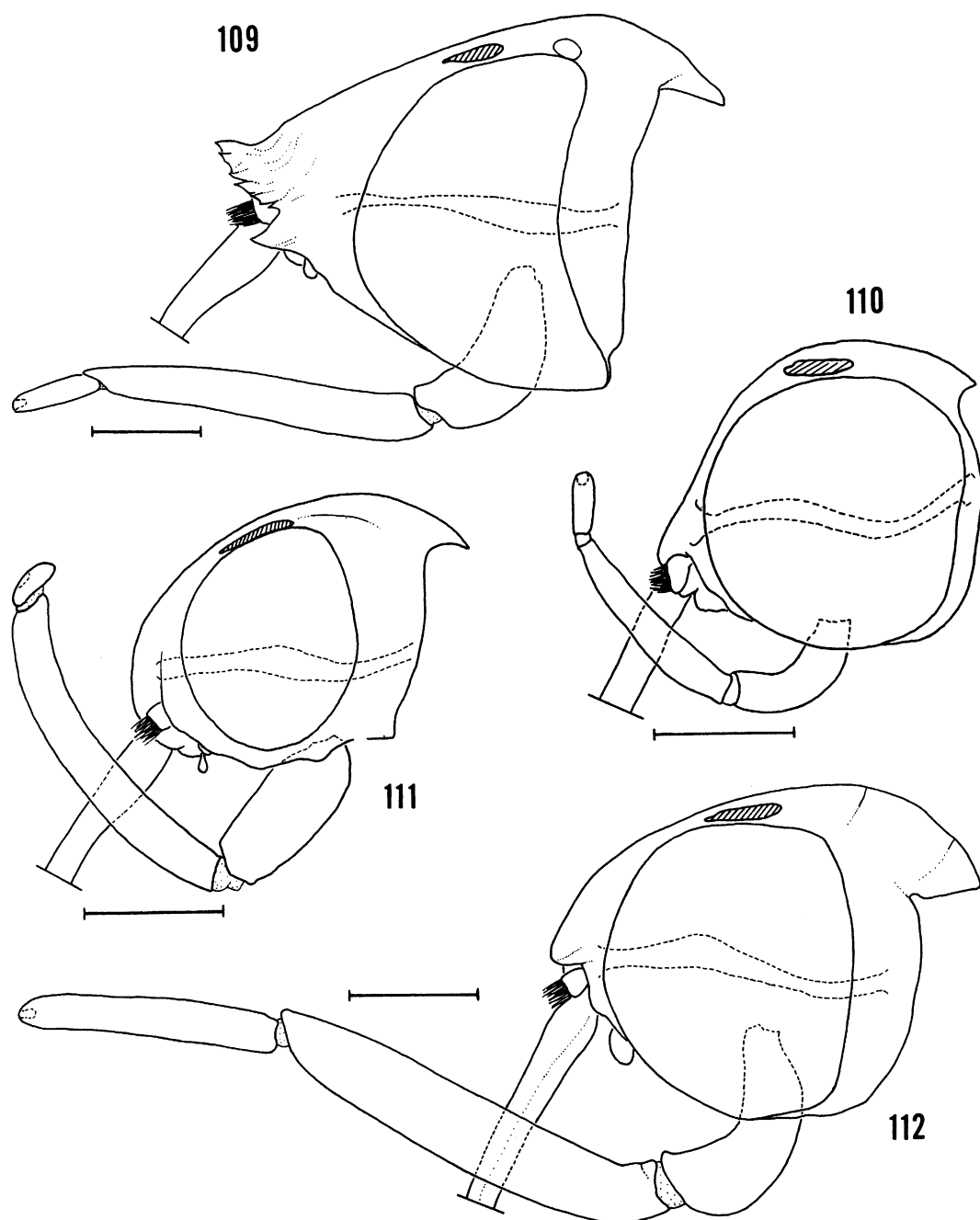


Figs. 105–108. Adult male heads in lateral view (anterior at left) with scales and antennae removed; antennal sockets indicated by cross-hatching. For long-tongued species only the base of the proboscis is shown. 105. *Anaphe panda*. 106. *Datana ministra*. 107. *Schizura biedermani*. 108. *Gargetta costigera*. Scale lines = 0.5 mm.

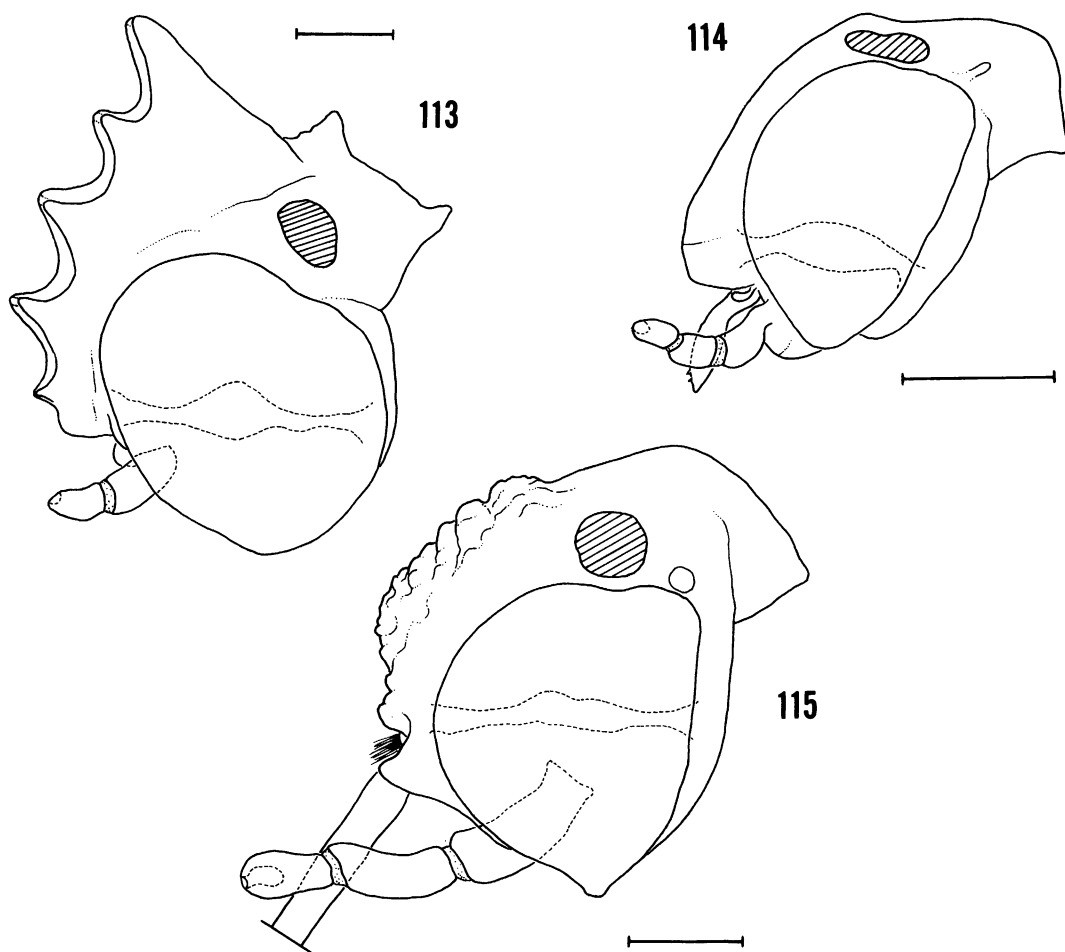
with huge ratchetlike teeth on it (fig. 113), and similar modifications are found in other thaumetopoeine genera (see figures in Bourgogne, 1951; de Freina and Witt, 1987). De Freina and Witt divided the Thaumetopoeinae into two groups based on presence or absence of the modified frons. The frons of

Thaumetopoea processionea, which I also scored as having the derived state, is sclerotized and bulges anteriorly, but it does not have teeth.

The frons of both *Alypia* (Agaristinae) and *Oenosandra* protrudes greatly and is highly sclerotized. This condition is found through-



Figs. 109–112. Adult heads in lateral view (anterior at left) with scales and antennae removed; antennal sockets indicated by cross-hatching. For long-tongued species only the base of the proboscis is shown. **109.** *Scrancia stictica* (female). **110.** *Zunacetha annulata* (female). **111.** *Phaeochlaena gyon* (male). **112.** *Hippia packardii* (male). Scale lines = 0.5 mm.



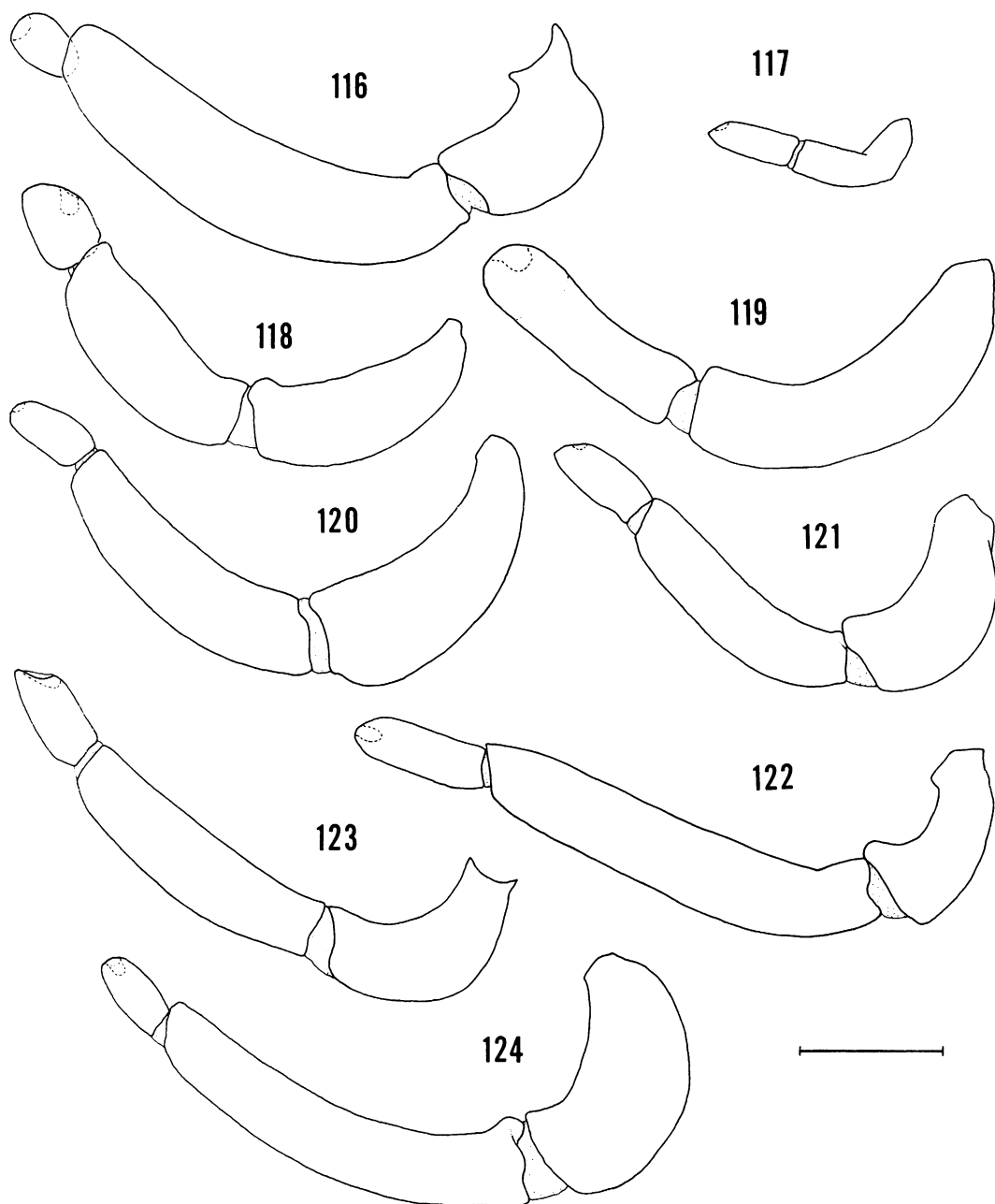
Figs. 113–115. Adult male heads in lateral view (anterior at left) with scales and antennae removed; antennal sockets indicated by cross-hatching. For long-tongued species only the base of the proboscis is shown. 113. *Traumatocampa pityocampa*. 114. *Ptilophora plumigera*. 115. *Goacampa variabilis*. Scale lines = 0.5 mm.

out the Agaristinae (Forbes, 1960; Kiriakoff, 1977). It also occurs in members of the noctuid groups Armadini (Ophiderinae) (Bourgogne, 1951; Kuznetsov, 1967; Wiltshire, 1979), Amphipyridae (Janse, 1939a), and Heliethinae (Hardwick, 1970). The frons of some desert-dwelling geometrids is remarkably similar to these (Rindge, 1959).

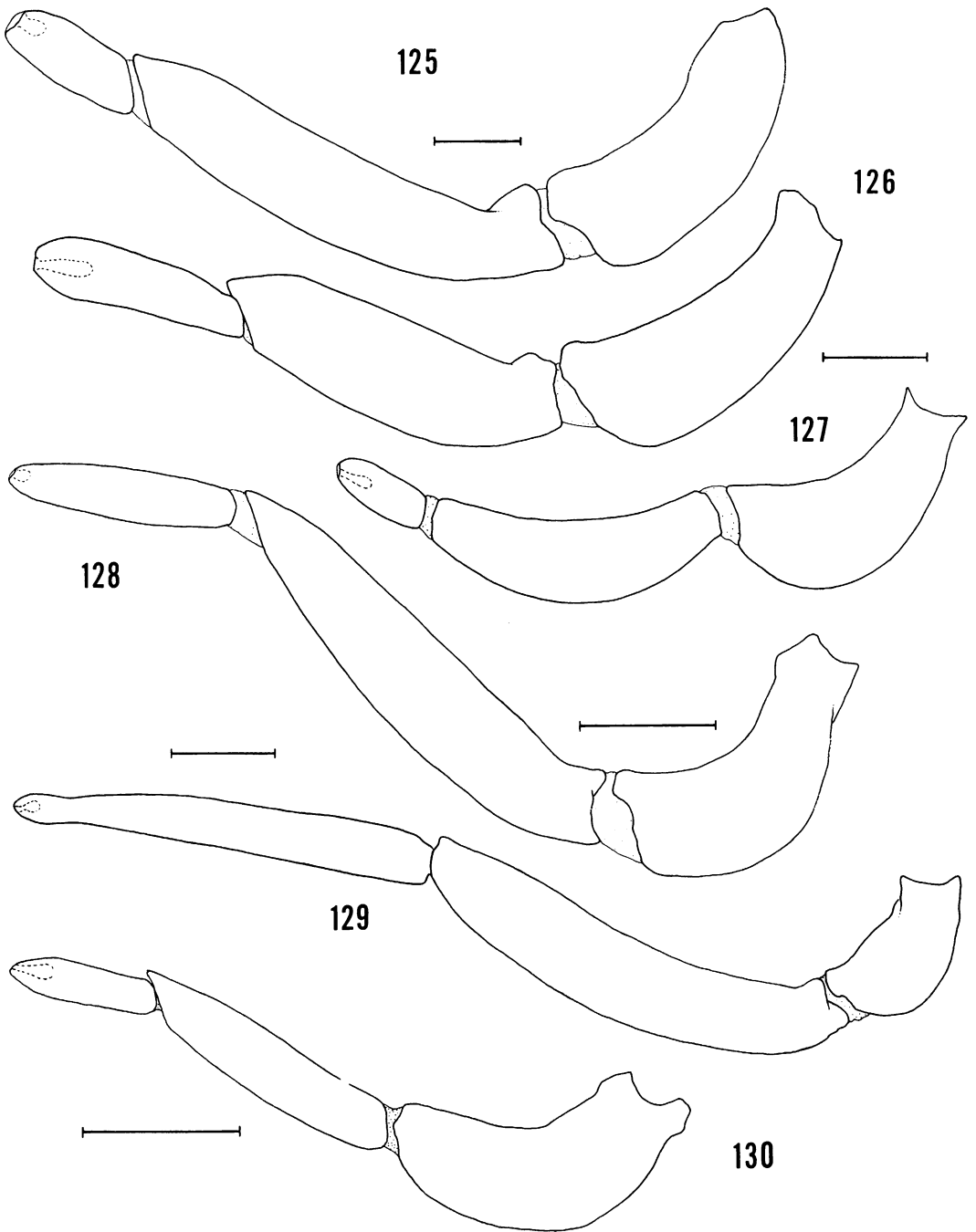
Though all the taxa above show slightly different types of frons modifications, the sclerotized protuberances may serve a similar function in each. They may be an adaptation to dry habitats with hard soils. The Armadini

and Heliethinae are often found in arid climates, and in both groups the structure is thought to assist the adult moth as it breaks through hard soil upon emergence from its subterranean pupa (Bourgogne, 1951; Hogue, 1963; Wiltshire, 1979; Lafontaine, 1981; Ryabov, 1988). Alternatively, these frontal processes may be used by the adult moth to break through specialized pupal chambers (Dodd, 1902; G. Godfrey, personal commun.).

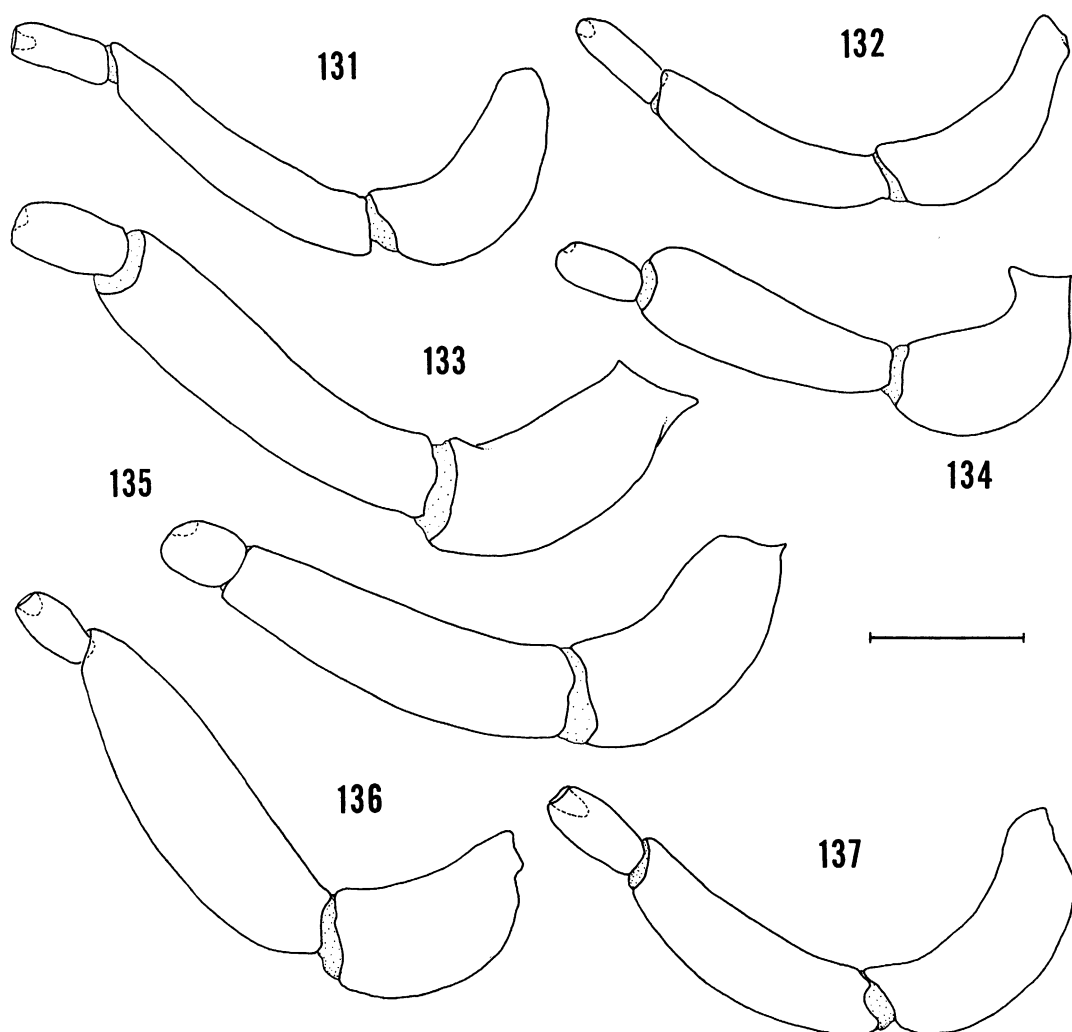
Labial Palpi: Size and shape of the labial palpi, extremely variable within the Notodontidae, have long been used as taxonomic



Figs. 116–124. Male left labial palpus (anterior at left). 116. *Clostera albosigma*. 117. *Gluphisia septentrionis*. 118. *Phalera bucephala*. 119. *Cerura liturata*. 120. *Antheua simplex*. 121. *Ellida caniplaga*. 122. *Nadata gibbosa*. 123. *Peridea angulosa*. 124. *Lirimiris truncata*. Scale line = 0.5 mm.



Figs. 125–130. Male left labial palpus (anterior at left). 125. *Dudusa synopla*. 126. *Tarsolepis japonica*. 127. *Hemiceras bilinea*. 128. *Symmerista albifrons*. 129. *Didugua argentilinea*. 130. *Josia ligata*. Scale lines = 0.5 mm.



Figs. 131–137. Male left labial palpus (anterior at left). 131. *Lochmaeus bilineata*. 132. *Schizura unicornis*. 133. *Cnethodonta griseascens*. 134. *Harpyia microsticta*. 135. *Stauropus fagi*. 136. *Spatalia jezoensis*. 137. *Fentonia ocypte*. Scale line = 0.5 mm.

characters (e.g., Stephens, 1829; Hampson, 1892; Dyar, 1897; Schaus, 1901; Turner, 1903, 1922; Nagano, 1916; Janse, 1920; Marumo, 1920; Matsumura, 1929b). Extremes range from the Thaumetopoeinae, where the palpi can be very small (fig. 113; Janse, 1920), to the Nystaleinae, many of which have extremely long palpi (figs. 112, 128, 129, 203; see also Weller, 1989).

Although labial palpi are of universal occurrence in Lepidoptera, their function is far from clear (Bourgonne, 1951). In all species

there is a sensory pit, first discussed by vom Rath (1887), at the apex of the third segment (figs. 101–137). Recent authors have argued that presence of vom Rath's Organ is a synapomorphy for the entire order Lepidoptera (Kristensen, 1984; Nielsen, 1989). Bogner et al. (1986) showed that the sensilla housed in this organ are highly sensitive to carbon dioxide, but the authors acknowledged that the biological significance of CO₂ perception in Lepidoptera is obscure.

The labial palpi show sexual dimorphism;

male palpi are frequently longer and show more striking variation than those of females. Males were therefore used for the three labial palpus characters in my analysis.

Character 3. Length of Palpus Segment 2. I recognized four character states concerning palpus segment 2. The first three measure segment 2 length relative to that of segment 1 (Appendix I). These states are (a) segment 2 approximately one to 1½ times as long as segment 1, (b) segment 2 shorter than segment 1, or (c) segment 2 more than twice as long as segment 1. The first (scored as "0") is exemplified by *Schizura beidermani* (fig. 107), *Antheua simplex* (fig. 120), and others. The second state ("1") applies to species such as *Notodonta pacifica* (fig. 102). The third state, having an extremely long second segment, is best seen in members of the Nystaleinae (figs. 112, 128, 129), but occurs in other species such as *Clostera albosigma* (fig. 116), *Nadata gibbosa* (fig. 123), and *Scrancia strictica* (fig. 109).

Although most members of the outgroup received a "0" score (e.g., *Peridroma saucia*, fig. 101), there is significant variation in palpus shape there as well. *Doa* (fig. 104), the lymantriids, and *Nola* have a long second segment, whereas that of *Oenosandra* is very short.

A fourth character state is restricted to the Dioptinae. In *Erbessa*, *Phaeochlaena* (fig. 111), and several other dioptine genera (Köhler, 1930; J. Miller, unpubl. data), the labial palpi are long and sickle-shaped with an elbowlike joint between the first and second segments. In these species the palpi are typically held against the frons, sometimes extending posteriorly over the head as far as the occiput. In contrast, the palpi of *Phryganidia californica* are relatively short (Miller, 1987a).

Character 4. Length of Palpus Segment 3. An elongate third palpus segment occurs in many species currently placed in the Nystaleinae (Weller, 1989). I scored segment 3 as being elongate if it is as long as or longer than segment 1 (figs. 112, 128, 129). Among the species I examined, this occurs in four members of the Nystaleinae. The trait cannot be used as a synapomorphy for the entire subfamily, however, because the palpi of *Nystalea* do not have an elongate third segment. The derived state applies to one outgroup

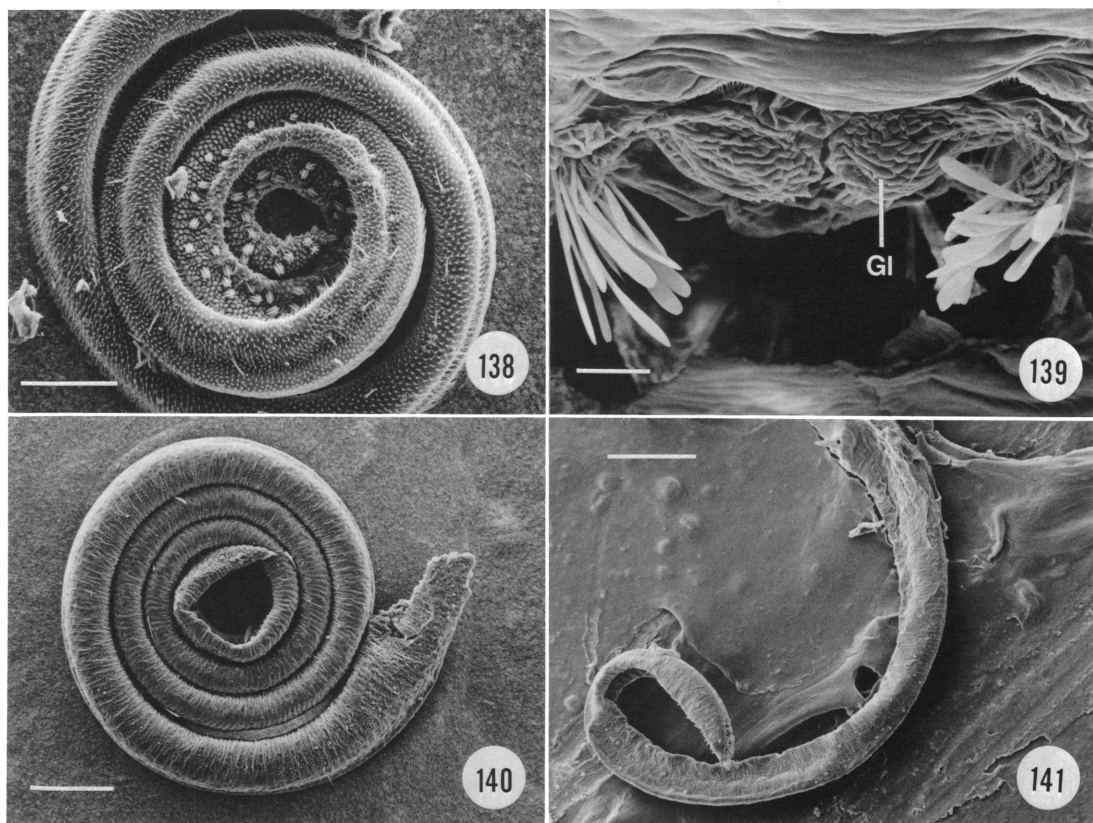
taxon as well, the noctuid genus *Nycteola* (Sarrothripinae). I recognized a second derived state, found only in *Erbessa* and *Phaeochlaena* among my species sample, in which segment 3 is extremely short and oblong in shape, with vom Rath's Organ located on the segment's anterior surface (fig. 111). This morphology occurs in other dioptine genera as well (J. Miller, unpubl. data).

Character 5. Fusion of Palpal Segments. The labial palpi of almost all Lepidoptera are three-segmented. However, adults of some Notodontidae have very small labial palpi with the second and third segments apparently fused so that the entire palpus appears to be two-segmented. This is found in *Liparopsis*, *Furcula* (fig. 103), *Cerura* (fig. 119), and *Gluphisia* (fig. 117), all members of the subfamily Notodontinae. In addition, thaumetopoeines exhibit a range of palpal development from fairly large (e.g., *Anaphe*, fig. 105) to highly reduced; each labial palpus in *Epicoma tristis* is represented by a single, tiny lobe. *Oenosandra* and *Panthea* have small palpi, but all three segments are clearly separated.

Fusion of labial palpus segments occurs in other families of Lepidoptera, for example, the Papilionidae (Miller, 1987b) and Hepialidae (Nielsen and Kristensen, 1989). In each case fusion appears to represent a derived state.

Proboscis: In Lepidoptera, elongate galeae of the maxillae interlock with legulae (fig. 149; Callahan, 1969; Davis, 1986) to form a sucking tube (figs. 146, 147), the haustellum or proboscis (Snodgrass, 1935; Oseto and Helms, 1976). Comparative morphology of notodontid proboscises provided a wealth of phylogenetic information. Many of these features were best observed by scanning electron microscopy. I examined the haustellum of all study taxa with SEM, but most proboscis characters could have been scored with a compound microscope. For two species the proboscises of conspecific males and females were studied. None of the characters I describe exhibit sexual dimorphism. For taxa lacking the haustellum (see Character 6), it was necessary to score proboscis fine structural features as missing data ("?").

Character 6. Proboscis Length. Noctuids exhibit wide variation in the degree of de-



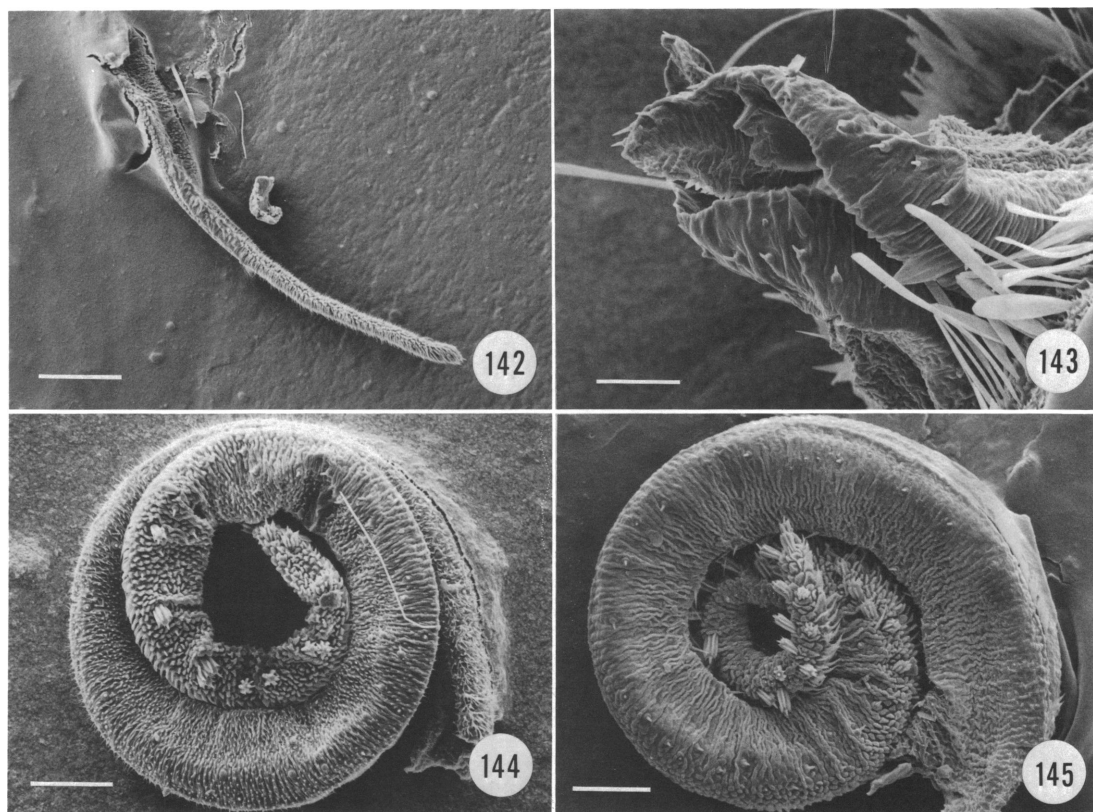
Figs. 138–141. Adult proboscis. **138.** *Nola pustulata* (Nolidae), lateral view (100 μ m). **139.** *Dasychira obliquata* (Lymantriidae), frontal view showing reduced galeae (GI) (50 μ m). **140.** *Schizura biedermani*, lateral view (200 μ m). **141.** *Cargida pyrrha*, lateral view (200 μ m). Scale lengths in parentheses.

velopment of the proboscis. For example, the proboscis is long in Noctuidae and Nolidae (fig. 138), but is reduced to two small lobes in Lymantriidae (fig. 139). The Notodontidae show a complete range of haustellum length. It can be long (figs. 140, 156, 168), of moderate length (figs. 141, 145), present as two small lobes (figs. 105, 114, 143), or absent (fig. 113). I attempted to categorize four character states (see Appendix I) based on proboscis length relative to head and thorax length. A long proboscis is characteristic of species that feed extensively as adults, and these probably have relatively long life spans (Weller, 1989). All Dioptriinae possess a long tongue, and I have observed species of several genera feeding at flowers during the late afternoon in Ecuador (unpubl. data). Notodontids with a reduced proboscis have previously been thought not to feed as adults,

suggesting that these live for shorter periods of time. However, Adler (1982) showed that adults of *Gluphisia* and *Clostera*, both of which have a small proboscis, take in extremely large amounts of water from puddles. For *Gluphisia* he found that puddling adults pass huge quantities of water through their system, up to 500 times their body weight per hour. In *Gluphisia*, the legulae are large and spatulate (figs. 148, 149) and loosely interlock, perhaps forming a “strainer” when the adult drinks.

Character 7. Proboscis Width. The haustellum in *Peridea angulosa*, *Odontotia elegans*, and *Nadata gibbosa* is unusually wide relative to its length (figs. 144, 145). Although in these genera the proboscis is fairly short, short proboscises are not always wide (e.g., fig. 142).

Character 8. Proboscis Surface Sculptur-



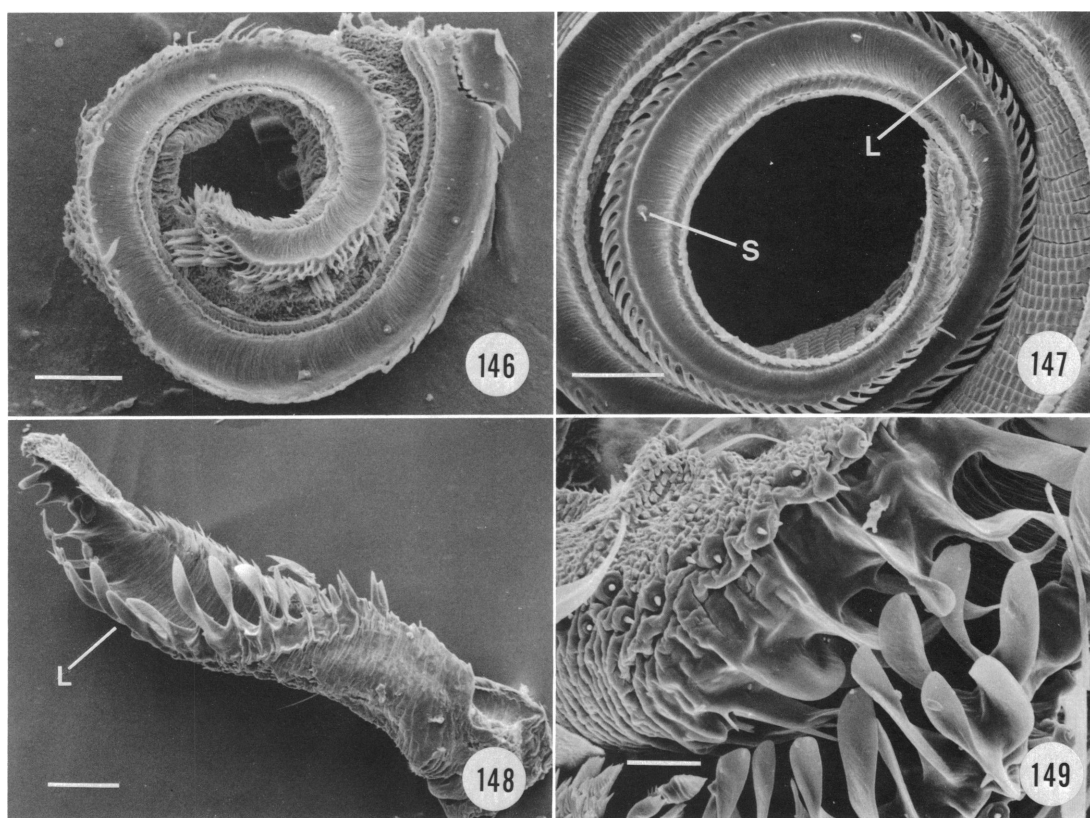
Figs. 142–145. Adult proboscis. **142.** *Furcula borealis*, lateral view (200 μm). **143.** *Clostera albosigma*, dorsal view (100 μm). **144.** *Peridea angulosa*, lateral view (100 μm). **145.** *Nadata gibbosa*, lateral view (100 μm). Scale lengths in parentheses.

ing. The galeae of the lepidopteran proboscis are composed of numerous sclerotized rings joined by membranous bands (Eastham and Eassa, 1955; Oseto and Helms, 1976; Common, 1979). Morphological variation in proboscis surface sculpturing is used as a taxonomic character for eumaeine lycaenids by Robbins (in press) and was discussed by Davis (1986) with regard to phylogeny of monotrysian Lepidoptera. Notodontids exhibit three distinct types of surface sculpturing (which I designate Types I–III) on these sclerotized rings. In Type I, also typical of the outgroup, the surface is covered with apically acute microprojections (e.g., figs. 138, 144, 150–155) that are usually dorsoventrally flattened (figs. 152, 153). The extreme base of the proboscis in all species I examined is covered with hairlike microprojections (fig. 161). To assure that these were not confused with

Type I microprojections, I scored Character 8 by examining an area approximately half-way between the head and the tip of the proboscis.

Two apomorphic surface types were observed, both unique to Notodontidae as far as I am aware. In Type II there are no microprojections and each ring has a series of distinct longitudinal ridges on its surface. The ridges of one ring are aligned so that they alternate with the ridges of the next (figs. 157, 158). Type II surface structure is characteristic of Dioprinae (figs. 147, 158), as well as most Nystaleinae (fig. 156) and Heterocampinae (figs. 157, 164, 168).

Some Notodontidae exhibit Type III, in which the galeae lack sculpturing altogether and appear instead to be composed of smooth rings (e.g., fig. 159). According to my analysis, Type III surface sculpturing has evolved



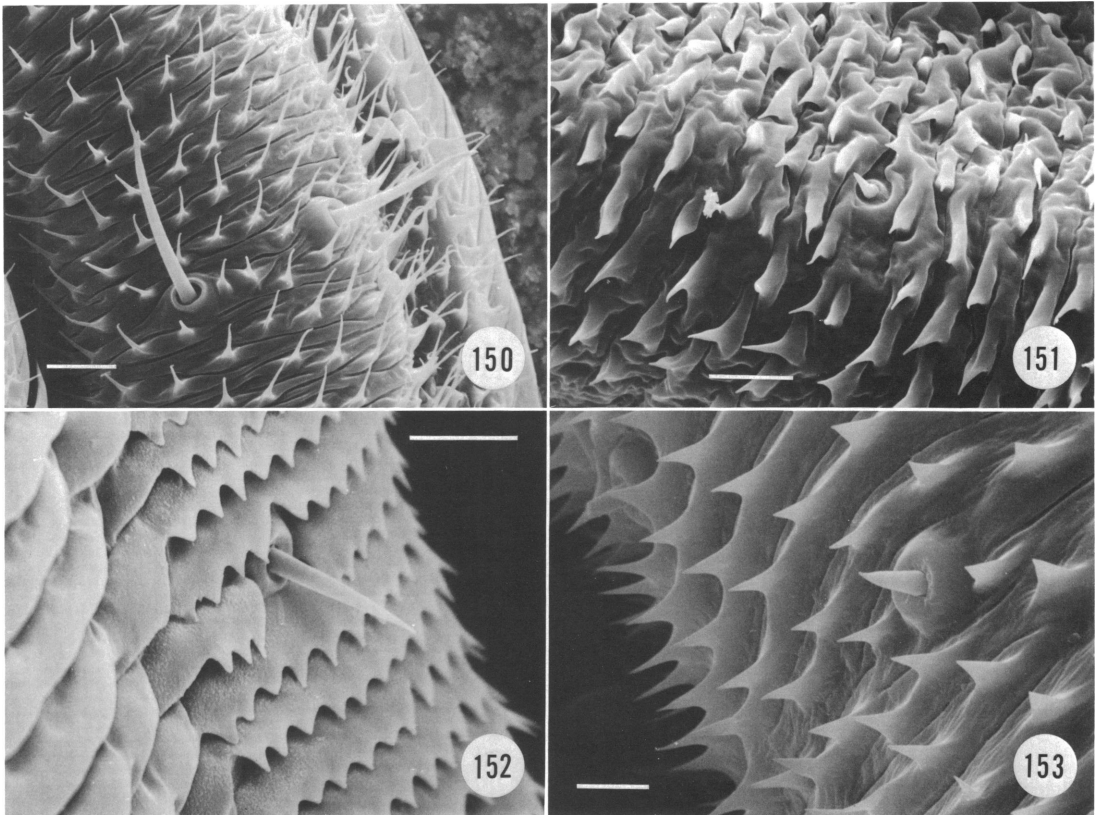
Figs. 146–149. Adult proboscis. **146.** *Lirimiris truncata*, mesal view of right galea showing internal surface of sucking tube (100 μ m). **147.** *Josia ligata*, mesal view of right galea (distal portion) showing internal surface of sucking tube; note legulae (L) and internal sensillae (S) (50 μ m). **148.** *Gluphisia septentrionis*, mesal view of right galea showing spatulate legulae (L) (100 μ m). **149.** *Gluphisia septentrionis*, ventral view of haustellum showing interlocking galeae (50 μ m). Scale lengths in parentheses.

separately in two subfamilies. First, it is a synapomorphy for the Dudusini that I studied (e.g., *Tarsolepis japonica*, fig. 190). Second, Type III occurs in the genus *Nystalea* (figs. 159, 195) of the Nystaleinae, where Type II is clearly the ground state.

Although I attempted to assign each taxon to one of the three states described above, some difficulties arose. Reduction of the haustellum appears to have occurred independently in almost every notodontid subfamily (see Character 6), and in species with a reduced proboscis, the surface sculpturing tends to become obscured (e.g., fig. 148). Occasionally, the sculpturing was not clearly one type or the other. For example, I could not assign a score to the proboscis of *Spatialia*

jezoensis in the Heterocampinae (fig. 165), so this taxon received a “?” for Character 8.

Proboscis Sensilla: Two types of sensilla occur on the lepidopteran proboscis. The first, called “R2” by Börner (1939), appear to be basiconic sensilla. Each consists of a short body and what I term the sensory cone (fig. 166), following Bourgonne (1951). R2 sensilla are found scattered along the tongue’s entire length (figs. 167, 168). The second type (“R1” of Börner, 1939), found only on the distal third of the haustellum, are large sensilla styloconica (Callahan, 1969; Davis, 1986). These sensilla, most numerous at the proboscis tip (figs. 138, 144, 145, 156, 168), show interspecific shape variation ranging from squat to elongate (figs. 170, 176), but a



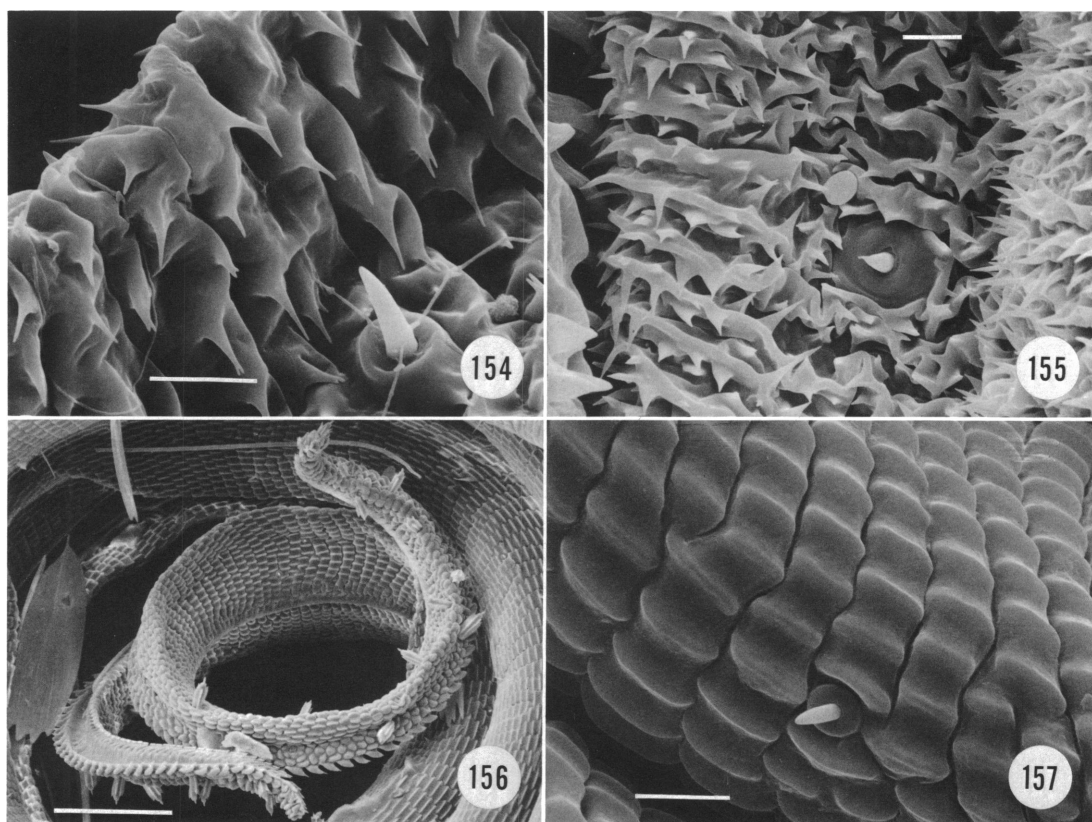
Figs. 150–153. Surface of the adult proboscis (photographs taken at approximately the proboscis midpoint). 150. *Nola pustulata* (Nolidae) (10 μ m). 151. *Panthea furcilla* (Noctuidae) (10 μ m). 152. *Scraucia stictica* (10 μ m). 153. *Hemiceras bilinea* (5 μ m). Scale lengths in parentheses.

single specimen can also exhibit slight height variation. Usually, each R1 sensillum consists of an elongate body with five to seven longitudinal flutes (fig. 171) and a relatively short sensory cone (figs. 170–179). It is not known whether these sensilla function as chemoreceptors or mechanoreceptors (Bourgogne, 1951; Sellier, 1975). Both Callahan (1969) and Ryabov (1988) claimed that they are taste receptors, but neither author provided supporting evidence.

In each lepidopteran group where they have been studied, R1 sensilla exhibit remarkable variation in shape (Bourgogne, 1951; Ikeuchi, 1962). Davis (1986) and Kitching (1987) were perhaps the first to use such variation for taxonomic purposes. Ryabov (1988) stressed sensillum shape as a potential taxonomic character in Noctuidae. I recognized

two character states involving the presence or absence of flutes (Character 9) and four states involving overall shape of the R1 sensilla (Character 10). With further study, more taxonomic information could be obtained from both character complexes. In some taxa with an extremely reduced haustellum, such as members of the Thaumetopoeinae, R2 sensilla occur, but R1 sensilla appear to be absent. These received “?” scores (= missing data) for Characters 9 and 10.

Character 9. Fluted R1 Sensilla. Fluted R1 sensilla have been reported in families of the Monotrysia (Davis, 1986), throughout the Papilionoidea (Bourgogne, 1951; Sellier, 1975; Robbins, in press), and in the Noctuidae (Callahan, 1969; Wiltshire, 1979; Kitching, 1987, 1988; Ryabov, 1988). In addition, Börner (1939) described them from families



Figs. 154, 155. Surface of the adult proboscis (photographs taken at approximately the proboscis midpoint). 154. *Antheua servula* (10 μm). 155. *Lirimiris truncata* (10 μm). Scale lengths in parentheses.

Fig. 156. Distal portion of the adult proboscis of *Hippia packardii*. Scale line = 100 μm .

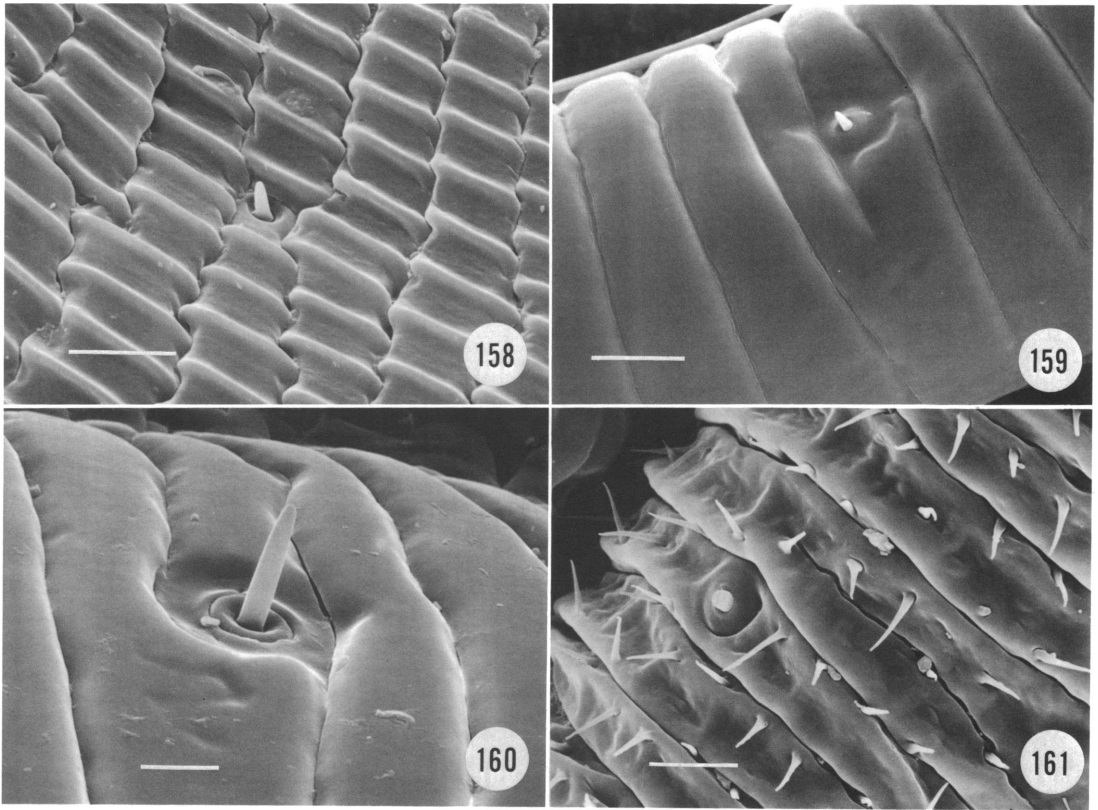
Fig. 157. Surface of the adult proboscis of *Lochmaeus bilineata* (photograph taken at approximately the proboscis midpoint). Scale line = 10 μm .

as widely divergent as the Castniidae, Tortricidae, and Uraniidae. In *Micropterix* there are two types of sensilla on the galeae: short, basiconic sensilla similar to the R2 sensilla in noctuids, and lamellate sensilla that lack the sensory cone (Chauvin and Fauchaux, 1981). The presence of fluted styloconic sensilla on the haustellum may be an apomorphy for all Lepidoptera above Micropterigidae.

In my study, fluted styloconic sensilla are found throughout the outgroup (figs. 177, 178). Kitching (1988) proposed that these are plesiomorphic within Noctuidae, and I regard that shape to be plesiomorphic for Notodontidae as well. A second state can occur where the R1 sensilla are smooth or the flutes are highly reduced. There appears to be a rough correlation between presence of a small

proboscis and loss of the R1 flutes (e.g., see Nielsen and Kristensen, 1989), a trend noted by Ryabov (1988) for Noctuidae as well. In *Oenosandra*, for example, the proboscis is short and the flutes are barely visible (fig. 180). Similarly, most notodontids with a reduced proboscis have simple sensilla (figs. 181, 182; see also *Clostera anastomosis* in Arru, 1965: fig. 3).

This derived state appears to have evolved separately in five notodontid lineages. All members of Clade 14 (Notodontini) that I studied have rather squat, smooth R1 sensilla (fig. 181). There are small projections on the body of the sensillum in *Odontosia elegans* (figs. 184, 185), possibly homologous with reduced flutes. Short, smooth sensilla also occur in some Dicranurini (fig. 182) and in the



Figs. 158–160. Surface of the adult proboscis (photographs taken at approximately the proboscis midpoint). **158.** *Phaeochaena gyon* (10 μ m). **159.** *Nystalea nyseus* (20 μ m). **160.** *Hapigia annulata* (10 μ m). Scale lengths in parentheses.

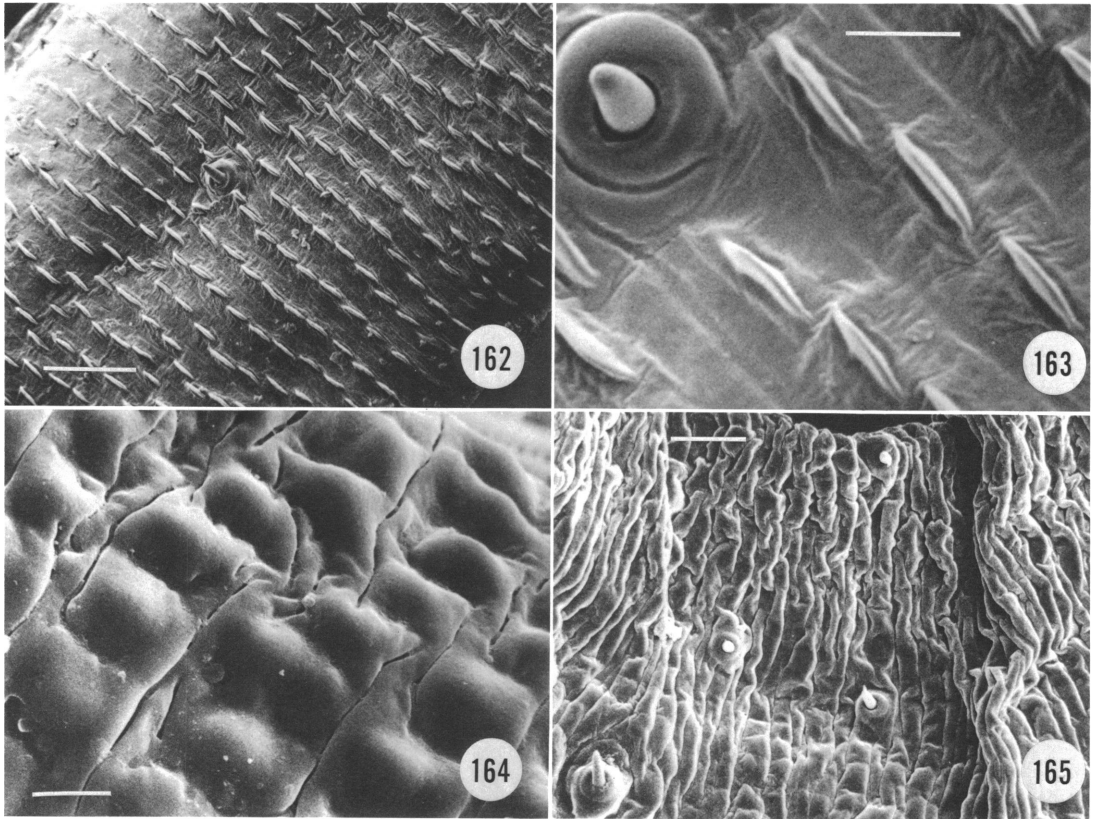
Fig. 161. Surface of the adult proboscis of *Schizura biedermanni* (photograph taken near the proboscis base). Scale line = 10 μ m.

Pygaerinae (fig. 183). Tall, smooth R1 sensilla are found in the genus *Nystalea*. Monophyly of the Nystaleinae is well supported, and other members of the tribe have typical fluted sensilla (fig. 156). I examined another *Nystalea* species (*N. eutalanta* Dyar; fig. 195) to confirm that the sensilla of *N. nyseus* (fig. 189) are not unique in the genus.

Presence of smooth R1 sensilla also provides a synapomorphy for the Dudusini (Clade 29). Here, they are quite different from those in Clade 14, being greatly elongate. In *Dudusa*, *Goacampa*, and *Cargida*, the sensilla are cylindrical with tiny remnants of the flutes distally (figs. 188, 192, 193, 198), while they are completely smooth and laterally compressed in *Crinodes* and *Tarsolepis* (figs. 186, 187, 191). *Gargetta costigera* has smooth

R1 sensilla, but *Scrancia stictica* does not. Character optimization could not resolve whether smooth R1 sensilla originally evolved in Clade 27 (Dudusinae) but reverted to the plesiomorphic condition in *S. stictica*, or whether smooth sensilla evolved separately in the Dudusini (Clade 29) and Scranciini (Clade 28).

Bänziger (1973, 1983, 1987, 1988a, 1988b, 1988c, 1989; Bänziger and Fletcher, 1988), in a fascinating series of papers, has described Asian Lepidoptera feeding on mammalian lachrymal secretions. He reported incidents of lachryphagy in the Geometridae, Pyralidae, Thyatiridae, Sphingidae, and Noctuidae. Most important to this study, he has shown that some Notodontidae are highly specialized tear drinkers (Bänziger, 1988a). His ob-



Figs. 162–165. Surface of the adult proboscis (photographs taken at approximately the proboscis midpoint). **162.** *Goacampa variabilis* (20 μm). **163.** *G. variabilis* (5 μm). **164.** *Fentonia ocypete* (5 μm). **165.** *Spatalia jezoensis* (20 μm). Scale lengths in parentheses.

servations (Bänziger, 1973, 1983, 1988a) are limited to relatively few notodontid genera. These are *Tarsolepis*, *Poncetia* Kiriakoff, and *Pydnella* Roepke. Of particular interest, Shannon (1928) reported that adults of *Crinodes besckei* in Argentina are attracted to horses at night. He did not directly observe tear drinking in *C. besckei*, but did in other moths taken at the same time. Shannon proposed two explanations for tear drinking in moths. First, he suggested that such behavior may result from a scarcity of flowers, making another food source necessary. Second, he thought that the moths might obtain essential salts from mammalian tears.

The studies cited above have interesting implications. My cladograms suggest that *Crinodes*, *Cargida*, *Goacampa*, *Dudusa*, and *Tarsolepis* belong in the tribe Dudusini (Du-

dusinae). Furthermore, these species have specialized proboscis sculpturing (Character 8) and modified R1 sensilla, morphological traits perhaps related to tear-drinking behavior. I would therefore predict that all Dudusinae with specialized proboscises are lachryphagous, and that *Crinodes* and other New World dudusines do indeed drink mammalian tears. It will be interesting to see whether *Poncetia* and *Pydnella* are dudusines and whether they exhibit morphological specializations of the proboscis.

Character 10. Shape of the R1 Sensilla. In addition to presence or absence of flutes, I recognized four states involving overall shape of the R1 sensilla (see Appendix I). Based on morphology in the outgroup, moderately elongate sensilla (figs. 169, 175, 179) represent the plesiomorphic state for Notodonti-

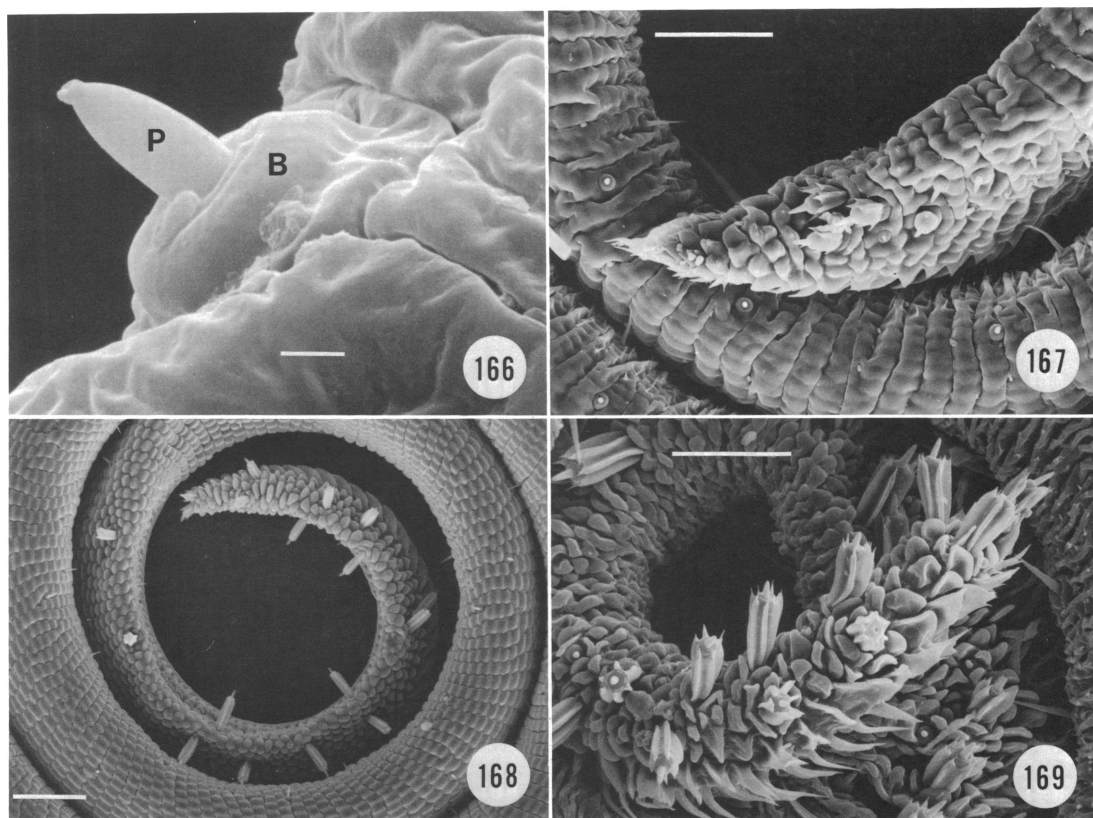


Fig. 166. R2 sensillum on the proboscis surface of *Cargida pyrrha*. B = body. P = sensory cone. Scale line = 2 μ m.

Figs. 167–169. Distal portion of the adult proboscis showing R1 and R2 sensilla. 167. *Schizura biedermani* (50 μ m). 168. *Lochmaeus bilineata* (50 μ m). 169. *Nadata gibbosa* (50 μ m). Scale lengths in parentheses.

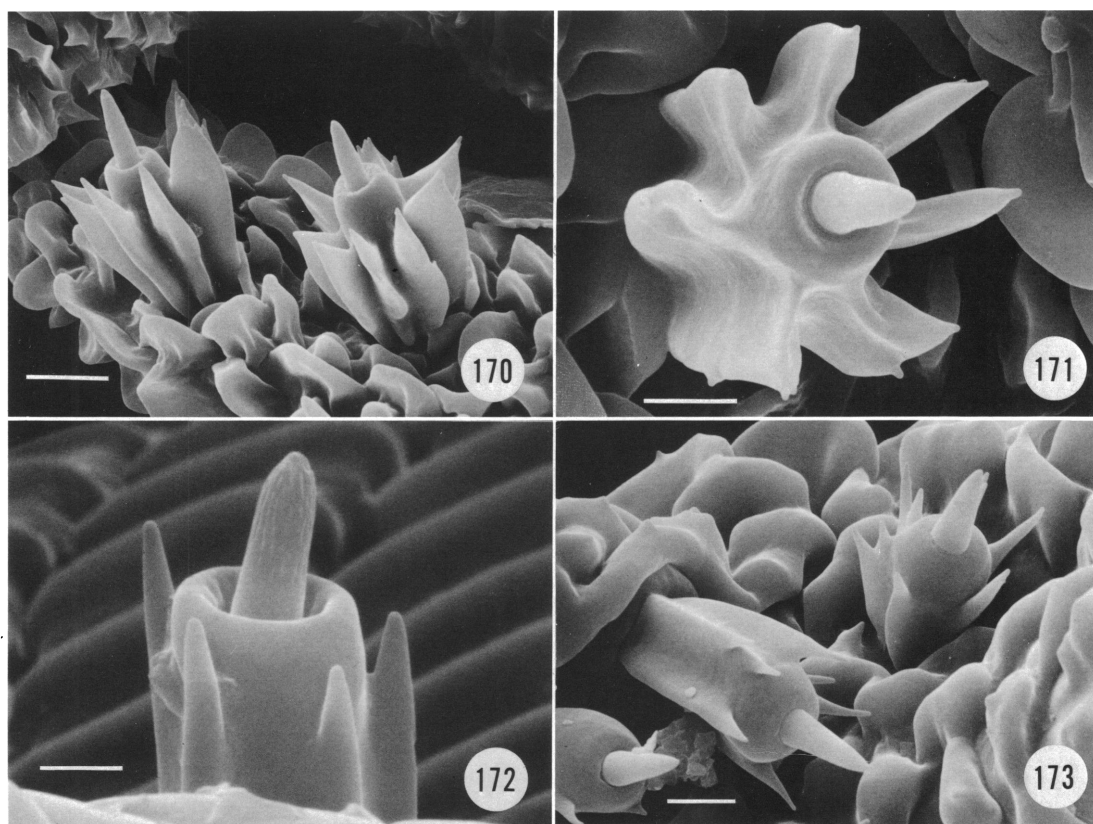
dae. Goblet-shaped sensilla, exemplified by those of *Odontosia* and *Notodonta* (figs. 181, 184, 185), were recognized as an apomorphic state, while highly elongate, laterally compressed sensilla, such as those found in some Dudusinae (figs. 186, 187, 191), are a third state. In the final derived state, the R1 sensilla are very short, hardly larger than R2 sensilla (e.g., *Clostera albosigma*; fig. 183). They could be distinguished from R2 sensilla only by their location.

Character 11. Absence of Pilifers. The pilifers, a pair of short, setose lobes above the haustellum (fig. 101), function to clean the proboscis. In some cases where the proboscis is greatly reduced, the pilifers are absent. This occurs in the Thaumetopoeinae (e.g., *Trau-*

matocampa pityocampa, fig. 113), some Notodontinae (e.g., *Ptilophora plumigera*, fig. 114), and Clade 38 ("Stauropini") of the Heterocampinae.

Eyes: Character 12. Eye Size. Prout (1918) noted that many dioptines have relatively small eyes. Eye reduction appears to be correlated with diurnal activity in other lepidopteran families (Powell, 1973; Davis, 1989), including day-flying Arctiidae (Ferguson, 1985). The same is very likely true for the Dioptinae. Ferguson (1985) also noted seasonal variation in eye size.

In dioptine species exhibiting the derived state, the eye does not extend to the anterior and ventral margins of the gena (fig. 111), leaving a scaleless region that is covered with



Figs. 170–173. R1 sensilla located near the proboscis tip. 170. *Peridea angulosa*, lateral view (10 μ m). 171. A single sensillum of *Peridea angulosa*, dorsal view, showing flutes (5 μ m). 172. *Josia ligata* (2 μ m). 173. *Schizura biedermani* (5 μ m). Scale lengths in parentheses.

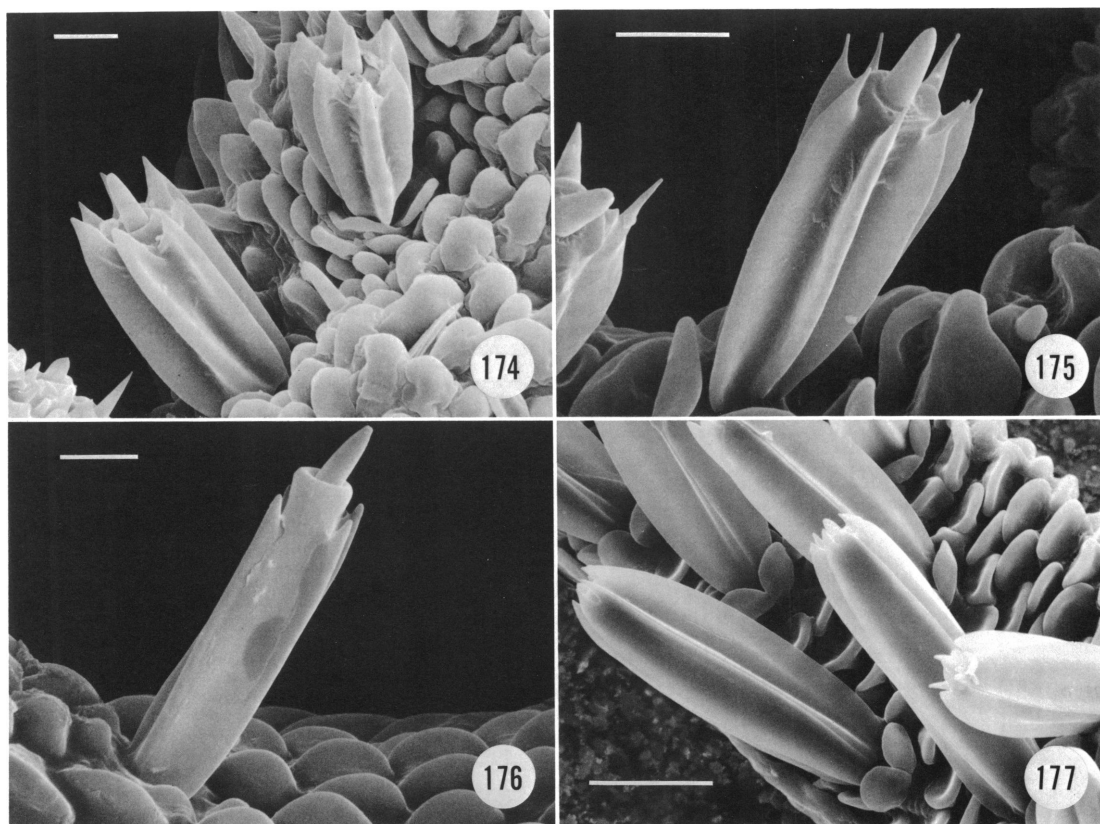
microprojections (Miller, 1989). This trait is not found in all Dioprinae, however. The eyes of *Zunacetha annulata* are large and extend to the genal margins (fig. 110), and *Z. annulata* is atypical of Dioprinae in that it flies almost exclusively at night (Wolda and Foster, 1978). This probably represents secondary loss of diurnal behavior because *Z. annulata* is a relatively derived dioptrine (J. Miller, unpubl. data; and see fig. 100) and more primitive species, like *Phaeochlaena gyon* (fig. 111), have small eyes.

Character 13. Hairy Eyes. One of the historically important characters in noctuid classification is the presence or absence of interfacetal setae on the eyes. So-called “hairy eyes” have been used since Hampson (1903) to define the noctuid subfamily Hadeninae. However, according to Kitching (1984a) this character shows a high level of homoplasy.

Among the Noctuidae I examined (which did not include a hadenine), hairy eyes occur only in *Panthea*. The functional significance of interfacetal setae is unknown.

This is also an important taxonomic character for the Notodontidae. Hairy eyes occur in relatively few genera, but the trait has long been used as a key character (e.g., Schaus, 1901; Nagano, 1916; Marumo, 1920; Janse, 1920). Presence of interfacetal setae has also figured in discussions of notodontid higher classification. Forbes described the Pygaerinae as having “eyes hairy” (e.g., *Clostera*; fig. 200) and the Notodontinae as having “eyes usually naked” (1948: 205). Exceptions in the latter subfamily include *Gluphisia* and *Notodonta* (figs. 201, 202). According to my cladistic results (fig. 99), the derived state has arisen separately in these three genera.

Male Antennae: There are innumerable

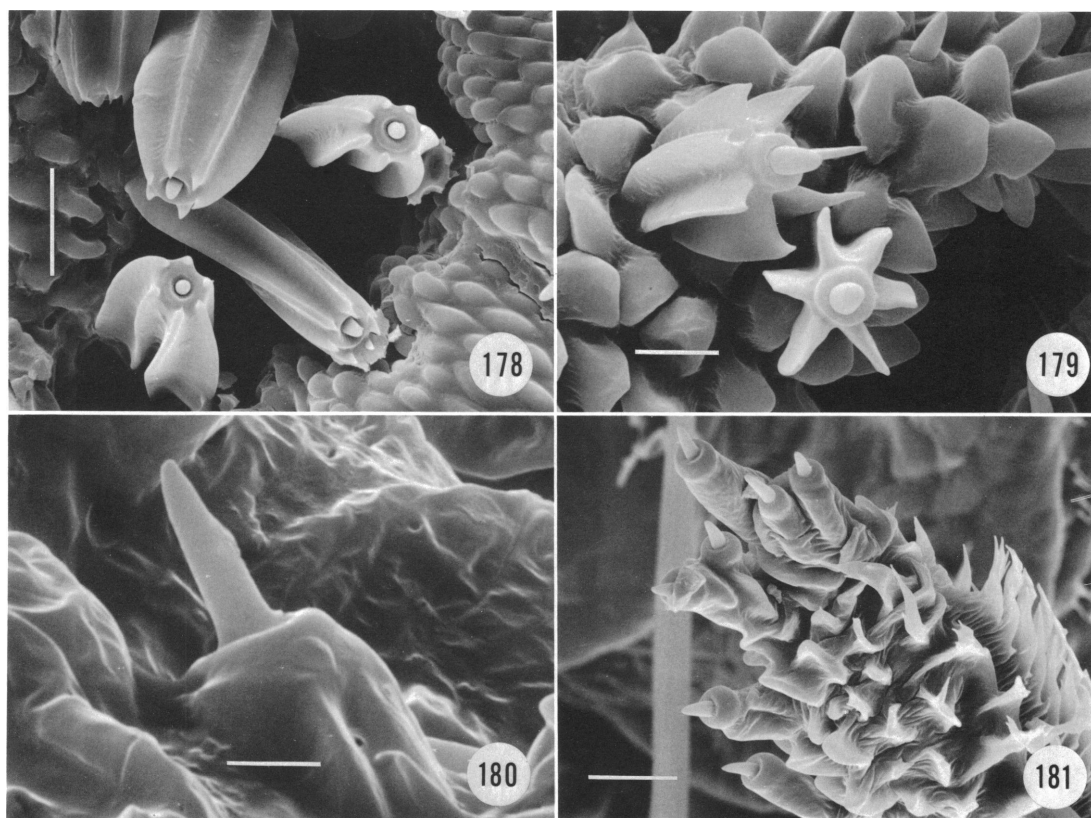


Figs. 174–177. R1 sensilla located near the proboscis tip. 174. *Lirimiris truncata* (10 μ m). 175. *Nadata gibbosa* (10 μ m). 176. *Zunacetha annulata* (5 μ m). 177. *Peridroma saucia* (20 μ m). Scale lengths in parentheses.

modifications of the male antennae among Noctuoidea. Within the Dioptinae alone, the antennae may be ciliate, bipectinate, or doubly bipectinate (Miller, 1987a, 1989). Comparative SEM studies, especially focusing on types and locations of antennal sensilla (e.g., Fauchaux, 1989, 1990), would invariably lead to a refinement of my character analysis and would result in the discovery of additional characters. Specialized antennal sensilla provide important characters for some lepidopteran groups (see Bodine, 1896), an example being the ascoid sensilla of Opostegidae (Nepticuloidea) (Davis, 1989). Lavoie-Dornik and McNeil (1987), using SEM, identified seven types of sensilla on the antenna of *Pseudaletia unipuncta* (Noctuidae), and Fauchaux (1990) recognized 10 different types in *Noctua pronuba* L. (Noctuidae). Flower and Hel-

son (1974) argued that placing sensillum types into well-defined categories poses a difficult problem. I did not attempt a detailed study, but instead examined those antennal characters discussed by previous authors on the Notodontidae. I have attempted to refine our knowledge of character state distributions.

One character, which I began to study but which proved very difficult to score, involves the relative length of pectinations on either side of the antenna. It has been noted that, in some Notodontidae, the pectinations are shorter on one side (Nagano, 1916; Weller, 1989). The difference in length becomes particularly obvious in species, such as *Antheua simplex* (fig. 212), where the pectinations themselves are somewhat reduced. After studying this character I discovered that the tendency toward uneven length is universal



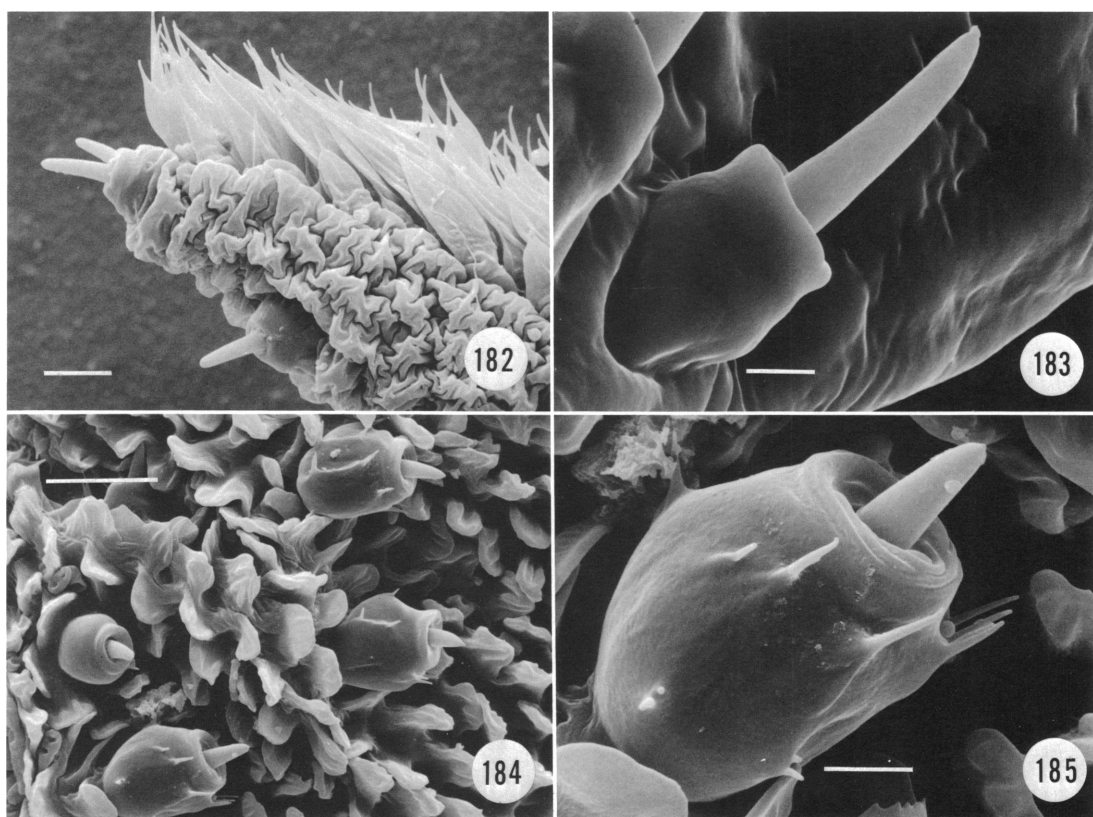
Figs. 178–181. R1 sensilla located near the proboscis tip. **178.** *Acronicta americana* (20 μm). **179.** *Nola pustulata* (5 μm). **180.** *Oenosandra boisduvalii* (4 μm). **181.** *Notodonta pacifica*, tip of the proboscis (20 μm). Scale lengths in parentheses.

among notodontids. In many species the length difference is extremely subtle and was beyond my ability to measure.

Character 14. Male Antennal Pectinations. I used four states to describe superficial morphology of male antennal pectinations. Male antennae with pectinations of moderate length (a score of “0”) occur in almost every notodontid subfamily. I recognized three additional states. First were those in which the male antennae are almost smooth, without pectinations. Only two examples of this, both in the Dioptinae, occurred among my study species. Next, I gave a separate score to species in which pectinations are not present, but in which each antennal segment bears a lateral row of stout bristles (fig. 210). This state exhibits a scattered distribution, occurring in three species of the Phalerinae (*Datana ministra*, *Phalera bucephala*, and *Peridea angu-*

losa), in *Nystalea nyseus* (Nystaleinae), and in *Crinodes besckei* (Dudusinae). Finally, I gave a score of “3” to species, such as *Liparopsis postalbida* (fig. 205) and *Ptilophora plumigera* (fig. 20), in which the antennal pectinations are extremely long (Stephens, 1829; Matsumura, 1929b). None of my categories produced consistent character state distributions. More detailed study would likely reveal that these states are not homologous among subfamilies.

Further difficulty arises from the fact that the outgroup species also exhibit a wide range of antennal types (see Appendix I). Antennae without pectinations are as common among my sample of quadrifid noctuoids as are those with pectinations. Kitching (1988) described dramatic antennal variation among species of *Ocalaria* (Noctuidae: Catocalinae), in which one has very long pectinations and an-



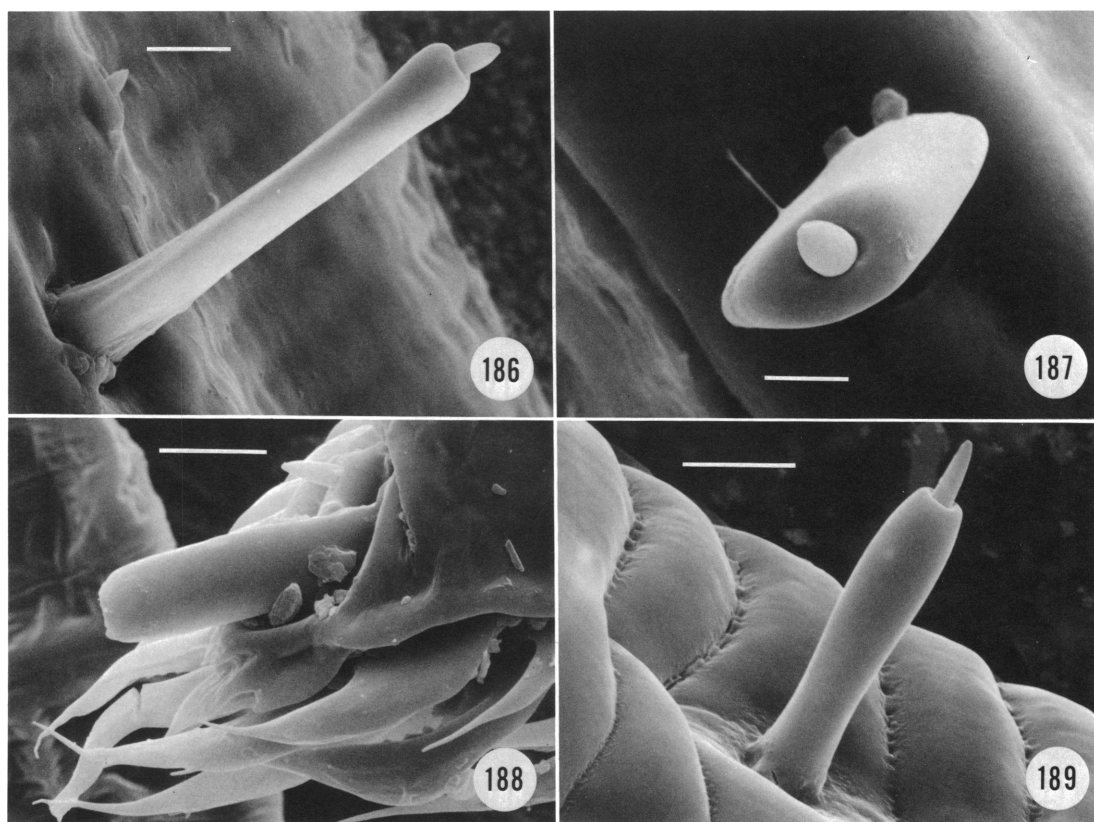
Figs. 182–185. R1 sensilla located near the proboscis tip. **182.** *Furcula borealis*, tip of the proboscis (10 μ m). **183.** *Clostera albosigma* (5 μ m). **184.** *Odontotia elegans* (20 μ m). **185.** A single sensillum from figure 184 (5 μ m). Scale lengths in parentheses.

other lacks pectinations altogether. It is not surprising, therefore, to find that antennal character states as I have scored them are extremely inconsistent (Appendix IV).

Character 15. Terminal Antennal Segments Simple. Males of many species have antennae in which the pectinations end abruptly approximately two-thirds out, the remainder of the antenna being simple (figs. 206–211). This trait has long been used as a diagnostic feature in the Notodontidae (e.g., Stephens, 1829; Neumoegen and Dyar, 1894a, 1894b; Packard, 1895a; Schaus, 1901; Nagano, 1916; Matsumura, 1929b; Forbes, 1939a, 1948). I characterized the plesiomorphic state as being an antenna in which there are fewer than 10 simple segments distally. In these, the antennae are usually pectinate almost to the tip (figs. 204, 205). The derived state applies to species with 15 or

more terminal segments simple. It is found in various members of the Heterocampinae (figs. 206, 207), Phalerinae, Dudusinae (fig. 209), and Nystaleinae. It also occurs in *Lirimiris* and *Hemiceras*. My analysis suggests that there is much homoplasy regarding this character (Appendix IV).

Character 16. Antennal Scale Tufts. A variety of types of scale tufts can occur on the antennal scape in male Notodontidae (Packard, 1895a; Weller, 1989). Most species have a small tuft located ventrally, and these appear to occur among the outgroup as well. A few Notodontidae have a long dorsal scale tuft in addition to the ventral one. When Forbes erected the tribe Nystaleini, one of his diagnostic characters was “male antennae with a high plume on scape dorsally” (1948: 206). He referred two New World genera, *Symmerista* and *Dasylophia*, to that tribe.



Figs. 186–189. R1 sensilla located near the proboscis tip. **186.** *Crinodes besckei* (10 μ m). **187.** *Crinodes besckei*, dorsal view of a single sensillum (5 μ m). **188.** *Cargida pyrrha*, tip of proboscis showing cylindrical R1 sensillum (sensory cone missing) (10 μ m). **189.** *Nystalea nyseus* (10 μ m). Scale lengths in parentheses.

First mention of this character (for *Dasylophia*) seems to date back to Neumoegen and Dyar (1894a). Todd noted the “large, erect, dorsally-pointed scale tuft” (1973: 266) on the antennal scape in his diagnosis for the genus *Nystalea*. Weller (1989) further refined the character and documented its distribution among nystaleine genera. I assigned the derived state to species having a long, dorsal tuft of stiff scales on the antennal scape. All other types of antennae tufts were regarded as primitive.

The dorsal scale tuft (figured in Weller, 1989) occurs in all five of the Nystaleinae I studied, but it appears to have been lost in some members of the subfamily (Weller, 1989). A nonhomologous case is found in *Schizura beidermani*, but not in other heterocampines. *Lirimiris truncata* has a long tuft of loose scales on the antennal scape,

again not homologous with the tuft of stiff scales in nystaleines.

Character 17. Antennal Segments Joined Obliquely. Species in the Thaumetopoeinae have antennae in which the segments, when viewed laterally, are joined obliquely (fig. 213). I did not observe this state elsewhere in the Notodontidae, but a similar condition occurs in *Doa ampla*.

Character 18. Antennal Spinules. Ferguson (1978; see also Holloway et al., 1987) described the presence of spinules at the end of each antennal pectination as a defining character for the Lymantriidae. Spinules are present in both of my study species from that family, but they seem to occur in some Arctiidae as well.

Female Antennae: Character 19. Presence or Absence of Pectinations. I scored pectinations in female antennae as being either

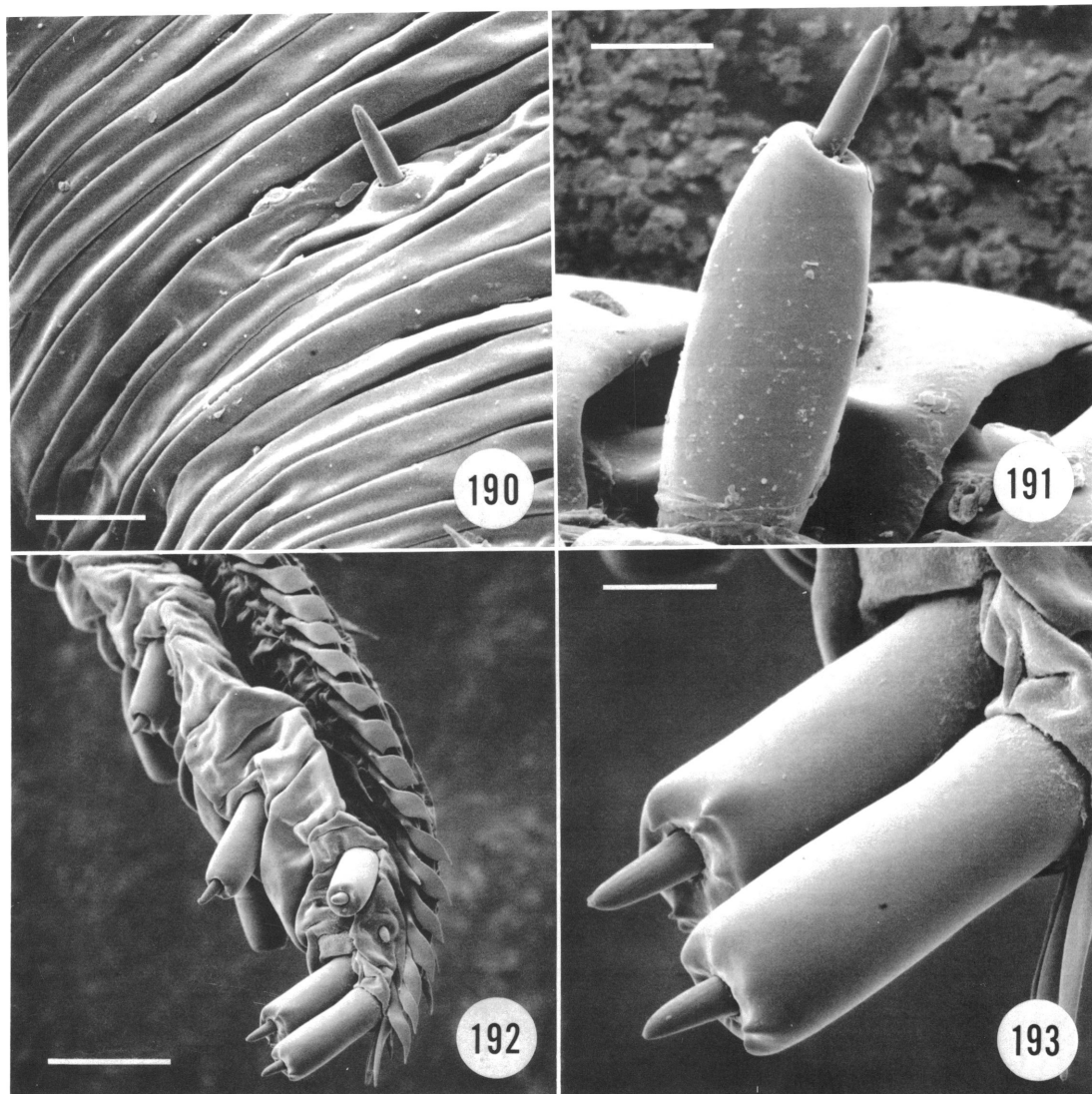


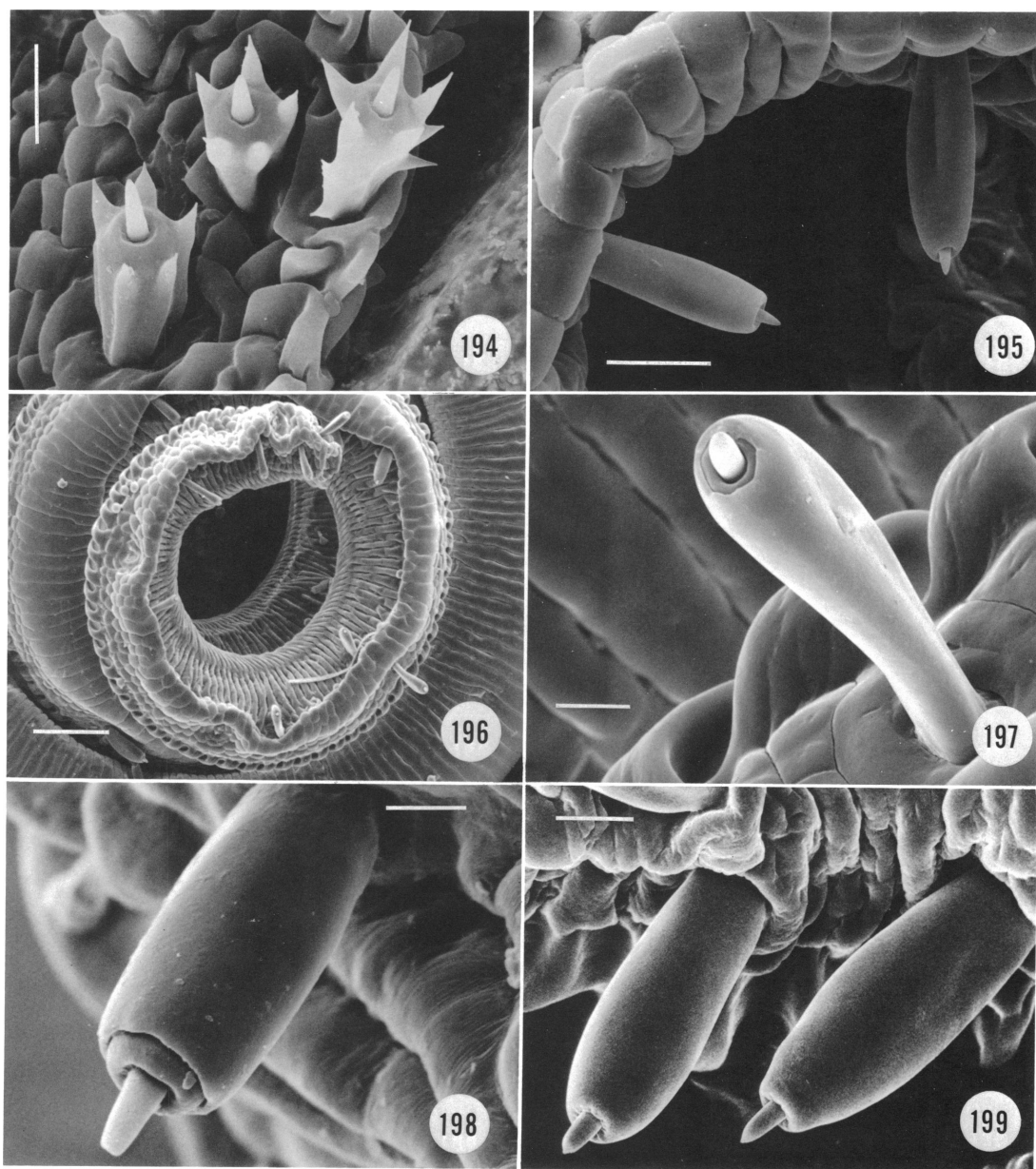
Fig. 190. Surface of the adult proboscis of *Tarsolepis japonica* (photograph taken at approximately the proboscis midpoint). Scale line = 10 μ m.

Figs. 191–193. R1 sensilla on the distal portion of the adult proboscis. 191. *Tarsolepis japonica* (20 μ m). 192. *Dudusa synopla* (40 μ m). 193. Two distal sensilla from figure 192 (10 μ m). Scale lengths in parentheses.

present ("0") or absent ("1"). Even though scoring did not present difficulties, the character shows poor consistency (Appendix IV). My results suggest that absence of pectinations on the female antennae is a synapomorphy for Clade 33 (fig. 100). Janse (1920) showed that, even though the African genus *Antheua* is well defined, within it there are species in which the female antennae are sim-

ple and species where pectinations are present.

Ocelli: *Character 20. Presence of Ocelli.* The presence or absence of dorsal ocelli has historically been important in theories of noctuid classification. For example, Hampson (1900) recognized three arctiid subfamilies—the Nolinae, Lithosiinae, and Arctiinae—and argued that the first two are derived, having



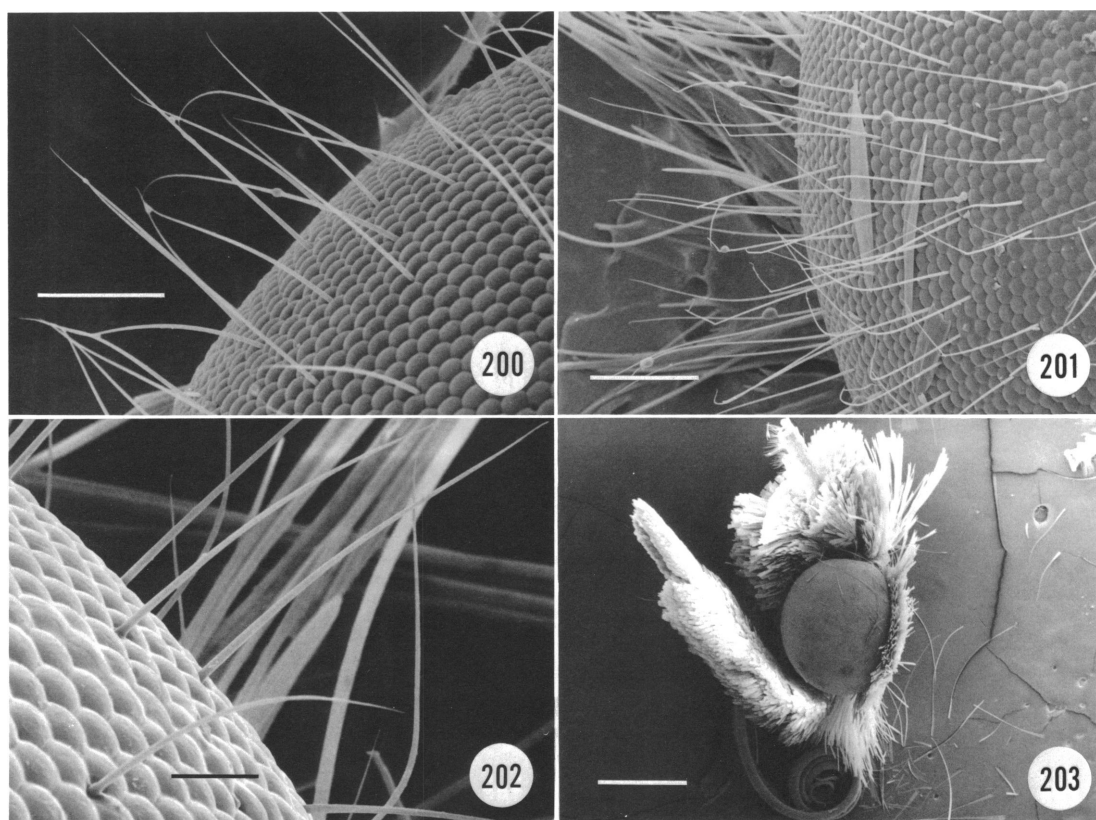
Figs. 194, 195. R1 sensilla located near the proboscis tip. 194. *Dasylophia anguina* (10 μ m). 195. *Nystalea eutalanta* Dyar (20 μ m). Scale lengths in parentheses.

Fig. 196. Proboscis of *Hapigia annulata* Schaus, distal portion. Scale line = 100 μ m.

Figs. 197–199. R1 sensilla located near the proboscis tip. 197. *Hapigia annulata* (10 μ m). 198. *Goacampa variabilis* (5 μ m). 199. *Spatalia jezoensis* (10 μ m). Scale lengths in parentheses.

lost the ocelli. As with hairy eyes (Character 13), however, the trait exhibits homoplasy. Among the outgroup species in my study, ocelli are present in all except *Doa*, the lymantriids, *Hypoprepia*, and *Nola*.

Forbes wrote that the Notodontidae can generally be characterized as having “strong tongue and ocelli” (1939a: 235). He then listed absence of ocelli as a defining character for both the Cerurinae (my Clade 20) and



Figs. 200–202. Eyes of adult male Notodontidae. **200.** *Clostera albosigma* (100 μ m). **201.** *Gluphisia septentrionis* (40 μ m). **202.** *Notodonta pacifica* (100 μ m). Scale lengths in parentheses.

Fig. 203. Head of adult male *Hippia packardii* with antennae removed. Scale line = 1.0 mm.

Dioptidae (Dioptinae). Marumo (1920), on the other hand, described ocelli as being “rarely present” in Notodontidae. I found that presence of well-developed ocelli is relatively uncommon within the family. In an attempt to refine the definition of this trait, I recognized three character states: (a) ocelli present (“0”), (b) ocelli rudimentary (“1”), and (c) ocelli absent (“2”).

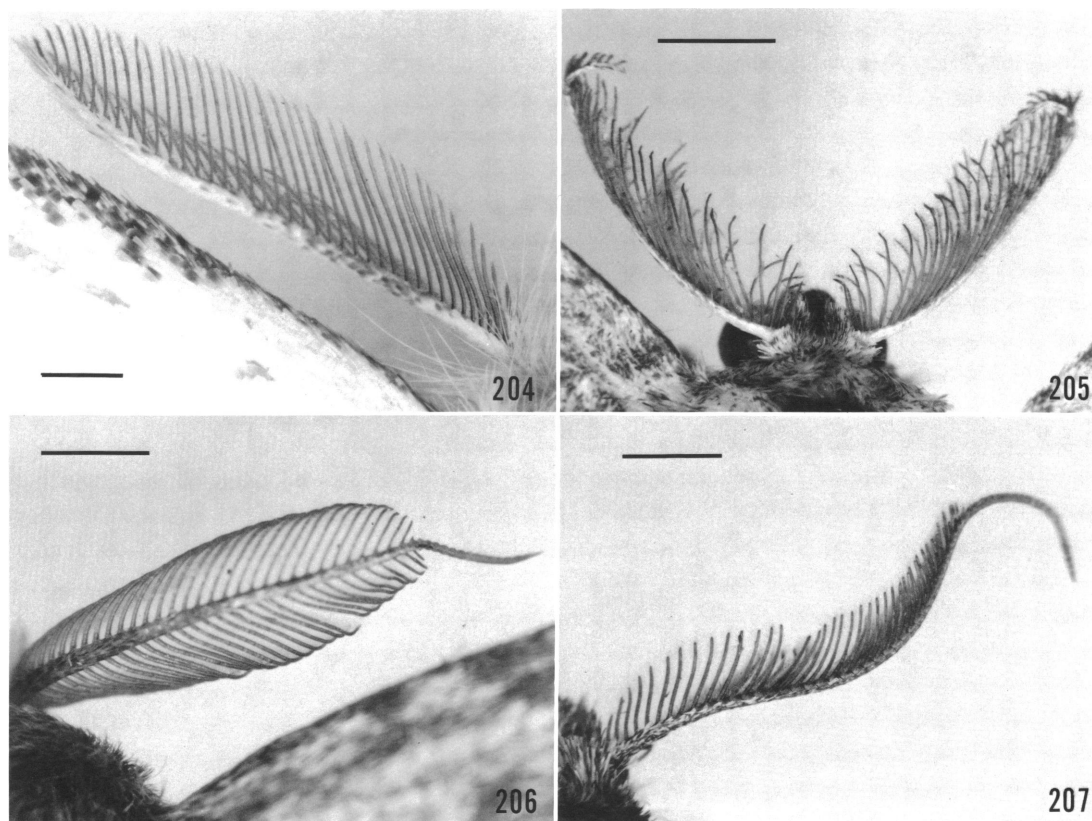
Among Notodontidae, presence of large ocelli is a synapomorphy for the subfamily Dudusinae (e.g., *Gargetta costigera* [fig. 108], *Scrancia stictica* [fig. 109], and *Goacampa variabilis* [fig. 115]). My results suggest that absence of ocelli is plesiomorphic for the Notodontidae. Both the Thaumetopoeinae (figs. 105, 113) and Pygaerinae lack ocelli. The Dioptinae (figs. 110, 111) can be characterized as having ocelli absent, but other subfamilies are not consistent; ocelli can be either small or absent.

The dorsal ocelli of moths are important in detecting ambient light levels, and they play a role in periodicity (Eaton et al., 1983). Wunderer and De Kramer (1989) have shown that occlusion of the dorsal ocelli in an arctiid, *Cretonotos transiens*, delays the onset of mating activity.

THORAX

This study did not rely heavily on internal thoracic skeletal morphology. Internal structures seem to exhibit subtle shape differences, but in most cases these are difficult to define. Similarly, there were only slight differences in shape of the tegulae and pleural sclerites on the pro- and mesothoracic segments. The most comprehensive study of lepidopteran thoracic anatomy is that of Weber (1924), but he did not describe the notodontid thorax.

Legs: Three potentially interesting char-

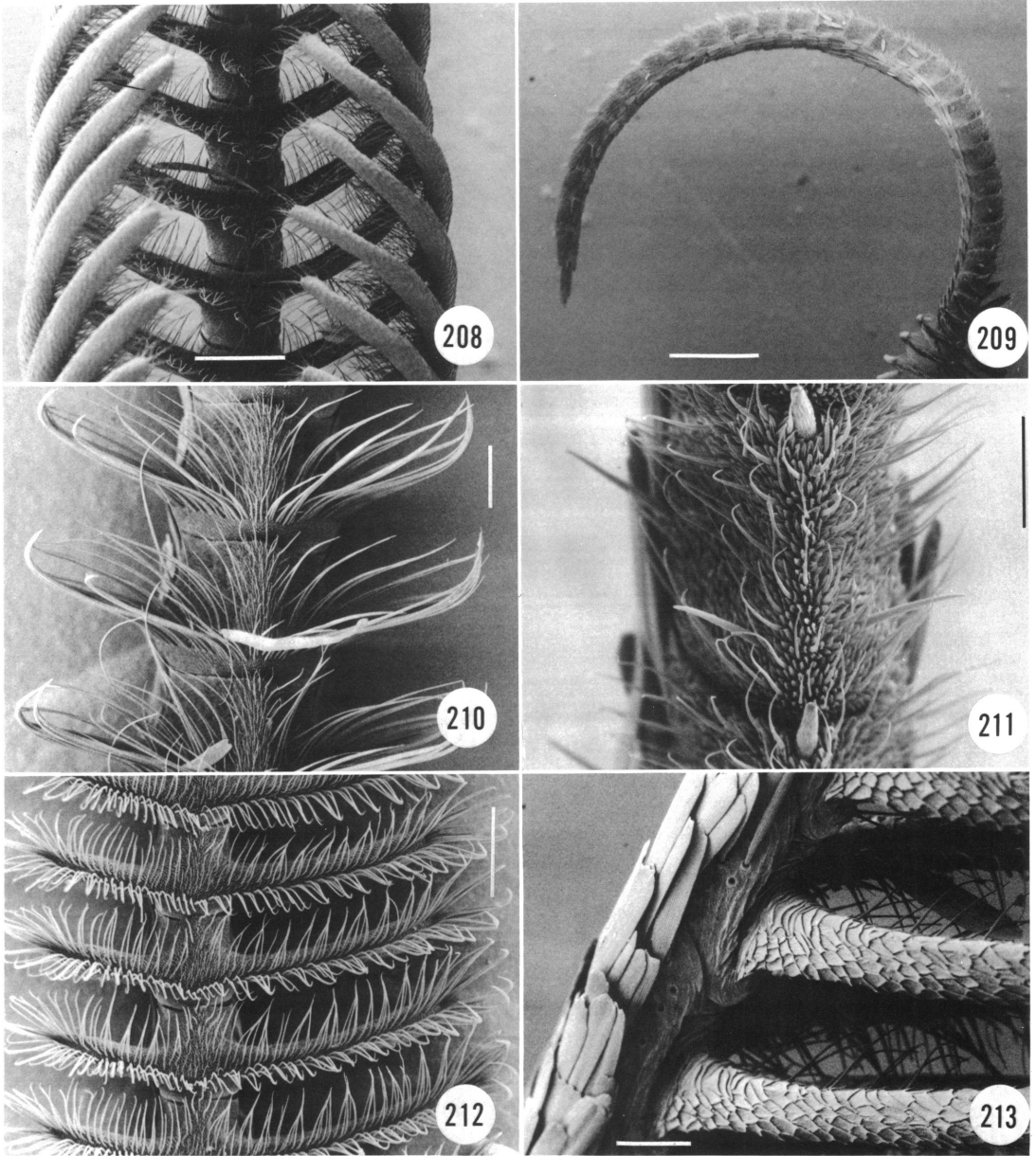


Figs. 204–207. Photographs of male antennae (dorsal view) of Notodontidae. **204.** *Epicoma melanosticta*, left antenna (1.0 mm). **205.** *Liparopsis postalbida* (2.0 mm). **206.** *Stauropus fagi*, right antenna (1.0 mm). **207.** *Heterocampa averna*, right antenna (1.0 mm). Scale lengths in parentheses.

acter complexes of the legs were not included because preliminary work suggested that all would require SEM analysis for each species, which would be beyond the scope of my project. The first two involve the pretarsus. I describe one basic difference in tarsal claw structure (Character 28), but there appears to be variation in shape of the unguitractor plate, paronychium, and pulvillus as well, all of which have been shown to be taxonomically useful in other lepidopteran families (Rothschild and Jordan, 1903; Davis, 1989). The third character is presence of serrate ventral margins on the tarsal claws. The plesiomorphic state appears to be smooth margins, but within the Notodontidae there are species with minute serrations (Jordan, 1923b; figs. 234, 236), as well as some, such as the thaumetopoeines (fig. 235), with smooth tarsal claws.

Weller (1989) detailed the structure of remarkable scent organs found on the prothoracic legs of some male Nystaleinae and Hemiceratini. These can be complex. Among my exemplar taxa, male foreleg scent organs occur only in *Nystalea*, and Weller's work should be consulted for a discussion of them. Similar structures can be found in males of some noctuid groups (Birch and Hefetz, 1987) as well as throughout the Sphingidae (Rothschild and Jordan, 1903). Rothschild and Jordan (1903) noted that, in sphingids, the presence of these structures is extremely variable; the structure can be present or absent in closely related species. Their observation seems to hold true for male scent organs of all types.

Character 21. Elongate Foretarsi. One of the characters that supports a sister-group relationship between *Scrancia* and *Gargetta* is

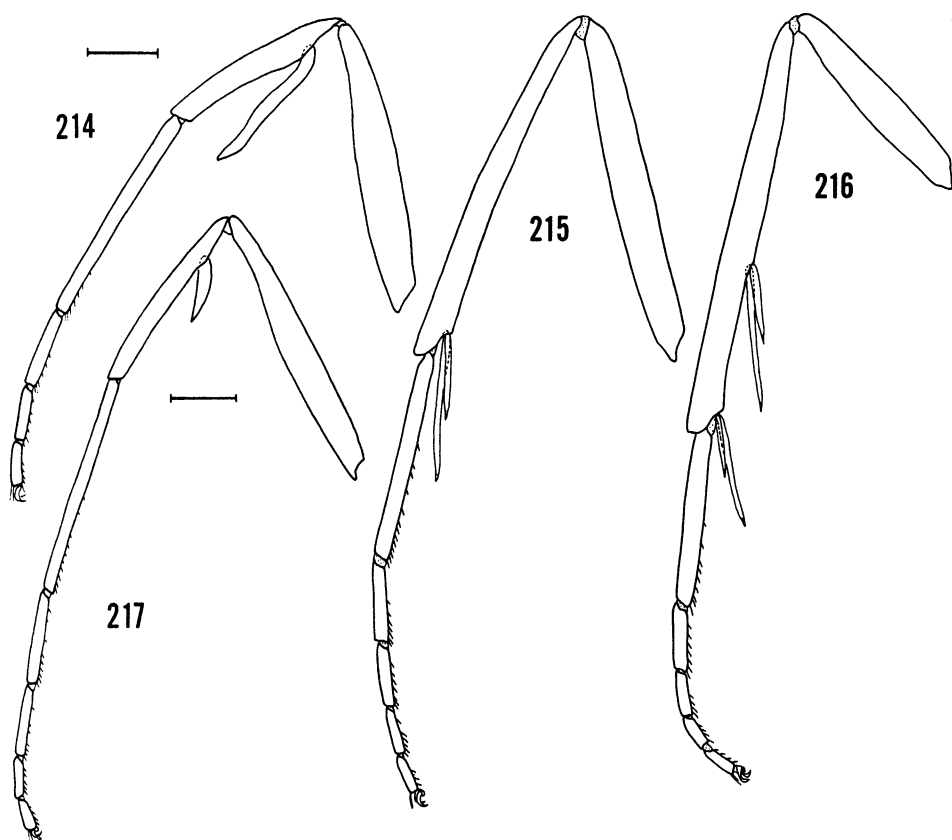


Figs. 208–213. Scanning electron micrographs of male antennae of Notodontidae. 208. *Tarsolepis japonica*, ventral view near antennal midpoint (200 μm). 209. *T. japonica*, lateral view of distal portion (500 μm). 210. *Nystalea nyseus*, ventral view near antennal midpoint (100 μm). 211. *N. nyseus*, ventral view near tip (50 μm). 212. *Antheua simplex*, ventral view of right antenna (200 μm). 213. *Traumatocampa pityocampa*, lateral view (50 μm). Scale lengths in parentheses.

the presence of extremely long foretarsi, described by Janse (1920) for *Scrancia*. The first tarsomere is as long as the others combined (figs. 214, 217). In *Gargetta*, one tarsomere of the foreleg appears to have been lost (fig.

214), apparently an autapomorphy for the genus.

Character 22. Epiphysis Shape. Presence of the foreleg epiphysis has been proposed as a synapomorphy for the Lepidoptera (Kris-



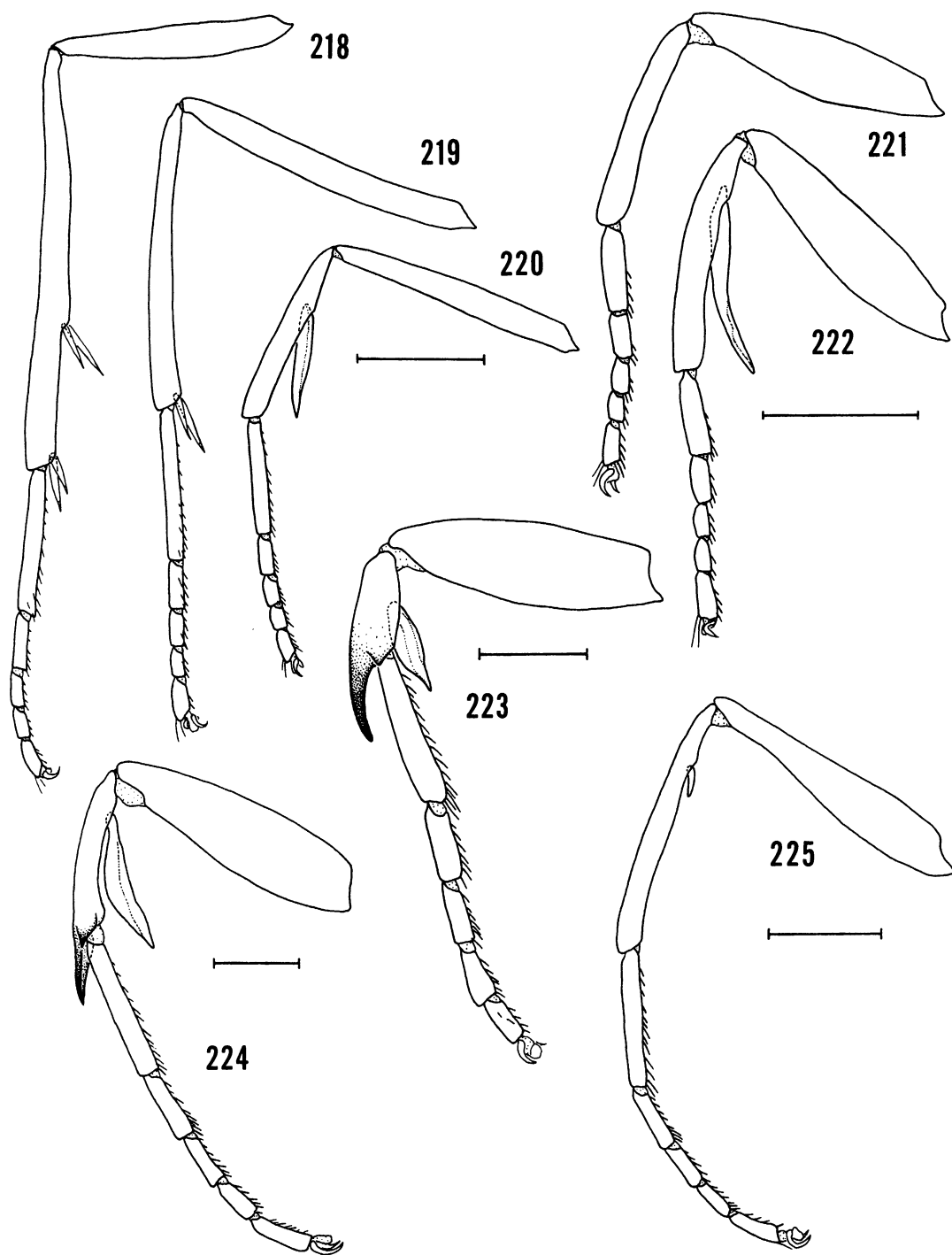
Figs. 214–216. Left legs of adult male *Gargetta costigera*. 214. Foreleg. 215. Middle leg. 216. Hind leg. Scale line = 1.0 mm.

Fig. 217. *Scrancia stictica*, left foreleg. Scale line = 1.0 mm.

tensen, 1984; Nielsen, 1989). Both Michener (1952) and Kuznetsov (1967) argued that the epiphysis is an enlarged tibial spur that has moved basally. The epiphysis exhibits a wide variety of shapes among Lepidoptera, and can sometimes vary within a single genus (e.g., Kitching, 1988). In the Notodontidae it is typically rather short and apically acute (figs. 217, 220, 223, 224). I recognized a derived state, found in almost all Notodontinae and exemplified by *Gluphisia septentrionis* (fig. 222), in which the epiphysis is long and flat. According to Weller (1989), the long flat type of epiphysis also occurs in some *Dasylophia* species (Nystaleinae). Marumo (1920) used epiphysis shape as a taxonomic character. He described and figured the epiphysis for at least one representative species in each of the Asian

genera he discussed. Further, it was Marumo who first noted the major shape difference I have described here.

Character 23. Loss of the Epiphysis. Females of *Gluphisia* (fig. 221) and *Epicoma* (Thaumetopoeinae) show no sign of the epiphysis. It has been suggested that the epiphysis is used to clean the antenna (Kuznetsov, 1967; Common, 1979), and one might predict that the female antennae in these genera should be ciliate rather than pectinate, but such is not the case. These two cases of epiphysis loss are convergent. A third case in the Notodontidae involves females of *Ptilophora plumigera* where the epiphysis is present but highly reduced (fig. 225). Having defined the derived state as reduced or absent (Appendix I), I scored *P. plumigera* as “1”.



Figs. 218–225. Left legs of adult Notodontidae. 218. *Phaeochlaena gyon* male foreleg. 219. *P. gyon* male middle leg; 220. *P. gyon* male hind leg. 221. Female foreleg of *Gluphisia septentrionis*. 222. Male foreleg of *Gluphisia septentrionis*. 223. Male foreleg of *Goacampa variabilis*. 224. Male foreleg of *Traumatocampa pityocampa*. 225. Female foreleg of *Ptilophora plumigera*. Scale lines = 1.0 mm.

My cladistic analysis suggests that the derived state is homologous in *Ptilophora* and *Gluphisia*, but that the female epiphysis was regained in Clade 18 of the Dicranurini (Notodontinae). This hypothesis should be further tested.

Character 24. Foretibial Spurs. In three of the notodontid species I examined, there is a strongly sclerotized distal spur on the foretibia. Forbes (1948) noted this spur in his diagnosis for the genus *Datana* (Phalerinae). I found that the distal spur is present in *Datana ministra*, but that it does not occur throughout the closely related genus *Phalera*; the foretibial spur is absent in *P. bucephala*. Two other notodontids have a large spur on the foretibia: *Goacampa variabilis* (Dudusiinae) (fig. 223) and *Traumatocampa pityocampa* (Thaumetopoeinae) (fig. 224).

Interestingly, considering cladistic relationships among the three taxa (figs. 99, 100), all of these must have evolved separately. Michener (1952), who described similar spines on the foretibiae of some Saturniidae, suggested that they are used to dig out of the ground after emergence from the pupa. Ryabov (1988) observed a correlation between presence of foretibial armature and head protuberances (see Character 2) among species of Noctuidae. This is known, for example, in Heliiothinae (Hardwick, 1970) and Stiriini (Hogue, 1963). Ryabov (1988) argued that the leg spines and head projection help the newly emerged imago exit from hard soil in arid habitats. It also appears likely that the foreleg spurs in *Goacampa* and *Traumatocampa* are used in conjunction with the frontal protuberances of the adult head. *Datana*, however, does not have a sclerotized frons.

Character 25. Legs Elongate. Long legs are characteristic of, but not unique to, the Dioprinae. All three pairs tend to be long (figs. 218–220), but I scored the character using hind legs only. In dioptrines the hind tibia is at least 1.5 times the length of the femur, and the two pairs of spurs are widely separated (fig. 218). The derived state also occurs in *Scrancia stictica* (Janse, 1920) and *Gargetta costigera* (fig. 216) (Scranciini), as well as in *Doa*.

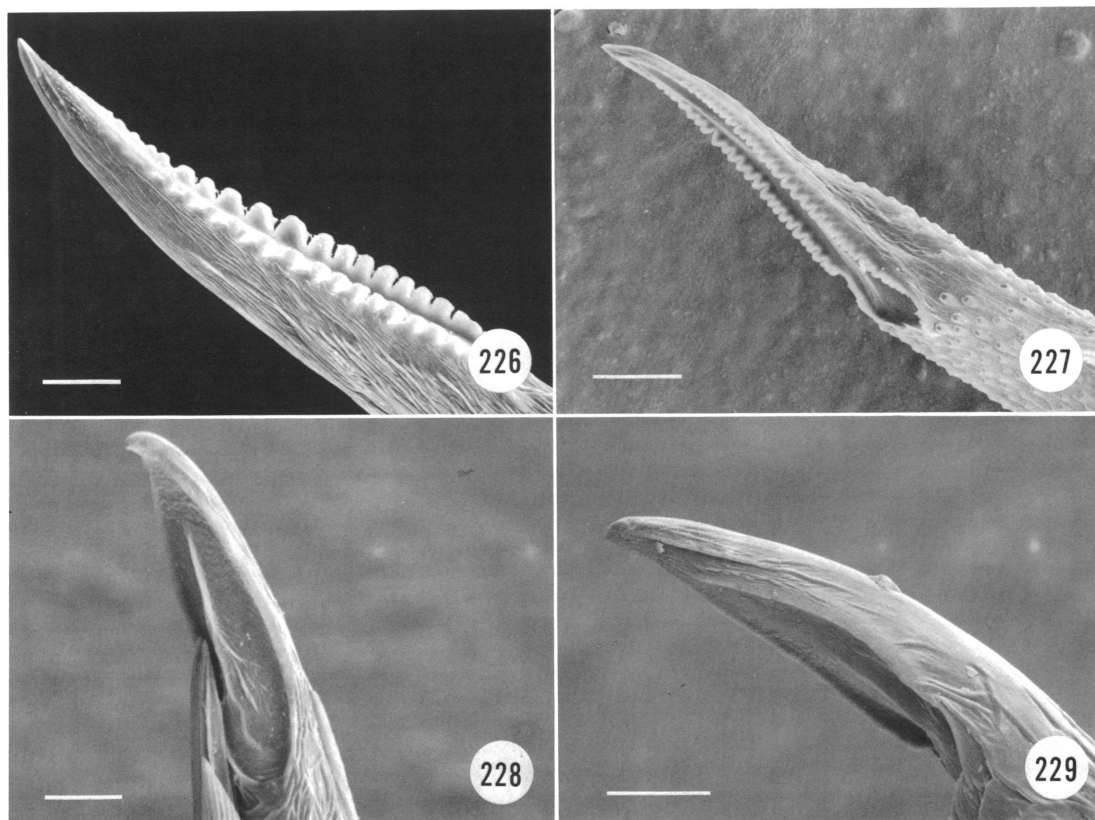
Character 26. Tibial Spur Apices Serrate. The sclerotized tips of the tibial spurs are serrate in the Notodontidae (fig. 226; Janse, 1920; Arru, 1965; Weller, 1987, 1989),

whereas they are smooth in most other noctuoids. Serrate spurs are apparently apomorphic, but they also occur in the Lymantriidae (fig. 227) and in *Panthea furcilla* (Noctuidae: Pantheinae). *Doa ampla* (fig. 228) and *Oenosandra boisduvalii* (fig. 229) have smooth spurs, but in thaumetopoeines they are serrate (Appendix I). Among tritid Noctuoidea, therefore, serrate tibial spurs provide a useful synapomorphy for the Notodontidae (but see discussion of *Platyhasma* in Addition of Taxa).

Character 27. Tibial Spur Formula. Throughout the Noctuoidea there is typically an epiphysis on the prothoracic tibia, one pair of tibial spurs on the mesothoracic legs, and two pairs of spurs on the metathoracic legs. This is often described as being a tibial spur formula of 0-2-4 (e.g., Common, 1979), the epiphysis not being considered a spur. The 0-2-4 formula occurs in most Notodontidae (figs. 214–216, 218–220, 230), but there are taxa in which only the distal pair of metathoracic spurs is present (formula 0-2-2). In species with the 0-2-2 formula, all spurs are relatively small (Stephens, 1829; compare figs. 230–232). Spur number has been discussed in most papers on taxonomy of the Notodontidae (e.g., Schaus, 1901; Turner, 1903; Nagano, 1916; Marumo, 1920; Matsumura, 1929a, 1929b).

The number of metathoracic tibial spurs has also received attention as an important character in notodontid classification. For example, Börner (1939, 1944) defined the Thaumetopoeinae and Cerurinae as having only a single pair of metatibial spurs. The rest of the family, which he placed in a single subfamily (the Notodontinae), was defined by the presence of two pairs. Packard (1895a) and Forbes (1948) characterized their Gluphiini and Cerurinae (both of which I place in the Notodontinae) as having the distal spurs only, but neither author recognized an association between the two groups on that basis. My analysis suggests that presence of a single pair of metathoracic tibial spurs is a derived state for the Notodontidae that has evolved in at least four separate groups: the Thaumetopoeinae, the Dicranurini (Clade 16, Notodontinae), some Dudusiinae (*Tarsolepis/Dudusa*, Clade 32), and some Heterocampinae.

The latter subfamily is particularly inter-



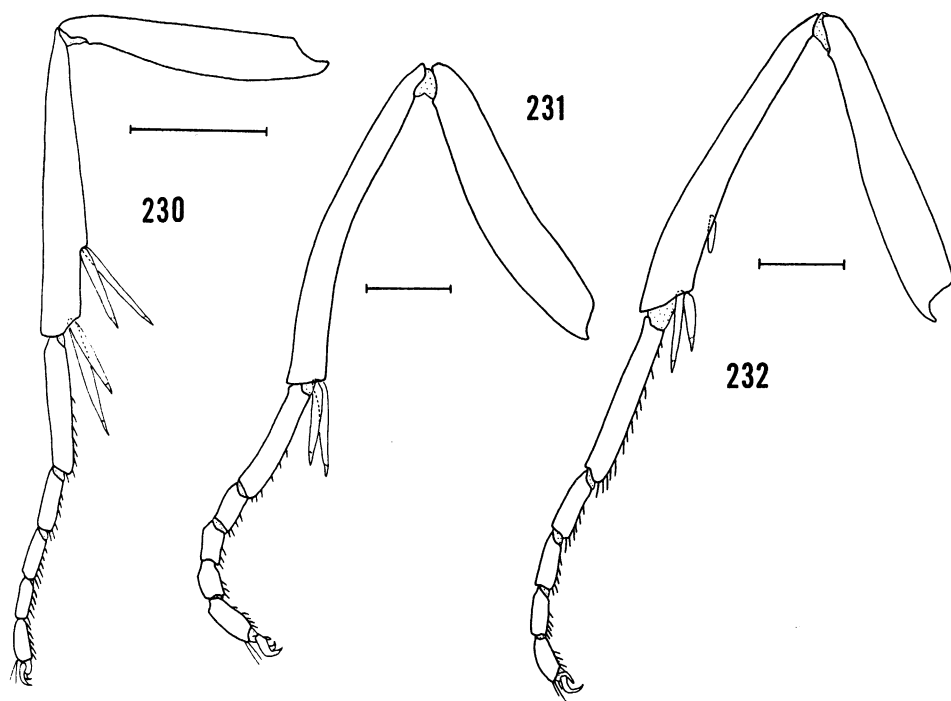
Figs. 226–229. Sclerotized tips of distal metatibial spurs. 226. *Ellida caniplaga* (40 μm). 227. *Lymantria dispar* (Lymantriidae) (100 μm). 228. *Doa ampla* (Doidae) (10 μm). 229. *Oenosandra boisduvalii* (20 μm). Scale lengths in parentheses.

esting with regard to tibial spur loss. Members of Clade 39 (the “Stauropini”) have only a single pair of spurs (fig. 231), but both of the *Schizura* species I examined show an apparently intermediate state: the two proximal spurs are very small and lack sclerotized tips. Both spurs are still present in *S. unicornis*, while *S. biedermani* has only a single tiny spur in the proximal position (fig. 232). *Spatalia jezoensis*, a basal member of the Heterocampinae (fig. 100), also exhibits reduced spurs. I scored the condition in *Schizura* and *Spatalia* as being a separate character state, intermediate between presence and absence of spurs, and treated Character 27 as additive.

Character 28. Tarsal Claws Bifid. In most Notodontidae there is a lobe at the base of each tarsal claw (fig. 234). Weller (1987, 1989, 1990), who observed this condition in *Litodonta hydromeli* Harvey (Notodontidae:

Heterocampinae) and in some Nystaleinae, termed such claws “bifid.” This basal lobe is ubiquitous throughout notodontid subfamilies except the Thaumetopoeinae (fig. 235) and Notodontinae (fig. 236). However, the basal lobe is frequently lost (Weller, 1989; and see Appendix II). For example, among the taxa I examined, all Dudusinae have bifid tarsal claws with the exception of *Dudusa*, and all Heterocampinae have bifid claws except *Stauropus* and *Harpyia*.

Bifid tarsal claws occur in other members of the Noctuoidea. I observed them in several noctuid subfamilies (Appendix II; see also Ryabov, 1988) and in both arctiid exemplars: *Spilosoma virginica* (fig. 233) and *Hypoprepia miniata*. Mitter and Silverfine (1988) observed simple tarsal claws in *Catocala* (Catocalinae: Noctuidae) and scored them as derived relative to the bifid state. The complex distribution of this trait suggests that



Figs. 230–232. Right hind legs of adult male Notodontidae. 230. *Cargida pyrrha*. 231. *Cnethodonta grisescens*. 232. *Schizura biedermani*. Scale lines = 1.0 mm.

bifid tarsal claws are not homologous in all noctuoid groups.

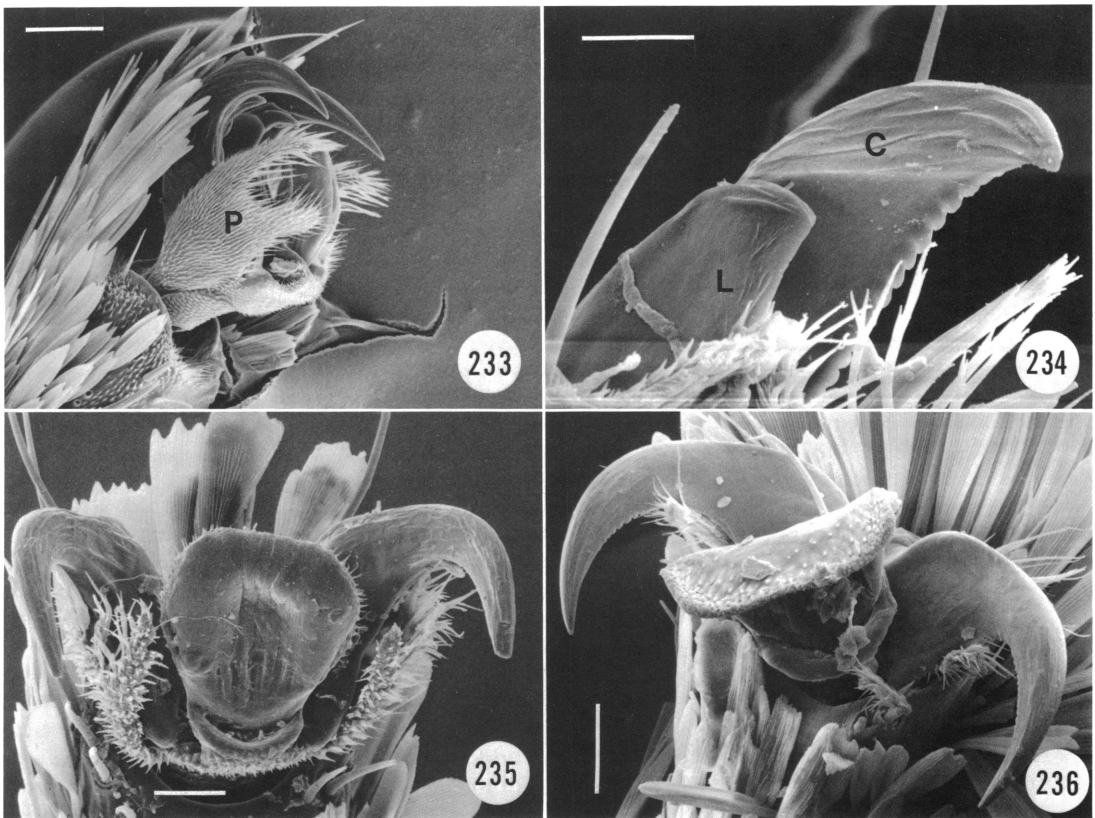
Metathorax: I used two characters of the metathoracic episternum. The first, described by previous authors, relates to the outgroup, and for that reason I do not provide figures. The second is found only among Dioptinae, and I describe it here for the first time.

Character 29. Tymbal Organs. Presence of metathoracic tymbal organs is a synapomorphy that unites most of the Arctiidae (Forbes and Franclemont, 1957; Kitching, 1984a; Ferguson, 1985; Minet, 1986). These structures occur in both arctiids that I examined, one species of Arctiinae and one of Lithosiinae. Among more recent papers, the arctiid tymbal organ has been figured by Fenton and Roeder (1974), Watson (1975), Ferguson (1985), and Surlykke (1990), all of whom discussed its function and taxonomic distribution in some detail. Fullard et al. (1979) suggested that the clicks produced by arctiid tymbal organs act to disrupt information processing by hunting bats as they approach their moth prey.

Fenton and Roeder (1974) discovered differences in tymbal organ fine structure between arctiid genera, and they suggested that such differences might be used as taxonomic characters. Presence of a tymbal organ in Thyretidae is the primary evidence for a relationship between that group and the Arctiidae (Holloway et al., 1987).

Character 30. Metepisternal Flange. In some Dioptinae the ventral portion of the metepisternum is heavily sclerotized and a lateral flange is present (fig. 241). I have not seen previous reference to this flange, and as far as I am aware its function is unknown. It is most highly developed in *Josia* and *Cyanotricha* and is absent in *Erbessa*. The ventral portion of the metepisternum can be sclerotized in species belonging to other notodontid groups, for example, *Tarsolepis japonica* (Dudusini). There, however, individuals seem to vary in the degree of sclerotization and no flange is present. I restricted my treatment to presence or absence of the lateral flange.

Character 31. Metafurcal Apophyses Rounded. The furcasternum is an internal



Figs. 233–236. Tarsal claws of adult Noctuoidea. 233. *Spilosoma virginica* (Arctiidae) (100 μ m), lateral view of pretarsus showing pulvillus (P). 234. *Hippia packardii*, mesal view of a single claw (C) showing lobe (L); note serrations on claw margin (20 μ m). 235. *Thaumetopoea processionea*, distal view of pretarsus (40 μ m). 236. *Gluphisia septentrionis*, distal view of pretarsus (50 μ m). Scale lengths in parentheses.

thoracic structure formed by fusion of the sternal apophyses and invaginated sternum (Weber, 1924; Snodgrass, 1935). For lepidopteran groups in which they have been described (e.g., Weber, 1924; Ehrlich, 1958b; Davis, 1986, 1989), the metafurcal apophyses are apically acute (fig. 242). All the Notodontidae I examined have acute furcal apophyses except the Dioprinae, which have posteriorly rounded ones (fig. 243). In addition, the furcal base of dioptrines is slightly elongate compared to that of other notodontids. The only other shape variation I observed concerns *Hypoprepia* (Arctiidae: Lithosiinae), in which the furcal apophyses are small (scored as “2”). The distribution of this character state should be surveyed in the Lithosiinae.

Tympanum: Brock claimed that “noctuid

tympanal structures are now among the best known regions of lepidopterous anatomy” (1971: 78). Morphology of the metathoracic tympanum has certainly been given inordinate attention by workers on noctuid phylogeny. Kiriakoff’s classifications (1950a, 1950b, 1950c, 1963a, 1963b) rely almost exclusively on tympanal characters. It was his contention that “tympanic structures undoubtedly are the most significant single set of characters that can be found in Lepidoptera” (1963a: 5).

Early works on the metathoracic tympanum include those of Forbes (1916, 1922a) and the important studies of Eggers (1919, 1928) and Sick (1935, 1940). Richards’s (1932) analysis is the most comprehensive. It covers 372 species from 300 genera, focusing on the Noctuidae, but also includes

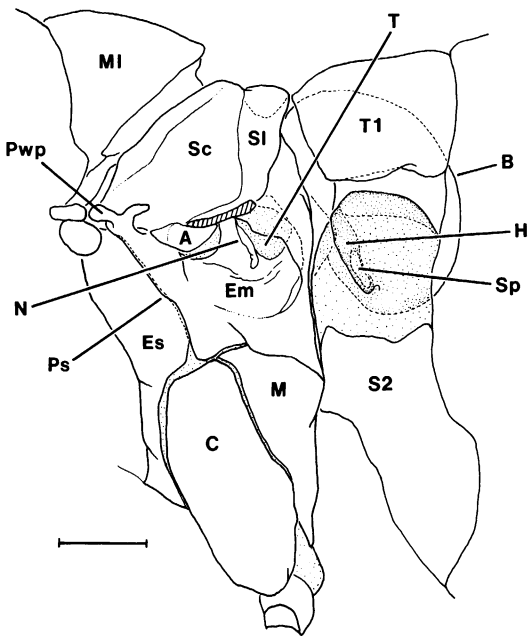


Fig. 237. Metathorax and first abdominal segment of female *Peridroma saucia* (Noctuidae) in lateral view with anterior at left (hind wing base shown with hatched lines). A = subalare. B = abdominal bulla. C = eucosta. Em = metepimeron. Es = metepisternum. H = counter-tympanal hood. M = metameron. MI = mesoscutellum. N = nodular sclerite. Ps = metapleural suture. Pwp = metapleural wing process. Sc = metascutum. SI = metascutellum. Sp = first abdominal spiracle. S2 = sternum 2. T = tympanal membrane. T1 = tergum 1. Scale line = 1.0 mm.

representatives of the other major noctuid lineages including the Arctiidae, Lymantriidae, and Notodontidae. Richards's conclusions form the basis for most of our current theories on relationships among noctuid families. Sick (1940), who studied tympanal morphology in a large number of dioptine species, included thaumetopoeines and other notodontids in his analysis.

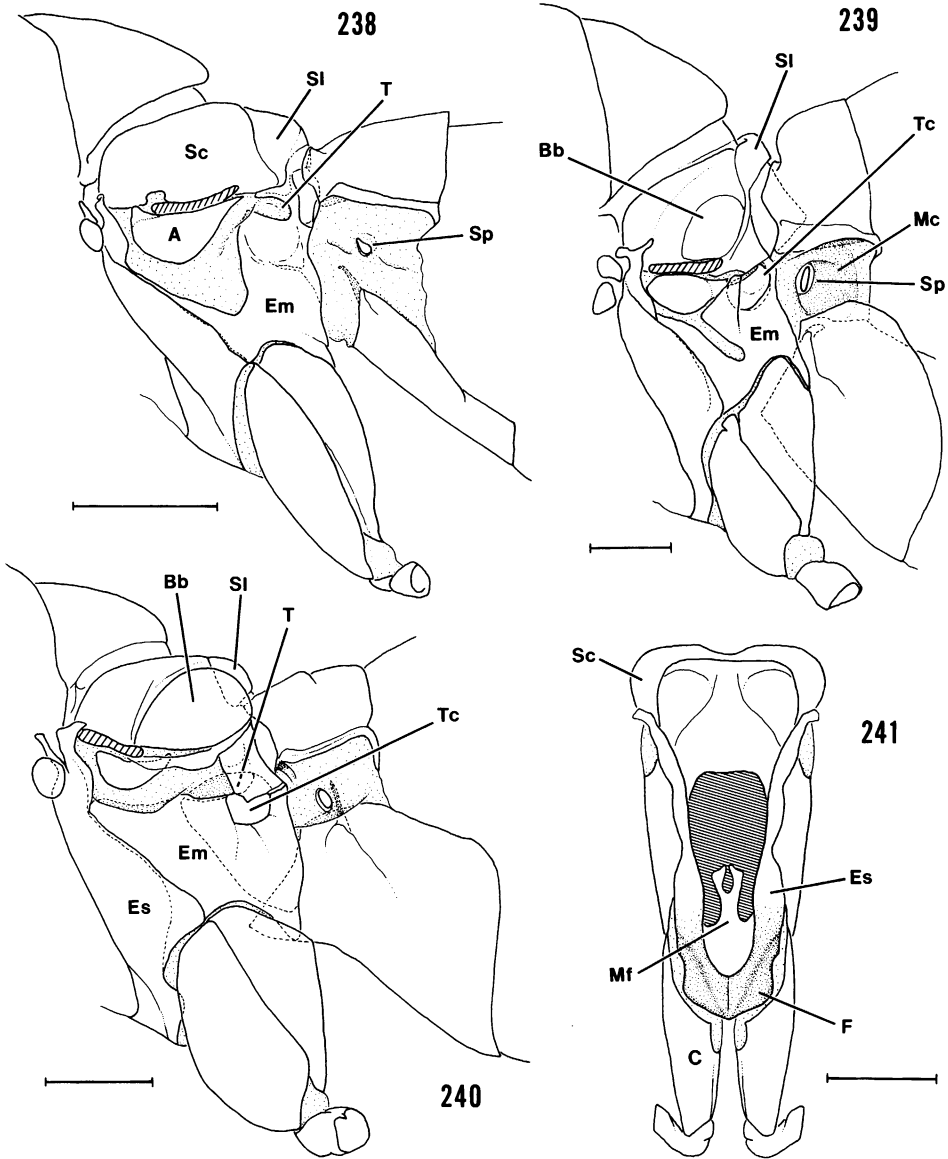
Roeder and Treat (1957), among the first to investigate the function of the metathoracic tympanum, concluded that it could serve two purposes. First, they suggested that the noctuid tympanum is effective in detecting high and low frequency cries of bats. They also found that it would be capable of de-

tecting the presence of other flying insects, such as individuals of the opposite sex. Spangler (1988) emphasized that acoustic communication is being discovered in more and more moth species. Sound production by noctuid adults is now known in Arctiidae (Peter, 1917; Blest et al., 1963; Conner, 1987; Krasnoff and Roelofs, 1990), in the noctuid subfamilies Agaristinae (Common, 1979; Alcock et al., 1989; Surlykke, 1990), Heliethinae (Matthews, 1987), Chloephorinae (Holloway, 1976), and Cuculliinae (Surlykke and Gogala, 1986), as well as in the Dioptriinae (Forbes, 1922b; Miller, 1989).

Surlykke (1984) and Spangler (1988) reported that the noctuid tympanal membrane is innervated by two auditory A cells, whereas the notodontid tympanum is innervated by only one. The phylogenetic significance of this trait remains uncertain because the character distribution is inadequately known (Weller, 1989). Surlykke (1984; see also Treat, 1956) noted that notodontids lack a nodular sclerite (Richards, 1932) and a "Bügel," a specialized site of attachment for the non-auditory B cell. On these grounds, she concluded that notodontids possess the simplest type of noctuid ear. However, her research showed that tympana of Notodontidae and Noctuidae are equally sensitive and that both groups show basically the same behavioral responses to sound.

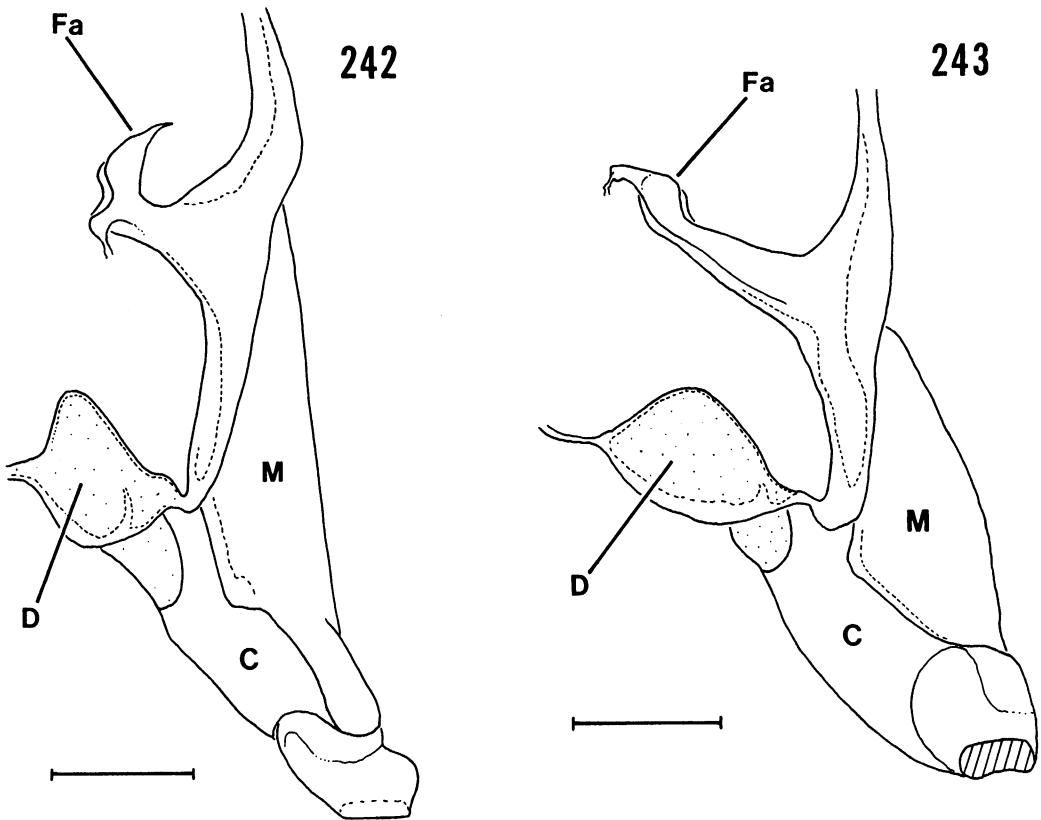
Considerable attention has been paid to the internal structure of the noctuid tympanum. Richards (1932) first described variation in the shape of what he termed "pockets I-IV." Most subsequent discussion has been obtuse, and terminology between workers often conflicts (Weller, 1989). According to Richards (1932), the thaumetopoeine tympanum lacks pocket IV, a potential synapomorphy for the group. Weller (1989), whose interpretations of pocket homology differ from those of Richards, stated that pocket IV in *Thaumetopoea processionea* is present but reduced. Weller (1989) also reported that pocket II is absent in the dioptriine species she studied. I chose to use external rather than internal tympanal characters. Those interested in the latter should consult Weller (1989).

Character 32. Orientation of the Tympanal Membrane. Orientation of the tympanal



Figs. 238–240. Metathorax and first abdominal segment in lateral view with anterior at left (hind wing base shown with hatched lines). For key to symbols see figure 237. **238.** *Doa ampla* (Doidae) male. **239.** *Cnethodonta grisescens* (Heterocampinae) male. As in most Notodontidae, the tympanal membrane in this species forms the roof of the tympanal cavity (Tc). Note also the metascutal bulla (Bb; Character 34), and “membranous cup” (Mc) on A1 (Character 46). **240.** *Josia ligata* (Dioptinae) female. Scale lines = 1.0 mm.

Fig. 241. Metathorax of *Josia ligata* male in frontal view showing the metepisternal flange (Character 30). Symbols as in figure 237 with the addition of: F = metepisternal flange. Mf = metafurca. The abdominal opening is shown with hatched lines. Scale line = 1.0 mm.



Figs. 242, 243. Metafurcasternum and metadiscrimen (D) in mesal view (anterior at left), showing furcal apophyses (Fa). 242. *Cargida pyrrha* male. 243. *Phryganidia californica* male, showing rounded furcal apophyses of Dioprinae (Character 31). C = metacoxa. M = metameron. Scale lines = 0.5 mm.

membrane differs between notodontids and the rest of the Noctuoidea (Richards, 1932; Common, 1979; Fullard, 1984; Weller, 1989). In notodontids the dorsal portion of the epimeron is strongly concave (Brock, 1971), causing the membrane to face obliquely ventrally. The concave epimeron and ventrally directed tympanal membrane also occur in *Doa* (fig. 238). In quadrid noctuoids (fig. 237) and in *Oenosandra boisduvalii*, the epimeron is not concave or is only moderately sunken around the tympanum, and the membrane faces posteriorly.

All authors who surveyed structure of the thoracic tympanum have noted the unusual tympanal morphology of *Josia* (Richards, 1932: fig. 153; Börner, 1939: fig. 41; Sick, 1940: figs. 1–4; Kiriakoff, 1950a: figs. 9, 10). In *Josia*, the metepimeron is deeply invaginated so that the tympanal cavity is a large

internal pouch, almost as large as the epimeron itself (fig. 240). The tympanal membrane forms the roof of the pouch, and the cavity opening is very small. On the basis of this highly derived condition, Sick (1940) proposed "Group V" of the "Dioptridae" to include eight genera (approximately 100 species). These same genera were recognized by Kiriakoff (1950a) as the subfamily Josiinae, all other species being placed in the "Dioptrinae." Among my list of exemplar taxa, the large internal pouch occurs in *Cyanotricha* as well as *Josia*.

Character 33. Nodular Sclerite Absent. The nodular sclerite (Forbes, 1923; Richards, 1932; Surlykke, 1984), or "epaulette" (Eggers, 1919, 1928; Callahan, 1969; Oseto and Helms, 1976; Common, 1979), is a small sclerite located between the epimeron and the anterior margin of the tympanal membrane

(fig. 237; Treat, 1956; Roeder and Treat, 1957). The structure can be morphologically complex in some Noctuidae, and Treat (1956) argued that in these cases it might serve as a barrier to parasitic mites. A nodular sclerite is found in all noctuoids except *Doa* and the Notodontidae (figs. 238–240). Richards (1932: 32) suggested that *Doa* has affinities with the Notodontidae because he discovered that it lacks the nodular sclerite and abdominal counter-tympanal hood (Character 45, below), but has a sunken tympanal region (Character 32, above).

My results contradict those of previous authors, all of whom have suggested that the notodontid-type tympanum is primitive in the Noctuoidea (e.g., see Common, 1975). Taken together, the character data suggest that *Oenosandra boisduvalii* is the sister group of *Doa* + Notodontidae (Clade 2; fig. 99). If this cladistic hypothesis is correct, then absence of the nodular sclerite, absence of the A1 hood, and presence of a sunken tympanal region all represent apomorphic states. The phylogenetic position of *Oenosandra*, obviously pivotal to such an argument, should be studied in great detail. In the interim, I hope my theories on noctuoid tympanal characters will spur fruitful debate.

Character 34. Metascutal Bulla. In most Notodontidae the region of the metascutum above the tympanum is swollen to form a bulla (Common, 1975, 1979; Holloway, 1983) demarcated by a fine sulcus (figs. 239, 240). Brock (1971) considered the metascutal bulla to be diagnostic for the Notodontidae. This structure, which may act as a counter-resonating organ for the tympanum, does appear to be unique to notodontids, but it is variously developed in the group. I recognized four character states concerning size and shape of the metascutal bulla (Appendix I). Presence of a teardrop-shaped bulla, characteristic of almost all Notodontidae, was scored as "1". Two additional apomorphic states are restricted to the Dioptinae, where the bulla is highly developed (fig. 240; Sick, 1940).

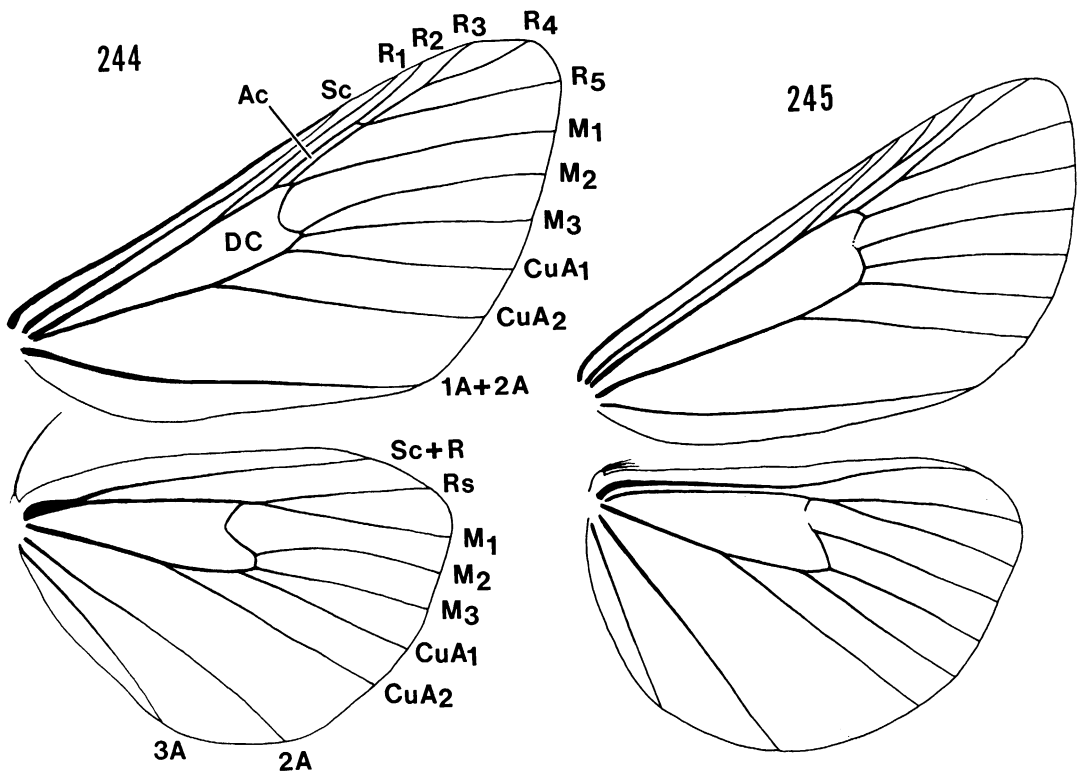
Kiriakoff (1950b) erected the subfamily Tarsolepidinae to include *Tarsolepis* and *Dudusa*, ignoring the fact that Matsumura (1929b) had already erected the subfamily Dudusinae for those same two genera. Kiriakoff's rationale was based on the observa-

tion that in both taxa the scutal phragma is similar to Noctuidae ("type phalénoïde"). If my interpretation is correct, the scutal phragma of Kiriakoff (1950b) and Sick (1940) is homologous with the metascutal bulla. The *Tarsolepis* and *Dudusa* species I examined do appear to have lost the bulla; a slight hump is present, but the sulcus is absent. The same is true of *Cargida pyrrha*, *Goacampa variabilis*, and *Crinodes besckei*. Thus, although these genera seem to exhibit the plesiomorphic condition of the metascutal bulla, it instead represents a case of derived loss and provides evidence for monophyly of Clade 29, the tribe Dudusini.

Forewings: I did not use wing pattern in this study. The research of Nijhout and colleagues (see, e.g., Nijhout, 1986; Nijhout and Wray, 1988) could potentially provide ways to identify homologous pattern elements. However, such an approach would probably be of little use in a study such as this, where the taxa are quite distantly related and their wing patterns are either highly divergent or convergent. An example of wing pattern convergence in the Notodontidae is the distinctive silver triangle seen on the forewing in several genera. My studies show that the silver triangle pattern evolved separately in the Heterocampinae (e.g., *Spatalia jezoensis*, fig. 21), Dudusinae (e.g., *Tarsolepis japonica*, fig. 51), and Nystaleinae (e.g., *Didugua argenteilinea*, fig. 65). An interesting problem will be understanding how the mimetic wing patterns of Dioptinae evolved from wing patterns of other Notodontidae, particularly the Nystaleinae.

Another character system that I did not study is variation in the axillary sclerites at the base of each wing. Sharplin (1963) showed that the wing bases of primitive Lepidoptera are very different from those of more derived groups, but she found surprisingly little variation within superfamilies.

Wing venation has been used by almost all previous notodontid researchers. For example, both Schaus (1901) in his revision of American notodontid genera and Prout (1918), who revised the genera of Dioptinae, based their works almost entirely on venation. Wing veins are relatively easy to see and involve a minimum of specimen preparation for study. However, they present difficult



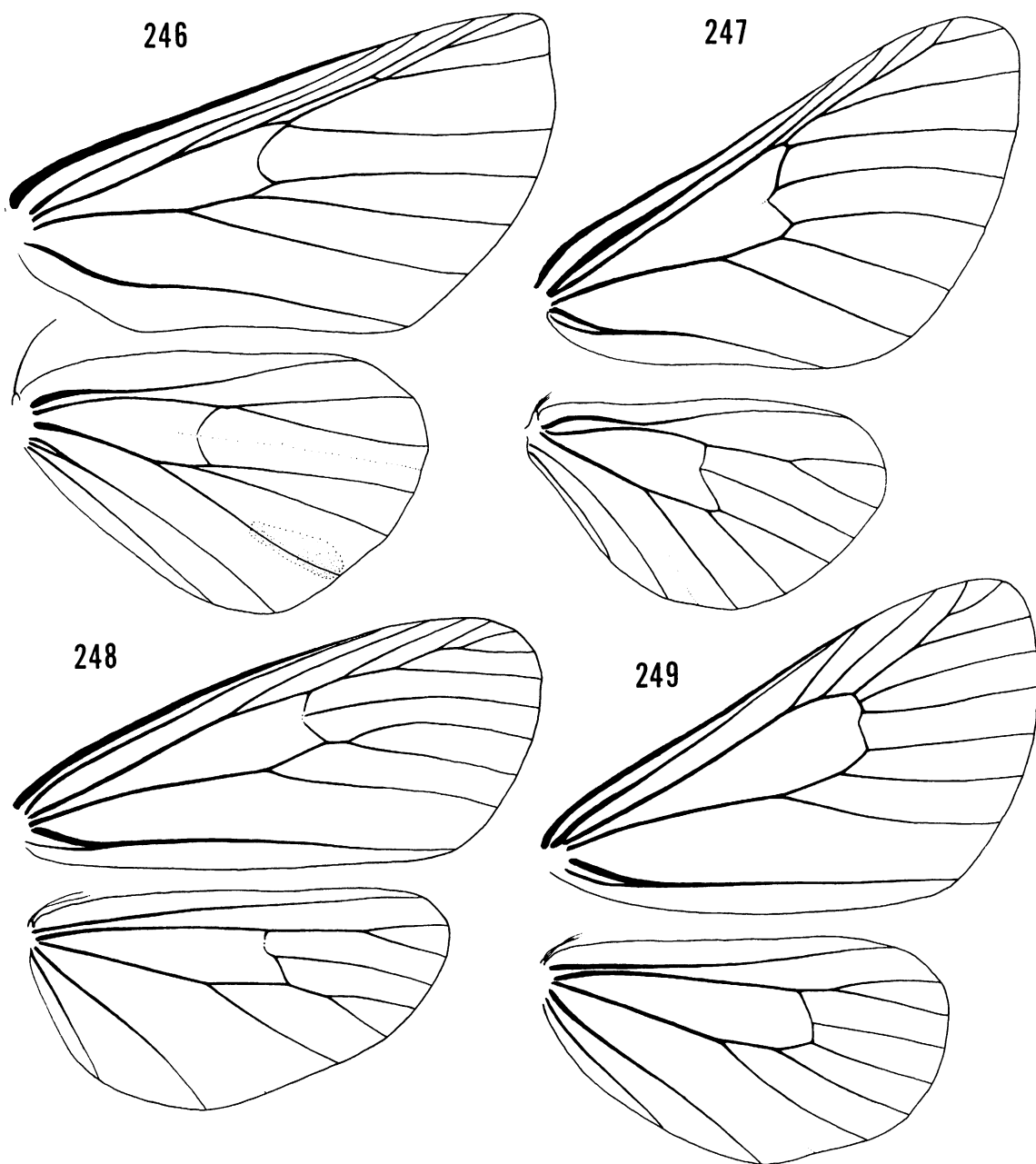
Figs. 244, 245. Right wings of Noctuoidea (FW lengths in parentheses). **244.** *Panthea furcilla* (Noctuidae) male (18 mm). **245.** *Doa ampla* (Doidae) female (15 mm). A = anal vein. Ac = accessory cell. CuA = cubital vein. DC = discal cell. M = medial vein. R = radial vein. Rs = radial sector. Sc = subcostal vein.

problems in homology. Workers attempting to use venational characters in higher classification studies have often resorted to complicated transformation theories (e.g., Brock, 1971). In addition, no matter how they are interpreted, wing vein characters show a large amount of homoplasy (Weller, 1989). Janse (1920) demonstrated that notodontid wing vein characters can vary dramatically within well defined genera. In this study I employed only those venational characters that have figured prominently in previous discussions on the Notodontidae.

Character 35. Forewing Trifold or Quadrifid. One of the long-standing subdivisions of the Noctuoidea has been based upon whether the forewing cubital vein is trifold or quadrifid (Packard, 1895a; Richards, 1932; Forbes, 1939a, 1948; see also Introduction). In trifold venation, the base of M_2 is positioned approximately midway between veins M_1 and

M_3 (figs. 245–249), whereas in the quadrifid condition it touches M_3 (fig. 244). The quadrifid forewing has long been assumed to be apomorphic in the Noctuoidea, whereas trifold venation has been considered plesiomorphic. Among the taxa I examined, trifold forewing venation occurs in members of the Notodontidae and in *Doa* (fig. 245). *Oenosandra boisduvalii* clearly exhibits the trifold condition. The only notodontid group with a quadrifid forewing is the Platychasmatinae (fig. 527; see Addition of Taxa).

Character 36. Forewing Accessory Cell. A forewing accessory cell or “areole” (Schaus, 1901, 1939; Nagano, 1916; Marumo, 1920), formed between veins R_2 and R_3 , occurs in many lepidopteran groups, including most members of my outgroup (e.g., *Panthea furcilla*, fig. 244). Ryabov (1988) considered its presence to be characteristic of Noctuidae, and Brock (1971) regarded the accessory cell



Figs. 246–249. Right wings of Notodontidae (FW lengths in parentheses). 246. *Hemiceras bilinea* male (22 mm); note lobe on anal margin of forewing (Character 39). 247. *Thaumetopoea processionea* female (18 mm). 248. *Josia ligata* female (17 mm). 249. *Phaeochlaena gyon* female (17 mm).

as primitive for the Noctuoidea. In notodontids the cell can be either present or absent (figs. 246–249; see also Forbes, 1939a, 1948), but both character states appear to be constant within genera (Weller, 1989). The areole

was used as a key character by several early notodontid researchers (e.g., Neumoegen and Dyar, 1894a, 1894b; Dyar, 1897; Janse, 1920). Assigning character states to the various positions of R_2 and determining ho-

mologies for the different cell shapes is extremely difficult. I therefore opted for a relatively straightforward interpretation.

I recognized three states for the origin of vein R_2 . First, it may arise from the discal cell when there is no accessory cell (e.g., *Phaeochlaena gyon*, fig. 249). Second, I recognized as a separate state cases where R_2 arises from the discal cell, and there is a short connecting vein between it and the other radials, forming an accessory cell (fig. 246). Finally, in taxa such as the Thaumetopoeinae and Pygaerinae, R_2 is fused with R_3 – R_5 (fig. 247) and no accessory cell is apparent. I do not have a transformational hypothesis concerning this character complex, and so treated these states as nonadditive. It appears from my results that the thaumetopoeine/pygaerine condition is plesiomorphic for Notodontidae.

The three accessory cell states I used do not fully describe variation within the Notodontidae concerning branching patterns of the radial system. In addition to differences in the branching order of veins R_2 – R_5 , M_1 can arise either from the discal cell (figs. 247, 249) or from the radial sector (figs. 246, 248). I found both characters extremely difficult to describe and score, and have excluded them from my analysis. Furthermore, they may be highly unstable. Nakamura (1973) has shown that venation of the radial system can vary within a species; in *Phalera himalayana* Nakamura, some specimens had an areole present while others did not.

Character 37. Forewing Accessory Cell Shape. The accessory cell varies in shape. Some members of the Heterocampinae (the taxa in Clade 42; fig. 100) have an unusually long cell. This state was first noted by Packard (1895a; see his fig. 80) for the genus *Heterocampa*. Forbes (1939a, 1948) used an elongate accessory cell as diagnostic for his Heterocampini. I also recognized an extremely short accessory cell as a separate state. This occurs in *Hippia* and *Symmerista* (Nystalinae). Finally, I recognized a fourth state for species with a short and wide accessory cell, referring in this case to *Scrancia stictica* and *Gargetta costigera* (Scranciini).

Character 38. Fusion of Forewing Veins M_3 and $CuA1$. Having forewing veins M_3 and $CuA1$ fused (fig. 248), a trait used extensively

by Prout (1918) in his revision of the Dioprinae, appears to be apomorphic for that subfamily (Miller, 1987a, 1989). However, except for the few exemplar outgroup taxa examined, I have not surveyed the quadrifid Noctuoidea for this character state. Fusion occurs in most diopline genera (Köhler, 1930) but not in *Erbessa* and *Phaeochlaena* (fig. 249), both of which I regard as plesiomorphic dioplines (fig. 100). The derived state is found in only one other species among my study sample, *Anaphe panda* (Thaumetopoeinae).

Character 39. Forewing Anal Margin with a "Prominence." The name *Notodonta* (from Greek; *notos* = back, *donta* = tooth) was proposed by Ochsenheimer (1810). Although he did not specify whether he was referring to the toothlike projection on the forewing of some species or to the dorsal projections frequently found on notodontid caterpillars (e.g., figs. 79, 84, 93), most subsequent authors (e.g., Seitz, 1912, 1932) claim that the family name is derived from the adult forewing projection. The projection is formed from elongate scales (fig. 250) attached to a rather shallow lobe on the forewing's anal margin (fig. 246). When the wings are folded over the body while the moth is at rest, these two projections meet dorsally to produce a tuft that breaks the insect's outline and aids crypsis (Seitz, 1912).

The forewing "tooth" actually exhibits a relatively limited distribution among Notodontidae. In my study, it occurs only in *Notodonta*, *Odontesia*, and *Pheosia* of the Notodontinae, as well as in *Peridea* (Phalerinae), *Spatalia* (Heterocampinae), and *Hemiceras*. There are two projections on the forewing anal margin in *Platyhasma virgo* (figs. 525, 526). The tooth also occurs in other notodontid genera that I did not study. My cladistic results thus suggest that the forewing tooth evolved at least five times within the family.

Character 40. Bar-shaped Retinaculum. The retinaculum, which occurs in males of almost all Lepidoptera, is a cuticular outgrowth from the forewing costa. It catches the frenular bristle from the hind wing, and together these function as a wing-locking mechanism (Braun, 1919, 1924). Hampson (1900) recognized a "bar-shaped" retinaculum as diagnostic for the Arctiidae, in which he included the Lithosiinae and Nolinae. In

addition to those groups, the retinaculum is long and bar-shaped in Sarrothripinae and Chloephorinae (Kitching, 1984a), both of which are subfamilies in the Noctuidae. I did not find variation in retinaculum shape within the Notodontidae.

Hind Wings: *Character 41. Fusion of Veins M_3 and CuA_1 .* Hind wing veins M_3 and CuA_1 are stalked (fig. 248) in five of the six dioptine genera included in this study (see also Prout, 1918; Köhler, 1930). Dioptinae are unique in that over 70% of the species have these veins fused in both the forewings and the hind wings (Miller, 1987a). The only other species in my sample with hind wing veins M_3 and CuA_1 stalked is *Hypoprepia miniata* (Arctiidae), obviously a separate derivation from the Dioptinae.

Character 42. Hind Wing Trifid or Quadrifid. Like the forewings, the hind wing cubital vein can be either trifid or quadrifid (Turner, 1946; Forbes, 1954; Ryabov, 1988), in this case related to both the position and development of vein M_2 . A quadrifid hind wing occurs only in some outgroup Noctuoidea. Among my exemplar species the quadrifid state is found in *Spilosoma virginica*, *Panthea furcilla* (fig. 244), and the Lymantriidae. Potential monophyly of the trifid Noctuidae has recently been discussed by Kitching (1984a) and Holloway (1989).

Character 43. Hind Wing Vein M_2 Absent. Forbes (1939a) defined the tribe Hemiceratiini based on a single character: absence of hind wing vein M_2 . A fold is present in the position of M_2 (fig. 246), but not a tubular vein. Interestingly, absence of hind wing vein M_2 is not restricted to the Hemiceratiini, but is much more widespread among Notodontidae. The first mention of this trait dates back to Schaus (1901), who used it in his key to Neotropical notodontid genera. The list of genera defined by his dichotomy ("vein 5 [= M_2] on secondaries absent" [Schaus, 1901: 263]) corresponds well with Forbes's concept of the Hemiceratiini. *Goacampa variabilis* (Dudusinae) also fell out at that point in Schaus's key. My examination confirmed that *G. variabilis* is, in fact, missing hind wing vein M_2 . Forbes (1948) later used loss of M_2 as a diagnostic character for both the Pygaerinae and Gluphisiini. I found that the vein is absent in *Clostera* (see also van Eecke, 1930),

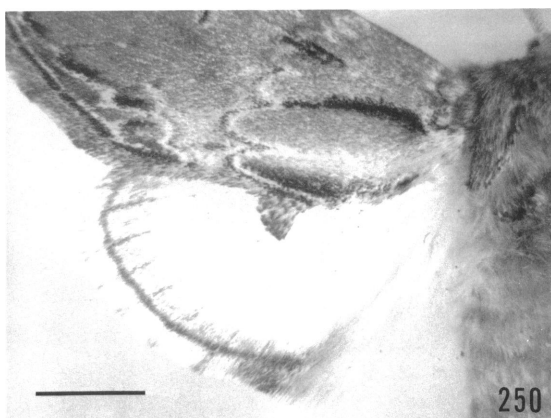
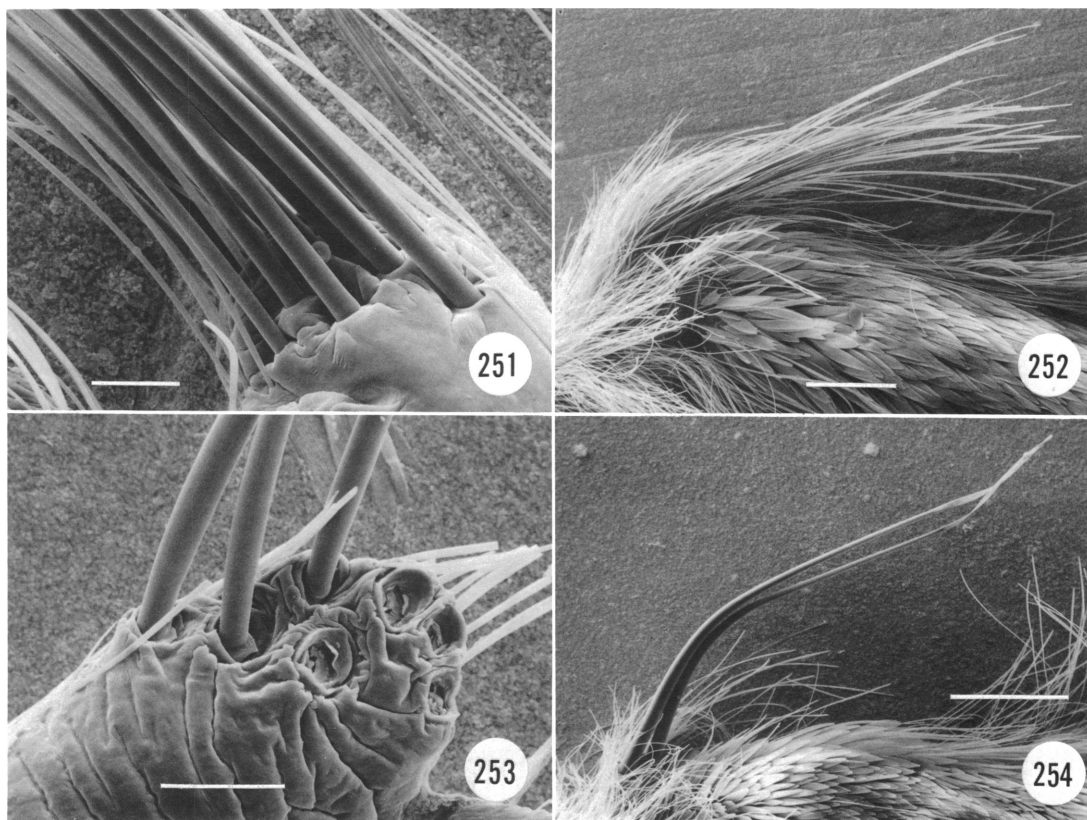


Fig. 250. Left wings (dorsal) of *Notodonta scitipennis* male, showing "tooth" on posterior margin of forewing. Scale line = 3.0 mm.

Gluphisia, *Ellida caniplaga*, *Goacampa*, and *Hemiceras*. Janse (1920) noted that in some African notodontid genera this vein is reduced or absent. I conclude that hind wing vein M_2 has been lost at least five times in the Notodontidae.

Character 44. Female Frenulum Bristle Number. The number of bristles comprising the female frenulum is extremely variable within Notodontidae. There are over 20 bristles in *Anaphe panda*, *Thaumatopoea processionea* (fig. 251), and pygaerine species (Arru, 1965). Other species have between four and eight bristles (e.g., *Peridea angulosa*; fig. 253), and there are only two in *Epicoma tristis* (Thaumatopoeinae), *Dasylophia anguina* (fig. 254), and others. The dioptines I examined have from two to eight bristles. Marshall (1922) showed that there is intraspecific variation in female frenulum number, so I did not attach particular importance to the precise number observed in each of my exemplar taxa. Rather, I used a form of gap coding to score this trait, recognizing only two states: female frenulum composed of 10 or fewer bristles, and frenulum composed of more than 15 bristles. The latter is found in all members of Clade 13 (e.g., *Odontosia elegans*; fig. 252) except *Liparopsis postalbida*. This species is unusual in that females lack a frenulum. In both sexes the hind wing humeral area is greatly expanded (fig. 28), analogous to the condition found in butterflies.



Figs. 251–254. Female frenulum on hind wing of Notodontidae. **251.** *Thaumetopoea processionea* with scales removed (50 μm). **252.** *Odontotia elegans* (500 μm). **253.** *Peridea angulosa* (100 μm) with scales and some frenular bristles removed. **254.** *Dasylophia anguina* (500 μm). Scale lengths in parentheses.

There is variation in female frenulum bristle number among other noctuoids as well. *Doa*, *Oenosandra*, and the Lymantriidae exhibit the “1” state (more than 15 bristles), whereas arctiid and noctuid species have either two or three (score of “0”). Character optimization thus suggests that presence of 15 or more frenular bristles is plesiomorphic for the Notodontidae.

Although male Lepidoptera have what appears to be a single frenular bristle, it is actually composed of fused bristles (Braun, 1919), and the number of these is known to vary (Marshall, 1922; Richards, 1981; Davis, 1986). I did not examine the male frenulum because an analysis would require scanning electron micrographs for all study taxa.

ABDOMEN (BOTH SEXES)

Segment 1: Character 45. Counter tympanal Hood. In quadrifid noctuoids there is a membranous evagination on the first abdominal segment termed the counter-tympanal hood (Eggers, 1919, 1928; Richards, 1932; Common, 1979). In previous discussions of noctuid classification (e.g., Forbes, 1954), much emphasis has been placed on whether this hood is prespiracular or postspiracular in position (fig. 237; see also figures in Common, 1979). A postspiracular hood is restricted to the Noctuidae, whereas among my study species a prespiracular hood occurs in *Nola*, *Spilosoma*, and the lymantriids. In some arctiids the prespiracular hood is very

large. Kitching (1984a) noted that the Herminiinae are unusual among Noctuidae in having a prespiracular hood.

Notodontids lack a hood, but they usually have a membranous cup around the A1 spiracle (Character 46 below). The hood is absent in *Doa* as well. Interestingly, in *Oenosandra*, the genus that has until now been placed in the Thaumetopoeinae, there is a well-developed prespiracular hood (see Character 33 and The Status of *Oenosandra*).

Character 46. A1 Membranous Cup. Fullard (1984) detailed the morphology of the "membranous cup" in Notodontidae, located in the pleural membrane around the first abdominal spiracle. The area of the cup is usually sclerotized slightly, and the surrounding scales are appressed to form a smooth cavity. Fullard suggested that the cup is homologous with the counter-tympanal hood of other noctuids and showed that it functions to localize sounds coming into the tympanum.

Within the Notodontidae there is variation in the degree to which this membranous cup is developed (Jordan, 1923b). For example, in members of the Dioprinae there is no sign of a cup (Jordan, 1923b), whereas in some Nystaleinae the cup is extremely large (Weller, 1989) and extends above the ventral margin of tergum 1. I recognized three character states to describe this variation. The first, that of having no cup around the spiracle, was found in the Thaumetopoeinae and Dioprinae (fig. 240). All other Notodontidae have a cup. Those with one of moderate size received a score of "1". It is large, extending above the pleuron (score of "2"), in two species of Nystaleinae I examined and in *Crinodes besckei*.

Character 47. A1 Sclerotized Bar. In Dioprinae there is a small, lightly sclerotized bar in the pleuron of A-1 dorsal to the spiracle (fig. 240). This structure, found in both sexes, is sometimes difficult to locate, but appears to be diagnostic for the group.

Character 48. A1 Abdominal Bulla. Some Noctuidae have a large internal abdominal bulla, formed from a deep invagination on the anterior face of A1. Among the outgroup species I examined, it occurs in *Diloba caeruleocephala*, *Peridroma saucia* (Noctuinae)

(fig. 237), and *Alypia octomaculata* (Agaristinae), being most highly developed in the latter. These three species belong to disparate groups according to most noctuid classifications. Kiriakoff (1977) defined the Agaristinae by presence of this structure, but Minet (1986) showed that the abdominal bulla is more widespread; he suggested this character as a potential synapomorphy for the Noctuidae. It certainly deserves study by future workers.

A similar abdominal bulla occurs in *Scrancia stictica* and *Gargetta costigera* (Scranciini). Cladistic results (figs. 99, 100) show that the scranciine structure is not homologous with that of Noctuidae. The taxonomic distribution of this A1 bulla within Notodontidae deserves further study. Minet (1986) noticed it in the notodontid genus *Pterostoma* Germar.

Segment 2: Character 49. Sternum 2 Apodemes Elongate. Anterolateral apodemes are found on sternum 2 (figs. 238, 239) in almost all Lepidoptera (Brock, 1971); it has been suggested that their presence is a synapomorphy for the Ditrysia (Kyrki, 1983; Nielsen, 1989). These apodemes are particularly long and thin in *Erbessa* and *Phaeochlaena*, but not in other dioptrines. I did not study subtle differences in apodeme shape.

Segment 4: Holloway et al. (1987) suggested that presence of a pair of pockets on the fourth sternum may be a synapomorphy for the Lymantriidae. Their figure of *Redoa* Walker shows fine corrugations in the pockets, and the authors suggested that this structure may produce sound. I did not find such an organ in my two lymantriid taxa.

ABDOMEN (FEMALE)

Segment 7: In many notodontids and in a few outgroup species, the female seventh segment is more heavily sclerotized than preceding ones. However, I was unable to reliably score the trait.

Character 50. Anal Scale Tuft. The female seventh tergum is sometimes large, membranous (strongly wrinkled in *Oenosandra*), and covered with a dense mass of short deciduous scales (fig. 257). This was termed the "anal tuft" by Common (1979). The tuft (not to be

confused with that of some male Notodontidae; see Character 77) occurs in thaumetopoeines (Turner, 1922), as well as in *Diloba caeruleocephala* (fig. 12). Its presence in *Oenosandra boisduvalii* (fig. 15) perhaps explains why Turner (1922) referred the genus to the Thaumetopoeinae. In addition, the anal tuft of *D. caeruleocephala* is perhaps the reason that this species has at times been placed in the Notodontidae (Kitching, 1987). A female scale tuft very similar to the one in thaumetopoeines occurs in several diopline genera (Miller, 1989), but it must have evolved there separately.

In addition to notodontids, a large anal tuft occurs in females of the noctuid genus *Bellura* (Levine and Chandler, 1976), as well as in many lymantriids, such as species of *Euproctis* (Ferguson, 1978). Females moths in these groups are known to cover their egg masses with the deciduous scales from their anal tufts (Stephens, 1829; Nagano, 1916; Levine and Chandler, 1976; Common, 1979), presumably as a defense against egg parasitoids. This may also be their function in notodontid groups where female tufts occur.

Segment 8: The female eighth segment in Notodontidae exhibits a wide range of morphological variation, whereas in most noctuoids it is unmodified. As with genitalic structures, determining the homology of these modifications is difficult because structural variation can be so extensive, even within genera.

Character 51. Pleural Region of A8 Membranous. The pleural region of segment 8 in noctuid females is typically sclerotized. However, within Notodontidae it varies from being membranous to being heavily sclerotized. I recognized three character states. A sclerotized pleuron on segment 8 was given a score of "0". If the pleuron was membranous, that species received a score of "1". In females of Clade 24 (Phalerinae in the restricted sense), the pleuron of segment 8 is heavily sclerotized and is emarginate posteriorly. The entire eighth segment of these species is fused into a sclerotized capsule (fig. 260).

Character 52. Dorsum of Female Tergum 8. The dorsum of female tergum 8 is usually completely sclerotized (e.g., figs. 262, 269). I found two apomorphic states among Noto-

dontidae. First, in some Dudusinae (e.g., *Cargida pyrrha*, fig. 263) there is a narrow, membranous region in the tergal midline. The other apomorphy is restricted to some genera of the Dioplineae. In *Josia* and *Cyanotricha* the female tergum 8 is reduced to two narrow straps that meet dorsally. This modification appears to allow the segment to expand during insertion by the male of an unusually broad aedeagus and vesica (Miller, 1988a). It is a synapomorphy for the species related to *Josia*, the "Josiinae" of Kiriakoff (1950a; see Character 32).

Character 53. Posterior Margin of Female Tergum 8. I recognized four character states for the posterior margin of female tergum 8, but these only roughly describe structural variation among taxa. Two of these states are autapomorphic; tergum 8 in *Phryganidia* is bifid with two long caudal protuberances (Miller, 1987a), and the posterior margin of tergum 8 in *Cnethodonta grisescens* has a single long projection (fig. 261).

Beyond these obvious character states, the situation becomes more difficult. The caudal margin of tergum 8 shows tremendous variation in shape, but the differences were not easy to characterize. I chose a simple scoring system. Members of the outgroup exhibit a sclerotized, often slightly emarginate margin, scored as "0". I scored the ingroup in a conservative manner, giving most species the plesiomorphic state even if the tergal margin is heavily sclerotized (e.g., *Hippia packardii*, fig. 264). Finally, I gave a "1" score to species in which the caudal margin of tergum 8 is crenulate or deeply emarginate (e.g., *Peridea angulosa*, fig. 265). Clearly, my approach could benefit from more detailed study.

Pheromone Glands: The ability to produce female pheromones is almost universal in the Lepidoptera (Nielsen, 1989; Wagner and Rosovsky, in press). For some families, gland chemistry appears to offer useful taxonomic information (Roelofs and Brown, 1982; Horak et al., 1988; Renou et al., 1988). For example, some tortricid tribes and subfamilies are characterized by pheromones of particular chain lengths or, in some cases, by unique chemical components (Horak et al., 1988). Renou et al. (1988) claimed that three "deltoïd" noctuid subfamilies—the Catocalinae, the Herminiinae, and the Rivulinae—have

female sex attractants with a unique chemical structure. The authors also suggested that pheromone chemistry provides apomorphies for particular genera. Male-emitted pheromones might also provide useful taxonomic characters (Birch, 1972a, 1972b). Unfortunately, characterization of noctuid gland morphology and chemistry is currently inadequate from a phylogenetic standpoint. Data are unavailable for many groups. Notodontidae are of little economic importance so few workers have studied their pheromone chemistry.

Hollander et al. (1982) discovered that in females of *Lymantria dispar* (Lymantriidae), both the dorsal and ventral regions of the 8/9 intersegmental membrane produce pheromone. Similar results were obtained by Teal et al. (1983) for *Heliothis virescens* (Noctuidae) and by Krasnoff and Roelofs (1990) for Arctiidae. Percy-Cunningham and MacDonald (1987) identified pheromone-producing cells in the terminal segments of female Notodontidae representing eight species. However, they noted that there was little consistency between species in the location of these cells. It therefore appears that in Noctuoidea, female pheromone production is generally associated with the 8/9 intersegmental membrane, but that two regions can be involved.

My treatment of pheromone gland morphology is superficial. Identifying glandular tissue and determining gland homology requires histological, behavioral, and chemical research. For the purposes of character analysis I simply scored the presence or absence of a clearly visible, invaginated glandular area. Two types of these occurred in the species I examined.

Character 54. Ventral Female Pheromone Gland. An invaginated glandular region occurs on the ventral surface of the 8/9 intersegmental membrane in Lymantriidae, Arctiidae, some Noctuidae, and in *Oenosandra boisduvalii*. I was unable to give a score to *Doa*, which has a complex membrane (fig. 304). Among ingroup species I found such a structure only in the Thaumetopoeinae (figs. 267, 268). Character optimization suggests that possession of a large, ventral, pheromone-producing region is plesiomorphic for the entire Noctuoidea, but that this was lost

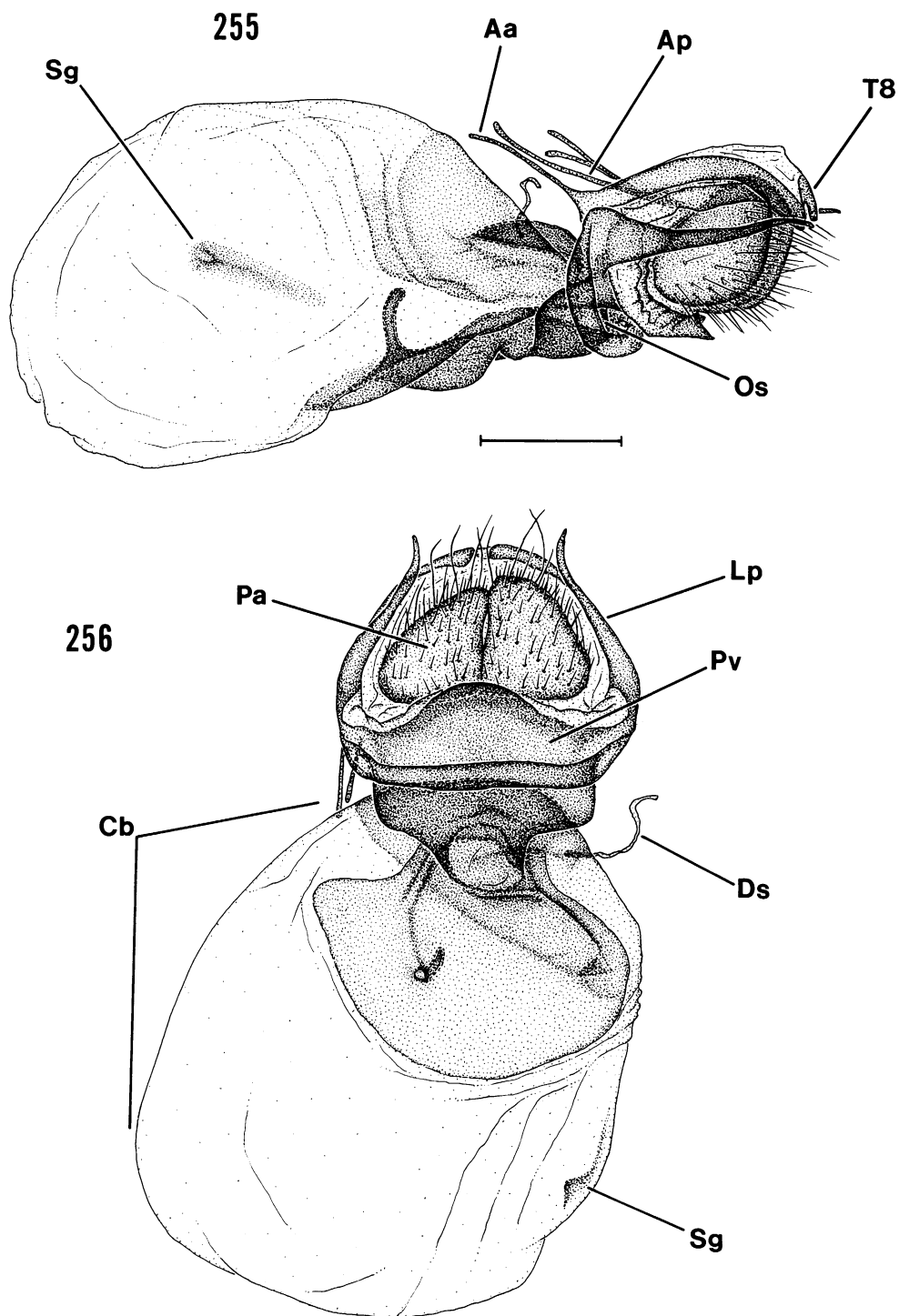
in Notodontidae above the Thaumetopoeinae (fig. 99).

Character 55. Dorsal Female Pheromone Gland. Both of the arctiid species I examined possess a female pheromone gland in the intersegmental membrane between tergum 8 and the papillae anales. It is a paired structure, invaginated anteriorly, and is quite long in *Spilosoma*. Studying the distribution of this trait was obviously beyond the focus of my paper, but judging from a perusal of the literature (e.g., Franclemont, 1966; Ferguson, 1985; Kôda, 1987, 1988), the gland is widely distributed in the Arctiidae. It is a complex structure apparently everted by blood pressure and retracted by longitudinal muscles (MacFarlane and Earle, 1970; Gupta, 1980). Krasnoff and Roelofs (1988) described the structure, chemistry, and mode of scent dissemination for the pheromone gland of *Pyr-rharctia isabella* (Arctiinae).

Genitalia: I limited my study to external genitalic characters. Petersen (1900) described differences among lepidopteran families in structure of the internal male and female genitalia. He examined 10 species of Notodontidae in his work, but did not find dramatic differences among those.

Although external genitalic characters are invaluable for distinguishing closely related species, they are less useful in higher classification studies. Among my study taxa, females show extreme divergence in most features. For example, signum shape and number can vary dramatically. The problem with these and other genitalic structures involves determining homology. As a case in point, there are numerous types of sclerotized regions on the female corpus bursa in addition to the signum. Should the sclerotized plate of *Nystalea nyseus*, with its unusual internal apodeme (figs. 255, 256), be considered homologous with the complex set of spines found in the bursa of *Zunacetha annulata* (fig. 262)? Perhaps a knowledge of function will aid in determining homology, but at present no such knowledge exists.

Because of these difficulties, I limited my analysis of genitalic morphology to cases where I had reasonable confidence concerning the homology of particular structures and to cases involving major structural modifications that are obviously uniquely derived,



Figs. 255, 256. Female genitalia of *Nystalea nyseus*. 255. Lateral view, anterior at left. 256. Ventral view, anterior at bottom. Aa = anterior apophysis. Ap = posterior apophysis. Cb = corpus bursae. Ds = ductus seminalis. Lp = lateral process of postvaginal plate. Os = ostium. Pa = papillae anales. Pv = postvaginal plate. Sg = signum. T8 = tergum 8. Scale line = 1.0 mm.

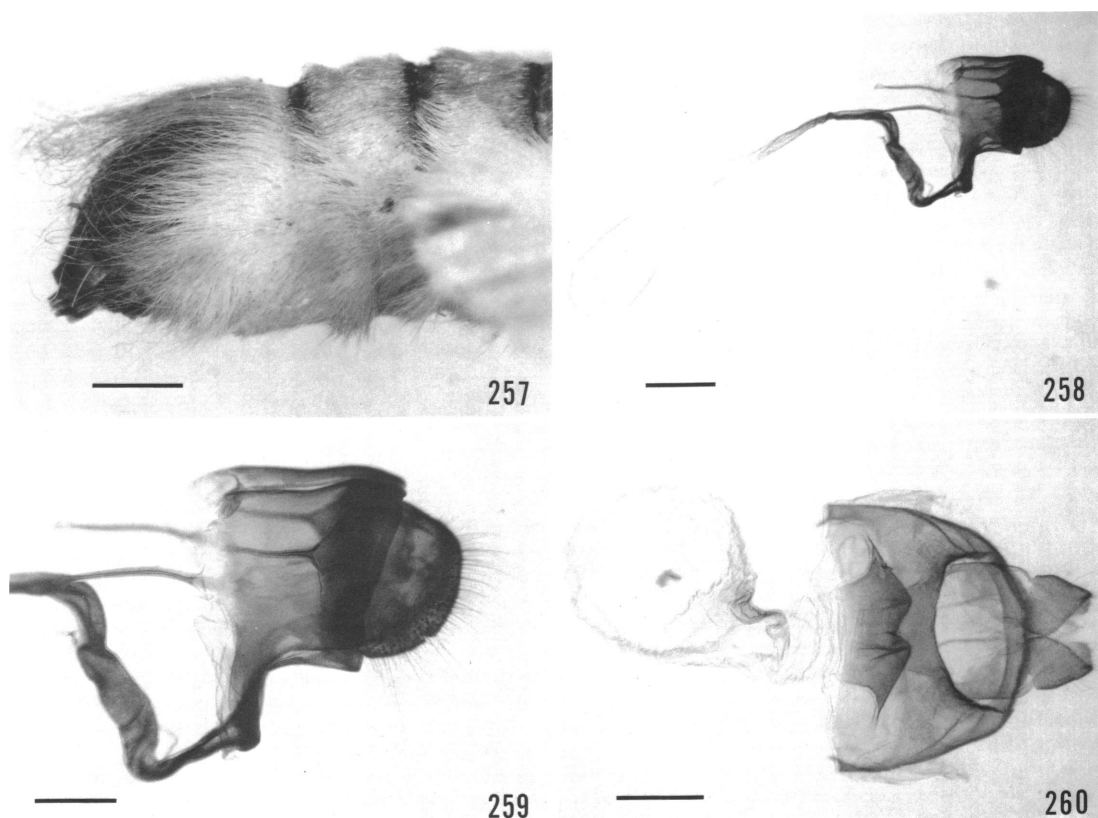


Fig. 257. Female abdomen of *Traumatocampa pityocampa* segments 6–8 (anterior at right), showing tuft of deciduous scales on segment 7. Scale line = 2.0 mm.

Figs. 258–260. Female genitalia of Notodontidae. 258. *Tarsolepis japonica*, lateral view with anterior at left (2.0 mm). 259. *T. japonica*, detail showing sclerotized pleuron of segment 8 (1.0 mm). 260. *Datana ministra*, ventral view with anterior at left (1.0 mm). Scale lengths in parentheses.

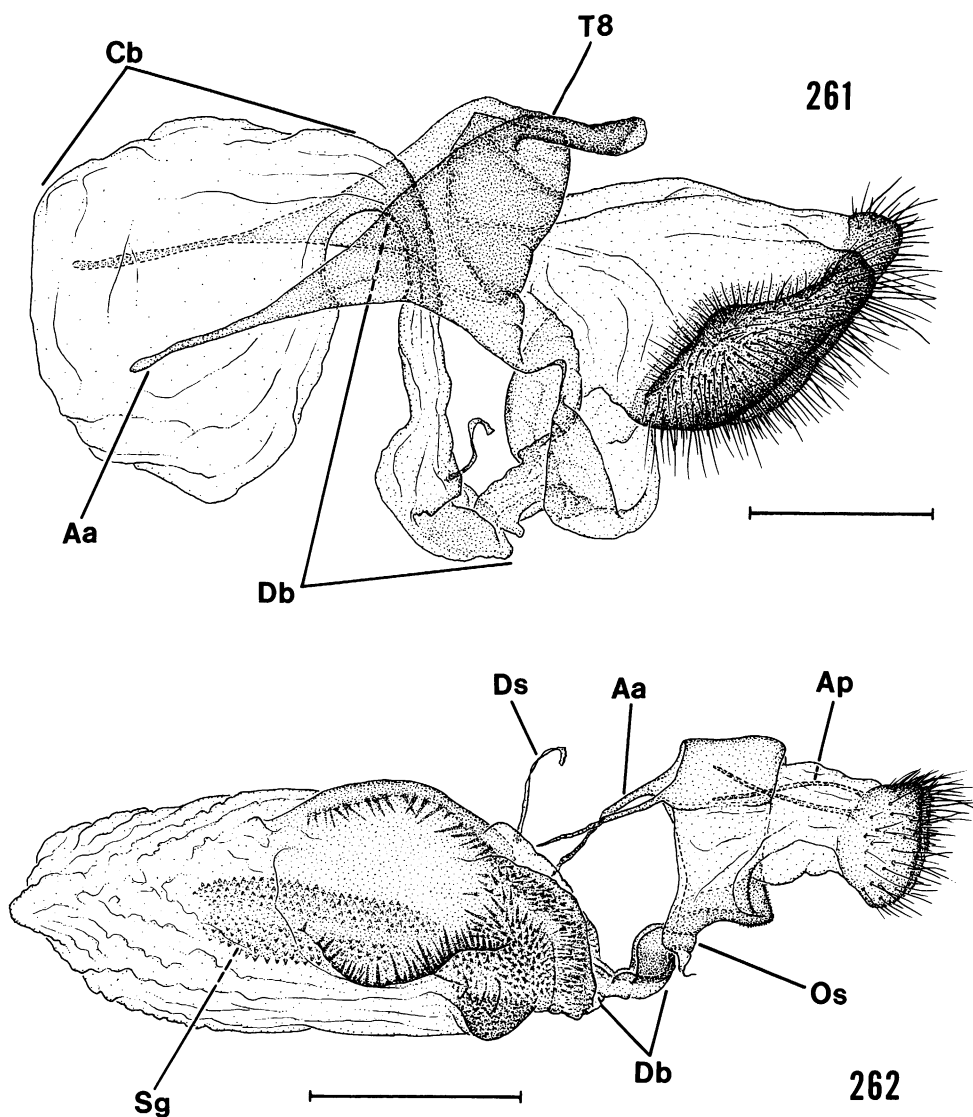
such as the stellate cornuti of the male vesica (Character 99). For a more detailed analysis of male and female genitalic morphology in Notodontidae, refer to Weller (1989, 1990).

Character 56. Modifications of the Ductus Bursae. The ductus bursae is usually defined as that region of the female genitalia between the ostium and corpus bursae (Klots, 1970). Degree of sclerotization and relative length of the ductus bursae, as so defined, is an extremely variable trait in almost all groups of Lepidoptera, including the Notodontidae. I used three character states of the ductus bursae. The first was for species with a membranous and elongate ductus bursae, examples being *Furcula borealis* (fig. 266) and *Fentonina ocypte* (fig. 269). This generally applied to outgroup species. The second was

given to taxa with the ductus bursae robust and heavily sclerotized (e.g., fig. 275). I gave a third score to taxa with a dorsoventrally compressed ductus bursae, an example being *Ellida caniplaga* (fig. 272).

None of these states was very consistent (Appendix IV). The sclerotized condition is typical of Phalerinae and some Notodontinae, but does not occur universally in either. The compressed ductus is found in most Nysaleinae (Weller, 1989), in two dioptine species, and in both arctiid exemplars.

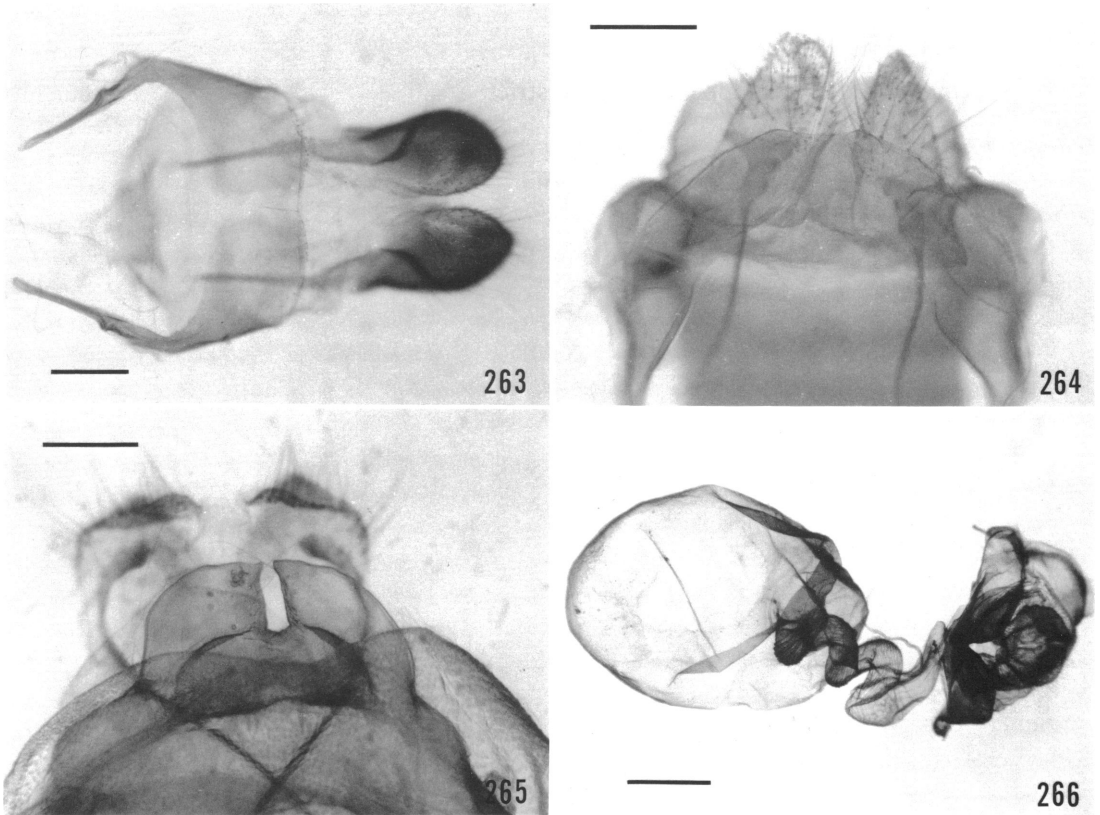
Character 57. Posterior Margin of the Female Postvaginal Plate. The postvaginal plate (PVP) exhibits numerous modifications. It is usually sclerotized, but can be large or small, and its posterior edge can be emarginate or not. An emarginate posterior edge can show



Figs. 261, 262. Female genitalia of Notodontidae in lateral view with anterior at left. **261.** *Cnethodonta grisescens*. **262.** *Zunacetha annulata*. **Db** = ductus bursae. For other symbols see figures 255 and 256. Scale lines = 1.0 mm.

many types of modifications, although I do not describe all of them here. My character states are relatively simple interpretations of the variation. The plesiomorphic condition was considered to be a PVP that is not unusually large and is not emarginate. A derived state was scored for species with a broad PVP that does not have an emarginate posterior margin. An example of this configuration is *Macrurocampa marthesia* (fig. 275). The nys-

taleines I studied, with the exception of *Symmerista albifrons*, have a unique type of PVP with long, posterolateral processes (see figs. 255, 256, 273, 274). These processes, first noted by Todd (1973), are found in additional nystaleine taxa (Weller, 1989). Finally, a synapomorphy for the lymantriids in my study is a cup-shaped PVP (see figures in Ferguson, 1978), a type I observed nowhere else. In the phalerines, where the entire eighth seg-



Figs. 263–265. Dorsal view of female tergum 8. 263. *Cargida pyrrha*, anterior at left (0.5 mm). 264. *Hippia packardii*, anterior at bottom (0.5 mm). 265. *Peridea angulosa*, anterior at bottom (0.5 mm). Scale lengths in parentheses.

Fig. 266. Female genitalia of *Furcula borealis* in ventral view with anterior at left. Scale line = 1.0 mm.

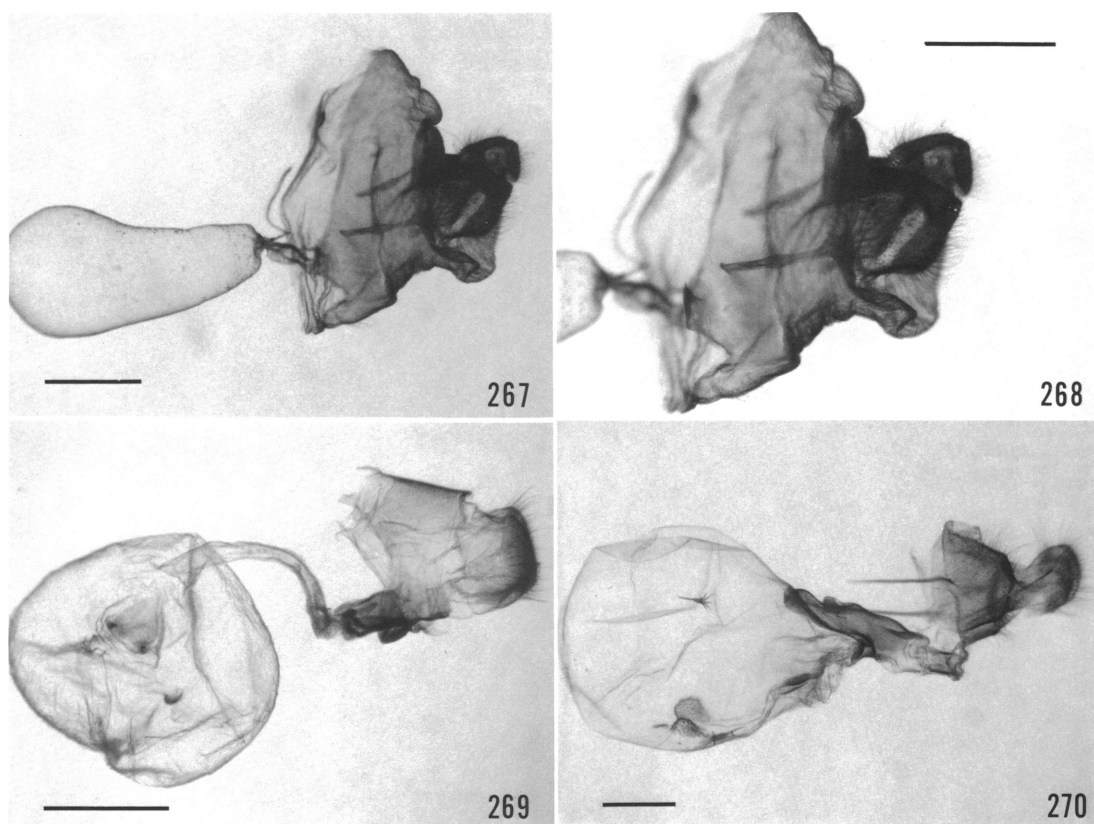
ment is fused into a sclerotized capsule (Character 51), I was unable to score this character because the PVP boundaries are indistinct.

Character 58. Medial Projection of the Postvaginal Plate. Some of the Heterocampinae I examined have a large medial projection on the ventral margin of the ostial opening (fig. 275). This apomorphy defines Clade 42 (the “Heterocampini”) of that subfamily; it is not found in the taxa closely related to *Stauropus* (Clade 40) or in *Schizura unicornis*. I have not seen this synapomorphy used in reference to the Heterocampinae, but it probably defines a fairly large monophyletic group.

Character 59. Surface of Corpus Bursae Spiculate. The external surface of the corpus bursae in Lepidoptera is almost always cov-

ered with numerous wrinkles. Sometimes these crenulations are conspicuous (e.g., figs. 271, 272). They probably allow the corpus to expand as the spermatophore is formed by the male during copulation. I noticed that the internal surface of the corpus bursae in two notodontines, *Gluphisia septentrionis* (fig. 276) and *Liparopsis postalbida*, as well as in *Lochmaeus bilineata* (Heterocampinae), is minutely spiculate. I did not examine this trait with SEM, and it is quite difficult to score. Perhaps a more detailed study will reveal additional character states for the surface of the corpus bursae and will show that this apomorphy is more widely distributed.

Character 60. Two Signa Present. Some authors (e.g., Stitz, 1901) thought that the signum of the corpus bursae, a structure found



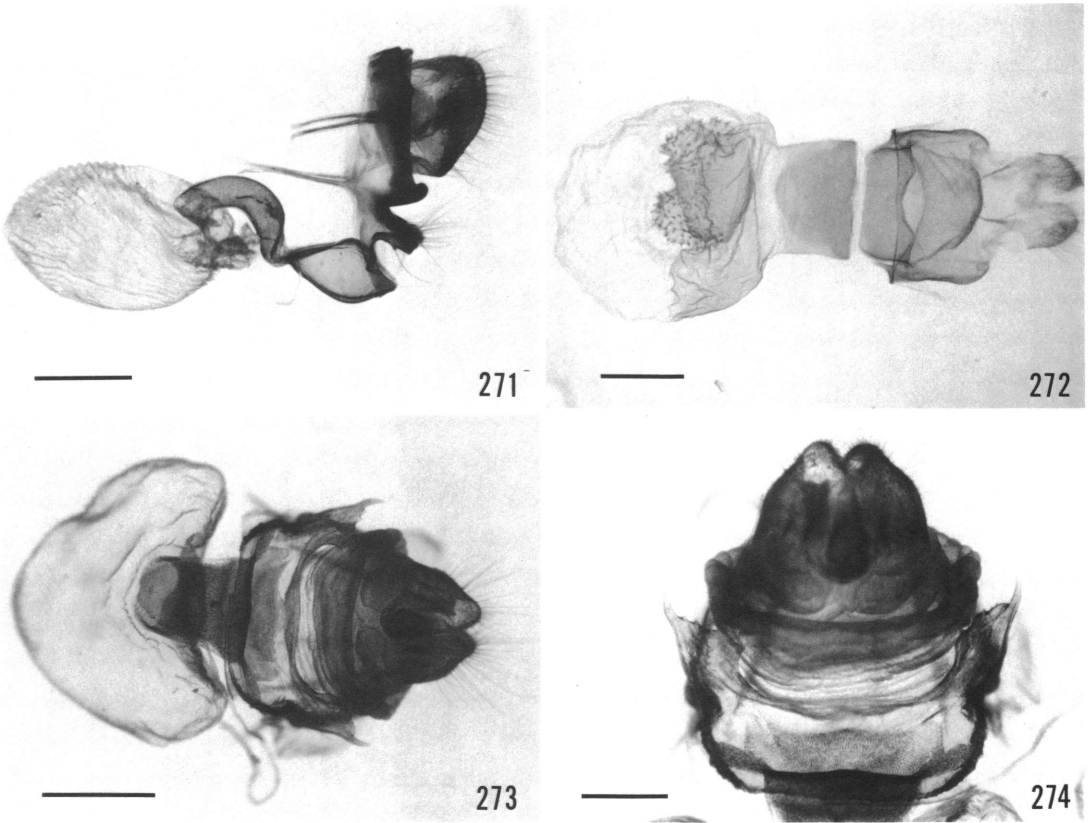
Figs. 267–270. Female genitalia of Notodontidae with anterior at left. 267. *Traumatocampa pityocampa* (1.0 mm). 268. *T. pityocampa*, close-up showing glandular area below papillae anales (1.0 mm). 269. *Fentonia ocypete* (2.0 mm). 270. *Goacampa variabilis* (1.0 mm). Scale lengths in parentheses.

almost universally in Lepidoptera, is used for breaking up the male's spermatophore. Others have suggested that the signum functions to hold the spermatophore in place (Petersen, 1907; Callahan, 1958). Both hypotheses require testing.

As noted above, signum shape varies widely among the taxa I studied. Further, the signum is absent in some species. I did not examine morphology of this structure in detail. In addition to the primary signum (at left in fig. 277), a round hump-shaped signum occurs in *Schizura biedermani*, *Schizura unicornis*, and *Lochmaeus bilineata*. This structure is not found in the other Heterocampinae I studied.

Character 61. Position of the Ductus Seminalis. The ductus seminalis enters either on the distal portion of the ductus bursae or on the corpus itself. I regard the plesiomorphic

condition to be the first of these, as seen, for example, in females of *Cnethodonta grisea* (fig. 261). In species with the derived configuration (e.g., *Zunacetha annulata*, fig. 262), the corpus bursae is frequently sclerotized near the point of attachment of the ductus seminalis. The sclerotized region can be fairly large and well defined (e.g., *Nystalea nyseus*, fig. 255), or it can be small and faint. Among ingroup species examined, the derived state occurs in five of the six dioptines and in all Nystaleinae except *Symmerista* and *Didugua* (fig. 273). The ductus seminalis attaches directly onto the corpus bursae in both Arctiidae. The derived state is not restricted to arctiids among quadrifid Noctuoidea however. It also occurs in many species of the Noctuidae not represented on my exemplar list (e.g., *Euxoa* species; Lafontaine, 1987). Ryabov (1988) considered position of the



Figs. 271–274. Female genitalia of Notodontidae with anterior at left. 271. *Hemiceras bilinea*, lateral view (1.0 mm). 272. *Ellida caniplaga*, ventral view (1.0 mm). 273. *Didugua argentilinea*, ventral view (1.0 mm). 274. *D. argentilinea*, detail (anterior at bottom) showing lateral processes of postvaginal plate (0.5 mm). Scale lengths in parentheses.

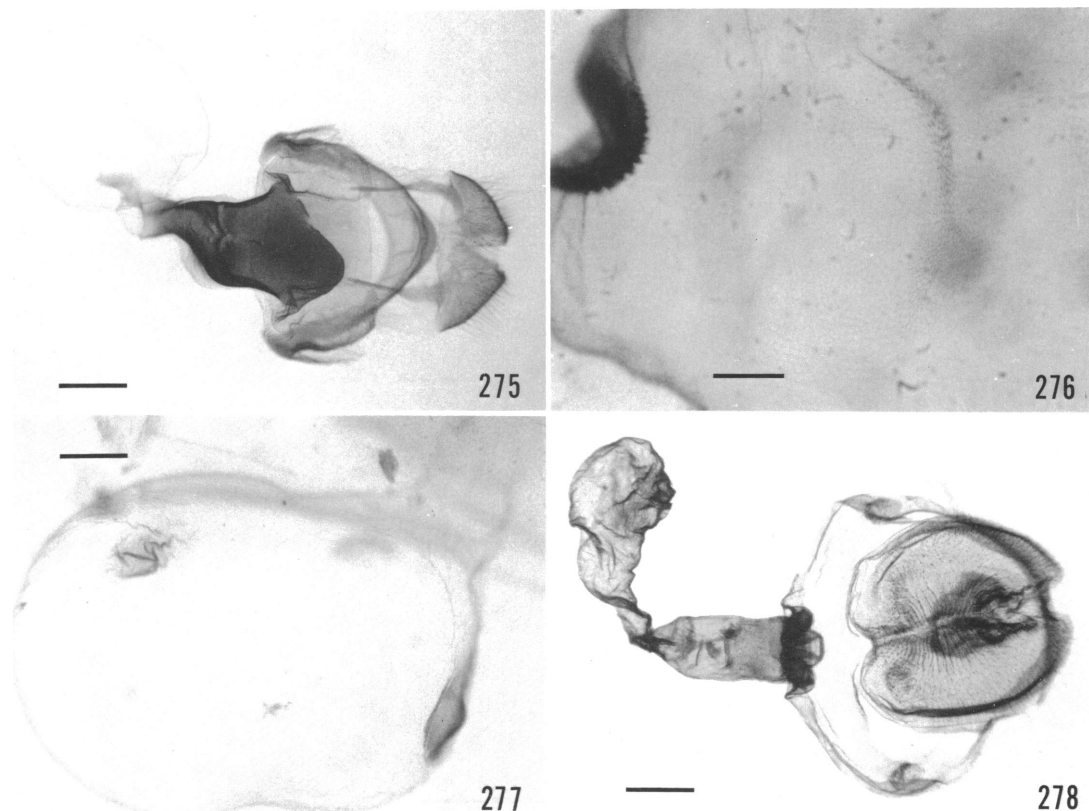
seminal duct to be an important character in the higher level classification of Noctuidae. Thiaucourt (1987) used position of the ductus seminalis to separate Neotropical species of *Rifargia* (Notodontidae).

Ovipositor Lobes: The female ovipositor lobes have been termed the papillae anales by most authors (e.g., Kuznetsov, 1967; Osoto and Helms, 1976), although Michener (1952) called them the proctigers. They are setose structures, thought to be derived from the ninth and tenth abdominal segments (Klots, 1970), through which the ovipore and anus exit. The lobes themselves vary greatly in shape among Noctuidae, and these differences are correlated with specialized oviposition behaviors (Ryabov, 1988). Weller (1989) described variation in form of the papillae anales setae among Notodontidae, a

character complex that has provided taxonomically useful information in other lepidopteran groups (e.g., the Papilionidae; Miller, 1987b), but I did not observe useful variation in setal structure among my study taxa. I used five characters involving the papillae anales, four of which relate to the in-group.

Character 62. Papillae Anales Broad. The papillae anales of four genera in the Notodontinae (*Liparopsis*, *Gluphisia*, *Cerura*, and *Furcula*) are broad, flattened, and membranous (fig. 278). The lobe surface of these tends to be finely creased. Papillae anales in other taxa are of various shapes and sizes, but they do not fit this description. The lobes in *Clostera albosigma* are also broad, but this state appears to have evolved separately.

Character 63. Base of Papillae Anales



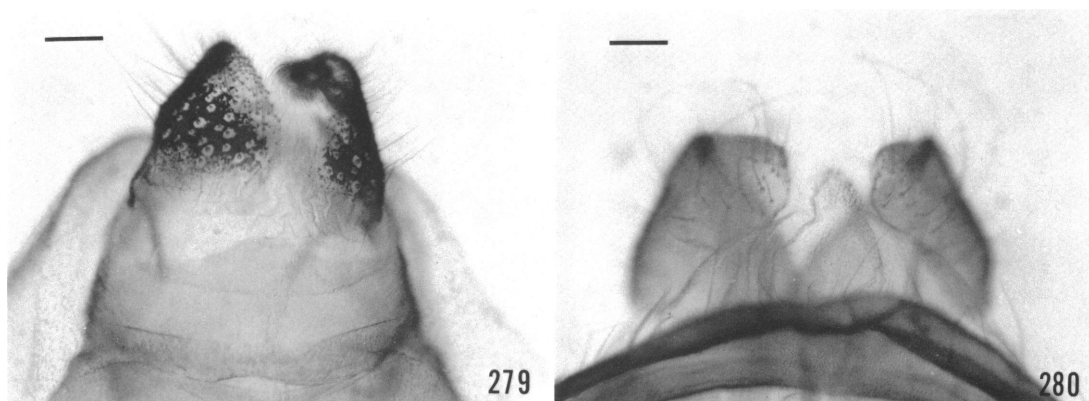
Figs. 275–278. Female genitalia of Notodontidae. 275. *Macrurocampa marthesia*, ventral view with anterior at left (1.0 mm). 276. Corpus bursae (ventral view) of *Gluphisia septentrionis* with signum at upper left, showing spiculate surface (0.25 mm). 277. Corpus bursae of *Schizura beidermani* showing two signa (0.5 mm). 278. *Liparopsis postalbida*, ventral view with anterior at left (0.5 mm). Scale lengths in parentheses.

Sclerotized. In both *Tarsolepis* and *Dudusa*, the basal portion of the papillae anales is heavily sclerotized and smooth (fig. 259). Again, there is a wide range of lobe types among the study group, but this apomorphy is easy to recognize. It adds further evidence for what, on other grounds, is a strongly supported sister-group relationship between these two genera.

Character 64. Posterior Edge of Papillae Anales Emarginate. The papillae anales appear to be more heavily sclerotized in some notodontids, and their posterior edges are somewhat emarginate. This is exemplified by the lobes of the heterocampines *Stauropus fagi* and *Schizura unicornis* (fig. 279). Typical lobes are membranous and have rounded margins (e.g., fig. 280). Some species are in-

termediate between these two types and were difficult to score. I found the derived state in four species of the Heterocampinae, as well as in females of *Scrancia stictica* (Scranciini).

Character 65. Dorsal Lobe of the Papillae Anales. In some Notodontidae there is a small, setose dorsal lobe in the membrane between the papillae anales (fig. 280). The apomorphic state (lobe present) exhibits an unusual taxonomic distribution. It occurs in *Doa* (fig. 304) and *Gargetta*, as well as in two species of the Phalerinae. These likely represent three separate derivations. Among the phalerine exemplars, a dorsal lobe between the papillae anales is found in *Antheua simplex* and *Datana ministra* (fig. 280). Study of additional phalerine species may reveal that presence of the lobe defines a fairly large clade.



Figs. 279, 280. Ovipositor lobes of Notodontidae. 279. *Schizura unicornis*, ventral view (0.25 mm). 280. *Datana ministra*, dorsal view showing medial spiculate lobe (0.20 mm). Scale lengths in parentheses.

Character 66. Ventral Lobe of the Papillae Anales. Females of *Lymantria dispar* and *Dasychira obliquata* (Lymantriidae) have a pair of small, ventral setose lobes at the base of the papillae anales. Again, detailing the distribution of this character was beyond the scope of my project, but I mention it because it might prove to be an important synapomorphy for this family (see Pierce and Beirne, 1941). The lobes appear in additional lymantriid species (e.g., figures in Pierce and Beirne, 1941; Ferguson, 1978).

ABDOMEN (MALE)

Abdominal Hair Pencils: Abdominal androconial organs are widespread in Lepidoptera. Whether they function solely as aphrodisiacs or also play a role in competition between males remains controversial (Birch and Hefetz, 1987; Birch et al., 1990). In Notodontidae androconia can occur on almost any segment; they have been reported on the second, third, fourth, fifth, and eighth segments (Thiaucourt, 1983; Weller, 1989). Among the species I studied, androconial structures are found on the second (in Noctuidae), third, and fourth (Dudusinae) abdominal segments. I reserve discussion of genitalic androconia for a later section.

Character 67. Stobbe's Gland. Males of many Noctuidae (those with a "trifid" hind wing; Forbes, 1954; Kitching, 1984a) possess an elaborate brush-organ on the second abdominal sternum (Kuznetsov, 1967; Birch,

1972a, 1972b; Ryabov, 1988; Holloway, 1989). Similar structures occur in the same location in many Sphingidae (cf. Rothschild and Jordan, 1903: pl. 63, fig. 1). In Noctuidae the brushes are composed of long androconia that distribute scent produced by a pair of glands, termed Stobbe's Glands (Varley, 1962a; Holloway, 1989) after their discoverer (Stobbe, 1912), found on the second abdominal segment. The brushes, held at rest in a pleural fold, are everted by the male during close-range courtship behavior (Birch, 1970; Birch and Hefetz, 1987). Varley (1962a), studying British *Leucania* (Noctuidae: Hadeninae), used brush-organs as a taxonomic character. Furthermore (1962b) he implored lepidopterists to consider these structures in their studies. Birch (1972a, 1972b) showed that the noctuid brush-organ involves at least five separate characters, and he argued convincingly that their comparative morphology and chemistry should prove to be extremely informative from a phylogenetic perspective. Unfortunately, noctuid taxonomists have not followed up on the pioneering works of Varley and Birch. Among my study taxa these androconial organs occur in two noctuid species, *Peridroma saucia* and *Alypia octomaculata*.

Character 68. Androconia on Segments A3 and A4. The pleura of abdominal segments 3 and 4 in males of *Crinodes*, *Tarsolepis*, and *Dudusa* bear sclerotized lobes (fig. 281) to which are attached brightly colored androconia. The abdominal androconia of *Tarso-*

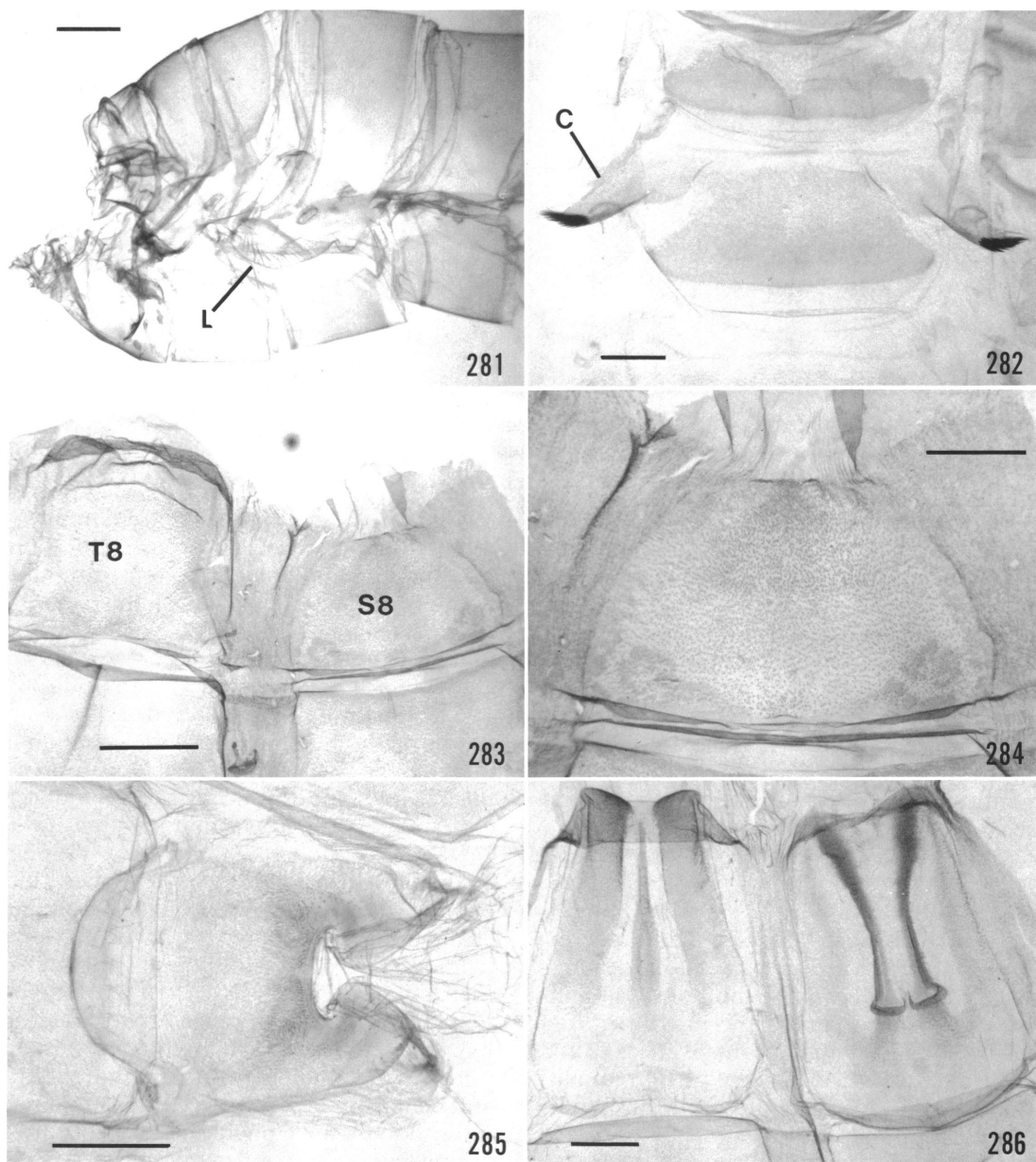


Fig. 281. First through fourth abdominal segments of male *Crinodes besckei* in lateral view (anterior at left) showing pleural lobes (L). Scale line = 2.0 mm.

Fig. 282. Fourth sternum of *Schizura beidermani* in ventral view showing cteniophore (C). Scale line = 1.0 mm.

Figs. 283, 284. Eighth segment of *Clostera albosigma* male. 283. Tergum (T8) and sternum (S8) (1.0 mm). 284. Detail of *C. albosigma*, male sternum 8 (0.5 mm). Scale lengths in parentheses.

Fig. 285. Sternum 8 of *Fentonia ocypte* in ventral view, anterior at left. Scale line = 1.0 mm.

Fig. 286. Tergum 8 (left) and sternum 8 (right) of *Spatalia jezoensis*. Scale line = 1.0 mm.

lepis species have been noted by previous authors (Butler, 1872; Marumo, 1920; Roepke, 1944), and Weller (1989) described those of *Crinodes*. The trait appears to be restricted to Dudusinae but is absent in several genera that I include in that subfamily.

Sternum 4: *Character 69. Cteniophore Present.* The cteniophore, a structure unique to males in the Notodontidae, was first described by Jordan (1923a). It consists of two winglike lateral flaps on sternum 4, each flap bearing a set of coarse distal spines (fig. 282; Holloway, 1983). Jordan claimed that a gland is located at the base of the cteniophore and that these structures constitute a male scent organ, but evidence to support his theory is lacking. I was unable to find a pleural gland, and to date no one has demonstrated a function for the cteniophore.

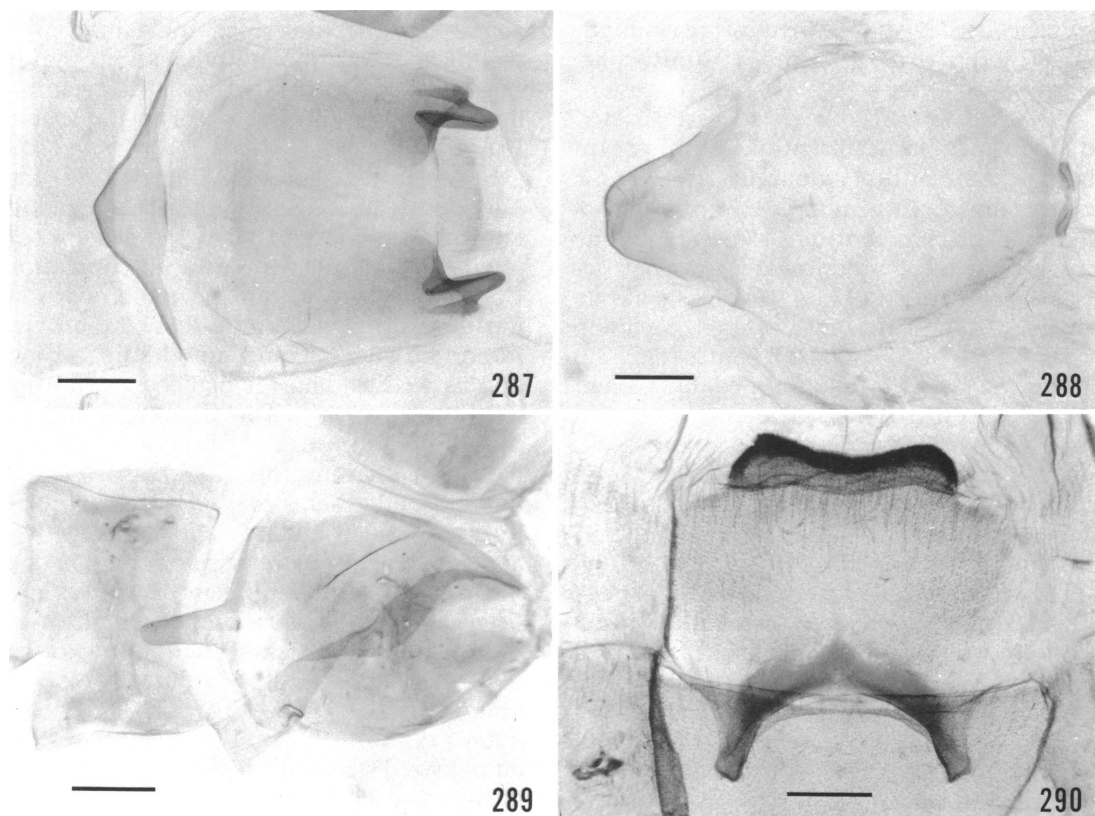
The taxonomic distribution of this structure has made its use in notodontid classification problematical. Among my list of exemplars, a cteniophore occurs in *Heterocampa* species, *Schizura biedermani* (fig. 282; but not *S. unicornis*), *Lochmaeus bilineata*, and *Spatalia jezoensis*, all belonging to the Heterocampinae. The structure occurs throughout the genus *Spatalia* (van Eecke, 1930). However, the cteniophore can be present or absent in what otherwise appear to be closely related taxa. For example, one occurs in *Heterocampa* males but not in *Macruracampa*. Based on other characters, these genera are very close. It is perhaps because of such problems that most previous workers, including Forbes (1939a, 1948), chose to ignore the character completely. Jordan (1923a) and Weller (1989) noted that the cteniophore of *Hapigia*, purportedly a member of the Hemiceratini (Forbes, 1939a), is highly developed. The structure occurs in members of *Farigia* Schaus (Thiaucourt, 1988b), a Neotropical heterocampine, and Jordan (1923a) and Holloway (1983) have reported it in some Oriental *Phalera* species. A cteniophore is not present in the phalerines I examined.

If Jordan's observations are correct, the cteniophore evolved at least three times within the Notodontidae. Further study may reveal associated characters, such as glands or male scent chemicals, and perhaps the distribution of these will be more informative.

Jordan (1923a) described male hind wing scaling and venational modifications that he suggested are associated with the cteniophore, but none of these occur in the species I studied.

Segment 8: I showed (Miller, 1988a) that Notodontidae are unusual among Lepidoptera because males of many species use segment 8 to grasp the female during copulation. Concordant with this are the numerous modifications of male sternum 8. These provide important characters in notodontid taxonomy, as well as data for higher classification (Holloway, 1983). The thaumetopoeines, most notodontines, and *Clostera* have a simple eighth sternum (figs. 283, 284), whereas in almost all other subfamilies there are variously modified anterior apodemes, as well as developments on the posterior margin (figs. 285–295) of sternum 8. These characters have been used by various workers to diagnose notodontid species and genera (e.g., Forbes, 1948; Kiriakoff, 1970b; Mutuura, 1973; Nakamura, 1974, 1976a, 1976b; Thiaucourt, 1984, 1988b, 1988c). Franclemont (1946) emphasized sternum 8 differences as a means to distinguish species of *Symmerista*, and I have used them to separate species in the Dioptinae (Miller, 1987a, 1989). Kitching (1988) and Holloway (1989) have shown that the male eighth segment provides diagnostic characters useful at the species and supra-generic levels in many noctuid subfamilies.

Character 70. Anterior Apodemes on Male Sternum 8. The anterior apodemes on male sternum 8, a derived character among Notodontidae, are probably sites of muscle attachment. The muscles may assist in pulling the female abdomen into that of the male during copulation (see Miller, 1988a). I recognized four character states involving these apodemes. Their absence in notodontids (fig. 284) is plesiomorphic. When present, the anterior apodeme can be a single narrow or broad projection (figs. 287–289; scored as "1") or it can be bifid (Weller, 1989; figs. 290, 292; scored as "2"). A single apodeme occurs in species representing most notodontid subfamilies, including the Notodontinae, Phalerinae, Heterocampinae, Nystaleinae (fig. 287), Dioptinae (figs. 288, 289), and Dudusinae. Double apodemes, almost equally scat-



Figs. 287–289. Sternum 8 of male Notodontidae in ventral view with anterior at left. **287.** *Hippia packardii* (0.75 mm). **288.** *Zunacetha annulata* (0.5 mm). **289.** *Erbesia glaucaspis* (0.75 mm). Scale lengths in parentheses.

Fig. 290. Sternum 8 of *Harpyia microsticta* in ventral view with anterior at bottom. Scale line = 0.75 mm.

tered in distribution, are found in the Notodontinae (Pierce and Beirne, 1941), the Heterocampinae (fig. 290), and *Gargetta*. Presence of double apodemes is characteristic of Clade 24 in the Phalerinae (fig. 292). Many heterocampines have a broad apodeme on S8, sometimes medially emarginate, with two foveae along the anterior margin (fig. 291; and figures in Forbes, 1948). This state was scored as “3”.

A pair of long anterior apodemes occurs on S8 in males of two outgroup species, *Nycteola* and *Nola*, but they are not homologous with the apodemes in Notodontidae. All other taxa in the outgroup list lack apodemes. Mitter and Silverfine (1988) described similar modifications of male sternum 8 in some Catocalinae (Noctuidae), but again these are not homologous with the structures described here.

Character 71. Medial Pits on Male Sternum 8. Forbes (1939a, 1948) listed the presence of paired pits on male sternum 8 in his diagnoses of both the Heterocampinae and Phalerinae, and speculated (1948) that the character might indicate a close relationship between the two groups. I regard the sternal pits of Heterocampinae (figs. 286, 291) and Phalerinae (fig. 292) to be nonhomologous, based on differences in both their position and shape. Paired invaginations occur on S8 of *Spatalia jezeonsis* (fig. 286), a basal member of the Heterocampinae (fig. 100). Torre and Alayo (1959) showed that they are present in members of the Neotropical genus *Disphragis* Hübner.

These pits can be either present or absent in species that otherwise seem to be closely related. For example, they are present and absent within the genus *Heterocampa* (Forbes,

1948) as currently defined (Franclemont, 1983). The pits are obviously involved with copulation, but their precise function is unknown.

Character 72. Posterior Margin of Male Sternum 8. The most dramatic modifications of male sternum 8 involve its posterior margin. Like the male genitalia proper, differences can often be used to separate species; two closely related species of *Cnethodonta*, *griseus* (Staudinger) and *japonica* Sugi, can easily be separated by the shape of the posterior margin on male sternum 8 (Sugi, 1980). I did not attempt to use all observable variation, but instead tried to categorize the study species into one of three basic groups. First are those with the posterior margin of S8 unmodified (fig. 284). The second character state I recognized includes species having the posterior margin of S8 sclerotized with a deep notch (figs. 285, 287, 292). Third were species with the margin sclerotized, but without a notch (fig. 288). The posterior margin of S8 in *Hemiceras bilinea* has, instead of a notch or sclerotized portion, a long medial strap projecting into the intersegmental membrane. I did not score this autapomorphy, but instead gave *H. bilinea* a "?" score.

Forbes (1939a, 1948) divided the Notodontidae into two groups, the Pygaerinae without a posterior notch and the rest of the family with a notch. He implied that pygaerines are the plesiomorphic sister group of all other notodontids. He did not discuss the Thaumetopoeinae, but I found that their male S8 is unmodified. My results (fig. 99) therefore roughly corroborate those of Forbes.

Character 73. Internal Apodeme on Male Sternum 8. A separate character was recognized for *Stauropus*, which has a long internal apodeme arising from the medial portion of S8 (fig. 293). This does not appear to be homologous with the paired pits described above. Pierce and Beirne (1941) and Tikhomirov (1979, 1981) noted that all aspects of the male genitalia in *Stauropus* are complex and difficult to homologize with other species. Male genitalic musculature of *Stauropus fagi* was described by Tikhomirov (1979).

Character 74. A8/A9 Intersegmental Membrane Long. The membrane between segment 8 and the genitalia (segment 9) can be extremely long in notodontid males (fig. 296).

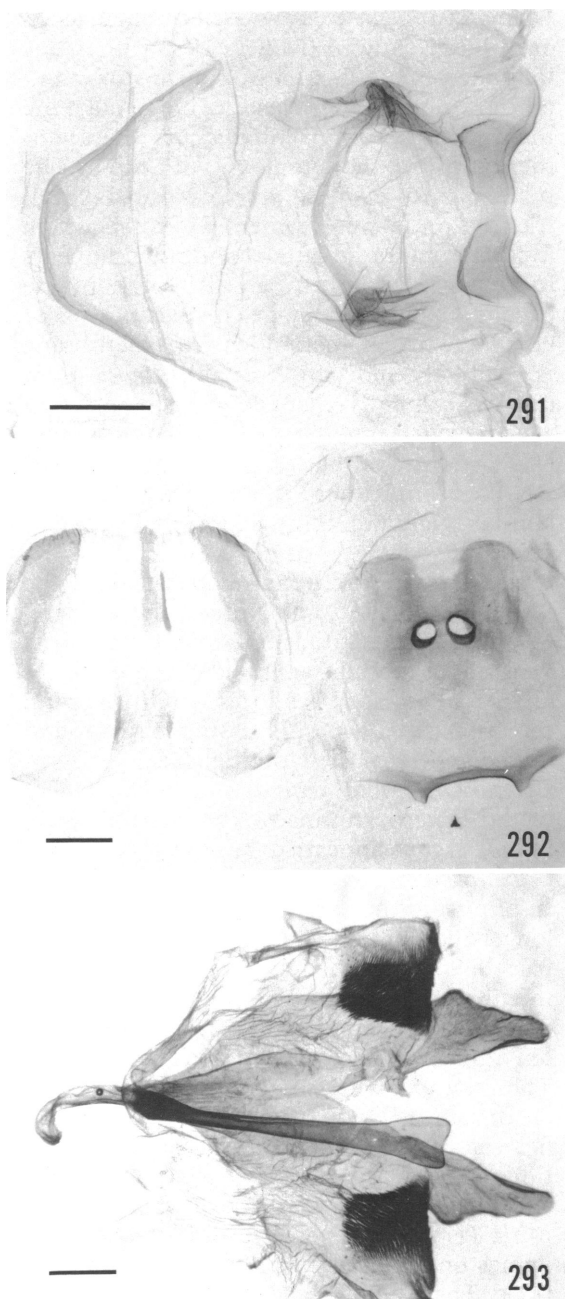


Fig. 291. Male sternum 8 of *Macrurocampa marthesia* in ventral view, anterior at left. Scale line = 1.0 mm.

Fig. 292. Male tergum 8 (left) and sternum 8 (right) of *Datana ministra* showing medial pits. Scale line = 1.0 mm.

Fig. 293. Male sternum 8 of *Stauropus fagi* in ventral view, anterior at left. Scale line = 1.0 mm.

Using *Cyanotricha necyria* (Dipterinae) as an example, I showed (Miller, 1988a) that this long membrane facilitates a means of copulation whereby, after clasping the female, the male withdraws its genitalia into the abdomen, drawing the female in with them. The male eighth segment applies dorsoventral traction on female segment 7. Presence of a long 8/9 intersegmental membrane appears to be a synapomorphy for all Notodontidae except Thaumetopoeinae. It does not occur elsewhere in the Noctuoidea. This membrane is relatively short in *Doa* and *Oenosandra* (fig. 295). A convergent case was reported in *Acrocercops* (Gracillariidae) by Kumata et al. (1988). Males of that genus exhibit notodontid-like modifications of segment 8 and have similar genitalic androconia as well (see Character 91).

There is an additional elaboration of the 8/9 membrane in some Notodontidae. Here, the membrane is longer dorsally than it is ventrally. When the genitalia of these species are extruded, they are oriented in a ventral direction (fig. 297). This apomorphy is found in two genera of the Notodontinae (*Liparopsis* and *Quadricalcarifera*) and in two genera of the Heterocampinae (*Harpyia* and *Stauropus*). It thus appears to have evolved twice.

Character 75. Length of Male Tergum 8. In almost all notodontids, male tergum 8 is longer than tergum 7 (figs. 296, 297). This is true of species with a long intersegmental membrane (Character 74) and a highly modified eighth sternum (Characters 70–72). The only groups where it does not occur are the Thaumetopoeinae, Scranciini, and *Goacampa variabilis* (Dudusinae). Again, this modification may be related to the holding function of segment 8 during copulation.

Character 76. Anterolateral Apodemes on Male Tergum 8. There are anterolateral apodemes on male tergum 8 in some Notodontidae. These apodemes occur in three groups: in some species of Notodontinae, in all Dudusini, and in *Hemiceras* (fig. 294). The trait has therefore evolved a least three times in the family.

Character 77. Terminal Scale Tuft. Previous authors have discussed the tuft of long scales arising from the terminal abdominal segments of some Notodontidae (e.g., Moore, 1882; Schaus, 1901; Marumo, 1920; Forbes,

1939a). I tried to refine the definition of this character. I recognized four character states. The plesiomorphic state is absence of a terminal scale tuft. Almost all notodontids, however, exhibit some type of terminal tuft. If the terminal scales are long and hairlike with simple apices, as for example in *Clostera albosigma* (fig. 298), I scored the character as "1". Although tufts are more prominent in some, this state was found in the vast majority of notodontid species. A third state, restricted to the Heterocampinae and Nysaleinae, applies to taxa with the scales arranged in a compact tuft that curves downward. Finally, members of Clade 31 in the Dudusinae have a terminal tuft composed of long, pedicellate scales with spatulate apices (fig. 299). Previous authors noted this trait in *Crinodes* (Forbes, 1939a; Torre and Alayo, 1959) and *Tarsolepis* (Marumo, 1920; Matsumura, 1929b), but none considered it evidence of shared common ancestry.

The function of this terminal scale tuft is unknown. Although not as well developed, it occurs in females as well and could not, therefore, be androconial. Kitching (personal commun.) noticed that when these moths are at rest the abdomen is curved up and the tuft is directed dorsally. He suggests that it may function as camouflage.

I studied scale shape, but not the shape of the tuft itself, which also seems to vary. Species such as *Spatalia jezoensis* (fig. 21), *Schizura beidermani* (fig. 39), and others (Schaus, 1901) have a distinctly bifid tuft.

Genitalia: Male genitalia are subject to the same problems of homology interpretation as female genitalia; differences are invaluable for distinguishing between species, but useful synapomorphies are difficult to identify. For that reason I have not emphasized male genitalic characters. I tried to focus on features that are phylogenetically conservative and those that might represent major evolutionary innovations. There are few studies on the Notodontidae in which genitalic morphology has been used except in a descriptive context, a noteworthy exception being the work of Weller (1989).

Character 78. Presence of Socii. Socii are paired setose structures located at the base of the uncus (figs. 300–303). Pierce and Beirne (1941) suggested that they may be a form of

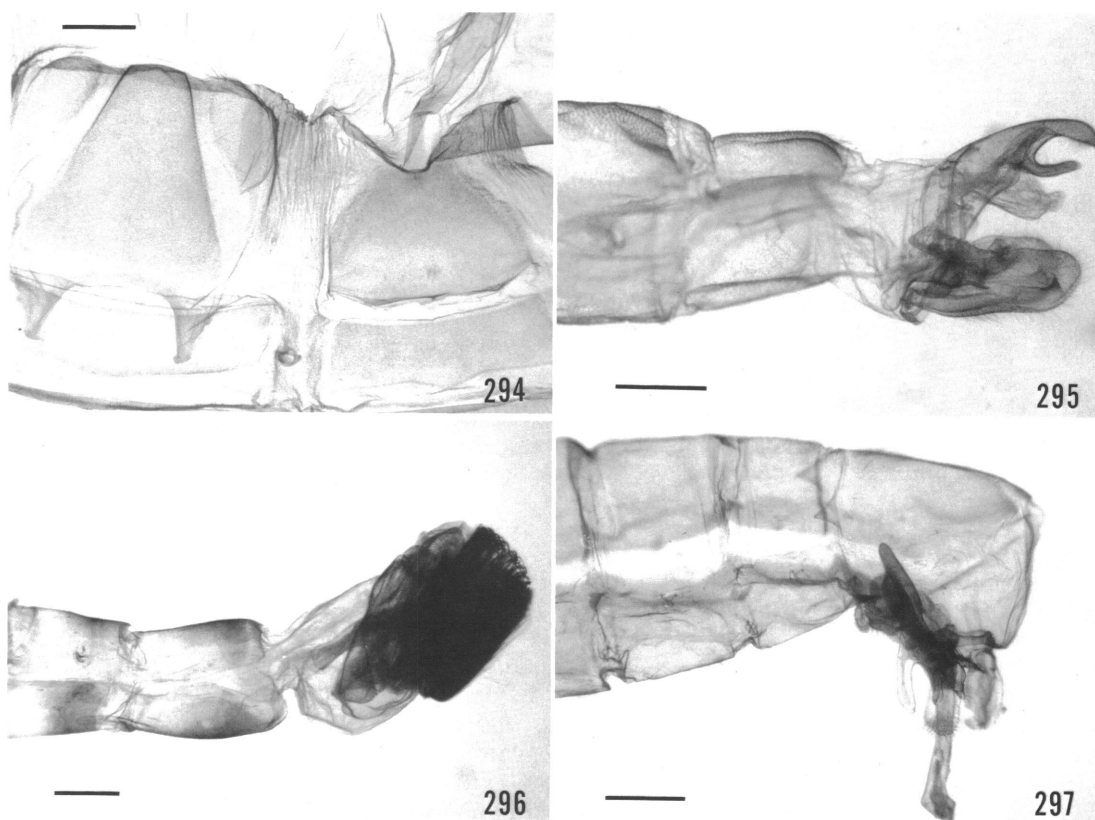


Fig. 294. Male tergum 8 (left) and sternum 8 (right) of *Hemiceras bilinea* (anterior at bottom), showing anterolateral apodemes on T8. Scale line = 1.0 mm.

Figs. 295–297. Terminal abdominal segments of male Notodontidae (lateral view, anterior at left). 295. Segments A7 and A8 and genitalia of *Oenosandra boisduvalii*. 296. Segments A7 and A8 and genitalia of *Erbesa glaucaspis*. 297. Segments A6, A7, and A8 and genitalia of *Liparopsis postalbida*. Scale line = 1.0 mm.

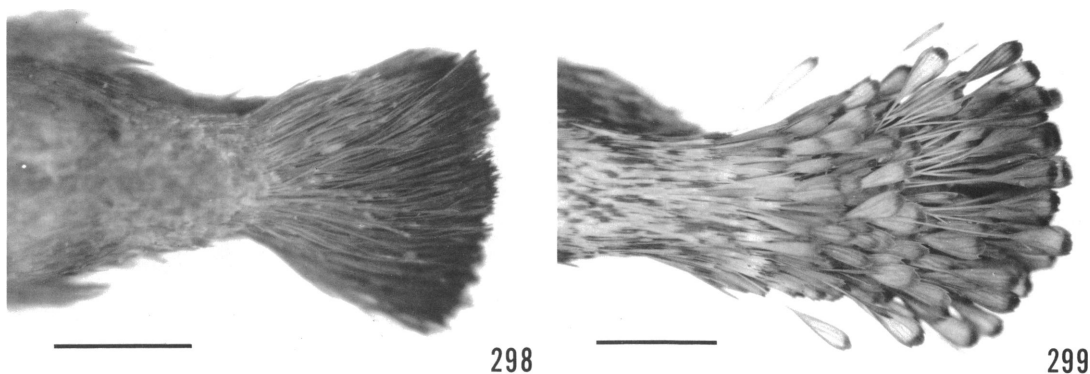
gnathos, and Tikhomirov (1979, 1981) called them together the “gnathos.” However, application of the two terms has historically been confusing. Similarly located structures have been called socii or gnathi in many families of Lepidoptera (Pierce, 1914; Klots, 1970).

Tikhomirov (1979, 1981) presented critical evidence that the socii of Notodontidae are not homologous with structures in other Lepidoptera. In Noctuidae, muscle M1 originates on the tegumen and inserts at the base of the uncus (Forbes, 1939b). Tikhomirov (1979) discovered that, unlike other Lepidoptera, M1 in Notodontidae inserts instead on the socii. He proposed this trait as a synapomorphy for the family (Tikhomirov,

1981). Following Tikhomirov’s hypothesis, I consider presence of socii in Notodontidae to represent a derived state.

Socii exhibit tremendous interspecific shape variation, but they are of almost universal occurrence within the Notodontidae. They do not occur in quadrifid noctuid groups (e.g., fig. 312; see also Pierce, 1909; Pierce and Beirne, 1941; Oseto and Helms, 1976).

Socii are present in all thaumetopoeines (figs. 313, 314). Interestingly, the male genitalia of *Oenosandra boisduvalii* exhibit socii (figs. 295, 310, 311). *Doa* is problematical. The male genitalia of *D. ampla* (fig. 305) have a structure arising from the base of the uncus composed of two thin straps that are joined medially. Because of its shape, most lepidop-



Figs. 298, 299. Terminal scale tuft of male Notodontidae in dorsal view, anterior at left. 298. *Clostera albosigma* (1.0 mm). 299. *Crinodes besckei* (2.0 mm). Scale lengths in parentheses.

terists would probably call this structure a gnathos rather than socii (see Character 83). Instead, I scored *Doa* as a question mark for Character 78 (Appendix II). Based on this set of interpretations, the socii of *Oenosandra* and Notodontidae are homologous and their presence is a synapomorphy for Clade 1 (fig. 99), the trifold Noctuoidea.

In two notodontine genera, *Gluphisia* and *Quadricalcarifera*, the socii are fused into a single process (fig. 318). I regarded this as a separate character state. Furthermore, the socii appear to have been lost in some species, including *Liparopsis postalbida* (figs. 297, 333) and *Scrancia stictica* (fig. 309).

Character 79. Uncus/Socii Joint Fused. Almost all noctuoids have the uncus and tegumen separated by a distinct suture, with the uncus capable of downward movement on this joint. In notodontids, the entire uncus/socii complex is movable and the uncus is inserted dorsally between the female papillae anales during copulation (Miller, 1988a). A few species among my study sample lack the suture. In these, the uncus and socii are fused with the tegumen. The apomorphic state (fused) evolved at least twice within the ingroup: in *Anaphe panda* (fig. 313) and in the Scranciini (fig. 309). According to Weller (1989), this character shows variation in the Nystaleinae, even within the nystaleine genus *Calledema* Butler. Among outgroup species, the derived state occurs only in *Oenosandra* (figs. 310, 311).

Character 80. Uncus with an Apical Notch. I did not attempt to describe all possible variation in uncus shape. Only two characters were used. The uncus is typically acute distally, although many exceptions exist. I scored as derived an uncus, exemplified by that of *Gluphisia septentrionis* (fig. 318), that is spatulate distally with an apical notch. In addition to *G. septentrionis*, the apomorphic state occurs in *Odontosia elegans* (fig. 319) and in species of *Pheosia* (Pierce and Beirne, 1941), all of which are members of the subfamily Notodontinae.

Character 81. Uncus Large and Triangular. Species in Clade 24 (Phalerinae in the restricted sense) have a characteristic uncus shape. It is large, triangular, and fused with the socii (fig. 320). In addition to *Antheua simplex*, *Phalera bucephala* and *Datana ministra*, this condition is found throughout the genus *Datana* (Forbes, 1948) and in other *Phalera* species as well (e.g., see figures in Kiriakoff, 1967; Nakamura, 1974, 1976a; Holloway, 1983; de Freina and Witt, 1987).

Character 82. Uncus with Ventral Prongs. Although the adult moths of *Crinodes besckei* and *Cargida pyrrha* are superficially very different (figs. 49, 52), their male genitalia are remarkably similar. An obvious similarity is the uncus shape, with a pair of ventral prongs at its base and a ventrally directed brush of setae (figs. 301, 321). The prongs are in addition to, not homologous with, socii. This shape was not observed in other species.

Character 83. Presence of a Gnathos. A gnathos is usually defined as a pair of processes arising from the tegumen below the uncus (Klots, 1970). The arms are often fused medially. Michener (1952) discussed confusion between the terms gnathos and transtilla as they are applied to the Saturniidae. Structures termed gnathi (also the "subscaphium" of Pierce [1909]) are found throughout the Lepidoptera, including some butterfly families and the Tortricidae (Klots, 1970). As so defined, a gnathos does not occur among the ingroup, but in the outgroup one can be found in *Dasychira*, *Nycteola*, *Acronicta*, *Panthea*, and *Alypia*. Such a distribution suggests that the gnathos is not homologous in these taxa.

Character 84. Tegumen Narrowed Dorsally. Among the nystaleines I examined, four (*Nystalea nyseus*, *Symmerista albifrons*, *Didugua argentilinea*, and *Hippia packardii*) exhibit a unique configuration of the tegumen. In these, the dorsal portion of the tegumen narrows, forming a "neck" to which the uncus/socii complex is joined (figs. 302, 324). This trait was discovered by Weller (1989), who figured additional taxa and further documented its distribution within the Nystaleinae (see also figures in Torre and Alayo, 1959).

Character 85. Presence of Penicilli. Penicilli ("peniculi" of Pierce, 1909) are setose lobate extensions on the ventral portions of the tegumen (Forbes, 1954; Klots, 1970). They occur in many Noctuidae, but I have not seen the presence of penicilli used as a higher classification character for the family. Among the noctuids in my outgroup sample, penicilli occur in *Acronicta*, *Alypia*, and *Diloba*. In *Peridroma saucia* (fig. 312) and in the genus *Euxoa* (Lafontaine, 1987), nonsetose lobes, perhaps homologous with penicilli, occur.

Character 86. Transtilla Shape. The transtilla is formed by two transverse extensions, often straplike in shape, arising from the costal base of each valve and passing above the aedeagus (Michener, 1952). In many species the two extensions are joined medially in the diaphragma (e.g., fig. 303). This structure is said to occur throughout the Lepidoptera (Klots, 1970), but whether it is homologous in all cases is uncertain. Judging from its sim-

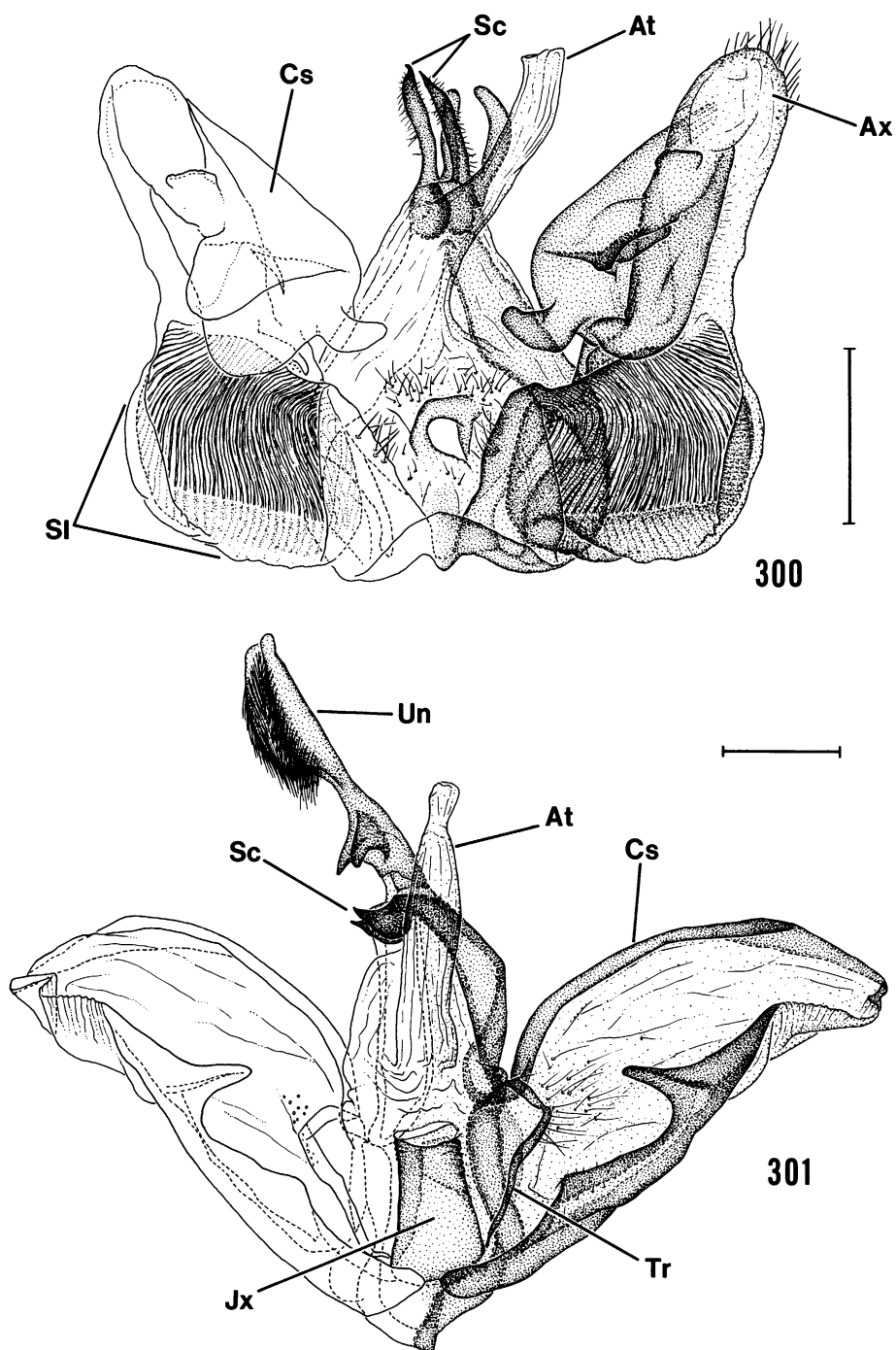
ilar shape and position among these groups, I suggest that the transtilla is homologous in much of the Lepidoptera.

Transtilla shape is extremely variable. For example, within the Dioptinae alone it ranges from thin in *Phryganidia* (Miller, 1987a) to a broad plate above the aedeagus in *Cyanotricha necyria* (Miller, 1988a). I used six character states in an attempt to describe structural variation in the transtilla. Two of these, scores "4" and "5" (below), are highly diagnostic for the Nystaleinae and Dudusinae, respectively. Other transtilla types were harder to define and proved to be of less taxonomic value.

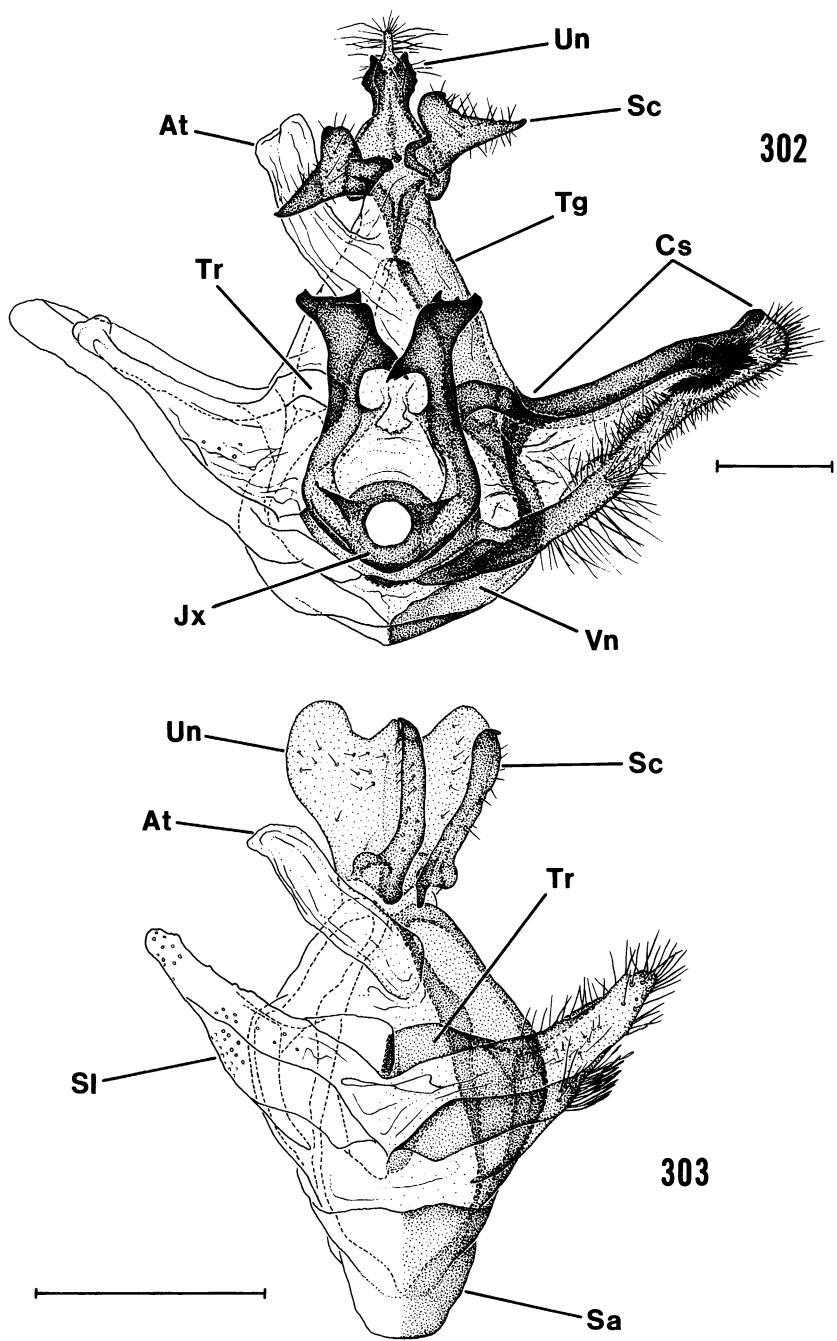
In the outgroup a transtilla is present in all but the two lymantriids. However, it can occur as one of two states: the plesiomorphic state (narrow bands joined medially above the aedeagus) or the derived state (scored as "1"), in which the bands are present but do not meet medially.

Among the ingroup species, I found complexity in transtilla morphology, as well as complexity in character state distribution. The plesiomorphic score (two bands joined above aedeagus) applies to all Dioptinae (figs. 303, 329, 330), as well as to individual species in the Thaumetopoeinae (fig. 313), Notodontinae, and Heterocampinae. The second state ("1") exhibits an equally scattered distribution. Absence of the transtilla (score of "2") is typical of many Notodontinae (figs. 318, 319, 322), Phalerinae, and Heterocampinae (fig. 327). A fourth state ("3" score) was observed in *Spatalia jezoensis* and *Heterocampa averna* (Heterocampinae). Here, there is a long, curved projection fused to the base of each valve (figs. 315, 325).

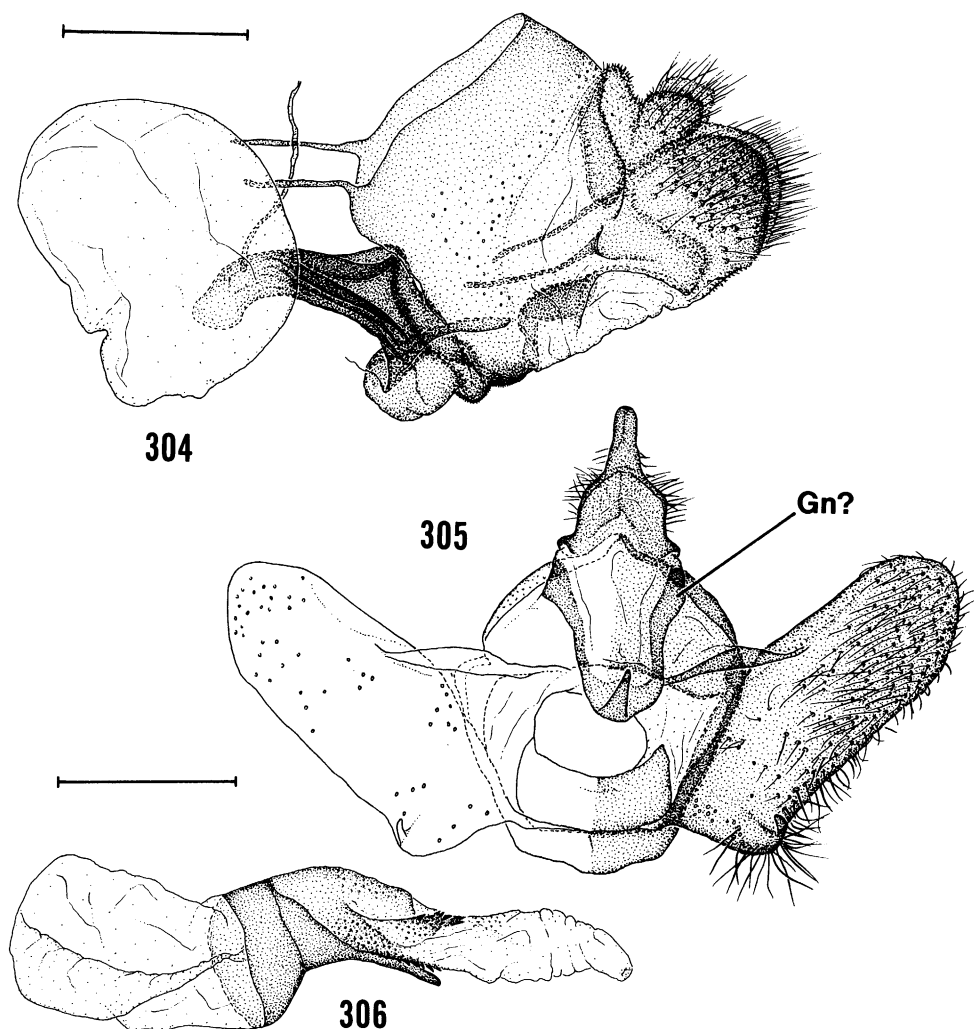
Two additional states provide reliable synapomorphies for the subfamilies in which they occur. Weller (1989, 1990) applied the term "costulae" to the long, horn-shaped projections arising from the base of each valve in Nystaleinae (fig. 324). These do not join above the aedeagus. Forbes used presence of the costula, which he described as "a large plate connected with costa of valve and sometimes inner face of valve and juxta" (1948: 206), to define the Nystaleini. Unlike the transtilla in *Heterocampa averna*, costulae appear to be articulated with the valval costa. Differ-



Figs. 300, 301. Male genitalia of Notodontidae in posterior view with aedeagus removed. **300.** *Hemiceras bilinea*. **301.** *Crinodes besckei*. At = anal tube. Ax = apex of valve. Cs = costa of valve. Jx = juxta. Sc = socii. SI = sacculus. Tr = transtilla. Un = uncus. Scale lines = 2.0 mm.



Figs. 302, 303. Male genitalia of Notodontidae in posterior view with aedeagus removed. 302. *Didugua argenteilinea*. 303. *Phaeochlaena gyon*. Sa = saccus. Tg = tegumen. Vn = vinculum. For other symbols see figures 300 and 301. Scale lines = 1.0 mm.

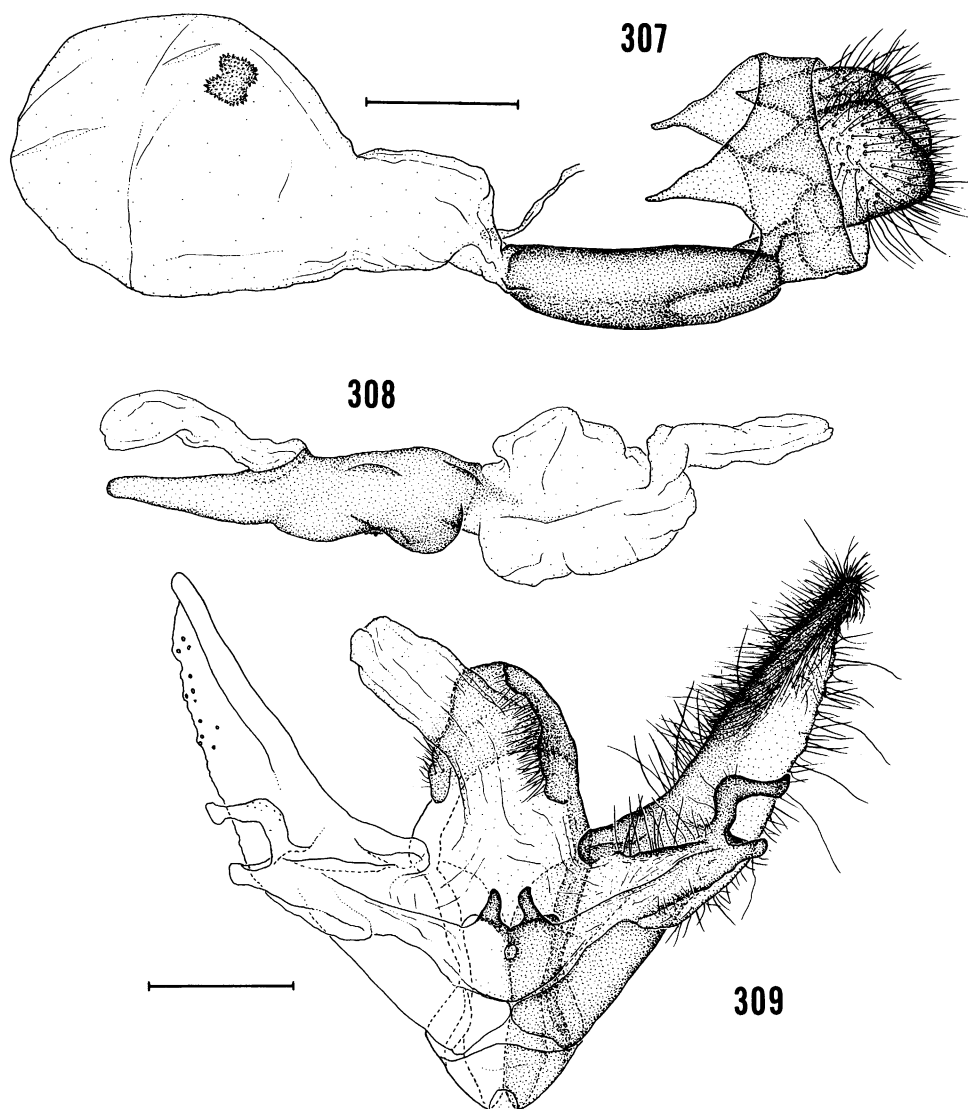


Figs. 304–306. Genitalia of *Doa ampla* (Doidae). 304. Female in lateral view, anterior at left. 305. Male in posterior view with aedeagus removed, showing a structure possibly homologous with the “gnathos” (Gn?). 306. Aedeagus in lateral view, anterior at left. Scale lines = 1.0 mm.

ences in costula shape provide species-specific characters in the Nystaleinae (Torre and Alayo, 1959; Todd, 1973; Weller, 1989, 1990). Among the nystaleines I studied, *Symmerista albifrons* lacks costulae, and I was unable to interpret the complex structure of *Didugua argentilinea* (fig. 302). It is possibly formed by fusion of the costulae and juxta (Forbes, 1948).

All taxa that I place in the Dudusini (Dudusinae) have a long thin strap arising from the valval costa and curving down to connect

on the ventral portion of the juxta. I interpret this structure as being homologous with the transtilla. It appears in all *Dudusa* and *Tarsolepis* species (see figures in Roepke, 1944; Holloway, 1983; Sugi, 1987b; Bänziger, 1988a), as well as in the New World taxa that I have placed in the Dudusini—*Crinodes* (fig. 301; see also Torre and Alayo, 1959), *Cargida* (fig. 321), and *Goacampa* (fig. 316). Based on figures in the literature, this feature is found in other notodontid genera, perhaps indicating the existence of a fairly large clade. Un-



Figs. 307–309. Genitalia of *Scrancia stictica* (Scranciini). 307. Female in lateral view with anterior at left. 308. Aedeagus in lateral view with anterior at left. 309. Male genitalia in posterior view with aedeagus removed. Scale lines = 1.0 mm.

fortunately, a similar morphology occurs in one notodontid not belonging to the Dudusini, *Fentonia ocypete* (fig. 317), which I place in the Heterocampinae. Other characters, particularly from the larvae, corroborate my placement of *F. ocypete*, so I must conclude that this type of transtilla arose separately in the two groups (fig. 100).

Character 87. Apical Portion of Valve

C-shaped. Valve shape is difficult to use as a taxonomic character. It is extremely variable, even among closely related species. One trait that appears frequently in Notodontidae is a valve with a C-shaped distal portion. Here, there is a medial costal process distally (perhaps homologous with the “projecting blade” of Nichols, 1989) and a valve apex that is expanded and often curved in a ventral di-

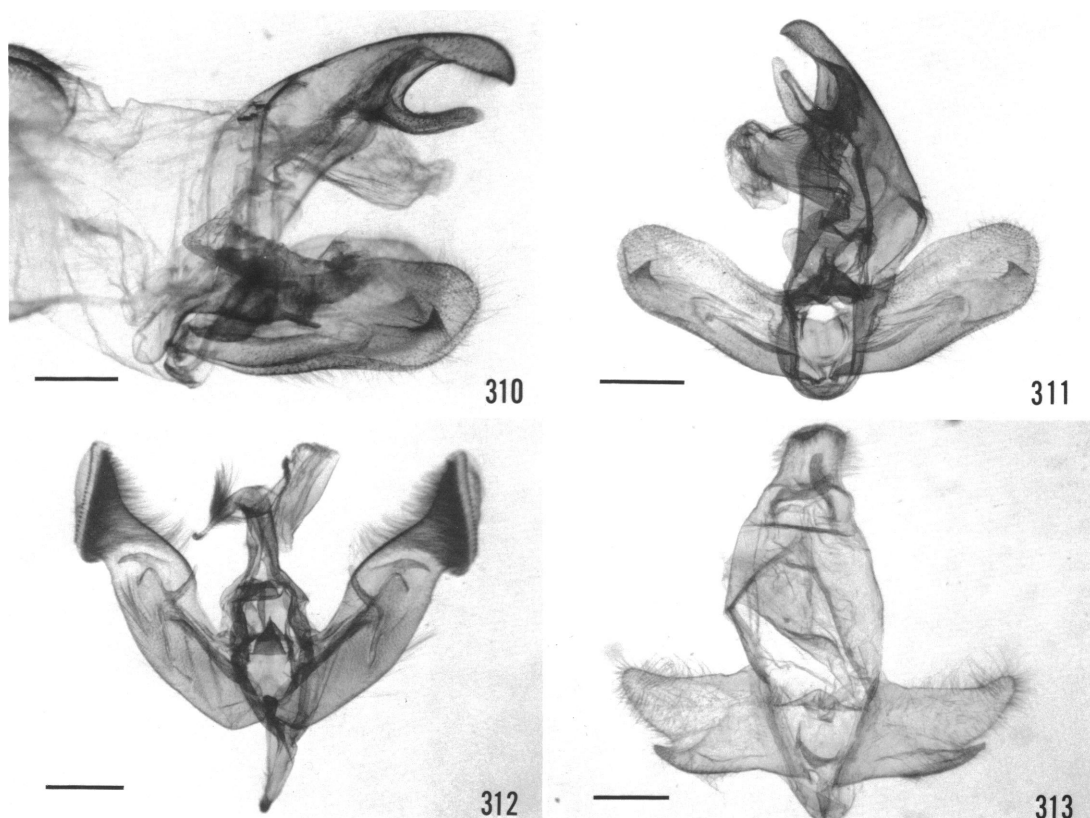


Fig. 310. Male genitalia of *Oenosandra boisduvalii* in lateral view, anterior at left. Scale line = 0.5 mm.

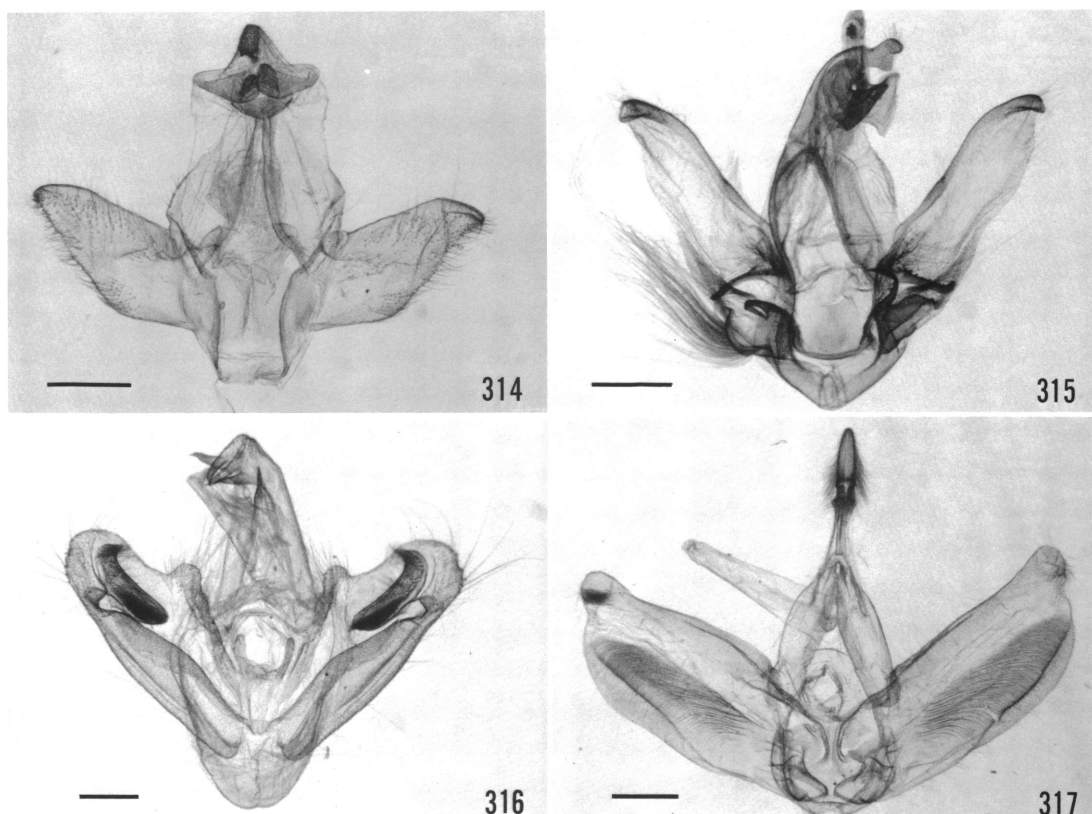
Figs. 311–313. Male genitalia of Noctuoidea in posterior view with aedeagus removed. 311. *O. boisduvalii* (0.75 mm). 312. *Peridroma saucia* (1.0 mm). 313. *Anaphe panda* (0.75 mm). Scale lengths in parentheses.

rection. These two features give the distal part of the valve a characteristic C-shape. Examples are the valves of *Peridea angulosa* (fig. 326) and *Macrurocampa marthesia* (fig. 327), members of different subfamilies.

Because of the variety of shape differences that can occur, scoring this character was difficult. I regarded the following species as having the derived state: *Datana ministra*, *Phalera bucephala*, *Antheua simplex*, *Nadata gibbosa*, *Peridea angulosa*, *Schizura biedermani*, *Macrurocampa marthesia*, and *Lochmaeus bilineata*. According to my subfamily definitions, therefore, the derived state is restricted to Heterocampinae and Phalerinae. Figures in Forbes (1948) and Holloway (1983) suggest that such valves occur in additional

Datana and *Phalera* species. This character could benefit from further refinement of its definition, but I am certain that it holds valuable phylogenetic information.

Character 88. Valve with a Basal Process. In *Notodonta* and related genera (Clade 14), as well as in *Ptilophora plumigera*, there is a distinctive process located at the base of the valve in the medial portion. In all cases it is flattened and setose (figs. 319, 322). Because of its relatively consistent shape and location, this structure is easily distinguished from other valval processes. I scored a second derived state, found only in *Spatalia jezoensis* among my species sample, where there is a large, pointed, sclerotized process at the base of the valve (fig. 315) in roughly the same



Figs. 314–317. Male genitalia of Notodontidae in posterior view with aedeagus removed. 314. *Thaumetopoea processionea* (0.5 mm). 315. *Spatalia jezoensis* (1.0 mm). 316. *Goacampa variabilis* (0.5 mm). 317. *Fentonia ocypte* (1.0 mm). Scale lengths in parentheses.

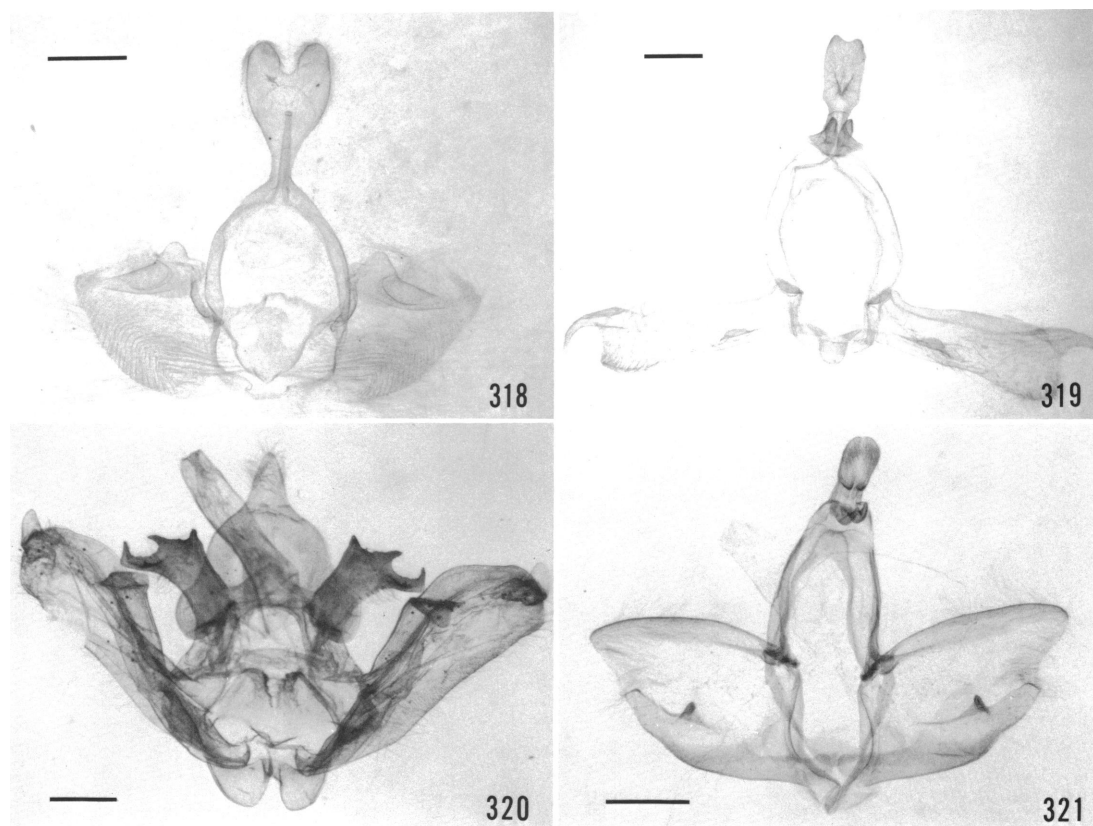
position as the structure found in *Notodonta*. The two types of processes are clearly not homologous.

Character 89. Distal Portion of Valve Bulbous. Another character state found in basal members of the Notodontinae involves the shape of the valve's distal portion. The derived state is presence of a sclerotized, bulbous, valval apex (fig. 322). This configuration is quite recognizable and appears to be fairly consistent. In addition to *Notodonta*, *Pheosia*, and *Ptilophora*, bulbous valval apices occur in *Nadata gibbosa*, apparently a separate derivation. A large number of other shapes occur in the family, but I did not attempt to characterize those.

Character 90. Central Portion of Valve Membranous. The male valve in some Dudusini has a characteristic shape. The valve

is broad and completely membranous in the central portion (figs. 301, 321). Its dorsal and ventral margins are lined by sclerotized bands, the ventral one usually with a projection about midway out. The valve apex in these species is simple and membranous with a fine series of folds. Among my study sample, the only species in the Dudusini that does not exhibit this type of valve is *Goacampa variabilis* (fig. 316).

Character 91. Sacculus Pleated. A remarkable genitalic modification found in Notodontidae is the pleated sacculus. Barth (1955) first described it in detail using *Hemiceras* (fig. 300) as his example. The organ is composed of a membranous sacculus, rather than a sclerotized one as occurs in other Lepidoptera (e.g., fig. 312), and a series of pleats that can unfold like an accordion. The pleats,



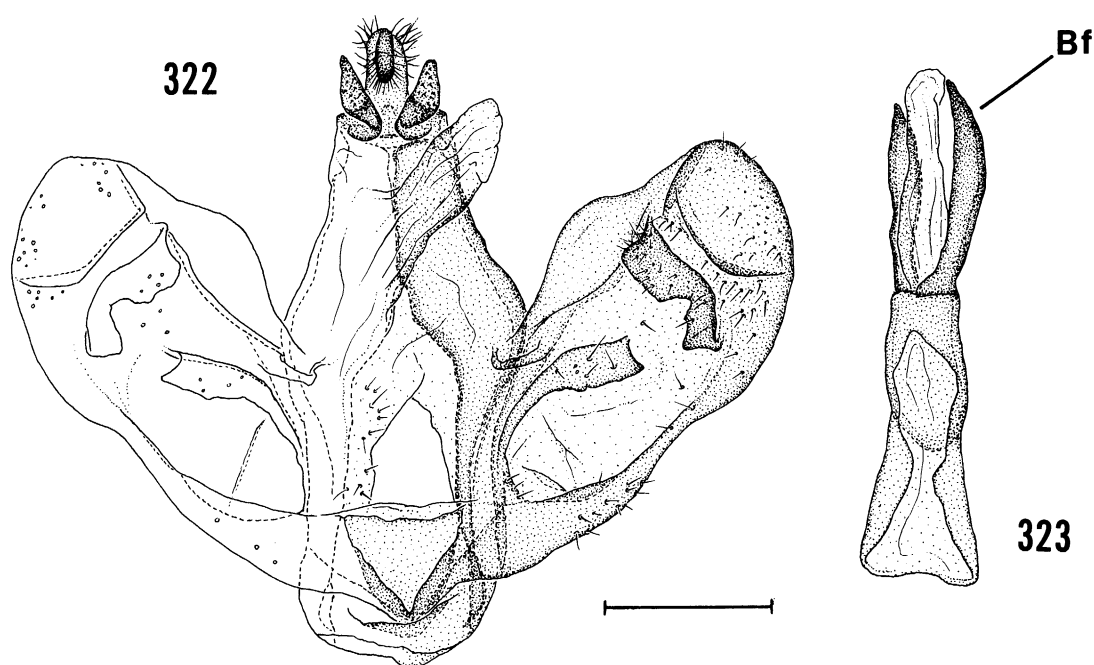
Figs. 318–321. Male genitalia of Notodontidae in posterior view with aedeagus removed. 318. *Gluphisia septentrionis* (1.0 mm). 319. *Odontosia elegans* (1.0 mm). 320. *Phalera bucephala* (1.0 mm). 321. *Cargida pyrrha* (0.75 mm). Scale lengths in parentheses.

which enclose long hairlike androconia (figs. 296, 329, 330), are thought to unfold during courtship, thus exposing these scent scales to the female (Barth, 1955; Weller, 1989). The pleated sacculus of notodontids has been discussed and figured by Forbes (1939a), Barth (1955), Franclemont (1970), Holloway (1983), Miller (1988a, 1989), Chistyakov (1989), and Weller (1989, 1990). All of these authors recognized the character as apomorphic for the Notodontidae, but the only one who used it to define higher group categories was Weller (1989, 1990).

Although the pleated sacculus has become modified in many ways within the Notodontidae, I chose to use a simple system of character states in an attempt to uncover broadly distributed synapomorphies. I was only marginally successful. I recognized four character

states of the sacculus (Appendix I). The plesiomorphic state, based on outgroup comparison, is obviously a sacculus without pleats. Ingroup taxa with a simple sacculus include the Thaumetopoeinae (figs. 313, 314) and most Notodontinae (figs. 319, 322). However, according to my analysis, complete loss of the saccular pleats has occurred in species belonging to almost every lineage of the Notodontidae.

Species, such as *Gluphisia septentrionis* (fig. 318) and *Zunacetha annulata* (fig. 329), in which the pleats are clearly present but the sacculus itself is not highly modified, were given a score of “1”. In some taxa, such as most Phalerinae (e.g., *Phalera bucephala*; fig. 320), the pleats are very faint and can be observed only by careful inspection. I scored this as “2”. A final character state (scored as



Figs. 322, 323. Male genitalia of *Ptilophora plumigera*. 322. Genitalia in posterior view with aedeagus removed. 323. Aedeagus in dorsal view, anterior at bottom, showing bifid distal portion (Bf). Scale line = 1.0 mm.

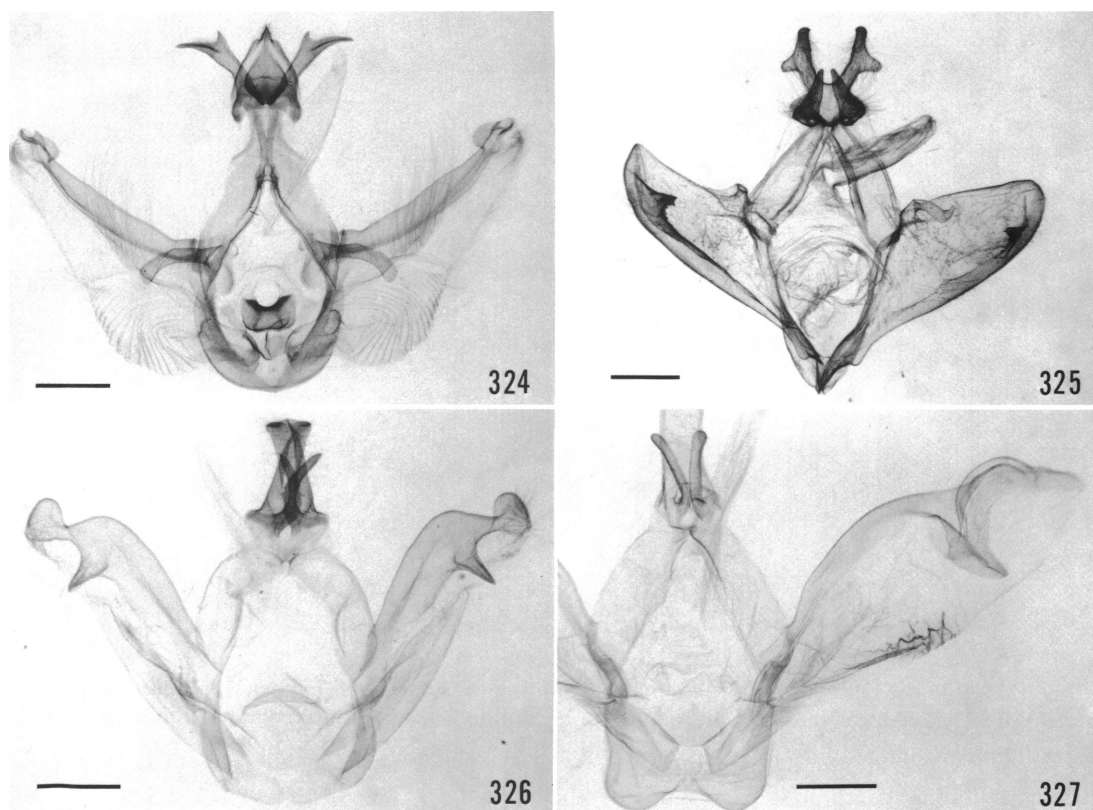
“3”) was applied to species in which the sacculus is huge and curls inward to enclose the pleats. Although in figure 300 I show the sacculus of *H. bilinea* in an expanded position, it is folded inward in its resting position. Weller (1989) restricted her definition of Barth’s Organ to a sacculus of the type found in *Hemiceras* (my state “3”). She argued that presence of Barth’s Organ is a synapomorphy for the Dioprinae (her Dioptrini) and Hemiceratina. I address this hypothesis in detail in my discussion on the status of the Hemiceratina.

Among the taxa I examined, the “3” score occurs only in species belonging to the Nystaleinae, the Dioptrinae (fig. 330), and the genus *Hemiceras*. It should be noted that relatively few dioptrines exhibit this type. Most have only moderately developed saccular organs (see fig. 329; also Miller, 1988a), and the pleats can be completely absent, as for example in *Phryganidia*, *Phaeochlaena gyon* (fig. 303), and others (Miller, 1987a, 1989). Many nystaleines, such as *Didugua argenteilinea* (fig. 302), also appear to have lost the saccular organs (discussed in Weller, 1989).

Valval androconia occur in other Lepidoptera. For example, in *Acrocercops* (Gracillariidae) long androconia are found laterally on the valves (Kumata et al., 1988). Based on my results and those of Weller (1989), Character 91 exhibits a large amount of homoplasy. Perhaps the chemicals associated with these saccular androconia will provide valuable data.

Character 92. Lateral Margin of Sacculus. In some species the sacculus projects from the valve’s lateral margin (e.g., fig. 324). This occurs in roughly the same species that possess Barth’s Organ (score of “3” for Character 91). However, it is also found in some Nystaleinae, such as *Symmerista* species, in which the saccular scent organ is only moderately developed. I recognized this by defining a separate character.

Character 93. Saccus Absent. According to Mehta (1933), the saccus, an internal extension of the ventral portion of the vinculum (Klots, 1970), is absent in notodontids (see also Miller, 1988a). Among outgroup taxa, the saccus is usually present as an elongate



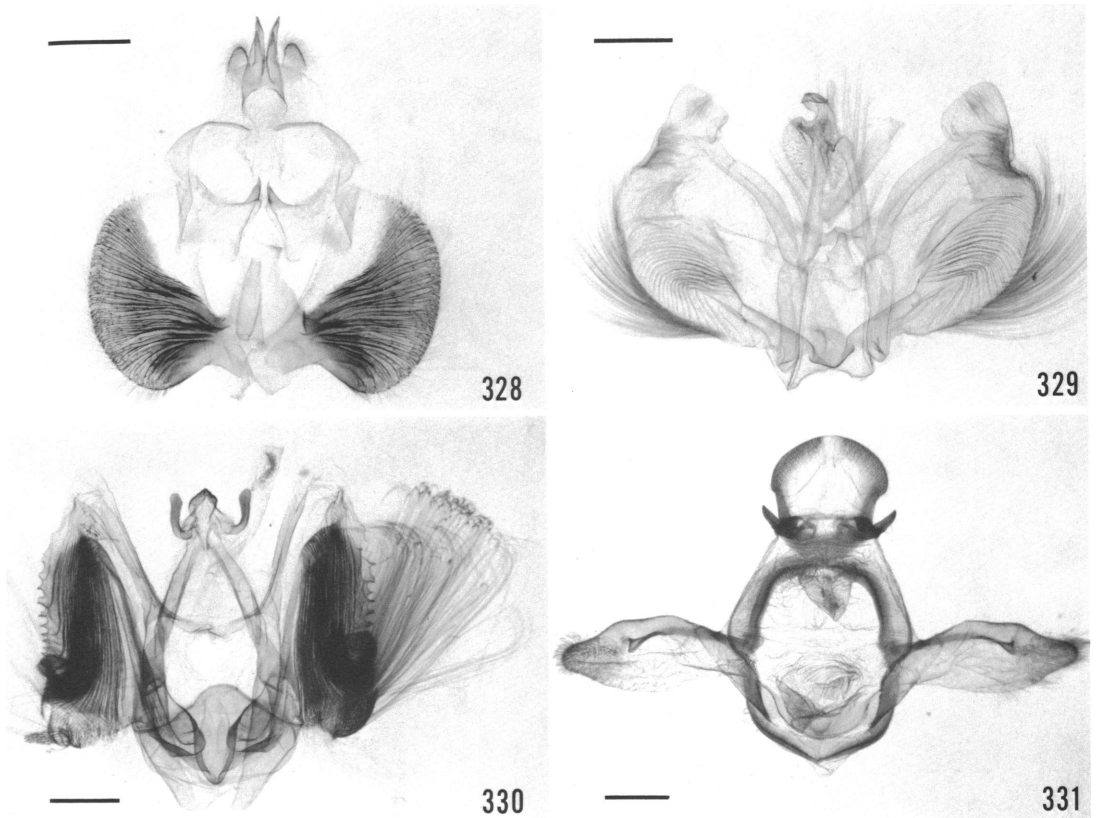
Figs. 324–327. Male genitalia of Notodontidae in posterior view with aedeagus removed. 324. *Hippia packardii*. 325. *Heterocampa averta*. 326. *Peridea angulosa*. 327. *Macrurocampa marthesia*. Scale lines = 1.0 mm.

structure (fig. 312). Absence of the saccus appears to be a derived character state uniting most of the Notodontidae. As a further refinement of this character, I recognized three states, the first (“0”) for species with a well-developed elongate saccus. An elongate saccus occurs sporadically within the ingroup. I observed it in one species of Thaumetopoeinae (*Epicoma tristis*), as well as in some Notodontinae (e.g., *Liparopsis postalbida*, fig. 333), Heterocampinae (*Cnethodonta grisea*, fig. 332), and Dudusinae (e.g., see figures in Roepke, 1944). Although I scored each of these as having the plesiomorphic condition, my analysis suggests that all represent separate derivations within the Notodontidae. Presence of the saccus is a synapomorphy for the genera *Liparopsis*, *Quadricalcifera*, and perhaps other close relatives that I did not examine (see figures in Nakatomi,

1980, 1981). The saccus is absent in *Doa ampla* (fig. 305) and *Oenosandra boisduvalii* (figs. 310, 311). Its loss is therefore an important synapomorphy for Clade 1 (fig. 99).

The third state (“2”) refers to notodontid species in which the saccus is essentially lost, but that region has a characteristic configuration. In these, what remains of the saccus is two shallow humps with a medial indentation. This apomorphy is found in phalerines (e.g., *Phalera bucephala*, fig. 320; *Peridea angulosa*, fig. 326) and three of my heterocampine exemplars (e.g., *Macrurocampa marthesia*, fig. 327).

Character 94. Manica Sclerotized. The manica is defined as that portion of the annular membrane where the aedeagus passes through (Nichols, 1989). The manica is attached to the aedeagus and holds it loosely in place. A unique condition occurs in the



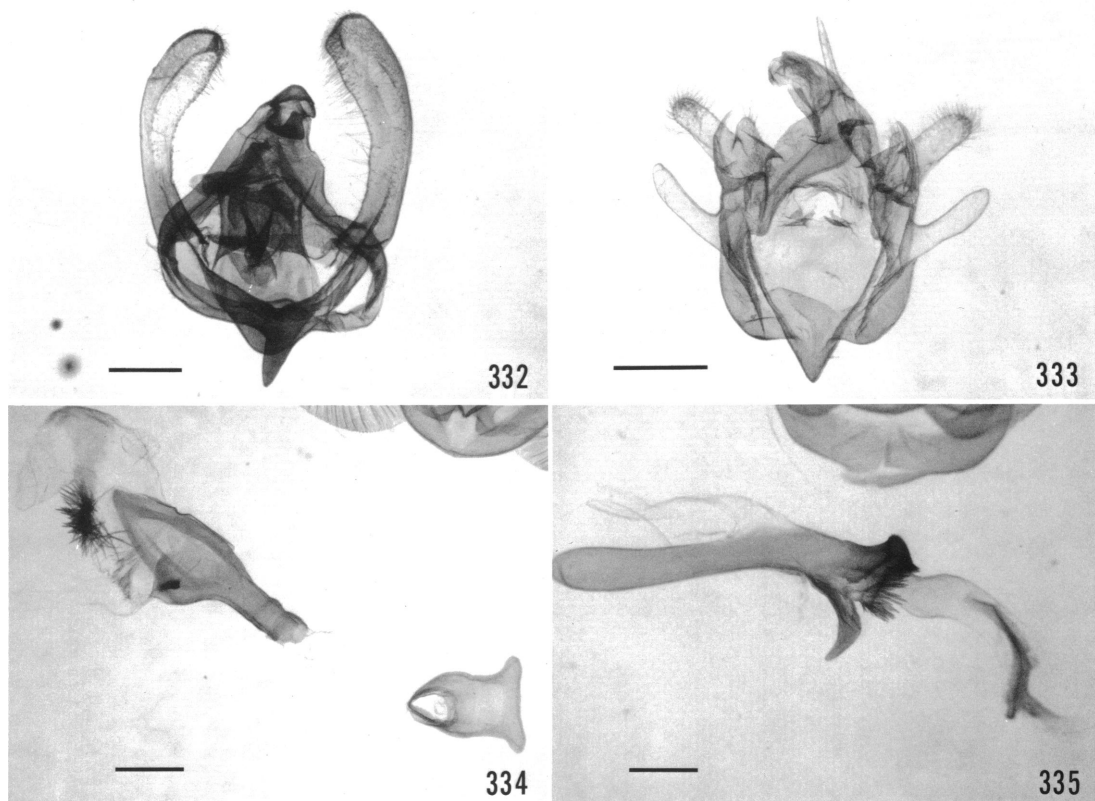
Figs. 328–331. Male genitalia of Noctuoidea in posterior view with aedeagus removed. 328. *Clostera albosigma* (0.75 mm). 329. *Zunacetha annulata* (0.75 mm). 330. *Erbesia glaucaspis* (0.75 mm). 331. *Harpyia microsticta* (1.0 mm). Scale lengths in parentheses.

Nystaleinae, where a heavily sclerotized manica is fused to the juxta, the two forming a single donut-shaped unit (figs. 302, 324). The aedeagus is held tightly in the diaphragma so that, when trying to remove the aedeagus during dissection, it must be broken in order to keep the juxta intact (fig. 334). This derived state was found in all the nystaleines I studied and, based on the figures in Weller (1989), may occur throughout the group.

Character 95. Shape of Aedeagus, Anterior. Not surprisingly, aedeagus shape is extremely variable among the study taxa. I attempted to define aedeagus characters so that each represents a basic structural difference rather than a subtle difference in shape. After lepidopteran genitalia are treated with potassium hydroxide, only the aedeagus, ductus ejaculatorius, and vesica remain. The ductus ejacu-

latorius is composed of a cuticular and a muscular portion (Callahan, 1958; Mitter, 1988), but the muscular portion dissolves during preparation.

I recognized five character states involving the anterior end of the aedeagus (Appendix I). The ductus ejaculatorius usually enters near the proximal end of the aedeagus (fig. 306). This is the type found throughout the out-group and I regarded it as plesiomorphic. In some species, the ductus is located more distally so that the aedeagus appears to have an anterior projection (e.g., fig. 335). For species with the latter configuration, I recognized four states. The anterior projection of the aedeagus frequently forms a long, simple, closed tube. This occurs in all Dudusinae (e.g., *Crinodes besckei*, fig. 336), in *Hemiceras* (fig. 341), as well as in various species of the Heterocampinae (fig. 335) and Notodontinae. A



Figs. 332, 333. Male genitalia of Noctuoidea in posterior view with aedeagus removed. 332. *Cnethodonta grisea*. 333. *Liparopsis postalbida*. Scale lines = 0.75 mm.

Fig. 334. Aedeagus of *Hippia packardii* in ventral view (distal portion at left) after removal from the manica and juxta. Scale line = 0.75 mm.

Fig. 335. Aedeagus of *Schizura beidermani* in lateral view with anterior at left. Scale line = 0.75 mm.

separate derived state was found in other notodontines, heterocampines, and all phalerines. Here, the anterior projection is membranous dorsally and roughly boat-shaped (fig. 342), rather than being a complete tube.

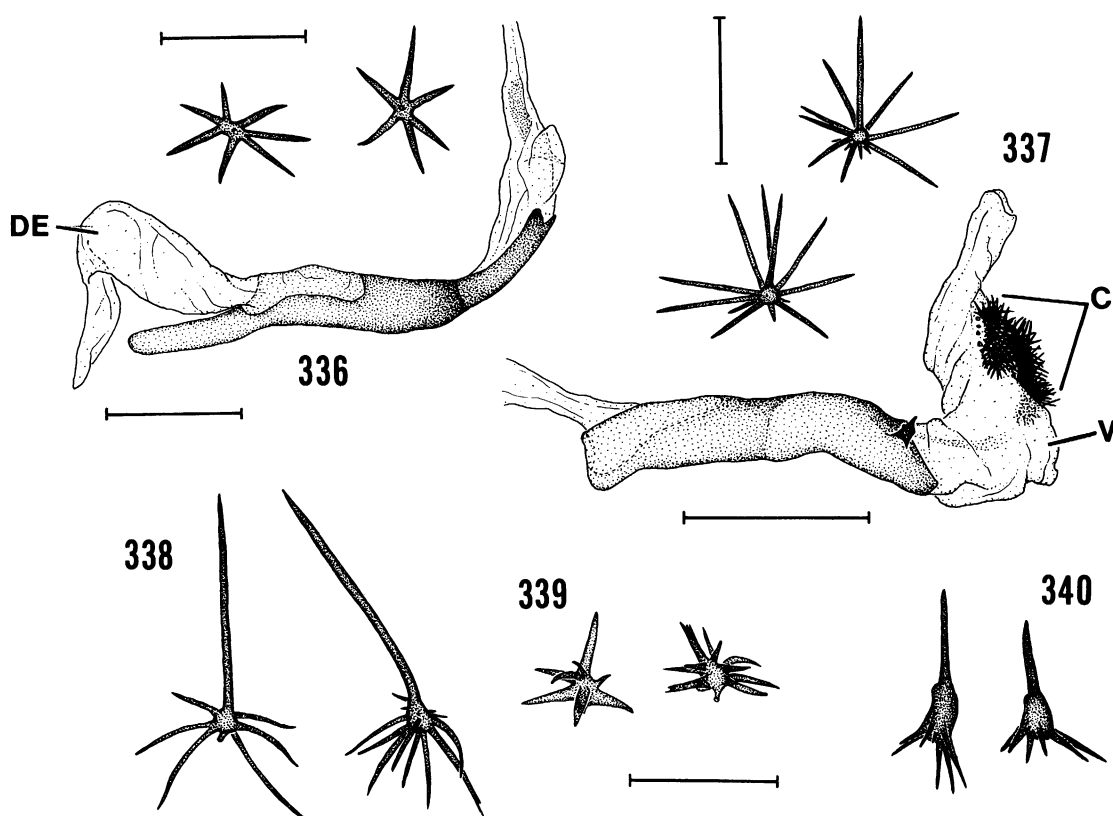
In Nystaleinae the anterior portion of the aedeagus has a unique configuration. It is broad, often with slight anterolateral projections (fig. 334), and is reflexed downward (fig. 343). Weller (1989) termed this structure the "callosum," and showed that it is a synapomorphy for 25 Neotropical genera, 18 of which she referred to the tribe Nystaleini. An analogous structure is found on the aedeagus of *Cerura liturata*.

A bulbous aedeagus (fig. 344) characterizes a large group of dioptine species related to

Josia (Miller, 1988a). The other dioptines in my species sample exhibit the plesiomorphic state for Character 95 (fig. 346).

Character 96. Aedeagus with Distal Spines. In several Notodontidae the distal portion of the aedeagus bears a patch of short spines. This occurs in two groups: Clade 19 of the Notodontinae (*Liparopsis* + *Quadricalcarifera*) and Clade 44 of the Heterocampinae (*Lochmaeus bilineata* [fig. 243 in Forbes, 1948] plus *Schizura beidermani* [fig. 335]). According to my analysis, the patch of spines has evolved separately in these two subfamilies.

Character 97. Shape of Aedeagus, Posterior. Beyond the few characters above, I made only a minor attempt to describe variation



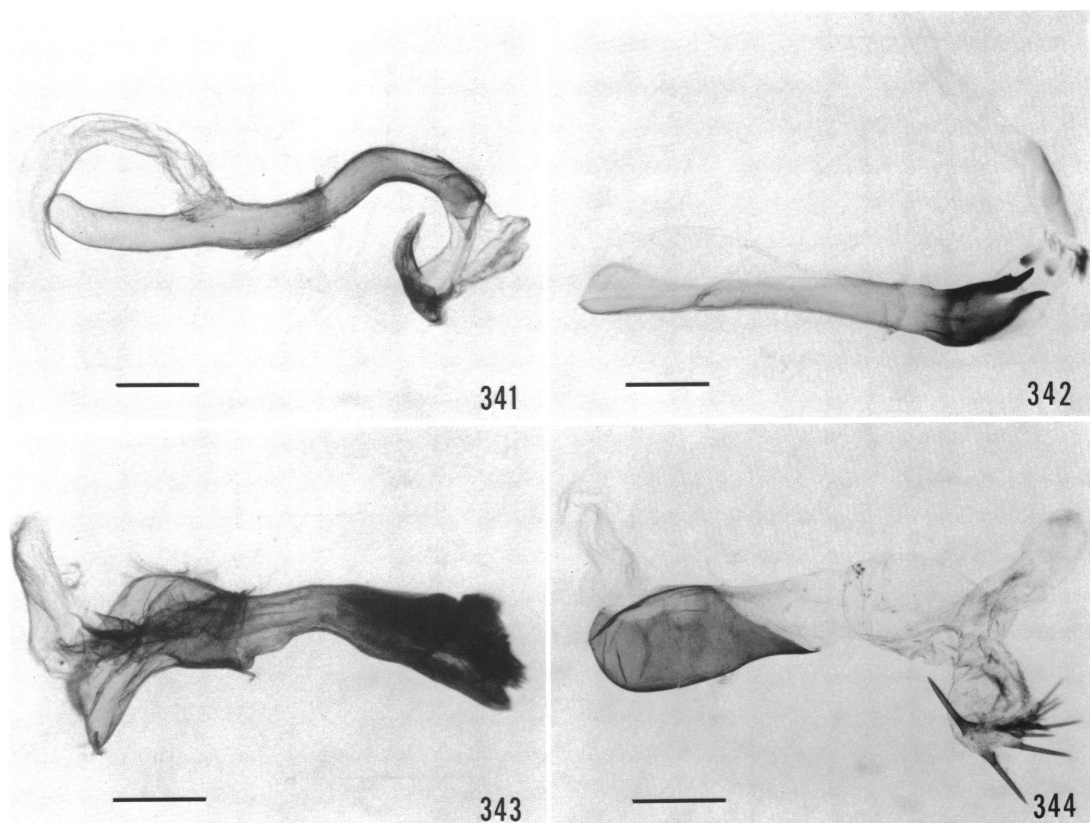
Figs. 336–340. Aedeagus and deciduous cornuti of Notodontidae. 336. *Crinodes besckei* aedeagus and cornuti (enlarged). 337. *Nystalea nyseus* aedeagus with deciduous cornuti still attached, and cornuti enlarged. 338. Cornuti of *Ellida caniplaga*. 339. Cornuti of *Antheua simplex*. 340. Cornuti of *Goacampa variabilis*. C = patch of deciduous cornuti. DE = ductus ejaculatorius simplex. V = base of vesica. Scale lines for aedeagi = 2 mm; for cornuti = 0.4 mm.

in aedeagus shape. I recognized three derived states for the distal portion of the aedeagus. In the first, the distal part is much wider than the middle. This characterizes the phallus of most nystaleine exemplars (figs. 334, 343), as well as that of *Ellida caniplaga*, a species I tentatively place in the Phalerinae. A second derived state is presence of a large ventral tooth on the aedeagus, found in the same two heterocampines, *Lochmaeus bilineata* (fig. 243 in Forbes, 1948) and *Schizura beidermani* (fig. 335), with the patch of spines on the aedeagus (Character 96). The final state applies to *Pheosia rimosa* and *Ptilophora plumigera* (Notodontinae), where the aedeagus is strongly forked distally (fig. 323; Pierce and Beirne, 1941).

Character 98. Vesica with Scobinate Cor-

nuti. There are innumerable modifications of the vesica among Notodontidae. I treated only those for which I have some confidence that the structures described are homologous. The proximal portion of the vesica in *Goacampa*, *Tarsolepis* (fig. 345), and *Dudusa* bears a patch of large scobinate cornuti. These have been figured by Roepke (1944), Holloway (1983), and Bänziger (1988a). Possibly, the scobinate patch is homologous in the genera above and represents a synapomorphy for the Dudusini (fig. 100) but was lost in *Crinodes* and *Cargida*. Two analogous cases occur, one in *Fentionia ocypte* and one in *Nadata gibbosa*.

Character 99. Stellate Deciduous Cornuti. Almost all Lepidoptera have some type of cornuti on the vesica of the aedeagus. Usually they are simple spinelike structures. An un-



Figs. 341–344. Aedeagus of Notodontidae in lateral view with anterior at left (vesica everted except fig. 343). **341.** *Hemiceras bilinea* (0.75 mm). **342.** *Macrurocampa marthesia* (1.0 mm). **343.** *Didugua argenteilinea* (0.75 mm). **344.** *Cyanotricha necyria* (0.75 mm). Scale lengths in parentheses.

usual character, widely distributed among notodontids, is the presence of deciduous stellate cornuti on the vesica (Forbes, 1939a; Pierce and Beirne, 1941; Franclemont, 1970; Holloway, 1983; Holloway et al., 1987; Weller, 1989). Outside of the Notodontidae, the only noctuid species where these are known is *Westermannia superba* Hübner (Noctuidae: Chloephorinae) (S. Sugi, personal commun.). These cornuti become detached during copulation and remain in the corpus bursae of the female (figs. 347, 348; Pierce and Beirne, 1941; Torre and Alayo, 1959). Their sharp points can sometimes be found lodged in the bursa membrane. The function of deciduous cornuti is unknown. Possibly they serve to break up the male's spermatophore, or perhaps, like the sphragis of butterflies, they discourage subsequent males

from mating. Among taxa with these structures, cornutus shape varies (figs. 336–340). In some cases shape differences might be useful in separating closely related species.

Occurrence of deciduous stellate cornuti is widespread in the family, but the character shows a complex taxonomic distribution. For example, such cornuti are found in the Dioprinae (see below) but appear to have been lost many times within that group. Stellate cornuti occur in all Phalerinae (e.g., *Ellida caniplaga*, fig. 338; *Antheua simplex*, fig. 339), in most Nystaleinae (e.g., *Nystalea nyseus*, fig. 337), in Dioprinae (e.g., *Erbessa glaucaspis*, figs. 346–348), in Platychasmatinae (see p. 197), and in some Dudusinae (e.g., *Crinodes besckei*, fig. 336). Among the heterocampines I examined, the only one with deciduous cornuti is *Fentonia ocypte*, a basal member of

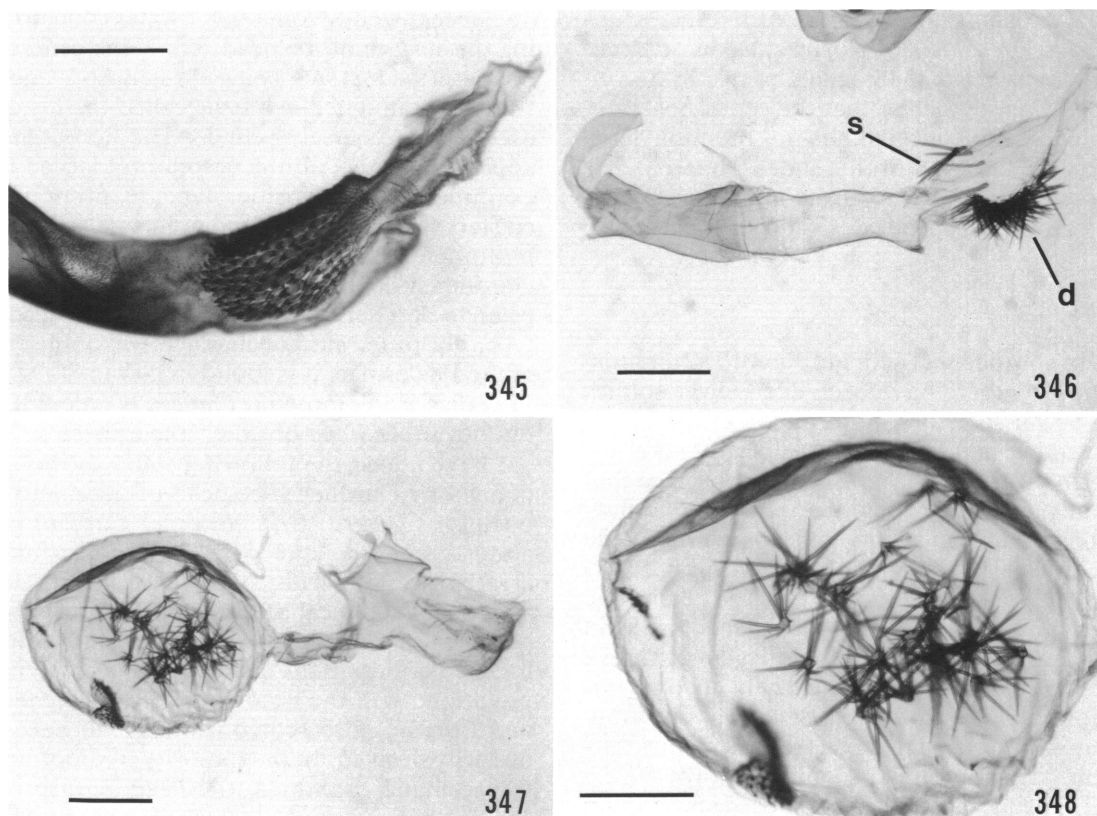


Fig. 345. Aedeagus of *Tarsolepis japonica* (distal portion) showing scobinations at base of vesica. Scale line = 0.5 mm.

Figs. 346–348. Genitalia of *Erbessa glaucaspis* in lateral view, anterior at left. **346.** Aedeagus, showing deciduous (d) and nondeciduous, spinelike (s) cornuti (0.75 mm). **347.** Female genitalia (0.75 mm). **348.** Detail of female, showing corpus bursae containing deciduous cornuti of male (0.5 mm). Scale lengths in parentheses.

that subfamily (fig. 100). The trait has clearly arisen (or has been lost) repeatedly within the Notodontidae.

Deciduous cornuti are known in additional nystaleine (Weller, 1989, 1990) and *Phalera* species (Holloway, 1983), as well as in numerous dioptine genera (J. Miller, unpubl. data). I have not done a detailed literature survey, but, as far as I know, the only notodontid subfamilies where deciduous stellate cornuti do not occur are the Thaumetopoeinae and Notodontinae.

Character 100. Vesica with Distal Sclerite. In some species there is a sclerite in the vesica located at approximately the point where the vesica narrows distally (figs. 335, 336, 341,

342). In phalerines, including *Nadata gibbosa* and *Peridea angulosa*, the sclerite is somewhat cup-shaped and appears to hold the deciduous cornuti. In most other taxa with deciduous cornuti, they are attached directly to the membranous portion of the vesica (figs. 337, 346).

Assuming that I have identified homologous structures, this sclerite exhibits a somewhat complex distribution. The distal sclerite of the vesica unites all Phalerinae (broad sense) except *Ellida caniplaga*, but also occurs in some Heterocampinae. The sclerite is found in *Spatalia jezoensis* and *Fentonia ocypete*, basal heterocampines (fig. 100), as well as in species belonging to Clade 42 (the

"Heterocampini"). Along with other characters, presence of this structure in *Schizura beidermani* (fig. 335), but absence in *S. unicornis*, is suggestive that the genus *Schizura*, as currently conceived, is not monophyletic. Finally, the apomorphic state is found in *Crinodes besckei* (fig. 336) and in *Hemiceras bilinea*, where it protrudes somewhat (fig. 341).

LARVAE

In comparison with notodontid adult morphology, there have been even fewer studies of larval structure. Caterpillars of the Notodontidae exhibit a remarkable diversity of form (figs. 67–98). Seitz (1912) suggested that many of the striking shapes and modifications have evolved to frighten predators, while some larvae are undoubtedly cryptic. Packard (1895a) first demonstrated the taxonomic significance of notodontid caterpillars, and Nagano (1916) emphasized that comparative study of larvae could potentially uncover obvious errors in the adult-based classification. Packard's (1895a) monograph remains perhaps the premier work on immatures for the family, but from a morphological standpoint, his larval characters were largely superficial. Gardner's (1943, 1946) papers on larvae of Old World Notodontidae presented more morphological detail but examined fewer species. Arru's (1965) study of the Italian notodontid *Clostera anastomosis* is comprehensive, and Weller (1987) described the immature stages of *Litodonta hydromeli*. The best recent work is that of Godfrey and Appleby (1987), whose treatment of the North American fauna provided diagnostic characters and general descriptions for many of the genera and species used in my study. Papers on specific larval structures are cited in the appropriate character descriptions.

HEAD

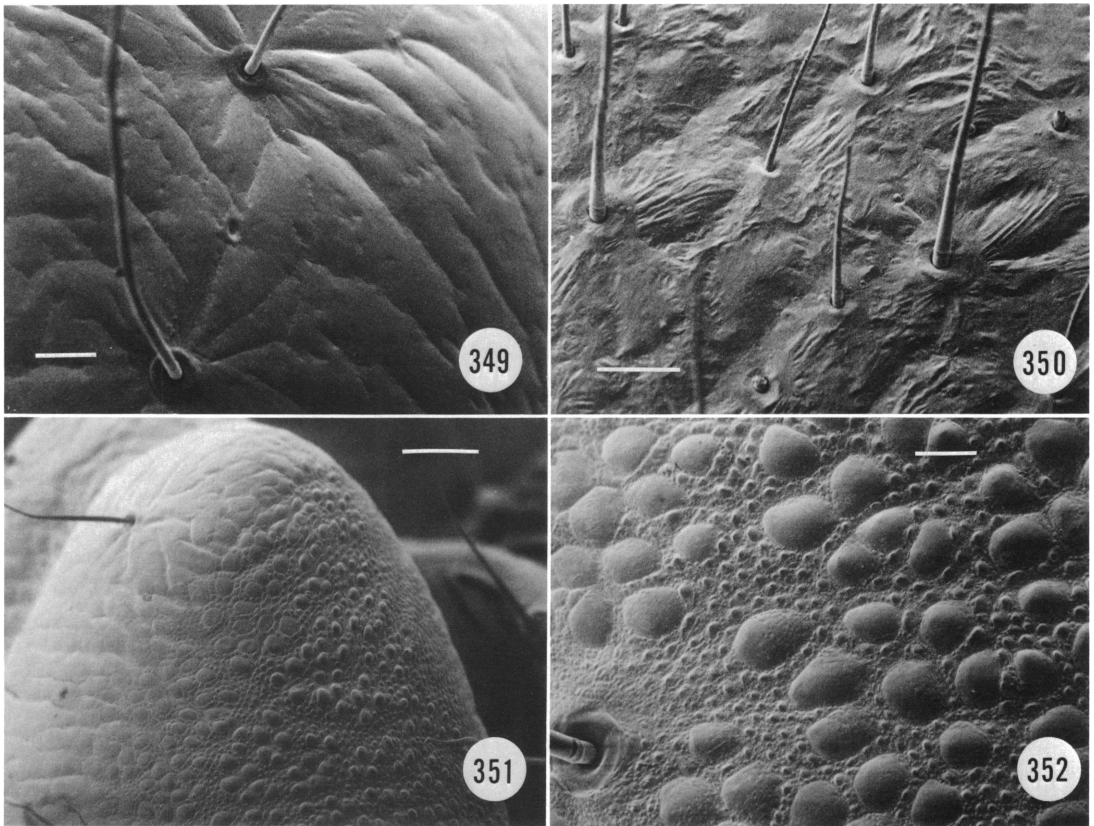
Microsculpture: *Character 101. Cranial Surface Sculpture.* Early workers noted that the head surface of some notodontid caterpillars appears granulate (e.g., see Bell, 1935). Nagano (1916) observed that some *Phalera* larvae have a "punctured" head. Gardner (1943), in his study of Indian notodontid lar-

vae, recognized two character states concerning the surface of the head. For some genera he described it as being "rugulose" and "closely granulate," while he called the head of *Phalera* "coarsely pitted." His first state applies to almost all the notodontid larvae I examined. The rugosities tend to occur in clusters (figs. 351, 352) and are usually most prominent near the stemmata (figs. 353, 354). Gardner's second state, coarsely pitted, appears to be a derivation of the granulate head type. The pitted surface characterizes a subset of the Phalerinae; it is found in larvae of *Datana* (figs. 355, 356) and *Phalera* (Clade 25), but not in *Antheua* or other phalerines.

I have added the following states to those defined by Gardner. The head of thaumetopoeines, *Clostera*, *Crinodes*, and *Cargida* is almost smooth, but with numerous fine creases (fig. 350). This character state (scored as "0"), also typical of the outgroup (including *Oenosandra*, fig. 349), is plesiomorphic for the Notodontidae according to my interpretation, with the head surface of *Crinodes* and *Cargida* (also scored as "0") being secondarily derived. In the majority of diopline larvae that I examined, the head surface is rugose, but the bumps are relatively small and are much more numerous than in other Notodontidae (figs. 357, 358). Another character state occurs in *Cyanotricha* and *Didugua*, both of which have an extremely smooth, almost glassy, head surface. This trait is also found in some *Josia* species, but not in the ones I studied. The final state characterizes the larval head of *Liparopsis postalbida*, which is covered with acute anteriorly directed spicules (figs. 359, 360).

Beck (1960) and Godfrey (1980) have shown that there is variation in larval head surface microsculpture within the Noctuidae as well. Careful study of cranial sculpturing in that family may prove to be phylogenetically informative.

Shape: Notodontidae exhibit considerable variation in larval head shape (Gardner, 1943; McCabe, 1991). The head of some taxa is broadly rounded, as is typical of most other Lepidoptera caterpillars and members of my outgroup (fig. 362). This is true, for example, of *Clostera* (fig. 364) and the Thaumetopoeinae. In other notodontids, the head is tall



Figs. 349–352. Larval head surface. **349.** *Oenosandra boisduvalii*, frontolateral view showing bases of P1 and P2 setae (100 μ m). **350.** *Clostera albosigma*, frontal view showing secondary setae (50 μ m). **351.** *Schizura unicornis*, lateral view with seta P2 in upper left (200 μ m). **352.** *S. unicornis* detail, base of seta P1 at lower left (50 μ m). Scale lengths in parentheses.

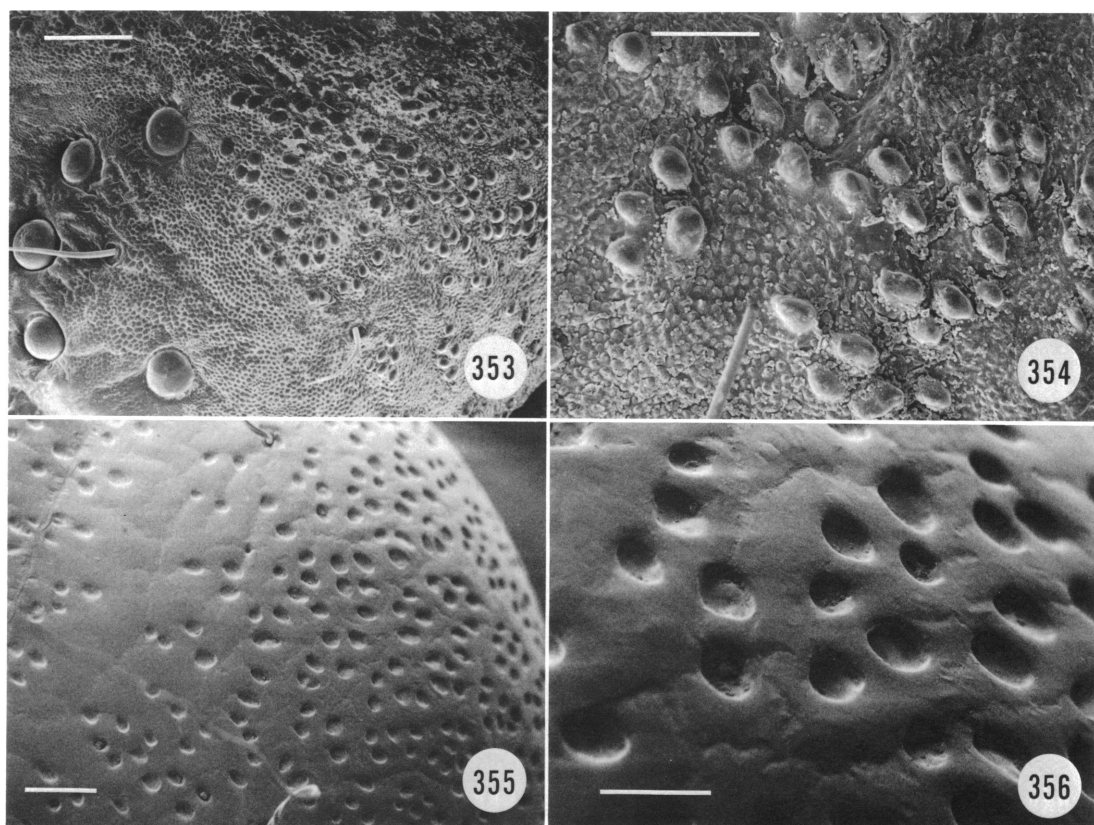
and the vertex is acute in lateral view (Stephens, 1829). Sometimes there is a deep medial groove on top of the head. Although the head shape extremes were easy to characterize, taxa with intermediate shapes were difficult to score.

Character 102. Head Height. I defined head height using only two states: head in lateral view (excluding mouthparts) taller than thorax (figs. 368, 370) and head not taller than thorax (figs. 362, 364), the latter being primitive. Usually, when the head is taller than the thorax, it is wider than the thorax as well (dorsal view).

The derived state occurs in some members of the Notodontinae (fig. 368), Heterocampinae, and Dioprinae, as well as in *Hemiceras*, *Scrancia*, and *Gargetta*. All Nystaleinae

(e.g., fig. 370) have the derived state. Definition of this character is unsatisfactory and might benefit from a morphometric approach.

Character 103. Epicranial Notch. A second head shape character involves the presence of a deep epicranial notch. The head of some species has a depression above the epicranial suture (frontal view) with the cranial halves produced upward (fig. 447). The plesiomorphic state is a head in which the cranium is only slightly depressed at the epicranial suture (e.g., *Clostera*, fig. 363). As with Character 102, the extremes were easy to recognize, but the states often intergrade. It should also be noted that, although Characters 102 and 103 are largely congruent, they are not completely so. For example, larvae of *Loch-*



Figs. 353–356. Larval head surface of Notodontidae. 353. *Heterocampa obliqua*, lateral view showing stemmata (300 μm). 354. *Schizura beidermani*, lateral view (100 μm). 355. *Datana ministra*, frontal view (200 μm). 356. *Datana ministra*, detail of pits (100 μm). Scale lengths in parentheses.

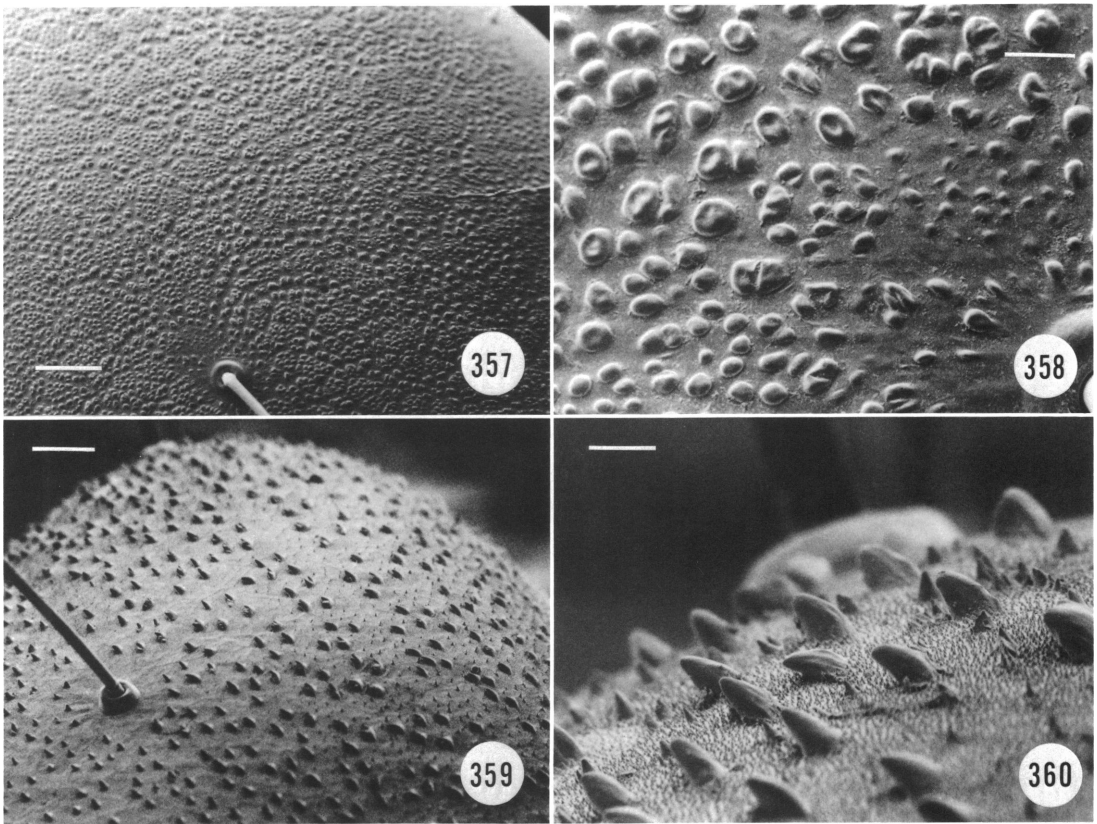
maeus bilineata and *Heterocampa averna* have heads that are not taller than the thorax (score of “0” for Character 102), but they do have a deep epicranial notch. Conversely, the diopline genera *Erbessa* and *Phaeochlaena* exhibit the derived score for head height, but they do not have a deep epicranial notch.

Setae: Lepidoptera caterpillars exhibit three types of body setae: primary, subprimary, and secondary (Fracker, 1915; Hinton, 1946; Peterson, 1962; Stehr, 1987a). Primary setae are relatively few in number and are quite constant in position. Dyar (1894) was among the first to use their location to classify Lepidoptera larvae. Subprimary setae are like primaries but appear at the second instar. The primary and subprimary setae are both termed primaries in later instars because they become difficult to distinguish (Stehr, 1987a). A wide variety of nomenclatorial systems have been applied to primary setae (see, e.g.,

the discussions in Janse, 1939b; Mutuura, 1956; MacKay, 1964), the most widely used being those of Fracker (1915), Gerasimov (1935), and Hinton (1946). For the most part, I follow the nomenclature used by Stehr (1987a), which is a slightly modified version of Hinton’s system, although in certain cases my findings disagree with Stehr’s. There are two categories of primaries: the tactile setae, which are macroscopic and usually long, and the microscopic proprioceptor setae (Stehr, 1987a).

The head MD setae (fig. 361), equivalent to the vertical (“V”) setae of Hinton (1946), were not used as characters because I found them difficult to locate. Similarly, I did not obtain character information from the various head pores (fig. 361).

Secondary setae can occur in addition to primary setae. Secondaries are more numerous and are usually found scattered over the



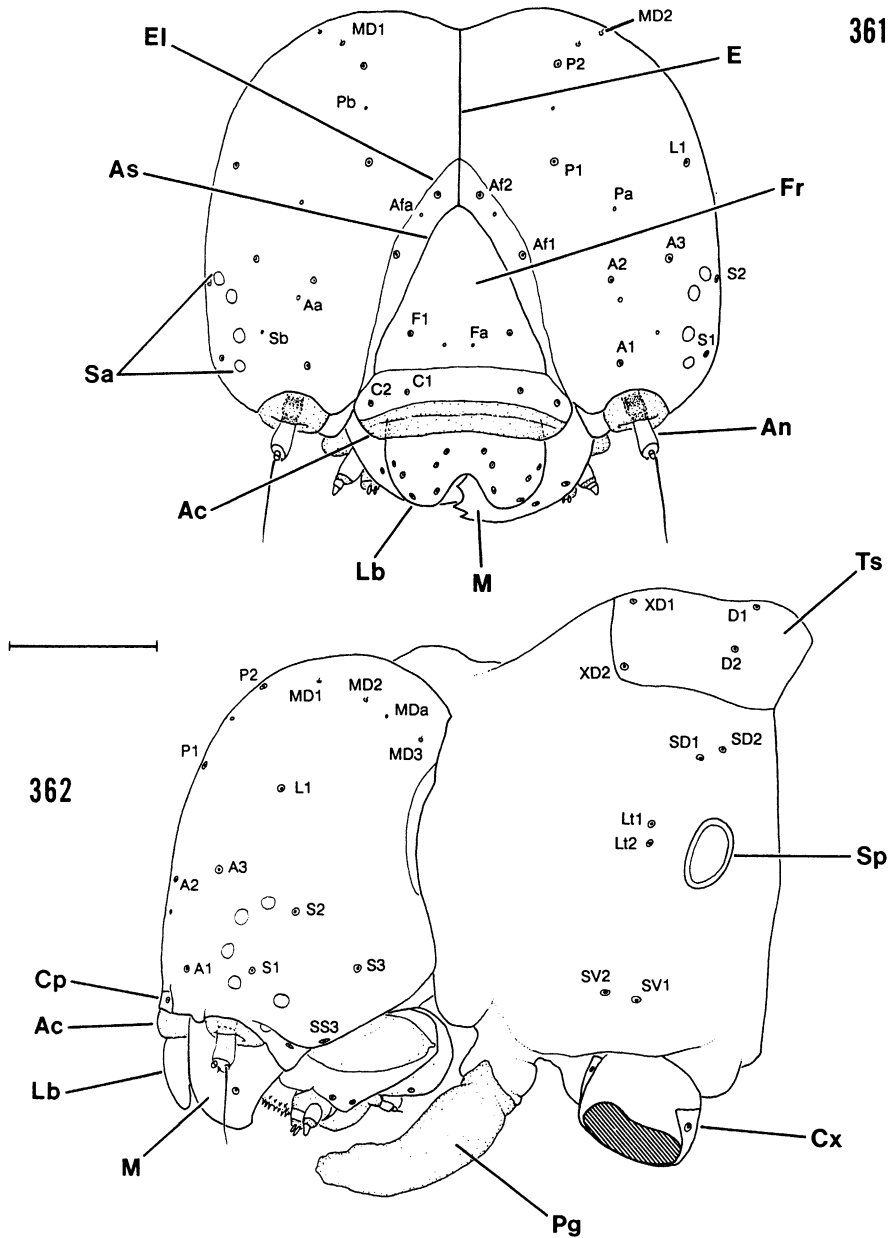
Figs. 357–360. Larval head surface of Notodontidae (lateral). 357. *Phryganidia californica*, seta L1 at bottom (100 μm). 358. *P. californica*, detail (20 μm). 359. *Liparopsis postalbida*, seta P1 at left (100 μm). 360. *L. postalbida* detail showing spicules, base of seta P2 above (20 μm). Scale lengths in parentheses.

entire body (e.g., fig. 504). If secondary setae are present, they often obscure the arrangement of primaries and this causes confusion when trying to score primary setal characters (Fracker, 1915). First instar larvae often lack such secondary setae (D. Lafontaine and D. Wagner, personal commun.) and they could potentially be used to score certain characters, but first instars were not available for this study. Thus, for some species with secondary setae in final instars it was necessary to score primary setal characters as missing data (“?” in Appendix II). For example, the last instar larval head of *Harpyia microsticta* is covered with short secondary setae (fig. 447) that are indistinguishable from the primaries. This species therefore received “?” scores for characters involving head primary setae. In contrast, the head of *Clostera albosigma* is covered with secondary setae (McCabe, 1991), but the primaries are significantly longer and

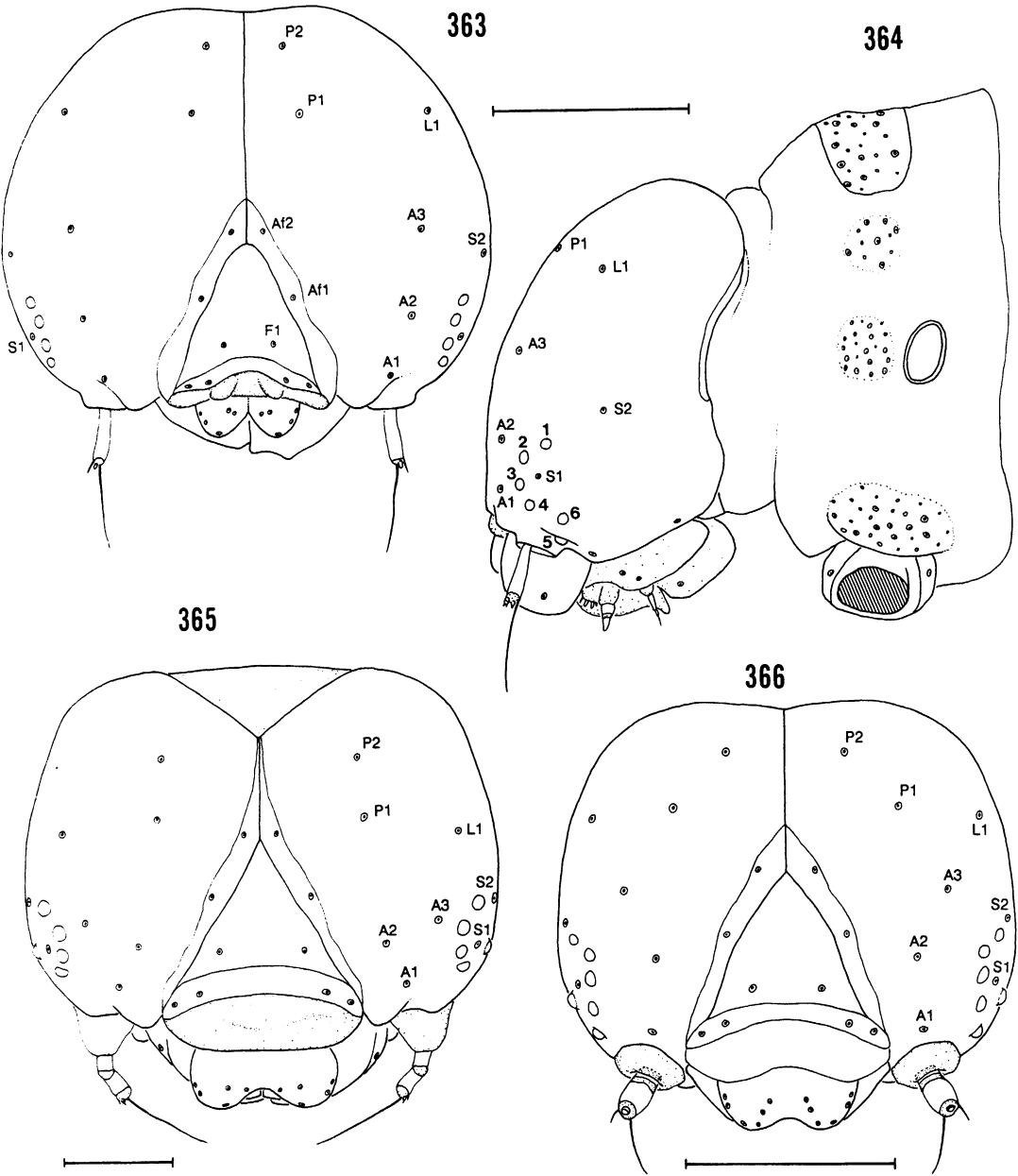
more robust than the secondaries. Primary setal characters of the head could therefore be reliably scored for *C. albosigma* (figs. 363, 364). Fortunately, this was the case for most of the Notodontidae I examined. Among out-group taxa, primary setae on the heads of *Panthea* (Noctuidae) and the lymantriids were obscured by secondaries.

A similar situation obtained for characters involving primary setae on the body. I could not score them for *Harpyia microsticta*, where the primaries are indistinguishable from secondary setae. However, in most taxa with numerous secondary setae, it was possible to distinguish the primaries because of their larger size and because each is often associated with a small pinaculum (e.g., figs. 503, 504).

When present on the head, secondary setae invariably occur on the thorax, abdomen, and legs as well. However, the reverse is not true;

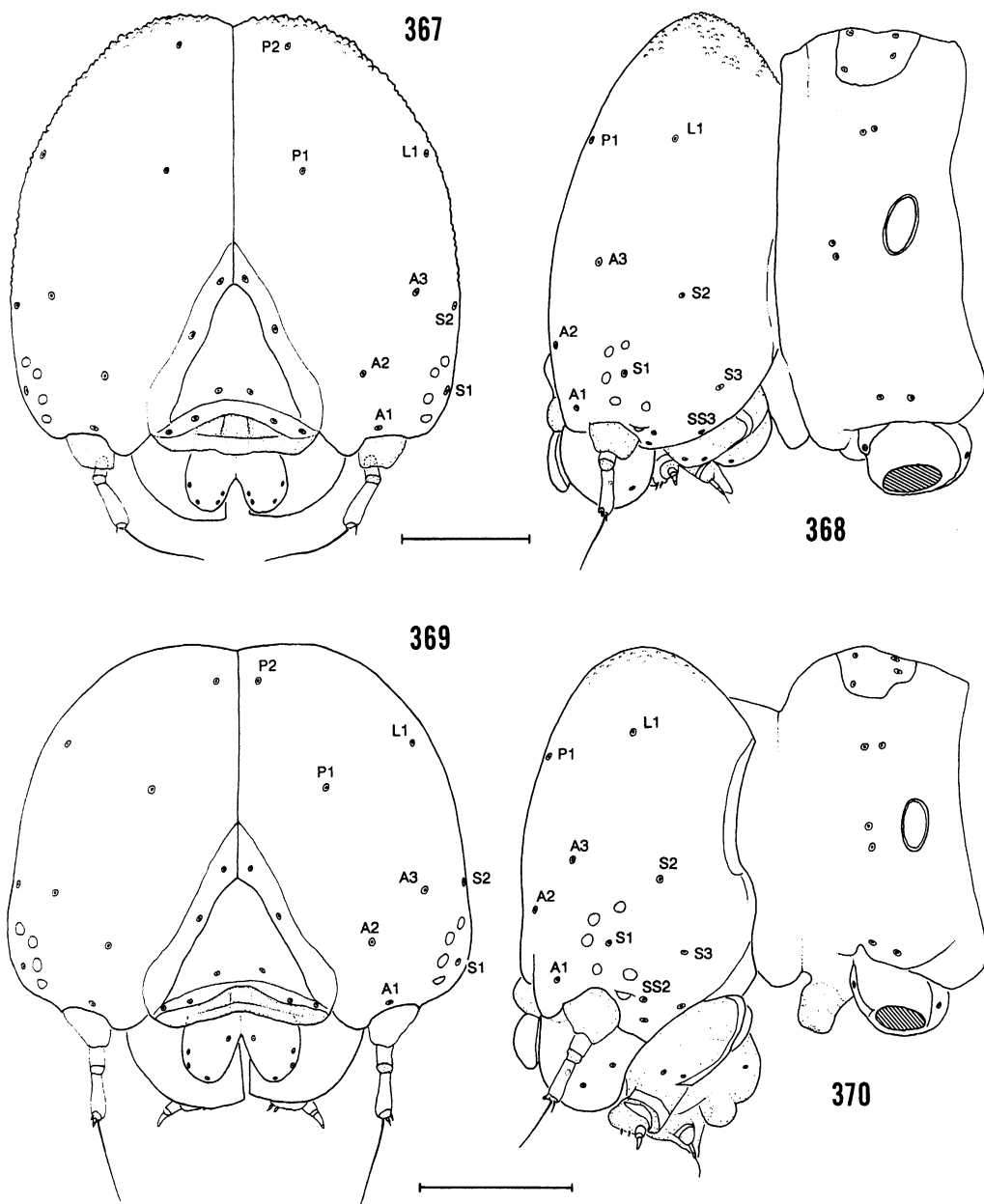


Figs. 361, 362. Final instar larva of *Alypia octomaculata* (Noctuidae). **361.** Head in frontal view. **362.** Head and first thoracic segment in lateral view. A = anterior seta. Aa = pore Aa. Ac = anteclypeus. Af = adfrontal seta. Afa = pore Fa. An = antenna. As = lateral adfrontal suture. C = clypeal seta. Cp = clypeus. Cx = prothoracic coxa. D = dorsal seta. E = epicranial suture. El = ecdysial line. F = frontal seta. Fa = pore Fa. Fr = frons. L = lateral seta (head). Lb = labrum. Lt = lateral seta (prothorax). M = mandible. MD = dorsal proprioceptor seta. MDa = pore MDa. P = posteriodorsal seta. Pa = pore Pa. Pb = pore Pb. Pg = prothoracic gland. S = stemmatal seta. Sa = stemmata. Sb = pore Sb. SD = subdorsal seta. Sp = prothoracic spiracle. SS = substemmatal seta. SV = subventral seta. Ts = prothoracic shield. XD = XD seta. Scale line = 1.0 mm.



Figs. 363, 364. Final instar larva of *Clostera albosigma* (Notodontidae). **363.** Head in frontal view. **364.** Head and first thoracic segment in lateral view. Scale line = 1.0 mm.

Figs. 365, 366. **365.** Final instar larva of *Oenosandra boisduvalii* (Oenosandridae); head in frontal view. **366.** Final instar larvae of *Doa ampla* (Doidae); head in frontal view. For key to symbols see figures 361 and 362. Scale lines = 1.0 mm.



Figs. 367–370. Final instar larvae of Notodontidae. **367.** Head of *Notodonta scitipennis* in frontal view. **368.** Head and first thoracic segment of *Notodonta scitipennis* in lateral view. **369.** Head of *Hippia packardii* in frontal view. **370.** Head and first thoracic segment of *Hippia packardii* in lateral view. For key to symbols see figures 361 and 362. Scale lines = 1.0 mm.

they are found less frequently on the head than on the body. For example, secondary setae occur on the thorax and abdomen, but not the head, in *Antheua* and *Datana* (Phalarinae). Typically, when secondary setae oc-

cur, all setae, including the primaries, are barbed (fig. 442; Bourgogne, 1951).

Character 104. Head with Secondary Setae. Packard (1895a) suggested that presence of secondary setae is primitive for the No-

todontidae. Optimization of Characters 104 and 140 supports his claim. However, presence of secondary setae on the larval head is an extremely homoplastic character state among both the ingroup and the outgroup. Taxa in the following notodontid subfamilies exhibit such setae: the Thaumetopoeinae, Pygaerinae, Phalerinae, Heterocampinae, Dioptinae, and Dudusinae. In my study, however, most subfamilies contained only one or two exemplar species with head secondary setae. This was true of the Dioptinae (*Cyanotricha necyria*), Phalerinae (*Phalera bucephala*), and Dudusinae (*Goacampa variabilis*). Indications are that the character state has arisen at least five times in the Notodontidae.

I used three states for this character. Absence of head secondary setae was assigned a "0" score, presence of long secondary setae was scored as "1", and presence of short secondary setae (in *Harpyia* [fig. 447], *Stauropus*, and *Goacampa*) was scored as "2".

Character 105. Location of Setae P1 and P2. There are two "P" setae on the upper portion of the larval face. There is some confusion in the literature concerning the proper nomenclature for these. Nakatomi (1977), in his figures of *Dudusa sphingiformis* caterpillars, labeled the dorsal one "V", perhaps misinterpreting Ripley (1923), Hinton (1946), and Gerasimov (1952). The "V" setae actually refer to proprioceptor head setae (equivalent to the "MD's" of Stehr, 1987a) located near the cranial vertex (Gerasimov, 1952; Stehr, 1987a; Merzheevskaya, 1988). I follow Stehr's terminology. In quadrifid noctuoids, seta P2 is located further from the epicranial suture than is P1 (fig. 361). This is shown in many papers on the larvae of Noctuidae (e.g., Ripley, 1923; Williams, 1953; Godfrey, 1972). In all Notodontidae, P2 is closer to the epicranial suture than P1, and P2 is usually relatively close to the epicranial notch (figs. 363, 367, 369; also fig. 50 in Arru, 1965). Interestingly, the same is true of *Doa* caterpillars (fig. 366; see also Brown, 1990). In *Oenosandra* the two setae are approximately equidistant from the suture (fig. 365). I scored this species as a question mark ("?").

This seems to be an extremely reliable diagnostic feature for the Notodontidae and provides important evidence that *Doa* is the

family's sister group. After discovering the character, I found that Forbes (1910) had already described it. In discussing setae P1 and P2 (his "setae i and ii"), Forbes noted that P2 is high up on the head in notodontids and that some species have P1 located lateral to P2. I have not seen other references to this character. Unfortunately, I could not determine the positions of P1 and P2 for thaumetopoeines, because in that group, the primary setae are indistinguishable from the numerous secondaries. Perhaps examination of first instar thaumetopoeine caterpillars will provide an answer.

Character 106. Distance Between Setae P1 and C1. There are always two pairs of clypeal setae, the C1 and C2 setae, and two pairs of adfrontal setae, Af1 and Af2 (Stehr, 1987a). Among members of the outgroup the distance between C1 and P1 is only slightly longer than the distance between C1 and Af2 (figs. 361, 365). Among Notodontidae and *Doa*, however, the distance between P1 and C1 is half again as long as the distance between Af2 and C1 (figs. 363, 366, 367, 369). I scored the latter as being derived. Again, some species having numerous head secondary setae, such as the thaumetopoeines, could not be scored. The derived state also appears in the outgroup taxa *Hypoprepia* and *Nycteola*, and the plesiomorphic state applies to *Oenosandra* (fig. 365). This character is probably correlated with head height, thus serving as an alternative to the epicranial index of Ripley (1923) and Beck (1960).

Character 107. Position of Seta S1. Lepidoptera larvae have three stemmatal, or "S", setae on the head (figs. 368, 370; the stemmata are numbered in fig. 364). The position of seta S1 varies with respect to stemmata 3 and 4. It can be located closest to stemma 3 (scored as "1") or closest to stemma 4 (scored as "0"). The first state (figs. 364, 368, 370, 394) is characteristic of all but a few of the Notodontidae I examined, while the second (fig. 362) is found more frequently in the quadrifid Noctuoidea (Appendix II). *Oenosandra* (fig. 365) exhibits the derived state, indicating a relationship with the *Doa*/Notodontidae clade. *Nycteola* (Noctuidae) also has S1 closest to stemma 3. According to my results, the plesiomorphic state has reappeared three separate times in the Notodontidae.

Stemmata: Character 108. Size of Stemma 3. There are six stemmata (sometimes incorrectly termed "ocelli"; e.g., Peterson, 1962) on the larval head in Lepidoptera. Their relative positions can vary, and the number of stemmata is sometimes reduced, especially among leaf-mining groups (Stehr, 1987a). Noctuid larvae seem to show little variation in stemmatal position, and I did not observe number reduction. In most Lepidoptera larvae the six stemmata are approximately equal in size (e.g., fig. 362). In caterpillars of Satyrinae (Nymphalidae), particular stemmata are enlarged relative to the rest (DeVries et al., 1985). Within the Notodontidae, there are species in which stemma 3 is enlarged. This is characteristic of some Notodontinae, including *Gluphisia*, *Quadricalcarifera*, and *Liparopsis* (fig. 394), but the state occurs in other groups, including *Hemiceras*, *Ellida*, *Clostera*, and all but two diopline genera.

The possible functional significance of having a single stemma larger than the others is unknown. MacKay (1962) described a remarkably similar condition in a tortricid. Stemma 3 is enlarged in *Cnephasia longana* Haworth (Tortricinae), but not in a closely related species, *C. virgaureana* Treitschke. She wondered whether this morphological difference is perhaps correlated with interspecific differences in microhabitat (MacKay, 1964).

Antennae: Character 109. Antennal Length. Larval antennae vary in length among notodontid species (figs. 373, 376–388). Gardner (1943) noted the short antennae of Thaumetopoeinae (fig. 376) and, in his 1946 paper, described the long antennae of *Hyperaeschra*. Dethier (1941), who included 11 notodontid species in his comparative study of lepidopteran larval antennae, noted the unusually long antennae of *Symmerista* species. Following Gardner (1946), I used the length of segment 2 relative to its width to characterize antennal length. I recognized two states: (1) length of segment 2 less than or equal to $2\frac{1}{2}$ times its width, and (2) length of segment 2 greater than $2\frac{1}{2}$ times its width (e.g., figs. 384, 387).

This character showed low consistency. Among my study taxa, at least one representative of each of the Notodontinae, Phalerinae, Heterocampinae, Dioplineae, and Dusinae exhibits the derived state.

I discovered that antennal surface structure

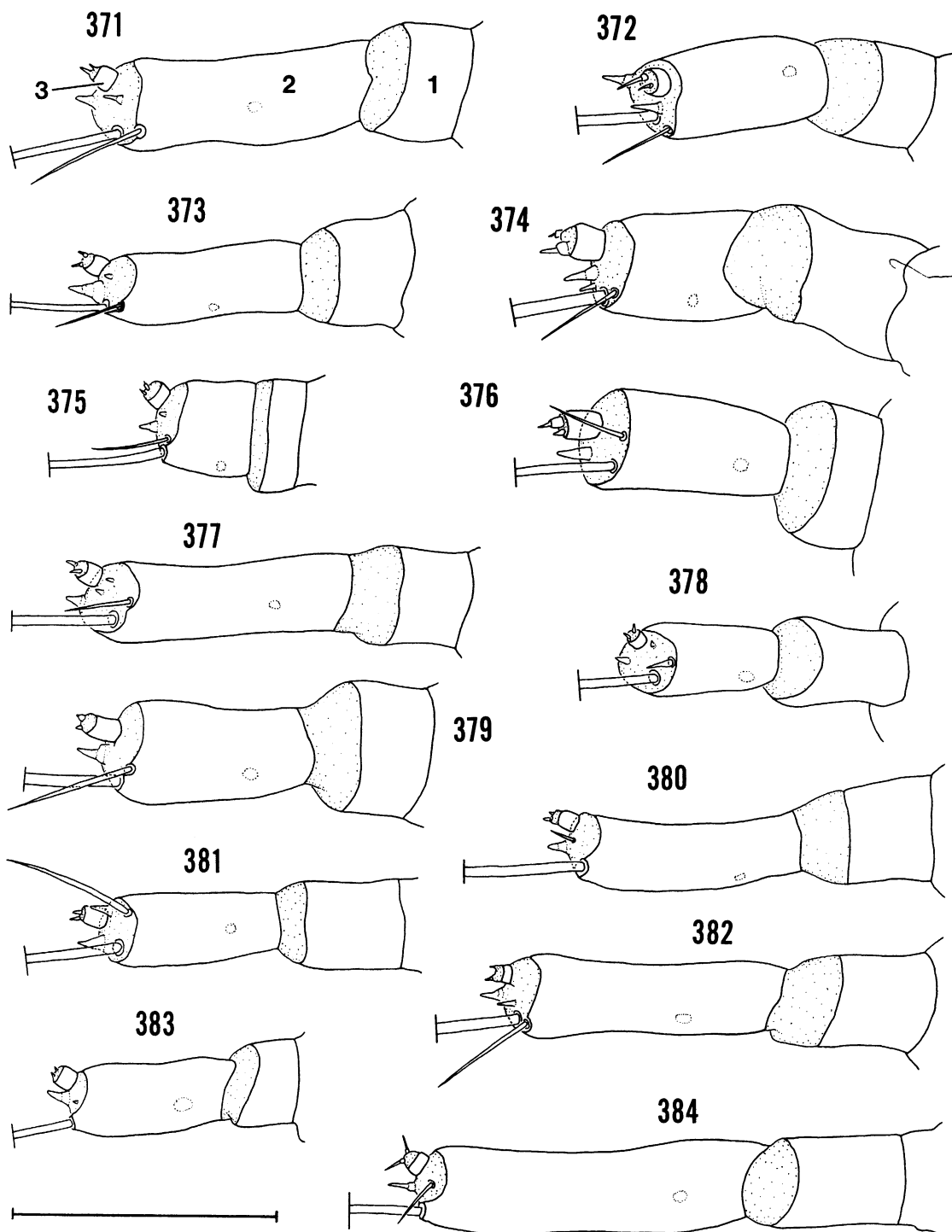
varies. It is typically smooth (fig. 393), but in *Liparopsis postalbida* there is a scalelike microsculpture covering the surface (fig. 392). I observed this in larvae of other notodontid taxa, but was unable to use the character because it could not be scored reliably without SEMs.

Labrum: Character 110. Depth of Labral Notch. The ventral margin of the notodontid larval labrum can have either a shallow or a deep notch (Gardner, 1943; Godfrey et al., 1989). Most members of the outgroup have a shallow curving labral notch (fig. 361), although there is variation in notch depth among Noctuidae (Crumb, 1956; Merzheevskaya, 1988). A shallow notch is found in *Oenosandra* (fig. 365) and *Doa* (fig. 366). In notodontids where the notch is deep, a medial groove is also present. A relatively shallow notch occurs in the Thaumetopoeinae (fig. 390; Gardner, 1943) and in *Clostera* (fig. 363; Arru, 1965), suggesting that this is plesiomorphic for Notodontidae. I characterized a deep notch, the derived state, as being one that is greater than two-thirds the height of the entire labrum. A deep labral notch (e.g., figs. 367, 369) occurs in all Notodontidae above Clade 10 (fig. 99) and in two outgroup taxa, *Lymantria* and *Acronicta*.

Godfrey et al. (1989) noted that first instar notodontid caterpillars have a shallow labral notch and that they skeletonize the leaf surface. They suggested that a deep notch, present only in later instars, all of which clip through the entire leaf, appears to aid in holding the leaf margin during feeding. I did not study the number and position of labral setae, although these might hold taxonomic information.

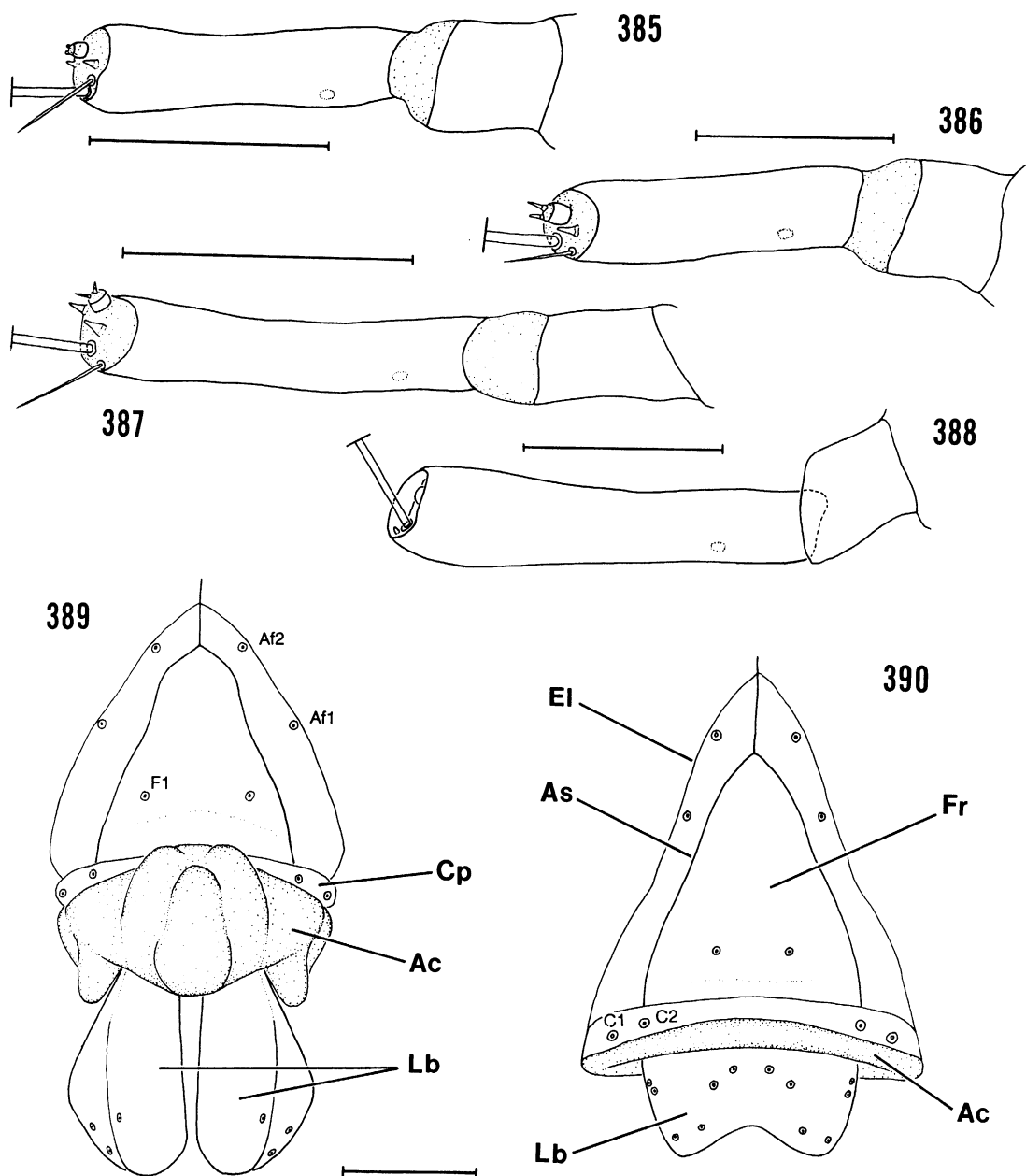
Character 111. Labral Lobes Swollen. In *Nystalea nyseus*, *Cnethodonta grisescens*, and *Liparopsis postalbida*, the labral notch extends all the way to the anteclypeus so that the halves of the labrum are completely separate (fig. 389). Furthermore, the two labral lobes are greatly swollen and protrude anteriorly (fig. 391). According to my analysis, this condition arose three separate times (see figs. 99, 100). I am not familiar with the feeding habits of these three species and so cannot speculate concerning the functional significance of the modification.

Anteclypeus: Character 112. Anteclypeus with Dorsoventral Folds. The anteclypeus is



Figs. 371–375. Left larval antenna of Noctuoidea in lateral view, anterior at left. 371. *Dasychira dorsipennata* (Lymantriidae). 372. *Peridroma saucia* (Noctuidae). 373. *Clostera albosigma* (Notodontidae). 374. *Oenosandra boisduvalii* (Oenosandridae). 375. *Doa ampla* (Doidae).

Figs. 376–384. Left larval antenna of Notodontidae in lateral view, anterior at left. 376. *Traumatocampa pityocampa*. 377. *Notodonta scitipennis*. 378. *Lochmaeus bilineata*. 379. *Antheua simplex*. 380. *Gluphisia septentrionis*. 381. *Gargetta costigera*. 382. *Quadricalcarifera viridimaculata*. 383. *Ellida caniplaga*. 384. *Hemiceras bilinea*. Segments numbered for *D. dorsipennata*. Only the base of the “long hair” (Dethier, 1941; Peterson, 1962) is shown. Scale line = 0.4 mm.



Figs. 385-388. Left larval antenna of Notodontidae in lateral view, anterior at left. 385. *Nadata gibbosa* (Phalerinae). 386. *Crinodes besckei* (Dudusini). 387. *Nystalea nyseus* (Nystaleinae). 388. *Stauropus fagi* (Heterocampinae). Scale lines = 0.4 mm.

Figs. 389, 390. Frontal region of larval Notodontidae. 389. *Liparopsis postalbida* (Notodontinae), showing greatly swollen anteclypeus (Ac) and completely divided labrum (Lb). 390. *Epicoma melanosticta* (Thaumetopoeinae), showing unmodified anteclypeus and labrum. For key to symbols see figures 361 and 362. Scale line = 0.5 mm.

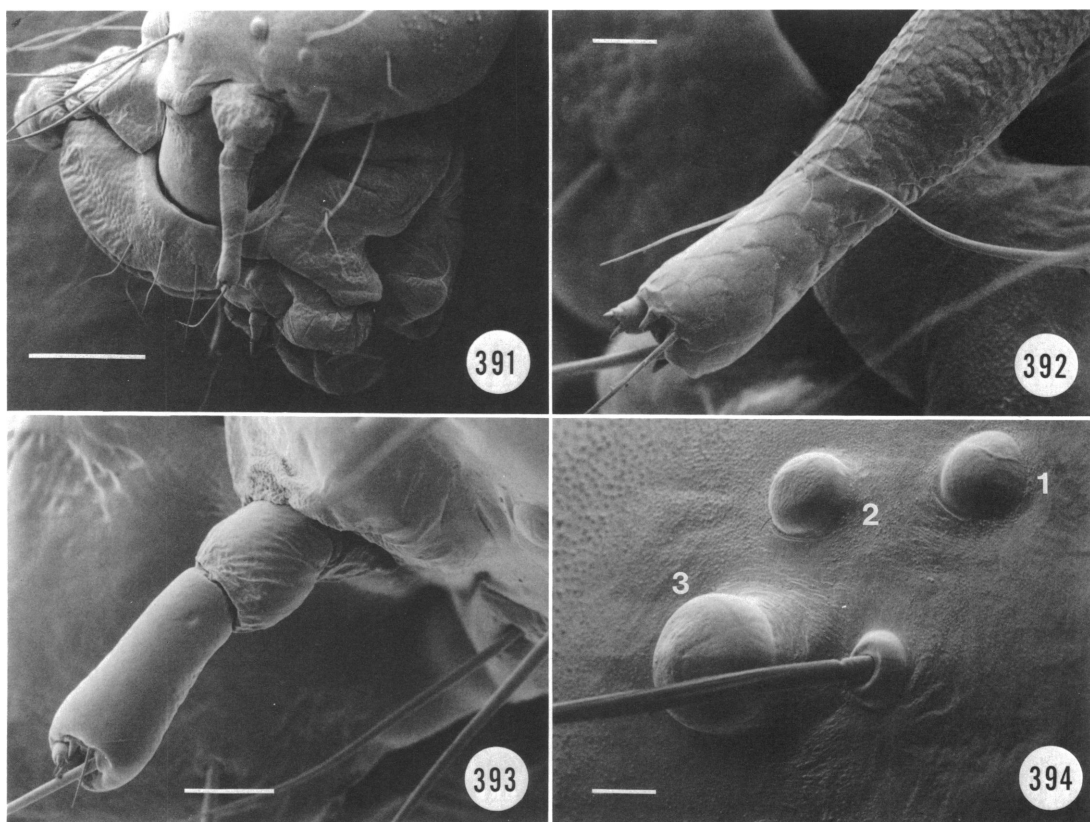


Fig. 391. Mouthparts and antenna of *Liparopsis postalbida* in lateral view (anterior at left). Scale line = 500 μ m.

Figs. 392, 393. Left larval antenna of Notodontidae. **392.** *Liparopsis postalbida*, distal portion showing surface sculpturing (50 μ m). **393.** *Schizura unicornis* (100 μ m). Scale lengths in parentheses.

Fig. 394. First three stemmata and seta S1 of *Liparopsis postalbida* (left side, anterior at left) showing enlarged stemma 3. Scale line = 50 μ m.

a somewhat membranous portion of the face located above the labrum and below the clypeus (figs. 389, 390). In all Notodontidae except the Thaumetopoeinae, the anteclypeus is expanded and has several dorsoventral folds (figs. 362, 367, 369, 389). When seen in lateral view, this type of anteclypeus protrudes from the face (figs. 391, 398). An unmodified anteclypeus, exemplified by *Alypia* (Noctuidae; fig. 361), *Doa* (fig. 366), and *Epicoma* (fig. 390), does not protrude, its upper and lower margins are roughly parallel, and there are no folds. The taxonomic distribution of the swollen anteclypeus is roughly congruent with presence of a deeply notched labrum (Character 110 above), but appears one node higher (in Clade 12; fig. 99) on my cladogram. The anteclypeus of *Liparopsis postalbida* is highly modified, being greatly swollen with

ventrolateral projections (fig. 389). The function of a swollen anteclypeus is unknown.

Mandibles: I used three mandible characters. SEM study of all taxa might provide additional information. For example, Godfrey et al. (1989) described a "transverse ridge" on the oral surface of the mandible in *Heterocampa obliqua* Packard and noted that this ridge is complex in *Crinodes besckei*. There appears to be additional variation in ridge structure but I did not examine it in detail, nor have I studied this character among members of the outgroup.

Character 113. Smooth Mandibular Margin. Many notodontid larvae exhibit an ontogenetic change in mandibular morphology (Weller, 1987; Godfrey et al., 1989). Early instars have serrate mandibles, usually with three or four large teeth. During the final in-

star, the mandibular cutting edge is smooth (figs. 396, 397). Almost all quadrid noc-tuoids, on the other hand, have a deeply serrate mandibular cutting edge in all instars (e.g., see figures in Ripley, 1923; Crumb, 1956; Beck, 1960; Godfrey, 1972, 1987b; Eichlin and Cunningham, 1978; Merzheevskaya, 1988; McCabe, 1991). Serrate mandibles occur in *Doa* (Brown, 1990) and *Oenosandra* (fig. 395).

The smooth notodontid mandible appears to be apomorphic for the family, but it is not found throughout (Godfrey et al., 1989; McCabe, 1991). Among the ingroup, serrate mandibles occur in three dioptine genera, as well as in *Gargetta* and *Scrancia*. *Cargida pyrrha* (Godfrey, 1984) and *Crinodes besckei* (see figures in Godfrey et al., 1989) exhibit the serrate mandible, but other Dudusini have a smooth margin. The serrate notodontid mandible is clearly secondarily derived from that found in other Lepidoptera and appears to have arisen at least twice (in dioptines and dudusines) within the family.

A third state, which I found in *Thaumatopoea* and *Traumatocampa* but not in other thaumatopoeines, is characterized by having the ventral portion of the mandibular cutting edge smooth, but shallow dentations on its dorsal margin. This appears to be a derivative of the smooth mandibular margin.

Character 114. Mandibular Carina. A carina occurs on the ventrolateral mandibular surface of some species. Unfortunately, this was a difficult character to score. The carina can be either weakly developed, as in *Clostera* (fig. 396), or strongly developed, as is typical of the phalerines I examined (fig. 397). Using a conservative judgement as to the carina's presence, I gave taxa with a strong carina the derived score and those without one or with a weakly developed one a "0" score. This procedure was only marginally successful; the character is extremely homoplastic. An apparently homologous condition occurs on the mandible of lymantriid larvae. A comprehensive SEM study of mandibular morphology might provide better data for Character 114.

Character 115. Mandibles with Secondary Setae. Gardner (1943) noted secondary setae on the mandibles of *Thaumatopoea cheela* Moore. I found secondary setae on the man-

dibles of all thaumatopoeines examined, but nowhere else among the study taxa. There are no secondary setae on the mandibles of *Oenosandra boisduvalii* (fig. 395).

Maxillary Complex: The larval maxillary complex was a particularly rich source of character information. The superb SEM studies of Grimes and Neunzig (1986a, 1986b) demonstrated tremendous variation among Lepidoptera in both the location and shape of maxillary sensilla. A detailed survey for the Notodontidae would undoubtedly provide information.

In Lepidoptera, each maxilla is composed of a mesal lobe (= laciniogalea) and a maxillary palpus. Grimes and Neunzig (1986b) categorized the mesal lobe sensilla as follows: the distal portion of each lobe bears three sensilla trichodea (numbered STI-STIII), two sensilla styloconica (MSS and LSS), and three sensilla basiconica (see figs. 399-403). The basiconic sensilla are relatively small, and I could not obtain character information from them without SEMs of all study species. The sensilla trichodea and styloconica, on the other hand, could be observed with a light microscope, and both sets of sensilla provided characters.

Character 116. Stipital Lobe Shape. Grimes and Neunzig (1986b) first described the stipital lobe, suggesting that it is unique to the Notodontidae. The stipital lobe is a fleshy protuberance, often minutely spiculate, arising from the base of the maxillary complex and located dorsal to the mesal lobe and maxillary palpus (fig. 398). Godfrey et al. (1989) showed that the stipital lobe is a valuable diagnostic character for the Notodontidae; they reported these lobes in 92% of the 154 notodontid species examined. Further, Godfrey et al. (1989) documented distinct interspecific shape variation in stipital lobes.

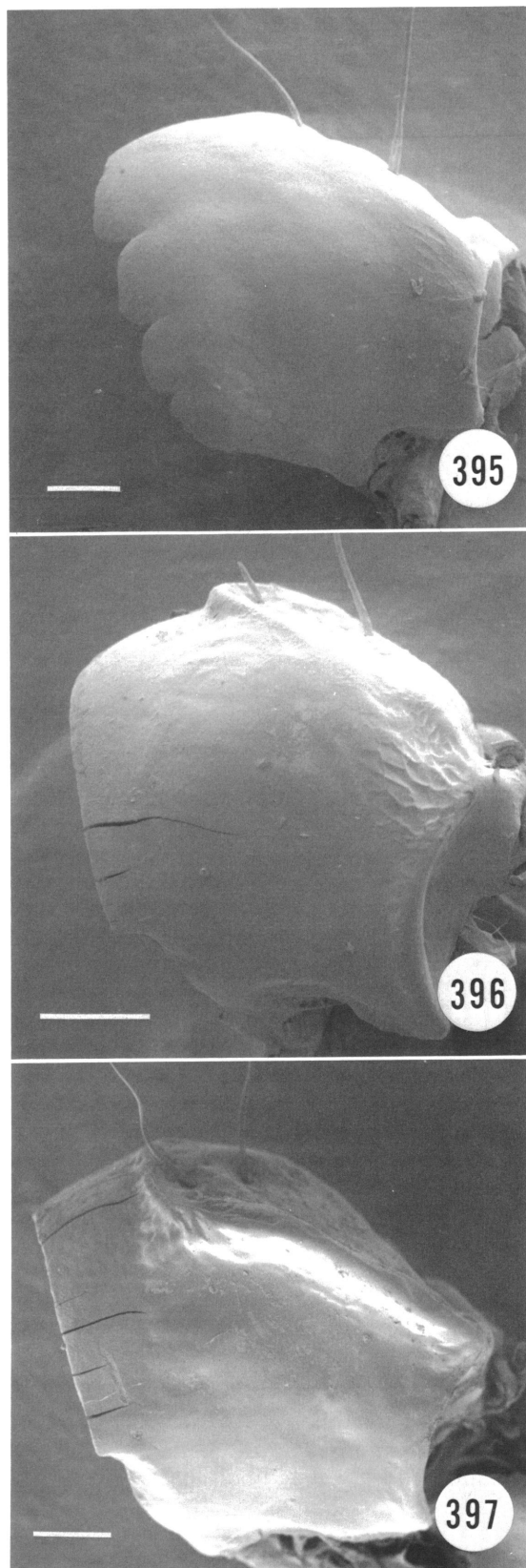
I recognized four character states involving shape and size of the stipital lobes: (1) absent (fig. 399), the plesiomorphic state; (2) short and broadly rounded (figs. 400, 402); (3) apically acute (figs. 401, 403); and (4) large, extending beyond the rest of the maxilla (when seen in dorsal view) (fig. 404). Interestingly, a stipital lobe is present in *Doa*, the sister group of the Notodontidae (fig. 99). The lobe of *Doa* is short, broad, and covered with long spicules (fig. 410). Intact specimens of *Oen-*

osandra boisduvalii exhibit a broadly rounded lobe, although its shape was not preserved in my SEM preparation (fig. 411). The lobe is absent in thaumetopoeines (Godfrey et al., 1989), but according to my analysis this represents secondary loss. Notodontid taxa with a broadly rounded stipital lobe include *Clostera*, *Phalera* (fig. 400), *Datana*, and *Nadata* (fig. 402). An apically acute lobe is the shape most frequently observed. Usually these can be seen in intact larval specimens, curving up in front of the mandible's ventral margin (fig. 408). The final state, a large stipital lobe, has a somewhat scattered distribution. It is found in species of the Heterocampinae, Nysaleinae, and Dioprinae (fig. 409), and in *Liparopsis postalbida*. The stipital lobe of *Nysalea* and *Erbessa* is extremely large, curving so far dorsally that it touches the labrum (Godfrey et al., 1989).

Grimes and Neunzig (1986b) proposed that stipital lobes aid the mandibles during mastication. Godfrey et al. (1989) have suggested that they might form seals between the mandibles and maxillae, thereby helping to hold leaf material in the oral cavity. Tests of these hypotheses will require direct observation of live notodontid caterpillars.

Character 117. Stipital Lobe Surface. As described above, the surface of the stipital lobe is minutely spiculate. In all heterocampine exemplars except *Lochmaeus bilineata* (fig. 404), the spicules are unusually large and slightly melanized, making them more conspicuous (see fig. 6 in Godfrey et al., 1989). Except for heterocampines, only *Doa ampla* (fig. 410) exhibits large spicules.

Character 118. Sensilla of Mesal Lobe Small. The sensilla trichodea and styloconica of the mesal lobe are very small in some species of notodontid caterpillars. Taxa with small sensilla usually have the mesal lobe broadly expanded (figs. 405, 406). Among taxa with the primitive state, STI is as tall as the maxillary palpus (figs. 399–404). How-



Figs. 395–397. Left mandible of final instar larvae (ventral view with anterior at left). 395. *Oenosandra boisduvalii*. 396. *Clostera albosigma*. 397. *Datana ministra*. Scale lines = 200 μ m.

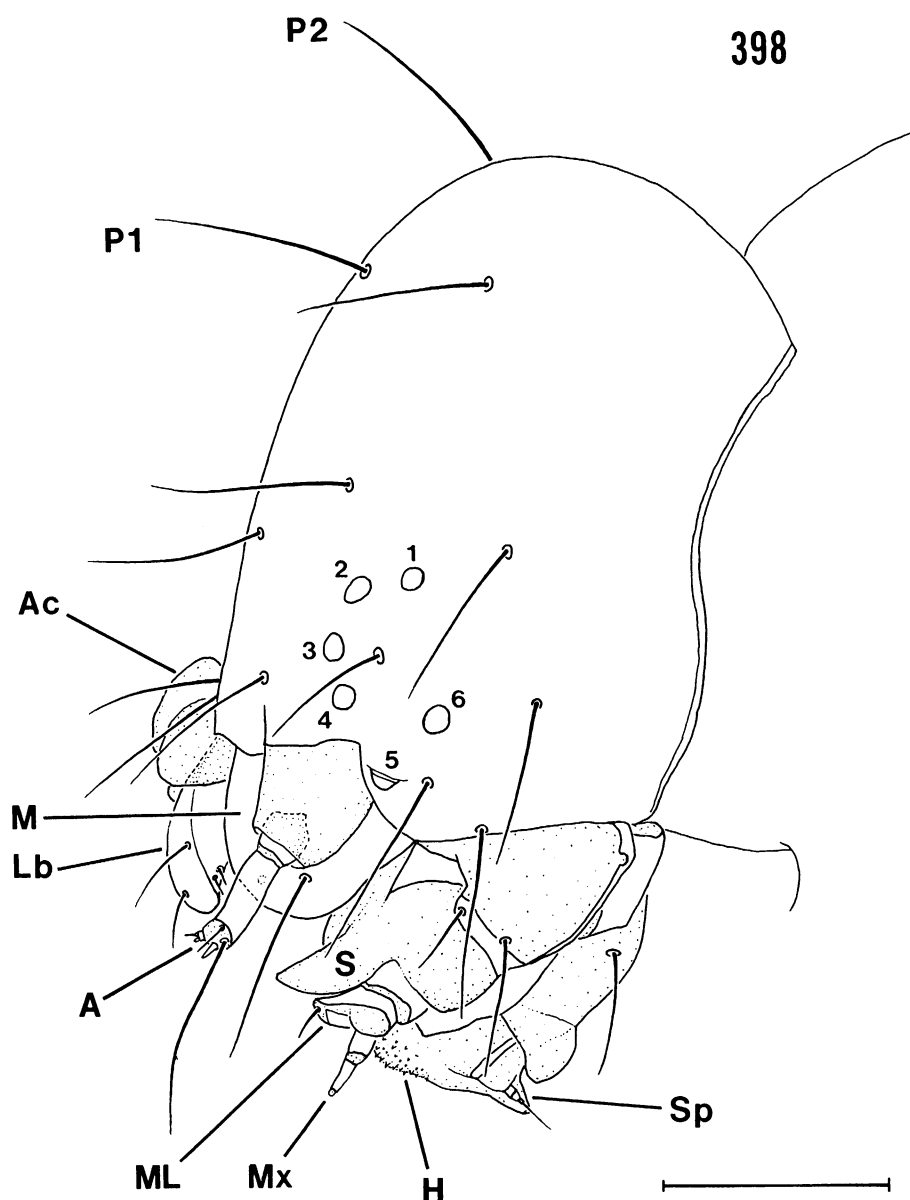


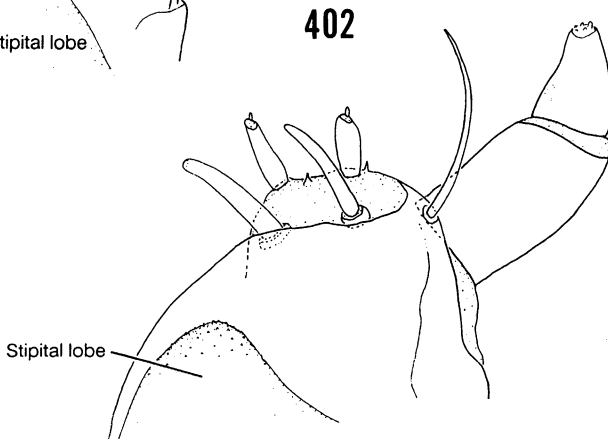
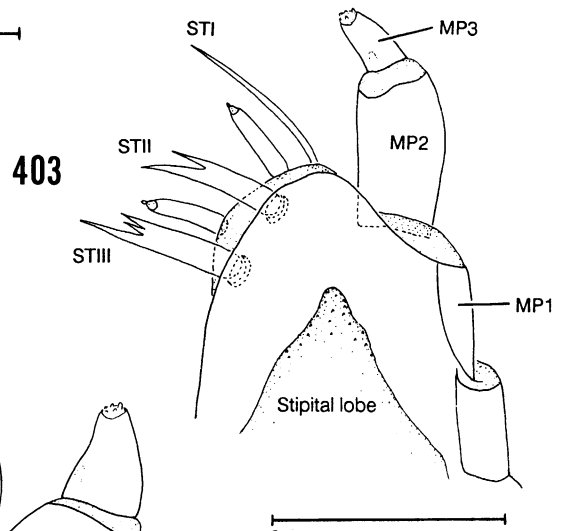
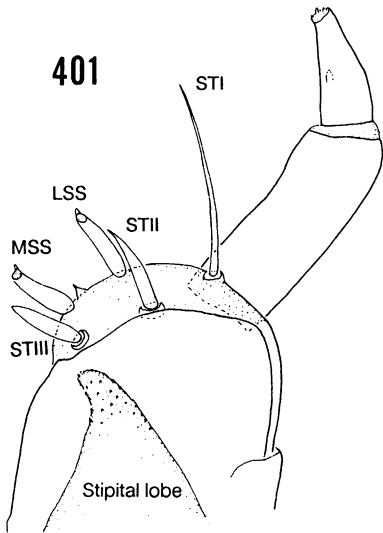
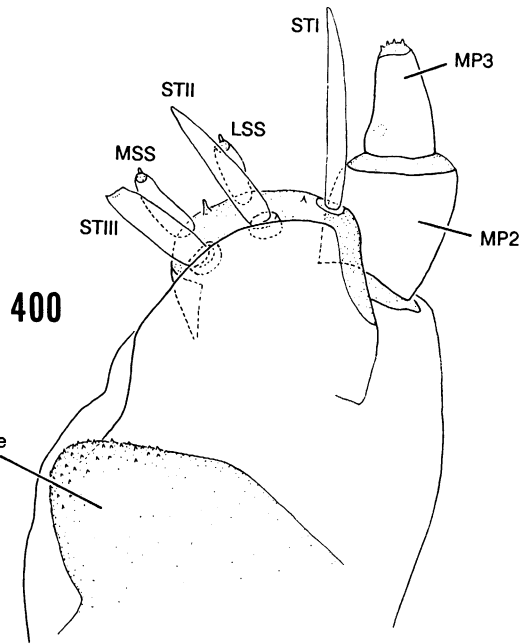
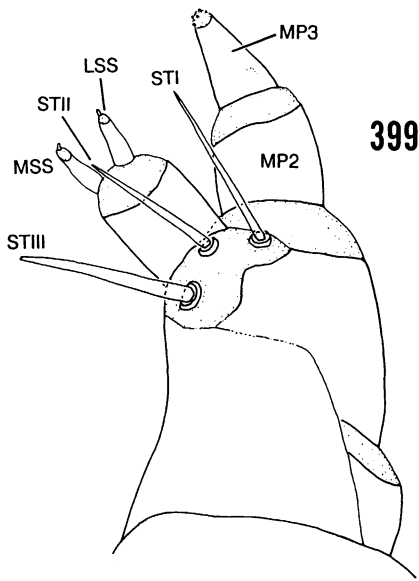
Fig. 398. Head of *Josia flavissima* Walker larva in lateral view. A = antenna. Ac = anteclypeus. H = hypopharynx. Lb = labrum. M = mandible. ML = mesal lobe. Mx = maxillary palpus. P1 = seta P1. P2 = seta P2. S = stipital lobe. Sp = spinneret (overlaid by labial palpus). Scale line = 1.0 mm.

ever, in species with the derived state, STI is shorter than the palpus (figs. 405–407, 409).

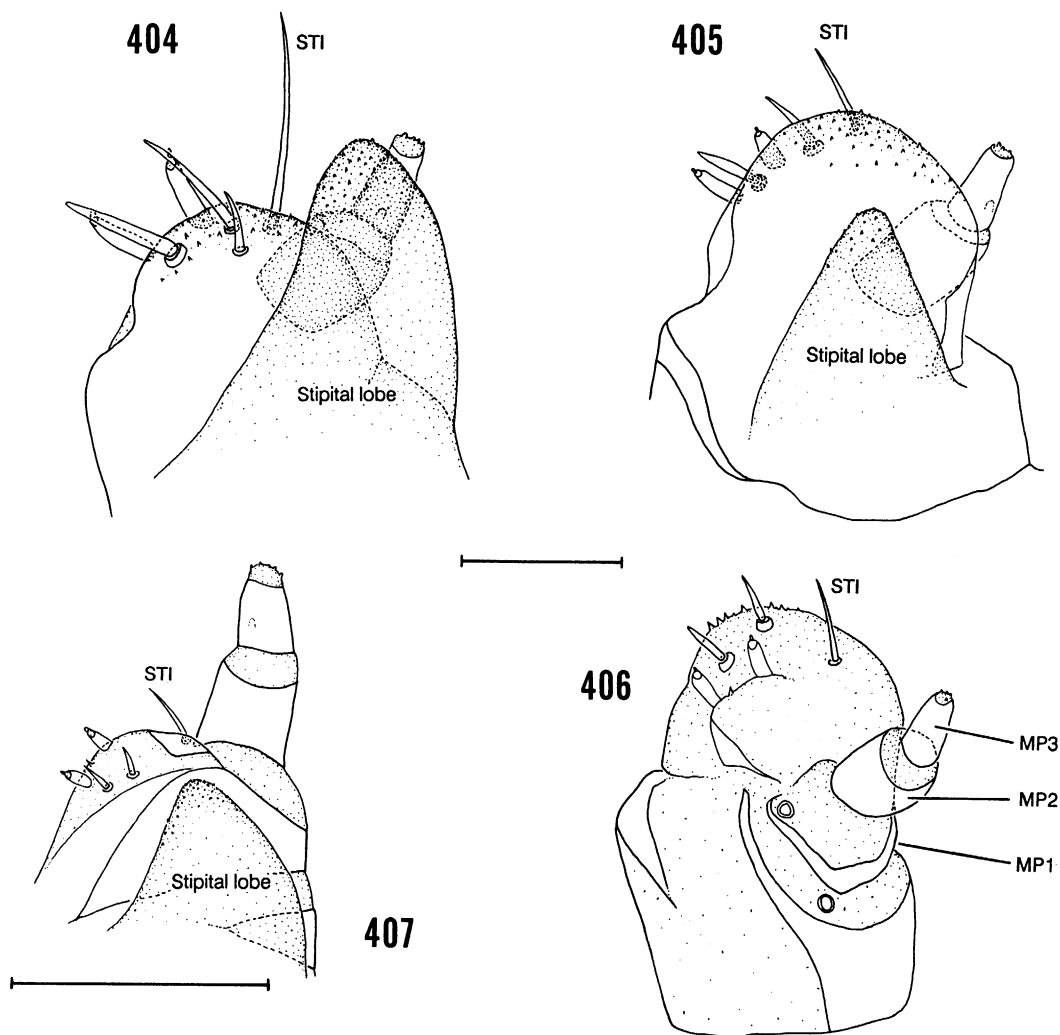
This character provides an important synapomorphy for the Nystaleinae + Dioptinae (Clade 45); small sensilla trichodea and styloconia occur in larvae of all the dioptines examined as well as in all five of the nystal-

eines. Among these, only *Josia* did not exhibit the broadly expanded mesal lobe (fig. 407). The derived state is not unique to Clade 45, however. It also occurs in *Quadricalcarifera* and *Liparopsis* (Notodontinae).

Character 119. Tips of Sensilla Trichodea Forked. Sensilla trichodea II and III on the



Figs. 399–403. Right mesal maxillary lobe and maxillary palpus of larval Noctuoidea, dorsoposterior view (anterior at top). **399.** *Peridroma saucia* (Noctuidae). **400.** *Phalera bucephala*. **401.** *Hemiceras bilinea*. **402.** *Nadata gibbosa*. **403.** *Crinodes besckei*. LSS = lateral sensillum styloconicum. MP = segment of maxillary palpus. MSS = medial sensillum styloconicum. ST = sensillum trichodeum. Scale line for figures 399–402 = 200 μ m; for figure 403 = 400 μ m.



Figs. 404–407. Right mesal maxillary lobe and maxillary palpus of larval Notodontidae, dorsoposterior view (anterior at top). **404.** *Lochmaeus bilineata*. **405.** *Symmerista albifrons*. **406.** *S. albifrons* (ventral view). **407.** *Josia ligata*. For symbols, see figures 399–403. Scale line for figures 404–406 = 400 μm ; for figure 407 = 100 μm .

mesal lobe have fork-shaped tips in three species: *Crinodes besckei* (fig. 403), *Goacampa variabilis*, and *Cargida pyrrha*, all members of the Dudusini. Occasionally, three distal points are observed on a single sensillum. The derived state is restricted to New World members of the Dudusini, but according to my data these species do not constitute a monophyletic group (fig. 100).

Character 120. Galeal Lobe Present. This character relates only to the outgroup. In some of the noctuid larvae I examined, the two

sensilla styloconica (MSS and LSS) are borne on a raised extension of the mesal lobe (fig. 399). An apparently identical structure, termed the “galeal lobe,” occurs in larvae of some Nymphalidae (Devries et al., 1985: fig. 1). Within Noctuidae, the galeal lobe may provide an important synapomorphy for a subset of lineages in the family. I found that the structure occurs in *Peridroma* (Noctuinae), *Alypia* (Agaristinae), and *Diloba*. Beck (1960) showed that it occurs in species of the Herminiinae and Plusiinae as well. The fig-

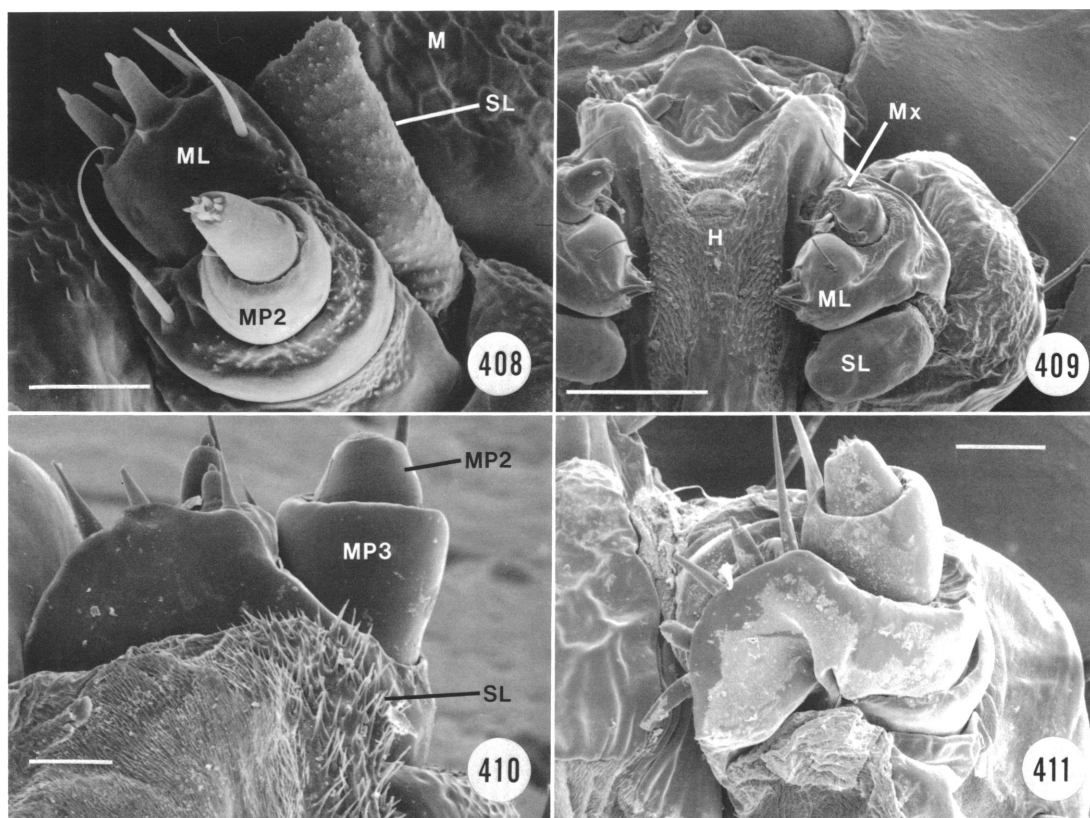


Fig. 408. Larval maxillary complex of *Zunacetha annulata* in frontal view with mandible intact, showing position of stipital lobe. Scale line = 50 μ m.

Fig. 409. Hypopharyngeal and maxillary complexes of *Phryganidia californica* larva in dorsal view with anterior at top. Scale line = 200 μ m.

Figs. 410, 411. Larval maxillary complexes of Noctuoidea in dorsoposterior view with anterior at top. **410.** *Doa ampla* (40 μ m). **411.** *Oenosandra boisduvalii* (100 μ m). H = hypopharynx. M = mandible. ML = mesal lobe. MP = maxillary palpus segment. Mx = maxillary palpus. SL = stipital lobe. Scale lengths in parentheses.

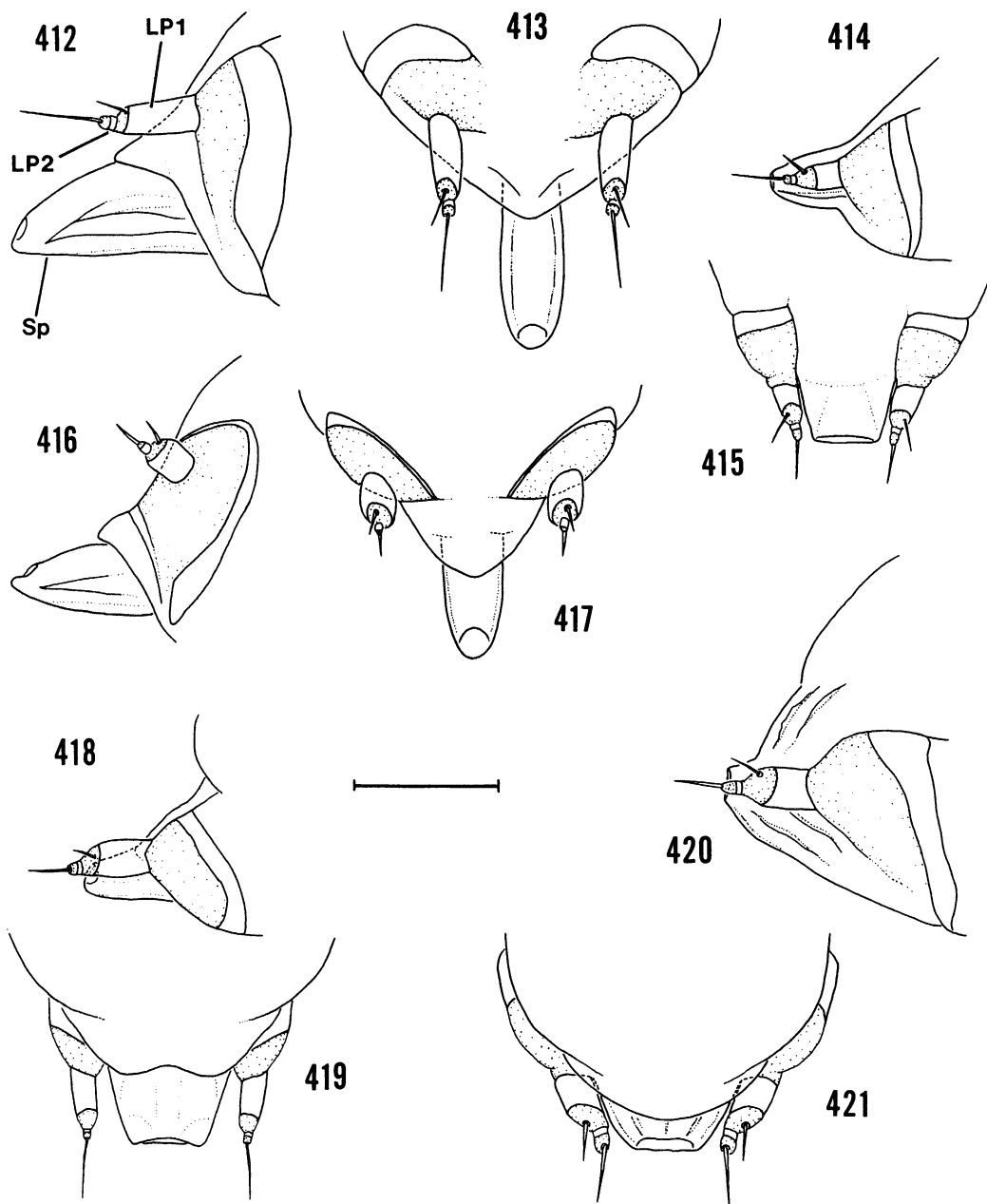
ures in Grimes and Neunzig (1986b) indicate that the galeal lobe occurs in Plusiinae and Heliiothinae. Detailed study of this character among additional members of the Noctuoidea is clearly warranted.

Character 121. Length of Maxillary Palpus Segment 3. I used two characters to describe the relative length of the maxillary palpus. The first was whether segment 3 is long and thin. In three species of Nystaleinae, in *Erbesa glaucaspis* (Dioptinae), and in *Hemiceras* (fig. 401), the third segment is elongate and narrows distally.

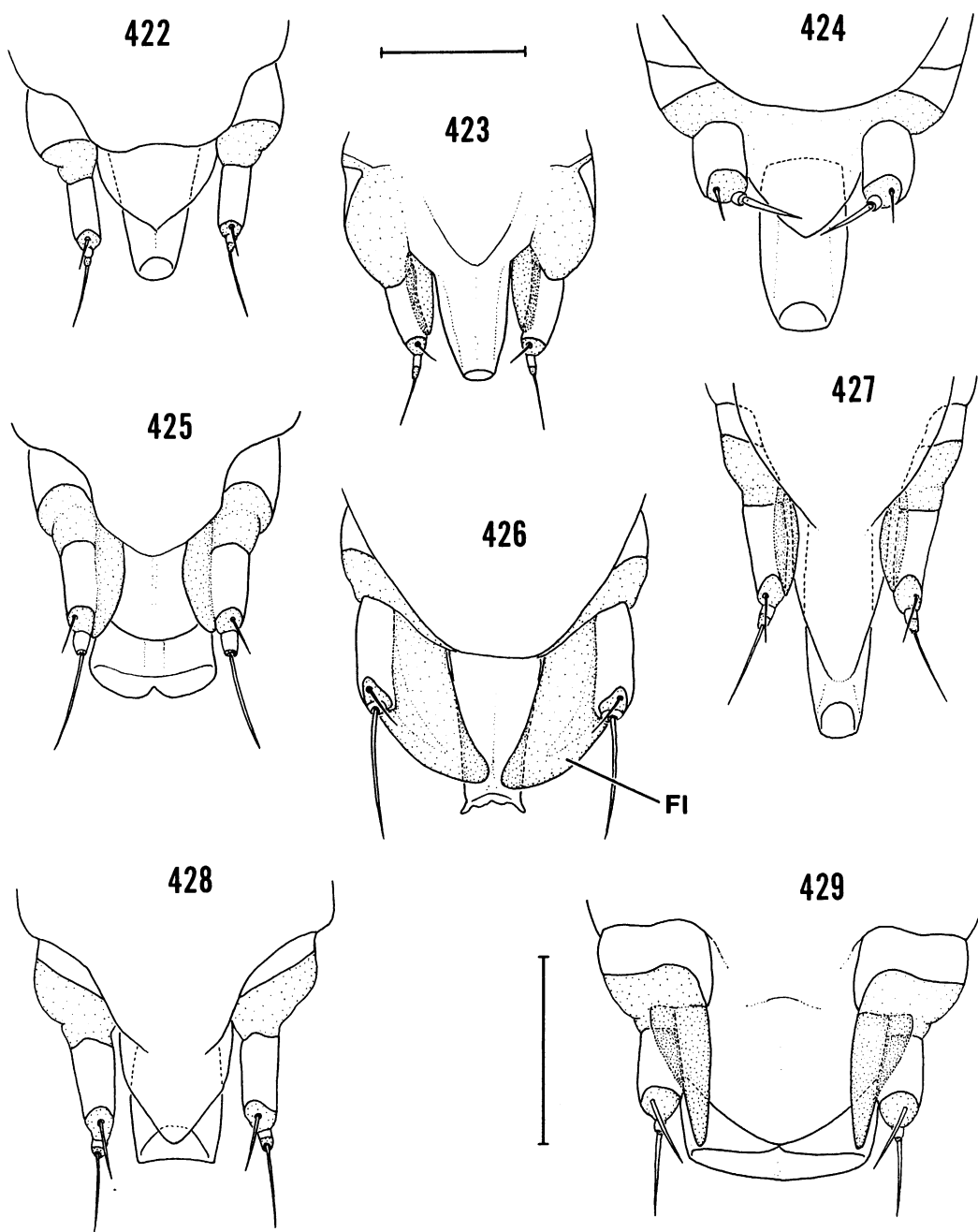
Character 121, as currently conceived, shows low consistency and I do not have much confidence in it. The derived state represents

one of the few apomorphies that *Hemiceras* shares with the Nystaleinae and Dioptinae. However, the majority of character evidence suggests that a direct relationship between *Hemiceras* and the nystaleine/dioptine clade is unlikely (see discussion in Classification of the Notodontidae).

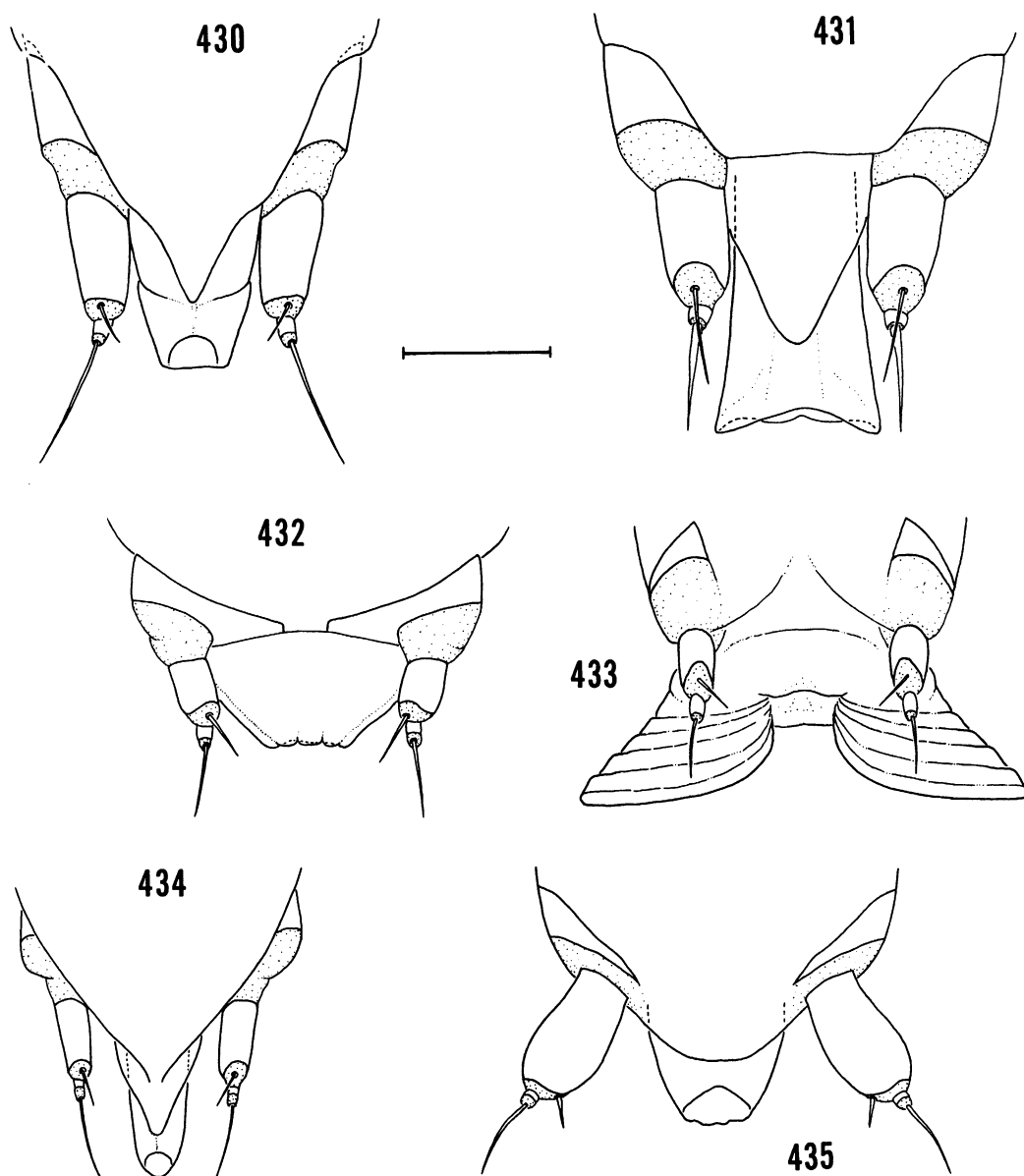
Character 122. Length of Maxillary Palpus Segment 2. The other character describing maxillary palpus length concerns segment 2. I gave the derived score (segment 2 elongate) only to taxa, such as *Hemiceras* (fig. 401), where there was no doubt. Contrary to expectation, species with a long third segment (Character 121) were not the same as those with an elongate second segment, with the



Figs. 412-421. Larval labial complexes of Noctuoidea. 412. *Dasychira dorsipennata* (Lymantriidae), lateral view with anterior at left. 413. *D. dorsipennata*, dorsal view with anterior at bottom. 414. *Josia flavissima*, lateral. 415. *J. flavissima*, dorsal. 416. *Traumatocampa pityocampa*, lateral. 417. *T. pityocampa*, dorsal. 418. *Symmerista albifrons*, lateral. 419. *S. albifrons*, dorsal. 420. *Macrurocampa marthesia*, lateral. 421. *M. marthesia*, dorsal. LP1 = labial palpus segment 1. LP2 = labial palpus segment 2. Sp = spinneret. Scale line = 200 μ m.



Figs. 422–429. Larval labial complexes of Notodontidae in dorsal view with anterior at bottom. 422. *Clostera albosigma*. 423. *Gluphisia septentrionis*. 424. *Antheua simplex*. 425. *Gargetta costigera*. 426. *Scrancia stictica*. 427. *Ellida caniplaga*. 428. *Notodonta scitipennis*. 429. *Cerura tattakana*. Note membranous medial flange (FI) on labial palpi in figures 423, 425–427, and 429. Scale line for figures 422–428 = 200 μm ; for figure 429 = 400 μm .

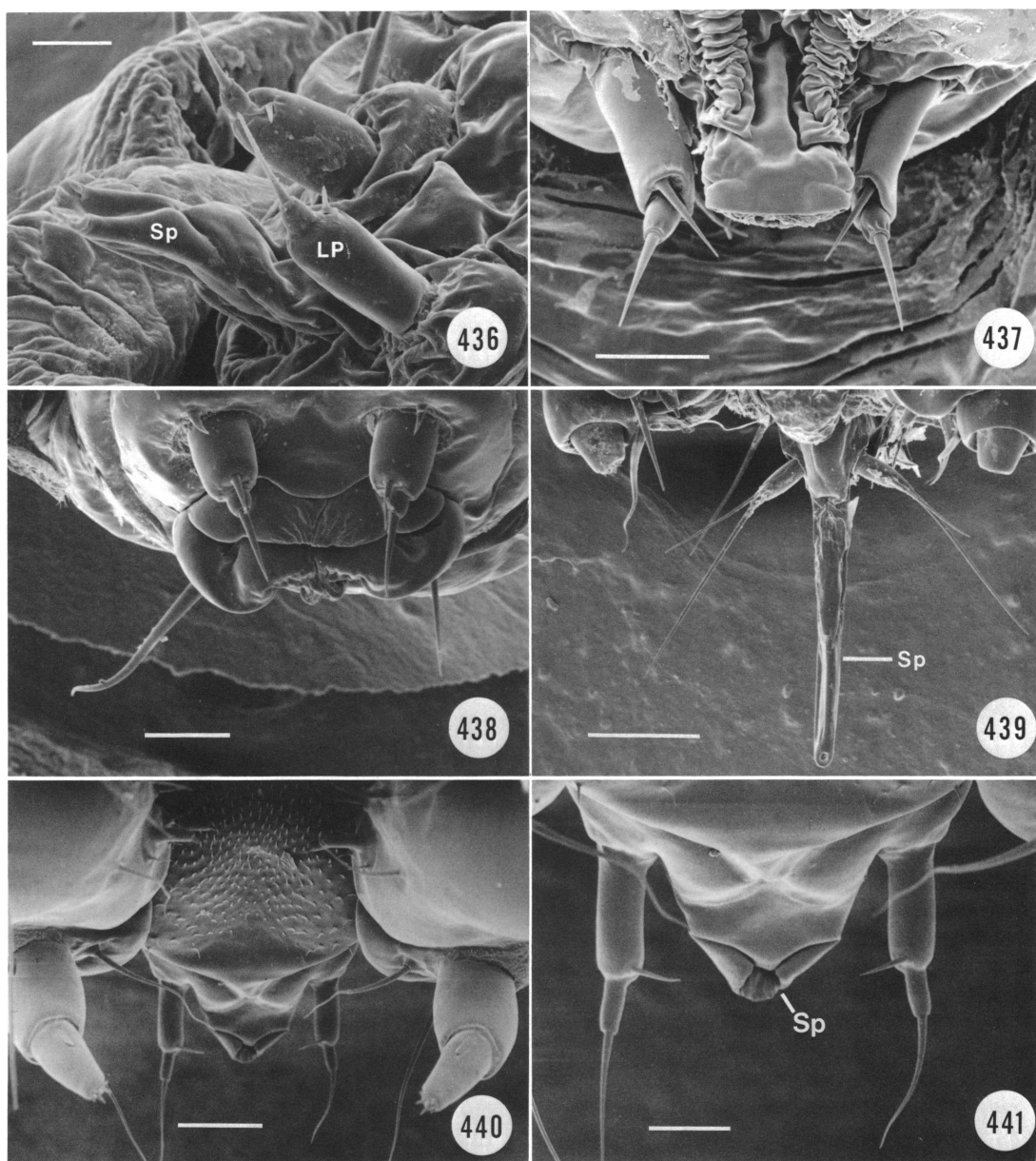


Figs. 430–435. Larval labial complexes of Notodontidae in dorsal view with anterior at bottom. **430.** *Nadata gibbosa*. **431.** *Tarsolepis japonica*. **432.** *Stauropus fagi*. **433.** *Cnethodonta grisea*. **434.** *Hemiceras bilinea*. **435.** *Phalera bucephala*. Scale line = 200 μ m.

exception of *Hemiceras*. Segment 2 of the maxillary palpus is also elongate in *Dudusa*, *Crinodes* (fig. 403), and *Lirimiris*. As with segment 3 (above), I have little confidence in this character.

Hypopharyngeal Complex: The hypopharyngeal complex comprises the hypopharynx,

labial palpi, and spinneret (Godfrey, 1972; Stehr, 1987a). I did not examine variation in fine structure of the hypopharynx, but based on the results of Godfrey (1972) and Beck (1960) for Noctuidae, this character may prove to be phylogenetically informative in the Notodontidae. The nomenclature I fol-



Figs. 436–439. Larval labial complexes of Noctuoidea. **436.** *Odontotia elegans*, dorsolateral view (50 μm). **437.** *Heterocampa obliqua*, dorsal view (80 μm). **438.** *Doa ampla*, dorsal view-20(40 μm). **439.** *Oenosandra boisduvalii*, dorsal view (200 μm). LP = labial palpus. Sp = spinneret. Scale lines in parentheses.

Figs. 440, 441. Larval mouthparts of *Didugua argentilinea* in dorsal view, anterior at bottom. **440.** Maxillary and labial complex (100 μm). **441.** Spinneret and labial palpi (50 μm). Sp = spinneret. Scale lengths in parentheses.

low is from noctuid workers (Ripley, 1923; Crumb, 1956; Beck, 1960; Godfrey, 1972).

Character 123. Hypopharynx Expanded Dorsally. I used only a single character involving the larval hypopharynx, although others undoubtedly exist. The character I used does not require SEM for study. Larvae of some Notodontidae have the hypopharynx greatly expanded dorsally. In these it also protrudes anteriorly, sometimes beyond the tip of the spinneret. Among the taxa I examined, the apomorphic state occurs in three closely related genera—*Stauropus*, *Cnethodonta*, and *Harpyia*—as well as in *Schizura unicornis*, *Erbessa glaucaspis* (Dioptinae), and *Scrancia stictica*. This trait indicates that the genus *Schizura* is not monophyletic (Clade 39, fig. 100).

Character 124. Length of the Labial Palpus. I recognized four character states involving structure of the labial palpus, only three of which relate to the ingroup. In evaluating length, I compared the labial palpus to the length of maxillary palpus segment 1 because the two appear to vary independently. In the majority of Notodontidae the labial palpus is approximately equal in length to segment 1 of the maxillary palpus (fig. 440). This is also true of all outgroup species. A derived state occurs in some Heterocampinae, in all Dioptinae, and in *Lirimiris*. Here, the labial palpus is small, much shorter than segment 1 of the maxillary palpus. In a third state, restricted to *Datana* and *Phalera* (fig. 435), the labial palpus is globose, wider distally than at its base. The final trait was observed only in the larva of *Oenosandra boisduvalii*, where the palpus and terminal seta are extremely long (fig. 439).

Character 125. Mesal Flange of the Labial Palpus. I discovered a character of the labial palpus that I have not seen previously described or figured, and that occurs only in Notodontidae as far as I am aware. Typically, the palpi are parallel-sided and segment 1 is entirely sclerotized. I observed a condition in which there is a membranous flange on the mesal margin of segment 1 in each palpus (figs. 423, 425–427, 429). These flanged labial palpi together with the spinneret seem to form a scoop-shaped structure. It may be that the flanges aid in applying silk during some sort

of specialized larval behavior, but I have no direct evidence.

Although palpus flanges are fairly easy to observe and I was confident in giving the derived score (flanges present = “1”), the taxonomic distribution of this trait conflicts somewhat with other character information. It provides corroborative evidence for the monophyly of Clade 17, that subset of the Notodontinae including *Gluphisia* and *Furcula* (fig. 99). However, the derived state also occurs in two anomalous positions on my cladogram, in *Gargetta* and *Scrancia* (Scranciini; figs. 425, 426), and in *Ellida caniplaga* (theoretically a member of the Phalerinae). The palpus flanges of *Scrancia* are highly developed, the largest I observed, and they are clearly present in *Ellida* (fig. 427). The phylogenetic position of the Scranciini is quite well supported, but that of *Ellida* is still far from clear (see Classification of the Notodontidae), and further research is required.

Character 126. Spinneret Length. Ripley (1923), Crumb (1956), and Merzhkevskaya (1988) regarded spinneret morphology to be a rich source of character information for the Noctuidae. Ripley suggested that “this appendage offers more extensive variation in caterpillars than any other structure” (1923: 20). Godfrey (1972) found that spinneret morphology provides useful diagnostic characters for some hadenine genera. I discovered numerous differences in spinneret morphology among notodontid species, and tried to describe these using five character states. However, I am not fully satisfied with my understanding of this character complex. Morphological differences in spinneret shape are probably associated with specialized behaviors; Ripley (1923) suggested that in Noctuidae, shape is correlated with mode of pupation. Increased knowledge of such specializations for notodontid caterpillars might provide clues concerning the characters themselves.

Based on my study, the primitive spinneret type is narrow in dorsal view and longer than the labial palpi. In these, the spinneret and palpi are not apposed. Examples are the spinnerets of *Traumatocampa pityocampa* (figs. 416, 417) and *Clostera albifrons* (fig. 422). A derived state occurring in many Notodonti-

dae is a spinneret that is shorter or barely longer than the labial palpi, with the palpi and spinneret apposed (scored as "1"). Taxa with this configuration include *Josia flavissima* (figs. 414, 415), *Didugua argentilinea* (figs. 440, 441), most heterocampine larvae (figs. 420, 421, 437), *Cerura* (fig. 429), *Furcula*, and *Lirimiris*. The only species outside the Notodontidae scored as "1" is *Doa ampla* (fig. 438). A third type, found in most Dudusini (e.g., fig. 431) and in *Ellida caniplaga* (fig. 427), is a spinneret that is approximately twice as long as labial palpus segment 1. According to my cladogram (figs. 99, 100), a short spinneret evolved at least three times in the Notodontidae: in *Lirimiris*; in Clade 20 of the Dicranurini; and in Clade 35, the group comprised of the Dioptinae, Nystaleinae, and Heterocampinae.

I recognized two additional states. The first is autapomorphic for *Cnethodonta griseus-cens*, where the spinneret is greatly modified with two huge winglike lateral flaps (fig. 433) that are covered with grooves. In the final character state, restricted to *Oenosandra* (fig. 439) and the Arctiidae, the spinneret is extremely long and narrow.

The only previous reference to notodontid spinneret size can be attributed to Gardner, who noted that in "many Notodontids the spinneret is truncate apically and projects only slightly beyond the basal segment of the labial palpi" (1946: 141). He figured the spinneret of *Cerura liturata* Walker as an example. Gardner contrasted this with the spinneret of *Thaumetopoea cheela* Moore, which he described as being slender and projecting well beyond the labial palpi. Other references to notodontid spinneret shape are rare. Sugi and Nakamura (1988) illustrated the spinneret and labial palpi of *Periergos magnus* (Matusmura), a species with uncertain subfamilial placement.

Beck (1960) and Godfrey (1987b) also used relative lengths of the spinneret and labial palpus as a character, both authors showing that numerous differences exist among larvae in the Noctuidae.

Character 127. Spinneret Dorsoventrally Compressed. I further characterized spinneret shape. In the plesiomorphic condition, the spinneret is roughly elliptical in cross section

and the opening is ovoid. This is true, for example, of *Clostera*, *Gluphisia*, *Antheua* (figs. 422–424), and the outgroup (fig. 413; and see fig. 28 in Beck, 1960). Some notodontid larvae have a dorsoventrally compressed spinneret. Examples are *Tarsolepis* (fig. 431), *Gargetta* (fig. 425), and *Cerura* (fig. 429). My cladistic results indicate that a flattened spinneret evolved separately in two notodontid subfamilies, the Notodontinae and Dudusinae.

Character 128. Hypopharyngeal Folds. In some Heterocampinae, there is a series of membranous folds located at the base of the spinneret and extending up onto the hypopharynx (fig. 437). This condition also occurs in larvae of *Quadricalcarifera viridimaculata*. I did not observe such folds in other caterpillars.

Character 129. Submentum with a Medial Cleft. According to Peterson, the spinneret and labial palpi are attached to the "stipes labii" (1962: fig. L4-G). Posterior to that are the mentum and submentum. In larvae of three notodontine genera (*Odontosia*, *Pheosia*, and *Liparopsis*) and one phalerine genus (*Peridea*), the submentum is swollen and has a deep medial cleft. Species with the plesiomorphic state have a submentum that is essentially flat, without a fold.

Character 130. Mentum Swollen. A modification of the mentum occurs in all nystaleine larvae I studied. Here the mentum is swollen and its surface has a glandular appearance. I found a further modification in two nystaleines, *Nystalea nyseus* and *Dasylophia thyatiroides*, where the mentum is swollen with two large lateral projections. Similar projections have been reported in earlier instars of notodontid caterpillars from other subfamilies (Godfrey et al., 1989), but for final instars I found them only in the two species above. It is not known whether the mentum of nystaleine larvae is truly glandular, and, if so, what its function might be.

THORAX

Integument: Character 131. Larval Integument "Shagreened". Scanning electron micrographs suggest that the larval integument of notodontids is usually crenulate (e.g., fig.

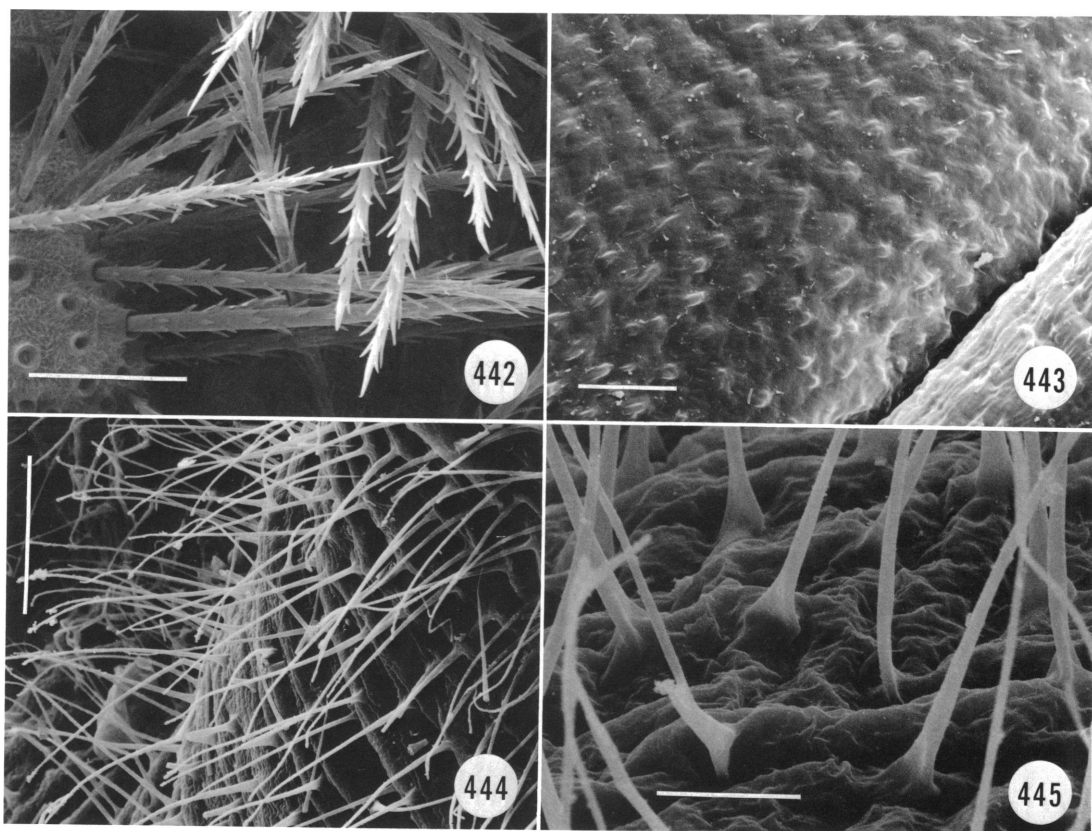


Fig. 442. Secondary setae on thoracic scoli of *Spilosoma virginica* (Arctiidae) larva. Scale line = 100 μ m.

Fig. 443. Cuticular surface of *Hippiia packardii* larva on eighth abdominal segment. Scale line = 20 μ m.

Figs. 444, 445. Cuticular surface of *Zunacetha annulata* larva. 444. Region near proleg base (segment A3) showing long microprojections (40 μ m). 445. Bases of microprojections in figure 444 (10 μ m). Scale lengths in parentheses.

443). Even in cases where the cuticle appears smooth when examined at $\times 60$ – 100 , SEM reveals a crenulate microsculpture. I found that all tagma except the head have the same type of integument sculpturing. Crumb (1956), Godfrey (1980, 1987b), and Merzheevskaya (1988) illustrated differences in skin texture between species of Noctuidae, some being granulate or spiculate. Leidy and Neunzig (1989) have demonstrated variation in integumental microsculpture even among closely related species of *Dioryctria* (Pyrilidae: Phycitinae). Unfortunately, it was not possible to study the cuticle of all exemplar species with SEM. I instead focused on two

unique modifications of the integument that have been discussed in the literature.

All diopline larvae have extremely long microprojections covering the entire body (figs. 444, 445, 519), a condition that has been termed "minutely rugose" (Forbes, 1939a) or "shagreened" (Peterson, 1962). Previous authors, all of whom relied exclusively on examination of *Phryganidia californica*, considered this to be a unique character for the Dioplineae (Fracker, 1915; Forbes, 1939a, 1948; Godfrey and Appleby, 1987). However, a similar integument structure occurs in *Closteria* (fig. 494). There the microprojections are not as long as in dioplines. The

larval skin of *Doa* shows unique "integumental spinules" (Donahue and Brown, 1987; Brown, 1990). Unlike the microprojections of dioptines and *Clostera*, these appear to be socketed. I therefore did not consider the condition in *Doa* to be homologous with a shagreened integument.

Cervical Gland: *Character 132. Presence of a Cervical Gland.* A cervical gland, or adenosma (Weller, 1989), occurs in larvae of many noctuoids, but gland morphology and chemistry have been most thoroughly studied for the Notodontidae (see discussion in Godfrey and Appleby, 1987). The cervical gland, located ventrally between the head and prothoracic legs (fig. 448), is eversible and produces a spray that contains formic acid and ketones (Packard, 1895a; Herrick and Detwiler, 1919; Eisner et al., 1972; Weller, 1987) shown to have a defensive function (Eisner et al., 1972; but see Chow and Tsai, 1989). Some species can eject the spray rapidly, accurately, and for fairly long distances (Packard, 1895b; Herrick and Detwiler, 1919; Forbes, 1948; Hintze, 1969). Kearby (1975) found that the formic acid in cervical gland secretions of *Heterocampa manteo* (Double-day) was concentrated enough to produce fairly severe skin lesions.

Larval cervical glands are known from other families of Lepidoptera, including the Yponomeutidae (Povel and Beckers, 1982), as well as the butterfly families Hesperidae, Pieridae, and Nymphalidae (Bourgogne, 1951; Peterson, 1962). In each group, the glands are thought to serve a defensive function. Bourgogne (1951) suggested that *Dicranura* (= *Cerura*) *vinula* larvae employ prothoracic gland secretions during formation of the cocoon, which is particularly tough in this species.

Chemicals associated with the cervical gland have not been described for members of the quadrid Noctuoidea, so they cannot be compared with those of Notodontidae. However, gland shape differs between notodontids and other noctuoids. In the former, the extruded gland is dorsoventrally compressed and is strongly bifid (fig. 448; Ash, 1892; Gardner, 1943; Bourgogne, 1951; Weatherston et al., 1979; Weller, 1987). In contrast, the everted cervical gland of Noc-

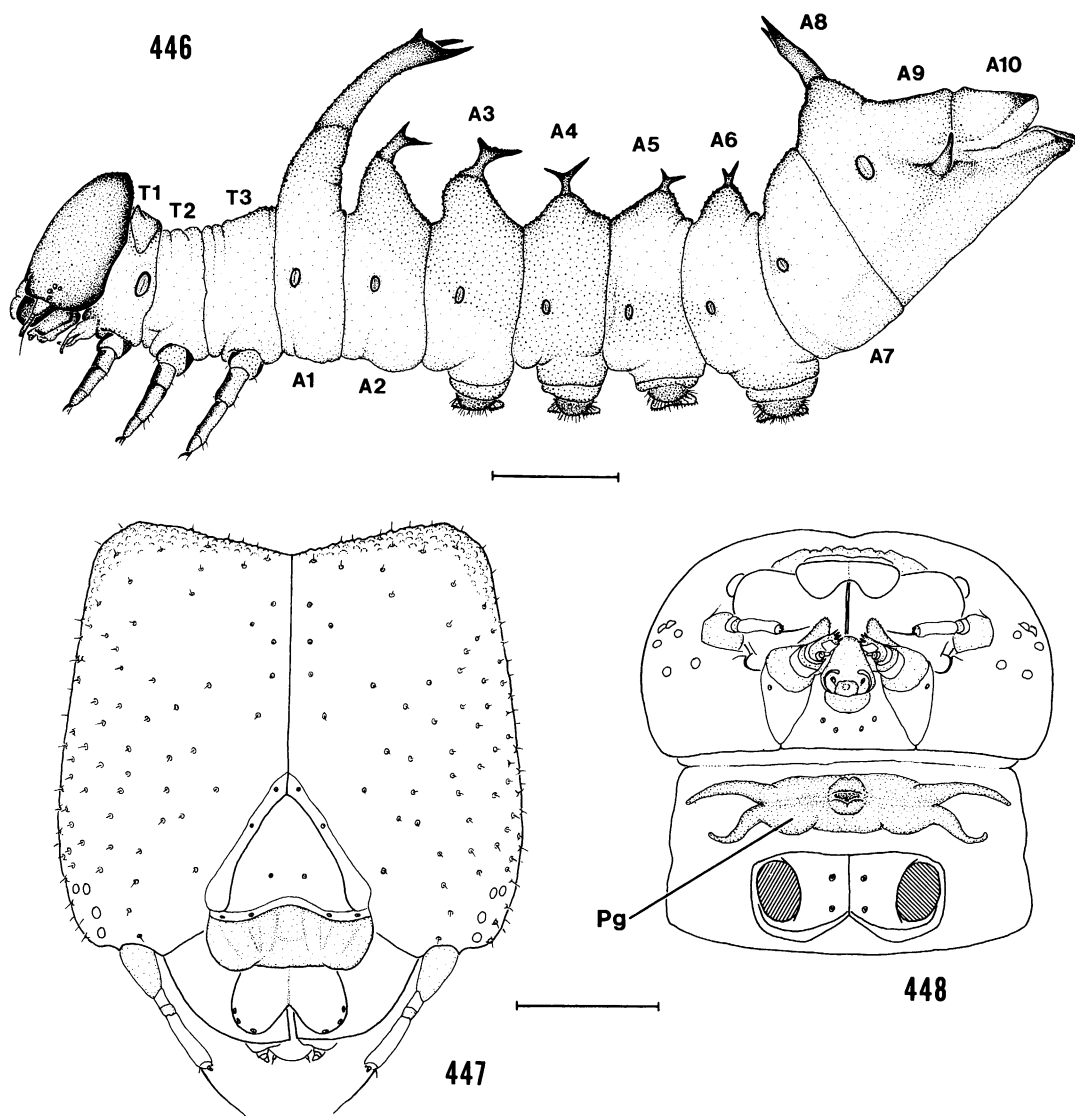
tuidae (e.g., *Alypia octomaculata*, fig. 362) is a simple smooth tube (Marti and Rogers, 1988) that is sometimes quite long. The cervical gland of dioptines is unusual among Notodontidae in having a noctuid-type shape. Unfortunately, I was unable to use cervical gland shape as a character for the ingroup. Interesting differences appear to exist, but the gland must be fully everted for such comparisons, and it was not possible to inflate it manually in preserved material.

Among the notodontid larvae I examined, a cervical gland is absent in the thaumetopoeines, *Clostera* (see also Godfrey and Appleby, 1987), *Lirimiris*, and *Platychasma* (see p. 197). Some notodontid larvae exhibit a well-defined groove where the cervical gland is usually located, but no invagination. I was able to study two species of *Quadricalcarifera*, and this was true for both. Larvae of *Hemiceras* also lack a cervical gland invagination. Based on other character evidence, and because a distinct groove is present, I hypothesized that both of these genera have lost the cervical gland, and therefore gave them a second derived score ("2"). All other notodontids have a large cervical gland and were scored as "1". The cervical gland is absent in *Doa* (Brown, 1990) and *Oenosandra*. Among outgroup species, it is restricted to some Noctuidae (Appendix II).

My analysis indicates that the cervical glands of Notodontidae and Noctuidae are not homologous. The organs in these two families should be critically compared. Furthermore, a detailed comparative study of the histology and chemistry of notodontid cervical glands might provide data concerning phylogenetic relationships within the family.

Prothoracic Shield: Godfrey and Appleby (1987) noted variation in the size, amount of pigmentation, and degree of sclerotization of the notodontid prothoracic shield. I was unable to find many characters involving these differences. Shield boundaries are often difficult to detect in alcohol-preserved material. I therefore included only characters that were relatively unambiguous.

Stehr (1987b) claimed that dioptines can be distinguished from other notodontids by the relative lengths of the XD and D setae on the prothoracic shield (figs. 449, 450).

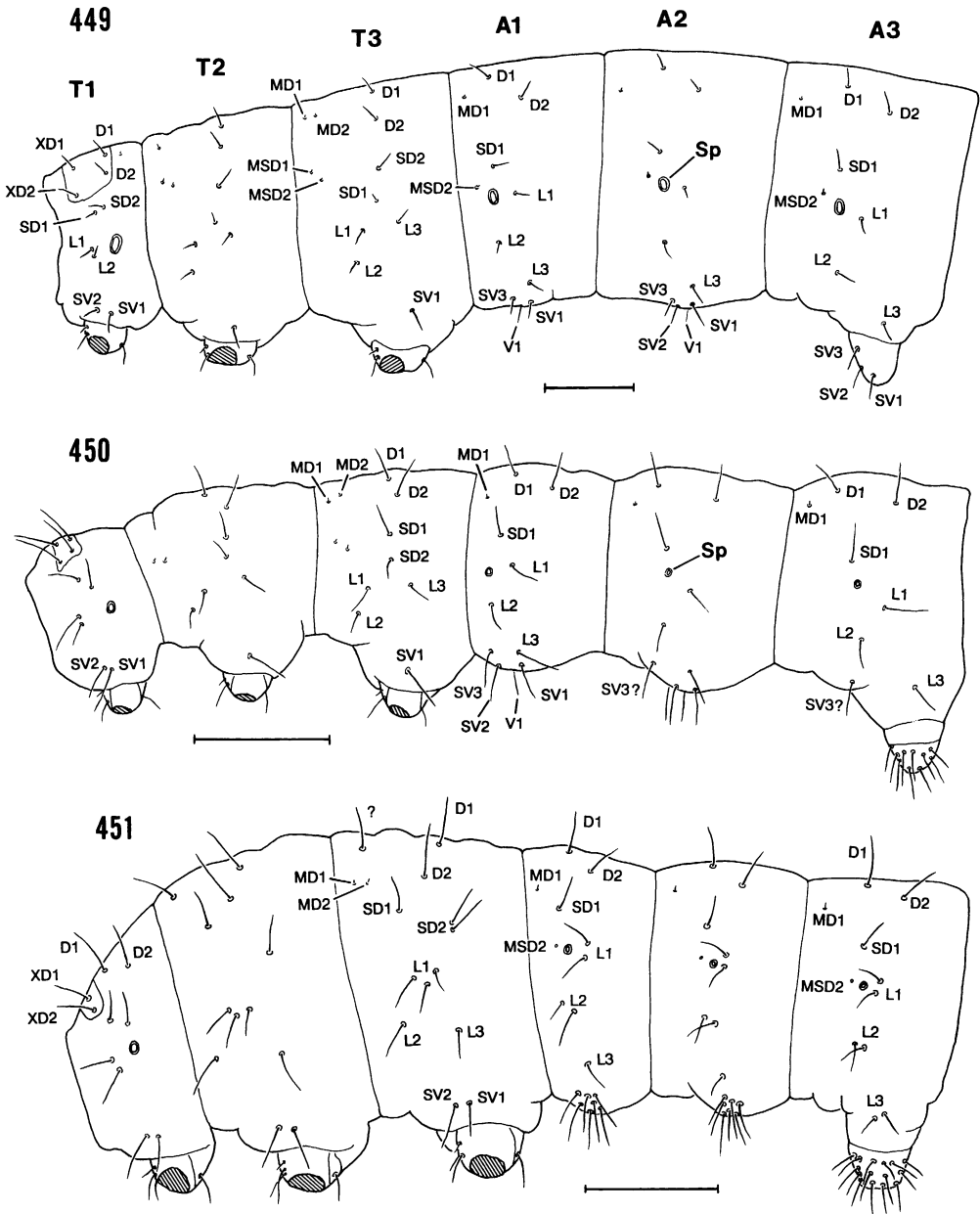


Figs. 446–448. Final instar larva of *Harpyia microsticta*. **446.** Habitus in lateral view. **447.** Head, frontal view. **448.** Head and first thoracic segment in ventral view (anterior at top), showing bifid prothoracic gland (Pg). A = abdominal segment. T = thoracic segment. Scale line for figure 446 = 5.0 mm; for figures 447 and 448 = 2.0 mm.

Dioptines purportedly have setae of equal length, whereas in other notodontid larvae the D setae are shorter than the XD's. I could not find reliable differences in setal length.

Character 133. Prothoracic Shield with Lateral Projections. Larvae belonging to two subfamilies, the Heterocampinae and Noto-dontinae, have lateral horns or bumps on the prothoracic shield (Packard, 1895a; Forbes, 1948; Klots, 1967; Weller, 1987). In both

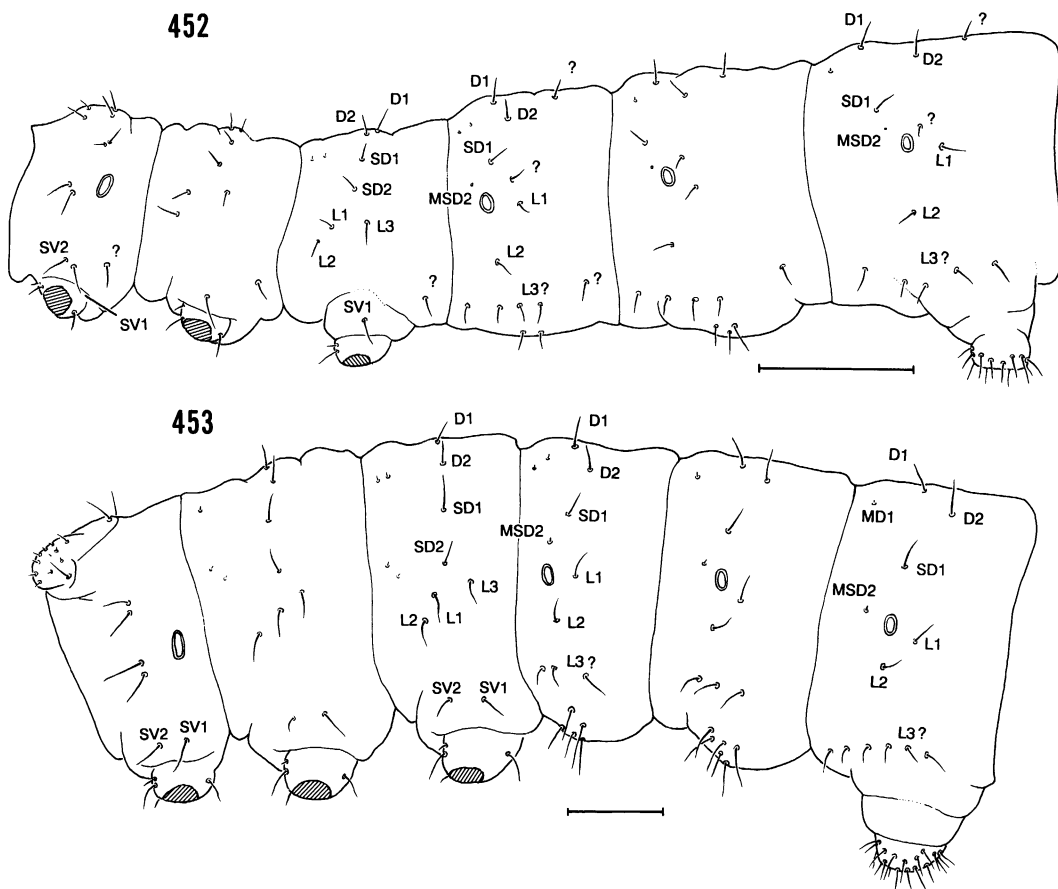
subfamilies, these protuberances bear the XD1 setae. The protuberances of heterocampine larvae are most pronounced during the first instar; Packard (1895a) and Gerasimov (1952) described the elaborate prothoracic "antlers" in first instars of some *Heterocampa* species and in *Macrurocampa*. Among noto-dontines, lateral prothoracic projections occur in *Quadricalcarifera*, *Cerura* (Issiki et al., 1969), and *Furcula* (fig. 453; Packard,



Figs. 449–451. Thoracic and first three abdominal segments of larval Noctuoidea in lateral view; thoracic legs and planta of proleg not shown. **449.** *Peridroma saucia*. **450.** *Josia ligata*. **451.** *Doa ampla*. A = abdominal segment. D = dorsal setae. L = lateral setae. MD = dorsal proprioceptor setae. MSD = subdorsal proprioceptor setae. SD = subdorsal setae. Sp = spiracle. SV = subventral setae. T = thoracic segment. V = ventral seta. XD = “XD” setal group. Scale lines = 2.0 mm.

1895a; Forbes, 1948). Packard showed that, as in Heterocampinae, the projections are more pronounced in early instars of *Furcula* species, although they are never antlerlike.

He used this ontogenetic similarity to claim that *Furcula* “has originated from the Heterocampinae” (1895a: 279). My results suggest that prothoracic projections are not ho-



Figs. 452, 453. Thoracic and first three abdominal segments of larval Notodontidae in lateral view; thoracic legs and planta of proleg not shown. **452.** *Gluphisia septentrionis*. **453.** *Furcula borealis*. For key to symbols see figures 449–451. Scale lines = 2.0 mm.

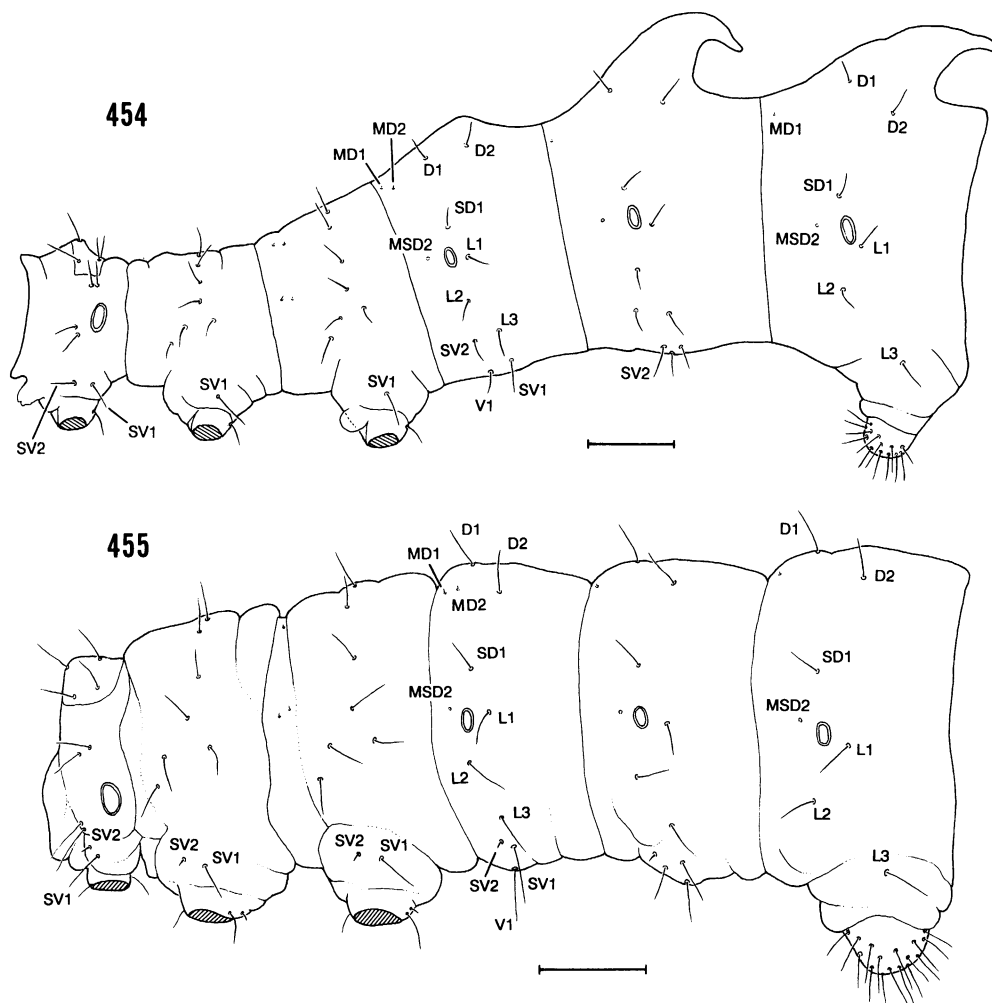
mologous in the two groups. There are obvious differences in tubercle shape, those of heterocampines being more acute and located in a more dorsal position.

Character 134. Prothoracic Shield Smooth. The prothoracic shield of *Crinodes*, *Cargida*, and *Goacampa* is large, smooth, and strongly sclerotized. It is almost square with an unpigmented medial line. Although a variety of prothoracic shield shapes exist among Notodontidae, none have such a configuration. Two larval characters, this one and Character 119 (presence of fork-shaped sensilla trichodea on the mesal lobe), indicate monophyly of the New World Dudusinae, although so far my data suggest otherwise (fig. 100).

Tactile Setae: I did not find variation in

number or shape for most primary setal groups on the thorax. However, the subventral (SV) thoracic setae provided three characters. For species with numerous secondary setae, these characters could not be scored because it was impossible to distinguish the SVs.

Character 135. SV Setal Formula. The number of SV setae on each thoracic segment (progressing from segment T1 to T3) is sometimes presented as a setal formula. These formulae, which vary among Lepidoptera, have been used as family level diagnostic features (e.g., Godfrey and Appleby, 1987). The formula typical of noctuid larvae is 2-1-1, as found, for example, in *Peridroma saucia* (fig. 449). Note that, for reasons unclear to me,



Figs. 454, 455. Thoracic and first three abdominal segments of larval Notodontidae in lateral view; thoracic legs and planta of proleg not shown. **454.** *Nystalea nyseus*. **455.** *Fentonia ocypte*. For key to symbols see figures 449–451. Scale lines = 2.0 mm.

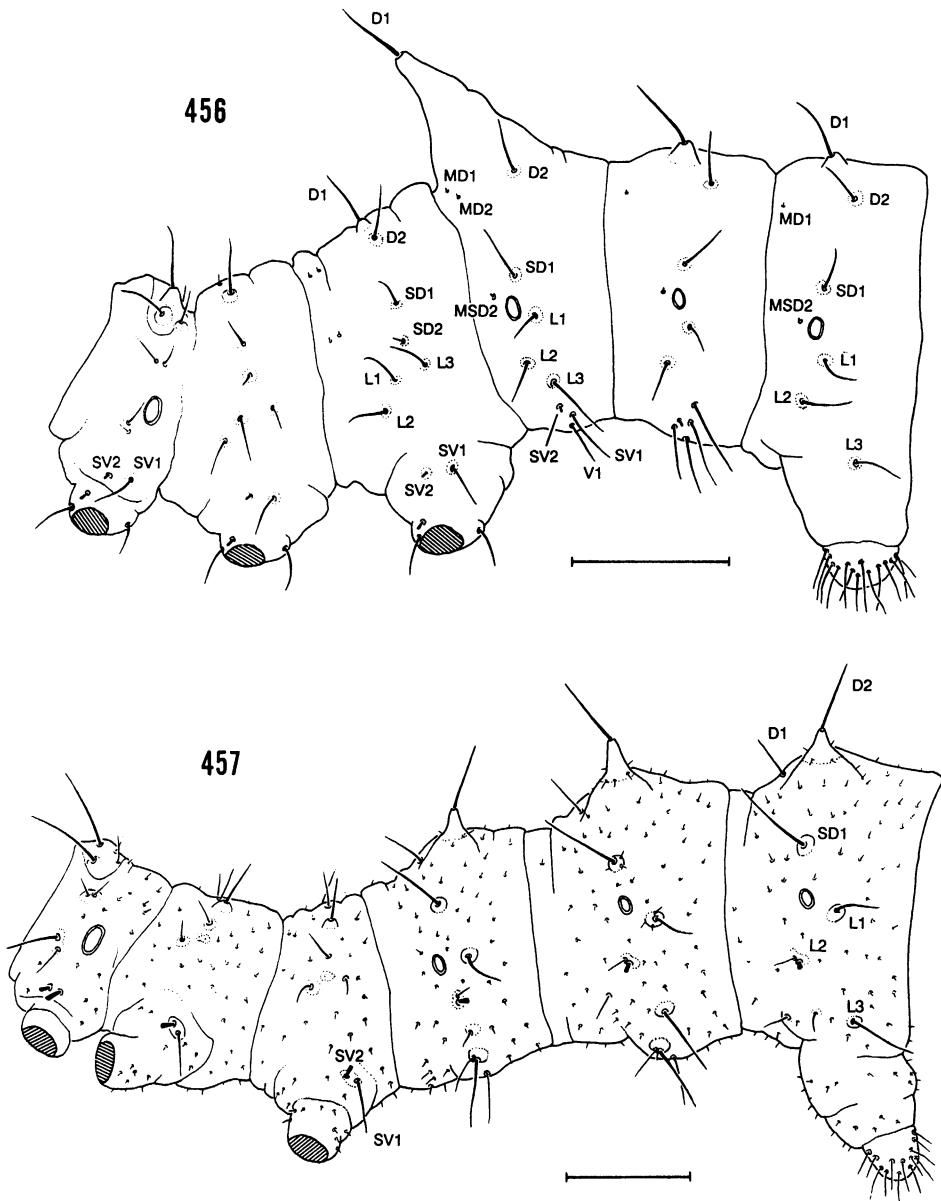
Hinton (1946) gave the anterior SV seta on T1 the number “2”.

Within the Notodontidae, the thoracic SV setae occur in either of two setal formulas. Most larvae exhibit the 2-1-1 condition (figs. 450, 452, 454) and these were scored as “0”. However, the SV setae of all Heterocampinae are in the formula 2-2-2 (figs. 455–457). This state shows a taxonomic distribution similar to the presence of protuberances on the prothoracic plate (Character 133); in addition to the Heterocampinae, it is found in *Quadricalarifera* and *Furcula* (fig. 453). Again, however, parsimony analysis suggests that the

2-2-2 SV formula evolved independently in the Heterocampinae and Notodontinae.

I had originally assigned a second derived state to the SV formula in *Gluphisia septentrionis*, which I characterized as being 3-2-2. After further study I realized that there is an additional seta (labeled “?” in fig. 452) in the SV region on all body segments of that species. I therefore amended my scoring so that *Gluphisia*, like *Liparopsis* in the Notodontinae, received a “0” score (2-1-1). This is, I believe, the correct interpretation.

Three outgroup species also exhibit the 2-2-2 formula. These are *Doa ampla* (fig. 451),



Figs. 456, 457. Thoracic and first three abdominal segments of larval Notodontidae in lateral view; thoracic legs and planta of proleg not shown. 456. *Schizura unicornis*. 457. *Cnethodonta grisescens*. For key to symbols see figures 449–451. Scale lines = 2.0 mm.

Hypoprepia miniata (Lithosiinae), and *Oenosandra boisduvalii*. Most arctiid caterpillars exhibit the 2-2-2 arrangement. Character optimization suggests that a 2-2-2 formula occurred in the common ancestor of Clade 2 (Doidae + Notodontidae). There are numerous taxa in both the ingroup and the out-

group where presence of secondary setae obscures the SV formula. These were given “?” scores (Appendix II).

Character 136. Shape of the SV Setae on T1. One of the most reliable synapomorphies for the Heterocampinae involves the shape of SV2 on the thoracic segments. As de-

scribed above, members of this subfamily have a 2-2-2 SV formula, and, in all species, SV2 on the first thoracic segment is short and usually spatulate (figs. 455–457). I am not certain whether modified SV2 setae occur in earlier instars as well. I have seen only one previous reference to these setae; Peterson (1962: fig. L25-C) noted their presence in larvae of *Heterocampa manteo* Doubleday.

As seems to be the case with almost every character I have studied, this one does not show complete consistency. In addition to the Heterocampinae, a short SV2 on T1 occurs in larvae of *Liparopsis postalbida* (fig. 460). There are two differences between the condition found in *L. postalbida* and the Heterocampinae. First, in the former, SV1 is also short, whereas SV1 in heterocampine larvae is as long as other primary setae (figs. 455–457). Second, the modified setae are spatulate in heterocampines (fig. 459) but round in *L. postalbida*. These differences suggest that the traits are not homologous. I did not study interspecific differences in SV setal shape among members of the Heterocampinae.

Character 137. Shape of the T2 and T3 SV Setae. The SV2 setae on thoracic segments 2 and 3 are sometimes modified as well, their shape being identical with the seta on T1 described above (Character 136). It appears that T1 and T2/T3 can be considered separate characters where presence of these specialized setae is concerned; there are species in which a short SV2 occurs on T1 but not on T2 and T3, but if T2 carries a modified seta T3 always does as well. I therefore recognized a second character to describe the presence of a short SV2 seta on T2/T3 (figs. 458, 459). This apomorphy occurs in all the heterocampine larvae I studied except *Stauropus fagi*. It does not occur in *Liparopsis postalbida*, providing further evidence that the modified seta on T1 is secondarily derived from the one in Heterocampinae.

Character 138. Primary Setae on Chalazae. The primary setae are borne on chalazae (Peterson, 1962; Merzhkevskaya, 1988) in four species of Heterocampinae. These chalazae are particularly pronounced for the dorsal setae. Taxa exhibiting the apomorphic state are *Schizura biedermani*, *Schizura unicornis* (fig. 456), *Stauropus fagi*, and *Cnethodonta griseascens* (fig. 457). Forbes (1948)

characterized three genera of the Heterocampinae—*Schizura*, *Hyparpax*, and *Oligocentria*—by the presence of chalazae, so the trait may be quite widely distributed in the subfamily. I also found chalazae in *Liparopsis postalbida*, and they occur in some noctuid larvae (Appendix II).

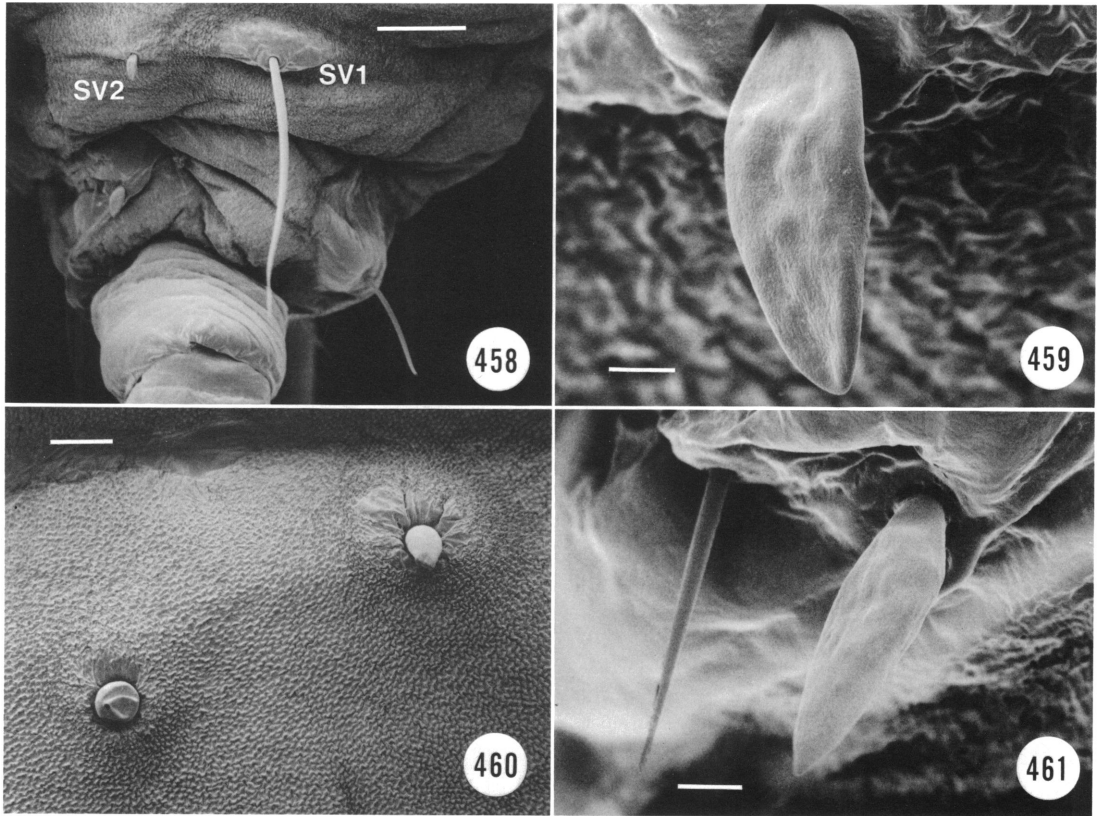
Proprioceptor Setae: Character 139. Metathorax with Two MD Setae. Hinton (1946) argued that the families Noctuidae, Lymantriidae, Arctiidae (including Lithosiinae), and Notodontidae (including Thaumetopoeinae) are related based on the presence of two, rather than one, MD proprioceptor setae on the metathorax, a derived condition in Lepidoptera according to him. I found this condition in all the taxa I examined (figs. 449–457). It may be an even more reliable synapomorphy for the Noctuoidea than presence of a metathoracic tympanum in adults, which is lost in some groups, such as members of the genus *Diophtis* (Forbes, 1916, 1922a).

Secondary Setae: Character 140. Body with Secondary Setae. Abbot (1927), who performed a series of experiments on *Datana* caterpillars, suggested that body secondary setae are sensitive to sounds of various frequencies.

Although the presence or absence of secondary setae has been accorded much phylogenetic significance in previous notodontid classifications (see, e.g., Forbes, 1948), this character shows an extremely high level of homoplasy. Secondary setae have evolved at least once in almost every major lineage. They occur in Thaumetopoeinae, *Clostera*, *Scranicia*, and *Lirimiris*, as well as in most members of the Phalerinae and in various genera of the Heterocampinae (*Stauropus* and related genera), Diophtinae (*Cyanotricha*), Nystalinae (*Dasylophia*), and Dudusini (*Goacampa*).

It is clear that not all of these cases are homologous. In an attempt to make some sense of this character, I tried to describe secondary setae in more detail than simple presence or absence by recognizing four character states. I feel that my approach is an improvement over previous discussions of the character, but it is still not entirely satisfactory. Recognizing four states, this character has a CI of 0.52.

A “0” score was given to species without



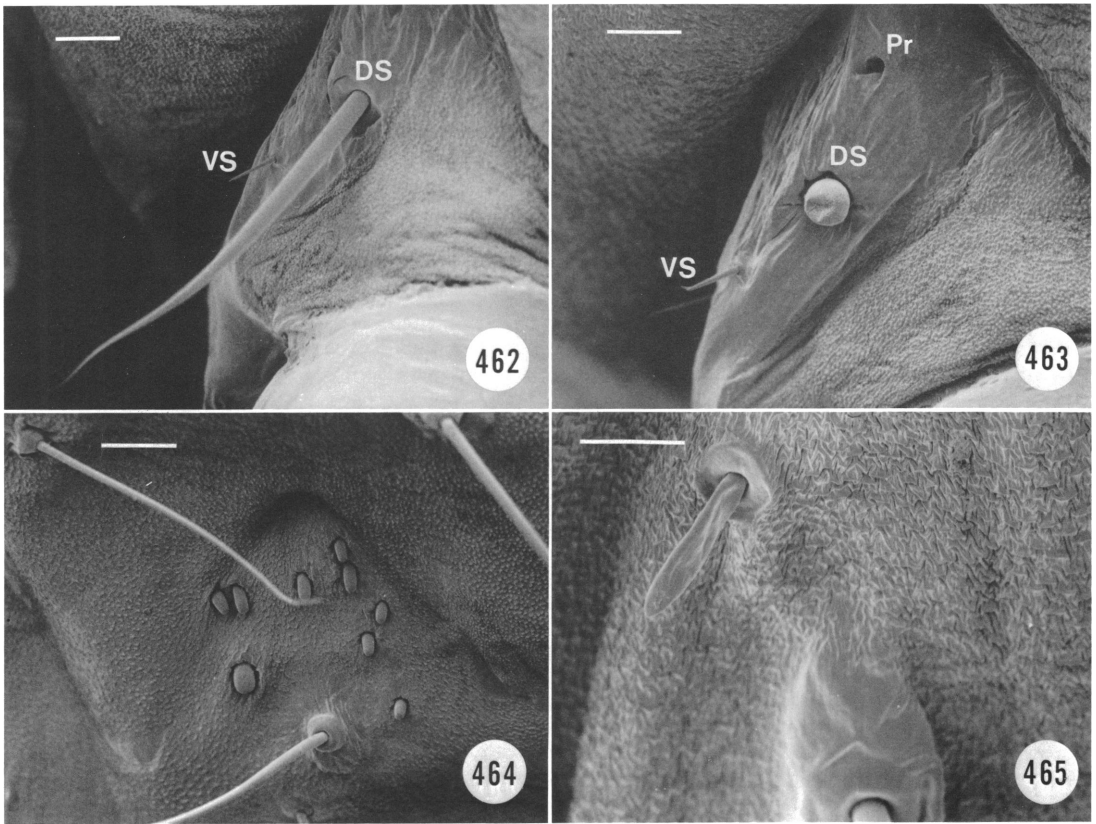
Figs. 458–461. Modified thoracic setae of notodontid larvae. **458.** Setae SV2 and SV1 on segment T3 of *Schizura unicornis* (200 μm). **459.** Detail of seta SV2 from figure 458 (10 μm). **460.** Setae SV1 and SV2 on segment T1 of *Liparopsis postalbida* (50 μm). **461.** Coxal setae on segment T2 of *Schizura unicornis* (20 μm). Scale lengths in parentheses.

secondary setae. However, there was considerable ambiguity involved in this decision, the problem being that in some species the body is not covered with secondary setae, but individual setae occur for which there are no primary setal names. *Gluphisia septentrionis* is an example (fig. 452). In that species there are from two to six setae on each body segment for which no names are available. I chose to give species such as *G. septentrionis* and *Hemiceras bilinea* (fig. 512) a score of “0” (secondary setae absent) on the albeit arbitrary grounds that the setae are not numerous enough. Taxa regarded as having secondary setae present were those where the setae are extremely numerous (e.g., *Clostera albosigma*, fig. 504).

For species with secondary setae I recognized three possible scores. First, the second-

aries are sometimes very long, but are grouped only at primary setal locations. Among Notodontidae, an example is *Antheua simplex* (fig. 506). This is also the state typical of outgroup species where secondary setae occur (Appendix II). A second state is exemplified by the thaumetopoeines and *Clostera* (figs. 503, 504), where the body is covered with secondary setae and the primaries are represented by groups of longer setae, sometimes borne on verrucae. In the final state, secondary setae are very short and are evenly scattered over the body. This occurs in Clade 40 (the three genera related to *Stauropus*) and in *Goacampa variabilis*. Whenever secondary setae occur either in the ingroup or the outgroup, they are almost always barbed (see discussion of head setae and fig. 442).

The presence or absence of secondary setae



Figs. 462, 463. Coxal setae of *Liparopsis postalbida* shown with anterior at left. **462.** Segment T1 (50 μ m). **463.** Segment T2 (50 μ m). DS = dorsal coxal seta. Pr = pore. VS = ventral coxal seta. Scale lengths in parentheses.

Figs. 464, 465. Modified SV setae on abdominal segments of Notodontidae. **464.** *Liparopsis postalbida* segment A2, showing the cluster of short SV setae (100 μ m). **465.** *Schizura unicornis* segment A1 (50 μ m). Scale lengths in parentheses.

has been given considerable taxonomic importance in discussions of quadrifid noctuid phylogeny, but I suggest that future workers define the character in a more precise way. Otherwise it should be regarded with caution.

Legs: Forbes noted the deeply cleft thoracic claws of thaumetopoeines (1910: fig. 97). I observed variation in claw shape among Notodontidae, but lacking SEMs for each species, I could not accurately characterize discrete states. Beck (1960) and Merzhkevskaya (1988) showed that marked differences in claw shape occur among various groups of the Noctuidae.

Character 141. Shape of the Coxal Setae. In all species I studied, the lateral surface of each thoracic coxa bears two setae. Typically,

the dorsal of the two setae is elongate and shaped like other primary setae, whereas the ventral one is short (fig. 462). Weller (1987) described an unusual condition in larvae of *Litodonta hydromeli* Harvey (Heterocampinae), where she termed the dorsal coxal seta "spindle-shaped." I found this to be true of all Heterocampinae examined (fig. 461) except *Lochmaeus bilineata*, where the plesiomorphic state occurs. Two genera in the Notodontinae also exhibit the derived state: *Liparopsis* (fig. 463) and *Cerura*. *Liparopsis* is unusual in that the modification occurs on T2 and T3, but not on T1. In Heterocampinae it occurs on all three thoracic segments.

Caterpillars of *Nystalea nyseus* appear to lack the ventral coxal seta. In addition, the

dorsal one is greatly elongate with a spatulate apex. The seta is located in a complex, ever-sible, membranous fold. Its function is unknown.

Character 142. Thoracic Legs Elongate. Larvae of *Stauropus* are famous for their greatly elongate thoracic legs (fig. 80; see also figures in Moore, 1882; Bourgogne, 1951; Gerasimov, 1952) and characteristic defensive posture, giving them the name "lobster moths" (Stephens, 1829; Grünberg, 1912; Pinhey, 1975; Carter, 1982). These caterpillars are thought to derive protection by mimicking spiders, although according to Sevas-topulo, the first instar *Stauropus* caterpillar is "a very good ant mimic both in appearance and behavior" (1947: 583).

Larvae of *Cnethodonta griseus* have femora and tibiae that are almost identical to *Stauropus*, and they assume the same posture (fig. 92; Issiki et al., 1969). In *Harpyia microsticta*, the femora and tibiae are elongate (figs. 79, 446), especially on the meta-thorax, although the legs of *H. microsticta* are not as highly modified as in *Stauropus* and *Cnethodonta*.

Tarsal Setae: One of the most interesting larval character complexes I studied involves the shape of tarsal setae found at the base of each claw (figs. 466–492). Although a nomenclature for thoracic leg setae is not in common usage, Beck (1960) did propose a numbering system for noctuid larvae. In his figure 80, he labeled the four tarsal setae simply "1, 2, 3, 4." Three of these are located on the mesal surface of the tarsus (fig. 467). Godfrey (1972, 1980), following Beck, applied the names "Ts1–Ts3" to them. The fourth is lateral in position, and Godfrey did not name it. I follow the systems of Beck and Godfrey, using the name "Ts4" for the lateral seta (fig. 467).

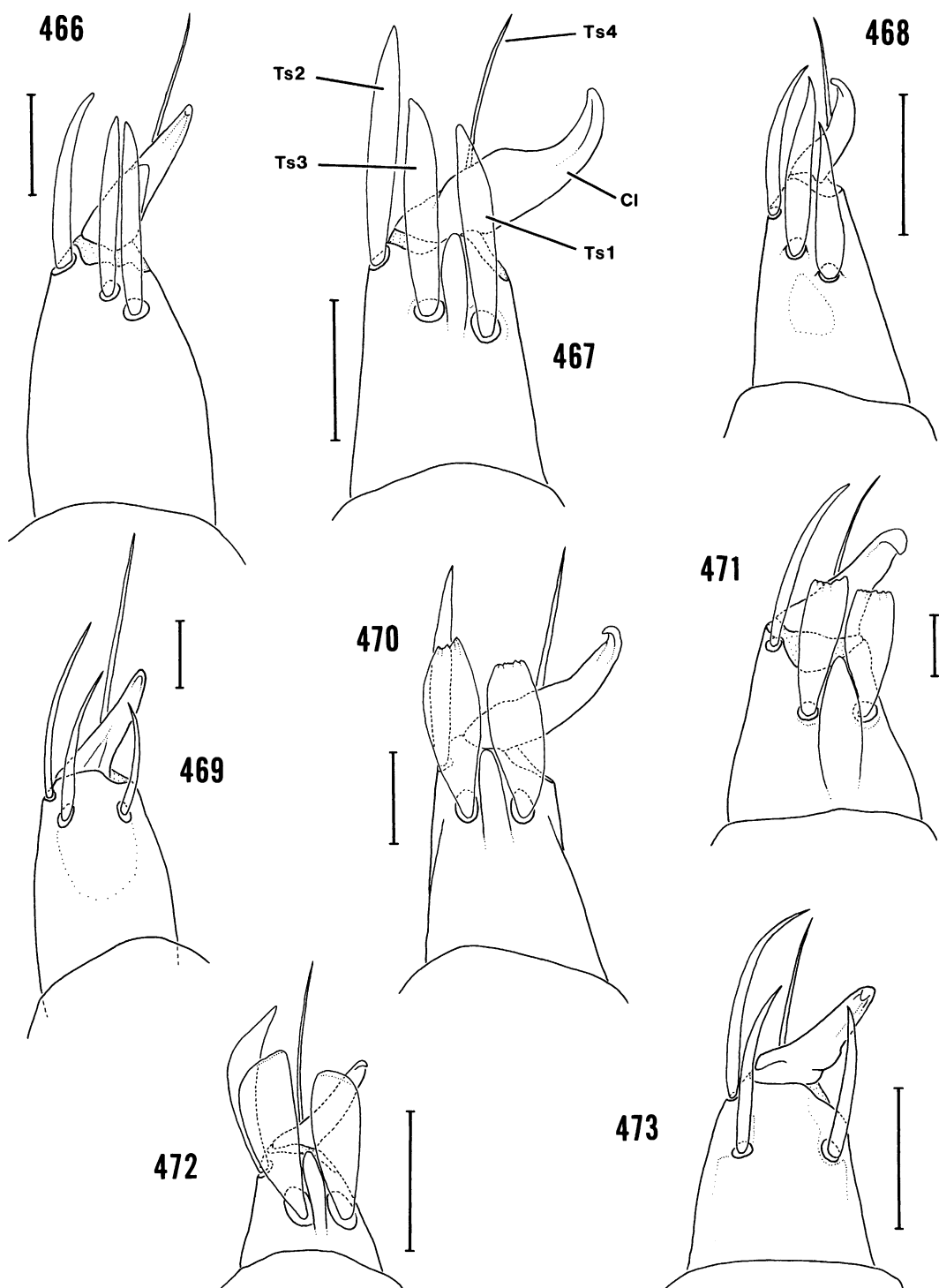
As far as I can determine by examining the literature, these four tarsal setae are found in all Lepidoptera. Their location is constant and setal homology can almost always be determined. Ts1 and Ts3 are more basal in position, while Ts2 is found in close proximity to the claw. Beck (1960) noted that, in Noctuidae, the basal tarsal setae, Ts1 and Ts3, are often broad, whereas Ts2 and Ts4 are normal in shape. Similarly, I found that in Notodontidae Ts1, Ts2, and Ts3 are modi-

fied; in almost all species they are flattened to some degree and are broader than other body setae. The lateral seta, Ts4, is always thinner than the mesal ones and it does not seem to show morphological variation. In my study, Ts4 did not provide useful character information.

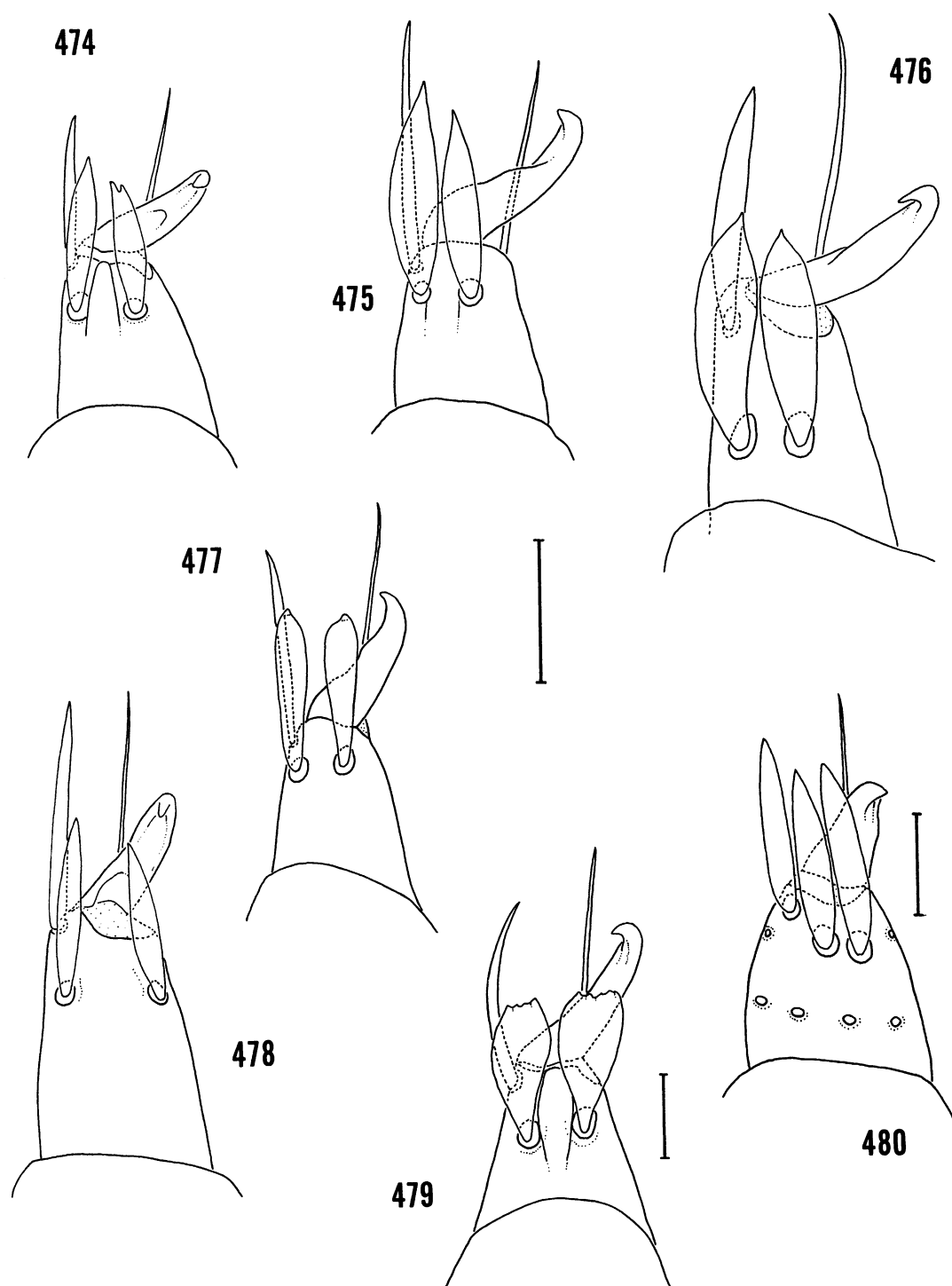
I found few previous discussions of tarsal setae for the Lepidoptera. They have been figured on occasion (e.g., Forbes, 1910: fig. 101; Godfrey, 1972: figs. 392, 393; Godfrey, 1980: figs. 16, 23), but have rarely been described in detail. Crumb (1956) and Merzheevskaya (1988) illustrated modified tarsal setae in various species of Noctuidae. Godfrey (1972) used the shape of Ts3 as a key character to separate two species of *Homorthodes* (Noctuidae: Hadeninae). Modified tarsal setae are not restricted to the Noctuoidea. Carter used "tarsi of thoracic legs with specialized flattened setae" ([with figure] in Holloway et al., 1987: 200) as a key character for the Agonoxenidae (Gelechioidea). This indicates that modified tarsal setae occur widely in the Lepidoptera. The only SEMs I found in the literature were published by MacKay (1972: fig. 52d), who showed modified tarsal setae in *Bucculatrix* (Lyonetiidae) species. She also presented line drawings showing shape variation among several microlepidopteran families. The function of these setae is unknown.

The surface of notodontid tarsal setae can be smooth (e.g., fig. 485) or sculpted, either with many fine grooves (e.g., *Heterocampa obliqua*, fig. 486; *Liparopsis postalbida*, fig. 489) or with a single shallow groove (e.g., *Epicoma melanosticta*, fig. 488). Close examination of the raised pad between Ts1 and Ts3 in *Nystalea nyseus* reveals that its surface is minutely rugose (fig. 490), possibly glandular. It should be noted that the setae are soft rather than being heavily sclerotized. Critical-point drying was necessary to prepare them for SEM, otherwise they shriveled when removed from ethanol. I did not find variation in setal shape between legs on different thoracic segments, except that they are present only on the prothoracic legs of *Stauropus* and *Cnethodonta* (Character 145).

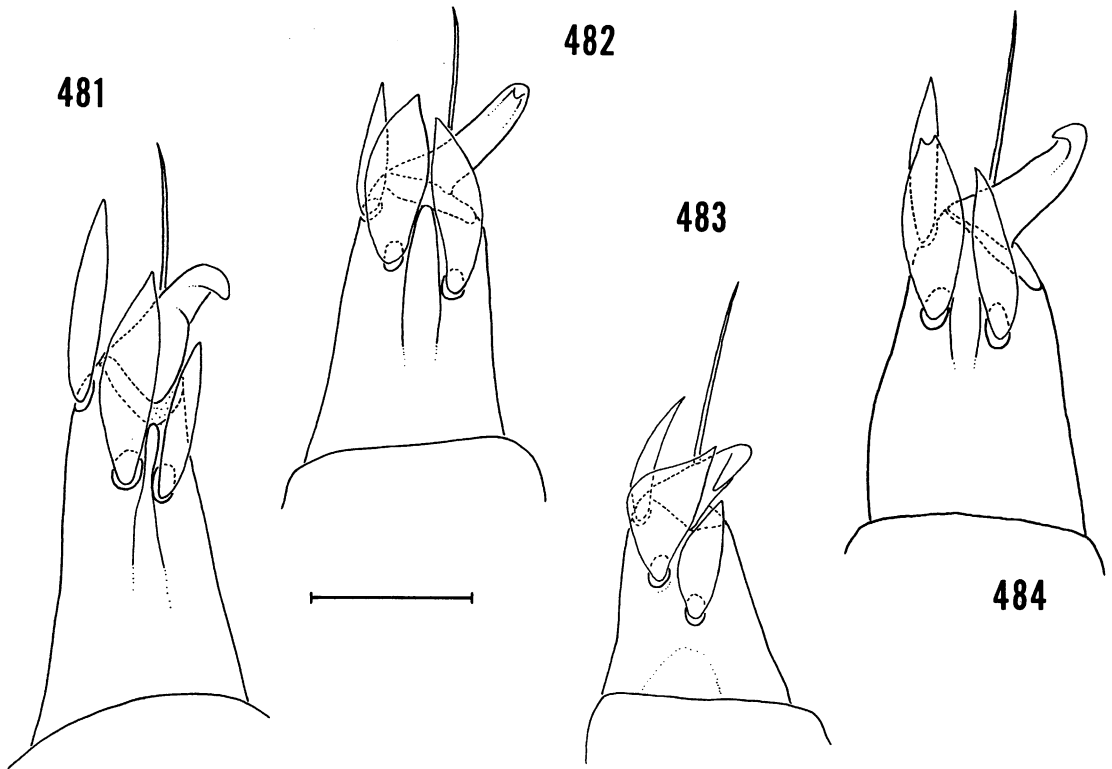
Within the Noctuoidea, the three mesal tarsal setae exhibit a remarkable array of shapes, many of which provide useful higher



Figs. 466–473. Right pretarsus of mesothoracic larval leg in mesal view. 466. *Dasychira dorsipennata* (Lymantriidae). 467. *Oenosandra boisduvalii*. 468. *Doa ampla*. 469. *Antheua simplex*. 470. *Quadricalcarifera viridimaculata*. 471. *Cerura tattakana*. 472. *Gluphisia septentrionis*. 473. *Notodonta scitipennis*. Cl = claw. Ts = tarsal seta. Scale lines = 200 μm.



Figs. 474–480. Right pretarsus of mesothoracic larval leg in mesal view. 474. *Ellida caniplaga*. 475. *Gargetta costigera*. 476. *Scrancia stictica*. 477. *Lochmaeus bilineata*. 478. *Cargida pyrrha*. 479. *Heterocampa averta*. 480. *Stauropus fagi* (prothoracic leg). Scale lines = 200 μ m (top scale applies to figures 474–478).



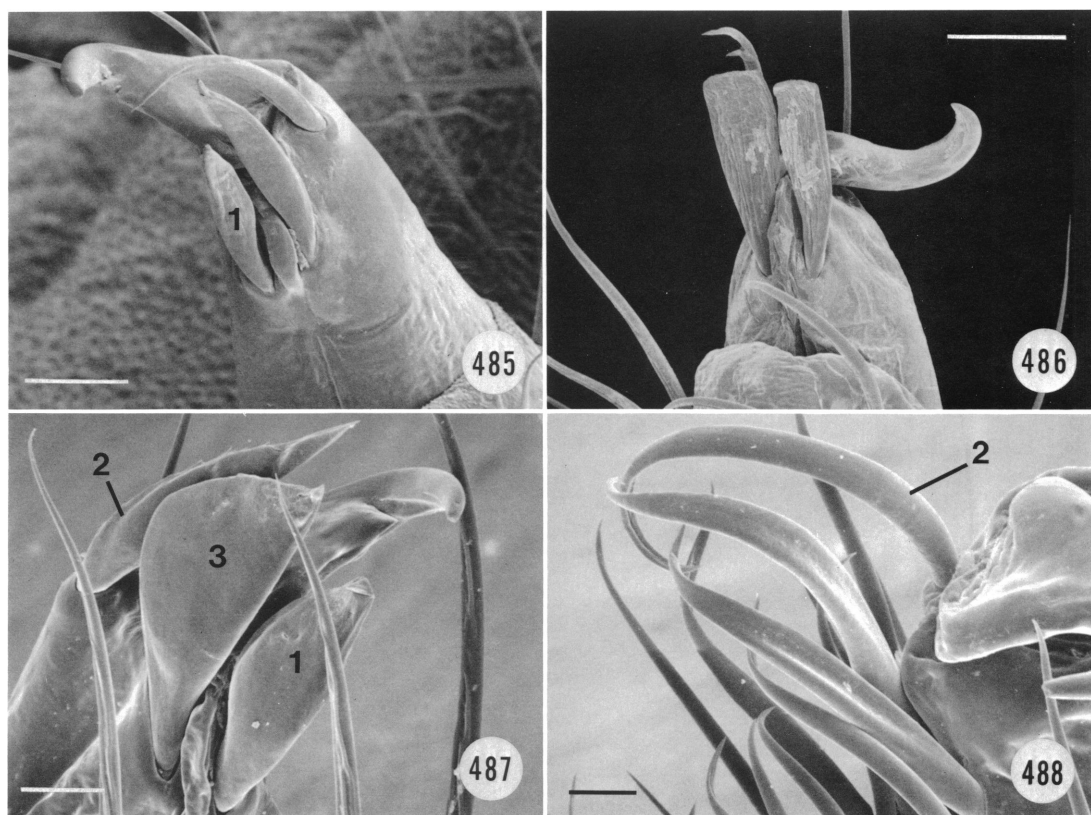
Figs. 481–484. Right pretarsus of mesothoracic larval leg in mesal view. **481.** *Hemiceras bilinea*. **482.** *Didugua argentilinea*. **483.** *Josia flavissima*. **484.** *Symmerista albifrons*. Scale line = 200 μ m.

group synapomorphies. I used three characters: one concerning various shapes of Ts1 and Ts3, which tended to look alike; one involving Ts2, the shape of which seemed to vary independently of the other two; and one for the loss of tarsal setae.

Character 143. Shape of Tarsal Setae 1 and 3. I recognized six character states for the two basal tarsal setae (Appendix I). The most frequent shape among the species I studied was lanceolate, with Ts3 slightly longer than Ts1 (figs. 466–468, 474–476, 478, 482). This type occurred in almost all outgroup species (see below), and I regarded it as primitive for the Notodontidae. Having the setae narrow (e.g., *Antheua simplex*, fig. 469) was considered a derived state. A third state was recognized for taxa in which the setae are parallel-sided but apically acute (e.g., *Lochmaeus bilineata*, fig. 477), found in five of the heterocampine species studied. In some Heterocampinae, as well as in Clade 18 of the Notodontinae, the setae have a characteristic morphology: they widen toward the end and have truncated distal margins (figs. 470, 471, 479, 486, 489)

rather than being acute. In these, the surfaces of Ts1 and Ts3 are covered with many fine striations and the distal portion is usually minutely dentate (fig. 489). All dioptine larvae so far examined have Ts1 broad and short, while Ts3 is extremely broad and leaf-shaped, with its apex deflected toward the tarsal midline (figs. 483, 487).

Among outgroup species, almost all exhibit the lanceolate type (score of “0”), with two exceptions. In *Hypoprepia miniata* (Lithosiinae), the tarsal setae are narrow (score of “1”) like those of Thaumetopoeinae (fig. 488). Finally, I observed a unique setal shape in larvae of *Spilosoma virginica* (Arctiinae) and *Nycteola frigidana* (Noctuidae: Sarrothripinae). These have almost identical, paddle-shaped tarsal setae (figs. 491, 492), a type found nowhere else among my study taxa. Crumb (1956) used tarsal setae “strongly spatulate” as a diagnostic feature for the Sarrothripinae, and figured them for larvae of *Sarrothripus* (= *Nycteola*) species. He showed that similar paddle-shaped tarsal setae occur in species of *Epizeuxis* (Noctuidae: Hermi-



Figs. 485–488. Pretarsus of larval thoracic leg showing tarsal setae. **485.** *Clostera albosigma*, left mesothoracic leg in mesal view (100 μ m). **486.** *Heterocampa obliqua*, right mesothoracic leg in mesal view (200 μ m). **487.** *Erbessa glaucaspis*, right mesothoracic leg in mesal view (40 μ m). **488.** *Epicoma melanosticta*, right prothoracic leg in lateral view (80 μ m). 1 = Ts1 (tarsal seta 1). 2 = Ts2. 3 = Ts3 (see text and figure 467). Scale lengths in parentheses.

niinae), but did not suggest that this character unites the two subfamilies. Merzheevskaya (1988) figured spatulate tarsal setae in larvae of *Herminia* Latreille (Herminiinae) and listed that as a generic character. Similarly, Godfrey (1980) described spatulate tarsal setae in *Renia*, another herminiine genus.

Character 144. Tarsal Seta 2 Short. The tarsal seta nearest to the claw (Ts2) is typically narrower than Ts1 and Ts3 and is usually curved toward the tarsus midline (e.g., figs. 466, 468, 471–473). In some Dioptrinae and Nystaleinae, Ts2 is short. I gave the derived score to species, such as *Didugua argentinella* (fig. 482) and *Josia flavissima* (fig. 483), in which Ts2 is shorter than Ts1.

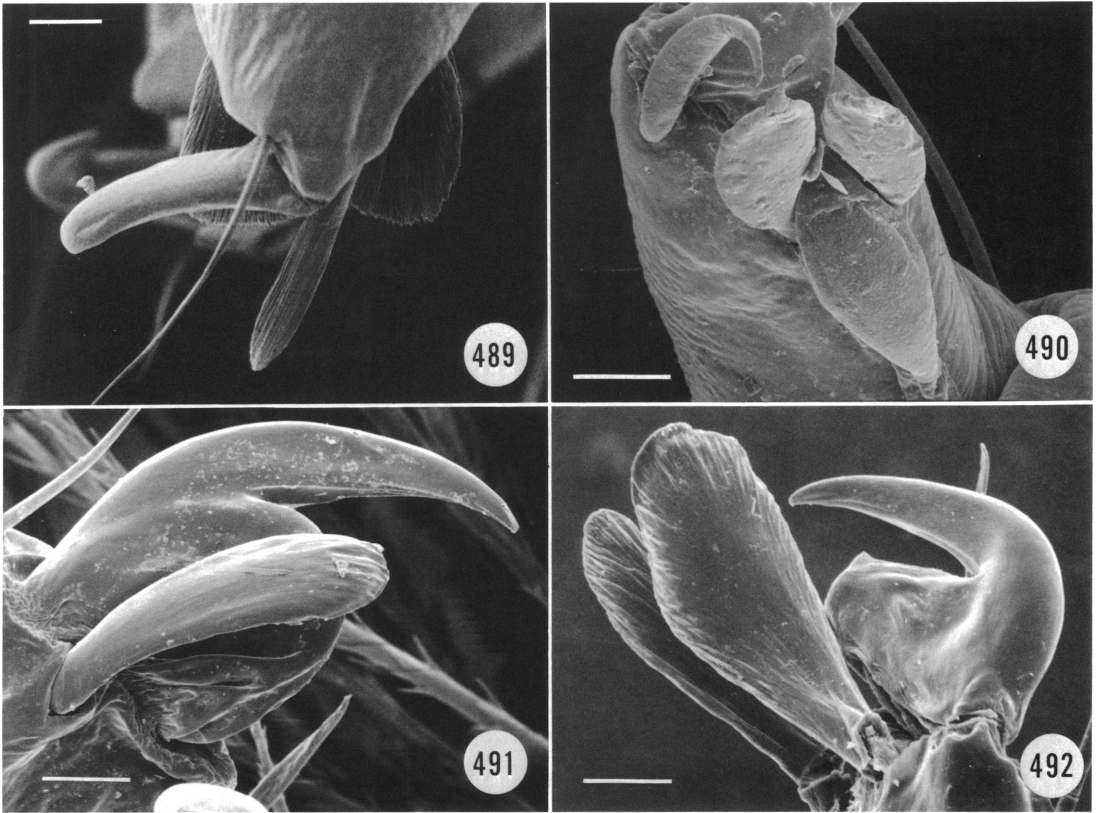
Character 145. Tarsal Setae Absent. A third character for the tarsal setae involves their loss on the meso- and metathoracic segments.

This occurs in only two of the taxa on my study list, *Stauropus fagi* and *Cnethodonta griseescens*, and is probably correlated with the highly modified legs of these species (see Character 142).

ABDOMEN

My discussion of abdominal morphology is arranged in the following manner. First, I list the proprioceptor, tactile, and secondary setal characters. Next, I describe the nonsetal characters used. For both sections, the character discussions are arranged in order from anterior segments to posterior ones.

Proprioceptor Setae: The microscopic “MD” proprioceptor setae are primary setae located on the anterior margin of most body segments (Stehr, 1987a). They are thought to



Figs. 489–492. Pretarsus of larval thoracic leg showing tarsal setae. **489.** *Liparopsis postalbida*, left mesothoracic leg in lateral view (50 μ m). **490.** *Nystalea nyseus*, right mesothoracic leg in dorsomedial view (80 μ m). **491.** *Spilosoma virginica* (Arctiidae), metathoracic leg in lateral view (50 μ m). **492.** *Nycteola frigidana* (Noctuidae: Sarrothripinae), prothoracic leg in lateral view (20 μ m). Scale lengths in parentheses.

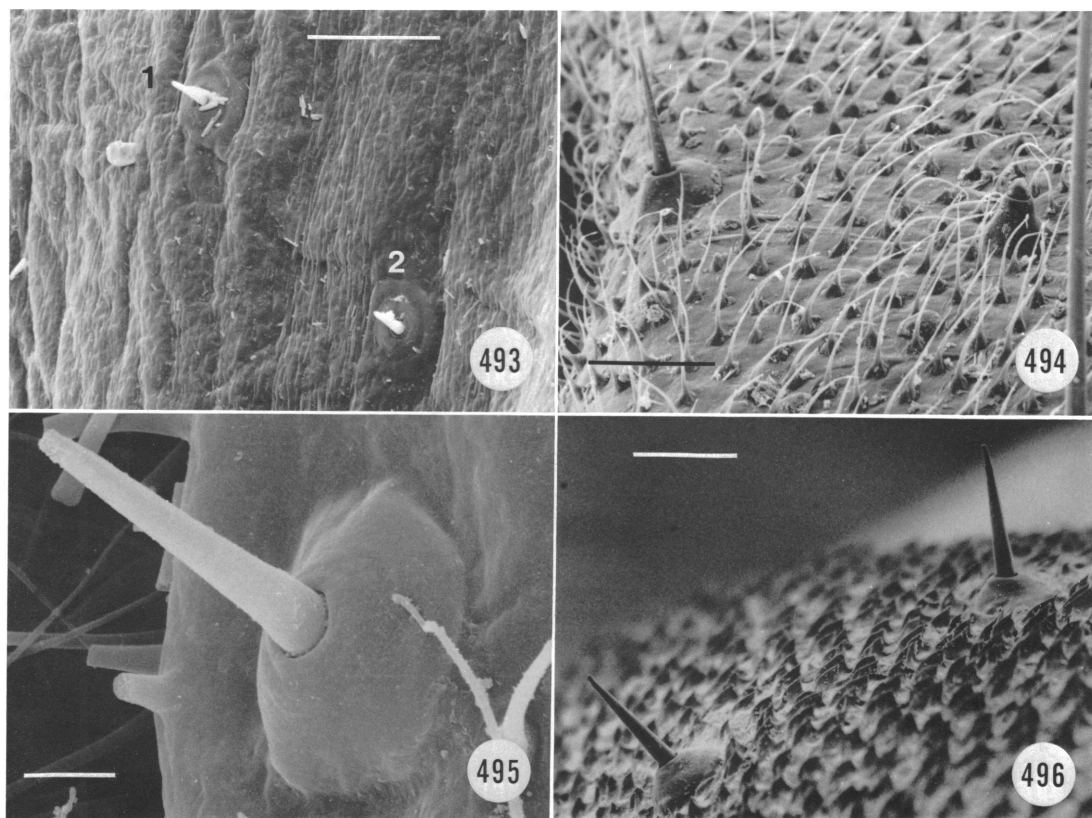
sense movement between adjacent segments. I used two characters involving MD setae. The first concerns the number of MD setae on segment A1, a character that has been of historical importance in discussions of noctuid phylogeny. The second character involves a seta called “SD2” by almost all previous workers (e.g., Stehr, 1987a). I argue below that this seta, which is found on the abdominal segments in all lepidopteran caterpillars, is not an SD seta at all but is instead homologous with MSD2, a proprioceptor.

Character 146. Segment A1 with Two MD Setae. Hinton (1946) first noted that there are two MD setae on segment A1 in notodontids (figs. 493, 494, 496) and only one in other Lepidoptera. Presence of the additional seta has been cited by almost all subsequent authors as a defining character for the Notodontidae. In the majority of notodontid

species, these MD setae can be seen with a dissecting microscope. *Clostera albosigma* appeared to have a single seta on A1 when the dissecting scope was used, but SEM revealed that a second very short one is present (fig. 494).

Presence of two MD setae on larval segment A1 remains one of the most reliable diagnostic characters for the Notodontidae. There is one major exception. All diopline larvae I examined have a single seta. This has been noticed by other recent workers (Weller, 1989; J. Rawlins, personal commun.). To confirm that Dioplineae lack the second MD seta, I examined all six exemplar species with SEM. The single MD on A1 of *Zunacetha annulata* is shown in figure 495. Both *Doa* (fig. 451) and *Oenosandra* exhibit the plesiomorphic condition.

Character 147. Position of Seta MSD2. On

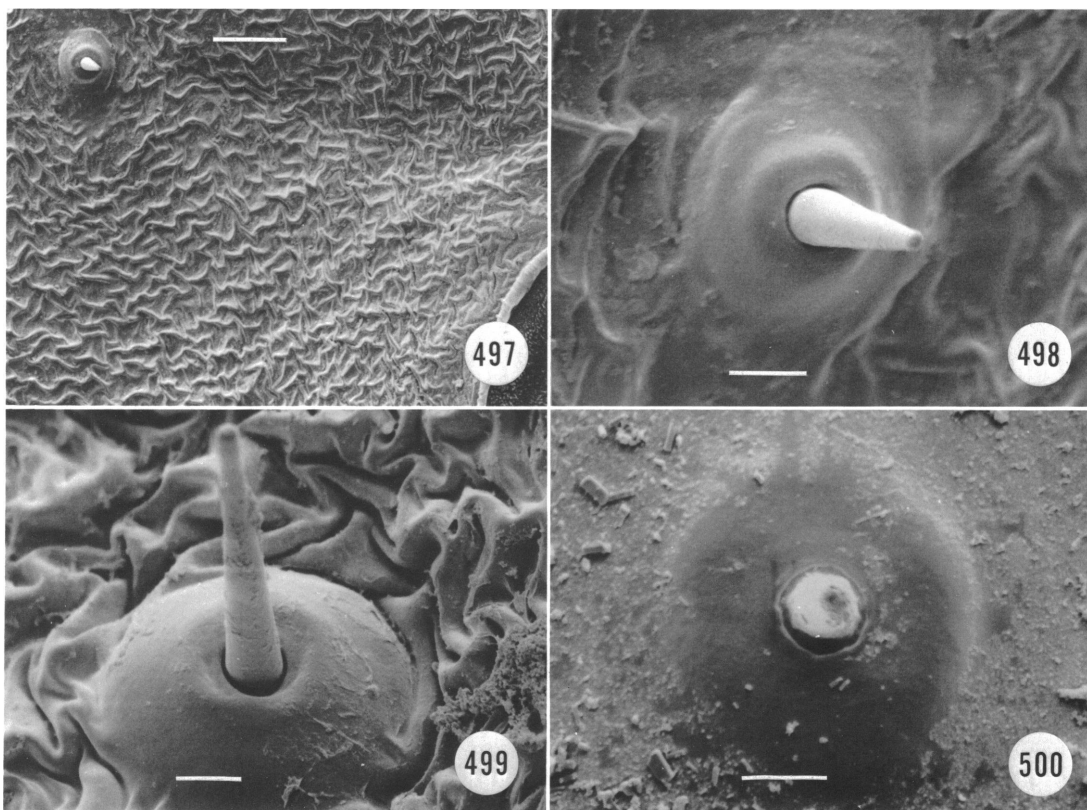


Figs. 493–496. Dorsal proprioceptor setae on segment A1 of notodontid larvae, shown with anterior at left. 493. *Hippia packardii* (40 μm). 494. *Clostera albosigma* (40 μm). 495. *Zunacetha annulata* (5 μm). 496. *Liparopsis postalbida* (20 μm). 1 = MD1. 2 = MD2. Scale lengths in parentheses.

the thoracic segments in Lepidoptera there are two MSD proprioceptor setae below the MDs (e.g., see fig. 449). On the abdominal segments there is a seta, located anterior to the spiracle, usually called “SD2” in the literature (e.g., Stehr, 1987a; Godfrey, 1972). This terminology seems to be attributable to Hinton (1946). When SD2 is examined with SEM, it becomes apparent that this seta is morphologically identical to an abdominal MD proprioceptor seta (compare figs. 495 and 498). Therefore, this seta could not be serially homologous with SD2 of the thorax. Kitching (1984b), studying danaine caterpillars, and Singh and Goel (1987), in their study of noctuid larvae, offered what I believe is the appropriate interpretation. These authors called SD2 of other authors proprioceptor seta “MSD2.” I follow the nomenclature of Kitching and Singh and Goel.

I found one informative character regarding the position of MSD2. In almost all larvae from both the ingroup and outgroup, MSD2 on A1–A7 is located anterior to the spiracle, approximately on a horizontal line with it (e.g., figs. 489, 494). In members of the *Dudusini*, MSD2 is located anterodorsally to the spiracle, on a horizontal line well above it (fig. 511). This state does not occur in either *Scrancia* or *Gargetta*.

Tactile Setae: There is probably more character information in the abdominal tactile setae than what I list below. However, the problem of scoring primary setal characters for species with numerous secondary setae somewhat limits the usefulness of these characters. Difficult homology problems exist, both between taxa and between abdominal segments (serial homology), but the relative positions of tactile setae are remarkably



Figs. 497–500. Proprioceptor setae on abdominal segments of larval Notodontidae. **497.** Seta MSD2 on A5 of *Liparopsis postalbida* (20 μm). **498.** Seta MSD2 on A6 of *L. postalbida* (5 μm). **499.** Seta MD1 on A6 of *Schizura unicornis* (5 μm). **500.** Seta MSD2 on A3 of *Didugua argentinelinea* (5 μm). Scale lines in parentheses.

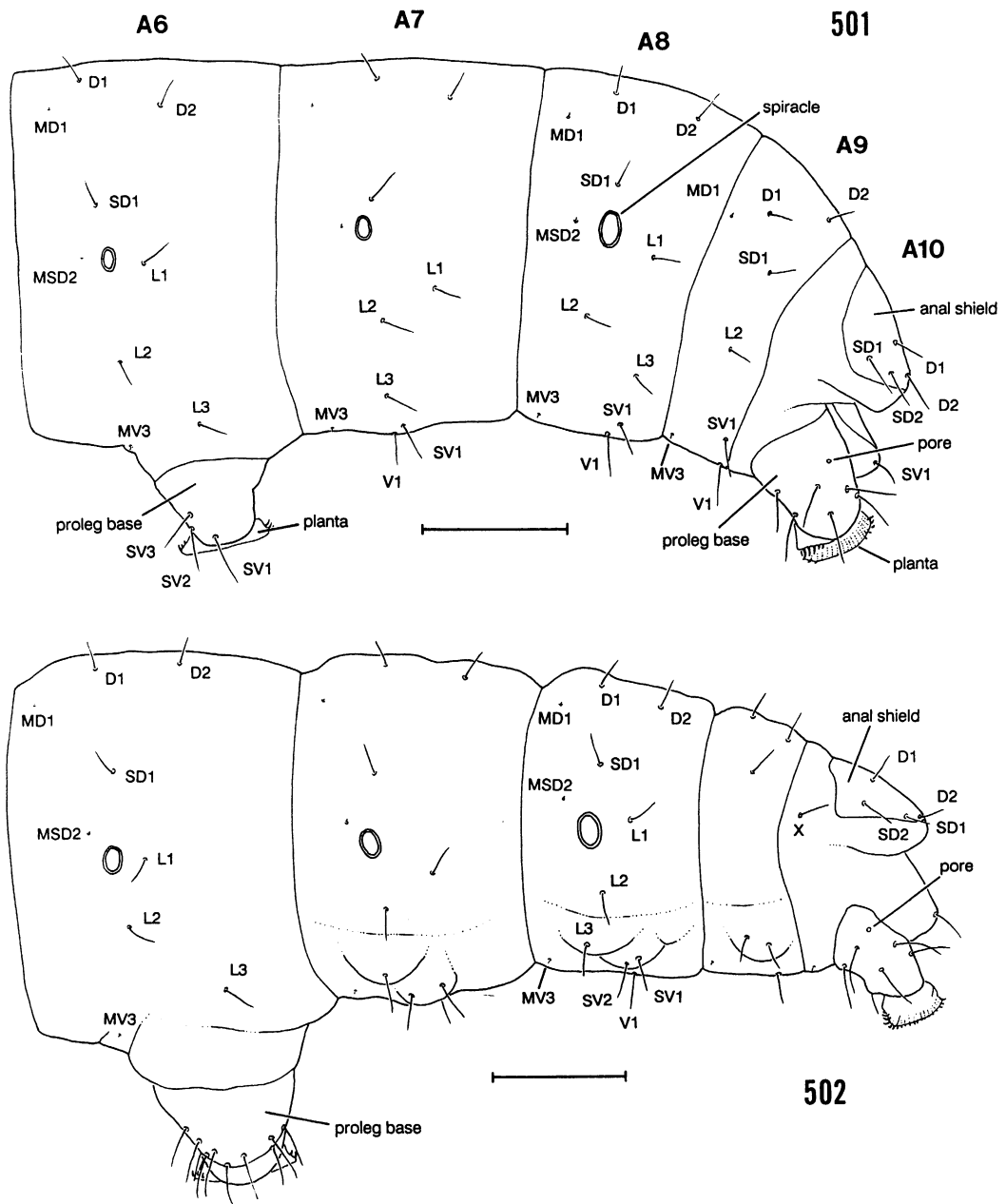
constant within notodontid lineages, and such data provide extremely useful phylogenetic information.

It is obvious that setal patterns between abdominal segments are correlated, and treating each abdominal segment as an independent unit would give undeserved weight to setal characters. However, some abdominal segment groups seem to vary independently from other abdominal regions. I addressed this issue by grouping the 10 abdominal segments into fewer body regions, treating each region as a separate character. For example, segments A3 through A6 are almost always identical in both the position and number of setae, and these were essentially treated as a single segment. Setal patterns on segments A1 and A2, which lack prolegs, were treated as separate from A3–A10. In addition, A8 and A10 exhibited setal characters unique to those segments. I used

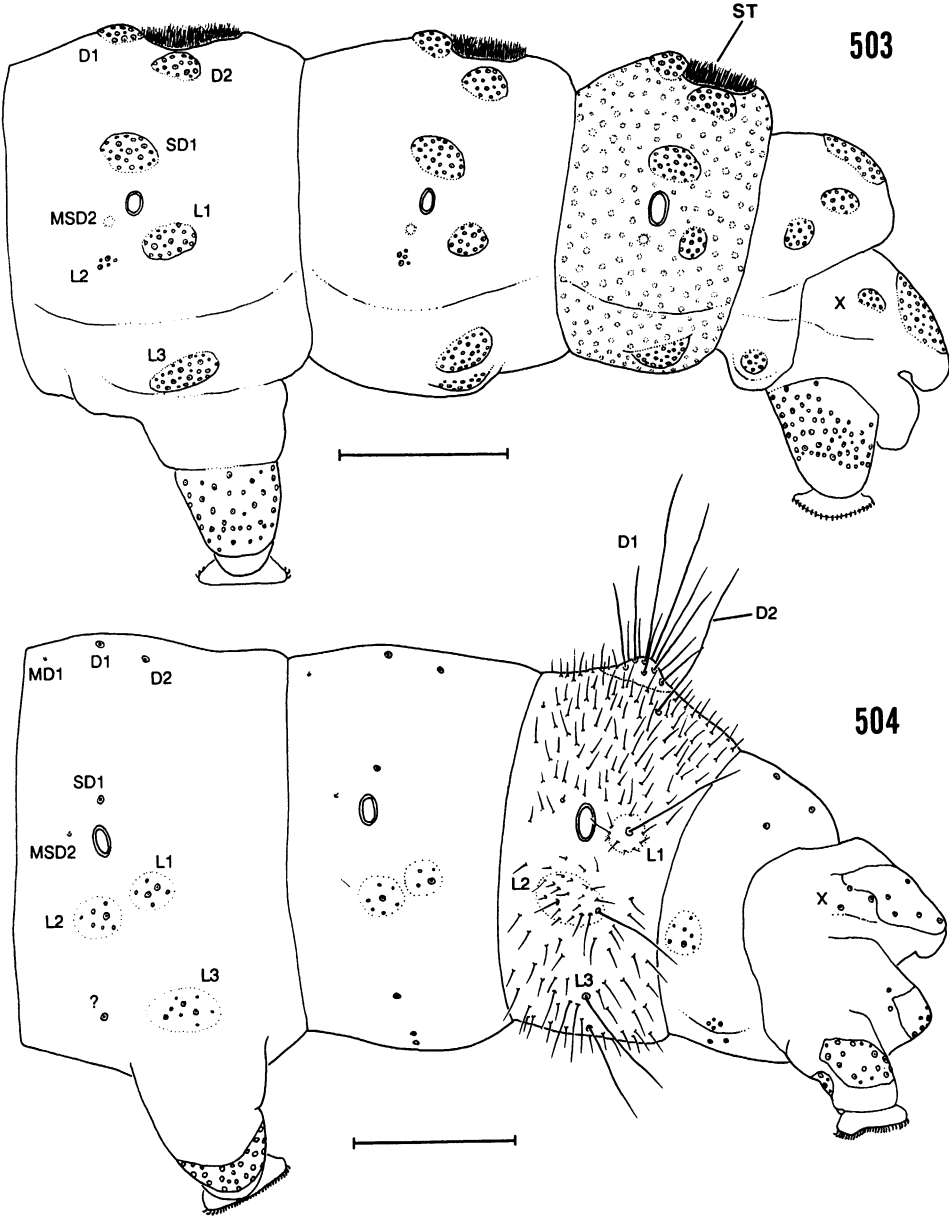
the following characters from abdominal tactile setae.

Character 148. Number of Primary Setae Below the Spiracular Line on A1 and A2. Among Notodontidae there is variation in the number of setae below the spiracular line on segments A1 and A2. These segments lack prolegs in all Lepidoptera except the Dalcidae, which have crochet-bearing prolegs on A2 (and A7 as well; Stehr, 1987a). Absence of prolegs creates confusion concerning the serial homology of setae in the regions of the L, SV, and V groups. After several unsuccessful attempts to resolve that confusion, I gave up and have instead followed current setal nomenclature to the best of my ability.

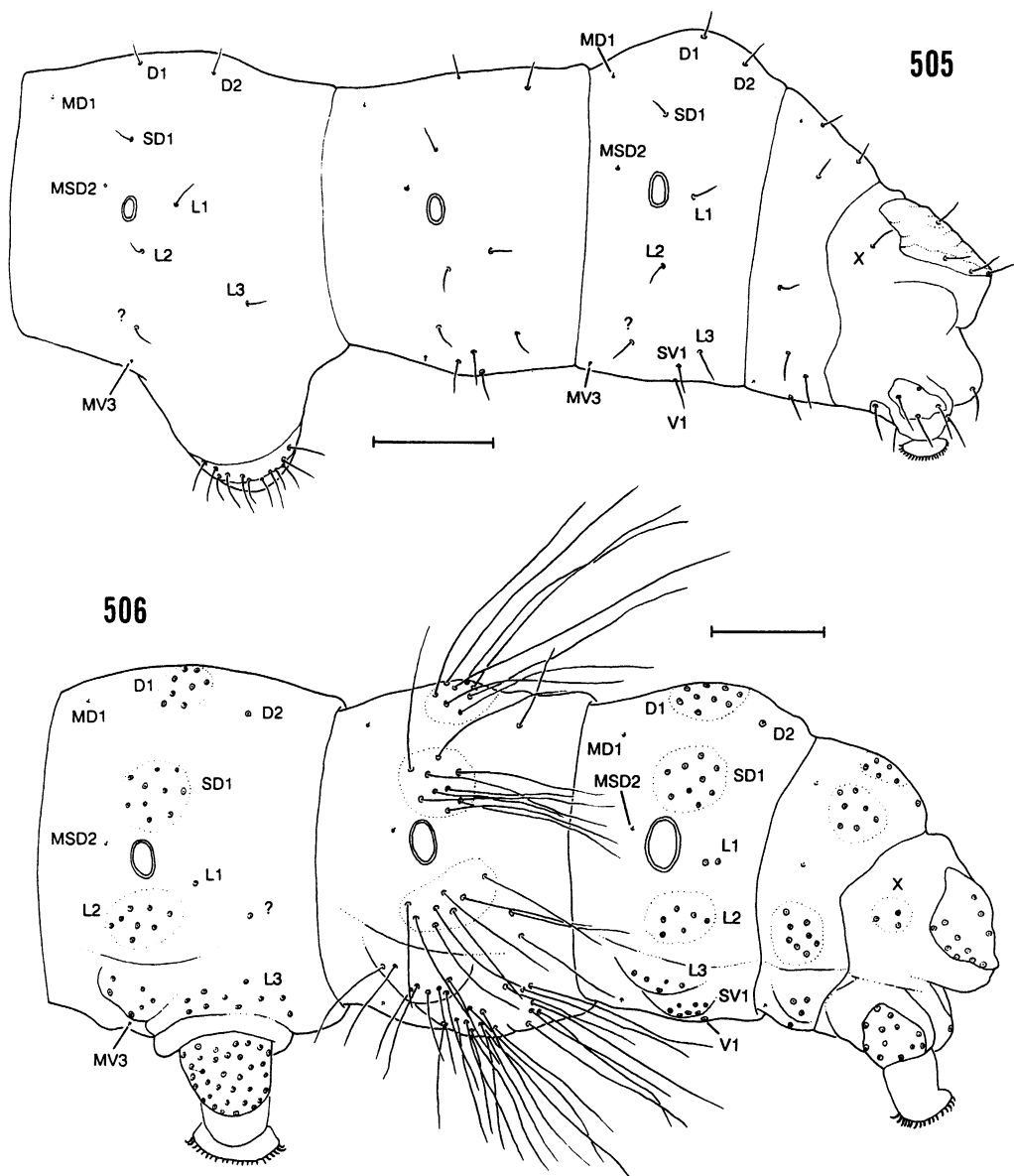
I created three categories to describe differences in the number of setae below the spiracular line. I gave a score of “0” to taxa with six to eight setae below that line. This was true for all scoreable outgroup species



Figs. 501, 502. Sixth through 10th abdominal segments of larvae, anterior at left. **501.** *Peridroma saucia* (Noctuidae). **502.** *Peridea angulosa* (Notodontidae). A = abdominal segment. D = dorsal setae. L = lateral setae. MD = dorsal proprioceptor setae. MSD = subdorsal proprioceptor setae. MV = ventral proprioceptor seta. SD = subdorsal setae. SV = subventral setae. V = ventral seta. X = seta X of Gerasimov (1935). Scale lines = 2.0 mm.



Figs. 503, 504. Sixth through 10th abdominal segments of larvae, anterior at left. **503.** *Epicoma melanosticta*. **504.** *Clostera albosigma*. ST = tuft of deciduous setae. For key to other symbols see figures 501 and 502. Scale lines = 2.0 mm.

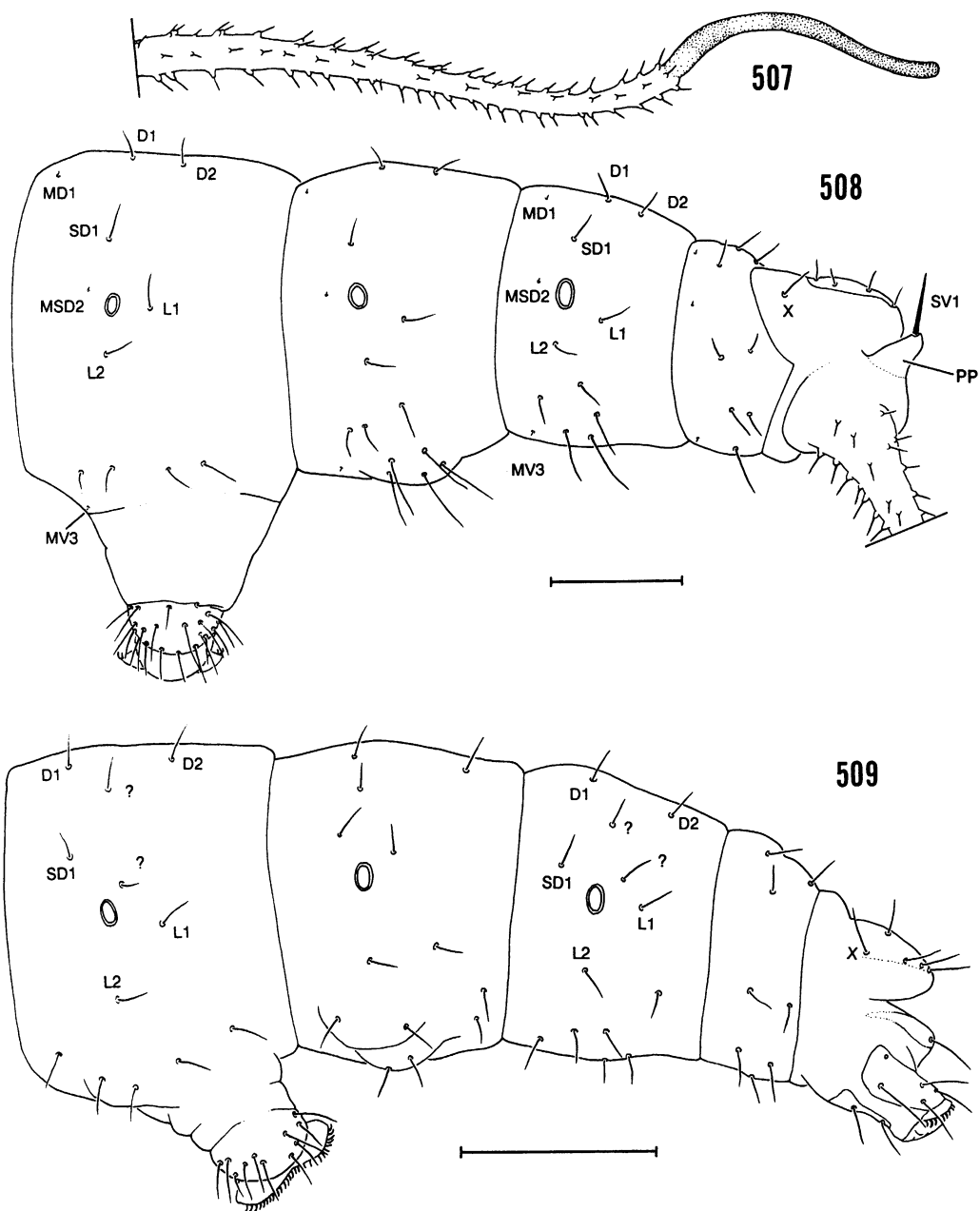


Figs. 505, 506. Sixth through 10th abdominal segments of larvae, anterior at left. **505.** *Odontosia elegans*. **506.** *Antheua simplex*. For key to symbols see figures 501 and 502. Scale lines = 2.0 mm.

and for the vast majority of Notodontidae. A second group contains species, all belonging in the Heterocampinae, with six to eight setae below the spiracular line, but with one SV seta (which I term SV2) short and spatulate (figs. 455, 456). The third character state applies to species with 10 or more setae below the spiracular line and includes many mem-

bers of the notodontine tribe Dicranurini (e.g., *Gluphisia septentrionis*, fig. 452; *Furcula borealis*, fig. 453).

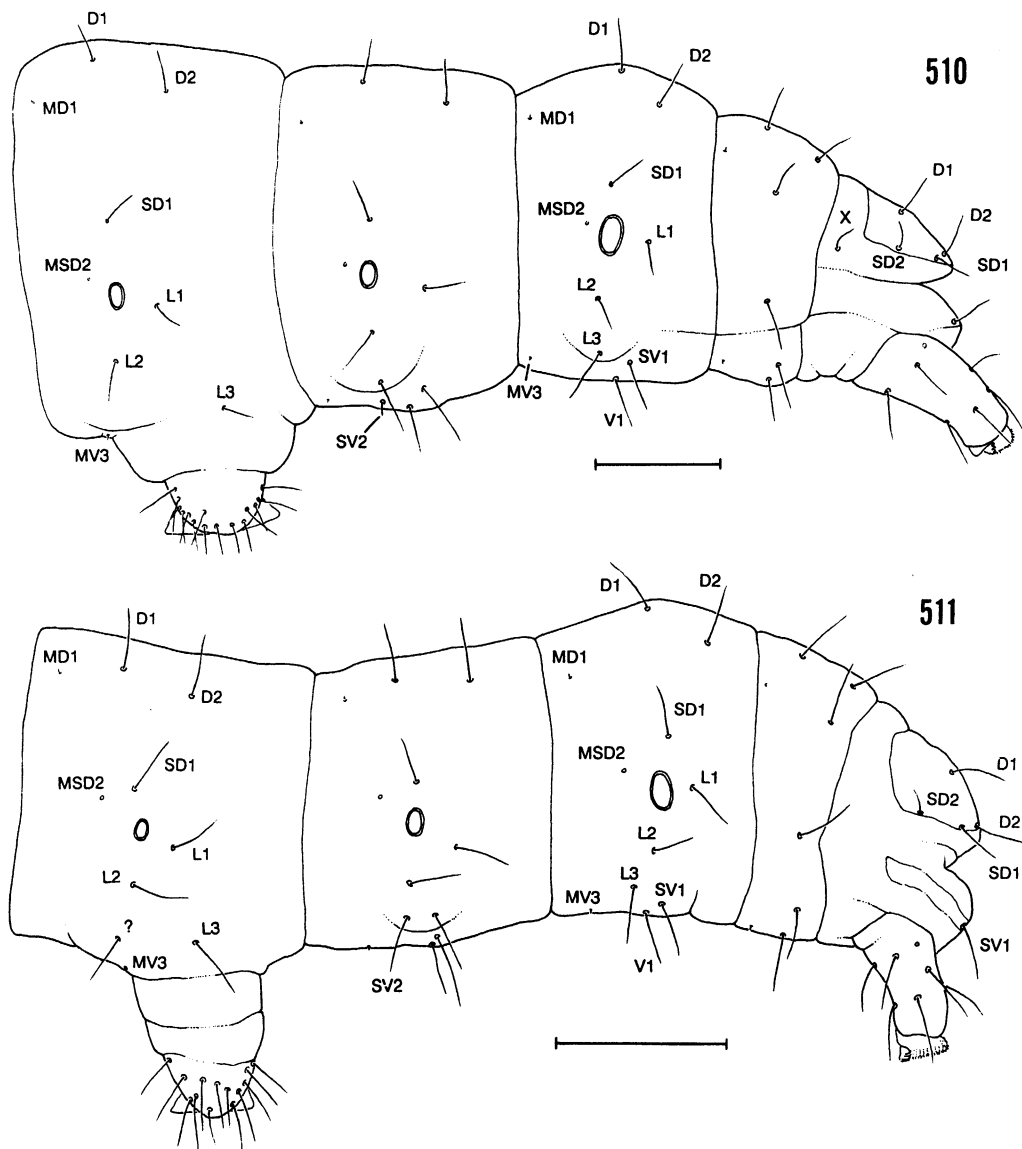
Character 149. An Additional Abdominal SD Seta Present. Among the quadrid noctuoids I studied and in most Notodontidae, a single SD seta (SD1) occurs on all abdominal segments (figs. 449–451, 454, 455). Some



Figs. 507–509. Sixth through 10th abdominal segments of larval Notodontidae, anterior at left. **507.** *Furcula borealis* (stemapod). **508.** *Furcula borealis*. **509.** *Gluphisia septentrionis*. PP = paraproct. For key to other symbols see figures 501 and 502. Scale lines = 2.0 mm.

notodontids have an additional SD seta. This occurs in two ways: SD can be bisetose on segments A2 through A7 and unisetose on A8 (scored as “1”), or SD can be bisetose on A2 through A8 (scored as “2”). The first of

these states occurs in two heterocampine genera, *Heterocampa* and *Macrurocampa*, as well as in *Tarsolepis* (Dudusinae). According to my analysis, these are not homologous. The second state is found in three genera of the

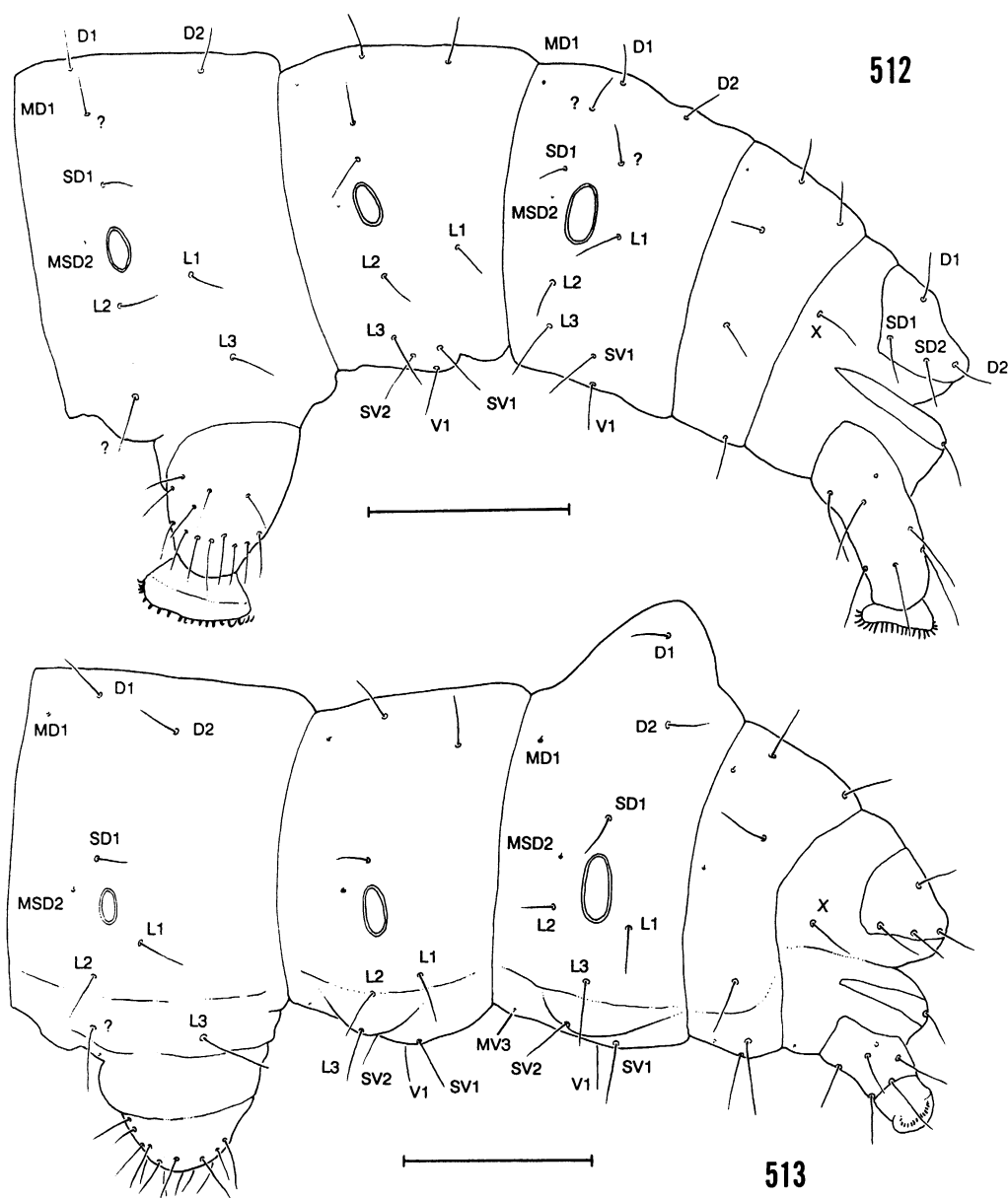


Figs. 510, 511. Sixth through 10th abdominal segments of larval Notodontidae, anterior at left. **510.** *Fentonia ocypte*. **511.** *Cargida pyrrha*. For key to symbols see figures 501 and 502. Scale lines = 2.0 mm.

Notodontinae: *Quadricalcarifera*, *Cerura* (but not *Furcula*), and *Gluphisia* (fig. 452). Unfortunately, there are 13 ingroup species in my sample for which I could not score Character 149 because of the presence of secondary setae (Appendix II).

Character 150. An Additional Abdominal D Seta Present. In the primitive condition, found almost throughout the Lepidoptera,

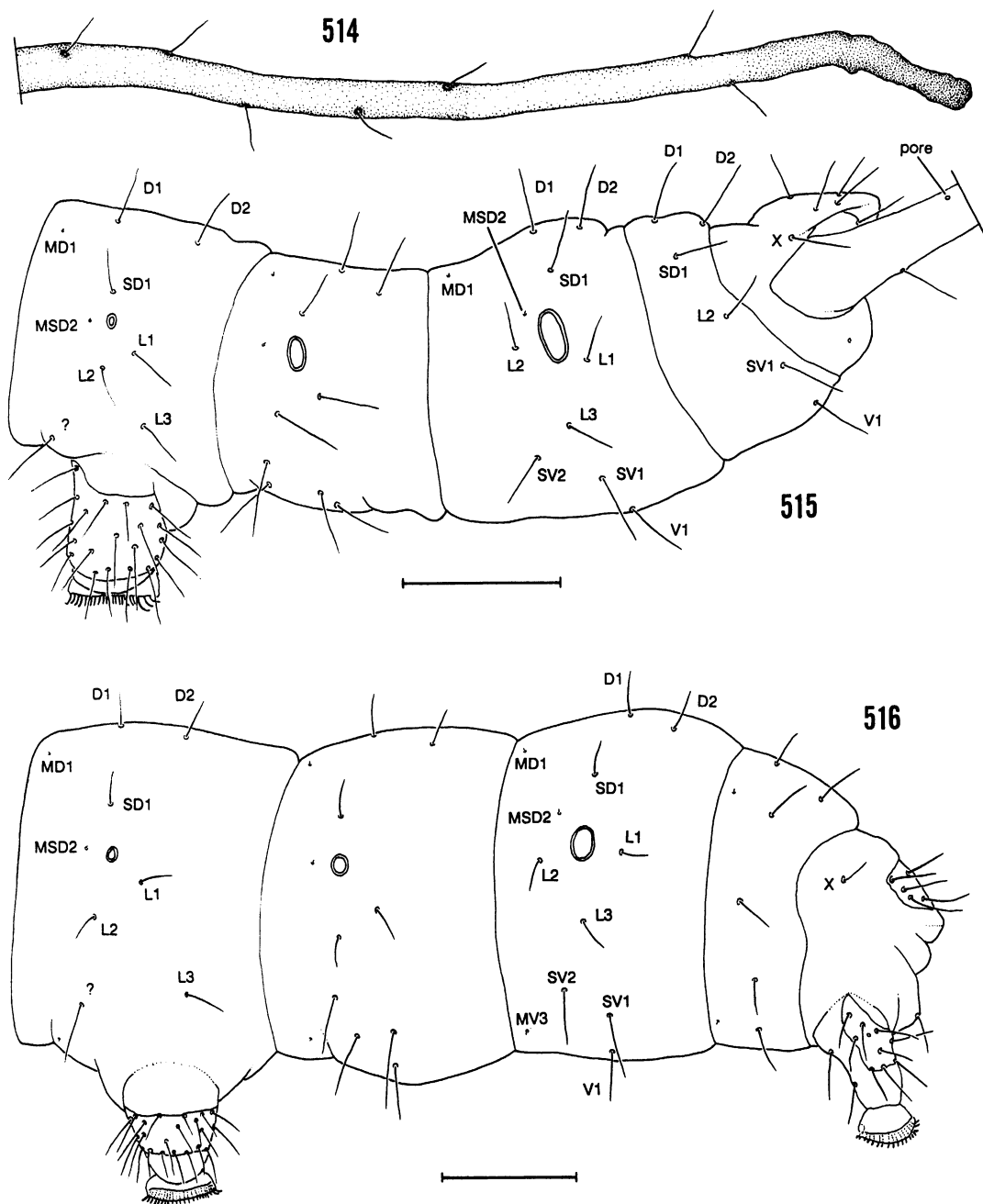
there are two dorsal setae (D1 and D2) and a single subdorsal seta (SD1) on the abdominal segments (e.g., figs. 449–451, 501, 502, 505, 508). Some notodontids have an additional seta, located approximately midway between the dorsal and subdorsal groups, on A2 through A7, and two such setae on A8. The derived condition occurs in four Notodontinae exemplars, including *Gluphisia sep-*



Figs. 512, 513. Sixth through 10th abdominal segments of larval Notodontidae, anterior at left. **512.** *Hemiceras bilinea*. **513.** *Didugia argenteilinea*. For key to symbols see figures 501 and 502. Scale lines = 2.0 mm.

tentrionis (figs. 452, 509), as well as in larvae of *Hemiceras* (fig. 512) and *Tarsolepis japonica*. I have labeled the novel seta with a question mark. Based on my cladistic results this trait evolved independently in the Notodontinae, in *Hemiceras*, and in the Dudusinae (*Tarsolepis*).

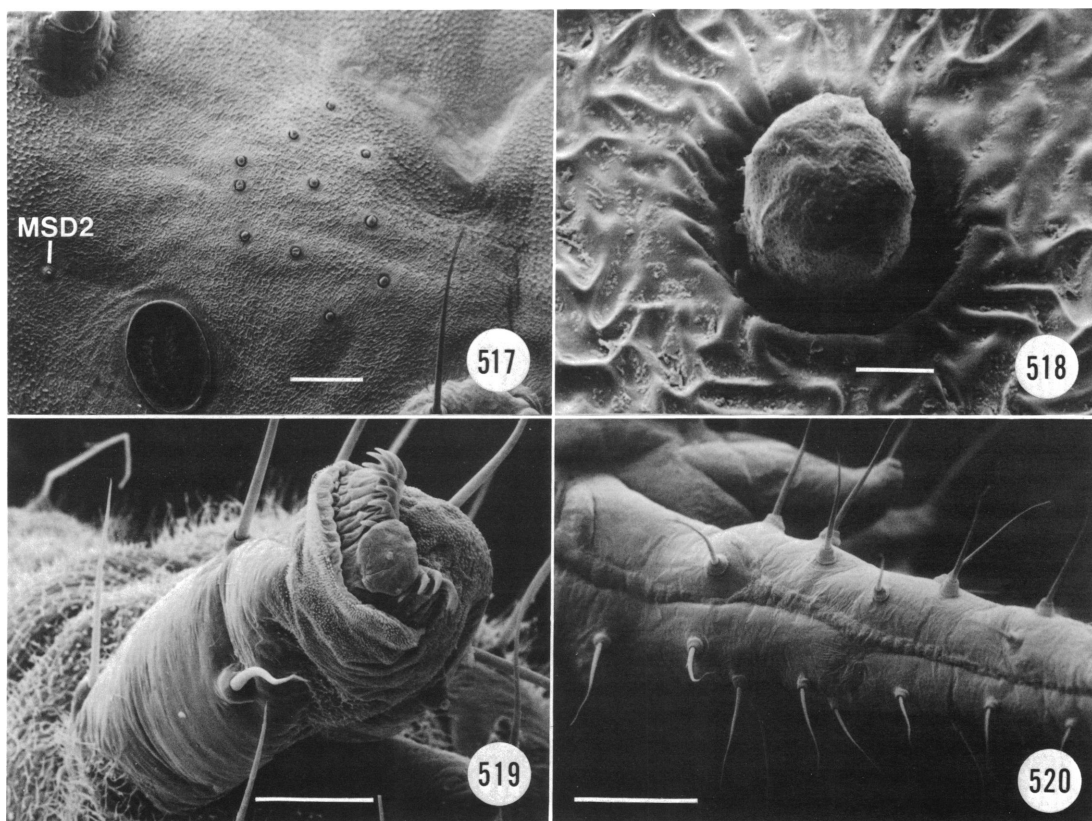
Character 151. The Number of Lateral Setae on Abdomen. Among ingroup species there is variation in the number of lateral (or L) setae on abdominal segments A3–A6. I recognized four character states to describe this variation. The primitive state, exemplified by *Peridroma saucia* (Noctuidae) and *Peridea*



Figs. 514–516. Sixth through 10th abdominal segments of larval Notodontidae, anterior at left. **514.** *Erbessa glaucaspis* (stemapod). **515.** *Erbessa glaucaspis*. **516.** *Josia ligata*. For key to symbols see figures 501 and 502. Scale lines = 1.0 mm.

angulosa (figs. 501, 502), is characterized by three L setae (L1–L3), with L1 being located near the spiracle and L3 being above the proleg base. A derived state (scored as “1”) oc-

curs where there are four setae in the L region. The novel seta (labeled “?” in figures) is located at approximately the same height as L3, but anterior to it. This character state is found



Figs. 517, 518. Fifth abdominal segment of *Liparopsis postalbida* larva. **517.** Spiracle and surrounding setae showing position of proprioceptor seta MSD2 (100 μ m). **518.** Modified peglike seta from figure 517 (5 μ m). Scale lengths in parentheses.

Figs. 519, 520. Left prolegs of Notodontidae. **519.** Anal proleg of *Zunacetha annulata* (100 μ m). **520.** Basal portion of anal proleg of *Liparopsis postalbida*, showing raised setal bases (400 μ m). Scale lengths in parentheses.

in many Notodontidae, but it shows homoplasy, occurring in some Notodontinae (e.g., *Odontosia elegans*, fig. 505), in all Nystaleinae and Dioprinae (figs. 513, 515, 516), and in some Heterocampinae. In addition, four L setae are present in *Cargida pyrrha* (fig. 511) and in *Hemiceras* larvae (fig. 512). A second derived state, found only in *Ellida caniplaga* among the taxa I studied, has five L setae. The last state I recognized (score of "3") is found only in members of the Dicranurini (Notodontinae). Here, there are from 6 to 12 L setae, with the novel ones located in a horizontal row at the height of L3 (figs. 508, 509). This condition, possibly a derivation of apomorphic state "1", is found in all members of Clade 17 except *Liparopsis*.

Character 152. Anterior Abdominal L Seta

Spatulate. In two heterocampine species, *Stauropus fagi* and *Cnethodonta grisescens* (fig. 457), the anterior L seta on each abdominal segment is spatulate rather than being hairlike.

Character 153. Position of Seta L2 on Segment A8. One of the most reliable synapomorphies for the Nystaleinae + Dioprinae (Clade 45) involves the relative position of seta L2 on segment A8. Typically L2 on A8 is located below the spiracle on a vertical line with it (figs. 501, 502, 504–506, 508–512). In dioptrine and nystaleine larvae, L2 has apparently moved anterodorsally, so that it is anterior to the spiracle and on a line approximately horizontal with it (figs. 513, 515, 516). Scoring the trait is clear-cut, at least for taxa without secondary setae, and among the spe-

cies I examined, the apomorphic state shows complete consistency. It will be interesting to see whether, with the discovery of larvae representing additional species from these two subfamilies, the synapomorphy retains its integrity.

Character 154. Peglike Body Setae Present. An autapomorphy for *Liparopsis* is the presence of a group of approximately 10 extremely short, peglike setae located posterior to the abdominal spiracles on each body segment (figs. 517, 518). Such setae were not observed elsewhere, but larvae outside the study group should be examined; presence of these may define a larger clade of notodontid genera. As with other autapomorphies, Character 154 was not included in the analysis.

Character 155. Seta X Present. Gerasimov (1935, 1937, 1952) described an extra primary seta in Notodontidae, which he termed seta "X", located on the anterolateral corner of the anal shield. This region of A10 has been called the "E area" (Stehr, 1987a). Stehr and Martinat (1987: fig. 180 in their key to families) used presence of seta X in the E area as diagnostic for the Notodontidae, and the character appears to be quite reliable. In notodontids with secondary setae, there is usually a cluster of setae or a verruca in the appropriate position (figs. 503, 506). Seta X can be located either close to the anterior boundary of the anal plate (fig. 509) or further from it (figs. 512, 513).

Seta X does not occur in members of the outgroup. Unfortunately, I was unable to determine whether it is present in larvae of *Doa* because numerous secondary setae occur on the anal shield and E area of that species. Among Notodontidae there is only one group in which seta X appears to have been lost: the subfamily Dudusinae. Godfrey and Appleby (1987) noted that seta X is absent in *Cargida pyrrha* (fig. 511), but I discovered that its absence is a synapomorphy for the entire subfamily.

Secondary Setae: Character 156. Number of Setae on the Proleg Bases. Presence of secondary setae on the proleg bases in the region of the SV group (fig. 519) has been used as a diagnostic character for the Notodontidae (e.g., Godfrey and Appleby, 1987). Some Noctuoidea possess only three setae (labeled SV1, SV2, and SV3 [fig. 501] by previous

workers) on the proleg bases. However, my study shows that many quadrid noctuoids exhibit the first of these traits (Appendix II). In fact, I am uncertain whether numerous setae, or three setae, is the ground plan state for Notodontidae. I scored species with more than three setae on the proleg base as "1", and those with three or less as "0".

Among my exemplar list, the only genera exhibiting the "0" state are *Oenosandra*, *Hypoprepia*, *Nycteola*, *Peridroma* (fig. 501), and *Alypia*, a disparate group of taxa. Genera, in addition to Notodontidae, with numerous setae on the proleg bases include *Diloba*, *Nola*, *Panthea*, *Spilosoma*, the lymantriids, and *Doa* (fig. 451). For species with numerous secondary setae on the rest of the body it was meaningless to score this character because secondary setae inevitably occur on the proleg bases as well.

Character 157. Abdomen with "Dorsal Pads". Caterpillars of many Thaumetopoeinae have tufts of short, deciduous, hairlike setae located in fleshy dorsal pockets ("dorsal pads" of Gardner, 1943) on abdominal segments 1 through 8. The setae are known to cause skin irritation in humans (Gilmer, 1925; Gardner, 1943; Pinhey, 1975; Common, 1979; Carter, 1984); Stephens described them as causing "very great irritation and acute pain" (1829: 46). Of the thaumetopoeines I examined, such tufts occur in *Thaumetopoea*, *Traumatocampa*, and *Epicoma* (fig. 503), but not in *Anaphe*. Tufts of deciduous setae are also found on segments A1–A4 and A8 in *Dasychira* (Lymantriidae) (Gilmer, 1925), but these differ in being longer, barbed rather than smooth, and located on raised dorsal patches rather than in depressions. My analysis indicates that the structures in thaumetopoeines and lymantriids are not homologous.

Spiracles: Character 158. Spiracles Small on A1–A6. Having examined larvae of *Phryganidia californica*, Stehr (1987b) listed small spiracles on segments A1–A6 as a diagnostic trait for the Dioptinae. The character seems reliable (figs. 450, 515, 516). *Gargetta* is the only other notodontid where I observed small spiracles. The spiracles on A1–A6 are small in four other genera: *Doa* (fig. 451; Brown, 1990), *Hypoprepia*, *Nycteola*, and *Nola*.

Prolegs (Segments 3–6): Lepidopteran pro-

legs consist of two parts (Stehr, 1987a): a proximal base on which the SV setae are found (fig. 519) and the planta bearing the crochets (see fig. 501). I did not find many useful characters involving A3–A6 prolegs. Proleg structure is fairly uniform among notodontid genera, and crochet arrangements (see below), which can vary significantly between lepidopteran groups (e.g., see Gerasimov, 1952; Peterson, 1962), were not found to differ among ingroup taxa. The presence or absence of secondary SV setae on the proleg bases was discussed above (Character 156).

Character 159. Arrangement of Larval Crochets. In most noctuid larvae the crochets are arranged in a uniordinal mesoseries (Forbes, 1954; Godfrey, 1987b). This is true for all Notodontidae and for all outgroup species in my study list except the following: those of *Doa* are in a biordinal mesoseries (Donahue and Brown, 1987; Brown, 1990); *Oenosandra* has biserial crochets; and Arctiidae, excluding some Lithosiinae such as *Hypoprepia* (Forbes, 1960), are distinguished by having heteroideous crochets (Gerasimov, 1952; Peterson, 1962; Habeck, 1987).

Character 160. Prolegs Reduced on A3. Caterpillars of *Scrancia*, *Gargetta*, and *Tarsolepis* are unique among the Notodontidae I examined in having smaller prolegs on A3 than on segments A4–A6. In each case, there is a correlated reduction in A3 crochet number (table 2). *Gargetta costigera* has A3 prolegs reduced to setose bumps, with no crochets present. According to Gardner (1943), other *Gargetta* species have small crochets present on A3; in his study, their absence was a key character for *G. costigera* only. *Scrancia* and *Tarsolepis* larvae exhibit a condition similar to *Gargetta* except that the A3 prolegs are not as highly reduced and crochets are present. Previous authors have discussed proleg reduction in *Scrancia* and *Gargetta* larvae (Janse, 1920; Gardner, 1943; Holloway, 1983), but no one seems to have noticed reduced A3 prolegs in *Tarsolepis*. It may be that as additional taxa are studied, this apomorphy will prove to be fairly widespread in both the Dudusini and Scranciini. Among outgroup species, A3 prolegs and crochets are absent in *Nola* (Stehr, 1987c; see table 2).

Character 161. Prolegs Reduced on A4. In addition to having reduced A3 prolegs, cat-

erpillars of *Gargetta costigera* and *Scrancia stictica* have smaller prolegs on A4 than those on A5–A6. In both species, the A4 prolegs bear substantially fewer crochets than on segments 5 and 6 (table 2). Reduction of the A4 prolegs occurs nowhere else in the Notodontidae as far as I am aware and may ultimately prove to be a synapomorphy for the Scranciini. According to Holloway (1983), *Gargetta* larvae use only the prolegs on A5 and A6 to grasp the substrate, and they walk in a “semi-looper” manner, a behavior also typical of some noctuid larvae, such as the Plusiinae, where reduced prolegs on A3 and A4 also occur (Eichlin and Cunningham, 1978; Kitching, 1987; Godfrey, 1987b).

Dorsum of Abdomen: Tubercles or humps frequently occur on the dorsum of the first and eighth abdominal segments, but they can occur on any body segment. For example, in *Nerice bidentata* Walker there are nine pairs of large fleshy humps on segments T3–A8 (Packard, 1895a; Forbes, 1948; McCabe, 1991). The caterpillar of *Harpyia microsticta* has fork-shaped protuberances on the dorsum of segments A1–A6 and A8 (figs. 79, 446), and *Nystalea* larvae have long, tapered protuberances on segments A1–A5 and A8 (fig. 454).

For this study, I did not rely heavily on larval body shape for character information, the main reason being that it is difficult to homologize various modifications. If tubercles on two different species differ only slightly in relative position but dramatically in shape (compare, e.g., *Harpyia microsticta* and *Nystalea nyseus*), should they be scored the same?

There is some evidence that larval body shape in Lepidoptera is controlled by relatively few genes. Greene (1989) demonstrated dramatic seasonal shape polymorphism in larvae of *Nemoria arizonaria* (Grote) (Geometridae). Larvae from spring broods mimic oak catkins, whereas summer larvae mimic oak twigs, and the difference appears to be mediated by dietary tannin levels. It would be interesting to know which morphological structures are associated with this polymorphism.

Character 162. Tubercle Present on A1. As noted above, larvae of many notodontid species possess some type of protuberance on

TABLE 2
Number of Larval Crochets (in final instar) for Study Species from the Genera Listed
(see table 1 for species names)
(Only a single specimen of each was examined. A = abdominal segment)

Taxon	Number of crochets					
	A3	A4	A5	A6	A10	10/6 ^a
Notodontidae						
<i>Thaumetopoea</i>	19	20	19	21	20	0.95
<i>Traumatocampa</i>	24	23	24	23	24	1.04
<i>Epicoma</i>	46	47	45	46	43	0.93
<i>Anaphe</i>	41	40	40	41	38	0.92
<i>Clostera</i>	35	38	37	40	37	0.92
<i>Lirimiris</i>	34	33	35	34	31	0.91
<i>Platychasma</i>	26	29	29	31	33	1.06
<i>Notodonta</i>	21	23	21	24	16	0.66
<i>Odontosia</i>	29	27	26	30	21	0.70
<i>Pheosia</i>	24	24	23	25	18	0.72
<i>Ptilophora</i>	22	20	22	21	19	0.90
<i>Gluphisia</i>	24	23	27	28	20	0.71
<i>Cerura</i>	50	53	53	56	0	0
<i>Furcula</i>	28	33	33	32	0	0
<i>Liparopsis</i>	50	52	53	52	0	0
<i>Quadricalcarifera</i>	52	49	50	51	41	0.80
<i>Phalera</i>	40	37	37	39	23	0.58
<i>Datana</i>	30	30	30	34	10	0.29
<i>Antheua</i>	27	26	27	27	23	0.85
<i>Nadata</i>	23	19	30	29	21	0.72
<i>Peridea</i>	24	25	25	26	20	0.76
<i>Ellida</i>	22	23	26	27	20	0.74
<i>Tarsolepis</i>	33	50	51	49	0	0
<i>Dudusa</i>	41	43	40	39	29	0.74
<i>Crinodes</i>	27	29	31	32	24	0.75
<i>Cargida</i>	25	28	29	28	24	0.85
<i>Goacampa</i>	18	18	20	20	13	0.65
<i>Gargetta</i>	0	16	30	31	0	0
<i>Scrancia</i>	35	40	57	58	0	0
<i>Hemiceras</i>	20	20	21	22	19	0.86
<i>Spatalia</i>	24	25	27	28	23	0.82
<i>Fentonia</i>	28	29	31	30	27	0.90
<i>Lochmaeus</i>	23	23	22	24	13	0.54
<i>Schizura biedermani</i>	27	28	30	29	20	0.68
<i>Heterocampa</i>	35	40	40	42	16 ^b	0.38
<i>Macrurocampa</i>	35	35	39	36	0	0
<i>Schizura unicornis</i>	22	24	23	24	12	0.50
<i>Cnethodonta</i>	32	33	32	34	24	0.70
<i>Harpyia</i>	39	42	41	43	0	0
<i>Stauropus</i>	32	31	30	32	0	0
<i>Erbessa</i>	24	25	28	27	16 ^b	0.59
<i>Phaeochlaena</i>	18	19	19	24	17 ^b	0.70
<i>Phryganidia</i>	25	26	27	25	19	0.76
<i>Zunacetha</i>	21	23	22	23	17	0.73
<i>Josia</i>	19	22	21	23	18	0.78
<i>Cyanotricha</i>	25	24	25	24	17	0.70
<i>Symmerista</i>	23	23	23	25	16	0.64

TABLE 2—(Continued)

Taxon	Number of crochets					
	A3	A4	A5	A6	A10	10/6 ^a
<i>Didugua</i>	19	20	21	21	18	0.85
<i>Hippia</i>	17	18	18	19	15	0.78
<i>Nystalea</i>	27	31	32	31	17	0.54
<i>Dasylophia</i>	21	23	23	23	18	0.78
Outgroup						
<i>Doa</i>	32	30	28	28	28	1.00
<i>Oenosandra</i>	140	140	138	138	142	1.02
<i>Lymantria</i>	55	58	55	62	63	1.01
<i>Dasychira</i>	53	51	52	50	49	0.98
<i>Spilosoma</i>	32	32	34	31	34	1.09
<i>Hypoprepia</i>	42	40	39	42	40	0.95
<i>Peridroma</i>	20	22	25	28	28	1.00
<i>Nycteola</i>	17	16	16	16	17	1.06
<i>Nola</i>	0	14	13	14	13	0.92

^a Ratio of crochet number on A10 divided by the number on A6.

^b Crochets extremely small and spinelike, not hook-shaped.

the first abdominal segment. For this and for the following character, I used a simple system of states; I scored larvae as either having a tubercle on A1 (score of "1") or not ("0"), disregarding the diversity of tubercle types. My rationale was that, by ignoring complexity, I might find useful information concerning basic similarity. This approach was hardly successful; Characters 162 and 163 show extremely poor consistency (Appendix III).

A tubercle on A1 is found in relatively few taxa among my study sample. In addition to three heterocampine species (e.g., fig. 456), one occurs on *Clostera albosigma* and a very short one is found in *Nystalea nyseus* (fig. 454).

Character 163. Tubercle Present on A8. Presence of a tubercle on A8 is taxonomically more widespread than presence of one on A1. In addition, A8 tubercles exhibit a greater variety of shapes and sizes, ranging from species with a slight hump (e.g., *Odontosia elegans*, figs. 69, 505) to species such as *Pheosia rimosa* (fig. 83), where the protuberance is long and spinelike. All were simply scored as having the apomorphic state, protuberance present. As with Character 162, the A8 protuberance exhibits an inconsistent taxonomic distribution (Appendix III). It occurs in the Pygaerinae (fig. 504), in the Notodontini (fig.

505), in *Ellida caniplaga*, in *Cargida pyrrha* (Dudusinae; fig. 511), in four species of the Heterocampinae (e.g., figs. 93, 446), and in all five nystaleine species I examined (figs. 82, 95, 96, 513). It appears likely that A8 tubercles have been lost and gained many times within the Notodontidae. Further study of Character 163 is certainly necessary.

Character 164. Middorsal Glands Present. An important synapomorphy for the Lymantriidae is presence of middorsal glands in the caterpillars (Bourgogne, 1951; Ferguson, 1978; Godfrey, 1987a). Often brightly colored, these almost always occur on segments A6 and A7 (e.g., in *Dasychira* and *Lymantria*), but they can be present on additional body segments (Ferguson, 1978). The glands are not associated with deciduous setae and are not homologous with the dorsal pads of thaumetopoeine larvae (see Character 157).

Character 165. Segments A7–A10 Triangular. Segments A7–A10 of some species are triangular in lateral view, the seventh segment being somewhat constricted and the eighth segment being high (fig. 446). This character state occurs in *Stauropus* and others, providing a synapomorphy for Clade 39. In live larvae, these segments usually arch upward and are carried erect (fig. 92; Stephens, 1829), a behavior characteristic of

several notodontid groups, including the Dudusinae, Phalerinae, Heterocampinae, Notodontinae, and Dioprinae.

Character 166. Segments A7 and A8 with a Lateral Ridge. Larvae of three species in my study sample—*Stauropus fagi*, *Cnethodonta grisescens*, and *Harpyia microsticta* (fig. 446)—have a well-defined lateral ridge on segments A7 + A8. The ridge is particularly prominent in the first two species. Its presence, along with many other larval characters, supports monophyly of Clade 40.

Abdominal Segment 10: The terminal abdominal segment of notodontid caterpillars is often highly modified. In particular, there is extreme variation in morphology of the anal prolegs. Taxa such as *Clostera*, *Lirimiris*, and members of the Thaumetopoeinae have anal prolegs that are not different from those on segments A3–A6. In others, the anal prolegs are not used for walking, lack crochets, and are remarkably modified into elongate “stemapods” (Gerasimov, 1952) bearing eversible distal glands. These glands, termed “lashes” by Holloway (1983), are everted when the larva is disturbed (Godfrey and Appleby, 1987; Holloway et al., 1987) and presumably emit a noxious chemical to deter predators (Chow and Tsai, 1989). Klotz (1969) found that *Cerura* caterpillars evert the stemapod glands in response to sound.

Within the Notodontidae, one finds a complete spectrum of anal proleg modification ranging between these two extremes. My results indicate, however, that dramatically different anal proleg types can be found in closely related species. For example, many authors have recognized a close relationship between *Dudusa* and *Tarsolepis*. Members of these genera have almost identical male genitalia (Roepke, 1944), and I provide additional synapomorphies from adult morphology. However, *Dudusa* caterpillars possess only slightly modified anal prolegs (fig. 89; Nakatomi, 1977) while in *Tarsolepis* larvae the prolegs are stemapodiform (fig. 90; Holloway, 1983). Similarly, I found marked differences in anal proleg morphology within the Dioprinae. Larvae of *Erbessa glaucaspis* have stemapodiform anal prolegs (fig. 514), whereas those of *Phryganidia californica* and *Josia* species are only moderately reduced

(figs. 97, 98, 516). These examples suggest that stemapod presence or absence is under fairly simple genetic control.

Notodontidae are unique among noctuoids in having modified anal prolegs, but non-homologous similarities can be found in caterpillars of other lepidopteran families. For example, the anal prolegs are highly reduced and not used for walking in some larvae of the Drepanidae (Peterson, 1962; MacKay, 1964).

Character 167. Modifications of the Anal Prolegs. I characterized size and shape of the anal prolegs in comparison with the A3–A6 prolegs using five character states (Appendix I). All outgroup species, including *Doa ampla* and *Oenosandra boisduvalii*, have anal prolegs that are equal in size to those on segments 3–6. I scored this state as “0”. Among ingroup species a “0” score was given to all Thaumetopoeinae (fig. 503), as well as to *Clostera* (fig. 504) and *Lirimiris*.

In the majority of notodontid species the anal prolegs are modified compared to those on segments A3–A6. Among this group I recognized four character states. First are the species in which the A10 prolegs are reduced compared to those on A3–A6 (figs. 502, 505, 506, 509, 510–513, 516). This score (“1”) applies to the vast majority of ingroup taxa (Appendix II) and can be found in species belonging to every subfamily except the Thaumetopoeinae, Pygaerinae, and Platychasmatinae (see Addition of Taxa). Next, I gave a score of “2” to species exhibiting larval stemapods. In every case, these are unmistakable, being greatly elongate, flexible, and whiplike (figs. 71, 72, 85, 90, 507, 514). Nevertheless, presence of stemapods shows homoplasy (Appendix IV). Stemapods occur in members of the Notodontinae (e.g., *Furcula borealis*, fig. 507), Heterocampinae (*Macrurocampa marthesia*), Dioprinae (*Erbessa* [fig. 514] and *Phaeochlaena*), and Dudusinae (*Tarsolepis*), including *Gargetta* and *Scranicia*. There is considerable evidence that the stemapods of dioptrines are not homologous with those of other notodontids (see discussion of Characters 169 and 170). Two additional states occur in the Heterocampinae. Larvae of *Stauropus* (fig. 80) and *Cnethodonta* (fig. 92) have elongate anal prolegs, but

rather than being flexible and whiplike they are sclerotized, stiff, and slightly expanded distally (Stephens, 1829). I gave these a score of "3". Finally, larvae of *Harpyia microsticta* have lost the anal prolegs altogether (figs. 79, 446; score of "4").

Character 168. Shape of the A10 Proleg Base. In an attempt to further characterize variation in development of the anal prolegs, I studied the shape of the A10 proleg bases. Some species with small anal prolegs have the proleg base slightly elongate (e.g., fig. 502). These were given a score of "1". In other groups, the A10 proleg bases are quite heavily sclerotized and are almost cylindrical in shape. This type, scored as "2", is characteristic of *Hemiceras*, the Heterocampinae, Nystaleinae, Dioprinae, and Dudusinae (figs. 510–513, 516). Species with stemapodiform anal prolegs were scored as missing data ("?") for Character 168 because the boundaries of the A10 proleg bases are completely obscured.

Character 169. Number of Setae on A10 Proleg Base. In almost all Notodontidae there are significantly fewer setae on the A10 proleg base than on the proleg bases of segments A3–A6. I gave a "0" score to taxa with fewer than 10 (figs. 502, 505, 509–513, 516). However, other notodontid species have more than 10 setae on the A10 proleg base. I broke this category into two states. In the first, the setal bases are not modified. This condition occurs in caterpillars of *Heterocampa* and *Quadricambarifera* species, as well as in *Doa ampla*. Second, in some larvae with stemapodiform anal prolegs (exemplified by *Furcula borealis* [fig. 507] and *Liparopsis postalbida* [fig. 520]) the proleg surface is covered with numerous secondary setae, each on a minute projection or "chalaza" (Peterson, 1962). However, note that the stemapods of *Phaeochlaena* and *Erbessa* (fig. 514) bear fewer than 10 setae and these are not on chalazae. This suggests that dioptrine stemapods are fundamentally different from those of other notodontids.

Character 170. Number of A10 Crochets. Larvae with reduced anal prolegs often have fewer crochets on A10 than on A2–A6. I counted the crochets on one side of the body of a single specimen for each of the study species and then divided the number of crochets on A10 by the number on A6. These

data are shown in table 2. I used three character states for this trait, the first (scored as "0") being for species in which the number of crochets on A10 is approximately equal to the number on A6 (a ratio of 0.9 or above). The second state included all species in which the ratio is 0.89 or less (scored as "1"), and the third (given a "2" score) was for those having no crochets on A10.

This character is obviously correlated with Character 167 (above), but there is one point of interest. All species with stemapodiform anal prolegs (scored as "2" for Character 167) lack crochets on A10 with the exception of the two dioptrines, *Erbessa glaucaspis* and *Phaeochlaena gyon*. In both, the planta is greatly elongate and is deeply withdrawn into the stemapod. Further, it bears a reduced number of small crochets (table 2). Thus, stemapods in dioptrines differ in two major respects from those found in other Notodontidae. First, they are the only stemapods to have retained crochets, and second, they have a different kind of setal pattern (see Character 169).

Character 171. A10 Prolegs with Crochets Withdrawn. Some notodontid caterpillars that appear to lack crochets on A10 actually have them, but they are withdrawn into the proleg. The ones in *Erbessa* and *Phaeochlaena* (Dioptrinae) were described above. Previous authors (e.g., Forbes, 1948) have characterized the Phalerinae as lacking A10 crochets. However, crochets actually do occur (table 2). In some, such as *Antheua simplex*, they are reduced in number but are clearly present. In others, such as *Datana* and *Phalera* larvae, the planta and crochets are deeply withdrawn into the A10 proleg, giving the appearance that crochets are absent. To score this character I dissected the anal prolegs of species where the derived state could possibly occur. As a result, I found that larvae of *Cnethodonta grisescens* (Heterocampinae) and *Goacampa variabilis* and *Dudusa synopla* (both Dudusinae)—all species that appear to lack A10 crochets—have them present but withdrawn into the proleg.

My analysis thus indicates that the derived state evolved at least four times within the Notodontidae. It is likely that in all these cases the anal prolegs are not used for grasp-

ing the substrate. Phalerine caterpillars are well known for holding the terminal segments aloft when at rest (Godfrey and Appleby, 1987).

Character 172. Size of the A10 Crochets. The A10 crochets, even in larvae with very few of them, are almost always the same general size and shape as those on segments A3–A6. However, in two clades the A10 crochets are small and spinelike rather than being curved. This occurs in *Erbessa* and *Phaeochlaena*, as well as in *Heterocampa* (table 2).

Character 173. Shape of the Anal Plate. There is considerable variation among notodontid caterpillars in the degree of sclerotization of the anal plate. However, there is little variation in anal plate shape, so I did not study this structure in detail. Two Notodontinae on my study list, *Pheosia rimosa* (see Godfrey and Appleby, 1987) and *Odonotosia elegans* (fig. 505), are remarkable in having the anal plate heavily sclerotized, with a deeply wrinkled surface. The anal plate of *Oenosandra boisduvalii* also fits this general description, but it is obviously a secondary derivation.

Character 174. Paraprocts Present. On A10, between the prolegs and the anus, each SV1 seta is borne on a fleshy conical projection. These projections, termed “paraprocts” by MacKay (1964) and “furcula paranalisis” by Kuznetsov (1967), are sometimes long. Various authors have noted the presence of paraprocts in *Furcula* and *Cerura* larvae (Pack-

ard, 1895a; Forbes, 1910; Gerasimov, 1952; Kuznetsov, 1967). Stehr (1987b) noted them in *Phryganidia californica* and other notodontids, and they occur in some Noctuidae (Crumb, 1956) and Geometridae (McGuffin, 1958) as well. It has been suggested that the paraprocts serve to eject frass pellets away from the body (Packard, 1895a; McGuffin, 1958). Forbes (1910) termed these structures “anal dung-forks” (which conjures up some unusual images). Paraprocts are not homologous with the “anal comb” or “anal fork,” a sclerotized structure found on the 10th larval segment in some butterflies, gelechiids, tortricids, and hedylids (Gerasimov, 1952; MacKay, 1963, 1964; Scoble, 1986). The anal comb is thought to have a function similar to paraprocts (MacKay, 1964).

Within the Notodontidae, there is almost always a pair of short lobes bearing the SV1 setae on A10 (figs. 502–506, 509–515), but these are characteristic of the outgroup as well (fig. 501). I chose to recognize only two character states. Species in which the SV1 setae are typical in shape and are each borne at the end of a short blunt lobe were scored as “0”. Taxa in which the SV1 setae on A10 are thickened and erect, and in which each lobe is elongate and tapered distally, were scored as “1”. The derived state occurs in *Cerura*, *Furcula* (fig. 508), and *Liparopsis* (fig. 520), all belonging in the Dicranurini (Notodontinae).

PROPOSED CLASSIFICATION FOR THE TRIFID NOCTUOIDEA

Three lineages in the Noctuoidea exhibit the so-called trifid condition of the forewing cubital vein, a plesiomorphic state for the superfamily: the Notodontidae (in which I include the subfamilies Dioptinae and Thaumetopoeinae), the Doidae, and *Oenosandra boisduvalii*, the last having formerly been placed in the Thaumetopoeinae. Below, I discuss my hypotheses concerning relationships among these three lineages, and I make recommendations concerning their status in the noctuid classification.

For all the discussions that follow, I list synapomorphies based on character optimization resulting from the “xsteps” procedure in Hennig86 (Farris, 1988). Two points should be made regarding this approach. First, the

character states so listed may apply to only some of the taxa above the relevant node on the cladogram. Furthermore, some of these derived states occur in various members of the outgroup, although this is not usually the case. For example, optimization of Character 20 (adult ocelli present or absent) suggests that absence is a synapomorphy for the trifid noctuid lineages, including the Notodontidae (see below). Yet there are quadrifid groups, such as the Lithosiinae (Arctiidae), that lack ocelli, and I regard presence of ocelli as a synapomorphy for the Dudusinae (Notodontidae).

In all the synapomorphy lists, I use the category “ambiguous” to refer to situations where optimization indicated more than one

way to parsimoniously fit character states on the tree. The character states in question are listed together, separated by a slash (/).

SYNAPOMORPHIES (Trifid Noctuoidea; Clade 1): **ADULTS**: R1 sensilla of proboscis short, only slightly larger than R2 sensilla; male labial palpus with segment 2 more than twice as long as segment 1, narrow; ocelli absent; female frenulum composed of 15 or more bristles; socii present; saccus small or absent. **LARVAE**: Head with seta S1 located closest to stemma 3; stipital lobe present on maxillary complex. *Ambiguous*: Female antennae pectinate/ciliate; counter-tympanal hood present, postspiracular/hood present, prespiracular.

Of those listed, the three most consistent synapomorphies are: (1) presence of socii in the male genitalia (Character 78); (2) presence of a small saccus in the male genitalia (Character 93); and (3) presence of a stipital lobe on the larval maxilla (Character 116). These are found almost universally in the trifid Noctuoidea.

I hereby propose that three trifid noctuid families be recognized: the Notodontidae, Doidae, and Oenosandridae. An alternative would be to place all three in a single family, the Notodontidae, and make the Doidae and Oenosandridae subfamilies. However, I feel that, given the current state of our knowledge, such a move would be premature, particularly with respect to *Oenosandra*, a taxon whose phylogenetic position requires further study (see below).

THE STATUS OF *OENOSANDRA*

Kiriakoff (1970b) listed three Australian species in *Oenosandra*, but other authors (Turner, 1903, 1922; Common, 1979) have considered *boisduvalii* to be the sole included species. I was able to examine only *O. boisduvalii*, and so cannot evaluate Kiriakoff's claim. All of these authors regarded *Oenosandra* to be a member of the Thaumetopoeinae, apparently because the adult female possesses a terminal tuft of deciduous scales, an apomorphy found in many Lymantriidae and some Noctuidae, as well as in the Thaumetopoeinae (see Character 50). Kiriakoff (1970b) figured the male and female genitalia of *O. boisduvalii*.

The phylogenetic position of *Oenosandra boisduvalii* is problematical. Presence of a

metathoracic tympanum clearly indicates membership in the Noctuoidea. My cladistic analysis demonstrates that *O. boisduvalii* does not belong in the Notodontidae, but I am unable to suggest another existing noctuid family in which to place it. The species exhibits a seemingly contradictory set of characters. Besides being trifid in the forewing, the male genitalia have what appear to be socii (figs. 310, 311). However, the tympanal morphology of *Oenosandra* is typical of quadrid noctuoids rather than notodontids: the membrane faces posteriorly, and a nodular sclerite is present. The counter-tympanal hood on abdominal segment 1 is prespiracular, the configuration found among Arctiidae, Lymantriidae, and some Noctuidae.

The unusual larva offers few clues. Except for the stipital lobe (Character 116), it does not exhibit any of the apomorphic traits of notodontid caterpillars. The mandible is serrate rather than smooth, the anal prolegs are fully developed (a primitive state), and the body is relatively smooth; there are scattered secondary setae, but not the dense covering and verrucae found in thaumetopoeine larvae. The arrangement of primary setae on the head, thorax, and abdomen is unlike any notodontid. There are few SV setae on the lateral surface of the prolegs on A3–A6 (Character 156), a condition found in the Lithosiinae and some Noctuidae (Appendix II).

Common (1979), who regarded *Oenosandra* to be an "aberrant" member of the Thaumetopoeinae, claimed that the larval crochets are biordinal. I found them instead to be biserial, a derived state that does not occur elsewhere in the Noctuoidea (see Character 159). The larvae of *O. boisduvalii* are "semi-gregarious" (McFarland, 1979). They do not rest in a silk nest, as do thaumetopoeine caterpillars, and McFarland suggested that their behavior resembles that of some Arctiidae. The eggs, elongate-cylindrical in shape with longitudinal grooves, are atypical for members of the Notodontidae (McFarland, 1972), most of which have dome-shaped eggs without surface sculpturing (Packard, 1895a; McFarland, 1972).

Given the character information at hand, I suggest that *Oenosandra boisduvalii* is the plesiomorphic sister group to Clade 3 (fig. 99), *Doa* + Notodontidae. Synapomorphies to support this hypothesis are listed above.

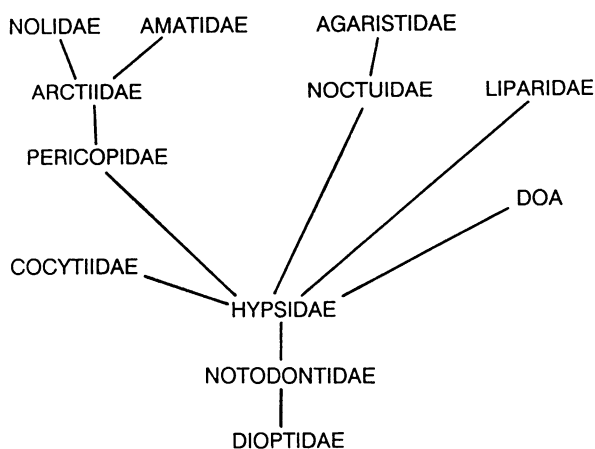


Fig. 521. Phylogeny for the Noctuoidea taken from Forbes's "Genealogy of the Families Related to the Noctuidae" (1923: fig. 2).

An alternative, but less parsimonious, hypothesis is that *Oenosandra* represents the plesiomorphic sister group to the quadrifid Noctuoidea. As far as I have been able to discover, *O. boisduvalii* does not exhibit synapomorphies of the Lymantriidae, Arctiidae, or Noctuidae, but my search was not exhaustive.

DIAGNOSIS (Oenosandridae; Clade 2): **ADULTS:** Proboscis short; labial palpi extremely short but clearly three-segmented; frons protruding, with a prominent sclerotized ridge; male antennae bipectinate to tip; female antennae simple; tibial spurs in the formula 0-2-4; sclerotized apices of tibial spurs smooth; tarsal claws simple; metathoracic tympanum similar to Lymantriidae and Arctiidae; male T8 and S8 simple; male genitalia with socii present, saccus small, valve simple, transtilla large and platelike, aedeagus short, vesica lacking cornuti; female abdomen with anal scale tuft; female T8 simple, not emarginate posteriorly; female genitalia with ostium simple, ductus bursae long and spiral-shaped, with an elongate sclerotized band, signum long, a small appendix bursae present. **LARVAE:** Surface of head covered with fine creases, no secondary setae present; mandibles serrate; labral notch shallow; antennae short; spinneret and labial palpi long; stipital lobe present, short and broadly rounded; prothoracic gland absent; thoracic SV setae in the formula 2-2-2; tarsal setae lanceolate; setal clusters present at most primary setal locations, but no covering of sec-

ondary setae; dorsal tubercles and prominences absent; all prolegs of equal size; A3–A6 prolegs with 3 or fewer SV setae on lateral surface; crochets biserial.

SYNAPOMORPHIES: ADULTS: Frons sclerotized; length of proboscis less than length of head; female T7 membranous, wrinkled, covered with deciduous scales; transtilla of male genitalia large and platelike. **LARVAE:** A3–A6 prolegs with three or fewer SV setae on lateral surfaces; crochets biserial, in two rows of equal length.

THE STATUS OF *DOA*

The phylogenetic position of *Doa* has proved to be one of the most controversial issues in noctuoid systematics. The genus has at one time or another been included in the Geometridae, Lymantriidae, Hypsiidae, Arctiidae, Pericopidae, and Dioptriidae (Watson et al., 1980; Donahue and Brown, 1987; see also Introduction). Most recently, it was given its own family, the Doidae (Donahue and Brown, 1987). When Forbes (1923) published his "Genealogy of the Families Related to the Noctuidae" (fig. 521), he placed *Doa* as a separate element arising from the base of the quadrifid Noctuoidea. Richards stated that *Doa* "is a connecting link between the trifid and quadrifid families" (1932: 32). He noted that *Doa* species lack a counter-tympanal hood and nodular sclerite, but possess a sunken metepimeron. These states are all typical of Notodontidae. He showed that the

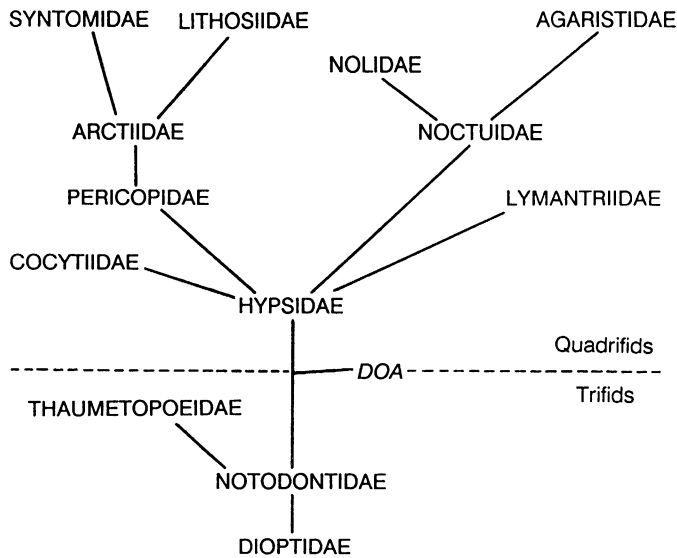


Fig. 522. Phylogeny for the Noctuoidea taken from Richards (1932: pl. 20) showing his placement of *Doa*.

tympanum of *Doa* has a well-developed pocket III like quadrifid noctuoids, and that the scutal phragma is similar to that of quadrifid species as well. Richards therefore placed *Doa* on his phylogenetic tree exactly between the quadrifids and trifids (fig. 522).

My analysis suggests that the sunken metepimeron and horizontally directed tympanal membrane are apomorphic. These would therefore be synapomorphies for the *Doa* + Notodontidae clade. The condition of the scutal phragma (which I term the "metascutal bulla," Character 34) in *Doa* and quadrifid species is similar; both groups lack the metascutal bulla. However, I regard absence as plesiomorphic. Neither Forbes nor Richards was able to study *Doa* larvae. I found that the caterpillars share two apomorphies with the Notodontidae (listed below). Unfortunately, I could not determine whether seta X is present on the larval anal plate in *Doa*. Presence of seta X is an important synapomorphy for the Notodontidae (Character 155), but that region is obscured in *Doa* by numerous secondary setae. Two synapomorphies for the Notodontidae do not occur in *Doa* species. First, the male genitalia do not appear to have *socii*. The unusual structure found in *Doa* genitalia (fig. 305), approximately in the location of *socii*, is problematic; I could not determine whether it is

homologous with *socii*. Second, the larvae have only a single MD seta on segment A1 rather than two, the latter being synapomorphic for all Notodontidae except Diop-tinae.

The evidence thus suggests that characters shared by *Doa* and the quadrifid Noctuoidea are symplesiomorphic and that *Doa* is the sister group of the Notodontidae. Donahue and Brown (1987) proposed using the family name Doidae, and I follow their recommendation. According to Franclemont (1983) and Donahue and Brown (1987), the genus *Leuculodes* Dyar also belongs in the Doidae. I have not studied *Leuculodes* adults to verify this, and as far as I am aware the immature stages are unknown. The character lists below are based on *Doa* only. Larvae of *Doa* species are described in Donahue and Brown (1987), and all immature stages are covered in Brown (1990).

SYNAPOMORPHIES (Doidae + Notodontidae, Clade 3): ADULTS: Dorsal portion of metepimeron strongly concave, forming a tympanum; tympanal membrane facing ventrally; tympanum without a nodular sclerite; segment A1 without a counter-tympanal hood. **LARVAE:** Head with seta P2 located near epicranial notch, closer to midline than P1; distance between P1 and C1 half again as long as the distance between Af2 and C1.

DIAGNOSIS (Doidae): ADULTS: Proboscis not as long as thorax but longer than head; labial palpi fairly long, second segment long, third segment short and round; male antennae bipectinate to tip; female antennae bipectinate; legs long; tibial spurs in the formula 0-2-4; sclerotized apices of tibial spurs smooth; tarsal claws simple; metathoracic tympanum similar to Notodontidae, metepimeron deeply sunken, nodular sclerite absent; male T8 and S8 simple; male genitalia with a gnathos (= socii?) present, saccus small, valve simple, transtilla short, not joined above aedeagus, aedeagus short and broad, vesica with small patches of scobinate cornuti; female abdomen lacking a terminal scale patch; female T8 simple; a dorsal, glandular invagination present between female segments 8 and 9/10; female genitalia with ostium simple, ductus bursae moderately long and sclerotized, signum absent, papillae anales with a pair of dorsal, setose lobes. **LARVAE:** Surface of head smooth, with shallow creases, no secondary setae present; mandibles serrate; labral notch shallow; antennae extremely short; spinneret short; stipital lobe present, broadly rounded, spiculate; prothoracic gland absent; thoracic SV setae in the formula 4-4-4; tarsal setae lanceolate; integument covered with long spicules; body not covered with secondary setae, except numerous setae in the region of L3 on all abdominal segments; dorsal tubercles and prominences absent, but thoracic segments distinctly humped dorsally; abdominal spiracles small; all prolegs of equal size; numerous SV setae on A3-A6 prolegs; crochets biordinal; numerous setae on anal plate.

SYNAPOMORPHIES (Doidae): ADULTS: Proboscis not as long as thorax, but longer than head; legs long, hind tibia approximately $1\frac{1}{2}$ times the length of femur, pairs of spurs widely separated; male genitalia with a gnathos (= socii?) present; transtilla not joined above aedeagus; female genitalia with a pair of setose dorsal lobes above papillae anales. **LARVAE:** Spinneret short; thoracic setae in the formula 4-4-4; thoracic segments humped; integument spiculate, each spicule arising from a socket; numerous setae in the region of L3 on all abdominal segments; abdominal spiracles small; crochets biordinal; numerous setae on anal plate.

MONOPHYLY OF THE NOTODONTIDAE

My results provide convincing support for monophyly of the Notodontidae. My concept of family boundaries conforms well to most previous classifications. I include the Thaumetopoeinae in the Notodontidae and give the group subfamilial status, as have many authors before me. I raise the Dioptini of Weller (1989) and Minet (1983, 1986) to subfamily status, but recognize the group's position as subordinate within the Notodontidae, following those authors. Compared to other families in the Noctuoidea, I would suggest that the Notodontidae (as here circumscribed) is one of the best defined.

SYNAPOMORPHIES (Notodontidae): ADULTS: Sclerotized apices of tibial spurs with margins serrate; metascutal bulla present, teardrop-shaped; vein R_2 stalked with R_{3-5} , no accessory cell present; pleuron of female segment 8 partially membranous; a ventral, invaginated, glandular region present in membrane between papillae anales and ostium; males with a terminal tuft of long hairlike scales, scale apices simple or serrate. **LARVAE:** Mandibular cutting edge smooth; body evenly covered with secondary setae, larger setae or sometimes verrucae present at primary setal locations; MD setae bisetose on A1; seta X located in E area near anterolateral corner of anal shield, or a verruca in that position; crochets uniordinal.

The most widely distributed of the synapomorphies listed above, and the ones that are therefore most diagnostic, are the following: Character 26, although serrate tibial spur apices also occur in Lymantriidae and Pantheinae (Noctuidae); Character 34, except that some Dudusini (Notodontidae) exhibit reduced metascutal bullae; Character 113, with reversal to serrate mandibles having occurred in some Dudusinae and Dioptinae; Character 146, the Dioptinae being unusual in showing the plesiomorphic state, a single MD seta on larval A1; and Character 155, again with Dudusinae being unique in having lost seta X on the terminal larval segment. Most of the other synapomorphies listed show low consistency and are unreliable as diagnostic features.

PROPOSED CLASSIFICATION FOR THE NOTODONTIDAE

In this section I propose a new subfamily classification for the Notodontidae. In certain cases I further divide subfamilies into tribes. My approach is relatively conservative; I have erected only one new family group name, the *Scranciini*. In addition, the classification reflects what I feel are the most well-substantiated, stable parts of my cladogram. Based on cladistic analyses of larval and adult morphological characters, I have identified nine major monophyletic groups in the Notodontidae (figs. 99, 100, 538), each of which I recognize as a subfamily. For certain genera I was not confident of subfamilial placement. These I have either placed incertae sedis or placed them in the subfamily indicated by the analysis, noting that their position is in doubt.

After giving a key to the subfamilies and tribes of the Notodontidae, I discuss each subfamily in turn. I describe the major differences and similarities between my subfamilial concepts and those of other authors. For each subfamily and tribe, I present a summary of diagnostic features for each group and a list of synapomorphies. These diagnostic characters, both apomorphic and plesiomorphic, are based exclusively on the exemplar taxa I examined. As future workers add species to these groups, some characters will likely need to be eliminated from the diagnoses and new ones will be added.

I also give an estimate of how many species are contained in each group and briefly discuss geographic distribution. Both of these are difficult to assess because the vast majority of notodontid species have never been assigned to a subfamilial or tribal category.

Although the majority of higher category names I use have been in existence for some time, membership in my groups is often radically different from what has previously been proposed. Many of the tribes and subfamilies of previous authors are paraphyletic. Others turned out to be highly derived elements within particular clades, and in such cases, I recommend that they be subsumed within the appropriate subfamily. Finally, I found that some subfamilies, such as the *Dudusinae* of authors, are much larger than previously thought.

KEY TO THE MAJOR SUBGROUPS OF TRIFID NOCTUOIDEA

The key below applies to all Noctuoidea with trifid forewing venation (see Character 35): the Notodontidae, Doidae, and Oenosandridae. An interesting exception is the subfamily *Platychasmatinae* (Notodontidae), the only notodontid with quadrifid venation (see Addition of Taxa). The key also treats notodontid tribes.

Initially I tried to write the key so that only adult specimens were required, the obvious reason being that caterpillars are unknown for the vast majority of taxa. However, often the best diagnostic features for notodontid groups are from larval morphology, and for some lineages (e.g., the *Heterocampinae*), no reliable adult characters exist. I was therefore forced to make a key based on both larval and adult characters.

1. Forewing with cubital vein quadrifid (fig. 244) 2
Forewing with cubital vein trifid (figs. 245–249) 3
- 2(1). Male genitalia with socii present (fig. 533); larval maxilla with a stipital lobe (e.g., fig. 398) *Platychasmatinae* (Notodontidae), p. 193
Male genitalia with socii absent (e.g., fig. 312); larval maxilla without a stipital lobe “*Quadrifid Noctuoidea*”
- 3(1). Metathoracic tympanum with membrane oriented horizontally, nodular sclerite absent (figs. 238–240); larval crochets in a uniseries; seta P2 on larval head closer to midline than seta P1 (e.g., figs. 367, 369); spinneret usually short or moderate in length (figs. 414–437) ... 4
Metathoracic tympanum with membrane facing posteriorly, nodular sclerite present (e.g., fig. 237); larval crochets biserial; setae P1 and P2 on larval head equidistant from midline (fig. 365); spinneret extremely long (fig. 439) ... *Oenosandridae* (*Oenosandra*), p. 169
- 4(3). Sclerotized apices of adult tibial spurs serrate (fig. 226); male genitalia with paired socii present below uncus (e.g., figs. 300–303); larval crochets uniordinal *Notodontidae* ... 5
Sclerotized apices of tibial spurs smooth (fig. 228); male genitalia with a fused structure (gnathos?) below uncus (fig.

- 305); larval crochets biordinal
..... Doidae (*Doa*), p. 170
- 5(4). Antennal segments joined at an oblique angle (fig. 213); female terminal segments with a large tuft of deciduous scales (fig. 257); larval mandibles with secondary setae
..... Thaumetopoeinae, p. 175
- Antennal segments joined vertically; female terminal segments without deciduous scales; larval mandibles without secondary setae (figs. 396, 397) 6
- 6(5). Male antennae pectinate for entire length (fig. 205); adult tarsal claws simple (fig. 236); proboscis extremely short (e.g., fig. 102) Notodontinae, p. 177 ... 7
- Male antennae often with apical segments simple (figs. 206, 207); adult tarsal claws usually bifid (fig. 234); proboscis variable in length 8
- 7(6). Anal margin of forewing with a prominent scale tuft (figs. 29, 30, 250); male antennal pectinations not long; larva with a dorsal protuberance on A8 (e.g., figs. 69, 83); stemma 3 not greatly enlarged (fig. 368); larval stemapods never present (fig. 505) Notodontini, p. 179
- Anal margin of forewing without a scale tuft (figs. 32–34); male antennal pectinations long (e.g., figs. 20, 205); larva without a protuberance on A8 (e.g., figs. 70, 508, 509); stemma 3 large (fig. 394); larval stemapods often present (figs. 71, 85, 507) Dicranurini, p. 180
- 8(6). Larva with anal prolegs unmodified, approximately the same size as those on segments A3–A6 (fig. 504) 9
- Larva with anal prolegs modified, either much smaller or more elongate than those on segments A3–A6 (e.g., figs. 506, 511, 512) 10
- 9(8). Adult eyes hairy (fig. 200); abdomen with a prominent terminal scale tuft (fig. 298); proboscis highly reduced, no fluted R1 sensilla present (fig. 143); larva with a short, sclerotized dorsal tubercle on segments A1 and A8 (fig. 504); larval integument covered with microprojections (fig. 494)
..... Pygaerinae (*Clostera*), p. 176
- Adult eyes naked; male abdomen without a prominent terminal tuft of scales; proboscis moderate in length, fluted R1 sensilla present (fig. 146); larva without dorsal protuberances on A1 and A8, dorsum smooth; larval integument minutely spiculate *Lirimiris*, p. 190
- 10(8). Adult ocelli present (figs. 108, 109, 115); proprioceptor seta MSD2 on segments A2–A6 located anterodorsally to spiracle (fig. 511); larval A10 with seta X absent (fig. 511); adult frons often sclerotized (figs. 108, 109, 115)
..... Dudusinae, p. 181 ... 11
- Adult ocelli rudimentary or absent (e.g., figs. 107, 110–112); proprioceptor seta MSD2 on segments A2–A6 located on a horizontal line with spiracle (e.g., figs. 454, 512); larval A10 with seta X present (e.g., figs. 510, 512, 513); adult frons never sclerotized (e.g., figs. 110–112) .
..... 12
- 11(10). Adult foretarsi long, first tarsomere longer than others combined (figs. 214, 217); transtilla of male genitalia absent (fig. 309) .. Scranciini (*Dudusinae*), p. 184
- Adult foretarsi not long (fig. 223); transtilla of male genitalia connected below aedeagus to ventral portion of juxta (figs. 301, 316, 321)
..... Dudusini (*Dudusinae*), p. 183
- 12(10). Hind wing vein M₂ absent (fig. 246); anal margin of forewing with a toothlike tuft; caterpillar with scattered, isolated secondary setae near D and SD groups (fig. 512) *Hemiceras*
("Hemicerati"), p. 191
- Hind wing vein M₂ present (figs. 248, 249); anal margin of forewing without a scale tuft (figs. 41–48, 55–65); caterpillar either without isolated secondary setae, or evenly covered with numerous secondaries (figs. 450, 454–457) 13
- 13(12). Seta L2 on larval segment A8 anterior to, and on a horizontal line with, spiracle (figs. 513, 515, 516) 14
- Seta L2 on larval segment A8 located below spiracle (figs. 506, 510) 15
- 14(13). Aedeagus with a callosum (fig. 343); scape of male antenna with a long dorsal plume; segment 3 of adult labial palpus often long (figs. 112, 128, 129); adult legs not unusually long; larval cuticle without microprojections (fig. 443); adult moth not brightly colored (figs. 61–65) Nystaleinae, p. 188
- Aedeagus without a callosum (figs. 344, 346); scape of male antenna without a long dorsal plume; segment 3 of adult labial palpus not unusually long, often small and globose (figs. 110, 111, 130); adult legs long (figs. 218–220); larval cuticle covered with long microprojections ("shagreened") (figs. 444, 445);

- adult moth often with striking patterns,
brightly colored (figs. 55–60)
..... Diopinae, p. 189
- 15(13). Larval thoracic SV setae in the formula
2-2-2, anterior SV setae short (figs. 455–
458) Heterocampinae, p. 185
- Larval thoracic SV setae in the formula
2-1-1 (e.g., fig. 454), anterior SV seta
(on T1) not short .. Phalerinae, p. 180

THAUMETOPOEINAE

The Thaumetopoeinae comprise 100 species in 23 genera (Kiriakoff, 1970b) occurring in Africa, the Mediterranean, southern Europe to northern India, Australia, and New Caledonia (Kiriakoff, 1970b; Holloway, 1979; Holloway et al., 1987). The group is reasonably well defined, but is in need of detailed revisionary work.

DIAGNOSIS (Clade 6): ADULTS: Frons sometimes sclerotized, with anterior processes (*Traumatocampa*); proboscis reduced or absent; labial palpi small, often highly reduced; male and female antennae pectinate to apex; ocelli absent; female with epiphysis sometimes absent (*Epicoma*); hind tibiae with distal pair of spurs only; tarsal claws simple; forewing radial system without an accessory cell, vein R_2 stalked with R_{3+5} ; FW lacking a scale tuft; female frenulum composed of more than 20 bristles; terminal segments of male with a tuft of long simple scales; terminal segments of female with a large mat of deciduous scales; female genitalia with T8 simple, signum present or absent; male eighth segment simple, no anterior processes or distal notch; male genitalia with valve simple, sacculus without pleats, socii present; vesica of aedeagus without deciduous cornuti. **LARVAE:** Head with secondary setae present, surface with shallow creases, not rugose; mandibles with secondary setae present, cutting edge smooth or with a few shallow dentations; labral notch shallow; antennae moderate in length; stipital lobe absent; spinneret moderately long; body covered with secondary setae, often on verrucae; prothoracic gland absent; tarsal setae narrow; anal prolegs not reduced.

SYNAPOMORPHIES (Clade 6): ADULTS: Proboscis absent or present as two small lobes; R1 sensilla short, only slightly larger than R2

sensilla; pilifers absent; male labial palpus with segment 2 approximately 1–1½ times the length of segment 1; male palpus small, often with division between segments 2 and 3 indistinct; antennal segments joined at an angle in lateral view; proximal pair of metatibial spurs absent (formula 0-2-2); female T7 membranous, covered with deciduous scales. **LARVAE:** Mandible with numerous secondary setae; stipital lobe absent; basal tarsal setae on thoracic legs (Ts1 and Ts3) narrow. *Ambiguous:* Larval abdominal segments 1–8 without dorsal patches of deciduous setae/dorsal pockets present on A1–A8, containing tufts of deciduous setae.

DISCUSSION: The major controversy concerning the processionary moths has been whether they should receive subfamilial or familial status (Watson et al., 1980). There has been considerable instability even among recent works in this regard. I have chosen to reflect what is clearly a sister group relationship between the Thaumetopoeinae and other Notodontidae (fig. 99) by using the subfamily name. Additional synapomorphies are needed for this subfamily.

I have shown that *Oenosandra* is not a member of the Thaumetopoeinae and should, in fact, be excluded from the Notodontidae. It would seem advisable, therefore, to review the Thaumetopoeinae for other incorrectly placed taxa. Gardner (1943) noted that mandibular secondary setae do not occur in the genus *Gazalina* Walker, purportedly a member of the Thaumetopoeinae. Based on the figures in Kiriakoff (1970b), the male genitalia of *G. apsara* (Moore) appear to lack socii. The genus had been referred to the Lymantriidae (e.g., Hampson, 1892), but was moved to the Thaumetopoeinae by Grünberg (1912). *Gazalina* should be examined to see whether it has been correctly placed.

Turner defined the Cnethocampinae (= Thaumetopoeinae) on the basis of having the tongue absent, the labial palpi highly reduced, the antennae pectinate to apex, and the "abdomen with a large apical tuft in both sexes, especially developed in the female" (1922: 362; see also Turner, 1946). None of these traits effectively define this subfamily. The tongue and labial palpi are reduced or absent in some species belonging to almost

every notodontid subfamily. Having the antennae pectinate to the apex, a plesiomorphic trait, occurs in Pygaerinae, Notodontinae, and some Phalerinae and Heterocampine. A male apical tuft is found almost throughout the Notodontidae. The female tuft of deciduous scales (Character 50) does appear to be a derived state within the Notodontidae and is a reasonably good synapomorphy for the Thaumetopoeinae. However, I noted previously that a similar female tuft occurs in Lymantriidae, some Dioprinae, *Oenosandra*, and some members of the Noctuidae.

Only two papers have addressed classification within the group. Kiriakoff (1970b) broke the "Thaumetopoeidae" into three subfamilies based on geographic distribution. The Thaumetopoeinae included all Palearctic and Oriental taxa, the entire African fauna was classified in the Anaphinae, and the Epicominae comprised all the Australian species. I did not study a sufficient number of taxa to test Kiriakoff's classification, but distributional data can hardly provide grounds for erecting subfamilies. In a discussion of western Palearctic Thaumetopoeinae, de Freina and Witt (1987) divided the genera into two groups: those without a modified frons (e.g., *Thaumetopoea*) and those with sclerotized processes on the frons (e.g., *Traumatocampa*). An unmodified frons is plesiomorphic for the subfamily, so a group formed on those grounds alone is likely to be paraphyletic. It will be interesting to see whether, with study of taxa from other biogeographic regions, de Freina and Witt's second group will prove to be monophyletic.

PYGAERINAE

Because the boundaries of the Pygaerinae are at present so vague, it is difficult to estimate the number of included species. Based on the distribution of *Clostera*, the subfamily is found worldwide. The genus, comprising 43 species (Gaede, 1934), occurs in the Nearctic, Neotropical, Palearctic, Indo-Australian, and African regions. *Clostera* has several easily recognizable male genitalic features that appear to support monophyly.

DIAGNOSIS (*Clostera*; Clade 9): **ADULTS:** Male antennae pectinate to apex; female antennae pectinate; eyes with interfacetal setae

present; proboscis short; labial palpi relatively long, segment 2 approximately $1\frac{1}{2}$ times the length of segment 1; frons unmodified, rounded anteriorly; forewing radial system lacking an accessory cell, vein R_2 stalked with R_{3-5} ; female frenulum composed of fewer than 15 bristles; tarsal claws bifid; hind tibiae with two pairs of spurs; abdomen with a terminal tuft of long scales; male segment 8 with tergum and sternum simple; male genitalia with pleated saccular scent organ, pleats sclerotized; vesica of aedeagus without deciduous cornuti; female genitalia with T8 simple, ductus bursae long, membranous, signum present. **LARVAE:** Head with secondary setae, surface with shallow creases, not rugose; labral notch relatively shallow; mandibular cutting edge smooth; stipital lobe short and rounded; spinneret moderate in length; labial palpi without medial flange; antennae moderately long; body covered with secondary setae, often on verrucae; prothoracic gland absent; tarsal setae lanceolate; segments A1 and A8 with a dorsal protuberance; anal prolegs not reduced.

SYNAPOMORPHIES (*Clostera*): **ADULTS:** Proboscis shorter than length of head; male epiphysis flat, almost as long as tibia, apex not acute; sacculus large, with accordion-like pleats. **LARVAE:** Long secondary setae present on head; stemma 3 larger than stemma 4; mandible with a pronounced ventrolateral carina; integument covered with microprojections; segment A8 with a dorsal protuberance.

DISCUSSION: The Pygaerinae, erected by Duponchel (1845), is one of the oldest subfamily categories in the Notodontidae, although the family name Melalophidae (based on *Melalopha* Hübner), first used by Grote (1895), has been adopted by many subsequent authors (e.g., Dyar, 1897; Forbes, 1948). Even though the Pygaerinae has been widely recognized, it remains poorly defined. Packard's (1895a) key character was presence of "hairy" larvae. Dyar (1897) expanded the subfamilial concept. He decided that presence of larval secondary setae was a highly significant character and that the group should therefore be considered a family. Hairy larvae occur throughout the Notodontidae (see Character 140), and a group formed solely on that basis has no chance of being monophy-

letic. Dyar's Melalophidae, characterized by having "hairy" larvae and adults with "tongue often absent" (1897: 2), included genera that belong in the Thaumetopoeinae and Phalerinae, as well as in the Pygaerinae.

The following characters were used by Packard (1895a), Matsumura (1929b), and Forbes (1948) to define the Pygaerinae: adults with eyes hairy; antennae pectinate to tips; labial palpi long; male abdomen ending in a tuft; larvae hairy, with a pair of tubercles on segments A1 and A8. Unfortunately, most of these occur in one form or another in other members of the Notodontidae. As far as I have been able to determine, consistent apomorphies for *Clostera* species are the unique type of sacculus in the male genitalia (fig. 328; see also figures in Holloway, 1983) and the setose tubercles on larval segments A1 and A8 (Packard, 1895a; Gardner, 1943; Issiki et al., 1969; Holloway, 1983; Godfrey and Appleby, 1987).

Whether other genera will be added to the subfamily based on presence of these traits remains to be seen. Duponchel (1845) placed two genera in the Pygaerinae: *Clostera* Samouelle and *Pygaera* Ochsenheimer. Janse (1920) formed "Group I" of the South African Notodontidae and in it placed two genera: *Clostera* and *Scalimicauda* Holland. I have not examined whether *Scalimicauda* shares apomorphies with *Clostera*; the diagnostic characters for Janse's Group I are uninformative. Forbes (1948) considered *Clostera* to be the only North American member of the Pygaerinae. Earlier (1939a), Forbes broke the subfamily into two tribes (table 5): the Melalophini and Rosemini, the latter to include a single Neotropical genus, *Rosema* Walker. Apparently, Forbes's rationale for including *Rosema* was based on an early larval description by Stoll (1790). Forbes stated, however, that adult characters of *Rosema* indicate membership in the "Notodontinae." The genus *Rosema* is large and complex, probably polyphyletic (S. Weller, personal commun.). I have not studied whether all or part of it should be included in this subfamily. When Nagano (1916) erected the genus *Micromelalopha*, he suggested that it is very close to *Clostera* based on both larval and adult structure. Tikhomirov (1981) studied male genitalic musculature in No-

todontidae. He argued that, on the basis of similarities in genitalic morphology, three genera in addition to *Clostera* belong in the Pygaerinae: *Gonoclostera* Butler, *Micromelalopha* Nagano, and *Pygaera* Ochsenheimer. It will be interesting to study larvae of these taxa in detail.

The cladistic position of this lineage, as sister group to all other Notodontidae except the Thaumetopoeinae (fig. 99), makes retaining subfamilial status advisable.

NOTODONTINAE

The list of taxa that I refer to the Notodontinae will likely be considered controversial. For example, I include all species from the Cerurinae of previous authors. Perhaps less controversial, I regard the "Gluphisinae" of Packard (1895a) (= Gluphisiini of Forbes, 1948) as belonging in this subfamily. My cladistic results suggest that *Cerura* and *Gluphisia* are closely related, a result that will surprise some workers. I tentatively recognize two tribes: the Notodontini and the Dicranurini. Further, I synonymize the Ptilophorinae of Matsumura (1929b; table 7) within the Notodontinae. *Ptilophora* appears on my cladogram as the basal member of the Dicranurini (fig. 99). I feel that the phylogenetic evidence to support these hypotheses is persuasive.

When the complete boundaries of the Notodontinae are eventually understood, it will likely prove to be a fairly large subfamily. Based solely on the genera I studied, there are at least 200 contained species (from Gaede, 1934; Kiriakoff, 1967). The subfamily occurs worldwide. *Cerura* alone has a global distribution, being most species rich in Asia. It is interesting to note that the vast majority of notodontine species occur in the Palearctic and Nearctic regions. For example, all species in *Notodonta*, *Odontosia*, *Pheosia*, *Gluphisia*, and *Ptilophora* are restricted to these regions. *Liparopsis* and *Quadricalcarifera*, on the other hand, are found in Asia. *Liparopsis* is most species rich in Sundaland (Bender, 1985), while the greatest diversity of *Quadricalcarifera* species occurs in New Guinea (Sugi, 1987a).

DIAGNOSIS (Notodontinae; Clade 13): ADULTS: Male antennae pectinate to apex,

pectinations often long; proboscis short and broad or absent, surface sculpturing of Type I; labial palpi often small; eyes hairy or naked; accessory cell present or absent; female frenulum composed of more than 20 bristles; tarsal claws simple; epiphysis usually elongate and flattened; terminal segments of male without a long scale tuft; male segment A8 usually unmodified; male genitalia with valve relatively simple, sacculus usually without pleats, rarely (*Gluphisia*) with, vesica without deciduous cornuti; female genitalia with T8 usually simple. LARVAE: Head without secondary setae, surface rugose; mandibular cutting edge smooth; labral notch deep; spinneret either moderate in length or short; labial palpi frequently with a mesal flange (Dicranurini); stipital lobe acute distally; body with scattered secondary setae (Dicranurini) or bare (Notodontini), never "hairy"; anal prolegs smaller than others, sometimes sterna-podiform.

SYNAPOMORPHIES: ADULTS: Proboscis shorter than length of head; male labial palpus with segment 2 approximately 1–1½ times the length of segment 1; tarsal claws simple. LARVAE: Four L setae on segments A3–A6, the ventral pair at approximately the same height. *Ambiguous:* Sensilla styloconica (R1) of adult proboscis fluted/R1 sensilla smooth, lacking flutes, or flutes reduced to small projections; male epiphysis broad, much shorter than tibia, apex acute/epiphysis flat, almost as long as tibia, apex not acute; female frenulum composed of 2–10 bristles/female frenulum composed of 15 or more bristles; base of male valve without a flange/base of valve with a setose, medial flange; apex of valve partially membranous, roughly acute, not bulbous/apex of valve sclerotized, rounded and bulbous.

DISCUSSION: The Notodontinae of Turner (1922) included all notodontid species except the Thaumetopoeinae. Although other authors have applied more restrictive definitions, the Notodontinae has tended to be a "catch-all" group (Tikhomirov, 1981). For example, Packard (1895a), who did not present reliable diagnostic characters, included the nystaleine genera *Symmerista* and *Dasylophia*. Dyar's (1897) "Ptilodontidae" (= Notodontinae) included all notodontids with the proboscis present and the larvae lacking

numerous secondary setae, a polyphyletic group composed of species from five of my subfamilies. Forbes's (1939a, 1948) Notodontinae was a large group comprising five tribes (table 5). Of those, I have raised his Nystaleini and Heterocampini to subfamily status. Perhaps an appropriate comparison would be between my Notodontinae and the Notodontini of Forbes, which he regarded as having a "very unsatisfactory definition at present" (1948: 217). A similarity between our classifications is inclusion of *Notodonta*, *Odontosia*, and *Pheosia*, while the major differences are my inclusion of Clade 17 and its genera (fig. 99) and my exclusion of *Ellida*, *Nadata*, and *Peridea*.

I have subsumed three groups from previous authors in the subfamily Notodontinae. These are the Gluphisiini, Cerurinae, and Ptilophorinae. All belong in a clade with *Notodonta*, as well as with *Odontosia* and *Pheosia*, two genera that have been considered close relatives of *Notodonta* (Forbes, 1948; Tikhomirov, 1979, 1981). Below, I explain how other authors have defined the Gluphisiini, Cerurinae, and Ptilophorinae, and justify my revised concept of the subfamily.

Packard (1895a) described the "Gluphisiinae" as having adults with a small head, hairy eyes, antennae with long pectinations extending to the apex, and small palpi. He described the larvae as having the body "noctuidiform." In addition to those characters, Forbes noted the proboscis "too short to be coiled" (1948: 205), a single pair of metatibial spurs, unspecialized male S8, and loss of hind wing vein M₂. These and all subsequent authors recognized *Gluphisia* as the sole included genus. Forbes described the Gluphisiini as a "degenerate holarctic type, without close relatives" (1948: 216). My results differ significantly. I have shown that *Gluphisia* belongs in Clade 13 (the Notodontinae sensu lato). There are numerous characters to support this hypothesis (see Appendix III). Until further study, the tribal name Gluphisiini should not be used.

Duponchel (1845) first erected the family group category "Dicranurides" to include the large and distinctive genus *Cerura*. Subsequent authors (e.g., Packard, 1895a; Matsu-mura, 1929b; Forbes, 1948) have used the name Cerurinae for this same group. I apply

the oldest available name, Dicranurini, to Clade 16 (fig. 99).

Cerura, which included approximately 60 species at the time of Gaede (1934), has since been broken into numerous genera. However, as Forbes noted, "there is no agreement on either the lines of separation nor the names to be used, and [*Cerura*] is really pretty homogeneous" (1948: 235). It is presumably because the adults are easily recognizable (figs. 33, 34) and the larvae have a striking habitus (figs. 71, 85) that the genus has been accorded subfamily status. Matsumura used a single character to define the Cerurinae, "antennae long, in both sexes plumose to the tips" (1929b: 88). In it he placed 11 genera from the Palearctic region. I included examples from three of those in my study: *Cerura*, *Liparopsis*, and *Cnethodonta*. My data support a relationship between the first two, but I place *Cnethodonta* in the Heterocampinae. Matsumura also regarded the following genera as members of the Cerurinae: *Dicranura* Boisduval, *Neocerura* Matsumura, *Gangaridopsis* Grünberg, *Nerice* Walker, *Microphalera* Butler, *Epizaranga* Matsumura, *Somera* Walker, and *Takashachia* Matsumura. I did not examine these.

A relationship between *Cerura* and *Gluphisia* has never been proposed, but the adult diagnostic characters noted by both Packard (1895a) and Forbes (1948) (hind tibiae with one pair of spurs, palpi short, proboscis obsolete, etc.) are nearly identical for the two groups. Superficial differences between the caterpillars appear to have confused these workers. However, upon close examination, even the larvae exhibit synapomorphies. One of the main differences is that *Gluphisia* caterpillars have small anal prolegs bearing crochets, whereas the larvae of *Cerura* and *Furcula* have greatly elongate stemapods, bearing eversible distal glands, but no crochets. I found that, among notodontids, the presence or absence of stemapods is extremely variable within otherwise well defined lineages (see Character 167).

The group Ptilophorinae was erected by Matsumura (1929b) and later recognized by Nam (1985). Neither author specified the included genera, and neither gave a list of diagnostic features for the Ptilophorinae. The following characters were taken from Mat-

sumura's subfamily key: forewings without a toothlike tuft, abdomen without a terminal tuft, and male antennae bipectinate to the tips. All of these are plesiomorphic. The only apomorphic feature in the key was in the final couplet, "antennae not decreasing the length of branches toward the tips" (1929b: 78), a reference to the plumose male antennae of *Ptilophora* (fig. 20). I have shown that presence of plumose male antennae is a synapomorphy for several notodontine genera (see Character 14).

Because the Ptilophorinae was never properly defined, I had to base my analysis solely on *Ptilophora*. The genus contains four species occurring from Europe to Japan (Kiriakoff, 1967), but as far as I am aware, larvae are known only for *Ptilophora plumigera*. The species exhibits all the derived states of Clade 16 in the Notodontinae. Adults have a highly reduced proboscis, extremely short labial palpi, a single pair of metatibial spurs, simple tarsal claws, a long, flattened epiphysis, and male genitalia very similar to *Notodonta*. There is little doubt concerning the subfamily placement of *Ptilophora*, and it is clear that the name Ptilophorinae should not be recognized.

On my cladogram (fig. 99) the Notodontinae is divided into two monophyletic groups: one consisting of *Notodonta*, *Odonotosia*, and *Pheosia* and the other a large assemblage comprising *Ptilophora*, *Gluphisia*, *Cerura*, *Furcula*, *Liparopsis*, and *Quadricalcarifera*. Fairly reliable synapomorphies support this division, and I here tentatively propose that two tribes be recognized, the Notodontini and Dicranurini. Pupal characters may provide additional synapomorphies for both. Tribal synapomorphies are as follows.

SYNAPOMORPHIES (Notodontini; Clade 14):
ADULTS: R1 sensilla goblet-shaped, with a distal constriction; anal margin of FW with a lobe and a tuft of scales forming a prominent, tooth-shaped projection; female frenulum composed of 15 or more bristles; base of valve with a setose medial flange. **LARVAE:** Segment A8 with a dorsal protuberance. **Ambiguous:** Female ductus bursae mostly membranous, elongate, not flattened/ductus bursae with a robust, sclerotized portion.

SYNAPOMORPHIES (Dicranurini; Clade 16): **ADULTS:** R1 sensilla smooth, lacking flutes, or flutes reduced to small projections; R1 sensilla short, only slightly larger than R2 sensilla; male palpus small, division between segments 2 and 3 often indistinct; antennal pectinations extremely long; male epiphysis flat, almost as long as tibia, apex not acute; proximal pair of spurs absent, only the distal pair present; FW vein R_2 stalked with R_{3-5} , no accessory cell; papillae anales broad and flattened, membranous. **LARVAE:** Stemma 3 larger than stemma 4. *Ambiguous:* Pilifers well developed/pilifers absent; female epiphysis present/female epiphysis reduced or absent; surface of corpus bursae crenulate/surface of corpus bursae spiculate.

Two aspects of my classification are doubtful. First, *Ptilophora* shares three distinctive male genitalic characters with the Notodontini (Characters 88, 89, 97), but other adult characters with the Dicranurini (listed above). The larvae more closely resemble the Notodontini in setal pattern, but shared features are likely plesiomorphic. The precise position of *Ptilophora* requires further study.

Second, *Liparopsis* and *Quadricalcarifera* (Clade 19) could very possibly be misplaced in the Notodontinae. In particular, the larvae exhibit apomorphic features found in the Heterocampinae. These include small sensilla on the mesal lobes (Character 118), a 2-2-2 thoracic SV setal formula (Character 135), and specialized tarsal seta shape (Character 143). Further, larvae in both genera are known to feed on plants in the Fagaceae (Sugi, 1987a), hosts typical for the Heterocampinae but highly unusual for the Notodontinae (table 8). However, adult characters seem to override the larval ones; throughout my analyses both genera consistently appeared in the Dicranurini clade.

PHALERINAE

The genera *Antheua*, *Datana*, and *Phalera* form a clade supported by two distinctive genitalic synapomorphies (see below). I also include *Peridea*, *Ellida*, and *Nadata* in the Phalerinae. These three genera have been of uncertain placement in the past, and my own proposal is made with a good deal of hesitation. When *Peridea*, *Ellida*, and *Nadata* are

included in the Phalerinae, all subfamily traits are highly inconsistent and the synapomorphy list is distressingly short. I therefore list the characters in two ways: first for my broad concept of the Phalerinae and second for Clade 24, the Phalerinae sensu stricto.

Because the taxonomic boundaries of this subfamily are unclear, I can say little about the group's distribution. Kiriakoff (1964) listed 34 *Antheua* species occurring in Africa and two in Indo-Australia. The genus *Phalera* is found in Africa (6 species), Indo-Australia (17 species), and the Palearctic region (15 species), while *Datana* (13 species in North America; Franclemont, 1983) appears to be mostly Nearctic in distribution. Based on similarities of genitalic morphology, the latter two are extremely close relatives. The three genera of doubtful placement—*Peridea*, *Ellida*, and *Nadata*—each occur in both the Palearctic and Nearctic regions.

DIAGNOSIS (Phalerinae in the broad sense; Clade 22): **ADULTS:** Male antennae pectinate or ciliate, terminal segments simple; proboscis shorter than length of thorax but longer than head, surface sculpture of Type I, sensilla styloconica fluted; labial palpi moderate in length, occasionally quite long, never highly reduced; forewing radial system with an accessory cell; female frenulum composed of fewer than 10 bristles; tarsal claws bifid; hind tibiae with two pairs of spurs; male S8 with a deep posterior notch; male genitalia with a faintly pleated sacculus, or pleats absent; vesica of aedeagus with deciduous cornuti; female genitalia with ductus bursae often heavily sclerotized. **LARVAE:** Head lacking secondary setae (except *Phalera*); mandibular cutting edges smooth; labral notch moderately deep; stipital lobe acute distally, or short and broad; spinneret moderately long; labial palpi without a mesal flange (except *Ellida*); antennae moderate in length (long in *Nadata*); body with or without secondary setae; prothoracic gland present; tarsal setae lanceolate; anal prolegs smaller than others.

SYNAPOMORPHIES (Phalerinae in the broad sense): **ADULTS:** Proboscis not as long as thorax but longer than head; sacculus relatively small, with faint pleats; vesica with deciduous stellate cornuti. *Ambiguous:* Female ductus bursae mostly membranous,

elongate, not flattened/ductus bursae with a robust, sclerotized portion/ductus bursae sclerotized, dorsoventrally compressed, broad.

DIAGNOSIS (Phalerinae sensu stricto; Clade 24): **ADULTS:** Male antennae with pectinations short, often fasciculate; proboscis relatively short and narrow, but coilable; labial palpi moderate in length; male S8 with two anterior apophyses, often with a pair of medial pits; male genitalia with reduced saccular pleats, uncus large and triangular, socii large; female genitalia with segment 8 heavily sclerotized, capsular. **LARVAE:** Head surface rugose (*Antheua*) or punctate (*Phalera*/*Datana*); body evenly covered with secondary setae, not located on verrucae; anal prolegs (*Phalera*/*Datana*) small and sclerotized, crochets withdrawn.

SYNAPOMORPHIES (Phalerinae sensu stricto): **ADULTS:** Pleuron of female segment 8 heavily sclerotized, entire eighth segment forming a capsule; male genitalia with base of uncus robust, uncus large and triangular.

DISCUSSION: Packard (1895a) included only the North American genus *Datana* in the Phalerinae (table 4). Few diagnostic characters for the subfamily were given, the most significant being "ciliate" adult male antennae and larvae "brightly banded and very hairy" (1895a: 104). Forbes, who also considered *Datana* to be the only American phalerine genus (table 5), gave the subfamily characters as: adults with male antennae "fasciculate," labial palpi moderately long, proboscis short but coiled; caterpillar with secondary setae, anal prolegs "rudimentary, chitinized, without crochets" (1948: 212). I have shown that the anal prolegs of *Datana* and *Phalera* larvae do have crochets that are withdrawn into the proleg (see Character 171).

In addition to *Phalera*, Gardner (1946) described the larval head of *Spataloides* and *Rosama*, two Indian notodontid genera, as being punctate. This suggests that both taxa may be derived members of the Phalerinae, in a clade with *Datana* and *Phalera*.

Janse (1920) first showed that *Antheua* is related to *Phalera*, and the latter has long been recognized as a close relative of *Datana*. These taxa, then, have classically been considered to constitute the Phalerinae. However, according to my analysis, *Ellida cani-*

TABLE 3
Classification of Neumoegen and Dyar (1894a, 1894b) Based on Adult Characters, Including Their Placement of North American Genera Used in This Study

Family Notodontidae
Subfamily Apatelodinae: <i>Apatelodes</i> (currently Bombycoidea: Apatelodidae)
Subfamily Notodontinae: <i>Notodonta</i> , <i>Nadata</i> , <i>Symmerista</i> , <i>Cerura</i> , <i>Clostera</i> , <i>Gluphisia</i> , <i>Pheosia</i> , <i>Peridea</i> , <i>Datana</i> , <i>Nystalea</i>
Subfamily Heterocampinae: <i>Dasylophia</i> , <i>Schizura</i> , <i>Heterocampa</i> , <i>Lochmaeus</i> , <i>Macrurocampa</i> , <i>Ellida</i>

plaga, *Nadata gibbosa*, and *Peridea angulosa* are plesiomorphic members of Clade 22 (fig. 99). When the latter three species are included in the Phalerinae, few unambiguous synapomorphies for the subfamily exist. Their larvae, which lack secondary setae, are not like those of species in the *Phalera* clade. Future research may show that all or some of these three genera are misplaced in the Phalerinae. Each has had a somewhat controversial history regarding their position in the classification. For example, *Ellida* has been placed in either the Heterocampinae (Neumoegen and Dyar, 1984a, 1984b; table 3) or Notodontinae (Packard, 1895a; Dyar, 1897; see table 4). Forbes (1948) included it, with *Nadata* and *Peridea*, in the Notodontini (table 5). Until additional data become available, I have followed my cladistic results and here place *Ellida*, *Nadata*, and *Peridea* in the Phalerinae. These taxa do not exhibit unambiguous synapomorphies of other notodontid subfamilies.

DUDUSINAE

Perhaps the most dramatic change I propose in our notodontid subfamilial definitions concerns the boundaries of the Dudusinae. When first recognized (Matsumura, 1929b), the Dudusinae consisted of six Asian genera: *Dudusa*, *Tarsolepis*, and four genera that Matsumura described. Matsumura erected three of these for species formerly in either *Tarsolepis* or *Dudusa*, and all three were later synonymized by Nam (1985). The fourth, *Tensha* Matsumura, includes two species; *striatella* Matsumura (1925) and *pos-*

TABLE 4

Classification of Packard (1895a) Based on Adult and Larval Characters, Including his Placement of North American Genera

Family Notodontidae
Subfamily Gluphisiinae: <i>Gluphisia</i>
Subfamily Apatelodinae
Subfamily Pygaerinae: <i>Datana</i>
Subfamily Ichthyurinae (= Pygaerinae): <i>Clostera</i>
Subfamily Notodontinae: <i>Notodonta</i> , <i>Pheosia</i> , <i>Odontosia</i> , <i>Nadata</i> , <i>Peridea</i> , <i>Hyperaeschra</i> , <i>Ellida</i> , <i>Nerice</i> , <i>Dasylophia</i> , <i>Symmerista</i>
Subfamily Heterocampinae: <i>Heterocampa</i> , <i>Macrurocampa</i> , <i>Hyparpax</i> , <i>Euhyparpax</i> , <i>Misogada</i> , <i>Schizura</i> , <i>Lochmaeus</i>
Subfamily Cerurinae: <i>Cerura</i> , <i>Furcula</i>

tobscura Holloway (1983). Thus, the Dudusinae formerly included *Dudusa*, *Tarsolepis*, and closely related species, and the group as defined was restricted to Asia. Matsumura (1929b) gave the following diagnostic characters: antennae bipectinate with ciliate or serrate apices; forewings crenulate; abdomen long, with an apical tuft of spatulate or penicillate scales.

I propose a significant broadening of Matsumura's concept. First, I have identified numerous synapomorphies that group three New World genera (*Crinodes*, *Goacampa*, and *Cargida*) with *Dudusa* and *Tarsolepis*. I term this assemblage (Clade 29) the tribe Dudusini. According to my findings, the Dudusini has a trans-Pacific rather than Asian distribution. *Crinodes* occurs from Argentina north to the southwestern U.S. *Cargida* and *Goacampa*, both monobasic (Gaede, 1934), are essentially Central American, the former extending north to the southwestern U.S. Furthermore, my analyses suggest that a firmly supported clade comprising *Scrancia* from Africa and *Gargetta* from Africa and Indo-Australia is the sister group of the Dudusini. I therefore place this second lineage in the Dudusinae and erect for it the tribe Scranciini. The Dudusinae in my broader sense, therefore, occurs on all continents of the world (obviously excluding Antarctica).

These findings resolve several long-standing problems concerning notodontid classification. *Crinodes* was previously placed in the Notodontini (Forbes, 1939a), while *Car-*

TABLE 5

Classification of Forbes (1939a, 1948) Based Largely on Adult Characters

(The proposed placement of genera used in this study and treated in his works is also shown)

Family Thaumetopoeidae: <i>Thaumetopoea</i> , <i>Traumatocampa</i> , <i>Anaphe</i> , <i>Epicoma</i>
Family Dioptidae: <i>Erbessa</i> , <i>Phaeochlaena</i> , <i>Phryganidia</i> , <i>Zunacetha</i> , <i>Josia</i> , <i>Cyanotricha</i>
Family Notodontidae
Subfamily Melalophinae (= Pygaerinae)
Tribe Melalophini: <i>Clostera</i>
Tribe Rosemini: <i>Rosema</i> (Neotropical)
Subfamily Phalerinae (= Pygaerinae of Packard): <i>Phalera</i> , <i>Datana</i>
Subfamily Notodontinae
Tribe Gluphisiini: <i>Gluphisia</i>
Tribe Notodontini: <i>Notodonta</i> , <i>Ellida</i> , <i>Nadata</i> , <i>Peridea</i> , <i>Pheosia</i> , <i>Odontosia</i>
Tribe Nystaleini: <i>Nystalea</i> , <i>Symmerista</i> , <i>Dasylophia</i> , <i>Crinodes</i> , <i>Lirimiris</i>
Tribe Heterocampini: <i>Heterocampa</i> , <i>Macrurocampa</i> , <i>Schizura</i> , <i>Lochmaeus</i> , <i>Spatialia</i> , <i>Fentonia</i> , <i>Stauropus</i>
Tribe Hemiceratini: <i>Hemiceras</i>
Subfamily Cerurinae: <i>Cerura</i> , <i>Furcula</i>

gida and *Goacampa* have never been assigned to a subfamily or tribe. Neither have *Scrancia* or *Gargetta* been assigned to an existing notodontid subfamily. Now that synapomorphies for the Dudusinae are known, and the Scranciini and Dudusini have been delineated, it will be exciting to discover additional members of these groups in other parts of the world. As I note in the discussion, the Scranciini is likely to be a large tribe with particularly strong representation in Africa. It may be that the Dudusini has many members in the Neotropics.

DIAGNOSIS (Dudusinae; Clade 27): ADULTS: Male antennae either pectinate to apex or pectinate with terminal segments simple; female antennae pectinate or ciliate; proboscis longer than thorax; proboscis with Type I surface sculpturing, or smooth (Type III); R1 sensilla lacking flutes (except fluted in *Scrancia*); labial palpi moderate in length, segment 3 not unusually long; tarsal claws bifid (except *Dudusa*); tibial spurs usually in the formula 0-2-4, sometimes 0-2-2 (*Tarsolepis* and *Dudusa*); forewing with an accessory cell; female frenulum composed of fewer

than 10 bristles; terminal segments of male abdomen with a tuft of hairlike scales or a tuft of long pedicellate scales; dorsum of female segment 8 simple; posterior margin of male S8 with a sclerotized notch; sacculus of male genitalia either lacking pleats or with faint pleats; deciduous cornuti of vesica usually absent, occasionally present (*Crinodes* and *Goacampa*). LARVAE: Head surface usually rugose, occasionally smooth (*Crinodes* and *Cargida*); head lacking secondary setae (except *Goacampa*); mandibular cutting edge either smooth or serrate; stipital lobe acute distally, occasionally lanceolate (*Goacampa*); sensilla on mesal lobes large; spinneret longer than labial palpi, often quite long; labial palpi either with (Scranciini) or without (Dudusini) a mesal flange; thoracic SV setae in the formula 2-1-1; tarsal setae lanceolate; dorsum generally without distinct tubercles or projections; anal prolegs modified, frequently stemapodiform.

SYNAPOMORPHIES (Dudusinae): ADULTS: Ocelli present, large; pleuron of female segment 8 sclerotized; postvaginal plate (PVP) not large, not emarginate; opening of ductus ejaculatorius simplex located posteriorly, anterior end of aedeagus forming a long tubular projection. LARVAE: E area of larval segment A10 lacking seta X. *Ambiguous:* Adult with frons broadly rounded anteriorly, no projections/frons protruding, strongly sclerotized, projections usually present; dorsum of female tergum 8 completely sclerotized/dorsum of T8 with a membranous medial suture; length of male T8 equal to or shorter than that of T7/T8 longer than T7; height of larval head equal to or less than that of thoracic segment 1, head not wider than thorax/head taller than thoracic segment 1 (lateral view, excluding legs), head wider than thorax; larval cranium rounded in lateral view, without a depression/cranium narrow in lateral view, with a posterior depression along epicranial suture.

DISCUSSION: Of the synapomorphies for the Dudusinae (Dudusini + Scranciini) listed above, the two most convincing are presence of well-developed ocelli in adults and absence of Gerasimov's seta X in the larvae. The other characters are either difficult to characterize accurately or occur widely in other notodontid subfamilies. The long list of

characters in the ambiguous category results from the fact that many traits, such as projections on the adult frons (Character 2), occur in some members of both the Scranciini and Dudusini, but are not found universally in the subfamily. Although monophyly of each of the two tribes in the Dudusinae is highly corroborated, it is necessary to identify additional synapomorphies at the subfamilial level. Below I treat the Dudusini and Scranciini separately.

Dudusini

My tribe Dudusini corresponds with the Dudusinae of Matsumura (1929b) and Nam (1985) and the Tarsolepidinae of Kiriakoff (1950b; see tables 6 and 7) but with the addition of New World taxa to the group. Numerous characters support this clade; many of them are unambiguous and easy to identify. At present, the tribe is found in Asia, North America, and the Neotropics. According to Gaede (1930), the Indo-Australian genus *Stigmatophorina* Mell (with two species) is similar to *Tarsolepis* in general appearance. Therefore, it probably belongs in the Dudusini. The size of the tribe is unknown. The exemplars I used come from relatively small genera, the largest being *Crinodes* with only 10 species (Gaede, 1934). Further study is required to refine tribal boundaries. Bänziger's papers have demonstrated that adults of the Dudusini are often lachryphagous, and I showed that their proboscises exhibit modifications possibly correlated with this unusual feeding behavior (Characters 5, 6, and 7). It will be interesting to see whether all members of the tribe turn out to be tear-feeders.

The subfamily diagnosis can be applied to the tribe. Many of the species are large moths, but there seems to be no overall gestalt that applies to the group. For example, upon further study it may turn out that *Crinodes* and *Cargida* are close relatives, but they differ dramatically in appearance of both adults and larvae (figs. 49, 52).

SYNAPOMORPHIES (Dudusini; Clade 29): ADULTS: R1 sensilla smooth, lacking flutes, or flutes reduced to small projections; metascutal bulla not present; dorsum of T8 with a membranous medial suture; tergum 8 with a pair of large anterolateral apodemes; tran-

TABLE 6
Classification of Kiriakoff (1950a, 1950b)

Family Thaumetopoeidae
Family Diopitidae
Family Notodontidae ^a
Subfamily Tarsolepidinae: <i>Dudusa</i> , <i>Tarsolepis</i>
Subfamily Notodontinae: all other genera
Incertae Sedis: <i>Gluphisia</i>

^aA third subcategory within the Notodontidae was formed for *Lobeza* Herrich-Schäffer, but no formal name was proposed.

stilla curving downward, connected to base of juxta. LARVAE: Height of head equal to or less than that of thoracic segment 1, head not wider than thorax; cranium rounded in lateral view, without a depression; sensilla trichodea II and III distally emarginate, often bifid; spinneret twice as long as segment 1 of labial palpus; prothoracic plate roughly square in shape, heavily sclerotized and smooth; proprioceptor seta MSD2 on larval segments A5–A7 located anterodorsally to spiracle. *Ambiguous*: Adult with frons broadly rounded anteriorly, no projections/frons protruding, strongly sclerotized, projections usually present; length of male T8 equal to or shorter than that of T7/T8 longer than T7; ventrolateral surface of larval mandible smooth/mandible with a pronounced ventrolateral carina.

DISCUSSION: Several authors have acknowledged a close relationship between *Dudusa* and *Tarsolepis*, usually on the basis of similarities in adult morphology (e.g., Roepke, 1944). Kiriakoff (1950b) noted that both genera have a modified type of metascutal bulla (see Character 34). On those grounds he erected the subfamily Tarsolepidinae for them (table 6), apparently unaware of Matsumura's (1929b) earlier work in which the Dudusinae was described (table 7). Kiriakoff further suggested that two tribes be recognized within the Tarsolepidinae, the Tarsolepidini and Dudusini, although he did not add constituent genera to these.

As the synapomorphy list above demonstrates, the clade is highly supported. Characters such as the unusual transtilla of the male genitalia (Character 86) are easy to observe and are highly diagnostic. But, as nature seems to prove time and time again, homo-

TABLE 7
Classification of Matsumura (1925, 1929b) and Nam (1985)

(The proposed placement of genera used in this study and treated in those works is also shown.)

Family Notodontidae
Subfamily Dudusinae: <i>Dudusa</i> , <i>Tarsolepis</i>
Subfamily Stauropinae: <i>Stauropus</i> , <i>Quadricalcarifera</i>
Subfamily Cerurinae: <i>Cerura</i> , <i>Furcula</i> , <i>Cnethodonta</i> , <i>Liparopsis</i>
Subfamily Notodontinae: <i>Notodonta</i>
Subfamily Phalerinae: <i>Antheua</i> , <i>Phalera</i> , <i>Datana</i>
Subfamily Spataliinae ^a : <i>Spatalia</i>
Subfamily Fentoninae: <i>Fentonia</i>
Subfamily Melalophinae: <i>Clostera</i>
Subfamily Ptilophorinae: <i>Ptilophora</i>
Subfamily Gluphisinae: <i>Gluphisia</i>
Subfamily Ceirinae ^b : <i>Ceira</i> , <i>Pydna</i>

^aIncluded genera were not listed for this and the following subfamilies.

^bLarvae representing the Ceirinae were not available for study.

plasy is a reality; this transtilla type also occurs in *Fentonia ocypte* (Heterocampinae).

With further research, it may become apparent that the three New World genera—*Goacampa*, *Crinodes*, and *Cargida*—form a clade separate from the Asian taxa. Bifid sensilla trichodea on the larval maxilla are present only in these taxa, and the male genitalia of *Crinodes* and *Cargida* are almost identical.

A derived state of the Dudusini, presence of serrate larval mandibles (Character 113), also occurs in *Theroa zethus* Druce (Godfrey et al., 1989), a species from Mexico and the southwestern U.S., perhaps indicating membership in this tribe.

Scranciini, New Tribe

Monophyly of the Scranciini is supported by numerous larval and adult synapomorphies. Furthermore, the group probably contains quite a large number of species. As I have delimited the tribe, it is known from Africa and Indo-Australia, but it will be important to search for representatives in other biogeographic regions.

As with the Dudusini, the subfamily diagnosis applies. The adult moths tend to be fairly small and light-bodied with elongate

legs and wings. All larvae so far known have a large head, reduced prolegs on A3 and A4, and stemapodiform anal prolegs lacking crochets (fig. 75).

SYNAPOMORPHIES (Scranciini; Clade 28): **ADULTS:** Tentorium narrow, without crests; frons protruding, strongly sclerotized, projections usually present; adult foretarsi long, first tarsomere longer than others combined; legs long, hind tibia approximately $1\frac{1}{2}$ times the length of the femur, spurs widely separated; large internal bullae present on anterior margin of tergum A1; length of male T8 equal to or shorter than that of T7; uncus/socii complex fused with tegumen; socii often absent. **LARVAE:** Head taller than thoracic segment 1 (lateral view, excluding legs), head wider than thorax; cranium narrow in lateral view, with a posterior depression along epicranial suture; labial palpus with a membranous flange on mesal margin; spinneret dorsoventrally compressed, distal opening wide and flat; A3 prolegs smaller than those on A5 and A6; A4 prolegs with fewer crochets than A5 and A6; A10 prolegs extremely long and flexible, developed as stemapods; proleg base with many setae, each on a raised tubercle; A10 crochets absent. *Ambiguous:* Sensilla styloconica (R1) of adult proboscis fluted/R1 sensilla smooth, lacking flutes, or flutes reduced to small projections; dorsum of female tergum 8 completely sclerotized/dorsum of T8 with a membranous medial suture.

DISCUSSION: There are two reasons for erecting the tribe Scranciini, based on the genus *Scrancia* Holland (1893b). First, *Scrancia* (approximately 20 species) from Africa and *Gargetta* (approximately 25 species) from Africa and Asia form an extremely well defined clade. The majority of synapomorphies are highly reliable and I have no doubt that the two genera constitute a monophyletic group. A relationship between these taxa was first suggested by Gaede, who placed them both in what he termed the "*Scrancia*-Group," containing "delicately built species with long legs" (1928: 422). In addition to having long legs, *Gargetta* and *Scrancia* have protuberances on the adult frons (see Character 2). Second, a brief review of the literature suggests that the Scranciini is a fairly large tribe. Janse (1920) broke the South African Notodontidae into eight generic groups,

one of these being the *Scrancia* group, comprising six genera. Gaede's (1928) *Scrancia* group contained 28 genera.

It is unlikely that all the species in these "*Scrancia* groups" form a monophyletic assemblage because the defining characters used by both Janse and Gaede leave room for interpretation. However, according to their diagnoses, many of the taxa they list exhibit the protruding sclerotized frons (Character 2). Janse (1920), who first described the modified frons of *Scrancia stictica* (see his pl. 8, figs. 12, 13), noted a similar modification in *Phycitomorpha* Janse, *Taeniopterix* Janse, and *Breyeria* Janse, as well as in *Notoxantha* Hampson (pl. 9, fig. 16). African species in *Lamoriodes* Hampson and *Lamorina* Gaede have a projection on the adult frons (Gaede, 1928). Kiriakoff (1968) reported a protruding frons in the Indo-Australian genera *Porsica* Walker and *Gallaba* Walker. The male genitalia of *Porsica* species (see figures in Holloway, 1983) are very similar to those of *Scrancia stictica* (fig. 309); they appear to lack socii and the valves are narrow. Larval morphology is also suggestive that other species belong in the Scranciini; caterpillars of *Porsica* have the first pair of prolegs reduced (Holloway, 1983). Based solely on the genera listed above, the Scranciini contains over 75 species, and many more taxa will certainly be added.

HETEROCAMPINAE

The subfamily Heterocampinae was recognized by Neumoege and Dyar (1894a, 1894b) and by Packard (1895a), but it is Packard's definition of the group (table 4) that is used today. Forbes's (1948) Heterocampini included essentially the same taxa as the Heterocampini of Packard (table 5). Forbes acknowledged, however, that the group "has a much wider distribution than the North American area where it is normally recognized" (1948: 225). My definition of the subfamily simply formalizes what Forbes had previously proposed (see below). In it, I include *Stauropus* and relatives from the Old World, as well as *Spatalia* and *Fentonia* from Asia, all three of which were placed in separate subfamilies (the Stauropinae, Spataliinae, and Fentoniinae; see table 6) by Mat-

sumura (1925, 1929b) and Nam (1985). At present, I am not entirely satisfied with the known synapomorphies for this subfamily because all are from larvae; I was unable to identify a single reliable synapomorphy from adult morphology. I hope that future research will clarify the situation. It is obvious that at least one reliable adult synapomorphy must be discovered in order to determine the correct placement of currently unplaced notodontid taxa for which larvae have not been described.

I am unfamiliar with Neotropical Heterocampinae. Forbes (1939a) placed six Neotropical genera in the group, but I have not studied those. The Heterocampinae will likely prove to be a large and extremely complex subfamily, with representatives found throughout the world.

DIAGNOSIS (Heterocampinae; Clade 36): **ADULTS:** Male antennae pectinate, distal portion usually simple; female antennae simple or pectinate; proboscis variable in length, either long (*Lochmaeus*) or short (e.g., *Stauropus*), usually shorter than length of thorax; proboscis with Type II surface structure; R1 sensilla almost always fluted (except *Spatalia*); labial palpi moderate in length, never long or reduced; tarsal claws usually bifid, sometimes simple (*Harpyia* and *Stauropus*); tibial spurs often with only distal pair present, proximal ones then either reduced (e.g., *Spatalia*, *Schizura*) or absent (e.g., *Stauropus*); forewing radial system usually with an accessory cell, accessory cell sometimes elongate (Heterocampini); female frenulum composed of from 2 to 10 bristles; abdominal segments with a scale tuft, sometimes distinctly bifid (e.g., *Schizura beidermani*); male S8 often with a pair of deep medial pits, posterior margin with a notch; male genitalia with sacculus pleated or not, sacculus never large; deciduous cornuti of vesica absent (except in *Fentonia ocypte*); vesica usually with a distal sclerite. **LARVAE:** Head surface rugose; head usually lacking secondary setae, when present (*Stauropus*) very short; mandibular cutting edge smooth; stipital lobe often large, covered with large spicules; spinneret short; labial palpi without a mesal flange; thoracic SV setae in the formula 2-2-2, the anterior seta of each pair short, conical; tarsal setae often apically truncate; anal prolegs

variable, always modified, sometimes ste-mapodiform.

SYNAPOMORPHIES (Heterocampinae): **ADULTS:** Proboscis not as long as thorax but usually longer than head; vesica with a small distal sclerite. **LARVAE:** SV setae on thoracic segments in the formula 2-2-2; anterior SV seta on T1 short, conical. *Ambiguous:* Male sacculus without pleats/sacculus large, with accordion-like pleats/sacculus smaller, with faint pleats; surface of larval stipital lobes minutely spiculate/stipital lobe with large spicules; three L setae on larval segments A3–A6/four L setae on segments A3–A6, the ventral pair at approximately the same height/six or more L setae on A3–A6, a horizontal row of 4–10 setae present at the height of L3.

DISCUSSION: Neumoegen and Dyar (1894a, 1894b) placed 10 North American notodontid genera in the subfamily Heterocampinae. Unfortunately, they did not list diagnostic features for the group. According to their key, the Heterocampinae can be distinguished by having “antennae of male pectinated for basal two-thirds or more, the tips bare,” as opposed to the Notodontinae, which have the antennae “bipectinated to the tip or simple” (1894a: 182–183). Packard gave only two definitive characters for the Heterocampinae: adult head “tufted on the vertex,” a character I did not observe, and male antennae “filiform in their distal fourth” (1895a: 183), a character state similar to the one used by Neumoegen and Dyar. Packard characterized the larvae as “varying greatly in shape, markings, and coloration” (1895a: 183). Forbes’s (1948) diagnoses (for the Heterocampini) were hardly more informative. He noted the dramatic interspecific variation in larval habitus and described the adult as having “nothing really characteristic” (1948: 225).

Even though none of these authors defined the Heterocampinae with precision, their lists of included genera overlapped greatly (tables 3–5). Further, my results indicate that their concept of the Heterocampinae was remarkably accurate; the group is monophyletic, with the exception of a few misplaced genera. A major difference in my classification is the inclusion of an Old World clade comprising *Stauropus* and related genera (Clade 40). However, even this was predicted by Forbes.

While introducing the subfamily he argued, on the basis of larval morphology, that *Stauropus* "is unquestionably a heterocampine" (1939a: 280). I have placed additional genera in the Heterocampinae; the larvae of *Stauropus*, *Cnethodonta*, and *Harpyia* exhibit numerous synapomorphies.

Matsumura defined the Stauropinae as having "antennae in the male plumose, at the apical part suddenly filiform, serrate or pectinate" (1929b: 82). Tikhomirov (1979, 1981), noting the bizarre male genitalia of *Stauropus fagi*, felt that subfamily status was justified. Matsumura included eight genera in the subfamily: *Stauropus*, *Quadricalcarifera*, *Kikuchiana* Matsumura, *Shachia* Matsumura, *Damata* Hampson, *Damatoides* Matsumura, *Hoplitis* Hübner, and *Netria* Walker. This is roughly similar to my hypothesis for Clade 40 since the type species of *Hoplitis* is a synonym of *Harpyia milhauseri* (Watson et al., 1980), and based on superficial appearance *Damata* belongs in this clade as well.

Matsumura (1929b) erected the subfamily Spataliinae, but he did not list the constituent genera (table 7). His key to subfamilies gave "primaries with two tooth-like tufts at the dorsum" (1929b: 78) as the defining character, referring here to the scale tufts on the forewing anal margin (see Character 39). I obtained larvae of a Japanese species, *Spatalia jezoensis*, and used that taxon as one of my exemplars. The forewing of *S. jezoensis* has a single scale tuft (fig. 21), as occurs, for example, in *Notodonta scitipennis* and *Hemiceras bilinea*. Therefore, Matsumura's key character for the Spataliinae is not definitive even for the genus *Spatalia* itself. According to my analysis, *Spatalia jezoensis* belongs in the subfamily Heterocampinae (fig. 100). The genus exhibits many apomorphic character states of the Heterocampinae: presence of a ctenophore; male S8 with a pair of widely spaced internal apodemes; a transtillar process similar to that of *H. averna*; and larvae with thoracic SV setae in the formula 2-2-2, with the anterior seta of each pair short. The Indo-Australian genera *Allata* Walker and *Ginshachia* Matsumura appear to be close relatives of *Spatalia* (Holloway, 1983).

As so often seems to be the case, Forbes (1948) predicted this result as well. He noted that larvae of European *Spatalia* have a dor-

sal protuberance on A1 similar to that in *Schizura*, and he therefore considered *Spatalia* to be a heterocampine. It is clear that the subfamily Spataliinae should be synonymized with the Heterocampinae.

I have also included *Fentonia ocypete* in the Heterocampinae. The species was placed by Matsumura (1929b) in its own subfamily, the Fentoniinae (table 7). *Fentonia ocypete* is unusual among heterocampines in having a vesica with deciduous cornuti and a transtilla apparently identical with that of the Dudusini (Character 86). However, several characters, such as the SV setal formula and presence of spatulate tarsal setae in the caterpillar, indicate membership in this subfamily. Again, Forbes hinted as much many years earlier. Based on larval morphology he wrote that *Fentonia* "is obviously very near *Dicentria* [a Neotropical heterocampine] and *Schizura*" (1939a: 280).

At least two distinct clades are apparent within the subfamily: Packard's (1895a) "Heterocampinae" form one group (Clade 42 in fig. 100) while *Stauropus* and relatives (Clade 39) form another. Interestingly, the two *Schizura* species I studied, *S. beidermani* and *S. unicornis*, fall out separately. I could recognize these two clades by using the tribal names Heterocampini and Stauropini for each, but in such a classification the genera *Spatalia* and *Fentonia* would not be accounted for. The names Spataliini and Fentoniini are available, but I feel that more research on phylogeny within the Heterocampinae must be done before a formal proposal is made. In particular, the Neotropical fauna should be studied. I present the characters that define Clade 42 (the "Heterocampini") and Clade 39 (the "Stauropini") below.

SYNAPOMORPHIES (Clade 42; "Heterocampini"): **ADULTS**: Ostium with a ventral medial projection; apodeme on male S8 broad, with two "windows." **LARVAE**: Prothoracic plate with a pair of anterolateral projections or horns. **Ambiguous**: Posterior margin of female tergum 8 sclerotized, often emarginate/margin crenulate or with a deep notch; male sternum 4 unmodified/ctenophore present on male S4; medial portion of male sternum 8 without pits or apodemes/medial portion of male sternum 8 with a pair of internal apodemes, widely spaced; no medial projec-

tion on valval costa/valval costa widened distally, "C-shaped" with a large medial projection; height of larval head equal to or less than that of thoracic segment 1, head not wider than thorax/head taller than thoracic segment 1 (lateral view, excluding legs), head wider than thorax.

SYNAPOMORPHIES (Clade 39; "Stauropini"): **ADULTS**: Female antennae pectinate; proximal pair of metathoracic tibial spurs reduced in size; vesica entirely membranous. **LARVAE**: Hypopharynx swollen, expanded dorsally; labial palpus small, much shorter than segment 1 of maxillary palpus; prothoracic plate with a pair of anterolateral projections or horns; primary setae located on chalazae; larval segment A8 with a dorsal protuberance; larval segment A8 expanded, laterally emarginate. *Ambiguous*: Male antennae pectinate, with fewer than 10 terminal segments simple, or terminal segments similar to proximal ones/male antenna with 15 or more terminal segments simple; male S8 with a single anterior apodeme/S8 with double apodemes.

If *Schizura unicornis* is excluded from the "Stauropini," there are numerous synapomorphies for the group, including the elongate larval thoracic legs.

NYSTALEINAE

The family group name based on *Nystalea* Guenée is relatively new, having been first proposed by Forbes in 1948. Weller (1989) recently revised the Nystaleinae. She provided a detailed analysis of adult morphology and a revised classification for the group. The subfamily comprises approximately 300 species and is restricted almost entirely to the Neotropics. Two genera, *Symmerista* and *Dasylophia*, have representatives occurring in North America as far north as Quebec and Nova Scotia (Forbes, 1948), while species of *Didugua*, *Notela*, and *Hippia* can be found in the southwestern U.S. *Nystalea* occurs in the North American Southwest and in Florida. There are no members of the Nystaleinae in the Old World as far as is known (Weller, 1989).

DIAGNOSIS (Nystaleinae; Clade 46): **ADULTS**: Male antennae ciliate (*Nystalea*), or pectinate with terminal segments simple;

female antennae ciliate; antennal scape with a long scale tuft; proboscis long, occasionally reduced (e.g., *Symmerista*); proboscis with Type II surface structure or smooth (*Nystalea*); R1 sensilla usually fluted; labial palpus long, segment 3 usually extremely long; tarsal claws bifid; ocelli rudimentary; tibial spurs in the formula 0-2-4; forewing with an accessory cell, cell sometimes small (*Symmerista* and *Hippia*); female frenulum composed of 2 or 3 bristles; female postvaginal plate with narrow posterolateral projections; posterior margin of male S8 with a sclerotized notch; male genitalia with sacculus usually pleated, often very large; deciduous cornuti usually present. **LARVAE**: Head surface rugose, lacking secondary setae; head taller than thoracic segment 1; mandibular cutting edge smooth; stipital lobes acute distally, sometimes very large; sensilla on mesal lobes small, mesal lobes broad; spinneret shorter than labial palpi; labial palpus without a mesal flange; thoracic SV setae in the formula 2-1-1, not modified in shape; tarsal setae lanceolate, Ts2 shorter than Ts1; anal prolegs small, tubular in shape, never stemapodiform, crochets present.

SYNAPOMORPHIES (Nystaleinae): **ADULTS**: Male labial palpus with segment 2 narrow, more than twice as long as segment 1; segment 3 of male labial palpus elongate, as long as or longer than segment 1; scape of antenna with a small ventral scale tuft and a large dorsal tuft of stiff scales; ductus bursae sclerotized, dorsoventrally compressed, broad; terminal tuft of male abdomen compact, curved downward; tegumen constricted dorsally, forming a "neck"; manica sclerotized, fused with juxta, enclosing aedeagus tightly; aedeagus with a callosum; opening of ductus ejaculatorius simplex located slightly posteriorly, anterior end of aedeagus broad, reflexed in a ventral direction; distal portion of aedeagus expanded, much wider than middle. **LARVAE**: Mentum swollen, appearing glandular; segment A8 with a dorsal protuberance. *Ambiguous*: Female postvaginal plate (PVP) large, broad, emarginate posteriorly/PVP large, sharply emarginate posteriorly, with narrow posterolateral projections; male sacculus not separate from rest of valve/sacculus separate from rest of valve, projecting from valve's lateral margin.

DISCUSSION: Weller (1989) surveyed 81 genera of Notodontidae and found that among those, 27 (largely Neotropical) genera are united by presence of a callosum, a uniquely derived condition of the aedeagus (see Characters 94, 95). After analyzing relationships among the 27 genera based on 82 characters from adult morphology, she argued in support of one preferred cladistic solution. That cladogram comprised two major lineages. The first, which Weller defined as the Nystaleini, includes *Nystalea* and 14 related genera. The second clade, which she determined is the sister group of the Nystaleini, contains *Dasylophia* and 11 additional genera.

I identified a well defined monophyletic group (Clade 46; fig. 100) comprising five Neotropical species including *Nystalea nyseus* and *Dasylophia thyatiroides*. All five of the genera in Clade 46 were shown by Weller (1989) to possess a callosum. I found two larval synapomorphies and eight from adults that support the monophyly of Clade 46. There are differences between my results and those of Weller concerning relationships among these five genera. However, because I studied so few species I do not place much confidence in the precise topology of Clade 46.

By combining my results with those of Weller (1989), there is considerable support for the following arrangement. Clade 46 should be recognized as the subfamily Nystaleinae, comprising 27 genera. The Nystaleinae would then consist of two subgroups: Weller's *Dasylophia* and *Nystalea* clades. Using this classification, the Nystaleini of Weller (1989) refers to a restricted set of 15 genera within my more inclusive subfamilial category. This leaves open the possibility of recognizing Weller's second lineage as the tribe Dasylophiini.

DIOPTINAE

The family name Dioptidae can be attributed to Walker (1865). The group has subsequently been accorded either familial or tribal status. I advocate a third alternative—subfamilial status. All 400 known species occur in the Neotropics (Prout, 1918; Hering, 1925; Bryk, 1930), with the exception of *Phryganidia californica* from the west coast

of the U.S. (Miller, 1987a). I consider it highly unlikely that dioptine taxa will be found in the Old World.

DIAGNOSIS (Dioptinae; Clade 49): ADULTS: Male antennae pectinate to apex or with pectinations completely lacking; female antennae either pectinate or ciliate; proboscis long, with Type II surface structure; R1 sensilla fluted; labial palpi usually moderate in length, sometimes long (*Erbessa* and *Phaeochlaena*); tibial spurs in the formula 0-2-4; tarsal claws bifid; forewing radial system never with an accessory cell; FW never with a scale tuft on anal margin; female frenulum composed of fewer than 10 bristles; posterior margin of male S8 with a notch; sacculus of male genitalia pleated or not, sometimes (e.g., *Erbessa*) extremely large; deciduous cornuti often present. LARVAE: Head taller than thoracic segment 1; head lacking secondary setae (except *Cyanotricha*); mandibular cutting edge either serrate or smooth; stipital lobe usually acute distally, sometimes large; sensilla on mesal lobe small, mesal lobes broad; spinneret shorter than labial palpi; thoracic SV setae in the formula 2-1-1; tarsal setae with Ts2 shorter than Ts1; dorsum of abdomen lacking distinct tubercles; anal prolegs either small and cylindrical in shape or stemapodiform, crochets present.

SYNAPOMORPHIES (Dioptinae): ADULTS: Eyes relatively small, genal area partially scaleless with surface spiculate; male antennae pectinate, with fewer than 10 terminal segments simple, or terminal segments similar to proximal ones; ocelli absent; legs long, hind tibia approximately 1½ times the length of femur, pairs of spurs widely separated; metafurcal arms blunt posteriorly; metascutal bulla prominent, round; pleural membrane surrounding A1 spiracle not sclerotized; a small, lightly sclerotized, setose patch located in pleuron above A1 spiracle; postvaginal plate not large, not emarginate; transtilla present, comprising two sclerotized bands in the manica, joined medially above aedeagus; ductus ejaculatorius simplex (DES) opening near anterior end of aedeagus. LARVAE: Head surface rugose, with rugosities extremely small; stemma 3 larger than stemma 4; labial palpus small, much shorter than segment 1 of maxillary palpus; integument covered with long microprojections ("sha-

greened"); Ts1 broad and relatively short with apex acute, Ts3 with lateral margin expanded, apex deflected toward midline; MD proprioceptor setae unisetose on A1; abdominal spiracles small. *Ambiguous*: Forewing vein R_2 arising from discal cell, not forming an accessory cell/ R_2 arising from discal cell, forming an accessory cell/ R_2 stalked with R_{3+5} , no accessory cell; hind wing with veins M_3 and CuA1 not anastomosed/ M_3 and CuA1 in HW anastomosed; anterolateral apodemes on sternum 2 moderate in length/apodemes on sternum long and thin; ductus seminalis entering on ductus bursae, or at junction of ductus and corpus bursae/ductus seminalis entering on corpus bursae; larval stipital lobe acute distally, not extending beyond maxilla/lobe large, extending beyond rest of maxilla (dorsal view).

DISCUSSION: Sick (1940) regarded the Dioptidae to be the sister group of the Notodontidae (Thaumetopoeinae + Notodontinae in the broad sense). Minet (1983, 1986), on the basis of superficial larval morphology, and Weller (1989), on the basis of adult morphology, placed the group (as the tribe Diopitini) within the subfamily Notodontinae. I have rejected previous definitions of the Notodontinae (see above). Furthermore, like Weller (1989) I found evidence that dioptines are the sister group of Clade 46, the subfamily Nystaleinae. Therefore, on one hand my results agree with the hypotheses of Minet (1983, 1986) and Weller (1989): the group is subordinate within the Notodontidae. On the other hand, in the context of a comprehensive family reclassification there is reason to recognize subfamilial status for the Dioptinae, a position first suggested by Franclemont (1970). Alternatively, I could propose that Clade 45 (Nystaleinae + Dioptinae) be subsumed in a single large subfamily. This group would receive the name Dioptinae and the two subordinate clades would be called the Nystaleini and Diopitini. I feel that such a solution would require extreme changes in our concepts of these group names and that it should be rejected on those grounds.

Members of the Dioptinae vary dramatically in superficial appearance (Prout, 1918; Jordan, 1923b; Hering, 1925), and there has been some doubt as to whether the group is monophyletic (Seitz, 1925; Köhler, 1930). As

the synapomorphy list above shows, I discovered more evidence to support monophyly of the Dioptinae than for almost any other group in the Notodontidae. The six exemplars I used represent highly divergent lineages among the 40 known dioptine genera (J. Miller, unpubl. data). Nevertheless, I have identified seven unambiguous subfamily synapomorphies from larval morphology and 12 from adults. The majority of these do not occur elsewhere in the Notodontidae. I am highly confident that when larvae of more genera become known, and character systems from pupae, eggs, and first instar larvae are studied, there will be additional data to support monophyly of the Dioptinae.

INCERTAE SEDIS

There are two taxa in particular whose placement in the notodontid classification I consider to be ambiguous: the genera *Lirimiris* and *Hemiceras*. *Lirimiris* appears on my cladogram as the sister group to all Notodontidae above the level of the Pygaerinae (Clade 12; fig. 99). Based on the characters I studied, *Hemiceras* is the sister group to the clade that includes the Heterocampinae, Nystaleinae, and Dioptinae (Clade 35; fig. 100). To arrange these genera in my classification, one family group name would have to be created, the "Lirimirinae," and the Hemiceratini would have to be raised to subfamily status. Rather than formally propose these changes, I place *Lirimiris* and *Hemiceras* incertae sedis with the hope that future research will provide more conclusive evidence on their phylogenetic positions. Below, I describe the groups in detail and provide my rationale for considering them incertae sedis.

Lirimiris

Lirimiris Walker includes 16 species occurring from southern Brazil to the southwestern U.S. (Gaede, 1934). *Lirimiris truncata*, the species I studied, is known from Ecuador to Arizona. Immature stages in the genus are poorly known, the only published report being Young (1983) for the larvae and pupae of *L. meridionalis* (Schaus). The status of *Lirimiris* in the notodontid classification has been controversial (Weller, 1989). Forbes (1939a: 269) described the genus as

being "somewhat related to *Dasylophia*" (Nystaleinae), but in the same sentence suggested that it "leads over into *Rosema*" (Pygaerinae: Rosemini). *Lirimiris truncata* exhibits a confusing set of characters. For example, adults have bifid tarsal claws and male antennae pectinate proximally but simple distally. The male genitalia are highly modified, with reduced valvae and no sacular scent organ. Larval morphology is particularly confusing. The caterpillar exhibits some derived features: long secondary setae occur in "clusters" similar to those of *Antheua* (fig. 506; Young, 1983), rather than in a dense covering like *Clostera* (fig. 504); the mandibular cutting edge is smooth; and an acute stipital lobe is present. On the other hand, it also shows primitive traits: there is no prothoracic gland, the anal prolegs are the same size as those on A3–A6, and A10 crochet number is not reduced.

Initially, I thought that *Lirimiris* might be related to *Clostera*, but I found no synapomorphies for these genera. Resolution of this problem will require accomplishing two things. First, additional species of *Lirimiris* must be studied, including their immature stages. Second, the complete boundaries of the Pygaerinae must be determined and synapomorphies identified. Until such work is done, I am unwilling to create a new subfamily for *Lirimiris*.

DIAGNOSIS (Based on *Lirimiris truncata*; Clade 11): **ADULTS:** Male antennae pectinate, terminal segments simple; female antennae pectinate; rings of proboscis covered with micropjections along length of tongue except at tip (surface Type I); R1 sensilla fluted; segment 2 of labial palpi long; ocelli rudimentary; tibial spurs in the formula 0-2-4; tarsal claws bifid; forewing with an accessory cell; female frenulum composed of fewer than 10 bristles; female T8 simple, with a medial suture; female genitalia with postvaginal plate broad, emarginate posteriorly, corpus bursae small with signum absent; a pair of (glandular?) internal pouches on either side of ostium; male genitalia with valve sclerotized, thornlike distally, sacculus not pleated, socii reduced; aedeagus long and narrow, vesica lacking cornuti. **LARVAE:** Head surface with creases, not rugose, secondary setae absent; mandibular cutting edge smooth; labral notch

deep; stipital lobe acute distally; sensilla on mesal lobes not small; spinneret short, conical in shape; tarsal setae lanceolate; body covered with short secondary setae on sides and venter, long secondary setae in SD and D regions; anal prolegs the same size as others; A10 crochet number not reduced.

SYNAPOMORPHIES: ADULTS: Proboscis not as long as thorax but longer than head; male antenna with 15 or more terminal segments simple; scape of male antenna with a small ventral scale tuft and a large dorsal tuft of stiff scales; male epiphysis flat, almost as long as tibia, apex not acute; pleuron of female segment 8 sclerotized. **LARVAE:** Seta S1 located closest to stemma 4; labial palpus small, much shorter than segment 1 of maxillary palpus; spinneret shorter or barely longer than labial palpi, palpi and spinneret apposed.

Hemiceratini

Guenée (1852) established the Hemiceridae and in it placed five genera—*Hemiceras*, *Canodia*, *Arcyophora*, *Plusiodes*, and *Achantodes*—all of which he described. Guenée considered this group to be a category within the Noctuidae, but *Hemiceras* and *Canodia* were later moved to the Notodontidae by Druce (1887) and Schaus (1901), respectively. Forbes (1939a) recognized the Neotropical tribe Hemiceratini, distinguished by having hind wing vein M_2 lost and the larvae "smooth or nearly so with elongate but functional anal legs" (1939a: 237). The latter description must have been based on caterpillars of *Hemiceras*, the only hemiceratine genus for which larvae are known. According to Forbes (1939a), the Panamanian fauna includes *Hemiceras* and six other genera: *Anita* Schaus, *Colax* Hübner, *Hapigia* Guenée, *Rhapigia* Schaus, *Chliara* Walker, and *Antaea* Hübner. Together these genera comprise approximately 200 species. Hampson (1892) listed *Hapigia obliqua* Walker as occurring in India, but his error can be traced to Walker, who misinterpreted the label data in his description of *H. obliqua* (I. Kitching, personal commun.).

Schaus (1901) noted absence of hind wing vein M_2 in his key to American notodontid genera, and that couplet separated essentially the same genera Forbes (1939a) listed as be-



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Fig. 523. Dorsal view of *Hapigia annulata* Schaus, male (Colombia, AMNH; FW length = 44 mm).

ing the Hemiceratini. Schaus, however, did not erect a formal group for these taxa. Apparent loss of hind wing vein M_2 , then, is the only adult apomorphy that has been used to define the tribe (Weller, 1989).

When absence of hind wing vein M_2 is surveyed comprehensively for the Notodontidae, distribution of the derived state is much more widespread than just the "Hemiceratini" (see Character 43). According to my analysis, the vein has been lost at least five separate times in the Notodontidae: in *Hemiceras*, in the Pygaerinae (*Clostera*), in the Notodontinae (*Gluphisia*), in the Phalerinae (*Ellida*), and in the Dudusinae (*Goacampa*). Further, Janse (1920) characterized three of six genera in his South African "Scrancia group" as having hind wing vein M_2 "obsolescent." In at least one of those, *Taeniopteryx* Janse, the vein is absent completely (Janse, 1920: pl. 8, fig. 14).

Unfortunately, I was unable to procure immature material for any of Forbes's (1939a) Hemiceratini except *Hemiceras*. Since I restricted this study to taxa for which I had larval data, I could not adequately test whether the group is monophyletic. I did examine adults of *Hapigia* Guenée, including SEM study of the proboscis (Characters 5–7) in *H. annulata* (fig. 523). The rings of the haustellum are entirely smooth (Type III; fig. 160), and the R1 sensilla are tall, without flutes (figs. 196, 197). Males of *Hapigia* have a well-developed cteniophore on S4 (Jordan, 1923b), and stellate cornuti are present on the male

vesica (Characters 69 and 99). None of these apomorphies occur in *Hemiceras*. A cteniophore is typical of some Heterocampinae, whereas the proboscis morphology of *Hapigia* is very similar to that of *Nystalea* (figs. 159, 189, 195) and the Dudusini.

Ultimately, larval material will be needed to resolve this problem. Until immatures for additional taxa become known, and adult and larval morphology is studied in detail, I consider monophyly of the tribe Hemiceratini to be doubtful.

Weller (1989), using *Hemiceras*, *Hapigia*, and *Apela* as representative Hemiceratini, concluded that the tribe is paraphyletic with respect to the Dioptriinae (my Dioptriinae) and that the hemiceratine/dioptriine clade is the sister group of the Nystaleinae (fig. 524). Weller characterized her theories as being "weakly supported." The strongest character evidence in support of a relationship between the Hemiceratini and Dioptriinae was presence of a large, pleated sacculus (Barth's Organ, Character 91). My hypothesis differs markedly. Three synapomorphies unite Clade 35 (fig. 100), and none of these occur in *Hemiceras*: the proboscis microsculpturing (Character 5) is Type II in Clade 35 but is Type I in *Hemiceras* (fig. 153); the larval spinneret is short in Clade 35 (Character 126) but long in *Hemiceras*; and finally, Clade 35 is united by the presence of a single anterior apodeme on male sternum 8 (Character 70), whereas *Hemiceras* lacks an apodeme altogether (fig. 294). My findings therefore suggest that, rather than *Hemiceras* being the sister group of the Dioptriinae, it is the sister group to a much larger clade that includes the Dioptriinae, Nystaleinae, and Heterocampinae.

Thiaucourt (1988a) discussed the Neotropical genus *Apela* in some detail, dividing the 20 recognized species into three groups. Below I present a diagnosis for the genus *Hemiceras*. An unusual feature of the male hind wing in most *Hemiceras* species, the "stigma" (Schaus, 1939; Weller, 1989) near the base of M_3 (fig. 246), makes male specimens easy to recognize in collections.

DIAGNOSIS (Based on *Hemiceras bilinea*; Clade 34): ADULTS: Male antennae pectinate with terminal segments simple; female antennae ciliate; proboscis long, with Type I surface structure; R1 sensilla fluted; labial

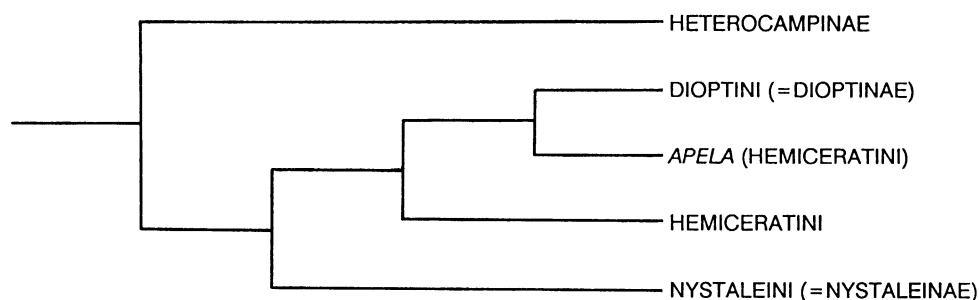


Fig. 524. Cladogram of Weller (1989) showing proposed relationships among the Hemiceratini, Dioptini, and Nystaleini (my rankings for these taxa are shown in parentheses). Note that in her scheme the Hemiceratini is paraphyletic with respect to the Dioptinae.

palpi moderately long, third segment not elongate; ocelli rudimentary; tibial spurs in the formula 0-2-4; tarsal claws bifid; forewing with an accessory cell; male hind wing of many species with a patch of androconia (stigma); female frenulum composed of 2 or 3 bristles; males lacking a cteniphore; female T8 simple; female postvaginal plate with setose lateral projections, ductus bursae long and sclerotized at base, signum absent; male S8 with a thin sclerotized strap projecting anteriorly into 8/9 membrane; male genitalia with an extremely large pleated sacculus (Barth's Organ); deciduous cornuti absent. LARVAE: Head surface rugose, lacking secondary setae; antennae long; mandibular cutting edge smooth; stipital lobe acute distally; sensilla on mesal lobes large; labial palpus lacking a mesal flange; spinneret moderately long; thoracic SV setae in the formula 2-1-1, setae not

modified in shape; tarsal setae lanceolate; dorsum of larva lacking projections or protuberances; body with scattered extra setae in D and SD locations; anal prolegs cylindrical in shape but not stemapodiform.

SYNAPOMORPHIES (*Hemiceras*): ADULTS: Anal margin of FW with a lobe and a tuft of scales forming a prominent tooth-shaped projection; female postvaginal plate large, sharply emarginate posteriorly, with narrow posterolateral projections; male tergum 8 with a pair of large anterolateral apodemes; male genitalia with Barth's Organ, saccus with two shallow humps and a medial indentation; aedeagus with opening of ductus ejaculatorius simplex located posteriorly, anterior end of aedeagus forming a long tubular projection. **LARVAE:** Stemma 3 larger than stemma 4; T1 cervical gland absent, only a shallow groove visible.

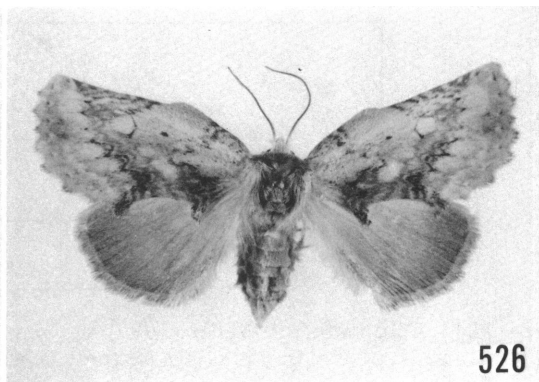
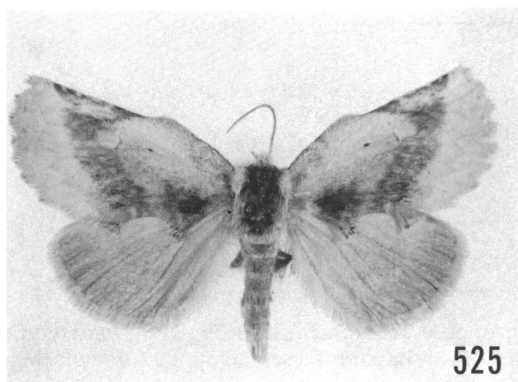
DISCUSSION

ADDITION OF TAXA (STATUS OF THE PLATYCHASMATINAE)

The exemplar method, while perhaps the only reasonable approach for beginning to understand the classification of a group as large as the Notodontidae, has obvious limitations. Clearly, if certain genera are not monophyletic, then selection of different representative species from those "genera" could produce different results. For example, I selected two species of *Schizura* (*S. unicornis* and *S. beidermani*) because J. G. Franclemont (personal commun.) had suggested that the genus may not be monophyletic. Indeed,

according to my analysis each belongs to a different clade in the Heterocampinae (fig. 100). However, even though selection of one or the other species would produce different results regarding the cladistic placement of "*Schizura*," the classification I have proposed would be unaffected. I consider it unlikely that such sampling problems have affected the major features of my classification.

A more important question is whether my hypotheses concerning composition of, and relationships among, notodontid subfamilies will change with the addition of taxa. There have been few studies concerning the effects



Figs. 525, 526. Adults of *Platychasma virgo* Butler (Notodontidae: Platychasmatinae) from Japan. 525. Male (FW length = 17 mm). 526. Female (FW length = 17 mm).

of taxon addition on cladogram structure. However, an analogous issue, and one with direct application to this problem, is the question of whether discovery of fossils can significantly alter a classification previously based on knowledge of extant taxa.

Gauthier et al. (1988) have argued that discovery of particular types of taxa, specifically plesiomorphic ones (in their case fossils), can significantly change cladogram structure, which in turn might have dramatic effects on a classification. Hennig (1966: 142–145) demonstrated that addition of taxa, such as through discovery of paleontological evidence, may fill in gaps in transformation series and may help determine character polarity. Further, he showed that knowledge of intermediate states can help to understand character homology. Patterson (1981: 218) concurred, noting that addition of fossil data might change ideas on character homology or polarity. However, Patterson felt that such findings would rarely overturn theories on relationship based on recent organisms. Doyle and Donoghue concluded that “addition of taxa can provide new character combinations that may necessitate changes in cladogram topology” (1987: 90). These changes could in turn necessitate major modification of an existing classification. Thus, while most authors seem to acknowledge that addition of taxa can be potentially enlightening with regard to character transformation, fewer believe it will affect cladogram structure.

Shigero Sugi (Tokyo) brought an unusual species to my attention at a point when I had

essentially completed the research for this study. Butler (1881) described *Platychasma virgo*, endemic to Japan and Korea (Inoue, 1956; Sugi, 1982), in the Notodontidae. The species has had a controversial history. The notodontid subfamily Platychasmatinae was erected by Nakamura (1956) for *Platychasma* (monobasic) and an Indian genus, *Cyphanta* Walker, on the grounds that both taxa are unique among Notodontidae in having a quadrifid forewing (see also Holloway, 1989:

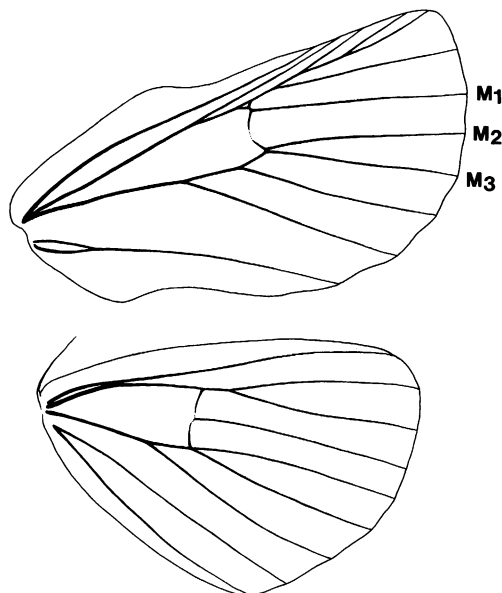
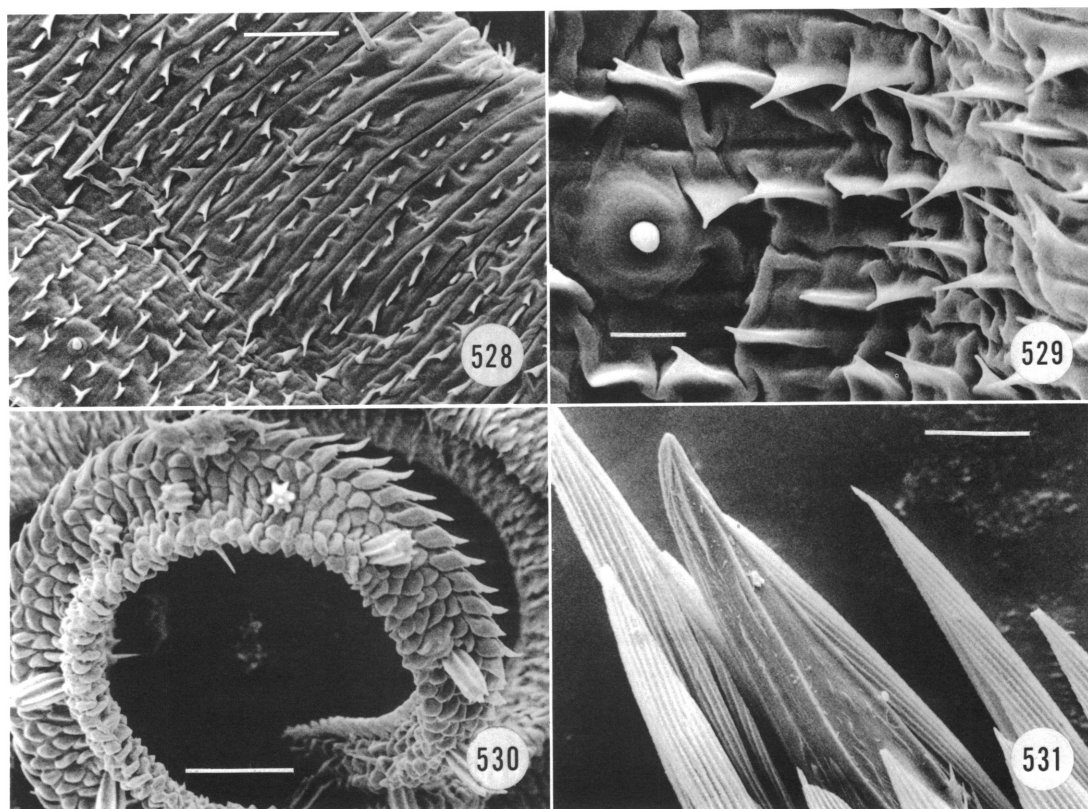


Fig. 527. Right wings of *Platychasma virgo* Butler male, showing quadrifid forewing venation. M = medial veins.

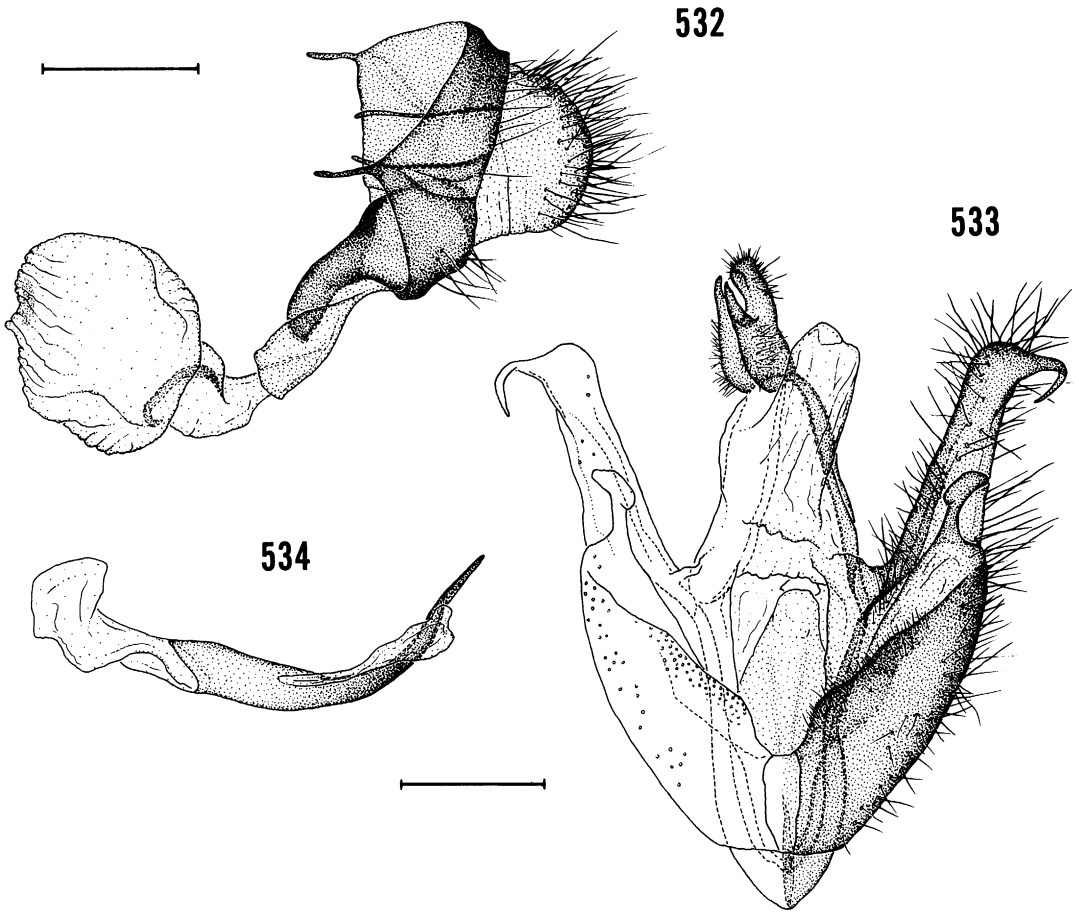


Figs. 528–531. Scanning electron micrographs of adult *Platychasma virgo*. 528. Middle portion of proboscis (20 μ m). 529. Close-up of proboscis surface (5 μ m). 530. Tip of proboscis (40 μ m). 531. Sclerotized tip of metatibial spur (20 μ m), showing smooth spur margin. Scale lengths in parentheses.

207). The Platychasmatinae was also recognized by Inoue (1956), but Kiriakoff subsequently removed *Platychasma* and *Cyphanta* from the Notodontidae and placed them in the Noctuidae near “group 2 of the Erebine-Catocaline complex of Richards” (1963b: 33). Sugi (1982, 1987a) disagreed with Kiriakoff and moved *P. virgo* back to the Notodontidae. Independent of these authors, Holloway (1983, 1989) argued that *Cyphanta* and a third genus, *Sphetta* Walker, should be transferred from the Noctuidae to the Notodontidae.

In order to test the effects of taxon addition on my cladogram and classification, and to resolve the status of the Platychasmatinae, I added *Platychasma virgo* to my analysis. Adults of *P. virgo* are characterized by having forewings with two toothlike scale tufts on the anal margin and a sinuate costal margin (figs. 525–527). As noted by Nakamura (1956), the forewing venation is quadrid (fig.

527). Kiriakoff (1963b) argued that the tympanum is of the type found in Noctuidae (see his figs. 1 and 2), but I disagree. The membrane is oriented somewhat posteriorly, a configuration that occurs in a few other notodontid species. However, there is no nodular sclerite, the epimeron is concave, and a metascutal bulla is present. These three characters are synapomorphies for Clade 2 (Doiidae + Notodontidae; fig. 99). An important synapomorphy for the trifold Noctuoidea (Clade 1) is presence of socii in the male genitalia (Character 78). These are well developed in *Platychasma virgo* (fig. 533). Most other adult characters, including those of the male and female genitalia (figs. 532–534), occur in the plesiomorphic state relative to other Notodontidae. The proboscis is long, but it shows plesiomorphic conditions of surface structure and sensillum shape (figs. 528–530). Interestingly, the tibial spur apices are smooth



Figs. 532–534. Genitalia of *Platychasma virgo*. 532. Female in lateral view, anterior at left. 533. Male in posterior view with aedeagus removed. 534. Aedeagus in lateral view, anterior at left. Scale lines = 1.0 mm.

(fig. 531) rather than being serrate as in all other Notodontidae (Character 26).

The larva, which is restricted to feeding on *Acer diabolicum* (Sugi, 1987a), exhibits the following suite of characters: head surface rugose (fig. 535), labrum deeply notched, mandibular margin smooth, stipital lobe present, and two MD setae on segment A1 (fig. 536). These are synapomorphies for almost all Notodontidae. The primary setal locations bear clusters of long secondary setae (figs. 536, 537). The caterpillar also shows primitive character states, such as fully developed anal prolegs (fig. 537).

My approach was to simply score adults and larvae of *P. virgo* for all 174 of the characters used, combine the data with my pre-

vious matrix, and run the new one using Hennig86 under the same conditions as before. The resulting cladogram is summarized in figure 538. *Platychasma* appears as the plesiomorphic sister group of all Notodontidae exclusive of the Thaumetopoeinae and Pygaerinae. Interestingly, even though *P. virgo* is a plesiomorphic species, and its addition to my study would be analogous to discovering a primitive fossil species (with complete data), cladogram topology was completely unaffected. Further, relatively few character transformations were affected, and none of those changes have implications regarding the origin of notodontid groups. Character state optimizations for the *P. virgo* tree produced no changes in my subfamilial synapomorphy

lists. It may be, therefore, that adding notodontid species will not greatly affect the classification I have proposed.

These results provide support for the hypothesis of Sugi (1982, 1987a) that *Platy-chasma virgo* is a member of the Notodontidae rather than the Noctuidae as suggested by Kiriakoff (1963b). The species is unique among Notodontidae with respect to two traits: the forewing is quadrifid and the apices of the tibial spurs are smooth rather than serrate. I recommend that the subfamily Platychasmatinae be retained. Below I list diagnostic characters and apomorphies for the subfamily (based on *P. virgo* Butler).

DIAGNOSIS (Platychasmatinae): ADULTS: Male antennae simple (fig. 525); female antennae simple (fig. 526); eyes lacking interfacetal setae; proboscis longer than length of thorax, surface with Type I surface sculpturing (figs. 528, 529); R1 sensilla fluted (fig. 530); labial palpi moderately long, segment 2 approximately $1\frac{1}{2}$ times the length of segment 1; frons unmodified, rounded anteriorly; forewing radial system with a very small accessory cell; forewing cubital system quadrifid (fig. 527); female frenulum comprising two bristles; tarsal claws bifid; hind tibiae with two pairs of spurs, tips of spurs not serrate (fig. 531); female genitalia (fig. 532) with T8 emarginate posteriorly but simple, ductus bursae moderately long, an elongate sclerotized band present at base of corpus bursae in addition to the signum; male segment 8 with tergum and sternum simple; male genitalia (fig. 533) with socii present, saccular scent organ absent, vesica of aedeagus membranous (fig. 534), with small deciduous cornuti. **LARVAE:** Head lacking secondary setae, surface rugose; seta P2 near epicranial notch, closer to midline than P1 (fig. 535); labral notch relatively deep, anteclypeus with folds; mandibular cutting edge smooth; stipital lobe present, rounded apically; spinneret moderate in length; labial palpus without medial flange; body not evenly covered with secondary setae, numerous setae at primary setal locations (figs. 536, 537), often on verrucae; prothoracic gland absent; tarsal setae lanceolate; segments A1 and A8 without dorsal protuberances; anal prolegs not reduced.

SYNAPOMORPHIES: ADULTS: Male antennae simple; female antennae simple; tibial

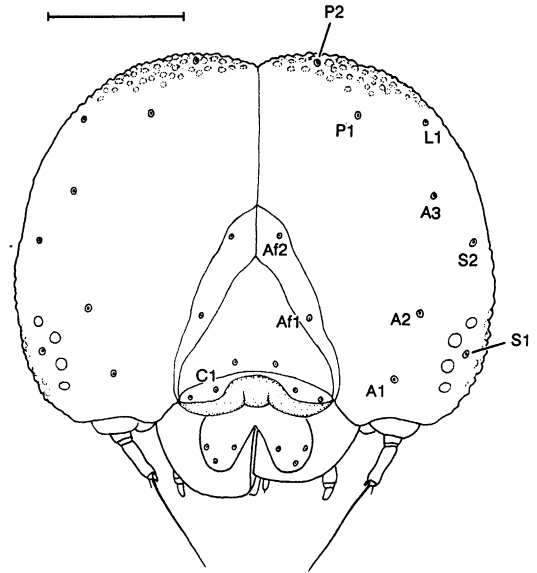
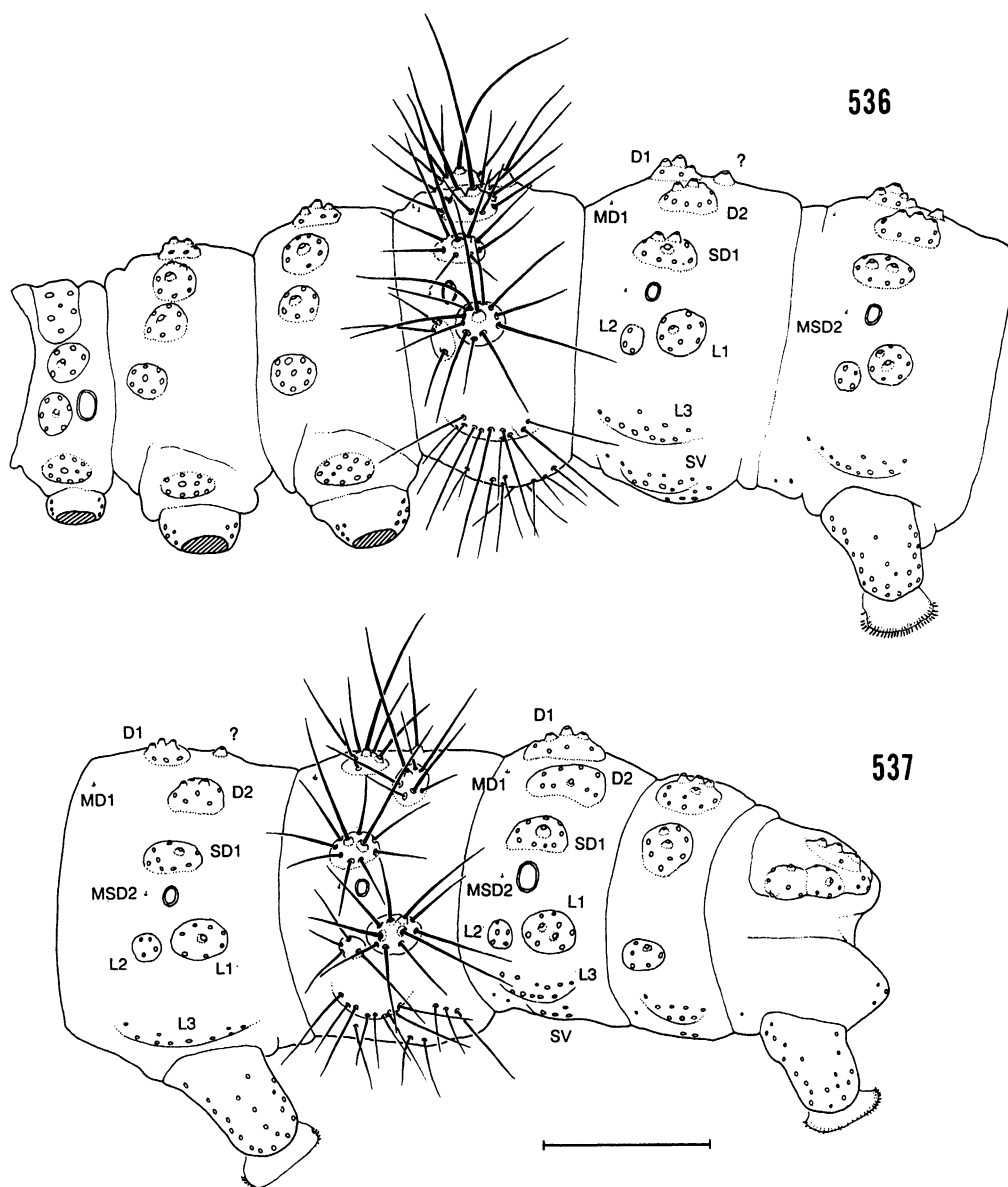


Fig. 535. Last instar larval head of *Platy-chasma virgo* in frontal view. For key to symbols see figures 361 and 362. Scale line = 1.0 mm.

spurs with margins simple; costal margin of forewing sinuate (fig. 527); radial system of FW with a very small accessory cell; forewing cubital system quadrifid; anal margin of FW with two tufts (figs. 525, 526), the proximal one comprising a lobe and a tuft of scales forming a tooth-shaped projection; female genitalia with a long sclerotized band at base of corpus bursae in addition to the signum (fig. 532); male genitalia with valvae narrow, valval apex with a long hook (fig. 533).

DISCUSSION: The cladistic placement of the Platychasmatinae (fig. 538) is strongly supported. Although I found several autapomorphies for adults, I could find none for the caterpillars. However, larvae of *Platy-chasma virgo* can easily be identified by the combination of traits listed in the diagnosis. I was unable to examine specimens of *Cyphanta* or *Sphetta* to see whether those too should be placed in the Platychasmatinae.

A rather disheartening realization is that, even within a relatively well defined family of insects such as the Notodontidae, all characters show homoplasy. Rarely did I find a subfamilial or tribal character that provides indisputable proof of membership. This



Figs. 536, 537. Last instar larva of *Platychasma virgo*. **536.** Thoracic and first three abdominal segments in lateral view with anterior at left (setae shown for A1 only). **537.** Segments 6–10 (setae shown for A7 only). For key to symbols see figures 449–451 and 501, 502. Scale line = 2.0 mm.

should not be surprising to a seasoned systematist, but the amount of homoplasy I discovered, even for characters of unambiguous interpretation, is high, and addition of species to these analyses will only increase the amount (Sanderson and Donoghue, 1989). The presence of quadrifid forewing venation

in *Platychasma virgo* shows that even supposedly “monolithic” characters will not survive unscathed. Our higher level groupings must therefore be based on most parsimonious interpretations of groups of characters, rather than on a single “silver bullet” character.

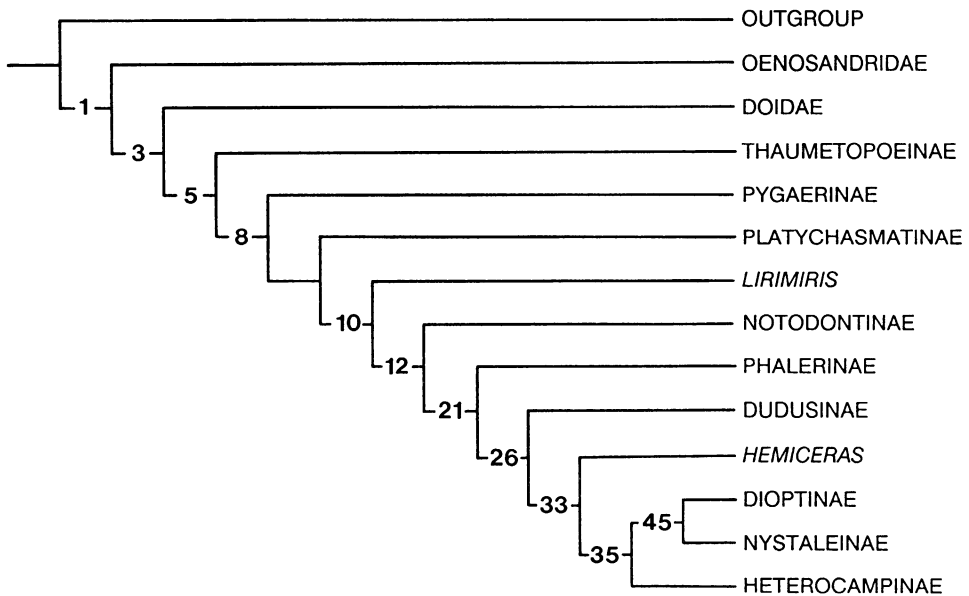


Fig. 538. Summary of results from a Hennig86 analysis of the original data set (63 taxa), with *Platychasma virgo* Butler (Platychoasmatinae) added. As in the original analysis, eight equally parsimonious trees were found (length = 868 steps, CI = 0.30, RI = 0.66). Cladogram topology was identical with that shown in figures 99 and 100. (Clade numbers correspond to those figures.)

RELATIONSHIPS AMONG NOTODONTID SUBFAMILIES

For the discussions that follow I have attempted to glean the intentions of early authors from their writings, but their ideas have usually been couched in an anecdotal context. Concerning cladistic relationships among notodontid subfamilies, I feel that my results are somewhat equivocal. Monophyly of each subfamily is usually well supported, but relationships among them are less clear. Nevertheless, the tree in figure 538 can be used as a working hypothesis, and it is generally in accordance with previous hypotheses.

Early, it was proposed that "hairy larvae" are primitive for the family (Packard, 1895a), and at least partially on that basis, most authors have regarded the Thaumetopoeinae to be the sister group to the rest of the Notodontidae (e.g., Turner, 1922; Sick, 1940). Using similar reasoning, Packard felt that the Pygaerinae, a group with secondary larval setae, is relatively primitive. My cladogram corroborates both of these proposals. Further, I place the genus *Lirimiris*, another taxon with hairy larvae, basally, on the node

above Pygaerinae. Character optimization suggests that, indeed, presence of secondary setae on the larvae (Character 139) is plesiomorphic for the Notodontidae, although the trait appears to have evolved subsequently in at least five other subfamilies.

My placement of the subfamily Notodontinae is supported by the following characters. Six larval synapomorphies support Clade 12 (fig. 538), which groups the Notodontinae with Clade 21 (comprising the Phalerinae, Dudusinae, Dioptinae, Nystaleinae, and Heterocampinae). These are head surface rugose, prothoracic cervical gland present, body not covered with secondary setae, A10 prolegs smaller than those on A2–A6, A10 proleg bases elongate, and A10 crochet number reduced. Clade 21 is characterized by three adult synapomorphies: R1 sensilla moderate in length, segment 2 of male labial palpus approximately 1–1½ times the length of segment 1, and posterior margin of male sternum 8 with a medial notch. Taken in total, I believe my evidence for the position of the Notodontinae is fairly conclusive.

One controversial issue apparent from past

discussions of notodontid classification is the placement of *Furcula*/*Cerura* (the Cerurinae of previous authors). I include the group within the subfamily Notodontinae, but others have argued that it belongs with the Heterocampinae. Both Duponchel (1845) and Moore (1882) placed *Stauropus* (Heterocampinae) in the Dicranurinae (= Cerurinae) with *Cerura* because caterpillars of both have steapodiform anal prolegs. For the same reason, Fracker (1915) proposed a relationship between *Cerura* and *Macrurocampa* (Heterocampinae). Forbes argued that larval steapods in Cerurinae "suggest a derivation from the Heterocampine group of *Macrurocampa*, *Misogada*, and *Stauropus*," but noted that "there is not great likeness in other ways" (1948: 235). I discovered additional larval characters shared by both the Dicranurini and Heterocampinae, including a 2-2-2 formula for the thoracic SV setae (Character 135), but according to my cladistic results, all such similarities evolved separately in the two groups.

The next clade, subfamily Phalerinae, has been considered a primitive lineage in the Notodontidae. Referring to the Phalerinae sensu stricto (see above), Packard wrote "I am inclined to think that this group may be the most generalized one of the family, owing to the smooth and hairy larvae, resembling those of the Nyctemeridae, Liparidae, etc." (1895a: 105). I believe that larval secondary setae in phalerines are secondarily derived from the condition in Thaumetopoeinae and Pygaerinae. Forbes (1948) suggested that the paired pits in the male eighth sternite of some Phalerinae (Character 71) are homologous with those in the Heterocampinae and that these reflect a relationship between the two groups. I argued that the pits are not homologous (see discussion of Character 71) and therefore scored them as separate character states. The list of synapomorphies for Clade 21 is short (see above), and of those I regard only Character 72 (presence of a sclerotized notch in the posterior margin of male S8) to be reliable. Further research is required to better understand the boundaries and placement of the Phalerinae.

The phylogenetic position of Clade 27, the Dudusinae, is also somewhat doubtful. Previous researchers have not commented on

the issue. Clade 26, comprised of the Dudusinae, Dioptinae, Nystaleinae, Heterocampinae, and *Hemiceras*, is supported by only two synapomorphies: adult proboscis longer than thorax (Character 3, state "0"), and A10 proleg bases cylindrical with mesal and lateral surfaces sclerotized (Character 168, state "2"). A third synapomorphy (Character 102, state "0"), involving height of the larval head, is ambiguous. Clade 33, made up of these subfamilies exclusive of the Dudusinae, is supported by four synapomorphies: adult male antennae pectinate with 15 or more terminal annulations simple (Character 15, state "1"), adult female antennae ciliate (Character 19, state "1"), larval cranium narrow in lateral view with a posterior depression (Character 103, state "1"), and four L setae on larval segments A3–A6 (Character 151, state "1"). However, these four synapomorphies result from character optimization; each of the derived states can be found in species within the Dudusinae, and some of them are reversed within Clade 33. Support for the monophyly of Clade 33 is therefore weak.

My analysis suggests that Heterocampinae are the sister group of Clade 45 (Dioptinae + Nystaleinae). Monophyly of Clade 35, which includes the Heterocampinae, Dioptinae, and Nystaleinae, is corroborated by the following: rings of proboscis with surface composed of alternating longitudinal ridges (Character 5, state "1"); male sternum 8 with a single anterior apodeme (Character 70, state "1"); and larval spinneret short (Character 126, state "1"). Although each of these characters exhibits homoplasy, I regard them as strong evidence in favor of my hypothesis. The unique structure of the proboscis in Clade 35 is particularly compelling because the modification is distinctive and it appears nowhere else in the Lepidoptera as far as I am aware.

Few cladograms have been published for the Notodontidae. Holloway (1987) showed cladistic relationships among subspecies in *Besida xylinata* and *Phalera* subgenus *Erconholda*. By far the most comprehensive cladistic analysis is Weller's (1989) study on the Nystaleinae. Weller (1989) found five synapomorphies based on adult morphology to support the hypothesis that dioptines and

nystaleines are sister groups (see fig. 524). Of her supporting characters, three were from the genitalia, one concerned shape of the epiphysis, and the fifth was presence of two frenulum bristles on the female hind wing. Heterocampine genera were used as outgroup taxa. Unlike my results, however, she also placed the Hemiceratini in this clade as the sister group to the Dioptinae (see Hemiceratini in Classification of the Notodontidae).

My results support the association of Nystaleinae and Dioptinae, but I have placed *Hemiceras* as the sister group to Heterocampinae + (Dioptinae + Nystaleinae). I found a single adult synapomorphy to support the Dioptinae + Nystaleinae clade, presence of an extremely narrow tentorium lacking crests (Character 1, state "1"), a condition that occurs in some other Notodontidae, such as the Scranciini. However, I discovered three synapomorphies in caterpillars of the two groups: sensilla trichodea and sensilla styloconica small, mesal lobe broad with lateral margin expanded (Character 118, state "1"); tarsal seta Ts2 shorter than Ts1 (Character 144, state "1"); and seta L2 on segment A8 located anterior to spiracle, on a line horizontal with it (Character 153, state "1"). Of these larval characters, I consider the last one to be the most reliable. Scoring it is unambiguous, and among the taxa in my study, the derived state did not occur outside the Dioptinae and Nystaleinae. Thus, based on two independent studies, my own and that of Weller (1989), these two Neotropical groups are sister taxa.

Schintlmeister (1985) used numerical phenetic methods to analyze relationships among 47 species of European Notodontidae in 22 genera based on 50 characters, mostly from adults. Thirteen of those genera were included in my study as well. Not surprisingly, there is little agreement between his phenogram and my cladogram. I therefore reanalyzed Schintlmeister's data set using Hennig86 in order to provide a more valid comparison. An artificial outgroup was created using "0" for all character states. I ran two analyses, one in which his nine multistate characters were treated as additive and another in which they were nonadditive.

The two runs produced almost identical results. In both, over 1300 equally parsimonious trees were found (the output over-

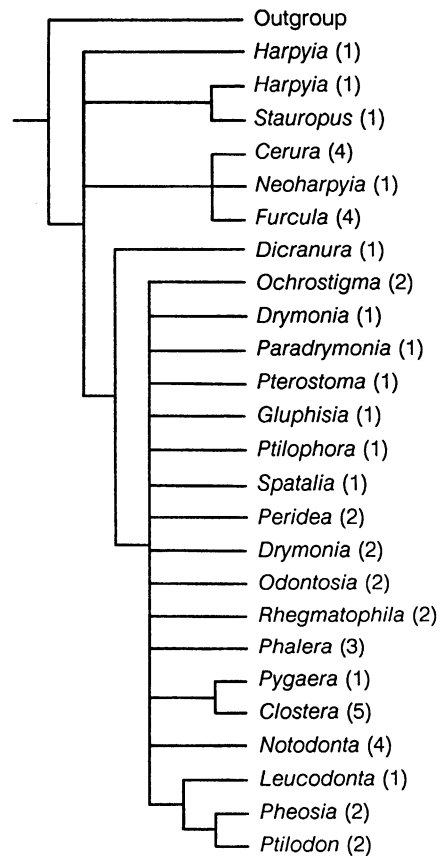


Fig. 539. Strict consensus cladogram resulting from a Hennig86 analysis of Schintlmeister's (1985) data matrix for European Notodontidae. My analysis produced over 1309 equally parsimonious trees (tree memory overflowed), each with a length of 261 and a CI of 0.26. Numbers in parentheses refer to the number of species included by Schintlmeister that belong in each clade.

flowed tree memory space). Additive coding gave a CI of 0.22, while for the nonadditive run it was 0.26. In both cases the strict consensus trees show extremely poor resolution, but it was slightly better for the second (shown in fig. 539). The areas of resolution involve species belonging in the same genus, and I illustrate only relationships between genera. It is not surprising that there are differences between Schintlmeister's cladogram and my own. His lack of resolution may reflect absence of larval data. Further, his group of study taxa was chosen on the basis of shared geography (European Notodontidae), a

method sure to produce specious phylogenetic results.

CONGRUENCE BETWEEN ADULT AND LARVAL DATA

It is obvious that combining independently derived data sets will increase cladogram resolution, whether one is combining molecular and morphological data, or separate morphological data sets (Hillis, 1987). It has often been claimed for holometabolous insect groups that study of immatures is crucial in determining taxonomic relationships. My data provided an opportunity to test congruence between larval and adult characters. I broke my complete matrix into two separate matrices, one based on larval morphology (74 characters) and one based on adults (100 characters). Each data set was then analyzed separately using Hennig86 under conditions of character coding and ordering identical to those that produced the tree in figures 99 and 100. As with that run, characters were unweighted.

Analysis of adult data produced 2296 equally parsimonious trees with a length of 499 steps, a CI of 0.30, and a retention index of 0.67. A strict consensus tree derived from those cladograms is shown in figure 540. Several points of general interest should be mentioned. First, there is extremely poor resolution at the base of the cladogram. In fact, according to my test there are no reliable adult synapomorphies for the subfamilies Thaumetopoeinae and Notodontinae. In contrast, monophyly of the subfamilies Dioprinae, Dudusinae, Phalerinae, and Nystaleinae is supported by adult characters, although the hypothesis of relationships among these differs markedly from that produced by the combined data set (figs. 99, 100). The other interesting observation is that, based on adult characters, the subfamily Heterocampinae is polyphyletic. This result is consistent with that of Weller (1989), who also used adult morphology. *Stauropus*, *Harpyia*, and *Cnethodonta* (Clade 40 of the "Stauropini") appear as part of a large basal polytomy. Even though there are numerous larval synapomorphies for Clade 40, the group is not monophyletic when only adult characters are used. Further, in figure 540 *Schizura unicornis* holds a relatively basal position quite far

removed from other heterocampines, and *Macrurocampa marthesia* appears as the sister group of the Phalerinae. These results are clearly anomalous; there is little doubt that both taxa belong in the Heterocampinae. I conclude that a study based solely on adult morphological data would produce an unsatisfactory subfamily classification.

The larval analysis produced a very different result. This time there were 810 equally parsimonious trees with a length of 300 steps, a CI of 0.36, and an RI of 0.73. The strict consensus of those is shown in figure 541. In general, better resolution was obtained, and the larval tree more closely matches the one produced by the combined data. Monophyly of the Dudusinae and Dioprinae is again supported, although the subfamily Phalerinae falls apart. Interestingly, the Heterocampinae, polyphyletic in the adult tree, is a monophyletic group according to the larval analysis, and topology of the group is in fairly good accordance with the combined result.

There are numerous subtle differences between the two cladograms. A classification based on either one alone would be highly controversial. The cladistic hypothesis and classification I have proposed for the Notodontidae require knowledge of adult and larval characters. This experiment shows that certain notodontid groups, such as the Dudusinae and Dioprinae, can be defined solely on the basis of adult data while others, such as the Heterocampinae, are readily defined by larval characters. An unfortunate conclusion results; it will be impossible to place many species of Notodontidae in the correct subfamily without specimens of larvae as well as adults. Particularly distressing is the fact that immature stages are known for such a small percentage of species in the family. I conclude that such knowledge is essential to further understand relationships within the Notodontidae.

It is interesting to note that Alexander (1990), in his study of nomadine bees, obtained results similar to mine when he compared cladograms produced by larval and adult data sets. The larval data showed less homoplasy and produced better cladogram resolution. When Alexander combined both data sets he found that some lineages are supported exclusively by larval characters and

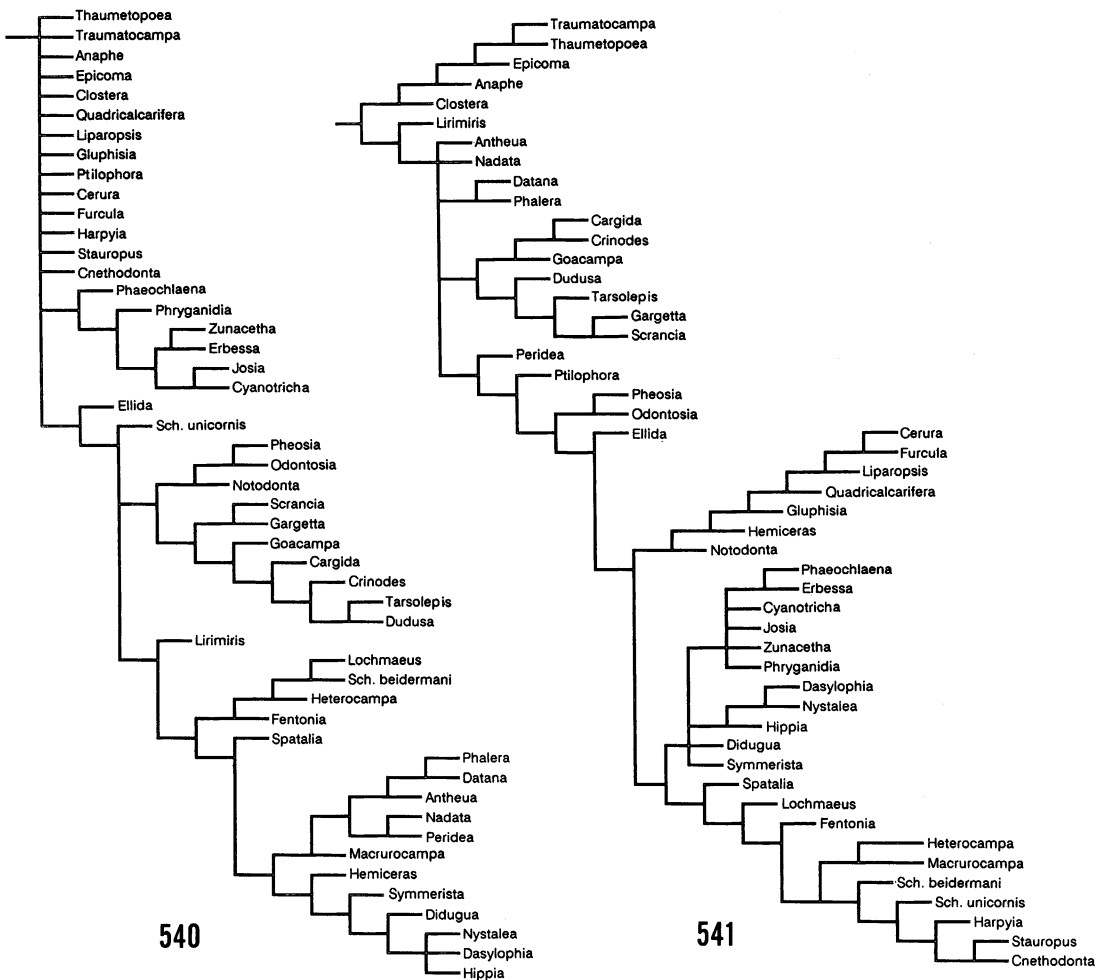


Fig. 540. Strict consensus tree derived from a Hennig86 analysis of adult characters (total = 100). The analysis found 2296 equally parsimonious trees, each with a length of 499 and a CI of 0.30.

Fig. 541. Strict consensus tree derived from a Hennig86 analysis of larval characters (total = 74). The analysis found 810 equally parsimonious trees, each with a length of 300 and a CI of 0.36.

others by adult characters. According to Alexander (1990), larval morphology in nomadine bees is less complex than that of adults. He suggested that larval characters may evolve more slowly and that when novel features do arise in a lineage they are subsequently conserved. His hypothesis may partially explain these findings for the Notodontidae. Forty-two of the 100 adult characters used in my study are from the male and female genitalia. It has long been suggested that characters of the genitalia evolve rapidly. Further, many authors have noted the difficulties involved in determining the

homology of genitalic structures (see my discussion of genitalia in the section entitled Character Analysis, Adults).

I limited my studies to final instar caterpillars, but earlier instars, as well as other immature stages, will probably provide important information. Access to first instar larvae may allow for accurate assessment of primary setal chaetotaxy in species with secondary setae because secondary setae are usually acquired only in the second to final instars. The pupae of Notodontidae exhibit many interspecific differences (Mosher, 1916, 1917; Nagano, 1916; Dolinskaya, 1989).

TABLE 8
Larval Host-plant Families for the Notodontid Study Species

	Host-plant family
Thaumetopoeinae	
<i>Traumatocampa pityocampa</i>	Pinaceae
<i>Thaumetopoea processionea</i>	Fagaceae
<i>Epicoma melanosticta</i>	Myrtaceae
<i>Anaphe panda</i>	Euphorbiaceae, Apocynaceae
Pygaerinae	
<i>Clostera albosigma</i>	Salicaceae
Platychasmatinae	
<i>Platychasma virgo</i>	Aceraceae
Notodontinae	
<i>Notodonta scitipennis</i>	Salicaceae
<i>Odontosia elegans</i>	Salicaceae
<i>Pheosia rimosa</i>	Salicaceae
<i>Ptilophora plumigera</i>	Aceraceae
<i>Gluphisia septentrionis</i>	Salicaceae
<i>Furcula borealis</i>	Salicaceae, Rosaceae
<i>Cerura tattakana</i>	Salicaceae
<i>Quadricalcarifera viridimaculata</i>	Fagaceae
<i>Liparopsis postalbida</i>	Fagaceae
Phalerinae	
<i>Phalera bucephala</i>	Generalist tree-feeder
<i>Datana ministra</i>	Generalist tree-feeder
<i>Antheua simplex</i>	Leguminosae
<i>Peridea angulosa</i>	Fagaceae
<i>Nadata gibbosa</i>	Fagaceae, others
<i>Ellida caniplaga</i>	Tiliaceae
Dudusinae	
Dudusini	
<i>Tarsolepis japonica</i>	Sapindaceae, Aceraceae
<i>Dudusa synopla</i>	Sapindaceae
<i>Crinodes besckei</i>	Rhamnaceae
<i>Cargida pyrrha</i>	Rhamnaceae
<i>Goacampa variabilis</i>	Leguminosae
Scranciini	
<i>Gargetta costigera</i>	Euphorbiaceae
<i>Scrancia stictica</i>	Euphorbiaceae
Heterocampinae	
<i>Spatalia jezoensis</i>	Fagaceae
<i>Fentonia ocypte</i>	Fagaceae, Hippocastanaceae
<i>Lochmaeus bilineata</i>	Ulmaceae
<i>Schizura biedermanni</i>	Fagaceae
<i>Heterocampa obliqua</i>	Fagaceae
<i>Macrurocampa marthesia</i>	Fagaceae, Rosaceae
<i>Schizura unicornis</i>	Generalist tree-feeder
<i>Cnethodonta griseascens</i>	Generalist tree-feeder
<i>Harpyia microsticta</i>	Fagaceae
<i>Stauropus fagi</i>	Generalist tree-feeder

TABLE 8—(Continued)

	Host-plant family
Dioptinae	
<i>Erbessa glaucaspis</i>	Leguminosae
<i>Phaeochlaena gyon</i>	Aristolochiaceae
<i>Phryganidia californica</i>	Fagaceae
<i>Zunacetha annulata</i>	Violaceae
<i>Josia ligata</i>	Passifloraceae
<i>Cyanotricha necyria</i>	Passifloraceae
Nystaleinae	
<i>Symmerista albifrons</i>	Fagaceae, Aceraceae, others
<i>Didugua argentilinea</i>	Sapindaceae
<i>Hippia packardii</i>	Sapindaceae
<i>Nystalea nyseus</i>	Myrtaceae
<i>Dasylophia anguina</i>	Leguminosae
Incertae sedis	
<i>Hemiceras bilinea</i>	Leguminosae
<i>Lirimiris truncata</i>	Tiliaceae
Outgroup Species	
<i>Doa ampla</i>	Euphorbiaceae
<i>Oenosandra boisduvalii</i>	Myrtaceae

Packard (1895a) described and figured pupae for most of the North American genera, and several cremaster characters of phylogenetic significance are apparent. In *Gluphisia* and *Furcula*, the cremaster is absent (see also Marumo, 1920; Ferguson, 1963), providing support for the monophyly of Clade 17 (fig. 99). In members of Clade 42 (the "Heterocampini"), the cremaster is distinctly fork-shaped. Other genera, such as *Symmerista* and *Dasylophia* (Nystaleinae), have a more typical cremaster bearing a cluster of curled, hook-shaped setae. In pupae of *Phryganidia californica* and other dioptines, there are hook-shaped setae on the dorsum of abdominal segments 7–10, as well as on the cremaster (Miller, 1987a), a trait apparently unique in the Lepidoptera. Pupal morphology will likely contribute crucial data as researchers attempt to further refine the classification of the Notodontidae.

In addition to pupae, ontogenetic studies involving all larval instars might help interpret particular characters. For example, Gardner (1943) noted that early instars of *Phalera* species possess stemapodiform anal

prolegs (Character 167), whereas in later instars the anal prolegs are short. Packard (1895a) and Gerasimov (1952) described remarkable modifications of the prothoracic plate in early instars of *Heterocampa* (see Character 133). These might provide important phylogenetic information, but they largely disappear in later instars.

Field researchers must diligently collect and preserve immature specimens of all developmental stages and carefully retain their association with the adult so that the species can later be identified. Only through an increase in such efforts will we be able to fully understand the classification and evolution of fascinating groups such as the Notodontidae.

HOST-PLANT ASSOCIATIONS IN THE NOTODONTIDAE

Notodontidae are unusual among Macrolepidoptera in that almost all species feed on trees, whereas few are found on herbaceous plants. Packard claimed that all Notodontidae "without any exceptions known to us, have trees as their principal, if not exclusive,

food plants" (1890: 496). Table 8 shows the larval hosts of species used in my study. Notodontid host records listed in publications such as Forbes (1948), Issiki et al. (1969), and Cai (1979a) further support Packard's contention. Notodontid species exhibit a fair degree of host specificity, but within well-defined clades, one can find a wide range of host use. For example, members of the Nystaleinae feed on trees representing a large number of unrelated plant families (Weller, 1989). Other notodontid groups, such as the Phalerinae, can be characterized as tree-feeding generalists (table 8). In contrast, the family Noctuidae includes many herbaceous-feeding lineages. There are certainly exceptions, an example being the genus *Catocala* (Catocalinae), where almost all included species feed on trees (Packard, 1890; Mitter and Silverfine, 1988). Nevertheless, the huge lineage comprising the tritid noctuid subfamilies can be characterized as an herbaceous-feeding radiation, and it includes many of the most damaging crop pests known (Holloway, 1989). The tree-feeding habit of notodontids clearly accounts for the dearth of pest species.

Even without species-level cladograms and detailed host records, it is obvious that the evolution of host association patterns in Notodontidae does not fit the type of scheme found in families such as the Papilionidae (Ehrlich and Raven, 1964; Berenbaum, 1983; Miller and Feeny, 1989) or Arctiidae (e.g., see Boppré and Schneider, 1989; Krasnoff and Roelofs, 1990). In these, host use appears to be mediated in large part by plant secondary chemistry. If host chemistry is an important determinant of food-plant use in the Notodontidae, the specific factors involved are far from obvious.

At present, I can say little about the evolution of host association patterns in the Notodontidae. My study involved few species relative to the size of the family, and species level cladograms will ultimately be required. However, three interesting points arise from my cladistic results. First, I place the Cerurinae and Gluphisiini of previous authors as internal elements within the subfamily No-

todontinae. This move, based on morphology alone, means that Salicaceae-feeding specialists are confined to the Notodontinae and Pygaerinae (table 8). As I pointed out earlier, morphological evidence suggests that *Quadricalcarifera* and *Liparopsis* may be misplaced in the Notodontinae. Their host plants are more typical of the Heterocampinae. Second, the Heterocampinae appears to be largely a Fagaceae-feeding lineage. *Fentonia* and *Spatalia* are Fagaceae-feeders. Thus, host associations provide independent support for parts of my phylogenetic hypothesis based on morphology.

Finally, my cladistic results (fig. 100) strongly suggest that the Dioprinae, many of which feed on toxic plants (table 8), have evolved from an ancestor that fed on trees lacking toxins. Although the hosts of few species are known, a picture is starting to emerge: almost all dioprine food plants contain highly toxic secondary chemicals, examples being the Aristolochiaceae and Passifloraceae. An exception is *Phryganidia californica*, the larvae of which feed on *Quercus* (Fagaceae). The Dioprinae thus appear to have made a dramatic shift in host utilization, unique to the Notodontidae. If this shift preceded the evolution of their diurnal habit, then it has subsequently given rise to the unusual behavioral and morphological characteristics of the Dioprinae. For example, along with their aposematic coloration, some dioprines possess male hind wing androconial organs (Herling, 1925) almost identical to those found in some swallowtail butterflies (Boppré, 1984; Miller, 1987b). Dioprine mating systems may differ in fundamental ways from those of other Notodontidae; they perhaps rely to a greater extent on visual cues. As another example, Weller (1989) suggested that the unusual tympanal morphology in Dioprinae may reflect their change from a nocturnal to a diurnal life style, where avoidance of bat predation would be unnecessary. I hope to address these interesting evolutionary problems in future research on dioprine phylogeny.

CONCLUSIONS

It is critical that future studies on noctuid phylogeny address the status of pivotal groups such as *Doa* and *Oenosandra*. Molecular data may be particularly informative. I also hope the research described here will provide a framework for an improved classification of the world Notodontidae. It is now important that researchers further test my phylogenetic hypotheses by studying additional characters and taxa, and that they work to more fully

resolve notodontid relationships. The process of improvement is an iterative one; undoubtedly new subfamilial and tribal categories will need to be recognized and some of my conclusions will require revision. Nevertheless, I look forward to future scrutiny with the full knowledge that only through such refinement can we truly advance our understanding of nature's underlying patterns.

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APPENDIX I

Characters used in the analysis. Characters or character states that occur only in the outgroup are noted with an asterisk. Characters or character states autapomorphic for the ingroup are indicated by a dollar sign (\$). Multistate characters were treated as either nonadditive [–] or additive [+].

ADULTS HEAD

1. Tentorial crests present (0); tentorium very narrow, without crests (1).
2. Adult with frons broadly rounded anteriorly, no projections (0); frons protruding, strongly sclerotized, projections usually present (1).
3. [–] Male labial palpus with segment 2 approximately 1–1½ times the length of segment 1 (0); segment 2 shorter than segment 1 (1); segment 2 more than twice as long as segment 1, narrow (2); segment 2 long and narrow, sickle-shaped, extending to top of cranium (3).
4. [–] Segment 3 of male labial palpus not elongate (0); palpal segment 3 elongate, as long as or longer than segment 1 (1); segment 3 small and oblong, Organ of vom Rath opening on segment's anterior surface (2).
5. [+] Male labial palpus with all segments clearly defined, palpus not unusually small (0); male palpus small, division between segments 2 and 3 often indistinct (1); palpus reduced to a single, tiny segment (2)\$.
6. [–] Proboscis longer than thorax (0); proboscis not as long as thorax but longer than head (1); proboscis less than length of head (2); proboscis absent or present as 2 small lobes (3).
7. Proboscis relatively narrow, not robust (0); proboscis wide, robust (1).
8. [–] Rings of proboscis covered with microprojections along length of tongue except at tip (0); microprojections at base only, remainder of proboscis rings with surface composed of alternating, longitudinal ridges (1); surface of rings smooth (2); tongue reduced, rings of proboscis obscured (?).
9. Sensilla styloconica (R1 sensilla of Börner, 1939) of proboscis fluted (0); R1 sensilla smooth, lacking flutes, or flutes reduced to small projections (1); R1 sensilla highly reduced (score of “3” for Character 7) (?).
10. [–] R1 sensilla of proboscis moderate in length, parallel-sided (0); R1 sensilla goblet-shaped, with a distal constriction (1); sensilla long, laterally compressed (2); R1 sensilla short, only slightly larger than R2 sensilla (3).
11. Pilifers well developed (0); pilifers absent (1).
12. Eyes large, occupying almost entire genal region (0); eyes relatively small, genal area partially scaleless with surface spiculate (1).
13. Eyes with interfacetal setae absent (0); eyes with interfacetal setae present (1).
14. [–] Male antennae pectinate (0); male antennae almost smooth, with a few scattered bristles

(1); male antennae without pectinations, a row of bristles present, oriented laterally (2); antennal pectinations extremely long (3).

15. Male antennae pectinate, with fewer than 10 terminal annulations simple, or terminal annulations similar to proximal ones (0); male antennae with 15 or more terminal annulations simple (1).

16. Scape of male antenna without a scale tuft, or with a small ventral tuft (0); scape of male antenna with a small ventral scale tuft, and a large dorsal tuft of stiff scales (1).

17. Joints of male antennal annulations perpendicular (0); antennal annulations joined obliquely in lateral view (1).

18.* Pectinations of male antennae lacking spinules (0); male antennae with spinules at end of each pectination (Lymantriidae) (1).

19. Female antennae pectinate (0); female antennae ciliate (1).

20. [+] Adults with ocelli present, large (0); ocelli present, small (1); ocelli absent (2).

THORAX

21. Adult foretarsi not unusually long, first tarsomere shorter than length of others combined (0); foretarsi long, first tarsomere longer than others combined (1).

22. Female epiphysis present (0); female epiphysis reduced or absent (1).

23. Male epiphysis broad, much shorter than tibia, apex acute (0); male epiphysis flat, almost as long as tibia, apex not acute (1).

24. Foretibia unmodified (0); foretibia with a strongly sclerotized distal spur (1).

25. Legs not unusually long, hind tibia less than $1\frac{1}{2}$ times the length of femur, spur pairs close together (0); legs long, hind tibia approximately $1\frac{1}{2}$ times the length of femur, pairs of spurs widely separated (1).

26. Sclerotized tips of tibial spurs with margins smooth (0); tips of tibial spurs with margins serrate (1).

27. [+] Two pairs of metathoracic tibial spurs present, both pairs equal in size (0); proximal pair of metathoracic tibial spurs reduced in size (1); proximal pair of spurs absent, only the distal pair present (2).

28. Adult tarsal claws simple (0); each claw with a basal lobe (1).

29.* Metepisternal tymbal organ absent (0); tymbal organ present (Arctiidae) (1).

30. [+] Ventral portion of metathoracic episternum without a flange (0); ventral portion of metathoracic episternum with a lateral flange (1); lateral flange of metathoracic episternum strongly sclerotized and concave (2).

31. [-] Secondary arms of metafurca acute posteriorly (0); metafurcal arms blunt posteriorly (1); metafurcal arms small (2)*.

32. [+] Dorsal portion of metepimeron not concave or only slightly so (0); dorsal portion of me-

tepimeron strongly concave, forming a tympanum, tympanal membrane facing ventrally (1); epimeral cavity forming an internal "pouch," pouch as tall as epimeron itself (2).

33. Tympanum without a nodular sclerite (0); a nodular sclerite present in tympanal membrane (1).

34. [+] Metascutal bulla not present (0); bulla present, teardrop-shaped (1); bulla prominent, round (2); bulla large, comprising almost the entire metascutum (3).

35. Vein Cu in forewing trifold (0); Cu in FW quadrid (1).

36. [-] FW vein R_2 arising from discal cell, not forming an accessory cell (0); R_2 arising from discal cell, forming an accessory cell (1); R_2 stalked with R_{3-5} , no accessory cell (2).

37. [-] Forewing accessory cell moderate in length, or absent (0); accessory cell narrow, greatly elongate, vein R_2 and the base of R_{3-5} parallel (1); FW accessory cell extremely short, M_1 arising from its apex (2); FW accessory cell wide, relatively short (3).

38. Veins M_3 and CuA1 not fused in FW (0); M_3 and CuA1 fused in FW (1).

39. Anal margin of FW smooth, no projection (0); anal margin of FW with a lobe and a tuft of scales forming a prominent, tooth-shaped projection (1).

40.* Retinaculum short, broad, not extending to vein CU (0); retinaculum long, narrow, extending almost to vein CU (Arctiidae and some Noctuidae) (1).

41. Hind wing with veins M_3 and CuA1 not anastomosed (0); M_3 and CuA1 in HW anastomosed (1).

42. Vein Cu in hind wing trifold (0); Cu in HW quadrid (1).

43. Hind wing vein M_2 present (0); HW vein M_2 absent (1).

44. Female frenulum composed of 2–10 bristles (0); female frenulum composed of 15 or more bristles (1); female frenulum lacking bristles, jugal area expanded (?).

ABDOMEN (BOTH SEXES)

45. [+] Segment A1 without a counter-tympanal hood (0); counter-tympanal hood present, postspiracular (1); hood present, prespiracular (2).

46. [+] Pleural membrane surrounding A1 spiracle not sclerotized (0); membrane surrounding A1 spiracle sclerotized, concave, forming a cup (1); spiracular cup very large, extending above top of pleuron (2).

47. Area above A1 spiracle not setose (0); a small, lightly sclerotized, setose patch located in pleuron above A1 spiracle (1).

48. Adults with internal bullae on tergum A1 not large (0); large internal bullae present on anterior margin of tergum A1 (1).

49. Anterolateral apodemes on sternum 2 mod-

erate in length (0); apodemes on sternum 2 long and thin (both sexes) (1).

ABDOMEN (FEMALE)

50. Female tergum 7 sclerotized, not covered with deciduous scales (0); female T7 membranous, covered with deciduous scales (1).

51. [-] Pleuron of female segment 8 sclerotized (0); pleuron of segment 8 partially membranous (1); pleuron of segment 8 heavily sclerotized, eighth segment capsulate (2).

52. [-] Dorsum of female tergum 8 completely sclerotized (0); dorsum of T8 with a membranous medial suture (1); female T8 composed of two narrow straps, meeting dorsally (2).

53. [-] Posterior margin of female tergum 8 sclerotized, often emarginate (0); margin crenulate or with a deep notch (1); posterior margin of female T8 with two long protuberances (2)\$; female T8 with a single medial projection (3)\$; female T8 highly reduced (?).

54.* No externally visible pheromone gland present in dorsal portion of female 8/9 intersegmental membrane (0); a deeply invaginated pheromone gland present in dorsal portion of female 8/9 membrane (Arctiidae) (1).

55. No ventral invaginated glandular region between ostium and papillae anales (0); a ventral, invaginated, glandular region present in membrane between papillae anales and ostium (1).

GENITALIA (FEMALE)

56. [-] Ductus bursae mostly membranous, elongate, not flattened (0); ductus bursae with a robust, sclerotized portion (1) ductus bursae sclerotized, dorsoventrally compressed, broad (2).

57. [+] Postvaginal plate (PVP) not large, not emarginate (0); PVP large, broad, emarginate posteriorly (1); PVP large, sharply emarginate posteriorly, with narrow posterolateral projections (2); PVP cup-shaped (3)*; PVP fused to pleuron, boundaries indistinct (?).

58. Ostium without a ventral medial projection (0); ostium with a ventral medial projection (1).

59. Surface of corpus bursae crenulate (0); surface of corpus bursae spiculate (1).

60. Corpus bursae with a single signum, or without one (0); bursa with two signa, one rounded, the other crenulate (1).

61. Ductus seminalis entering on ductus bursae or at junction of ductus and corpus bursae (0); ductus seminalis entering on corpus bursae (1).

62.* No ventral lobes present below papillae anales (0); paired, ventral setose lobes present below papillae anales (Lymantriidae) (1).

63. Papillae anales not unusually broad or flattened (0); papillae anales broad and flattened, membranous (1).

64. Basal portion of papillae anales not heavily sclerotized (0); basal portion of papillae anales heavily sclerotized, smooth, distal portion of lobes membranous (1).

65. Posterior margins of papillae anales rounded, lobes membranous (0); posterior margins of papillae anales acute, lobes sclerotized (1).

66. Dorsal membrane between papillae anales unmodified (0); a spiculate, mediodorsal lobe between papillae anales (1).

ABDOMEN (MALE)

67.* Sternum of A2 without hair pencils (0); lateral hair pencils present on sternum of A2 (some Noctuidae) (1).

68. Male pleuron on all abdominal segments membranous (0); male with sclerotized lobes on pleuron of segments A3 and A4, bearing hair pencils (1).

69. Male sternum 4 unmodified (0); cteniphore present on male S4 (1).

70. [-] Male sternum 8 without an anterior apodeme (0); male S8 with a single anterior apodeme (1); S8 with double apodemes (2); apodeme on S8 broad, with two "windows" (3).

71. [-] Medial portion of male sternum 8 without pits or apodemes (0); medial portion of male sternum 8 with a pair of internal apodemes, widely spaced (1); male S8 with a pair of small, closely spaced medial pits (2).

72. [-] Posterior margin of male sternum 8 not modified, no notch (0); posterior margin of S8 with a medial notch (1); margin of S8 sclerotized but without a notch (2); margin with a thin, sclerotized strap projecting into intersegmental membrane (?).

73.\$ Male S8 with anterior apodeme only (0); S8 with an additional, extremely long, internal apodeme arising from the base of anterior apodeme (1).

74. [+] Male abdomen with 8/9 intersegmental membrane shorter than the length of T7 (0); 8/9 membrane equal to or longer than T7 (1); 8/9 membrane with dorsal portion long, ventral portion short, genitalia facing ventrally (2).

75. Length of male T8 equal to or shorter than that of T7 (0); T8 longer than T7 (1).

76. Male tergum 8 without anterolateral apodemes (0); tergum 8 with a pair of large, anterolateral apodemes (1).

77. [-] Males without a terminal scale tuft (0); males with a terminal tuft of hairlike scales, scale apices simple or serrate (1); male terminal tuft compact, curved downward (2); terminal tuft composed of long, pedicellate scales, scale apices spatulate (3).

GENITALIA (MALE)

78. [+] Socii absent (0); socii present (1); socii fused into a single, long process (2).

79. Uncus/socii complex hinged on tegumen (0); uncus/socii complex fused with tegumen (1).

80. [-] Uncus narrow, acute distally (0); uncus spatulate, with a distal notch (1); distal portion of uncus flattened ventrally, with a brush of fine setae (2); uncus strongly forked (3).

81. Base of uncus not robust (0); base of uncus robust, uncus triangular (1).

82. Uncus without ventral prongs (0); uncus with a pair of ventrally directed prongs in addition to socii (1).

83.* Male genitalia without a gnathos (0); male genitalia with two projections arising from the tegumen and curving below the anal tube to form a gnathos (some quadridid Noctuoidea) (1).

84. Sides of tegumen not constricted dorsally (0); tegumen constricted dorsally, forming a "neck" (1).

85.* Tegumen without a setal tuft (0); a setal tuft (penicillus) present on tegumen (some Noctuidae) (1).

86. [-] Transtilla present, composed of two sclerotized bands in the manica, joined medially above aedeagus (0); transtilla not joined above aedeagus (1); transtilla absent (2); a long projection present at base of each valve, fused to valval costa (3); transtilla composed of free sclerites at the base of each valve, with long, horn-shaped projections ("costulae" of Weller, 1989) (4); transtilla curving downward, connected to base of juxta (5).

87. No medial projection on valval costa (0); valval costa widened distally, "C-shaped" with a large medial projection (1).

88. [-] Base of valve without a flange (0); base of valve with a setose, medial flange (1); base of valve with a sclerotized, thornlike medial process (2).

89. Apex of valve partially membranous, roughly acute, not bulbous (0); apex of valve sclerotized, rounded and bulbous (1).

90. Valve not unusually broad, margins not narrowly sclerotized (0); valve broad, membranous in middle, with narrow, sclerotized bands on dorsal and ventral margins (1).

91. [-] Sacculus without pleats (0); sacculus large, with accordion-like pleats (1); sacculus small, with faint pleats (2); sacculus greatly expanded, curled inward to enclose pleats (3).

92. Sacculus not separate from rest of valve (0); sacculus separate from rest of valve, projecting from valve's lateral margin (1).

93. An elongate saccus present (0); saccus small or absent (1); saccus comprised of 2 shallow humps, with a medial indentation (2).

94. Manica almost entirely membranous (0); manica sclerotized, fused with juxta, enclosing aedeagus tightly (1).

95. [-] Ductus ejaculatorius simplex (DES) opening near anterior end of aedeagus (0); opening of DES located posteriorly, anterior end of aedeagus forming a long tubular projection (1); opening of DES located posteriorly, anterior end of aedeagus forming a boat-shaped structure, membranous dorsally (2); opening of DES located slightly

posteriorly, anterior end of aedeagus broad, re-flexed in a ventral direction (3).

96. Distal portion of aedeagus without a patch of short spines (0); distal portion of aedeagus with a patch of short spines (1).

97. [-] Distal portion of aedeagus expanded, much wider than middle (1); distal portion of aedeagus with a large ventral tooth (2); distal portion of aedeagus strongly forked (3); aedeagus not as above (0).

98. Base of vesica without scobinate cornuti (0); base of vesica with a patch of large scobinate cornuti (1).

99. Vesica without deciduous cornuti (0); vesica with deciduous stellate cornuti (1).

100. [+] Vesica entirely membranous, either with or without cornuti (0); vesica with a small distal sclerite, sometimes bearing deciduous cornuti (1); sclerite in vesica finely crenulate [2].

LARVAE

HEAD

101. [-] Microsculpture of larval head surface mostly smooth, with fine creases (0); head surface rugose with rugosities in clusters (1); head surface covered with pits (2); rugosities extremely small (3); head surface smooth, glassy (4); head surface spiculate (5)\$.

102. Height of head equal to or less than that of thoracic segment 1, head not wider than thorax (0); head taller than thoracic segment 1 (lateral view, excluding legs), head wider than thorax (1).

103. Cranium rounded in lateral view, without a depression (0); cranium narrow in lateral view, with a posterior depression along epicranial suture (1).

104. [-] Larval head without secondary setae (0); long secondary setae present on head (1); short secondary setae present (2).

105. Seta P2 located far from epicranial notch, lateral to P1 (0); P2 located near epicranial notch, closer to midline than P1 (1).

106. Distance between setae P1 and C1 only slightly longer than the distance between Af2 and C1 (0); distance between P1 and C1 half again as long as the distance between Af2 and C1 (1).

107. Seta S1 located closest to stemma 4 (0); S1 closest to stemma 3 (1).

108. Stemma 3 approximately the same size as stemma 4 (0); stemma 3 much larger than stemma 4 (1).

109. Length of antennal segment 2 less than or equal to $2\frac{1}{2}$ times its width (0); length greater than $2\frac{1}{2}$ times its width (1).

110. Labral indentation less than two-thirds labrum height, no medial groove (0); labral indentation at least two-thirds labrum height, a medial groove present (1).

111. Larva with labral lobes not swollen (0); labral lobes greatly swollen, halves completely separate (1).

112. Anteclypeus without folds, dorsal and ventral margins roughly parallel (0); anteclypeus expanded medially, with large dorsoventral folds (1).

113. [+] Mandibular cutting edge sharply dentate (0); mandibular cutting edge smooth (1); ventral half of mandibular margin smooth, dorsal half with shallow dentations (2).

114. Ventrolateral surface of mandible smooth (0); mandible with a pronounced ventrolateral carina (1).

115. Mandible without secondary setae (0); mandible with numerous secondary setae (1).

116. [-] Stipital lobe absent (0); stipital lobe present, rounded (1); stipital lobe acute distally, not extending beyond maxilla (2); lobe large, extending beyond rest of maxilla (dorsal view) (3).

117. Surface of stipital lobes minutely spiculate (0); stipital lobe with large spicules (1).

118. Sensilla trichodea and styloconica not unusually small, mesal lobe not broad (0); sensilla trichodea and styloconica small, mesal lobe usually broad, lateral margin expanded (1).

119. Sensilla trichodea (ST) II and STIII tapered to a single point (0); STII and STIII distally emarginate, usually bifid (1).

120.* Sensilla styloconica (MSS and LSS) not on a raised process (0); MSS and LSS on a raised process of the mesal lobe (some Noctuidae) (1).

121. Segment 3 of maxillary palpus not narrow and elongate (0); segment 3 of maxillary palpus narrow, elongate (1).

122. Segment 2 of maxillary palpus not elongate (0); segment 2 of maxillary palpus elongate (1).

123. Hypopharynx not greatly swollen (0); hypopharynx swollen, expanded dorsally (1).

124. [-] Labial palpus parallel-sided, moderate in length, approximately same length as segment 1 of maxillary palpus (0); labial palpus globose (1); labial palpus small, much shorter than segment 1 of maxillary palpus (2); labial palpus elongate, terminal seta extremely long (3)*.

125. Mesal margin of labial palpus smooth, without a flange or lobe (0); labial palpus with a membranous flange on mesal margin (1).

126. [-] Spinneret longer than labial palpus, palpi and spinneret not apposed (0); spinneret shorter or barely longer than labial palpus, palpi and spinneret apposed (1); spinneret twice as long as segment 1 of labial palpus (2); spinneret narrow, greatly elongate (3)*; spinneret with large, winglike lateral projections (4)\$.

127. Spinneret roughly elliptical in cross section, distal opening ovoid (0); spinneret dorsoventrally compressed, distal opening wide and flat (1).

128.-20 Base of spinneret smooth (0); base of spinneret deeply wrinkled (1).

129. Larval submentum without a medial cleft (0); submentum swollen, with a deep medial cleft (1).

130. [+] Larval mentum not swollen, without lateral projections (0); mentum swollen, appearing glandular (1); mentum swollen, with large lateral projections (2).

THORAX

131. [-] Surface of integument crenulate (0); integument covered with long hairlike spicules ("shagreened") (1); integument spiculate, each spicule with a socket (2); integument covered with short, sharp spicules (3).

132. [+] T1 cervical gland absent (0); cervical gland present (1); a groove visible but no gland present (2).

133. Prothoracic plate simple, no projections (0); prothoracic plate with a pair of anterolateral projections or horns (1).

134. Prothoracic plate not heavily sclerotized, not square in shape (0); prothoracic plate roughly square in shape, heavily sclerotized and smooth (1).

135. SV setae on thoracic segments in the formula 2-1-1 (0); SV setae in the formula 2-2-2 (1).

136. Anterior SV seta on T1 unmodified (0); anterior SV seta on T1 short, conical (1).

137. Anterior SV setae on T2 and T3 unmodified (0); anterior SV setae on T2 and T3 short and broad (1).

138. Larva without chalazae (0); primary setae located on chalazae (1).

139. Segment T3 with a single MD proprioceptor seta (0); T3 with two MD setae (1).

140. [-] Body not covered with secondary setae (0); body with long secondary setae, mostly grouped at primary setal locations (1); body evenly covered with secondary setae, larger setae or sometimes verrucae present at primary setal locations (2); body with very short secondary setae (3).

141. [-] One coxal seta short, the other long (same shape as other primary setae) (0); both coxal setae short, ventral one thin and dorsal one spatulate (1); only one extremely long, spatulate coxal seta present (2)\$.

142. Femur and tibia of thoracic legs not unusually long (0); femur and tibia elongate (1).

143. [-] Basal tarsal setae (Ts1 and Ts3) on thoracic legs lanceolate, Ts3 slightly longer than Ts1 (0); both setae narrow (1); both setae roughly parallel-sided, acute distally (2); both setae spatulate, with minute striations, apices dentate or broadly rounded (3); Ts1 broad and relatively short with apex acute, Ts3 with lateral margin expanded, apex deflected toward midline (4); both setae paddle-shaped (5)*.

144. Seta Ts2 of larva roughly equal in length to Ts1 and Ts3 (0); Ts2 shorter than Ts1 (1).

145. Tarsal setae of larva present on all thoracic

segments (0); tarsal setae absent on meso- and metathoracic segments (1).

ABDOMEN

146. MD proprioceptor setae unisetose on A1 (0); MD setae bisetose on A1 (1).

147. Proprioceptor seta MSD2 on segments A5–A7 located anteriorly to spiracle, on a line approximately even with it (0); MSD2 on A5–A7 located anterodorsally to spiracle (1).

148. [–] Six to 8 setae below line of spiracle on A1 and A2, all SV setae approximately equal in size (0); 6 to 8 setae below line of spiracle on A1 and A2, one SV seta short and conical or spatulate (1); 10 or more setae below line of spiracle on A1 and A2 (2); secondary setae obscuring arrangement of primaries (?).

149. [–] SD group on segments A3–A8 unisetose (0); SD group bisetose on segments A3–A7, unisetose on A8 (1); SD group bisetose on segments A3–A8 (2); numerous setae in SD group (?).

150. No additional seta present between the SD and D groups on A2–A8 (0); an additional seta present between the SD and D groups on segments A2–A8 (1).

151. [–] Three L setae on A3–A6 (0); 4 L setae on segments A3–A6, the ventral pair at approximately the same height (1); 5 L setae on segments A3–A6 (2); 6 or more L setae on A3–A6, a horizontal row of 4 to 10 setae present at the height of L3 (3); secondary setae obscuring arrangement of primaries (?).

152. Posterior L seta on each abdominal segment narrow in shape (0); posterior L seta on each abdominal segment spatulate (1).

153. Seta L2 on larval segment A8 located below spiracle and approximately on a vertical line with it (0); L2 on A8 located anterior to spiracle, on a line horizontal with it (1).

154. \$ No peglike setae located posterior to abdominal spiracles (0); a group of peglike setae located posterior to each abdominal spiracle (1).

155. "E area" (Stehr and Martinat, 1987) of larval A10 without a seta (0); a seta (seta X of Gerassimov) located in E area near anterolateral corner of anal shield, or a verruca in that position (1).

156. A3–A6 prolegs with 3 or fewer SV setae on lateral surface (0); proleg base with more than 3 setae on lateral surface of leg base (1); entire body, including proleg bases, covered with secondary setae (?).

157. [–] Larval abdominal segments 1–8 without dorsal patches of deciduous setae (0); dorsal pockets present on A1–A8, containing tufts of deciduous setae (1); tufts of deciduous setae present, not located in pockets (2)*.

158. Abdominal spiracles not small (0); abdominal spiracles small (1).

159. [–] Crochets uniordinal (0); crochets biordinal (Doidae) (1); crochets biserial, in two rows of equal length (Oenosandridae) (2); crochets heteroideous (some Arctiidae) (3).

160. Prolegs on larval segment A3 equal in size to those on A5 and A6 (0); A3 prolegs smaller and with fewer crochets than those on A5 and A6 (1).

161. Prolegs on larval segment A4 with same number of crochets as other segments (0); A4 prolegs with fewer crochets than A5 and A6 (1).

162. Segment A1 of larva without a dorsal protuberance (0); A1 with a dorsal protuberance (1).

163. Segment A8 without a dorsal protuberance (0); A8 with a dorsal protuberance (1).

164.* Segments A6 and A7 without middorsal glands (0); middorsal glands present (Lymantriidae) (1).

165. Seventh through 10th abdominal segments of larva not triangular in lateral view (0); larval segments A7–A10 triangular in lateral view, arched upward, carried erect (1).

166. Larval segment A8 not laterally emarginate (0); A8 expanded, laterally emarginate (1).

167. [+] A10 prolegs approximately equal in size to others (0); A10 prolegs modified, usually smaller than those on A2–A6 (1); A10 prolegs extremely long and flexible, developed as stemapods (2); A10 prolegs greatly elongate, but sclerotized rather than flexible (3); A10 prolegs absent (4).

168. [+] A10 proleg bases not elongate (0); A10 proleg bases elongate (1); A10 proleg bases elongate, almost tubular, with mesal as well as lateral surfaces sclerotized (2); stemapods present, A10 leg bases obscured (?).

169. [+] Fewer setae on A10 proleg base than on A3–A6 prolegs (0); numerous setae (more than 10) on A10 proleg base (1); proleg base with many setae, each on a raised tubercle (2); entire body covered with secondary setae (?).

170. A10 crochet number approximately equal to the number on A6 (a ratio of 0.9 or more; see table 2) (0); fewer crochets on A10 than on A6 (a ratio of 0.89 or less) (1); A10 crochets absent (2).

171. Larval A10 crochets exposed (0); A10 crochets withdrawn into proleg (1).

172. A10 crochets curved, similar in shape to those on other prolegs (0); A10 crochets small and spinelike, not curved (1).

173. Anal plate without sclerotized folds and wrinkles (0); anal plate heavily sclerotized, with numerous folds and wrinkles (1).

174. Paraprocts not unusually elongate (0); paraprocts elongate, bearing an enlarged SV1 seta (1).

Appendix II

Data matrix for 51 species of Notodontidae and 12 outgroup species. For complete taxonomic names see Table 1. For character state descriptions, see Appendix I and Character Analysis

ADULTS	20		40		60		80		100	
THAUME	010013????	1000001002	0000012000	0101020000	0001000001	0000100000	0000000000	0000001100	0000000000	0010000000
TRAUMA	010013????	1000001002	0001012000	0101020000	0001000001	1000100000	0000000000	0000001100	0000020000	0010000000
ANAPHE	000013????	1000001002	0000012000	0101020100	0001000001	1000100000	0000000000	0000001110	0000000000	0010000000
EPICOM	007023????	1003001002	0110012000	0101020000	0000000001	1100100000	0000000000	0000001100	0000070700	0000000000
CLOSTE	0020020073	0010000002	0010010100	0101020000	0010010000	1000000000	0010000000	0001101100	0000000000	1010000000
PLATYC	0000000000	0001000011	0000000100	0101112010	0000010000	1000000000	0000000000	0000007100	0000000000	0010000010
LIRIMI	0020010000	0003110001	0010010100	0101010000	0000010000	0000001000	0000000000	0201101100	0000020000	0010200000
NOTODO	0010020711	0010000011	0000010000	0101010010	0001010000	1000011000	0000000000	0001101100	0000020110	0010100001
ODONTO	0010021011	0000000001	0000010000	0101010010	0001010000	1000011000	0000000001	0001101101	0000020100	0010200002
PHEOSI	0010120711	0000000001	0000010000	0101020010	0001010000	1010001000	0000000000	0201101101	0000020110	0010203002
QUADRI	0020037773	1003000002	0010010000	0101020000	0000010000	1000010000	0000000001	0102111200	0000000000	0000110000
LIPARO	0010137777	1003000002	0010012000	0101020000	0007010000	1000000010	0010000001	0002111000	0000070000	0000010000
GLUPHI	0010120073	0013000001	0110012000	0101020000	0011010000	1000000010	0010000000	0001111201	0000000000	1010000000
PTILOP	0010120073	1003000011	0110012000	0101020000	0000010000	1000001010	0010000000	7201101100	0000020110	0000203000
CERURA	0010120073	1003000002	0010012000	0101020000	0001010000	1200001000	0010000002	0101111100	0000020000	0010300000
FURCUL	0010120073	1003000002	0010012000	0101020000	0001010000	1000001000	0010000001	0001101100	0000020000	0010000000
DATANA	0000010000	0002700011	0001010100	0101010000	0000010000	2000007000	0000001002	2101101100	1000021000	2020200011
PHALER	0000010000	0002700011	0000001010	0101010000	0000010000	2000017000	0000000002	2101101100	1000021000	2020200011
ANTHEU	0000010000	0000100001	0000010100	0101010000	0000010000	2000017000	0000010002	0101101100	1000021000	2020200011
NADATA	0020011000	0000000001	0000010000	0101010000	0000010000	1000011000	0000000001	0101101100	0000011010	2020200111
PERIDE	0000011000	0002100011	0000001010	0101020010	0000010000	1010011000	0000000001	0101101100	0000021000	2020200011
ELLIDA	0000010000	0000000002	0000010100	0101020000	0010010000	1000021000	0000000000	0101101100	0000000000	2010301010
SPATAL	0000010710	0000100071	0000011100	0101010010	0007010000	0000001000	0000000017	1001101100	0000030200	2020200001
FENTON	0000010100	0000100011	0000001010	0101011000	0000010000	1000001000	0000000001	0101101102	0000050000	1000200111
HETERO	0000020703	0000100011	0000001010	0101011000	0000010000	1010001100	0000000001	0101101100	0000030000	0020200001
BEIDER	0000010100	0000110012	0000001100	0101011000	0000010000	1010001101	0000100013	1101102100	0000021000	2010112001
UNICOR	0000010700	0000000001	0000011100	0101010000	0000010000	1000001001	0000100002	0201102100	0000020000	1020100000
MACRUR	0000020703	0000100011	0000001010	0101020000	0000010000	1000011100	0000100003	1101102100	0000021000	2020200001
LOCHMA	0000000100	0000100011	0000001010	0101011000	0000010000	1010001111	0000000013	1101102100	0000021000	1010212001
HARPYI	0000027773	1003100002	0000012000	0101020000	0001010000	0000001000	0000000002	0202101100	0000020000	0010200000
STAURO	0000030777	1003100012	0010012000	0101020000	0000010000	1000000000	0000100001	0112101100	0000070000	0010200000
CNETHO	0000037777	1000000002	0010012100	0101020000	0000010000	1030000000	0000000000	0101102100	0000000010	0000200000
NYSTAL	1020000212	0002110011	0000001010	0101010000	0000020000	1200022000	1000000002	0101102100	0001040000	3111300010
SYMMER	0021020773	0000011011	0000001010	0101012000	0000010000	1000011000	0000000001	0101102100	0001010000	2111301000
DASYLO	1021000100	0000011011	0000001010	0101010000	0000020000	1000022000	1000000002	0101102100	0000040000	2111301000
HIPPIA	1021000100	0000011011	0000001010	0101012000	0000010000	1000022000	1000000001	0101101100	0001040000	3111301010
DIDUGU	1021000100	0000011011	0000001010	0101010000	0000010000	1000022000	0000000001	0101102100	0001070000	0011301000
REBESS	1032000100	0101000012	0000011010	1102000000	1000001000	1000020000	1000000001	0101100100	0000000000	3120000010
PHAECC	1032000100	0100000002	0000011010	1102000000	0000001010	1000000000	0000000001	0101100100	0000000000	0000000000
PHRYGA	1000000100	0100000002	0010110101	1102020100	10000001010	1020000000	1000000001	0101100100	0000000000	0010000000
ZUNACE	1000000100	0001000012	00000110101	1103020100	1000001010	1000020000	1000000001	0101100100	0000000000	1020000010
JOSIA	1000000100	0100000012	00000110102	1203000100	1000001010	1270000000	1000000001	0101100100	0000000000	1010700000
CYANOT	1000000100	0100000012	00000110102	1203020100	1000001010	1270000000	1000000001	0101100100	0000000000	1010700000
HEMICE	0000000000	0000100011	0000001010	0101010010	0010010000	1000012000	0000000000	0701111100	0000020000	3120100001
GARGET	1100000712	0000000000	1000010100	0101013000	0000001010	0100000000	0000010002	0101001110	0000020000	0010100000
SCRANC	1120000000	0000000000	1000011010	0101013000	0000001010	0000010000	0000100000	0101001010	0000020000	0020100000
CRINOD	0020000212	0002100011	0000001010	0100001000	0000020000	0100000000	0000000101	0101113102	0100050001	2010100011
CARGID	0000000210	0000000000	0000001010	0100001000	0000010000	0100000000	0000000000	0101111102	0100050001	2010100000
GOACAM	0110000010	0000000010	0001010100	0100011000	0010010000	0100000000	0000000000	0101011103	0000050000	0010100110
TARSOL	0000000212	0000100000	0000012100	0100010000	0000010000	0100000000	0001000101	0101113103	0000050001	2000100100
DUDUSA	0000010212	0000100000	0000012000	0100010000	0000010000	0100000000	0001000101	0101113103	0000050001	0000100100
DOA	0020010073	0000001002	0000010000	0100000000	0001000000	0001000000	0000010000	0000007000	0070010000	0010000000
OENOSA	0110020003	0000000012	0000000000	0010010000	0001200011	0000100000	0000000000	0000000110	0000010000	0010100000
DASYCH	0020037773	1003000102	0010070000	0010100000	0101200000	0000010300	0100000000	0000000000	0010020000	0000100000
LYMANT	0020037777	0003000102	0000010000	0010120000	0101200000	0000010300	0100000000	0000000000	0000020000	0000100000
HYPOPR	1000010000	0001000012	0000000110	2010100000	1000000000	1001120000	1000000000	0000000000	0000000000	0000000000
SPILLOS	0000010000	0000000000	0000000110	0010100001	0100200000	0001120000	1000000000	0000000000	0000001000	0000000000
NYCTEO	1001000000	0001000010	0000000100	2010110001	0000100000	0000000000	0000000002	0001010000	0070000000	0000100000
PERIDR	0000000000	0001000010	0000000100	0010110000	0000100100	0000000000	0000001000	0000000000	0000000000	0000000000
ACRONI	0000000000	0001000010	0000000100	2010100000	0000100000	0000000000	0000000000	0000000000	0000110000	0000000000
PANTHE	0000120000	0010000010	0000001000	0010110000	0100100000	0000100000	0000000000	0000000000	0000000000	0000000000
ALYPPIA	0100000000	0001000010	0000000100	0010110000	0000100100	0000000000	0000001000	0010100000	0010100000	0000000000
NOLA	1020000000	0001000012	0000000000	2010170001	0000200000	0000000000	0000000002	0001010070	0070000000	0000000000
DILLOBA	0000020073	0000000000	0000000000	0010110000	0000100101	0000000000	0000000000	0000001000	0000100000	0000000000

LARVAE	120	140	160
THAUME	?0011??000	0021100000	0000000000
TRAUMA	0001??0000	0021100000	0000000000
ANAPHE	0001??1000	0011100000	0000000000
EPICOM	0001??1000	0010100000	0000000000
CLOSTE	0001111100	0111010000	0000000000
PLATYC	1100111101	0110010000	0100000000
LIRIMI	0000110001	0110020000	0102010000
NOTODO	1110111011	0111020000	0000000000
ODONTO	1000111001	0110020000	0000000000
PHEOSI	1000111001	0110020000	0000000000
QUADRI	1110111111	0110020100	0000101100
LIPARO	5110111111	1110030100	0000111010
GLUPHI	1000111111	0110020000	0000100000
PTILOP	1000111101	0110020000	0000000010
CERURA	1000111011	0110020000	0000111000
FURCUL	1000111011	0110020000	0000111000
DATANA	2000111001	0111010000	0001000000
PHALER	2001111001	0111010000	0001000000
ANTHEU	1000111001	0111020000	0000000000
NADATA	1000111011	0110020000	0000000000
PERIDE	1000111001	0110020000	0000000010
ELLIDA	1000111101	0110020000	0000120000
SPATAL	1110111001	0110021000	0000011000
FENTON	1110111001	0110020000	0000011110
HETERO	1010111001	0110031000	0000010100
BEIDER	1000111001	0111021000	0000010100
UNICOR	1110111001	0110031000	0012010100
MACRUR	1010111001	0110031000	0000010100
LOCHMA	1110111001	0110030000	0000010000
HARPYI	1112??0011	0110021000	0012010000
STAURO	1112??0011	0111021000	0012010000
CNETHO	1110111011	1110031000	001204?000
NYSTAL	1110111011	1110030100	1000010002
SYMMER	1110111001	0110020100	0000010001
DASYLO	1110111001	0110020100	1000010002
HIPPIA	1110111001	0110020100	1000010001
DIDUGU	4110111001	0110021000	0000010001
ERBESS	3100111101	0100030100	1012010000
PHAECC	3100111101	0100030100	0002010000
PHRYGA	3000111101	0110030100	0002010000
ZUNACE	3000111111	0110020100	0002010000
JOSIA	3000111001	0110030100	0002010000
CYANOT	4001111001	0100020100	0002010000
HEMICE	1110111111	0110020000	1100000000
GARGET	1110110001	0100020000	0000101000
SCRANC	1110111001	0100020000	0010101000
CRINOD	0000111011	0100020000	0100020000
CARGID	0000111001	0101020010	0000020000
GOACAM	1002111001	0111020010	0000020000
TARSOL	1000111001	0110020000	0000021000
DUDUSA	1000111001	0110020000	0100001000
DOA	0000111000	0000011000	0000010000
OENOSA	0000?01000	0000010000	0003030000
DASYCH	0001??0000	0001000000	0000000000
LYMANT	0001??0001	0101000000	0000000000
HYPOPR	0000010000	0000000000	0000030000
SPILOS	0000000000	0000000000	0000030000
NYCTEO	0000011000	0000000000	0000000000
PERIDR	0000000000	0000000001	0000010000
ACRONI	000000?001	0000000000	0000000000
PANTHE	0001??0000	0000000000	0000000000
ALYPYA	0000000000	0000000001	0010010000
NOLA	0000000000	0100000000	0000000000
DILOBA	3000000000	0000000001	0000000000

APPENDIX III

Apomorphic character states for nodes of the cladogram in figures 99 and 100. Listed are character number (character state). Asterisks indicate that the state changes within the relevant clade.

Clade 1 (Trifid Noctuoidea): 7(3); 9(2); 19(0/1); 20(2); 43(1); 44(1/2); 77(1); 92(1); 106(1).

Clade 2 (Oenosandridae): 3(2); 49(1); 155(0); 158(2).

Clade 3 (Doidae + Notodontidae): 32(1); 33(0); 44(0); 104(1); 105(1).

Clade 4 (Doidae): 3(1); 25(1); 85(1); 130(2); 157(1); 158(1).

Clade 5 (Notodontidae): 26(1); 34(1); 36(2); 50(1); 54(1); 76(1); 112(1); 139(2); 145(1); 154(1); 158(0).

Clade 6 (Thaumetopoeinae): 3(3); 7(3); 8(1); 9(0); 11(1); 17(1); 27(2); 49(1); 114(1); 115(0); 142(1); 156(0/1).

Clade 7: 2(1); 113(2); 114(1); 157(1).

Clade 8 (Notodontidae excl. Thaumetopoeinae): 28(1); 43(0); 73(1); 74(1); 103(1); 111(1); 113(0/1).

Clade 9 (Pygaerinae): 3(2); 23(1); 90(1); 103(1); 107(1); 113(1); 130(1); 162(1).

Clade 10 (Notodontidae excl. Thaumetopoeinae, Pygaerinae): 20(1); 36(1); 56(1); 85(2); 94(2); 109(1); 115(2).

Clade 11 (*Lirimiris*): 3(1); 7(0); 15(1); 16(1); 23(1); 50(0); 106(0); 123(2); 125(1).

Clade 12 (Notodontidae excl. Thaumetopoeinae, Pygaerinae, *Lirimiris*): 100(1); 131(1); 139(0); 166(1); 167(1); 169(1).

Clade 13 (Notodontinae): 3(2); 6(0/1); 9(1); 23(0/1); 28(0); 43(0/1); 87(0/1); 88(0/1); 150(1).

Clade 14 ("Notodontini"): 6(0/1); 7(1); 38(1); 43(1); 55(0/1); 87(1); 88(0/1); 100 (1); 162(1).

Clade 15: 80(1); 100(2); 129(1); 173(1).

Clade 16 ("Dicranurini"): 6(1); 7(3); 8(0/1); 11(1); 14(3); 22(0/1); 23(1); 27(2); 36(2); 43(0/1); 58(0/1); 62(1); 87(0/1); 88(0/1); 107(1).

Clade 17: 57(0/1); 76(1); 86(0/2); 88(0); 89(0); 95(0); 109(1); 125(1); 143(3); 148(2); 149(0/2); 150(1); 151(3).

Clade 18: 8(1); 20(2); 22(0); 70(1); 126(0/1); 127(1); 133(1); 135(0/1); 167(1/2); 169(1/2); 170(1/2); 174(0/1).

Clade 19: 3(3); 57(0); 74(2); 93(0); 95(1); 102(1); 103(1); 118(1).

Clade 20: 44(1); 57(1); 59(0); 86(2); 108(0); 126(1); 167(2); 169(2); 170(2); 174(1).

Clade 21 (Phalerinae + Dudusinae + Diopitinae + Nystaleinae + Heterocampinae): 7(0); 9(0); 71(1).

Clade 22 (Phalerinae—broad sense): 3(1); 55(0/1/2); 90(2); 98(1).

Clade 23: 4(0/1); 15(0/1); 56(1); 70(1); 87(1); 93(2); 100(1).

Clade 24 ("Phalerini"): 50(2); 80(1).

Clade 25: 14(2); 19(1); 71(2); 101(2); 116(1); 124(1); 140(2); 171(1).

Clade 26 (Dudusinae + *Hemiceras* + Diopitinae + Nystaleinae + Heterocampinae): 3(0); 101(0/1); 167(2).

Clade 27 (Dudusinae—broad sense): 2(0/1); 6(0/1); 20(0); 50(0); 51(0/1); 56(0); 74(0/1); 94(1); 101(0/1); 102(0/1); 112(0/1); 154(0).

Clade 28 (Scranciini): 1(1); 2(1); 6(0/1); 21(1); 25(1); 47(1); 51(0/1); 74(0); 78(1); 101(1); 102(1); 124(1); 126(1); 159(1); 160(1); 166(2); 168(2); 169(2).

Clade 29 (Dudusini): 2(0/1); 6(1); 34(0); 51(1); 74(0/1); 75(1); 85(5); 101(0); 102(0); 113(0/1); 118(1); 125(2); 133(1); 146(1).

Clade 30: 2(0); 5(2); 75(1); 80(2/3); 82(0/1); 90(1); 91(2); 101(0/1).

Clade 31: 7(2); 15(1); 68(1); 70(1); 77(3); 114(0); 122(0/1).

Clade 32: 27(2); 64(1); 80(3); 82(0); 93(0); 98(1); 101(1); 113(1); 119(0); 127(1); 134(0); 171(0/1).

Clade 33 (*Hemiceras* + Diopitinae + Nystaleinae + Heterocampinae): 15(1); 19(1); 99(0/1); 102(1); 150(1).

Clade 34 (*Hemiceras*): 38(1); 56(2); 75(1); 90(3); 92(2); 94(1); 107(1); 131(2).

Clade 35 (Diopitinae + Nystaleinae + Heterocampinae): 5(1); 69(1); 125(1).

Clade 36 (Heterocampinae—broad sense): 3(1); 90(0/1/2); 99(1); 116(0/1); 134(1); 135(1); 150(0/1/3).

Clade 37: 37(0/1); 128(1); 137(1); 141(1); 143(3); 148(1); 151(0).

Clade 38 (Heterocampini + Stauiropini; excl. *Fentonia* and *Spatialia*): 76(2); 115(3); 116(1); 127(1); 132(1); 136(1); 140(1); 142(3); 147(1); 150(0).

Clade 39 ("Stauiropini"): 15(0/1); 19(0); 27(1); 69(1/2); 99(0); 122(1); 123(2); 132(1); 137(1); 162(1); 165(1).

Clade 40: 3(3); 7(0/3); 8(1); 20(2); 23(0/1); 27(2); 36(2); 57(0/1); 91(0); 109(1); 128(0); 140(3); 142(1); 143(2); 145(0/1); 152(0/1); 166(1); 167(3); 169(2); 171(0/1).

Clade 41: 14(3); 15(1); 28(0); 74(2); 77(1); 104(2); 116(2); 170(1/2).

Clade 42 ("Heterocampini"): 52(0/1); 57(1); 68(0/1); 69(3); 70(0/1); 86(0/1); 101(0/1); 132(1).

Clade 43: 3(2); 7(3); 93(2); 102(0); 149(1).
Clade 44: 37(1); 53(1); 60(1); 69(1); 71(1); 87(1); 96(1); 97(2); 143(2).
Clade 45 (Dioptinae + Nystaleinae): 1(1); 76(0/1/2); 117(1); 143(1); 152(1).
Clade 46 (Nystaleinae): 9(2); 10(1); 16(1); 55(2); 56(1/2); 76(2); 83(1); 91(0/1); 93(1); 94(3); 96(1); 129(1); 162(1).
Clade 47: 57(2); 61(1); 86(4); 91(3); 92(1); 99(0/1); 121(1).
Clade 48: 46(1); 70(2); 130(2).

Clade 49 (Dioptinae): 12(1); 15(0); 20(2); 25(1); 31(1); 34(2); 36(0/1/2); 40(0/1); 45(0); 46(1); 48(0/1); 56(0); 60(0/1); 76(0); 85(0); 94(0); 100(3); 107(1); 115(2/3); 123(2); 130(1); 142(4); 145(0); 157(1).
Clade 50: 9(3); 10(2); 36(0); 113(0); 116(3); 167(2); 171(1); 172(1).
Clade 51: 30(1); 36(2); 38(1); 41(1); 49(1); 61(1); 102(0).
Clade 52: 34(3); 91(1).
Clade 53: 30(2); 32(2); 52(2); 108(0).

APPENDIX IV

Number of steps, CI, and RI for each character used in the analysis. The eight cladograms found (consensus shown in figs. 99 and 100) were 853 steps long, each with a CI of 0.30 and an RI of 0.66.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
5	5	16	2	3	5	11	5	13	4	6	2	4	13	8	3	2	1	15	14	1	3	8	3	3	3	12	8	1
20	20	18	50	66	20	27	20	23	50	33	50	25	23	12	33	50	100	6	14	100	33	12	33	33	33	16	12	100
71	33	64	0	93	60	57	66	58	60	60	75	0	54	63	66	75	100	53	67	100	0	41	0	75	77	65	69	100
30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
2	3	2	1	4	1	15	7	2	4	2	3	3	5	7	6	4	1	3	3	3	8	6	6	2	2	14	13	1
100	66	100	100	75	100	13	42	50	25	50	33	33	20	14	33	50	100	33	33	33	25	33	50	50	50	14	23	100
100	87	100	100	95	100	53	33	75	40	50	60	33	0	53	71	91	100	50	60	60	75	55	25	50	88	33	68	100
59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
4	2	4	1	3	1	5	4	1	1	3	14	5	9	1	5	3	5	9	5	3	6	1	2	2	2	3	19	3
25	50	25	100	33	100	20	25	100	100	33	21	40	22	100	40	33	20	33	40	33	50	100	50	50	50	33	26	33
0	50	66	100	60	100	0	0	100	100	33	65	50	74	100	81	89	63	77	76	33	50	100	0	0	66	0	56	71
88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116
3	5	1	18	4	16	1	15	2	6	4	8	7	9	7	6	8	1	3	4	7	8	3	4	3	7	10	1	12
66	20	100	16	25	12	100	20	50	50	25	12	28	55	14	16	25	100	33	25	14	12	33	25	33	28	10	100	25
66	0	100	31	40	54	100	67	66	50	25	41	66	84	68	73	45	100	66	70	40	46	86	0	85	75	30	100	67
117	118	119	120	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145
4	2	2	2	3	4	4	5	3	12	5	4	5	2	4	5	4	2	5	2	2	6	0	13	5	1	10	2	2
25	50	50	50	33	25	25	60	33	33	20	25	20	100	75	40	25	50	20	50	50	16	100	23	40	100	50	50	50
62	91	50	50	50	0	50	81	71	75	55	40	20	100	88	78	62	50	69	90	85	16	100	52	66	100	78	88	0
146	147	148	149	150	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174
2	2	5	5	5	9	2	1	1	2	4	3	5	3	3	2	6	9	1	2	1	10	4	9	9	6	1	2	2
50	50	40	40	20	33	50	100	100	50	25	66	20	100	33	50	16	11	100	50	100	40	50	22	22	16	100	50	50
94	80	70	25	33	68	0	100	100	91	25	50	60	100	33	50	0	46	100	75	100	80	94	53	74	28	100	50	50

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