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PARALLELISMS IN THE EVOLUTION OF THE SATURNIID MOTHS

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Parallelism or convergence in evolution is so well known that any biologist can list examples of organisms which look alike or have certain similar structures but nonetheless are only distantly related. The best known instances of convergence, such as the similarity of body form of whales and fish, or of foreleg structure of mantids (Orthoptera) and Mantispids (Neuroptera), involve adaptations of very dissimilar animals to similar modes of life. The examples of parallelism found in the Saturniidae are of a different sort, involving independent acquisition of similar characters by closely related moths. The Saturniidae is a particularly favorable group for this study because the survival of numerous annectent forms has made possible a rather clear understanding of the phylogeny of the group. Without this knowledge of the phylogeny, parallelisms such as those discussed below would not be recognizable as such. The purpose of this paper, then, is to list similar characteristics which have arisen repeatedly in the course of the evolution of these moths, and to consider the reasons for this repetition.

The present analysis is based upon a detailed morphological study of the genera of the saturnioid moths of the western hemisphere, and a less thorough study of those of the eastern hemisphere. The full results of this investigation will be published elsewhere. Two South American genera, each known from a single species, are omitted from consideration here because insufficient material has been available to me. Their relationships are roughly known, however, and their inclusion in the study would not materially affect the conclusions.

In the western hemisphere there are 93

genera and subgenera. The number of species is doubtful but there appear to be at least 700 and perhaps 1000 or more good species, many of them with numerous recognizable subspecies.

PHYLOGENY AND DISTRIBUTION

On the basis of a comparative morphological study, in which some fifty characters received special analysis, a phylogenetic tree for the Saturnioid moths was devised. It is believed that this tree (fig. 1) indicates the relationships with reasonable accuracy. Since there are no known saturniid fossils of any significance, the construction of such a tree is possible only because of the existence of unspecialized or primitive genera or species in which for some reason evolution of the principal characters ceased. Such forms provide the intermediate or annectent links necessary to establish the relationships of other genera. If certain specialized characters are ignored, these primitive living groups closely resemble the putative ancestral forms. Thus the trees used in this paper are actually only schemes of relationships based on living forms, not phylogenies in time. It is impracticable to discuss in detail here the characters used in establishing the phylogeny; in any case, the details are of no concern to evolutionists generally. They will be presented, however, in a larger paper to be published elsewhere.

The closest relatives of the Saturniidae are the small South American families Oxytenidae and Cercophanidae. These moths lack many of the peculiar features of the Saturniidae, to which family belong all of the other groups shown in the phylogenetic tree. The Saturniidae have been

divided into seven subfamilies as can be seen in figure 1.

Although all of these subfamilies contain primitive genera, the Rhescyntinae as a whole is the most primitive as shown

by several characters shared with the family Oxytenidae. For example, the proboscis bears numerous carinate papillae in the Oxytenidae. Such papillae are present also in many Rhescyntinae, but are want-

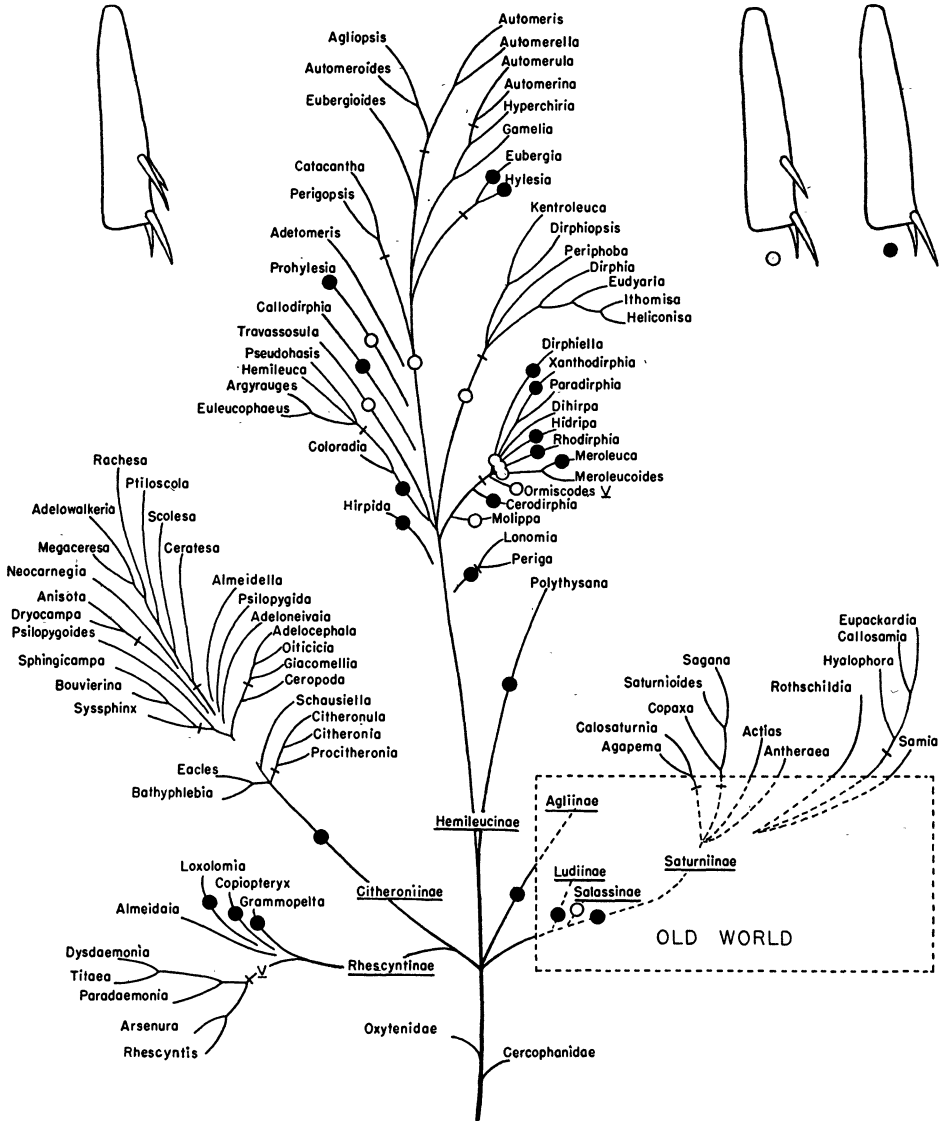


FIG. 1. Phylogenetic tree of the Saturniidae of the New World. The number of subapical hind tibial spurs is primitively two. In forms located beyond a circle there is but one, in forms beyond a black disk there are none. The letter "v" means variable from none to two. Note that *Adetomeris* has two.

A short cross line indicates that the names beyond such a line belong to a single genus and are to be considered as subgenera. Other symbols, if at the end of a line, show that only some species of the genus or subgenus have the character indicated, while if not at the end of a line, they indicate that all forms beyond the symbol have the character.

TABLE 1. *Some of the characteristics of the subfamilies of Saturniidae*

	Rhescyntinae	Citheroniinae	Agliinae	Hemileucinae	Ludiinae	Salassinae	Saturniinae
Frons convex at sides	-	+	-	-	-	-	±
Frontal protuberance present	+	+	-	+	-	+	-
Antennae, if quadripectinate, with apical rami adjacent to basal rami of following segment	+	+	+	+	±	+	-
Antennal cones multiple	±	-	-	-	±	0	+
Pilifers with bristles	+	-	-	-	-	-	-
Anepisternum large	+	+	+	-	+	+	-
Vein M ₂ arising in front of middle of apex of cell	-	±	+	+	-	+	+
Larvae with large thoracic horns in early stages	+	+	+	-	-	-	-
Mature larvae with large thoracic horns	-	+	-	-	-	-	-

+ Agreeing with statement at left.

- Not agreeing with statement at left.

± Variable, agreeing or not.

0 Structure absent.

In a few cases where a few specialized members of a subfamily have lost a character, this is not indicated in the table.

ing in all other Saturniidae. Numerous other characters indicate the same relationship. The Rhescyntinae are large, broad-winged moths, as are at least the more primitive members of most of the other subfamilies.

It is a relatively minor step from the Rhescyntinae to the primitive members of the Citheroniinae, such as *Bathyphlebia*. The principal characters by which *Bathyphlebia* differs from the more primitive *Rhescyntinae* are the convex lateral margins of the frons, the absence of bristles on the pilifers, the shorter tibial spurs, the absence of the subapical spurs of the posterior tibiae and the absence of tarsal spines. From the large broad winged *Bathyphlebia* the principal direction of evolution in the Citheroniinae has been reduction in size, especially in wing size, so that the more characteristic members of the subfamily are small with the thorax very robust and the wings or at least the forewings slender and powerful so that the shape of the insect as a whole is similar to that of certain Sphingidae.

The remaining subfamilies of the Saturniidae are probably not quite so closely

related to the Rhescyntinae as is the Citheroniinae, although in the Agliinae the larval characters are very similar to those of the Rhescyntinae. The adults of the Old World Agliinae, however, are similar to those of the New World Hemileucinae. The subfamily Hemileucinae is the largest of the American groups, and it contains a number of forms (e.g. *Lonomia*) whose relationships are not evident as shown by the broken bases of the lines of the accompanying tree. The relationships of most members of the groups, however, are evident.

The genus *Polythysana* is so different from other Hemileucinae that it has been placed in a tribe by itself and perhaps should be placed in a separate subfamily. While most of its characteristics considered individually can be matched within the rest of the Hemileucinae, the combination of characters is suggestive of certain Saturniinae, except for the wing venation which is not at all like that of the Saturniinae. Probably *Polythysana*, which occurs in Chile, is a relict type, like *Agliia* (Agliinae) and *Salassa* (Salassinae).

The Ludiinae, Salassinae, and Saturni-

inae are rather closely related. In spite of certain specialized characters, most features of the Ludiinae and Salassinae are more primitive than those of the Saturniinae.

Table 1 indicates the more outstanding characteristics of the various subfamilies. It is hoped that, studied in connection with figure 1, this table will give the reader an idea of some of the characteristics regarded as of phylogenetic significance and of the principal lines of evolution in the Saturniidae.

The distributional pattern shown by the various groups of Saturniids is extremely interesting. The Oxytenidae and Cercophanidae are entirely neotropical, all but one genus of the latter family being Chilean. Although the family Saturniidae is almost world-wide except for far northern and far southern regions, its most primitive groups are neotropical. The Rhescyntinae is entirely neotropical. The Citheroniinae is principally neotropical, although a few genera and species extend well north into the Nearctic region. The same is true of the Hemileucinae, although there are more nearctic genera and species than in the Citheroniinae. This great diversity of entirely American groups in the Saturniidae, together with the occurrence in the neotropics of the only families which appear to be very closely related to Saturniidae, suggests that the group as a whole arose in the Western Hemisphere and no doubt in the American tropics.

There are, however, very numerous genera and species of Saturniidae in the Old World, particularly in the Old World tropics. The bulk of these belong to the subfamily Saturniinae which is more richly represented in the Old World than in the New World. The small subfamily Ludiinae, however, is confined to Africa, and the Salassinae to Asia. If one ignores some of the highly specialized features of the Ludiinae such as the reduced size and the reduced labial palpi, the characters of this subfamily might well be regarded as ancestral to those of the Saturniinae.

The Salassinae also exhibits primitive characters, such as the frontal protuberance. It therefore seems not unlikely that a common ancestor of the Ludiinae, Salassinae, and Saturniinae reached the Old World not long after the Saturniids became widespread in the New World and that in the Old World it gave rise to the Saturniinae as well as to the modern Ludiinae and the relict Salassinae. The greater part of the evolutionary history of the Saturniinae seems to have taken place in the Old World and, because of lack of material, is not indicated on the accompanying phylogenetic tree. The Saturniinae became wide-spread and eventually, on several different occasions as indicated in figure 1, migrated back into the Western Hemisphere. New World genera of this subfamily are the scattered representatives which were able to migrate from Asia to North America. There are, in fact, three genera of Saturniinae which occur in both hemispheres. All are far better represented in Asia than in America and they may be regarded as having arisen in the Old World and spread to the New World relatively recently. The New World Saturniinae are North American except for *Copaxa* and *Rothschildia* which are well represented in the Neotropics.

The existence of several relict groups has already been indicated. The most outstanding of these are *Polythysana* with four species from Chile (Hemileucinae?), *Aglia* with a single Palearctic species (Aglinae), and *Salassa* with a few species from southern Asia (Salassinae). Each is an exceedingly isolated group. There is a good possibility that *Aglia* and *Polythysana* are related to one another more closely than either is to any other group, in spite of the fact that one is Eurasian, the other Chilean.

The distribution of a group of the more primitive saturniid subfamilies (for example, the Rhescyntinae, Agliinae, Ludiinae, Salassinae, and *Polythysana*) taken together is very discontinuous. The resulting map would be similar to some of

those given by Ander (1942) in his excellent study of the modern distribution of various insect groups represented in the Baltic amber. It seems worth suggesting, therefore, that the saturniids probably arose sometime in the early tertiary or before and may well have been a part of the early tertiary fauna, samples of which are preserved in the Baltic amber.

An interesting feature of distribution of the Saturniidae is their almost complete absence from the West Indies, although the group is extremely well represented around the coasts of the Caribbean and there are a number of species in the southern United States. It is evident that these American forms are poor colonizers of islands. Perhaps this is because the females are relatively sluggish and do not fly much, in spite of their large wings, for there are certainly suitable host plants and climatic conditions in the West Indies. In view of this situation it is interesting that in the Old World the Saturniinae have spread through the East Indies to New Guinea and to Australia.

REDUCTION OR LOSS OF STRUCTURES

Independent variations. The characters discussed below are only a few of the better examples of repeated reduction or loss of structures in the Saturniidae. Many others might easily be cited. In each instance the character has been reduced or lost independently, so far as can be learned, from other characters.

In most moths, including the Oxytenidae, the posterior tibiae bear a pair of subapical spurs in addition to the apical pair. The subapical pair is retained in many members of the large genus *Rhescyntis* (Rhescyntinae) and is retained, or perhaps regained, in *Adetomeris* and some *Ormiscodes*, members of the subfamily Hemileucinae. In all other saturniids, as shown in figure 1, one or both of the subapical spurs are wanting. Both are absent in all members of some of the large groups such as the Citheroniinae and Saturniinae. In the Hemileucinae one is absent in most

groups and all stages in the reduction of the remaining one can be found in several genera. As shown in figure 1, the loss of this remaining subapical spur has occurred independently 14 times in the Hemileucinae. Allowing for some misinterpretations of phylogeny, the spur must have been lost at least 10 times.

The epiphyses, or anterior tibial spurs, are frequently lost in the Saturniidae. They are more stable in males than in females, having disappeared in males only four times as shown in figure 2. All groups lacking epiphyses in males also lack them in females. In addition, they are wanting in females of 12 other groups. Assuming the possibility of errors in the phylogenetic tree of the subgenera of *Ormiscodes*, this means that the epiphyses of the female were independently lost at least 10 times during the evolution of the Saturniidae.

The labial palpi in the Saturniidae vary from large three-segmented structures projecting far in front of the head, as in most Lepidoptera, to small one-segmented globules, which may become fused together. The latter condition occurs twice in American Saturniidae, once in *Hemileuca* (Hemileucinae) and once in *Saturnia* (Saturniinae) (shown in figure 3 as *Calosaturnia* and *Agapema*, the American subgenera of *Saturnia*). In the phylogenetic tree (fig. 3) labial palpi are marked as "reduced" in groups in which they extend but little beyond the clypeus and are one- or incompletely two-segmented (feebly three-segmented in *Psilopygoides*). This degree of reduction was reached eleven times according to the phylogenetic tree. If, as seems quite possible, the "Old World" portion of the tree is inaccurate in detail, there nonetheless must have been such reduction in at least eight different groups.

In most groups of Saturniidae the male genital harpes are freely articulated to the ninth abdominal sternum. In the Hemileucinae, however, there is a tendency for the harpes to lose the articulation and become fused to this sternum; they may be

partially fused as in *Automeris* and its allies or completely fused as in *Dirphia* and *Hemileuca*. Some degree of fusion has arisen independently in seven different groups of the Hemileucinae, as shown in figure 3.

The occurrence of parallel evolution in genital structures is noteworthy since they

are hidden from the outside and hence presumably relatively little affected by direct selection from the outside environment.

Correlated variations. The characters discussed below involve structures whose reduction or loss is correlated with changes in other structures.

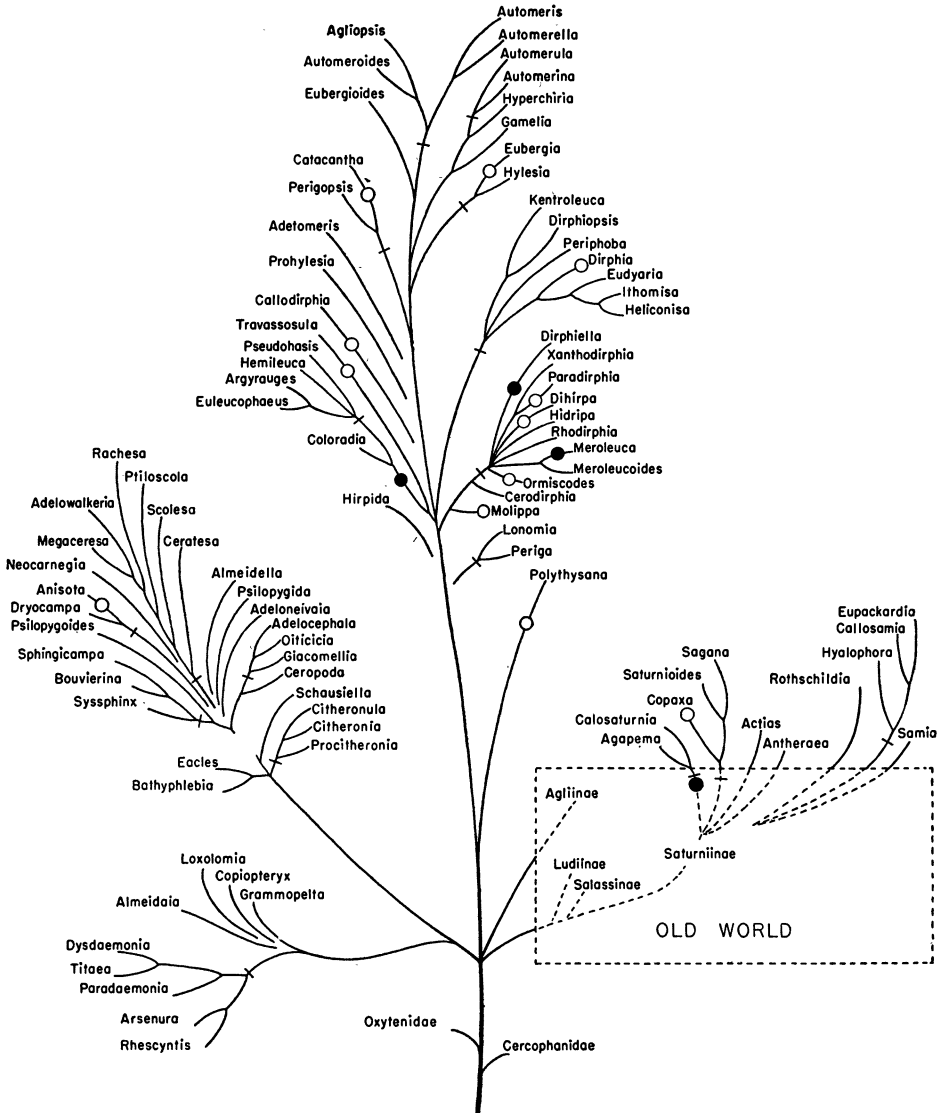


FIG. 2. Phylogenetic tree of the Saturniidae of the New World. Epiphyses are primitively present in both sexes. They are absent in the female in groups marked with a circle, and are absent in both sexes in groups marked with a black disk. For additional explanation see figure 1.

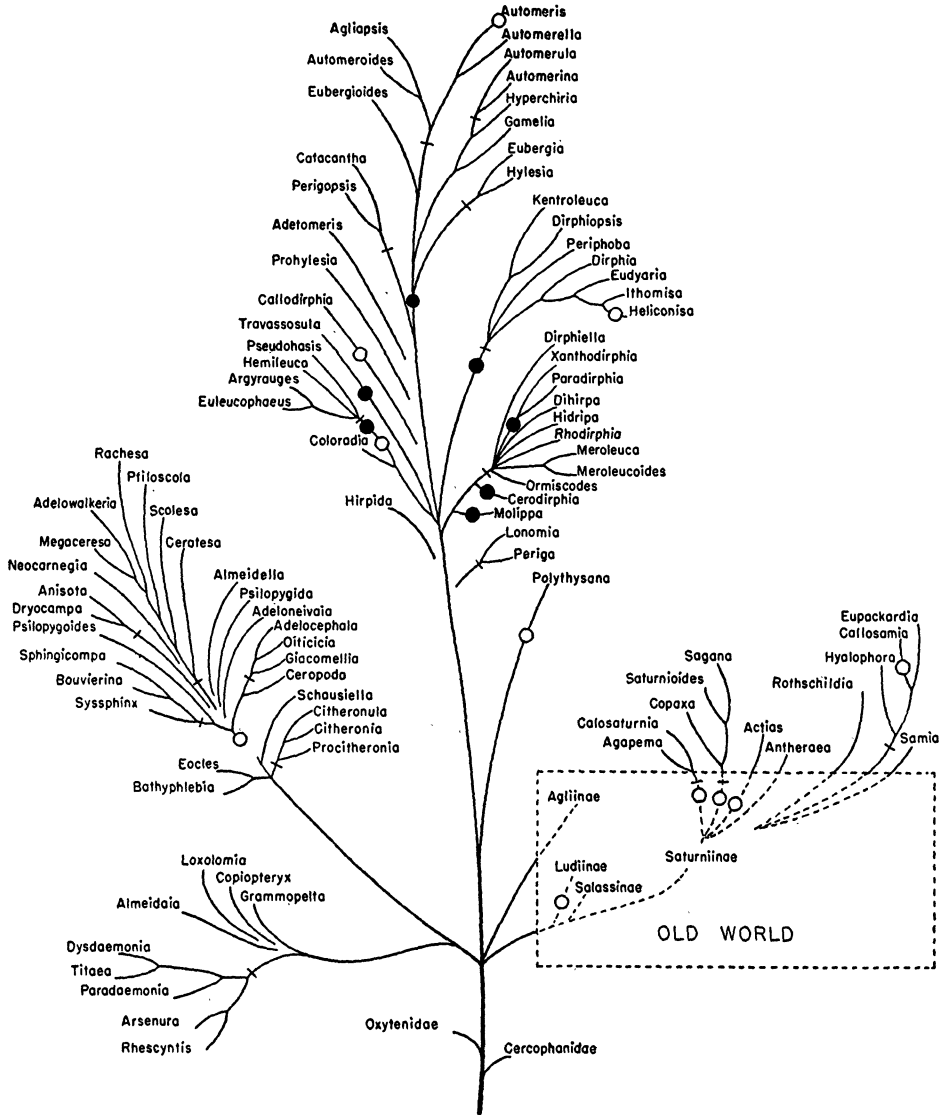


FIG. 3. Phylogenetic tree of the Saturniidae of the New World. The labial palpi are primitively long. They are reduced in forms marked with a circle. The male genital harpes are primitively freely articulated to the ninth segment. They are fused to it in forms marked with a black disk. For additional explanation see figure 1.

In the more primitive Saturniidae the antennae of the male are quadripectinate; that is, each segment bears four projecting processes or rami, a basal pair and an apical pair. In the Hemileucinae there are a number of groups in which the apical rami are reduced or lost. In some groups, especially in certain subgenera of *Dirphia*,

every stage in reduction can be observed in different species. The apical rami are lost, that is, the antennae become bipectinate, eight times independently in the Hemileucinae, as shown in figure 4.

Curiously enough, the reduction in the apical rami is correlated with certain characteristics of the basal rami. In forms

with quadripectinate antennae the rami are relatively short and straight (fig. 5) and the setae of the distal rami are directed basad while those of the basal rami are directed distad. When the antennae are bipectinate, however, the rami (basal) are long and strongly curved downward (fig. 5) and their setae are directed downward. When the distal rami are represented by short stubs, an intermediate condition also prevails as to the length

and curvature of the basal rami and the direction taken by their setae.

The eyes of saturniids are large in relation to the head, but their size is variable. As a measure of the eye size, the relation between the length of an eye and the length of the shortest line that can be drawn between the eyes has been used. If the distance between the eyes is one-fifth of the length of an eye, as in some of the Citheroniinae, the eyes are considered very large, while if it is one and one-half times the length of an eye, the eyes are very small. In preparing figure 6 the eyes were considered small if the distance between them were one half the length of an eye or more. It will be seen that this degree of reduction in eye size was achieved 18 times according to figure 6. Even if several of these apparent reductions result from phylogenetic misinterpretations, such reduction must have occurred at least 14 times.

Small eye size is usually correlated with changes in other structures of the head capsule. For example, the ordinarily very small distance between the latero-frontal sutures and the eyes is greatly increased as the eyes are reduced. Moreover, the proboscidal fossa and the frontal protuberance are reduced in all forms with small eyes and in but few others. It is as if the entire head capsule were less fully developed than in ordinary saturniids. Perhaps this is the effect of a group of genes which governs the rate of growth of the head.

Correlated characters of this sort may be very deceptive to the systematist who ordinarily works on the principle that organisms differing by several characters are less closely related than those differing in but one discernible character. It is obvious, however, that the head characters (likewise the antennal characters) described above should be given the weight of but one character even though several differences are involved, for these differences are consistently correlated and behave as a single character.

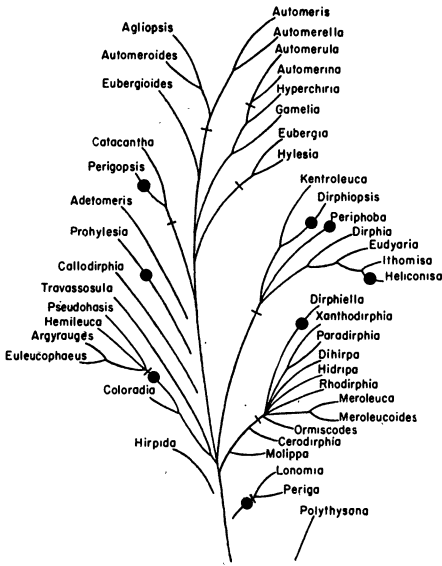


FIG. 4. Phylogenetic tree of the Hemileucinae. The antennae of the male are primitively quadripectinate. In forms marked with a disk they are bipectinate. For additional explanation see figure 1.

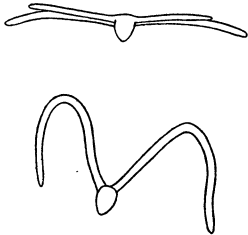


FIG. 5. Above: Apical view of an isolated segment of the male antenna of *Automeris*, a form with quadripectinate antennae. Below: Apical view of isolated segment of male antenna of *Hemileuca*, a form with bipectinate antennae.

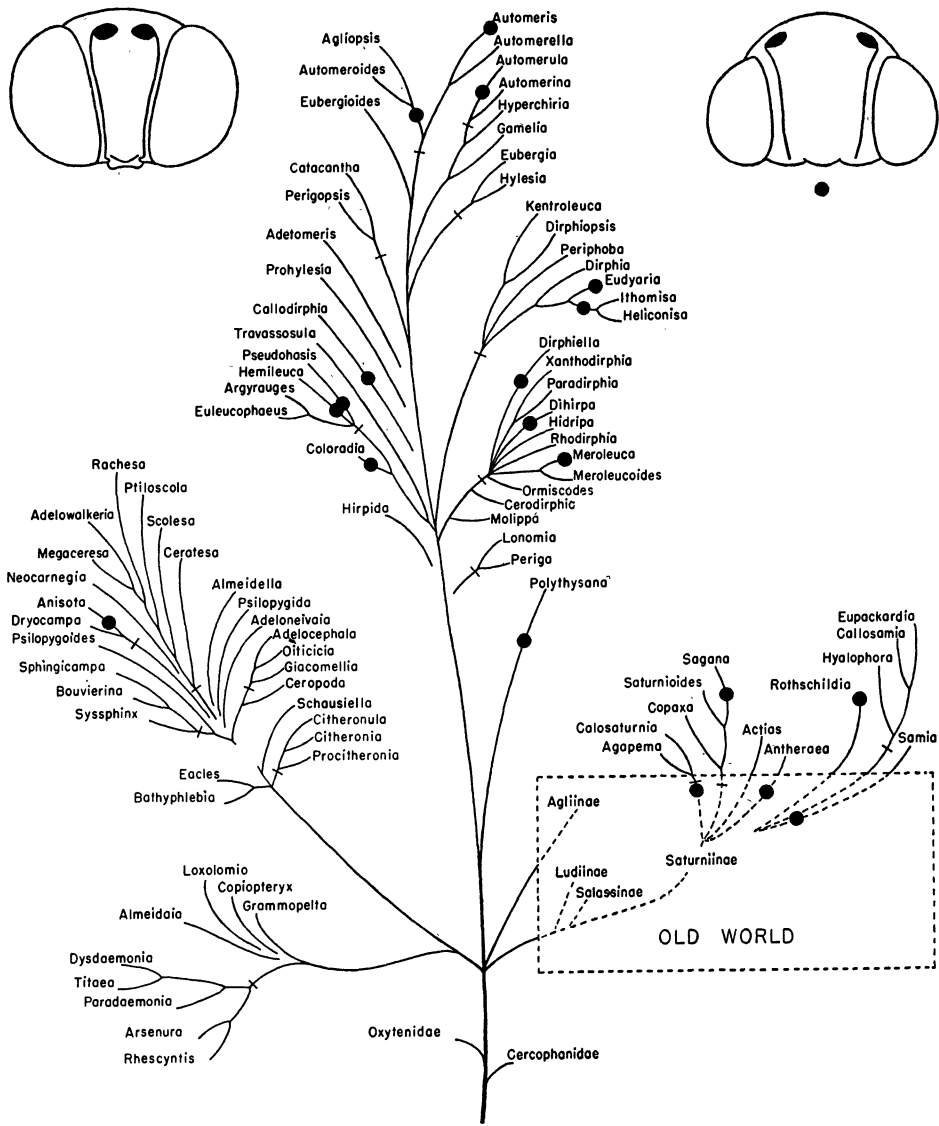


FIG. 6. Phylogenetic tree of the Saturniidae of the New World. The eyes are primitively large. In forms marked with a black disk the eyes are reduced so that the distance between them is one-half the length of an eye or more. For additional explanation see figure 1.

INDEPENDENT ACQUISITION OF A STRUCTURE

The examples of parallel evolution in the Saturniidae described above all involve reduction or loss of certain structures. However, the following example involves the acquisition of a structure found neither in the Oxytenidae and Cercophanidae

nor in the more primitive Saturniidae, such as the Rhescyntinae. In these groups the front tibiae are approximately as long as the tarsi and are unarmed (fig. 7). However, as shown in figure 8, there are scattered groups, nine in all, in the Citheroniinae and Hemileucinae in which each front tibia bears a horny spine arising from its outer apical angle (fig. 7).

Some of these groups also have a spine arising from the inner apical angle and even from the apex of the middle tibia. In every case, tibiae bearing such spines are markedly shorter than unarmed tibiae and shorter than the tarsi. Similarly short spined tibiae are found in some Old World Saturniinae.

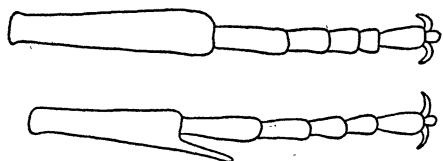


FIG. 7. Above: Normal fore tibia and tarsus. Below: Fore tibia and tarsus of a form with anterior tibial spine.

RELATIVE FREQUENCY OF LOSS AND GAIN OF STRUCTURES

Although the preceding parts of this paper give examples of the loss and gain of structures, they do not give any numerical information on the frequency of loss of old structures or of acquisition of new ones.

In a tabulation of 46 evolutionary trends (table 2), each of which can be observed in one or more parts of the phylogenetic tree of the Saturniidae, it can be noted that there are nearly 3.5 times as many trends toward reduction as toward increase in size of a structure and nearly 10 times as many trends toward reduction as acquisitions of new structures. Many of these trends occur as parallelisms in different groups of the Saturniids, but each is counted but once for the upper row of figures in table 2.

The lower row of figures in table 2 indicates the number of times that such

trends have occurred in the Saturniidae of the Western Hemisphere. The differences between the lower numbers and the upper are an indication of the frequency of parallelisms. From the lower figures, it will be seen that trends toward reduction occurred over 5.4 times as frequently as trends toward increase in size of a structure. Trends toward reduction occurred over 8.2 times as frequently as acquisition of new structures. The figure 147, for the number of times which trends toward reduction or loss have occurred, might have been considerably larger. This is because some judgment is involved in determining when a structure is "reduced." For example, labial palpi range from rather long, 3-segmented structures to minute unsegmented spherical bodies hidden under the vestiture. For purposes of this count they were considered reduced when they were 2-segmented but there are some forms with short 3-segmented palpi which might well have been called reduced.

Several examples of reduction or loss of structures have already been given. An example of the increase in size of a pre-existing structure may be seen in the changes in the frontal protuberance. In primitive groups this structure is present as a conspicuous transverse ridge. In scattered groups it becomes a strong snout, a trend recorded in the second column of table 2. Incidentally in other groups it may be reduced or absent (e.g. subfamily Saturniinae) so that the same structure is involved in a trend counted in the first column of table 2.

Under acquisition of new structures are included the tibial spines mentioned in the preceding section of this paper. These

TABLE 2. *Frequency of forty-six different evolutionary trends in the Saturniidae*

	Reduction or loss of a structure	Increase in size of a pre-existing structure	Acquisition of new structure	Not classifiable
Number of trends	29	9	3	5
Number of times trends have occurred	147	27	18	25

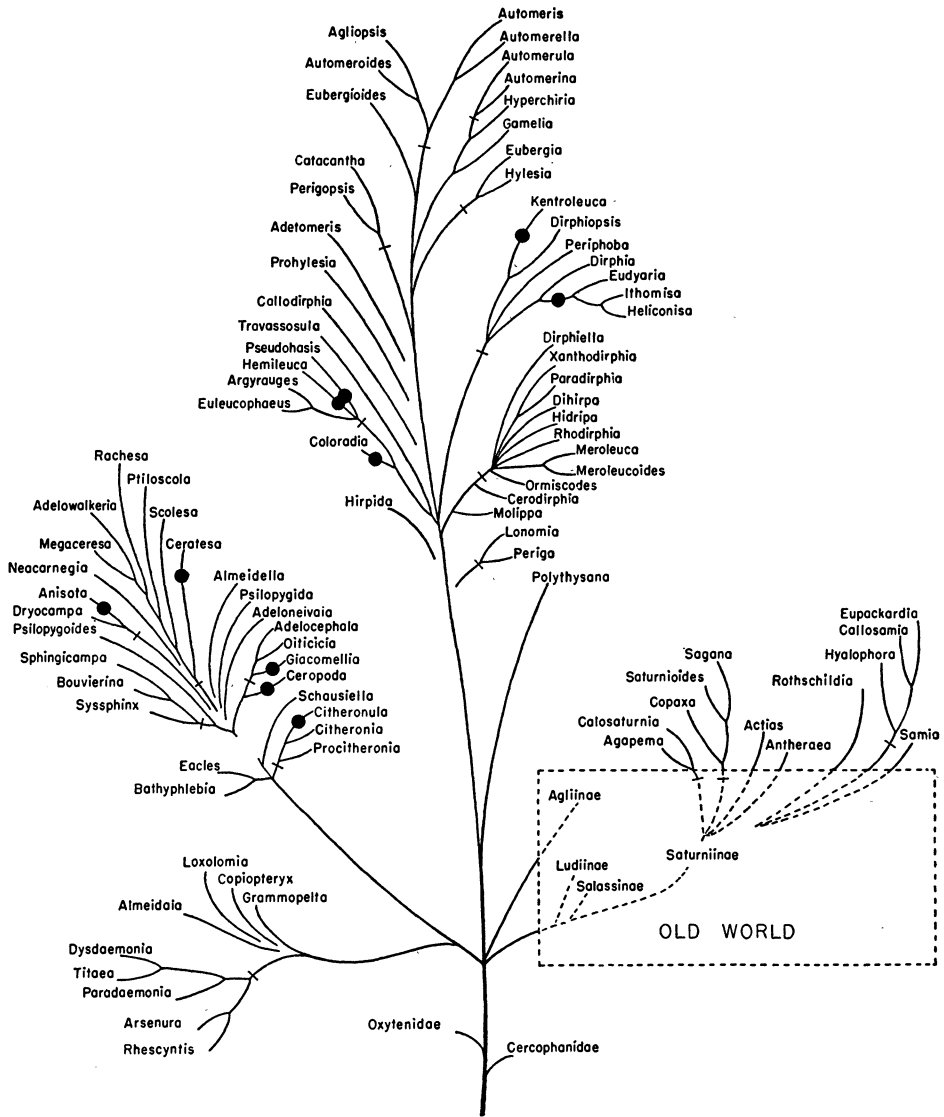


FIG. 8. Phylogenetic tree of the Saturniidae of the New World. The tibiae primitively lack spines. In forms marked by a disk the front tibiae bear at least one strong apical spine.

might have been interpreted as more than one trend, since inner apical spines are not always present, and since the middle tibiae as well as the front ones sometimes have spines. Another structure which seems to be newly acquired is the multiple antennal cone. Apparently each of the distal antennal segments bears, primitively, a single sharp conical projection on its under surface near the apex. In certain

groups, instead of a single projection, there is a broad lobe bearing a group of small points. In such groups the antennal cones are termed "multiple." Another minor new structure is a sharp ridge or carina along the under surface of the antenna. This ridge is often produced at the apex of each segment so that simple antennal cones extend nearly to the base of each antenna.

Under "not classifiable" in table 2 are included such trends as that from a large to a small anepisternum. At first sight this would seem to be a reduction, but actually it is merely a change in the course of the anepisternal suture, for as the anepisternum is reduced in size the kat-episternum is correspondingly enlarged. In the same category falls the change from nocturnal to diurnal habits. This involves not only the gain of diurnal flight habits, but also the loss of nocturnal ones.

DISCUSSION

The potentiality for similar changes, resulting in parallel characters, no doubt results from the fact that related animals have homologous chromosomes and genes (see Sturtevant and Novitski, 1941). It is evident that certain characters have changed repeatedly in the same manner, while others are relatively stable or changed but once so that the altered feature is regarded as of phylogenetic significance.

Why should certain characters change repeatedly in this fashion? It is well known that in those animals which have been studied genetically mutations occur or at least survive at certain loci more frequently than at others. Mayr and Vaurie (1948) give examples of the occurrence of parallel changes in birds comparable to those here described for the Saturniidae. In these groups, perhaps in all groups, there are much greater potentialities for changes of certain sorts than for those of other sorts. The independent acquisition of, for example, tibial spines in various saturniids may indicate such a predisposition to spined tibiae because of high mutability of a gene locus controlling such spines.

However, as Simpson (1944) has emphasized, there is no necessary relationship between mutation rate and rate of evolution. A high mutation rate at a certain locus might be completely unexpressed in evolution because of the inviability of the mutants. Moreover, there is no certain way of judging whether the presence

of spines in various unrelated saturniids is due to separate mutations or is due to alleles common to all or most saturniids but unexpressed in most because of the action of modifiers. Mather (1943) has pointed out that an organism's response to natural selection must depend largely upon stored variability such as this and not upon new mutations.

The significant point is that tibial spines have arisen at least ten times during the course of saturniid evolution. It is certain that selection has played the principal role in determining what variants survive. Simpson (1944) has ably discussed its importance. Both Rensch (1939) and Muller (1939) have pointed out that parallel evolution occurs in animals having similar genetic makeups and subject to similar conditions of selection. In connection with this last point, it is interesting that all American forms having such spines occur in the more or less temperate regions of the United States and Canada or in temperate or nearly temperate areas of southern Brazil, Paraguay, Uruguay, and Argentina. None of the numerous tropical saturniids have tibial spines. So far as known, forms with these spines pupate below the surface of the ground and the spines are thought to be important to the adult in digging its way to the surface. Pupation in the soil is probably one of the ways in which these insects are able to protect themselves from cool winters, although many other northern types survive cold by means of other sorts of adaptations, for they pass the winter as pupae in cocoons hanging in trees.

The remarks already made concerning mutation rates and selection apply equally to the reduction or loss of structures. As Wright (1929, 1940) and Muller (1939) have pointed out, there is considerable mutation pressure against most structures, so that unless they are preserved by selection, they tend to disappear. We must conclude that in at least some groups the selection pressure has relaxed for such structures as the epiphyses, which have been lost at least 10 times (in females) in

saturniid evolution. It is obviously much easier for an organism to lose a previously established character in this way than to acquire a new one. The extent to which this is true is indicated by the numerical data already presented.

A relationship exists between reduced eye size and diurnal habits. Like most moths, most saturniids are nocturnal, but those with reduced eyes are mostly, if not all, diurnal or crepuscular. Perhaps in daylight smaller eyes can perform the functions for which large eyes are necessary at night. Hence small eyes, which would be selectively disadvantageous in most saturniids, are at least not seriously disadvantageous in diurnal forms.

Reduction in eye size is correlated, as already stated, with reduction of other parts of the head capsule; the indication is that this is an example of disharmonic or allometric growth (see Huxley, 1932), the head capsule growing more slowly in relation to the rest of the body than in most saturniids.

Acknowledgments

Grateful acknowledgment is made to Mr. Frank Johnson for the funds made available, both at the American Museum of Natural History where this study was begun and at the University of Kansas. Thanks to his generosity, technical assistants have been available to make dissections and drawings which have aided greatly in the comparative morphological work which is the basis of this study. Doctor Ernst Mayr and Mr. Hewson H. Swift have read the manuscript and offered many valuable criticisms.

SUMMARY

The phylogeny of the Saturniid moths is discussed and several examples are

given of independent origin of similar characters in unrelated Saturniids. For example, the loss of a hind tibial spur has occurred independently at least 10 times in one subfamily, of the epiphyses of the female at least 10 times in the family, and of the articulation of the male genital harpes 7 times. Reduction of the labial palpi has occurred at least 9 times, and of the eyes and structures of the head capsule at least 14 times. Large spines are acquired on the front tibiae at least 10 times. A discussion is given of the possible reasons for this extensive series of parallelisms.

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