THE STATUS OF THE GLYPHIPTERIGIDAE AND A REASSESSMENT OF RELATIONSHIPS IN YPONOMEUTOID FAMILIES AND DITRYSIAN SUPERFAMILIES[1]

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Current studies of the North American Glyphipterigidae have revealed major fundamental morphological and behavioral characters which demonstrate that the inclusion of the choreutid and glyphipterigid groups within a single family is untenable. The discordant characters involved have been shown in the past by other workers to be so fundamentally and evolutionarily conservative in Lepidoptera phylogeny that it is not even possible to consider the two groups to have evolved within the same superfamily.

Glyphipterigid moths have long been considered of unusual interest because of apparent affinities to the Yponomeutidae and the Sesiidae, as well as to the Tortricidae. Most early workers considered them as distinct groups: the choreutids were placed with the tortricids and the glyphipterigids *sensu stricto* were placed among the tineoid moths. This segregation was rarely altered until Meyrick (1914) combined them into one family. Meyrick's classification was based largely on general facies—the two groups share a number of superficial characters—and not fundamental relationships. He also relied strongly on wing venation and did not use genitalia, internal morphology or larval characters. He formed a conglomeration of what now are no less than nine distinct families in several superfamilies, although he realized the true affinities of many of the included genera in later years. Current revisionary studies on the choreutids and glyphipterigids, using modern systematic techniques, are revealing the true affinities of these moths. The results of these studies to date have confirmed the polyphyletic nature of the Glyphipterigidae *sensu lato*, first indicated by Brock (1967).

Glyphipterigid Discordancies

Brock (1971) revealed certain previously unused characters of ditrysian internal morphology of which the sternal abdomino-thoracic articulation provides a significant character for Lepidoptera phylogeny and

the affinities of families. Whereas most genitalic characters are evolutionarily plastic at the species level in most groups, due to the selective pressures for reproductive isolation, it is clear that characters not likely to be involved in active selection should remain relatively stable and, consequently, useful in assessing the relationships of higher categories. The abdominal articulation in Lepidoptera appears to be such a stable character.[3]

Two types of sternal articulation are found in adult Ditrysia: the Tineoidea type, having elongated sternal rods internally in the second sternal sclerite and with apodemal projections into the thoracic lumen, and the Tortricoidea type, having simple apodemes. There are minor variations in these types, but only the two major conformations of abdominal articulation are found in Lepidoptera. Having examined 16 genera of choreutids and 9 genera of glyphipterigids, including all 50+ Nearctic species assignable to these two groups, and many species of Pantropic and Palearctic origins, I have found no discrepancy in the abdominal articulation of any in terms of assignment to either group. All the choreutids have tortricoid apodemes, and all the glyphiptergids have tineoid rods. This articulation discordancy, consequently, indicates that the two groups have not evolved from a recent common ancestor.

Another lepidopteran character considered evolutionarily conservative at the family level is the chaetotaxy of larvae, with particular interest here involving the lateral pre-spiracular setal group of the larval prothorax (Werner, 1958; MacKay, 1963; Peterson, 1965; Common, 1975). The glyphipterigid *sensu stricto* larvae have a bisetose pre-spiracular setal group on the prothorax. The choreutids have a trisetose pre-spiracular setal group. The polyphyly of the Glyphipterigidae *sensu lato* is here again demonstrated by a character used in the Lepidoptera.

A third fundamental character useful in the higher classification of Lepidoptera is pupal behavior at adult ecdysis and again the two groups show no recent common ancestry. The glyphipterigids do not protrude the pupa at adult ecdysis, and the choreutids do protrude the pupa. The protrusion or non-protrusion behavior is characteristic of superfamilies in the Ditrysia. It should be noted that this behavior involves the presence or absence of genetic components that form the pupal exterior spination, which is usually necessary for the pupa to be able to protrude from the cocoon. Some yponomeutids protrude only the head.

Table 1 summarizes the three fundamental characters noted above for each of the families and superfamilies comprising the microlepidop-

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[3] The sexual dimorphism in abdominal articulation noted by Hodges (1974) in certain Oecophoridae is one of degree only and while some tortricoid tendencies occur, these do not form a simple apodemal articulation but retain the tineoid rod conformation.

TABLE 1.   Characters of Ditrysian Microlepidoptera.

Abdominal Articulation	Superfamily		Larval L-group Setae	Protruded Pupa
tineoid rods	Tineoidea	(2 in *Scardia*)	3	yes
tineoid rods	Gelechioidea		3	no
tineoid rods	Copromorphoidea	- Copromorphidae	2	no
		Carposinidae	2	no
		Epermeniidae	2	no
		Glyphipterigidae	2	no
tineoid rods	Yponomeutoidea	- Douglasiidae	3	yes
		Argyresthiidae	3	yes
		Yponomeutidae	3	yes
		Plutellidae	3	yes
		Acrolepiidae	3	yes
		Heliodinidae	3	yes
apodemes	Sesioidea	- Immidae	3	yes
		Sesiidae	3	yes
		Choreutidae	3	yes
apodemes	Tortricoidea		3	yes
apodemes	Cossoidea		3	yes
apodemes	Castnioidea		3	yes
apodemes	Zygaenoidea		3	yes
apodemes	Pyraloidea		2	yes

terous Ditrysia. Taken together the three characters provide strong evidence that the glyphipterigids and choreutids have not evolved from a recent common ancestor and, consequently, are distinct families belonging to different superfamilies in our present concept of these higher categories.

Affinities and Rearrangements

Rearrangements I propose for a new classification of the lower Ditrysia are as follows: Glyphipterigidae *sensu stricto* and Epermeniidae transferred from Yponomeutoidea to Copromorphoidea, and Choreutidae and Sesiidae restricted to Sesioidea, with the Copromorphoidea being shifted between the Gelechioidea and the Yponomeutoidea, while the Tortricoidea are placed after the Sesioidea in a linear arrangement altered from that proposed by Common (1970). There are also two Nearctic genera placed in Glyphipterigidae *sensu lato* that will be transferred to Copromorphidae in a future paper: one of the genera was already assigned to Carposinidae by MacKay (1972) based on larval characters, but larval differences from true carposinids apparently apply to Copromorphidae.

Meyrick (1928) was the first to combine Copromorphidae and Carposinidae as a new superfamily, the Copromorphoidea (plus Alucitidae), but the Glyphipterigidae and Epermeniidae were not associated with the

superfamily. The discordances noted above show that the characters of the glyphipterigids *sensu stricto* conform to Copromorphoidea. Their naked haustellum and bisetose larva excludes them from the Gelechioidea. Their bisetose larva and the non-protruded pupa excludes them from the Yponomeutoidea.

The Epermeniidae have the same three major character states as the glyphipterigids, which also places the family outside of Gelechioidea and Yponomeutoidea. There is some doubt about the bisetose pre-spiracular condition of epermeniid larvae since MacKay (1972) noted larvae of an *Epermenia* species to be bisetose, but Forbes (1923) noted another to be trisetose. Common (1970) states that epermeniid larvae are bisetose. My own examination of reared epermeniid larvae in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., produced only bisetose larvae. It may be possible that both bi- and trisetose larvae occur in the family as in Tineidae where *Scardia* larvae are bisetose (Hinton, 1956) while other tineids are trisetose. The bisetose condition appears to be an apomorphic development prevalent in endophagous larvae, although as seen in Table 1, this character is generally conservative enough evolutionarily to serve as a useful character for higher classification. Not all endophagous larvae, however, are bisetose; for example, the trisetose endophagous Sesiidae (MacKay, 1968) among others.

The epermeniids are placed between Carposinidae and Glyphipterigidae because of genitalic features showing affinities to Carposinidae, e.g., the uncus, and because of advanced wing venation and other characters showing a close relationship to the glyphipterigids. Some epermeniids superficially resemble glyphipterigids, for example, the Palearctic *Epermenia pontificella* Hübner. As with the superficial resemblance of some choreutids with glyphipterigids, the Epermeniidae also have wing maculation that could be the result of convergent adaptive strategies as diurnal moths, although it is unclear whether all epermeniids are diurnal. Choreutids and glyphipterigids, as also some similar heliodinids, are diurnal in adult activity.

A distinctive feature of the Copromorphidae and the Carposinidae is the anal pectin of the hind wings, but not all species in these families have this feature (Common, 1970). The raised scale tufts of the forewings also are not found in all species of the families, which otherwise is a distinctive character for both families. Both characters would appear to be apomorphic in these two families and, thus, the lack of either in epermeniids and glyphipterigids should not exclude them from the superfamily. Some Gelechiidae and Oecophoridae (e.g., *Tonica* spp.) also have raised scale tufts on the forewings. The Epermeniidae often have

a scale tuft on the dorsal forewing margin that may indicate an affinity with the raised scale tufts of copromorphids and carposinids, although it may be a peculiarity of many epermeniids.

An interesting cohesive character of the Copromorphoidea is the enlarged spiracles of the prothorax and abdominal segment 8. Spiracles of the 8th abdominal segment also are more dorso-caudally positioned than is usual in Lepidoptera larvae (Common, 1970). While spiracle size is close to normal in Carposinidae (MacKay, 1972), a striking enhancement of this character has been illustrated and described by Moriuti (1960) and Kodama (1961) in the larva of the Japanese species, *Glyphipterix semiflavana* Issiki. The larvae have the spiracles of the 8th abdominal segment not only dorso-caudally positioned but elevated on what look like scoli. The larva of a new *Glyphipterix* species from Florida has protruding and enlarged spiracles as in the Japanese species. Larvae of the glyphipterigid genus *Machlotica* also have this unusual spiracle enlargement. I have examined reared *Epermenia* larvae, and these also showed the protruding spiracles. I have not seen larvae of Copromorphidae and follow Common (1970) in his notes for the family. The character may be apomorphic in endophagous larvae, having some unknown adaptive function. MacKay (1959) noted that tortricid larvae with more caudally positioned spiracles of the 8th abdominal segment invariably were borers, although this apparently does not hold for sesiid larvae (MacKay, 1968). Inasmuch as all Copromorphoidea larvae known thus far have enlarged spiracles to greater or lesser degree, but more than usual for Lepidoptera larvae, it appears to indicate a common ancestor for the four families. The unusual spiracle development of epermeniid and glyphipterigid larvae indicates that these two families are closely related. MacKay (1972) also noted other chaetotaxic characters which show affinities of epermeniids to Carposinidae.

The Copromorphoidea, as arranged in Table 1, have a reduction in wing venation from Copromorphidae to Epermeniidae, while retaining a chorda in Glyphipterigidae and vestiges thereof in Epermeniidae. The presence of the chorda has in the past retained the glyphipterigids and epermeniids in the Yponomeutoidea—the same can be noted for the choreutids—but the wing venation of these two families can be accepted as specializations within the Copromorphoidea.

The Douglasiidae are an anomalous family with little known about their biologies. The larvae are stated to be trisetose (Common, 1970), which I have confirmed in larvae of *Tinagma balteolella* (Fisher von Roeslerstamm). The pupa apparently is protruded at adult ecdysis, although this is unclear from published information. I retain them in Yponomeutoidea pending further investigation on their immature stages.

The family appears to be the most primitive yponomeutoid in relation to such characters as wing venation, a reduced uncus, and no socii. The remaining yponomeutoid families appear to form a monophyletic super-family and require no further notation in the context of this paper. The most recent research of European and Japanese workers is followed by the separation of Argyresthiidae, Plutellidae, and Acrolepiidae from Yponomeutidae. The superfamily progresses to the Heliodinidae, which would appear to be the most specialized yponomeutoid family.

The Choreutidae and Sesiidae have usually been considered in the Yponomeutoidea, especially due to their similar wing venation, which is also very similar between the two families, although very specialized in the sesiids. In fact, in the "choreutid" genus *Sagalassa* the two families nearly merge, with many species in the genus having hyaline wing areas as in Sesiidae. Larvae in at least one Neotropical species, *Sagalassa olivacea* (Busck), appear to be indistinguishable from true sesiid larvae (Duckworth & Eichlin, pers. comm.). The naked haustellum and other characters of *Sagalassa* indicate a close relation to Sesiidae, but with af-finities to *Imma*. Since the Sesiidae also have tortricoid apodemes at the abdominal articulation and are otherwise closely related to the Choreutidae, although extremely specialized, I follow Brock (1971) in assigning both to a separate superfamily, the Sesioidea. Although very specialized, the Sesiidae retain ancestral features (e.g., genitalic charac-ters) that allow their placement before Choreutidae in a linear arrange-ment of primitive to advanced.

The Pantropical genus *Imma*, in the past included in the glyphi-pterigids, may be assigned to **Immidae**, new family (type-genus: *Imma* Walker [1859]), the most primitive family of the Sesioidea. A thorough revision for a clarification of the true affinities of Immidae is needed.

Forster (1954) was the first to combine the Sesiidae and Glyphip-terigidae into one superfamily which he called Glyphipterygoidea, but he included the Glyphipterigidae *sensu stricto*. Meyrick (1928) had anticipated Forster by segregating the two families from Yponomeutoidea to Glyphipterygoidea—which was not followed by other workers—but he included Heliodinidae and Heliozelidae. Turner (1947) also had relationships mixed among several families, yet it is noteworthy that he seems to have been the first to note a possible relationship between Sesiidae, Glyphipterigidae *sensu lato*, and the Copromorphidae. Nicu-lescu (1964) also noted a relationship to Copromorphidae. Brock (1971) used the name Aegerioidea, but since Sesiidae is senior to Aegeriidae through the relative genus pertaining to each name, Sesioidea is the cor-rect superfamily name.

The Sesioidea remain distinct from the Tortricoidea through larval

characters, wing venation, labial palpi, head vestiture, and genitalic features. Among these characters in the Choreutidae are many tortricoid affinities. The largely tropical genus *Hilarographa*, heretofore considered choreutid, has remarkable genitalic resemblance to Chlidanotinae tortricids from Australia and New Guinea (Diakonoff, XV International Congress of Entomology, August 1976, Washington, D.C.) and, together with the related *Idiothauma* and *Mictopsichia*, will be transferred to Tortricidae in the near future.

The Choreutidae have a peculiar feature in their scaled haustellum, which is characteristic of gelechioids but not of sesiids or tortricoids (the three genera to be transferred to Tortricidae have naked haustellums, as do *Sagalassa* and *Imma* species). The state of haustellum scaling is usually useful at the superfamily level in Lepidoptera classification in terms of cohesive groups of families either having a scaled or a naked haustellum. As with other characters, isolated groups are found not to conform to some major character while otherwise having all the characteristics of the particular taxa they are related to. I believe the situation is the same with choreutids in their character complex between Sesiidae, Yponomeutidae, and Tortricidae. The Pyralidae also are the only pyraloid family having a scaled haustellum. As with the choreutids, the haustellum scaling appears to represent the retention of an ancestral character to some related group (e.g., choreutid relatives in the gelechioids?) or an apomorphy.

Figure 1 illustrates my understanding of the evolution of the Ditrysia by evidence presented herein and arranged linearly, but I do not wish to discuss all the details involved as this has been extensively covered by other authors (see Common, 1975). The taxa shown in the figure have lineage heights in relation to the general amount of evolutionary change (as a rate vector) that the group has undergone from ancestral forms: for example, Yponomeutidae evolved from an ancestral yponomeutoid but at a slower rate than Douglasiidae and, thus, the latter family is placed on a higher rate vector although the douglasiids have other characters which indicate they are more primitive yponomeutoids.

Superfamily Relationships

For a linear arrangement of the ditrysian microlepidopterous superfamilies, I follow Common (1970) as modified by the studies of Brock (1971). Thus, the Tineoidea and Gelechioidea are considered the most primitive due to their articulation and wing venation. However, such an understanding of their phylogenetic ancestral relationships does not preclude the many specializations found within the Gelechioidea, being a result of differential rates of evolution in the various included families.
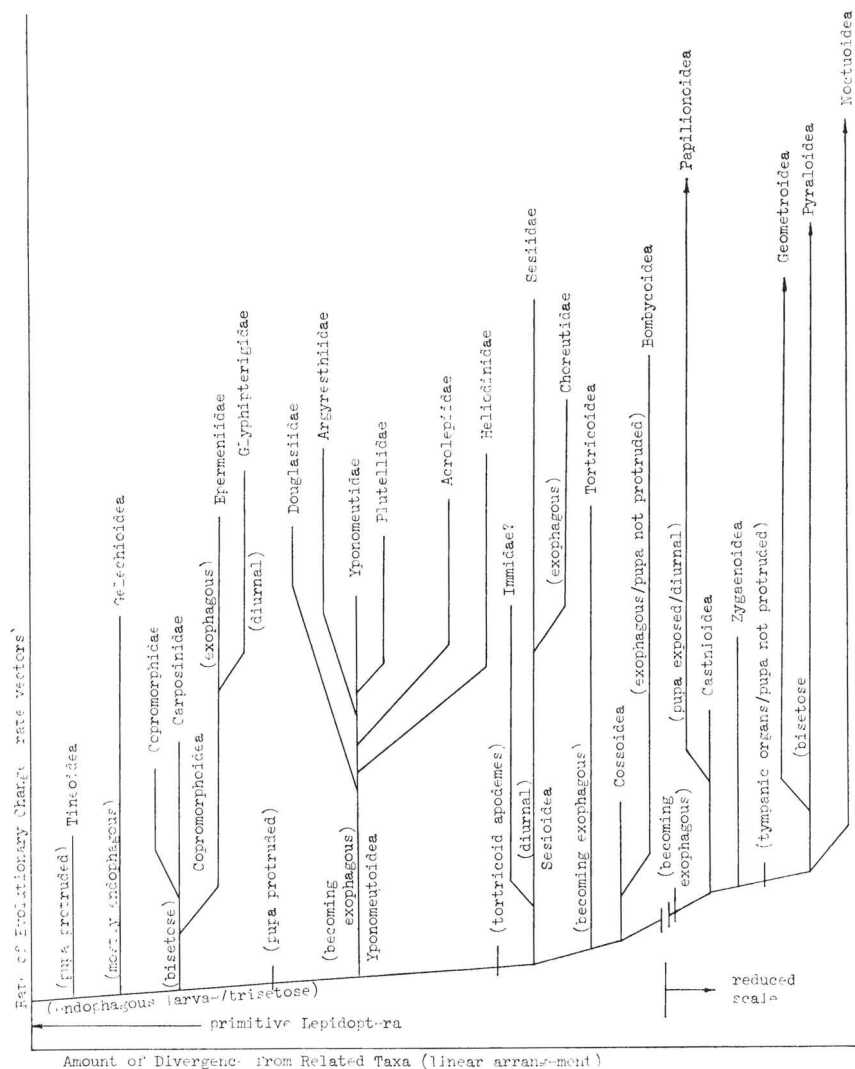
Fig. 1. Evolution of Ditrysia.

In contrast to Common (1970), I place the Copromorphoidea after Gelechioidea due to their tineoid abdominal articulation and the non-protruding pupal behavior, which is not tortricoid. Copromorphids have an abdominal articulation resembling the apodemal type, yet retain the tineoid sternal rods: the apodemal resemblance is actually enhanced due to the stoutness of the rods. The trisetose larvae and protruding pupal

behavior of Yponomeutoidea indicates closer affinities to Sesioidea than to Gelechioidea, thus, placing them after Copromorphoidea.

The apodemal nature of the abdominal articulation of Tortricoidea is a derived condition and demonstrates closer affinities to the higher Ditrysia, which all have the apodemal articulation, than to the Tineoidea, as followed by Common (1970). Larval studies by MacKay (1959) have also shown that most tortricids are more advanced than Tineoidea. As noted above, the mixed character complexes of the Sesioidea indicate ancestral relationships to both Yponomeutoidea and Tortricoidea, placing them in the middle in a linear arrangement. The Cossoidea I consider having evolved at a very slow rate of evolution in relation to the related Tortricoidea and, while more primitive in many ways compared to tortricoids, they are more advanced than ancestral tortricoids, thus allowing a more convenient placement after Tortricoidea for a linear arrangement. The remaining superfamilies are arranged after Common (1970) except for the Alucitidae. The alucitids were placed in the Copromorphoidea by Meyrick (1928) and Common (1970) but the tortricoid abdominal articulation would better place them in the Pyraloidea (Brock, 1971), which also have bisetose larvae and non-protruding pupae.

CONCLUSIONS

The long maintained assimilation of the Glyphipterigidae and Choreutidae as one family was due to their overall resemblance. Evaluation of more fundamental characters, as noted above, has elucidated the discordances in considering the two groups as one family in relation to the desire to maintain only monophyletic groupings of related taxa. Actually, the two groups evolved from distinct ancestral lines and must be considered distinct families.

Evaluation of related families indicates that the Epermeniidae are much more closely related to Glyphipterigidae than previously considered, with both showing common ancestry with the Copromorphidae and Carposinidae. Thus, the four families are here considered in one superfamily, the Copromorphoidea. Fundamental characters also distinguish the Sesiidae and Choreutidae as Sesioidea (together, probably, also with Immidae), not Yponomeutoidea, and their placement between the yponomeutoids and the tortricoids appears sound. Immidae will be discussed further in a forthcoming paper.

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AN "ALBINIC" *PIERIS SISYMBRII* (PIERIDAE) FROM THE CALIFORNIA SIERRAS

"Albinic" or "depigmentized" forms largely or wholly lacking melanin pigment from the wings are known in several pierid butterflies. Within the genus *Pieris* a weakly melanized form is known from *P. protodice* Bdv. & LeC. (Shapiro 1970, Wasmann J. Biol. 28: 245–256) and Gardiner (1962, Ent. Gaz. 13: 97–100; 1963, J. Res. Lep. 2: 127–136) has reported a form from *P. brassicae* L. in which the normally black scales lack pigment altogether, producing a translucent "shadow" pattern. In both of these cases the genetics is known. Crowe (1967, J. Lepid. Soc. 21: 121) reported a female *P. sisymbrii* Bdv. from Harney Co., Oregon which seems to resemble Gardiner's form of *P. brassicae* in totally lacking melanin on the wings. Although the accompanying photograph does not show a "shadow" pattern, it is mentioned in the text. On 23 May 1975 a very similar male with "shadow" pattern was taken flying among normal individuals on Washington Road, off state Highway 20 in Nevada Co., California. As in Crowe's specimen, the normally dark wing-veins contrast strongly with the ground color and the body, legs and antennae are normally pigmented. This male was kept alive for two days but no virgin females were available and I could not induce wild females to mate. The Washington Road population is unusual in that it is an isolated colony on the highest-elevation outcrop of serpentine soil (elev. 5000 ft) in the central west-slope Sierra. The vegetation on this atypical site is digger pine-manzanita-scrub oak, contrasting strongly with nearby stands of mixed montane coniferous forest on non-serpentine soils; the nearest known *sisymbrii* colony is seven miles away. This is the first aberrant individual I have seen among about 750 wild *P. sisymbrii* in about 20 California populations.

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