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A COMPARISON OF THE EXTERNAL ANATOMY OF THE LOWER LEPIDOPTERA AND TRICHOPTERA FROM THE STANDPOINT OF PHYLOGENY.

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Dr. August Busck and Dr. Bethune-Baker have very generously furnished the material upon which the following observations on the Lepidoptera were based, and Mr. Nathan Banks has kindly identified the adult Trichopteron described in the following discussion. To these gentlemen I would express my very sincere gratitude and appreciation for their generous assistance which has made this study possible.

One hundred years ago, that keen observer Leach, 1817 (Zoöl. Misc., Vol. 3) linked together the orders Trichoptera and Lepidoptera in a group to which Haeckel, 1896, applied the term "Sorbentia"; and most entomologists since Leach's time have agreed in regarding the orders Lepidoptera and Trichoptera as extremely closely related. Speyer, 1839 (Oken's Isis, 1839, p. 94) was, so far as I am aware, the first to suggest that the lepidopterous "family Micropterygidæ" forms a transitional group leading to the Trichoptera, and later in 1870 (Stett. Ent. Zeit., 1870, p. 202), he carried the comparison between the two groups still further. Subsequent investigations have served to confirm Speyer's views, and since the micropterygoids occupy such an important position from the standpoint of the phylogeny of the Lepidoptera, their affinities have been much discussed.

Chapman, 1894 (Trans. Ent. Soc. London, p. 335) divides the micropterygoids into two families, the Micropterygidæ and Eriocephalidæ. Meyrick, 1912 (Genera Insectorum, Fasc. 132) treats them as a single family, the Micropterygidæ, and divides them into three subfamilies, the Mnesarchæinæ, Eriocranianæ and Micropteryginæ. In the following discussion, these insects (which belong

to three distinct families) will be treated as comprising a single superfamily, the Micropterygoidea, which constitutes the lepidopterous suborder Prolepidoptera.

Packard, 1895 (Monogr. Bombycine Moths, Part 1, Notodontidæ) makes *Eriocephala calthella* the "type" of a distinct suborder of Lepidoptera which he calls Lepidoptera laciniata, or Protolepidoptera, while he places *Micropteryx* in another suborder which he calls the Paleolepidoptera. Chapman, 1916 (Trans. Ent. Soc. London, 1916–1917, p. 310) raises *Micropteryx* to ordinal rank, proposing for it the name Zeugloptera, thus differing from practically all of his predecessors, who agree in regarding the micropterygoids as lepidopterous.

On page 307 of Part II of his treatise on Insects (Cambridge Nat. Hist.), Sharp, 1909, in discussing the fact that Brauer's distinction between the Lepidoptera and Trichoptera on the basis of the presence of mandibles in the pupæ of Trichoptera no longer holds good, makes the statement that "unless it should be decided to transfer *Micropteryx* to Trichoptera, and then define Lepidoptera and Trichoptera as distinguished by the condition of the pupa, it would appear to be very difficult to retain the two groups as distinct." On page xvii of the Proceedings of the Ent. Soc. of London, Sharp, 1896 had likewise suggested that the micropterygoids "should be treated as a group of Trichoptera whose larvæ are not aquatic in habits." Comstock, 1918, in his book on the "Wings of Insects," has followed these suggestions, treating the Micropterygina as a suborder of the Trichoptera, and referring to them as terrestrial Trichoptera. In reviewing Comstock's book, Tillyard, 1919 (Ent. News for May, 1919, p. 149) criticizes him for removing the micropterygoids from the Lepidoptera to the Trichoptera from the study of the wing-veins alone, and states that "even from the point of view of the wing-venation it is scarcely defensible, for a careful study of the freshly turned pupæ of any of the older families of Lepidoptera will show that their wing-tracheation agrees closely with that of *Micropteryx*, particularly in the different courses of Cu and I A in fore and hind wings. Moreover the pupal wing of *Micropteryx* has a complete tracheation; the imaginal wings have broad well developed scales of a higher type than any found in the Trichoptera; the fore wing does not possess a separate M^4; and the hind wing has a definite frenulum.

In all these points this family is definitely Lepidopterous. Neither the larval form nor the imaginal mouthparts are Trichopterous, so that there is really no justification for so radical a change, which must remain as a serious blemish in a fine work."

In order to test the validity of Tillyard's criticism, it has seemed preferable to examine structures other than the wing veins in comparing the micropterygoids with the Tricoptera, and for this purpose, I have chosen the primitive little Trichopteron *Philopotamus distinctus*. These small caddice-flies are particularly interesting because the females have only rudimentary wings—a condition which, so far as I am aware, has been recorded but once before among North American Trichoptera. The bodies of both males and females are of a dusky black color, and the wings of the males are of a slightly ashen hue. Both sexes are found on stones along the banks of swiftly running streams, particularly in the neighborhood of waterfalls, and those found about Amherst first appear the latter part of April. The females have rather long hind legs enabling them to flee rapidly over the surface of the water with quick leaping movements, when disturbed, while the males under these conditions dart to the surface of the water, and after making a short series of "leaping" flights, come to rest on the bank a short distance from the place whence they were dislodged. At the beginning of the season, neither males nor females are readily disturbed, and may be easily captured by a quick grasp with a pair of forceps. The small white larvæ which appear to be those of *Philopotamus* crawl over stones in swift-running brooks, and pupate in their cases made of sand, usually attached to the upper surface of stones. The pupæ, if I remember aright, are protected by a parchment-like case lining the outer one made of sand. I am hoping to find out more of the life history of these insects later, since the habits and œcology of insects should be studied in addition to their structures, in attempting to determine their affinities; but for the purpose of the present paper, it will be sufficient to compare the chief features of their anatomical details with those of the micropterygids.

The head capsule of *Philopotamus* (Plate II, Fig. 2) is surprisingly like that of the micropterygid *Mnemonica* (Fig. 4) in outline, and these two types of head approach the nearest to that of the neuropterous ithoniid *Oliarces clara*, Banks (an insect which should be

placed in the family Ithoniidæ, judging from the nature of its thoracic sclerites, head capsule, and other features, although this has not yet been done in any grouping of the Neuroptera which I have seen thus far). In fact, it is very probable that the ithoniids are quite like the forms which gave rise to the lines of descent of the Lepidoptera and Trichoptera, though Tillyard and Handlirsch seem to think that the Mecoptera (or their fossil relatives) represent the ancestors of these two groups. The galeæ of the maxillæ (see structures labeled "mx" in Fig. 4, of the micropterygid) are not developed in the Trichopteron shown in Fig. 2, but Ulmer, 1905 (Zoöl. Anz. 28, p. 56) and Cummings, 1913 (Ann. Nat. Hist. XI, p. 308) describe the maxillæ of the Trichopteron *Dipseudopsis* having the parts well developed, and with the galeæ[1] as long as those of *Mnemonica* ("mx" of Fig. 4). The pupa of *Mnemonica* (Fig. 9) has huge crossing mandibles suggestive of the type found in Trichoptera (Fig. 7), but I have not found any Trichoptera in which the mandibles are enlarged at the tips as in *Mnemonica*, nor have any of the trichopterous pupæ which I have examined, a frontal process like that labeled "e" in Fig. 9 of the pupa of *Mnemonica*.

The lateral region of the thorax of *Mnemonica* (Fig. 1) is astonishingly like that of the Trichopteron (shown in Fig. 3), the outlines of the upper and lower divisions of the mesothoracic episternum ("aes_2" and "kes_2") being very similar in both instances. It may be remarked in passing, that the region labeled "aes" is *not* the entire episternum, nor is the region labeled "kes" the trochantin (which is labeled "tn" in both figures) as is usually stated to be the case, and the hinder portions of the coxæ labeled "me" are *not* detached portions of the epimeron "em," which have become adherent to the coxæ—but these features have been thoroughly discussed in an article dealing with the basal segments of the leg in insects (Zoöl. Jahrb. Abt. Anat., 39, p. 1) and need not be gone into further here.

As is true of all Lepidoptera which I have examined, the mesothoracic merocoxa "me_2" (Fig. 1) or posterior division of the coxa extends along the *entire posterior border* of the anterior coxal division "vc_2" in *Mnemonica* (Fig. 1), and there is *no* "*basicoxite*"

[1] The proboscis of *Plectrotarsus* is not "coiled," as was formerly stated to be the case, but is merely folded.

like that labeled "cm" in the Trichopteron (Fig. 3). On the other hand, the merocoxa "me_2" of Fig. 3 extends only *part way* down the remainder of the coxa in all of the Trichoptera which I have examined, and in all of them *there occurs a mesothoracic basicoxite* "cm" (Fig. 3) *which is absent in all of the Lepidoptera* I have seen. Since these features seem to be constant in the groups under discussion, they are probably diagnostic for the orders in question, and by applying this test to the micropterygids, they are seen to be clearly Lepidoptera and not Trichoptera! I would especially emphasize the importance of this apparently conclusive test, since it is the only feature (of which I have any knowledge) *which holds good in all cases examined*, and on this account it should be of great diagnostic value in attempting to determine whether an insect is lepidopterous or trichopterous.

The tergal region of the thorax is very similar in the lower Lepidoptera and Trichoptera (Figs. 5 and 8), but the mesothoracic scutellum of *Mnemonica* (Fig. 8, "sl_2"), as is the case in most of the other Lepidoptera, tends to become somewhat "transversely oval" in outline, while that of the greater part of the Trichoptera (Fig. 5, "sl_2") is more triangular in outline. This feature may also prove to be of diagnostic value; but I doubt that it will be found to hold in all cases, although I have been unable to find any exceptions thus far. In most Lepidoptera examined, there occurs a tegula-bearing rod labeled "t" in Fig. 8 of *Mnemonica;* but I do not find exactly this type of structure in most of my caddice-fly material. Both of these primitive representatives of the orders Trichoptera and Lepidoptera have a wing-coupling apparatus of the jugo-frenate type (*i. e.* both jugum "j" and frenulum "fr" are present in the insects shown in Figs. 5 and 8) so that Tillyard's distinction between the two orders on this score, will not hold. Since I have not made a study of the wing veins, I shall not attempt to discuss this phase of the matter; but so far as the nature of the jugum-bearing region "jf" and the alar ossicles "np," "ba," "a," etc., are concerned, the basal portions of the wings, like the tergal sclerites, are strikingly similar in the two insects under discussion.

In all of the Trichopterous larvæ which I have examined, homologues of the styli or gonopods ("s" of Fig. 6) are to be found in the posterior region of the abdomen; but I have been unable to find these structures in any lepidopterous larvæ, and since the larvæ of

the micropterygids seem to lack these structures, this feature may also be of value in distinguishing between the orders Lepidoptera and Trichoptera. The styli labeled "s" in the larva shown in Fig. 6 are apparently represented by the so-called gonopods, or gonostyli "s" of the adult male Trichopteron shown in Fig. 15 (Plate III). Even when the gonopods "h" are well developed in male Lepidoptera (Fig. 13), they apparently retain only one distinct segment "h," while in those Trichoptera in which the gonopods are exceptionally well developed, the gonostyle portion labeled "s" in Fig. 15, usually consists of two distinct segments. Furthermore, the dorsal lobes "sg" are of a different type in the two groups of insects, and these features may be of some value in further distinguishing between the Lepidoptera and Trichoptera.

McLachlan, 1874–1880 (Monographic Revision of the Trichoptera) on page 206 states that "*Enoicyla* is the only authenticated example of terrestrial habits in the larvæ of recent Trichoptera. . . . The genus is scarcely less remarkable by its practically apterous female. . . . The pupæ . . . have very distinct spiracles. . . . The larva lives under moss, etc., at the foot of trees, chiefly in woods, and often at great distances from water." Since some of the larvæ of the micropterygoids feed on mosses (Musci) and occur in somewhat similar locations, these facts lend additional weight to the view that Trichoptera and Lepidoptera are very closely related.

In discussing the protocerebrum of *Micropteryx*, Buxton, 1917 (Trans. Ent. Soc. London, 1917–1918, p. 135) states that "In *Micropteryx* paired ocelli are present, but the median ocellus is not developed here, or in any other Lepidopteron or Trichopteron." This is very probably true of the Lepidoptera as a whole, but I find a median ocellus in many Trichoptera (see Fig. 11 of article on head region of insects in Annals Ent. Soc. America, 1917, p. 339, and Fig. 2 of the present paper). If no median ocellus occurs in any Lepidopteron, and does occur in some Trichoptera, this may be regarded another feature of some value in distinguishing between the orders.

Mr. Banks has called my attention to the fact that "scales" occur on the wings of certain Trichoptera, and their presence is therefore not diagnostic for the order Lepidoptera. Thus McLachlan (l. c. p. 274) in describing the trichopterous genus

Lepidostoma speaks of the wings of the male as "clothed with scattered black 'scales' regularly placed . . . ," and somewhat similar "scales" occur in certain Leptocerids as well as in the Sericostomatid mentioned above. It must be admitted however, that the "scales" of Trichoptera are not exactly like those of Lepidoptera (see Kellogg, 1895, American Naturalist), though their function in certain cases (*e. g.* androconia-like structures of *Mystacides* wing, described by Kellogg, 1895) may be very like that of the scales of Lepidoptera.[1] Cummings, 1914 (Proc. Zoöl. Soc. London, 1914, p. 461) states that "The occurrence of typical unicellular scent glands at the bases of hairs in Trichoptera as well as Lepidoptera is interesting, and in view of the close relationship between these two orders not wholly unexpected. . . . In *Sericostoma* they (scales) occur on the maxillary palpi, a position in which, I believe, they are undescribed in Lepidoptera." The absence of scales from the maxillary palpi in all Lepidoptera and their presence in some Trichoptera, may prove to be another distinguishing feature in defining the two orders.

From the foregoing discussion it is quite evident that the similarity in the head capsule, the general character of the mouthparts (both adult and pupal), the nature of the thoracic sclerites, the wing venation and presence of a coupling apparatus of the primitive jugo-frenate type, the general character of the terminal abdominal structures, and the occurrence of moss-inhabiting larvæ, are features indicating an extremely close relationship between the lowest Lepidoptera and Trichoptera, so that Comstock's removing the micropterygoids from the Lepidoptera to the Trichoptera has considerable justification. On the other hand, the subdivision of the mesothoracic coxa *for its entire length*, into eucoxa "vc" and merocoxa "me" (Fig. 1) in all Lepidoptera studied, and the *merely partial* subdivision of the mesothoracic coxæ of all Trichoptera examined (Fig. 3 "vc" and "me"), together with the presence of a basicoxite "cm" (Fig. 3) marked off by a downward-sweeping line of demarcation in the mesothoracic coxa of all Trichoptera studied, and the absence of this type of structure in all Lepidoptera examined furnish us with an appar-

[1]Busck, 1914 (Proc. Ent. Soc. Washington, 16, p. 50), calls attention to the fact first observed by Spuler, that if the scales are removed from the wing of a micropterygid, its surface is seen to be covered with minute curved spines (like those of Trichoptera) occurring "between the scales and much more numerous than these."

ently decisive test for determining whether an insect is lepidopterous or trichopterous, and when this test is applied to the micropterygoids, they are seen to be clearly lepidopterous, not trichopterous! The "transversely ovate" outline of the mesothoracic scutellum (Fig. 8, "sl_2") in most Lepidoptera as opposed to the triangular scutellum of most Trichoptera (Fig. 5, "sl_2"), the absence of a median ocellus in all known Lepidoptera and its presence in some Trichoptera, the presence of "scales" on the maxillary palpi of some Trichoptera and their absence in all known cases in Lepidoptera, and the presence of structures homologous with the posterior abdominal styli in all trichopterous larvæ examined, coupled with the absence of such structures in lepidopterous larvæ are features of value serving to support the above mentioned test, when applied to the micropterygoids, and the evidence furnished by these features (which seem to have a very general application throughout the two orders) should be conclusive. I would therefore maintain that the micropterygoids are lepidopterous, not trichopterous, although I too would emphasize the remarkably close relationship between the lower Lepidoptera and Trichoptera (See Trans. Ent. Soc. London, 1919, p. 93).

In the appended diagram (text figure 1) the lines of descent of the Lepidoptera and Trichoptera are represented as though diverging from a common Lepidoptero-Trichopteron stem composed of forms combining in themselves the primitive ancestral features of the two orders. Just after these two lines of descent begin to diverge as they emerge as distinct orders (the common stem, however, was probably trichopterous) the line of development of the micropterygoids appeared, carrying over from the common ancestry many primitive features occurring in the Trichoptera, yet exhibiting certain peculiarly lepidopterous characters. The line of development of such Trichoptera as *Philopotamus* likewise arose very near the point of origin of the micropterygoid line of development, as shown in the diagram, but since *Philopotamus*' line of development is on the side of the Trichoptera, it did not acquire any peculiarly lepidopterous features, though it has developed certain features in common with all other Trichoptera, as would naturally be expected. This simple and self-evident explanation will serve to show how the micropterygoids may be truly Lepidoptera, and the *Philopotamus*-like forms may be truly

Trichoptera, despite the fact that both micropterygoids and lower Trichoptera exhibit a remarkable degree of similarity; and it is therefore quite evident that it is not necessary to remove the micropterygoids from the Lepidoptera to the Trichoptera, nor is it necessary to regard them as representing a distinct order.

It has seemed unnecessary to append a "bibliography" at this point, since the more important reference works dealing with the anatomy on the insects in question have been given in the text of this article. If the reader is interested in the further study of the anatomy of the micropterygoids, the following works, in addition to those previously cited, may be of interest. Walter, 1885 (Jen. Zeit. f. Wiss., 8, p. 755), on the mouthparts; Tillyard, 1918, Proc. Linn. Soc. N. S. Wales, xliii, pp. 298, and 626, for wing structures; and the excellent general description of the anatomy of all stages of *Mnemonica*, by Busck and Böving, 1914 (Proc. Ent. Soc. Washington, 16, p. 151).

The following list of abbreviations applies to the figures of Plate IV (illustrating the following article on genitalia of higher insects) as well as to the plates of the present paper, and will therefore serve equally well for both articles. Since homologous structures bear the same label throughout the series of figures, it will be unnecessary to give a more detailed description of the various anatomical features of the insects under discussion.

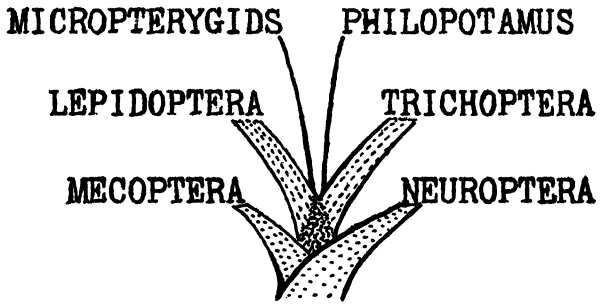

Fig. 1. Lines of descent of Lepidoptera and Trichoptera.

Abbreviations (Plates II, III, IV).

a.....posterior notal wing process (adanale).
aes.....upper division of episternum (anepisternum).
b .....thread of penis (penisfilum).
ba .....wing ossicle at base of anal veins (basanale).
c.....clypeus.
ca.....cerci.
cm.....coximarginal sclerite (basicoxite).
cx.....coxa.
d .....tergal plate and setæ of ninth segment.
e.....frontal process (frontonasus).
em.....epimeron.
ep.....epiproct (uncus, tegumen, or pygidium), also proctiger or structure bearing anus.
eps.....epipodal setæ.
es.....epicranial suture.
f.....frons.
fp.....frontal (tentorial) pits.
fr.....frenulum.
g.....“stipes” of gonopods (gonostipes).
gp .....genal process.
h .....harpago or clasp; last segment of gonopod, also called “harpes” and cochlearium.
ha .....hypandrium, or plate under genital apparatus of male.
ip.....interpleurite.
j.....jugum, or “clavus.”
jf.....jugum-bearing region (jugifer).
kes.....lower division of episternum (katepisternum).
l.....labrum.
lc.....lateral cervical plates.
lp.....labial palpus.
ls.....laterosternite.
m.....median wing ossicle (mediale).
md.....mandible.
me.....posterior division of coxa (merocoxa, or meron).
mp.....maxillary palpus.
mx.....maxilla.
np .....notal wing ossicle (notopterale).

o.....ocelli.
p .....styliger or "coxite" bearing styli (also called cardo, or gonocardo).
pa .....parietal region of head, prealar bridge of thorax.
pc.....postcranial region of head.
pf.....parafrons.
pfi .....paranotal fringe (parafimbrium).
pl.....propleuron.
pn .....pronotum.
pp .....gonopleurite.
pr.....plates on either side of anus (paraprocts or parapodial plates).
ps.....podal setæ.
psl.....postscutellum.
pt.....patagium, or patagial areas.
pv .....penisvalvæ, penis, ædeagus or phallus.
s.....styli, or gonopods (gonostyles).
sa.....plate under wing (subalare).
sal .....anterior tergal wing process (suralare).
sc.....scape of antenna.
sct.....scutum.
sg.....process above gonopod (surgonopod) probably homologous with dorsal lobes rather than cerci.
sl.....scutellum.
t.....tegula-bearing rod (tegulifer).
tf.....terminal filament (telofilum).
tg.....tegula.
tn.....trochantin.
vc.....anterior division of coxa (eucoxa or veracoxa).

Explanation of Plates II and III.

Fig. 1. Lateral view of thorax of *Mnemonia auricyanea*, Wals. (Micropterygoid).

Fig. 2. Frontal view of head of *Philopotamus distinctus* (Trichopteron).

Fig. 3. Lateral view of thorax of *Philopotamus*.

Fig. 4. Frontal view of head of *Mnemonica auricyanea*, Wals.

Fig. 5. Dorsal view of thorax and wing bases of *Philopotamus*.

Fig. 6. Lateral view of terminal structures of larval Trichopteron.

Fig. 7. Frontal view of pupal head of *Philopotamus* only mandibles shown.

Fig. 8. Dorsal view of thorax and wing bases of *Mnemonica auricyanea*, Wals.

Fig. 9. Frontal view of pupal head of *Mnemonica auricyanea*, Wals.

A COMPARISON OF THE GENITALIA OF MALE HYMENOPTERA, MECOPTERA, NEUROPTERA, DIPTERA, TRICHOPTERA, LEPIDOPTERA, HOMOPTERA, AND STREPSIPTERA, WITH THOSE OF LOWER INSECTS.

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Since the same plates have been used to illustrate both the present paper, and the preceding one dealing with a comparison of the lower Lepidoptera with the Trichoptera, the same list of abbreviations will serve for both papers, and by referring to the explanation of the labeling, given on page 32, this will obviate the necessity of repeating in the present paper, the list of abbreviations there given. For the Strepsipteron here described, I am indebted to Dr. C. T. Brues. Dr. Bethune-Baker has loaned me the lepidopterous material used; Dr. R. J. Tillyard has furnished the neuropterous material; and Mr. S. A. Rohwer has furnished the sawfly material used in the preparation of this paper. Mr. Nathan Banks has very kindly identified the Trichopteron referred to, and Mr. A. N. Caudell has had the Homoptera identified for me. To all of these gentlemen, I would express my deep appreciation of their generosity and assistance so freely given.

The genitalia of male insects have been discussed in several recent articles; but the correct interpretation has not been given to the parts in all cases. Recently, however, I have been able to examine a far wider and more inclusive range of forms than was at first available for study, and the added evidence, together with that furnished in Dr. Walker's excellent account of the parts of the