

TECHNICAL COMMENTS

LOGIC AND PHYLOGENY: A CRITIQUE OF SCOTT'S PHYLOGENIES TO THE BUTTERFLIES AND MACROLEPIDOPTERA

J. A. Scott (1985, *J. Res. Lepid.* 23:241-281; 1986, *J. Res. Lepid.* 25:30-38) proposed phylogenies to the Macrolepidoptera superfamilies (Fig. 1) and the butterfly families (Fig. 3, in part). Although he presented an impressive amount of data on comparative morphology and behavior, in many cases these data do not support his phylogenies. Because nonsystematists might easily overlook this problem among the pages of morphological detail, I present one example from each paper showing that his data are inconsistent with his results.

MACROLEPIDOPTERA

Ability to hear the ultrasounds produced by bats and other predators evolved at least three times in moths (Sales, G. & D. Pye 1974, *Ultrasonic communication by animals*, Chapman & Hall, London, 281 pp.). The Geometroidea and Pyraloidea possess an abdominal tympanum, the Noctuoidea a thoracic tympanum, and the Choerocampinae (Sphingidae) a tympanum on the head (labial palps). Scott (1985, above) proposed that the Noctuoidea, Bombycoidea, Sphingoidea, and butterflies form a monophyletic group. His evidence was that the geometroid abdominal tympanum evolved into a thoracic tympanum in the ancestor of these taxa (point T in Fig. 1). As he stated, "The tympana moved to the metathorax."

The noctuid-to-butterfly grouping is not supported by the data. The bombycoids, sphingoids, and butterflies lack the thoracic tympanum. Scott's assumption that the abdominal geometroid tympanum is homologous with the thoracic noctuid one is contradicted by the morphology and physiology of these structures (Forbes, W. T. M. 1916, *Psyche* 23:183-192; Richards, A. G. 1932, *Entomol. Am.* 13:1-43; Kiriakoff, S. G. 1952, *Rev. Fr. Lepid. Fasc.* 11-12:6 pp.; Maes, K. 1985, *Nota Lepid.* 8:341-350). No other characters support Scott's noctuid-to-butterfly grouping. A slightly different, but simpler phylogeny (Fig. 2) reflects the lack of support for the noctuid-to-butterfly grouping and requires only one evolutionary change as opposed to two (gain and loss of the thoracic tympanum) in Fig. 1.

BUTTERFLIES

There are three major types of male forelegs among the butterflies (Bates, H. W. 1861, *J. Entomol.* 1:218-245; Ford, E. B. 1945, *Butterflies, the new naturalist*, Collins, London, 368 pp.; Jander, U. 1966, *Z. Tierpsychol.* 23:799-844; Robbins, R. K. 1987, *J. Lepid. Soc.* 40:138-157).

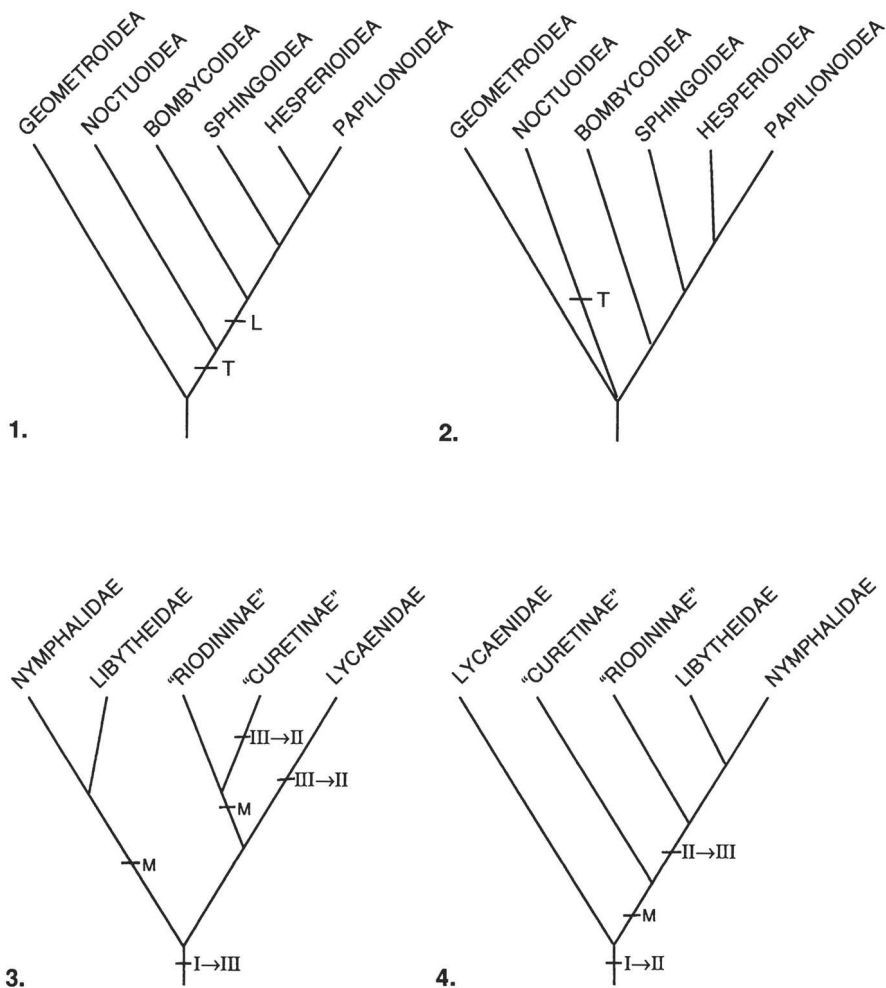
TYPE I (Hesperiidae, Papilionidae, Pieridae). Foretarsi five-segmented with "spines," sensilla, and pretarsal claws. Forelegs used for walking and cleaning the antennae.

TYPE II (Lycaenidae *sensu* Eliot, J. N. 1973, *Bull. Brit. Mus. (Nat. Hist.) Entomol.* 28: 371-505, including the Curetinae). Foretarsi fused into one segment, retain "spines" and sensilla, but not pretarsal claws. Forelegs used for walking but not for cleaning the antennae.

TYPE III (Riodininae, Libytheidae, Nymphalidae *sensu* Ehrlich, P. R. 1958, *Univ. Kans. Sci. Bull.* 39:305-370). Foretarsi partially or wholly fused, covered dorsally and ventrally with long scales (the "brush foot"), devoid of "spines," sensilla, and pretarsal claws, and greatly reduced in size. Forelegs not used for walking or cleaning the antennae.

There are some exceptions to this summary (Type III forelegs occasionally have one or two "spines" or sensilla, some male lycaenids have a segmented and clawed foretarsus), but they are irrelevant to my argument.

Scott (1985, above) stated that the ancestor of the Lycaenidae-Libytheidae-Nymphalidae



FIGS. 1-4. 1, 2. Phylogeny to the Macrolepidoptera. The thoracic tympanum evolved at point T, but was lost at point L. 1, Scott's phylogeny requiring two evolutionary steps; 2, An alternate phylogeny requiring one change. 3, 4. Phylogeny to the butterfly "families." Pupal midleg touching the eye evolved at point M. Evolution from one male foreleg type to another is represented by Roman numerals. The Stygines are omitted because of controversy over their male foreleg morphology (Forbes, W. T. M. 1960, *Lepidoptera of New York and neighboring states*, New York State College of Agriculture, Ithaca, 188 pp.); 3, Scott's phylogeny requiring five evolutionary steps; 4, An alternate phylogeny requiring three evolutionary steps.

had a small leg that could not clean the antennae. Since Type III forelegs are the only ones that are significantly reduced in size, Scott's statement implies that butterfly male forelegs evolved from Type I to Type III (in the lycaenid-nymphalid ancestor) to Type II (I-III-II hypothesis). This hypothesis, however, is less parsimonious than a I-II-III

proposal in Bates (above). The I-II-III hypothesis requires foreleg walking to be lost once (change from Type II to III) while the I-III-II hypothesis requires foreleg walking to be lost (change from I to III) and regained (change from III to II).

Scott's I-III-II hypothesis is inconsistent with his phylogeny (Fig. 3). The I-III-II hypothesis requires the Type II foreleg to evolve twice, once on the lineage to the Lycaenidae and once to the Curetinae (Fig. 3). The I-II-III hypothesis, on the other hand, implies an alternate phylogeny (Fig. 4) on which each male foreleg type evolves only once.

Scott further supported his I-III-II hypothesis by noting that the pupae of Curetinae have the midleg touching the eye, as in Nymphalidae, but again, this information does not support his phylogeny. As background, the Curetinae possess a Type II male foreleg. Scott noted that the pupal midleg character state occurs in Curetinae, Libytheidae, and Nymphalidae, but it also occurs in Riordinidae (Chapman, T. A. 1895, *Entomol. Rec. J. Var.* 6:101-107, 125-131, 147-152). Scott's phylogeny requires this character state to evolve twice (marked M in Fig. 3) while only one character change is necessary on the alternate phylogeny (point M in Fig. 4).

Scott presented much information besides that on male forelegs, and his phylogeny (Fig. 3) may be better supported by these other characters than the alternate phylogeny (Fig. 4). The important point is not which phylogeny is "correct" but that Scott incorrectly supported his I-III-II hypothesis with male foreleg and pupal midleg characters. This finding casts doubt on the validity of his analyses in general.

Phylogenies are basic to classification and to interpreting evolutionary hypotheses, but rigorously analyzed characters and character state distributions are needed to infer phylogenies. Scott claims to use cladistic methods, but his analyses appear to be inconsistent with cladistic methodology (Lundberg, J. G. 1972, *Sys. Zool.* 21:398-413; Farris, J. S. 1983, *Adv. Cladistics* 2:7-36). The prodigious amount of information that Scott presented on macrolepidopteran morphology and behavior will contribute to phylogenetic inference and, in this respect, is a major contribution to lepidopterology. However, it does not strongly support his conclusions.

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LOGIC AND PHYLOGENY: REPLY TO R. K. ROBBINS

Robbins is correct in questioning the homology of the noctuid tympanum with other tympana. About the only use of tympana is to help indicate that Geometroidea split off the Macrolepidoptera line before Noctuoidea, although its detailed structure may provide useful traits within each superfamily. A fourth origin of the tympanum may be indicated by the dorsal as well as the usual ventral abdominal tympanum in *Habrosyne* (Thyatiridae). Strong characters are used to devise branching schemes, and weak characters such as the tympanum are merely dragged along to wherever the strong characters place them. The position of Noctuoidea in J. A. Scott (1986, *J. Res. Lepid.* 25:30-38) merely minimizes the number of character changes in the overall Macrolepidoptera tree. Geometroidea and Noctuoidea seem the most primitive Macrolepidoptera because their larvae generally lack secondary setae and retain uniordinal crochets, their pupae retain the temporal cleavage line and the visible prothoracic femur, adults retain ocelli and the upper sector of the paracoxal sulcus, and, with Bombycoidea, adults retain the parepisternal rift and an areole. Geometroidea is at the base of the Macrolepidoptera tree because its abdominal tympanum may be phylogenetically related to the Pyraloidea abdominal tympanum, and