

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 Riodinidae (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.

I gratefully acknowledge John Burns, Gerardo Lamas, Scott Miller, Michael Pogue, Alma Solis, and Susan Weller for reviewing this comment.

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*Journal of the Lepidopterists' Society*  
41(4), 1987, 216-218

#### 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



because its flat eggs are more primitive than upright Noctuoidea eggs. The position of Noctuoidea after Geometroidea is also assigned by default because the cluster Bombycoidea-Sphingoidea butterflies share five derived traits (16–20 of Scott, above) which place this cluster on its own branch. Therefore, even when we discard the Noctuoidea tympanum because it evolved independently, Noctuoidea will have to stay put until new evidence to the contrary appears. The possible origin of Bombycoidea-Sphingoidea at the X of my Fig. 1 before Noctuoidea of Robbins' fig. 1 is equivalent to moving Noctuoidea to between Sphingoidea and Hesperioidea on Robbins' fig. 1, so I also was uncertain about the position of Noctuoidea. Currently, only these statements seem clear within Macrolepidoptera: 1) Geometroidea is the most primitive and Noctuoidea is next; 2) Bombycoidea and Sphingoidea are closely related; and 3) Hesperioidea-Papilionoidea are on their own branch. What is needed are new characters, which readers will hopefully provide.

Robbins' fig. 2 is improbable because we know that in nearly all cases two rather than three species evolve at one time, so a three-branch split is improbable on a phylogeny. Even if a three-branch split occurred during species-level evolution, the subsequent great animal extinction rate (estimated at 99%) would make the survival of all three taxa to the present exceedingly unlikely. Some authors draw as many as half a dozen lines branching from one point, but this merely reflects their uncertainty.

Among butterflies, the varying degrees of degeneration of the foreleg, especially the male foreleg, are weak traits that merely follow the strong traits when branching sequences are devised. I (below, pp. 256, 266) did not state that forelegs evolved from type I to III to II, only that the ancestor of Nymphalidae-Libytheidae-Lycaenidae had small forelegs, so that antennal cleaning by the middle leg evolved. Modifications of the foreleg such as tarsal fusion, claw loss, and scale elongation, or reversals of these states, apparently came later and proceeded differently in the various taxa. Libytheinae-Nymphalidae and Lycaenidae contain many groups with small forelegs, and they both clean the antenna with the middle leg; the logic that a small foreleg forced a switch from foreleg to middle leg cleaning seems inescapable. But just how small the ancestral foreleg was is not clear. Robbins assumes that it was his type III. Libytheinae was the first lineage to evolve from the nymphalid line, and its male foreleg is about one-half normal size while the female foreleg is about two-thirds normal size; even such a minimal reduction, occurring mainly in one sex, would have been enough to cause a shift to the middle leg. Or, a fusion of tarsal segments or loss of tarsal claws could have eliminated the ability of the leg to curve over the antenna shaft, reducing its utility in cleaning and causing the shift. Or, could a mere reduction of body size to lycaenid dimensions, together with a less-than-linear reduction of antennal shaft thickness due to a need to retain shaft rigidity to support the club, have reduced the ability of the antenna to flex backward with a small enough radius to be cleaned by the foreleg? If true, this ancestor would have a small foreleg in absolute dimensions, but a normal foreleg relative to the small middle and hind legs. One can classify the forelegs in various ways, many of which do not fit Robbins' I-II-III system, which is too simple and unnatural. For instance, Riodininae and Curetinae both have the male foreleg coxa extending spinelike below the articulation with the trochanter, an odd trait that may show their phylogenetic relatedness (both share other traits cited by Scott, J. A. 1985, *J. Res. Lepid.* 23:241–281, including the middle leg touching the pupal eye, noticed in Riodininae by Chapman, T. A. 1895, *Entomol. Rec. J. Var.* 6:129). Many Lycaeninae have a segmented and clawed male tarsus (Eliot, J. N. 1973, *Bull. Brit. Mus. [Nat. Hist.] Entomol.* 28:373–505), contrary to Robbins' type II; Eliot (pp. 394–395) argues that some groups have reacquired segmented and clawed male forelegs. Nymphalidae also show varying degrees of modifications of the tarsus (Ehrlich, P. R. 1958, *Univ. Kans. Sci. Bull.* 39:305–379). It seems difficult to avoid the conclusion that there have been many independent modifications of male foreleg details, including reversals. Robbins is correct that a I-II-III sequence would be more parsimonious; however, parsimony of entire phylogenetic trees overrides parsimony within a single character, and trees forced to obey Robbins' I-II-III sequence would require numerous added character changes in the tree because this sequence requires Nymphalinae to be evolved from the Lycaeninae-Curetinae ancestor.

Robbins' fig. 4 is impossible because of the massive number of shared derived traits of



Lycaenidae (including Riodininae, Miletinae, Curetinae, Lycaeninae), some newly discovered on the first stage larva by D. M. Wright. Fully 28 strong shared derived traits now define Lycaenidae, and seven shared derived traits define Nymphalidae (including Libytheinae) (Scott above, and Scott, J. A. & D. M. Wright, Butterfly phylogeny and fossils, in Kudrna, Otakar (ed.), Butterflies of Europe, Vol. 2, Aula-Verlag, Wiesbaden, in press). Just as the principle of parsimony has its final judgment on entire trees rather than single characters, phylogenies must be based on numerous characters—the more the better—and not on single characters. There will always be characters that are weak or difficult to interpret, or that show reversals, and even when worthless characters are discarded the remaining characters will not be of equal value; robust characters should be given greater weight. The shift to middle leg antenna cleaning is a strong character, but the detailed modifications of the male foreleg represent weak characters. The evolutionary history of weak characters is best determined by devising a phylogenetic tree using all characters (weighting the strong characters more heavily) and then using that tree to determine what happened to the weak traits. Using this method, the ancestral nymphalid-lycaenid foreleg may have shrunk to Libytheinae size, then later in Nymphalidae the male and female foreleg shrank further, while in Lycaenidae the Libytheinae-type foreleg changed to a feather-duster type male foreleg in Riodininae, and in Lycaeninae the foreleg became larger again, etc.; but all we know for certain is that the ancestral nymphalid-lycaenid foreleg was small in at least one sex.

The character of the pupal middle leg touching the eye would have to evolve only once on my phylogeny (in the ancestor of Nymphalidae-Lycaenidae) contrary to Robbins, and would have to be lost only once (in the ancestor of Lycaeninae, because Riodininae also have the trait).

It is good to question phylogenies, but one should not waste much time on weak characters; better to look for new characters, because the more one looks at a group of organisms, the more characters one finds. In most groups one can quintuple the known list of characters with hard work using morphology and behavior of all life stages.

My two papers are "cladistic" because they use the main two principles of cladistics, that a branch must be defined using shared derived traits, and that each branch must be monophyletic. Of numerous rules in cladistic variants, only those two rules are really necessary. It is also important to list all the character changes that must have occurred on the branches of the chosen tree to produce the character states observed in the living taxa; thus some weak characters are inevitably listed even though not given much weight in choosing the branching sequence of the chosen tree.

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Scott, J A. 1987. "Logic and phylogeny: reply to R.K. Robbins." *Journal of the Lepidopterists' Society* 41, 216–218.

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