

On the functional foreleg tarsus in *Caerulea* males (Lepidoptera: Lycaenidae: Polyommattini)

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Abstract. With very few exceptions, males in the butterfly family Lycaenidae have fused foreleg tarsomeres lacking distal claws. Functional five-segmented male foretarsi with claws are for the first time reported from the species-rich Lycaenidae tribe Polyommattini. In the *Glaucopsyche* section, both species of the Sino-Tibetan endemic subgenus *Caerulea* (*coeligena* Oberthür 1876, *coelestis* Alpheraky 1897) uniquely share this unusual trait. The phylogenetic significance of that character within the Lycaenidae is discussed.

Leg structures of arthropods often yield valuable characters for phylogenetic inferences. Among the Lepidoptera, leg morphology has been amply used in attempts to resolve questions concerning the higher classification. Recent examples for the Papilionoidea, or true butterflies, were published by Robbins (1988a & b, 1989). A five-segmented tarsus with one distal pair of claws on all legs constitutes the groundplan of butterfly tarsal structure. This groundplan is preserved in the families Papilionidae and Pieridae, whereas in the Riodinidae and Nymphalidae (sensu Harvey 1987, 1991) foretarsi of both sexes show various degrees of reduction (females) or fusion (males) of tarsomeres and bear no claws. In particular, forelegs are not used for walking in these two families.

In the family Lycaenidae a different pattern prevails. Female lycaenids always possess functional and fully segmented foretarsi, whereas males of almost all species have entirely fused tarsomeres and foretarsal claws are absent (so-called ankylosed tarsi). However, in both sexes the foretarsi are used in walking. As a rare exception (ca. 70 out of roughly 4500 described species, cf. Bridges 1988), segmented foretarsi with claws occur in males of a few Lycaenidae genera. The taxa recorded thus far are: *Liphyra*, *Euliphyra*, *Aslauga*, *Paraslauga*, *Egumbia*, *Lachnocnema* and *Thestor* (together constituting the predominantly Ethiopian tribe Liphyrini of the subfamily Miletinae); the East Asian genera *Artopoetes*, *Japonica*, *Ussuriana*, *Coreana* and *Protantigius* (all in the Theclini-Thecliti); the New Guinean *Titea* (Theclini-Luciiti); one species of the Oriental genus *Pratapa* and the Bornean endemic *Sukidion inores* (Eumaeini-Iolaiti); and the Neotropical *Theclopsis* (Eumaeini-Eumaeiti; see Eliot 1973, Robbins 1988b; higher classification largely following Scott & Wright 1990 and Fiedler 1991). We here report on the first observation of males with functional foretarsi in the large cosmopolitan tribe Polyommattini, representing more than 1000 described species.

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Fig. 1. Adults of the *Glaucopsyche* group of related species. Column 1, male upperside; 2, female upperside; 3, underside. Row 1, *Glaucopsyche alexis*, Spain; *Maculinea arion*, France; *Iolana iolas*, Spain; *Caerulea coelestis*, Tibet; *C. coeligena*, Tibet; *Phengaris atroguttata*, Taiwan (female, India).

In the course of morphological studies on the *Glaucopsyche* section sensu Eliot (1973) (this grouping is also referred to as Scolitantidini, Mattoni 1977), the senior author discovered functional foretarsi in both species of the taxon *Caerulea* Forster 1938. The Holarctic *Glaucopsyche* section comprises about 15 recognized nominal genera with some 50

species and several hundred so-called subspecies (Mattoni 1977, Bridges 1988). The phylogenetic relationships between the "genera" are not yet established, nor have all species or subspecies been revised. *Caerulea* contains only two species: *C. coeligena* (Oberthür 1876) with ssp. *pratti* (Hemming 1931), and *C. coelestis* (Alpheraky 1897) with ssp. *dubernardi* (Hemming 1931). Both are poorly known from a limited geographical area in southern China: Szechuan, Hupeh, and the eastern border of Tibet. Sometimes considered to constitute a single species only (Bridges 1988), they appear to be partly sympatric supporting their status as two valid species with two subspecies each (Hemming 1931, Mattoni unpubl.). Their life-histories and ecology are totally unknown, except that they occur at relatively high altitudes and are early spring fliers (implying a probable pupal hibernation, as usual in the *Glaucopsyche* section except in *Maculinea*).

The phylogenetic relationships of *Caerulea* are uncertain, although the male genitalia are quite similar to *Maculinea*. Forster (1938), in erecting *Caerulea*, classified it as a subgenus of *Glaucopsyche* together with *Maculinea*. The legs of *Caerulea* are quite dissimilar to other members of the *Glaucopsyche* complex. In addition to the possession of distinct male tarsomeres, femur and tibia are robust in *Caerulea* and the fore tibia has a well developed distal process (much smaller in *Glaucopsyche* s. str., absent in *Maculinea*). Furthermore, *Caerulea* males do not possess androconia. Figure 1 shows adult specimens, both sexes and undersides, of representatives of the presumptive closely related genera or subgenera involved in this discussion. Figure 2 illustrates the male genitalia of the same set of species. These figures present an overview of the very rich set of character states available for study in this group of insects.

Figs. 3-6 illustrate both male and female forelegs, with a detailed ventral view of the tarsomeres in both sexes. The chaetotaxy is different between the two sexes, particularly conspicuous is the greater spine number (A-type trichoid sensilla) of the female. The limited sample comprising two different subspecies of *C. coeligena* precludes a definite statement about sexual dimorphism in *Caerulea* leg chaetotaxy, but such dimorphism is quite usual among the Lycaenidae (Robbins 1988b, Mattoni unpubl.).

The ankylosed condition of the foretarsus, obviously an apomorphic character state relative to the Papilionoidea groundplan, is male-limited in lycaenid butterflies. In any population, therefore, genetic competence exists for developing a functional tarsus, since such competence is present, and the character invariably expressed, in the females. Secondary reversion of the functional male foretarsus would consequently represent a form of "decoupling" as discussed by Vane-Wright (1979).

We suggest that the ankylosed condition originated by a unique "macromutational" event. This event occurred in the ancestral stem lineage giving rise to the Lycaenidae, Riodinidae and Nymphalidae (these 3 families together form a well-defined monophyletic unit:

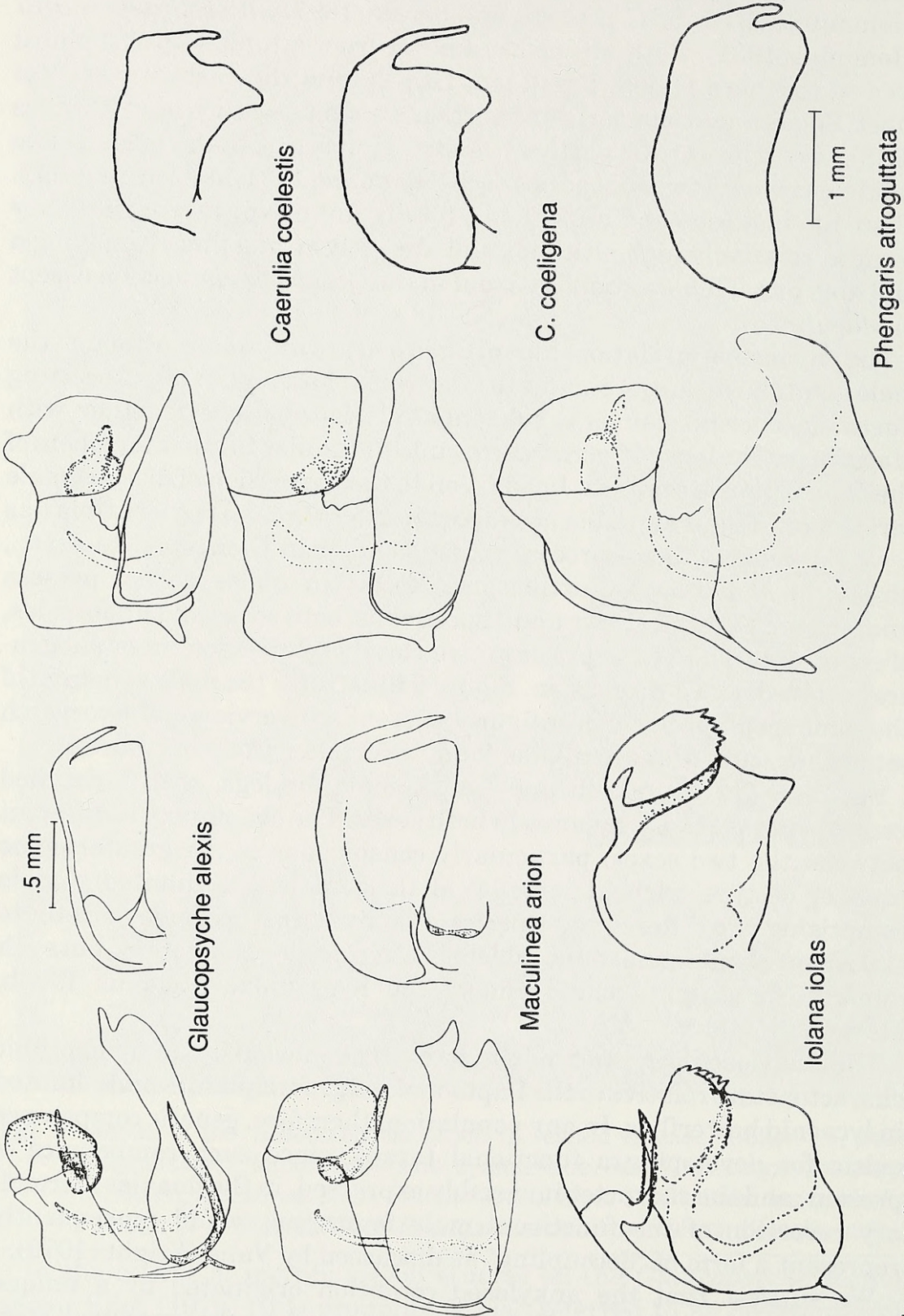


Fig. 2. Male genitalia, lateral view and valve. Species shown in figure 1 and discussed in text.

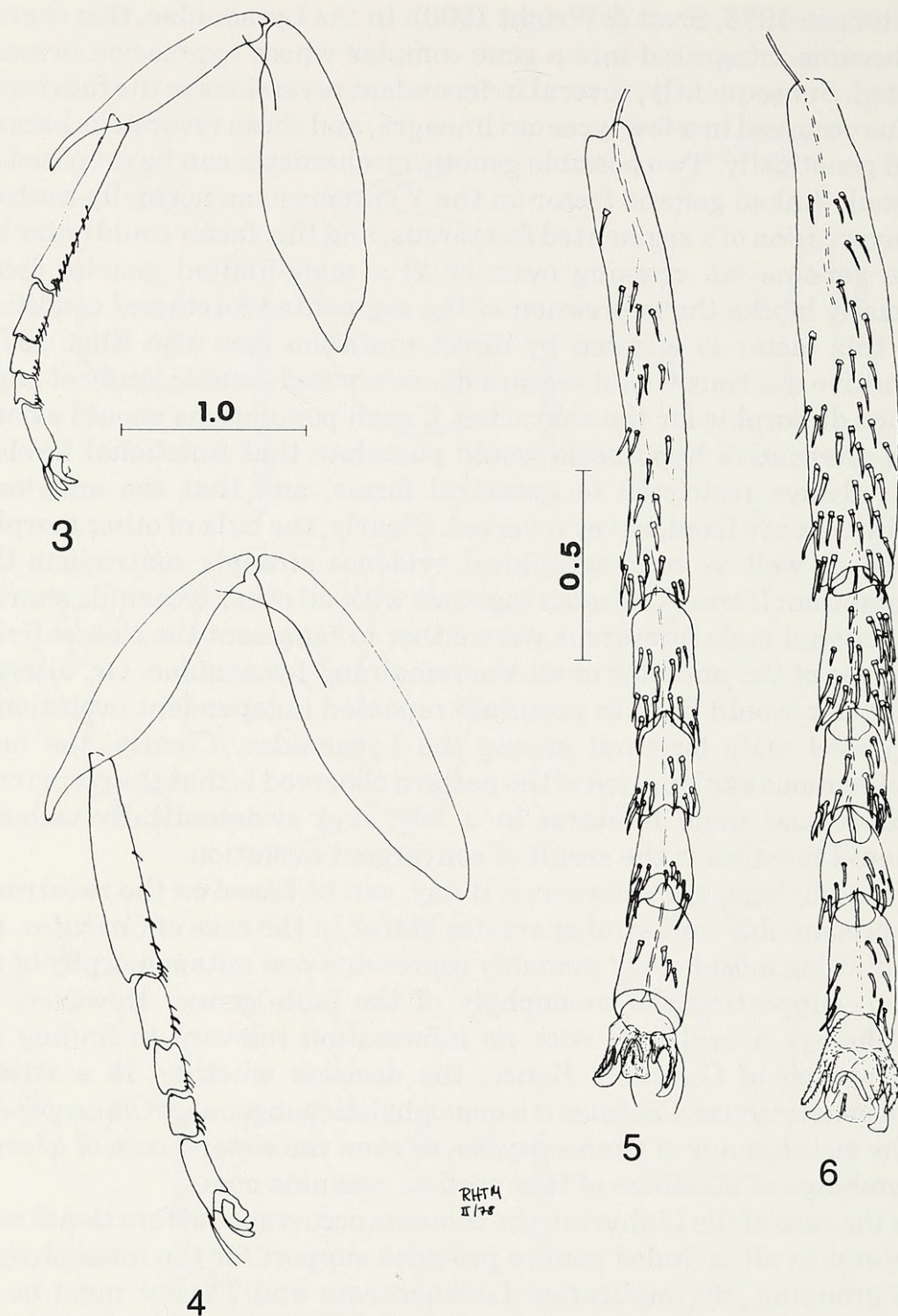
Kristensen 1976, Scott & Wright 1990). In the Lycaenidae, this character became integrated into a gene complex whose expression is male-limited. Subsequently, several independent reversions to the functional tarsus occurred in a few lycaenid lineages, and these reversions became fixed genetically. Two possible genetic mechanisms can be proposed: 1) a female-linked genetic factor on the Y chromosome normally controls the expression of a segmented foretarsus, and this factor could enter the male genome via crossing over; or 2) a male-limited genetic factor normally blocks the expression of the segmented foretarsal condition, and this factor is affected by direct mutation (see also Eliot 1973). Definitive analysis would require discovery and genetic study of populations dimorphic for the character, if such populations should exist.

An alternative hypothesis would postulate that functional forelegs were always restricted to ancestral forms, and that the ankylosed condition, once fixed, never reverted. Clearly, the bulk of other morphological as well as zoogeographical evidence strongly contradicts this assumption. If true, *Caerulea* together with all other lycaenids sharing a functional male foretarsus were either to represent the closest living relatives of the ancestor of all the remaining Lycaenidae. Or, alternatively, one would have to postulate repeated independent evolution of ankylosed male foretarsi among the Lycaenidae. Clearly, the most parsimonious explanation of the pattern observed is that the recurrence of functional male foretarsi in a few, and systematically isolated, lycaenid lineages is the result of convergent evolution.

What phylogenetic inferences, if any, can be based on the recurrence of a presumably ancestral character state? In the case of *Caerulea*, the peculiar leg morphology probably represents one autapomorphy of the group, supporting the monophyly of the (sub-)genus. However, leg morphology provides us with no information relevant to finding the sister-taxon of *Caerulea*. Hence, the decision whether, in a strictly phylogenetic sense, *Caerulea* is a monophyletic subgenus of *Glaucopsyche*, or the sister-genus of *Glaucopsyche*, or even the sister-taxon of a larger assemblage of members of that section, remains open.

In the case of the Liphyrini, the common occurrence of functional male foretarsi in all included genera provides support for the monophyly of this grouping. By implication *Lachnocnema* and *Thestor* must be removed from the Miletini sensu Scott & Wright (1990). This alteration in tribal arrangement, also suggested by Eliot (pers. comm.), well reflects the zoogeography of the Miletinae. Liphyrini in the new sense adopted here are then wholly Ethiopian with the single exception of *Liphyra* (probably a secondary invader of the Oriental region), whereas vice versa Miletini become Oriental with one African (*Megalopalpus*) and one Nearctic (*Feniseca*) extension.

Four of the Thecliti genera with functional male foretarsi (*Artopoetes*, *Coreana*, *Ussuriana*, *Japonica*) belong to a common clade with larval hostplants in the Oleaceae. Thus, loss of the ankylosed male foretarsus



Figs. 3-6 *Caerulea* forelegs.

Fig. 3. Femur, tibia, and tarsus. *C. coelestis coelestis*, male, China, Tatsienlou, Tibet, no date, ex coll. Oberthür. RHTM #128.

Fig. 4. Femur, tibia, and tarsus. *C. coeligena pratti*, female, China, Ichang, Hupeh, no date. RHTM #129.

Fig. 5. Ventral view of tarsomeres. *C. coeligena coeligena*, male, China, Tibet, 1887, leg. R. Dejean. RHTM #127.

Fig. 6. Ventral view of trasomeres. *C. coeligena pratti*, female, same specimen as in Fig. 2.

might be a synapomorphic trait of this assemblage. However, the Iberian *Laeosopis roboris* clearly belongs to this same group (based on morphological grounds as well as hostplant association), but retains the ankylosed condition (D. Kovac, pers. comm.). A definitive treatment requires a phylogenetic analysis of the Thecliti as a whole.

In all other lycaenids with functional male foretarsi, this trait can at best be used as additional autapomorphy defining small genera (like *Titea* or the monotypic *Sukidion*), or species-groups. Nevertheless, the recurrence of presumed ancestral character states is in itself an interesting phenomenon, and it remains to be seen whether further cases can be discovered in the course of morphological studies of hitherto insufficiently known Lycaenidae subgroups.

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