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A dated molecular phylogeny of the Proctolabinae (Orthoptera, Acrididae), especially the Lithoscirtae, and the evolution of their adaptive traits and present biogeography

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Abstract

We present a phylogeny of the Proctolabinae derived from their 12S and 16S mitochondrial ribosomal gene sequences, using 15 genera and 24 species. Phylogenetic analysis was performed using 4 different methods embodying different assumptions (maximum parsimony, neighbor-joining, maximum likelihood and Bayesian probability methods), all of which result in closely similar trees. The results largely corroborate the relationships and classification previously suggested by morphology. A phylogenetic tree including members of the Oedipodinae, Proctolabinae and Melanoplinae, fulfills the criteria of a molecular clock, which we calibrate using the divergence of the Oedipodinae from the other acridid subfamilies (Gaunt & Miles 2002). The major "star-burst" radiation of acridid subfamilies, previously documented by the present authors on the basis of a different analysis, and here represented by the divergence of the Proctolabinae and Melanoplinae, is estimated to have occurred 60 Mya, at the K/T boundary. The modern tribes and subtribes of the Proctolabinae were established in the subsequent 10 My, and most of the current genera were established between 25 and 35 Mya. We examine the phylogenetic distribution of food-plant specialisation, and of the correlated traits of flightlessness and of endo- and epiphytic oviposition, primarily within the subtribe Lithoscirtae. The original specialisation of this group was apparently on the Solanaceae, soon after the origin of that family around 38 Mya, with later radiation onto the Asteraceae and other unrelated families. The spectrum of food plants used is not based on relationship but rather on ecological proximity. Oviposition in or on the food-plant is primitive for this subtribe, and has been developed in different ways in the various clades. The power of flight has been lost and/or regained and wing form modified independently in several different lineages throughout the subfamily. The modern and historical biogeography of the subfamily is discussed in the light of its apparent antiquity and of the current understanding of Central American plate tectonics.

Key words

phylogeny, molecular clock, Orthoptera, Acrididae, Proctolabinae, Oedipodinae, Melanoplinae, host-plant specialization, brachyptery, biogeography

Introduction

The Proctolabinae are a subfamily of acridid grasshoppers, first raised to that status by Amédégnato (1974) and further classified, principally on the basis of their male genitalia, by Amédégnato (1977), Amédégnato and Poulin (1987), Descamps (1976, 1980, 1981), Descamps and Rowell (1978, 1984) and Rowell (2000). The subfamily currently contains 29 genera and 202 species, and more are in process of description. The current classification is given in Table 1 [derived from Amédégnato & Poulain (1987), who also briefly review the biology and biogeography of the subfamily].

To summarize the information contained in these works, the Proctolabinae are restricted to the Neotropics, extending from southern Mexico to northern Paraguay and southern Brasil, and live in wet forest up to about 2000 m elevation. Ecologically, most fall into 1 of 2 categories. The members of the first category are fully winged and mostly arboreal; they occur in both primary and secondary forest throughout the range of the subfamily, but are most diverse in South America. This ecological category includes the tribe Coscineutini and 3 of the 4 subtribes of the tribe Proctolabini (the Proctolabae, the Eucephalacrae and the Saltonacrae) and accounts for the majority of the genera and species. The second category consists mostly of brachypterous or micropterous genera which are found on woody forbs, shrubs or colonizing tree species in secondary successional areas within the forest, such as in light-gaps or at forest edges. This category is confined to Central America and corresponds roughly to the fourth subtribe of the Proctolabini, the Lithoscirtae. Occasionally otherwise flightless genera of the Lithoscirtae contain fully winged species convergent with the Proctolabae, such as *Ampelophilus coeruleus* and all species of the genus *Leioscapheus*. Conversely, *Proctolabus*, a Mexican genus of the Proctolabae, is ecologically convergent with the Lithoscirtae and some of its species are brachypterous, as is the little-known Colombian *Azotocerus*.

The Central American Lithoscirtae are notable ecologically for two features: they are oligophagous or even monophagous, and the genera are composed of assemblages of geographically separated but ecologically similar species, often with very restricted ranges, usually all eating the same or closely related plants (Rowell 1978, 1983, 2000). The different genera, on the other hand, sometimes eat very different plants and a similar diversity of food plants is present between species of a few genera. This suggests that past food-plant shifts may have been associated with taxon generation. This pattern, one of correlated trophic and morphological adaptation, with approximately generic-level foodplant specialisation plus local vicariant speciation, is familiar in some other groups of herbivorous insects [*e.g.*, psyllid Homoptera (Burckhardt & Lauterer 1989), chrysomelid Coleoptera (Farrell 1998, Termonia *et al.* 2001), some Lepidoptera (Ehrlich & Raven 1964)]. It is however unusual within the phytophagous Orthoptera Caelifera, which are often moderately wide-range oligophages or, somewhat less frequently, food-plant specialists (Gangwere 1972, Otte & Joern 1977, Rowell 1978); usually in this group there is no detailed correlation between feeding habits and systematics, though there are rough trends of this sort at the tribal or subfamilial level (*e.g.*, most gomphocerines eat grasses, most coptacridines eat composites, and many copiocerines eat palms). Associated with their specialisation on woody or semiwoody forest plants, many Lithoscirtae have changed their

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Table 1. Classification of the genera of Proctolabinae, after Amédégnato & Poulain 1987. In parentheses, the number of currently described species in each genus.

Subfamily Proctolabinae
Tribe Coscineutini
Coscineuta Stål 1873 (7)

Tribe Proctolabini
Subtribe Lithoscirtae
Ampelophilus Hebard 1924 (4)
Drymacris Descamps & Rowell 1978 (1)
Drymophilacris Descamps 1976 (7)
Leioscapheus Bruner 1908 (7)
Lithoscirtus Bruner 1908 (4)
Tela Hebard 1932 (4)
Paratela Descamps & Rowell 1978 (1)

Subtribe Proctolabae
Adelotettix Bruner 1910 (9)
Azotocerus Descamps 1976 (1)
Balachowskyacris Descamps & Amédégnato 1972 (6+)
Cercoceracris Descamps 1976 (10)
Cryptocloeus Descamps 1976 (4)
Dendrophilacris Descamps 1976 (14)
Dorstacris Descamps 1978 (1)
Halticacris Descamps 1976 (2)
Kritacris Descamps 1976 (1)
Poecilocloeus Bruner 1910 (59, in 9 species groups)
Proctolabus Saussure 1859 (8)
Witotacris Descamps 1976 (3)
Zodiacris Descamps 1980 (3)
Zosperamerus Bruner 1908 (7)

Subtribe Saltonacrae
Eucerotettix Descamps 1980 (1)
Harpotettix Descamps 1981 (2)
Loretacris Amédégnato & Poulain 1987 (1)
Saltonacris Descamps 1976 (8)
Ypsophilacris Descamps 1980 (1)

Subtribe Eucephalacrae
Eucephalacris Descamps 1976 (17)
Pareucephalacris Descamps 1976 (3)

oviposition habits from the plesiomorphic soil-depositing type to epi- or possibly endophyllous oviposition, with corresponding changes in the structure of the ovipositor. A parallel morphological development appears in the arboreal South American Saltonacrae (Descamps 1976, 1980; Amédégnato & Poulin1987); it is however not yet known whether these too are foodplant specialists, as could be expected from this morphology.

The Proctolabae fall rather clearly into 2 groups. One group is found in Northern South America and Central America, and, with the exceptions noted above, consists of fully winged species of relatively unmodified morphology. The other group is Amazonian, are canopy dwellers, and tend to have modified cycloid wings; in our sample this is represented only by the genus *Poecilocloeus*. The Coscineutini contains the single genus *Coscineuta*, which is found from northern Amazonia to Trinidad and Panama, and is morphologically similar to the northern group of the Proctolabae. On the basis of genital and cercal structure, both Descamps (1976) and Amédégnato & Poulain (1987) considered *Coscineuta* the most primitive proctolabine taxon.

Knowledge of phylogeny is an important prerequisite to a discussion of the evolution of morphological, ecological and behavioral adaptations (see *e.g.*, Brooks & McLennan 1991, Harvey & Pagel 1991). Current views on the phylogeny of the Proctolabinae are based on morphology; only Descamps (1976) and Amédégnato (1977) presented trees which allow the formulation of testable hypotheses. Since then, many more taxa have been described and more knowledge of the genital structures of both sexes obtained.

In this paper we present a phylogeny of these insects derived from their mitochondrial ribosomal gene sequences, and show that it largely corroborates the relationships and classification suggested by morphology. We show that a phylogenetic tree including members of the acridid subfamilies Oedipodinae, Proctolabinae and Melanoplinae fulfills the criteria of a molecular clock; we derive from this phylogeny a temporal framework within which to examine the evolution of the group and their current biogeography. The subfamily apparently diverged from other acridid subfamilies around 60 Mya, and most of the current genera were established between 25 and 35 Mya. We present data on the food plant specialisation of most of the genera of Central American proctolabines, add the reported food plants of some of the South American genera (Descamps 1980, Amédégnato 1997), and map the results onto the molecular phylogeny. We also examine the phylogenetic distribution of the morphological correlates of flightlessness and of endo- and epiphytic oviposition, both of which can plausibly be associated with food-plant specialisation (Rowell 1978, Braker 1989b).

The sequences used in this investigation were derived by P.K. Flook, who was also responsible for their original alignment and for the LINTRE analysis. All other analyses and data presented are due to C.H.F. Rowell.

Methods

1. Molecular phylogeny.

Collection and sampling.— Most taxa were collected in the field and immediately preserved in 2 changes of >95% ethyl alcohol, in which they were then kept at *ca* 5°C until their DNA was extracted. In most cases this was done from a single leg. A few sequences were derived from pinned and dried specimens, some up to 15 y old. Some of these were checked by comparing the sequences with those derived from alcohol material; there were no significant differences. Unfortunately, very few pinned specimens yielded sequenceable DNA, probably because they had been humidified after the initial collection by being relaxed for preparation. This prevented us from including many Amazonian taxa in the phylogenetic analysis; the sample is thus heavily weighted towards those taxa which we could collect in the field in Central America, supplemented by some others from South American and Mexico which were donated by colleagues. The subtribe Saltonacrae (infrequent and confined to Amazonia) were unfortunately not available for analysis at all and are ignored in the remainder of this article. The final taxon set including outgroup taxa (see below), comprised 44 species. Table 2 lists the species used, their origins, and the reference numbers of the deposited sequences.

The remaining laboratory methods have been presented in detail by Flook and Rowell (1997a). In brief, fragments of the mitochondrial 12S and 16S ribosomal RNA genes were amplified by PCR and both strands sequenced. The sequences were aligned and

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ambiguous portions rejected. As no significant phylogenetic conflict between the 2 fragments could be detected, the 2 fragments were combined for phylogenetic analysis in a "total evidence" approach (for details and rationale see Flook & Rowell 1997a, 1997b). The initial length of the combined sequences was 959 bp, of which 395 bp were derived from the 12S gene. 208 bp were excluded from the analysis as being ambiguously aligned, leaving a final length of 751 bp. Of these, 132 bp were invariant, 92 uninformative, and 527 informative. GC content was 31%. The alignment was derived from a larger alignment of sequences from over 200 orthopteran species. Sequences were aligned manually but reference was made to the secondary structure models of Buckley *et al.* (2001). The alignment can be obtained on request from the authors.

Phylogenetic analysis was carried out using the programmes PAUP* 4.0 [version Beta 10 (Swofford 2002) and earlier versions] and MrBayes (Huelsenback & Ronquist 2002), both in their Macintosh versions. A ratio of 2:1 was used for weighting transversions against transitions, following our 1997 work. Analyses were made using maximum parsimony, neighbor-joining, maximum likelihood and Bayesian probability methods. More details of procedures are given in the appropriate figure captions. Recent work (Rokas *et al.* 2003) makes a powerful case for believing that the sequences of 20 or more independent genes need to be analysed in order to resolve a phylogenetic tree fully. This level of data collection is and was beyond our means. We are however concerned to derive the tree that is most strongly supported by the data that we do have. To this end we employed 4 very different methods of analysis, differing greatly in their assumptions, to examine the consistency of the results. All methods produced closely similar trees, as shown below; we take this to indicate that tree topologies presented are not especially sensitive to the exact method of analysis chosen, and within the limits of the small molecular sample, adequately represent the probable phylogeny which can be deduced from it.

As outgroup we originally used members of the subfamily Copiocerinae, which have been shown in our previous work (Flook & Rowell 1997a) to be part of the same acridid radiation, and on morphological grounds (Amédégnato 1977) are probably the closest living relatives of the Proctolabinae. However, maximum likelihood methods of analysis (though not the others) sometimes produced trees which placed some of the Copiocerinae we used inside the Proctolabinae, suggesting that this group is too closely related for our purpose. We therefore ultimately used as outgroup members of the Oedipodinae and the Lentulidae, which we have previously shown (Flook & Rowell 1997a, Rowell & Flook 1998) to be early clades of the acridoid radiation. There were no differences in the topology recovered within the Proctolabinae using the two different sets of outgroups.

To plot the phylogenetic distribution of morphological or behavioral characters we used MacClade v. 3.0.6 (Maddison and Maddison 1996).

2. Molecular clock hypotheses and dating of phylogenies.

If molecular evolution took place at a constant rate (a "molecular clock"), it is obvious that a date on any node of a phylogeny which included genetic distances would allow one to calculate the ages of all other nodes. The date of a node is usually estimated by a geologically dated fossil (which, of course, provides only a minimum estimate of time to the node in question, as the fossil almost certainly postdates the original evolution of its taxon). The problem is that molecular evolution does not proceed at a constant rate; a variety of statistical methods have therefore been elaborated to test phylogenetic trees against their original sequence data and to calculate the probability that the observed changes are compatible with the assumption of a molecular clock.

There are relatively few Caeliferan fossils appropriate for calibrating molecular phylogenies. The most desirable is the eumastacid **Archaeomastax jurassicus* Sharov 1968 (Upper Jurassic). To use this it is necessary to derive a tree which includes minimally the eumastacids, the Proctolabinae and another acridid subfamily of appropriate age to date the divergence of the former. For this purpose we selected a sample (n = 6) of Melanoplinae, which our previous work had shown to be adequately sampled, clearly monophyletic and of approximately the same age as the Proctolabinae. We used a sample of eumastacids (n=15, not listed in Table 1) representing 5 of the 8 to 9 extant eumastacid families, which produced a tree concordant with their morphological groupings. As outgroup we used the Tetrigoidea, the sister group to the Eumastacoidea plus all later caeliferans (Flook *et al.* 1999). Trees containing only these 4 taxa resulted in unstable or poorly resolved proctolabine phylogenies, probably because of the considerable genetic distance between the root taxa and the 2 modern acridid subfamilies. Restoring the proctolabine tree structure required including a taxon of intermediate age, such as the Oedipodinae (n = 9). Attempts to reduce the number of taxa in either the proctolabine or the eumastacoid samples (to simplify computation) also destabilised their phylogeny, presumably because of the relatively weak phylogenetic signal contained in their 12S/16S sequences. The tetrigoid outgroup could be reduced to 3 taxa of the family Batrachideidae without adverse effects. The final sample contained 58 taxa.

To test for constancy of the rate of change of the DNA sequences we used a likelihood ratio test (Felsenstein 1988, Goldman 1993). PAUP* 4.0 b10 was first used to perform a maximum parsimony heuristic search with 10 replicates, and the best resultant trees used as starting trees for maximum likelihood (ML) analyses. Likelihood estimates were found to be optimal when using the general time-reversible model of substitution, with all ratio matrix values estimated from the data, and a gamma distribution with shape parameter (alpha) also estimated from the data. Using these parameters, a ML heuristic search was performed; to reduce computation time we constrained all nodes which received bootstrap values of 90% or higher in the parsimony analysis. This procedure yielded a best tree with -ln L =9028.843. We then repeated the search with the added constraint of a molecular clock. The best tree found had -ln L = 9087.907. Treating the doubled difference of the two likelihoods as a value of χ^2 with (n-2) = 56 degrees of freedom, indicates a very significant difference between the 2 scores ($P \leq 0.005$), showing that a clock-like model of molecular evolution cannot be supported for this tree. We confirmed this negative result using a different test of rate constancy (Takezaki *et al.* 1995) as implemented in LINTRE (Takezaki 1996). [We also examined the relative rates of evolution of the different clades using the programme RRTree (Robinson-Rechavi & Huchon 2000), comparing the rate of change of the proctolabine taxa with that of each of the other taxa (Eumastacoidea, Oedipodinae, Melanoplinae) in turn, using the best parsimony tree as a constraint tree. This procedure yielded no significant differences, a result which appears to conflict with the previous one.]

Gaunt and Miles (2002) have recently presented a phylogeny of the insects based on 5 insect orders and the second codon of the cytochrome oxidase 1 gene, and shown that it does satisfy the requirements of the molecular clock hypothesis. They dated it using the mid-Carboniferous origin of the Blattaria, which are well represented in the fossil record. Their analysis includes 2 grass-

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Table 2. Taxa sequenced in this investigation.

Genus, species, author	Locality	Collector	GenBank Acquisition No.
Proctolabinae			
Coscineuta coxalis (Serville 1839).	PANAMA: Panama: Barro Colorado National Monument.	K. Harmes	AY569246 AY569212
Coscineuta cicatricosa Bolívar 1890.	ECUADOR: Sucumbios: S. Pablo de Kantesiya.	K. Riede	AY569247 AY569213
Coscineuta sp.	ECUADOR: Napo: Río Tiputiki.	C. Amédégnato & S. Poulain	AY569248 AY569214
Leioscapheus guapiles Roberts 1973.	COSTA RICA: Alajuela: Virgen del Socorro.	C.H.F. Rowell	AY569249 AY569215
Leioscapheus gracilicornis (Bruner 1907).	COSTA RICA: Puntarenas: Osa Peninsula.	C.H.F. Rowell	AY569250 AY569216
Ampelophilus truncatus Rehn 1905.	COSTA RICA: Cartago: Tres Ríos.	C.H.F. Rowell	AY569251 AY569217
Ampelophilus coeruleus Descamps & Rowell 1984.	COSTA RICA: S. José: Río Paynor.	C.H.F. Rowell	AY569252 AY569218
Ampelophilus olivaceus (Giglio-Tos 1897).	COSTA RICA: Puntarenas: Gamba.	C.H.F. Rowell	AY569253 AY569219
Paratela ovatipennis (Rehn 1905).	COSTA RICA: Limón: Río Toro Amarillo.	C.H.F. Rowell	AY569254 AY569220
Tela viridula (Bruner 1908).*	MEXICO: Veracruz: Montepio.	C. Amédégnato & S. Poulain	AY569255 AY569221
Tela neeavora Descamps & Rowell 1978.	COSTA RICA: Heredia, Puerto Viejo.	C.H.F. Rowell	AY569256 AY569222
Lithoscirtus viceitas Rehn 1929.	COSTA RICA: Limón: Cerro Uatsi.	C.H.F. Rowell	AY569257 AY569223
Lithoscirtus daedalus Rehn 1929.	COSTA RICA: Cartago: Tapantí.	C.H.F. Rowell	AY569258 AY569224
Drymophilacris monteverdensis Descamps & Rowell 1978.	COSTA RICA: Puntarenas: Monteverde.	C.H.F. Rowell	AY569259 AY569225
Drymophilacris bimaculata (Rehn 1905).	COSTA RICA: Heredia: Puerto Viejo.	C.H.F. Rowell	Z93288 Z93250
Drymacris nebulicola (Rehn 1929).	COSTA RICA: Cartago: Tres Ríos.	C.H.F. Rowell	AY569261 AY569227
Eucephalacris borellii (Giglio-Tos 1897).	BRASIL: Sao Paulo: Itirapina.	C.S. Carbonell, A. & P. Mesa	Z93289 Z93251
Poecilocloeus sp.	ECUADOR: Napo: Coca/Tena Loreto.	C. Amédégnato & S. Poulain	AY569263 AY569229
Kritacris arboricola Descamps 1976.*	COSTA RICA: Alajuela: Upala.	F.D. Parker	AY569264 AY569230
Zosperamerus sp.	COSTA RICA: Limón: Cerro Uatsi.	C.H.F. Rowell	AY569265 AY569231
Balachowskyacris olivaceus (Bruner 1908).	COSTA RICA: Heredia Puerto Viejo.	C.H.F. Rowell	AY569266 AY569232
Balachowskyacris olivaceus (Bruner 1908) (dried).*	COSTA RICA: Heredia Puerto Viejo.	C.H.F. Rowell	AY569267 AY569233
Adelotettix gigas Descamps & Rowell 1978.*	COSTA RICA: Guanacaste: Río Naranjo	F.D. Parker	AY569268 AY569234
Adelotettix sp.	ECUADOR: Napo: Coca/Tena: Loreto.	C. Amédégnato & S. Poulain	AY569269 AY569235
Proctolabus mexicanus (Saussure 1859 .	MEXICO: Morelos: Cuernavaca.	T.H. Hsiao	Z93287 Z93249

* Taxa marked with an asterisk were sequenced from dried material, all others from fresh or alcohol-preserved material.

hoppers, the oedipodine *Locusta migratoria* and the gomphocerine *Chorthippus parallelus*; the best date associated with their divergence is *ca* 97 Mya. If this date is accepted, it allows the possibility of dating the proctolabine phylogeny without including the Eumastacoidea. A further ML analysis with and without clock constraints was performed using only the Proctolabinae, Melanoplinae and Oedipodinae (total n=40), with the Oedipodinae as outgroup. The starting tree was obtained by neighbor joining. To reduce computation time the 3 nodes defining the 3 subfamilies were constrained. This procedure yielded a doubled difference in likelihood scores of (4625.0978 - 4606.6020) × 2 = 36.99. Treated as χ^2 with n-2 = 38 degrees of freedom, this corresponds to $p \geq 0.5$, indicating no significant difference between the constrained and unconstrained models. A molecular clock can therefore be accepted for this tree.

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Table 2 continued.

Genus, species, author	Locality	Collector	GenBank Acquisition No.
Melanoplinae			
Melanoplus sanguineus (Fabr. 1798)	USA: Utah: Logan:	C.H.F. Rowell	AY569270 AY569236
Scotussa lemniscata (Stål 1860)	URUGUAY: Dpto. Treintetrés: 10 km. NE of Cerro Chato, source of Río Olimar	C.H.F. Rowell & C.S. Carbonell	AY569271 AY569237
Hesperotettix viridis (Thomas 1874)	USA: Utah: Logan: Green Canyon	C.H.F. Rowell & P. Ruben	AY569272 AY569238
Aidemona azteca (Saussure 1861)	MEXICO: Veracruz: Fortín-Orizaba. 930 m.	R. Sanchez	AY569273 AY569239
Jivarus americanus Giglio-Tos 1898	ECUADOR: Azuay: Sigsig. 2500-2900 m.	C. Amédégnato & S. Poulain	AY569274 AY569240
Jivarus sp.	ECUADOR: Loja: 2600 m.	C. Amédégnato & S. Poulain	AY569275 AY569241
Oedipodinae			
Aiolopus thalassinus (Fabricius 1781).	UGANDA: Buganda: Entebbe, 1100 m.	C.H.F. Rowell	AY352427 AY352428
§ *Mecostethus parapleurus* (Hagenbach 1822).	SWITZERLAND: Solothurn: Seewen.	C.H.F. Rowell	AY352431 AY352432
Oedipoda coerulescens (Linn 1758).	SWITZERLAND: Baselland: Pratteln.	C.H.F. Rowell	Z93293 Z93255
Locusta migratoria migratoria (Linn 1758).	Laboratory culture, origin unknown.		Z93294 Z93256
Morphacris fasciata (Thunberg 1815).	ISRAEL: no other locality data.	L. Mizrahi	AY352429 AY352430
Arphia conspersa Scudder 1875.	USA: Colorado, Fort Collins.	C.H.F. Rowell	Z93295 Z93257
Sphingonotus fuscoirroratus (Stål 1860).	ECUADOR: Galapagos Islands: Isla Floreana.	D. Otte	AY352433 AY352434
Sphingonotus haitensis (Saussure 1861).	DOMINICAN REPUBLIC: Santiago: Janico.	D. Perez	AY352435 AY352436
Trimerotropis cincta (Thomas 1880).	USA: Colorado: Fort Collins.	C.H.F. Rowell	AY352437 AY352438
Lentulidae			
Lentula obtusa (Stål 1878).	SOUTH AFRICA: Natal: Inchenga.	M. van Staaden	AY569276 AY569242
Eremidium nr. equuleus (Karsch 1896).	SOUTH AFRICA: Natal: Inchenga.	M. van Staaden	AY569277 AY569243
Karruia sp.	SOUTH AFRICA: Fraserburg Dist. Minverwagspoort.	J. Irish	AY569278 AY569244
Usambilla sagonai (Ramme 1929).	UGANDA: Buganda: Mpanga Forest.	C.H.F. Rowell	AY569279 AY569245
Rhainopomma montanum (Kevin 1950).	KENYA: Teita Hills: Mwaganini Forest.	M. Mungai	Z97617 Z97601

§ The name *Mecostethus parapleurus* follows Coray and Lehmann (1998). Most orthopterists know this species as *Parapleurus alliaceus* (Germar 1817).

3. Food plant determination.

Food plant use within the Lithoscirtae was determined principally by field observations in Costa Rica over a period of some 25 y, supplemented by less comprehensive and more recent observations in Panama. These were checked by experimental food-choice trials and by microscopic examination of epidermal patterns and trichome structures in the faeces and gut contents of both wild-caught and captive insects, with subsequent comparison with preparations of putative food plants [as originally described by Mulkern and Anderson (1959) and Brusven & Mulkern (1960)]. We have used the data of other authors (listed in Tables 3 & 4) for South American and Mexican species.

4. Morphology.

Adult females were relaxed and positioned as necessary to display the ovipositor valves. These were drawn in lateral and dorsal view at 25 × magnification with a drawing tube, and the following measurements taken with a digital stage micrometer, used in conjunction with an eyepiece graticule. 1) Length of the dorsal valves, measured from the base of the cercus to the tip of the valve; 2) the width of the individual dorsal valve at its widest point distal to the end of the supra-anal plate; and 3) the span of the 2 dorsal valves, being the widest point measured between the outer margins of both valves, distal to the supraanal plate. The length of the dorsal valve was then compensated for the differing sizes of the taxa by being expressed as the percentage of the length of the hind femur; both width and span were expressed as a percentage of the length of the dorsal valve. Additionally, notes were made on the shape of

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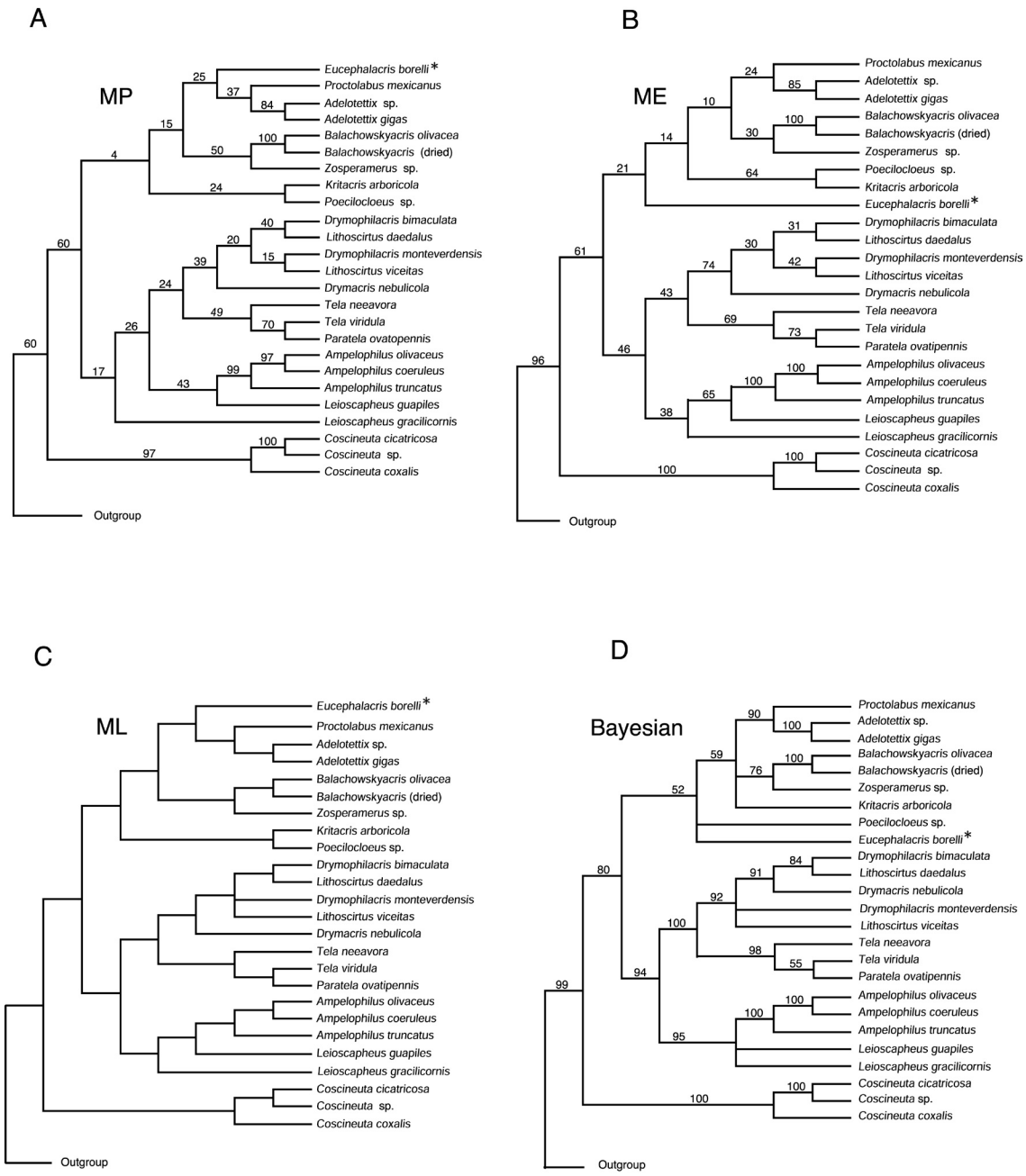


Fig. 1. The topologies recovered by 4 different methods of phylogenetic analysis. For all analyses, a transition:transversion weighting ratio of 2:1 was used, no sites were assumed to be invariable, and all sites were considered equal. DNA substitution models where applicable were General Time Reversible (GTR) or HKY85, and a gamma distribution was assumed with shape parameter 0.3 (estimated). The branch-swapping algorithm used was tree bisection/reconnection (TBR). Note that all 4 methods give essentially identical topologies, with exception of the taxon *Eucephalacris* (asterisked), which is placed as the sister taxon to all Proctolabae by Minimum Evolution and Bayesian methods, but subsumed within the Proctolabae by Parsimony and Maximum Likelihood methods. **A.** Maximum Parsimony, a cladistic method. Bootstrapped tree, 100 repetitions, each of 10 replicates. The numbers on the tree are bootstrap percentages. Starting tree(s) were obtained via stepwise addition, the addition sequence was random and a single tree was held at each step during stepwise addition. 7438 trees were used to calculate the 50% majority-rule consensus. **B.** Minimum Evolution, a distance method. Starting trees obtained via neighbor joining. Bootstrapped tree, 1000 repetitions. The numbers on the tree are bootstrap percentages. Distance measure = HKY85. Negative branch lengths allowed, but set to zero for tree-score calculation. 1016 trees were used to calculate the 50% majority rule consensus. **C.** Maximum likelihood. The starting tree was the best tree found by a heuristic search using Minimum Evolution and the HKY85 distance measure. From this were calculated its likelihood, the empirical base frequencies, the transition/transversion ratio, and the gamma shape constant, assuming an HKY85 model for unequal base frequencies and that rate variation is gamma distributed. These parameters were then used in the likelihood analysis. In this, the initial branch lengths were calculated using the Rogers-Swofford method, and the addition sequence was random. Trees with a likelihood removed by more than 5% from the target value were rejected. The calculation took about 5h with a 600 MHz computer — therefore no bootstrap was attempted. There was no change in topology when the starting tree was a parsimony tree. **D**. Bayesian probability. A GTR model and gamma-distributed rates were assumed. The analysis was run for 250,000 generations, with trees saved every 200 generations, producing 1,250 saved trees. The first 250 trees were ignored ("burn-in") when calculating the consensus, shown here. Numbers on the tree are the percentage of occurrence of the relevant branch in the 1000 remaining trees, and correspond to their Bayesian posterior probabilities.

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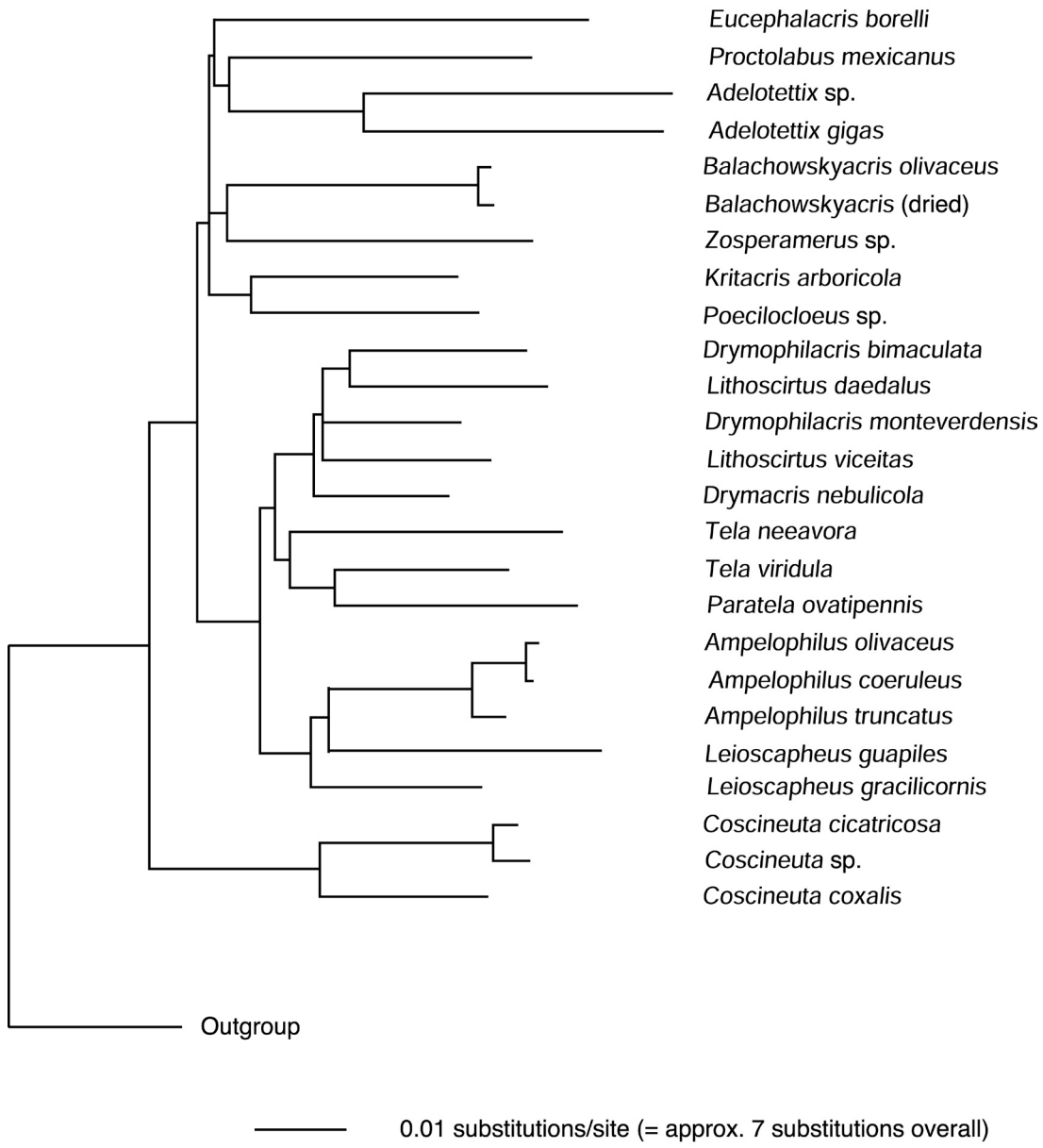


Fig. 2. Maximum Likelihood phylogram, showing branch lengths. The taxa with the most conservative sequences in each group are *Drymacris nebulicola* (Lithoscirtae), *Kritacris arboricola* (Proctolabae), and *Coscineuta coxalis* (Coscineutini), respectively. The most differentiated taxon is *Adelotettix*, with *Eucephalacris borelli* and *Leioscapheus gracilicornis* as runners-up.

the valves, the presence or absence of teeth, and the length of the ventral valves relative to the dorsal ones. In some species, in which the available individuals were not measurable for some reason, measurements were made on congeneric species, *e.g.*, *Tela viridula* was replaced by *Tela chlorosoma*.

The hind wings of flighted species were dissected from relaxed pinned specimens, spread and pinned to plastic foam with the aid of Minutennadeln, air dried and drawn under 12 × magnification. Venation was named after Ragge (1955).

Results

1. Phylogeny.

Fig. 1A-D presents the phylogenies recovered under parsimony, neighbor-joining, maximum likelihood and Bayesian analysis respectively. The details of the methods are indicated in the captions; for an exhaustive discussion of the first 3 methods and their application to this data set, see Flook & Rowell (1997a & b). Non-parametric bootstrap support for many of the nodes in the first 2 trees is weak, especially for the parsimony tree; the maximum likelihood tree was not bootstrapped, owing to computational constraints; the Bayesian method gives the highest (posterior) probability values overall, as has been remarked upon by other workers (Suzuki *et al.* 2002). The topology of all the trees is however essentially identical, except for the position of the Eucephalacrae (see below).

In all analyses, a strongly supported *Coscineuta* (forming the tribe Coscineutini) is the most basal taxon, followed by a dichotomy within the Proctolabini between the predominantly South American subtribes (Proctolabae + Eucephalacrae) and the

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Table 3. Food plants of Central American proctolabines. Data from Rowell, unpub. and Rowell 2000, except for the records of *Tela viridulus* and *Proctolabus* spp. (Amédégnato, pers. com.), and of *Coscineuta* (Popov *et al.* 1994). The actual specificity of the individual proctolabine species is often much higher than suggested here, as they are typically confined to one or a few plant species of the genera named.

Taxon	No. spp. (No. spp. for which food plants determined)	Food plant: Family (Genera)	Sequenced? Yes/no
Adelotettix	9 (0)	unknown	y
Ampelophilus	4 (4)	Asteraceae (*Verbasina, Vernonia*), Solanaceae (*Solanum, Acnistus*)	y
Balachowskyacris	6 (1)	Euphorbiaceae (*Plukenetia*), possibly more.	y
Coscineuta	7 (1-2)	Numerous tree species and cultivated dicots. Not investigated in detail.	y
Drymacris	2 (1)	Solanaceae (*Solanum, Witheringia*)	y
Drymophilacris	7 (3)	Solanaceae (*Solanum, Witheringia, Lycium*); *D. nigrescens* also takes some Asteraceae.	y
Kritacris	1 (1)	Ulmaceae (*Trema*)	y
Leioscapheus	7 (2-3)	Ulmaceae (*Trema*); sometimes Solanaceae (*Solanum*)	y
Lithoscirtus	4 (4)	Solanaceae (*Solanum, Witheringia, Acnistus*); or, Solanaceae & Asteraceae	y
Paratela	1 (1)	Asteraceae (*Vernonia*)	y
Proctolabus	8 (3)	Solanaceae (*Solanum*)	y
Tela	5 (2)	Nyctaginaceae (*Neea*). Solanaceae (*Solanum*)	y
Zosperamerus	6 (1)	Ulmaceae (*Trema*)	y

Central American Lithoscirtae. The latter divides into 2 clades, corresponding to the groupings *Drymacris/Drymophilacris/Lithoscirtus* (the Lithoscirtus clade) plus *Tela/Paratela* (the Tela clade), and *Ampelophilus/Leioscapheus* (the Ampelophilus clade). In the Bayesian analysis, virtually all nodes within the Lithoscirtae have posterior probabilities of 90% or better; in the other analyses, bootstrap support is often considerably weaker.

Within the Lithoscirtus clade (Baysian P = 92%) the constituent 3 genera are never properly resolved. Mitochondrial ribosomal RNA genes are generally slowly evolving, and therefore not well suited for resolution of species or closely-related genera. *Drymacris*, however, is usually placed basally, as expected from morphology. Within the Tela clade (Baysian P = 98%), *T. neeavora* is always basal to *Paratela* and *T. viridula*; this suggests that the genus *Tela* is paraphyletic with respect to *Paratela*. The Tela and Lithoscirtus clades are sister-groups in all methods, with support reaching P = 100% in the Bayesian analysis.

Within the Ampelophilus clade (Baysian P = 95%), the 2 *Leioscapheus* spp. are not very tightly linked, never being strongly clustered (parsimony even puts *L. gracilicornis* outside the clade, as the basal lithoscirtan, but morphology and the other computational methods all suggest that this is wrong). Within *Ampelophilus* the micropterous *A. truncatus* (and NOT the fully winged *A. coeruleus*) is invariably basal.

Within the Proctolabae (itself supported by a Bayesian probability of only 52%) relationships are less satisfactorily resolved than within the Lithoscirtae.

Eucephalacris (asterisked in Fig. 1) is placed as basal in Bayesian and NJ ME analyses (as expected if the Proctolabae and Eucephalacrae are indeed separate subtribes), but not in parsimony or ML analyses, where this genus is included within the Proctolabae. The molecular analyses thus do not clearly differentiate the Eucephalacrae from the Proctolabae; however, the former are badly undersampled in our study, being represented by only a single sequence, and this may explain this anomaly.

Within the Proctolabae all methods place *Poecilocloeus* at or close to the base of the clade, either alone or with *Kritacris* as its sister-genus. As the former is the only purely Amazonian genus of the Proctolabae in our analysis, this result may suggest an early division of the Proctolabae into an Amazonian group and a Central American/Northern South American group, comprising the rest of the present sample. A larger sample is required to check this point. *Adelotettix*, a genus with a rather plesiomorphic morphology, is surprisingly not resolved as basal within the Proctolabae, but instead

Table 4. Food plants of South American proctolabines (data from Descamps 1980, and Amédégnato 1997 and pers. com. 1998).

Taxon	No. spp. for which food plants determined	Food plant	Sequenced? Yes/No
Coscineuta	3	Many different dicot. trees and lianas.	y
Dendrophilacris	1	Lauraceae (*Bielschmieda*)	n
Eucephalacris	0	Unknown	y
Pareucephalacris	1	Bark?	n
Poecilocloeus	2	Flacourtiaceae	y
Saltonacris	1	Polyphagous	n
Witotacris	1	Vochysiaceae (*Qualea, Ruizterania*)	n
Cryptocloeus	1	Melastomataceae (*Loreya*)	n

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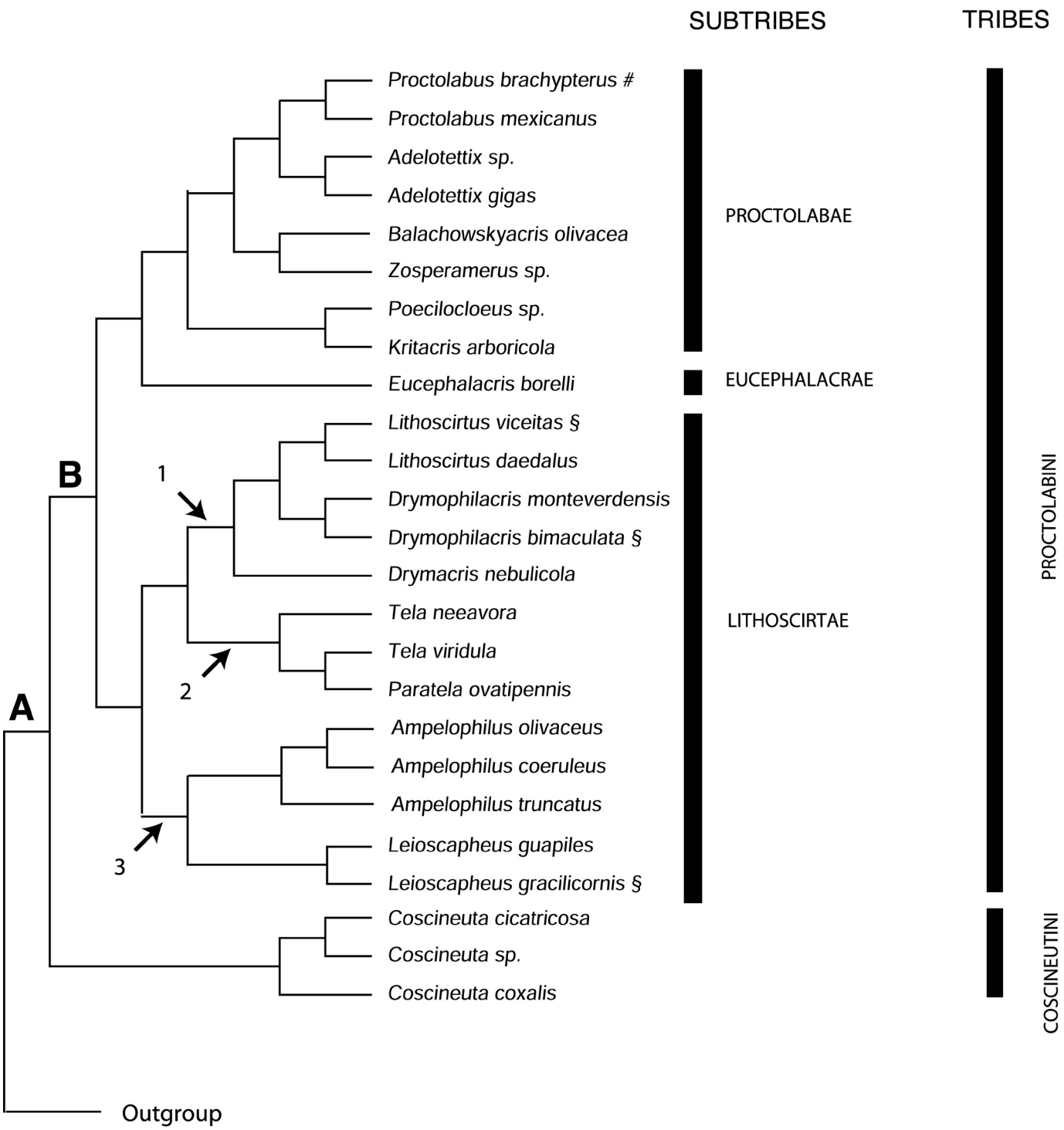


Fig. 3. The topology adopted for the remainder of this paper. It corresponds to the topology recovered by the ME and Bayesian methods (*i.e.*, with the Eucephalacrae resolved as the sister taxon of the Proctolabae, as also suggested by morphology), with the following alterations: a. the genera *Lithoscirtus, Drymophilacris* and *Leioscapheus* have each been made monophyletic, on morphological grounds; the taxa which have been moved are indicated with the symbol §. b. The taxon *Proctolabus brachypterus* (not sequenced, indicated with the symbol #) has been added as the sister taxon of *P. mexicanus* (which was sequenced). Node A corresponds to the division of the Proctolabinae into the tribes Coscineutini and Proctolabini. Node B shows the division of the Proctolabinae into 2 lines, the Central American subtribe Lithoscirtae and the predominantly or entirely South American subtribes Proctolabae + Eucephalacrae. The branches marked 1, 2, and 3 correspond to the *Lithoscirtus/Drymophilacris/Drymacris* clade, the *Tela/Paratela* clade, and the *Leioscapheus/Ampelophilus* clade respectively. The black bars to the right show the morphology-based systematic divisions. Note the close correspondence to the phylogenetic topology.

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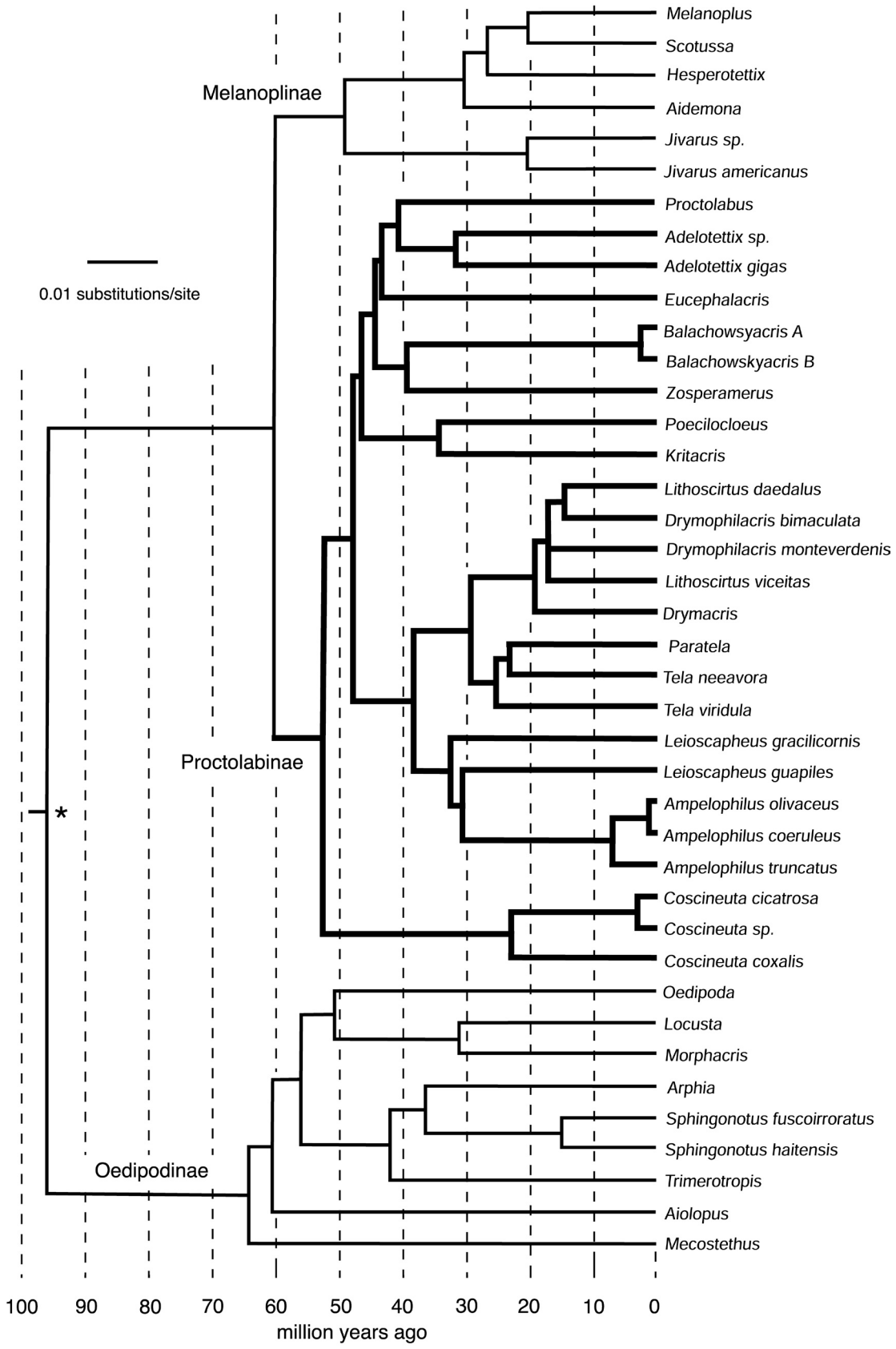


Fig. 4. Estimated timing of the evolution of the Proctolabinae, Melanoplinae and Oedipodinae. The tree is the strict consensus of 3 ultrametric ML trees with a molecular clock constraint; the calibration is based on the divergence (asterisked) of the Oedipodinae and remaining subfamilies at 97 Mya (Gaunt & Miles 2002). Further explanation in the text.

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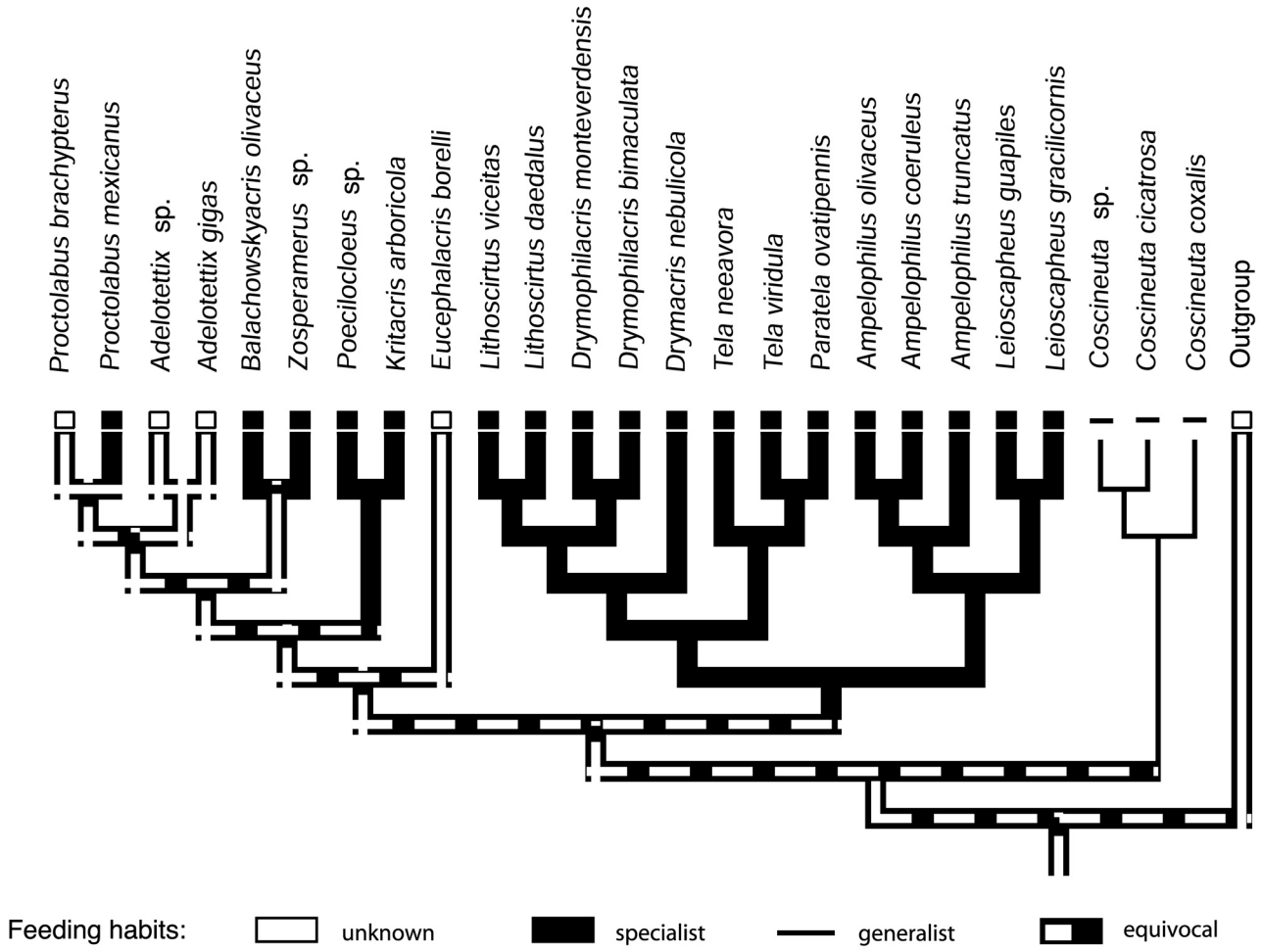


Fig. 5. Evolution of food plant preference in the Proctolabinae. I. Generalist/Specialist. The most parsimonious reconstruction makes the Coscineutini primitively polyphagous and the Lithoscirtae primitively oligophagous; the Proctolabae are all specialists as far as is known to date, but the primitive state is equivocal due to lack of data.

is consistently indicated as a derived form, with *Proctolabus* as its sister group; the same pairing was derived by Descamps (1976: Fig. 1) on morphological grounds. Otherwise, little can be said about the branching order within the *Proctolabae*; in the Bayesian analysis, only the groupings *Proctolabus* + *Adelotettix* (P = 91%) and *Balachowskyacris* + *Zosperamerus* (P = 76%) have reasonable support. The phylogram (Fig. 2) shows that the initial radiation of this group took place within a very short period of evolutionary time.

Summarizing, the different methods of analysis produce a consistent interpretation from the molecular data. The agreement between this molecular phylogeny and the morphological one (Descamps 1976, his Fig. 1; Amédégnato 1977) is reassuringly good (Fig. 3). There is complete agreement on the splits between the Coscineuti and the Proctolabini and between the Proctolabae and the Lithoscirtae. Within the Lithoscirtae, the genus groupings suggested by morphology are supported by sequence similarities. Where more than one species of a genus has been analysed, the molecular data in most cases support the generic grouping. The exceptions are within the closely related genera of the Lithoscirtus clade, which are poorly resolved. In these cases, however, the morphological evidence for the current genera (apomorphies in the structure of male genitalia and female subgenital plates, see Rowell 2000) is very strong. Mitochondrial ribosomal DNA is not in general well suited for analyses at the species level, due to its relatively slow rate of evolution.

The internal phylogenetic topology of the two outgroup clades was almost invariable in all analyses. The exception is the genus *Lentula*, which was variously placed as a basal lentulid (its normally accepted position), as an independent group of its own, or even as a basal oedipodine. It does not seem to be closely related to either of the other two clades of lentulids resolved here, consisting of the South African *Karruia* + *Eremidium* and the genetically and morphologically highly differentiated *Usambilla* + *Rhainopomma* from the wet forests of East Africa. Within the Oedipodinae (see Fig. 4), the genera *Mecostethus* and *Aiolopus* are basal, as expected from morphology; the remaining "band-wing" genera divide into 2 clades, corresponding to the New World genera (*Arphia, Sphingonotus, Trimerotropis*) and Old World genera (*Oedipoda, Locusta, Morphacris*) respectively.

2. Dating the phylogenetic tree.

As shown in the Methods section, the hypothesis of a molecular clock can be accepted for the ML phylogenetic tree derived for the Oedipodinae, Melanoplinae and Proctolabinae. The clock-constrained ML procedure found 3 ultrametric trees of the same log

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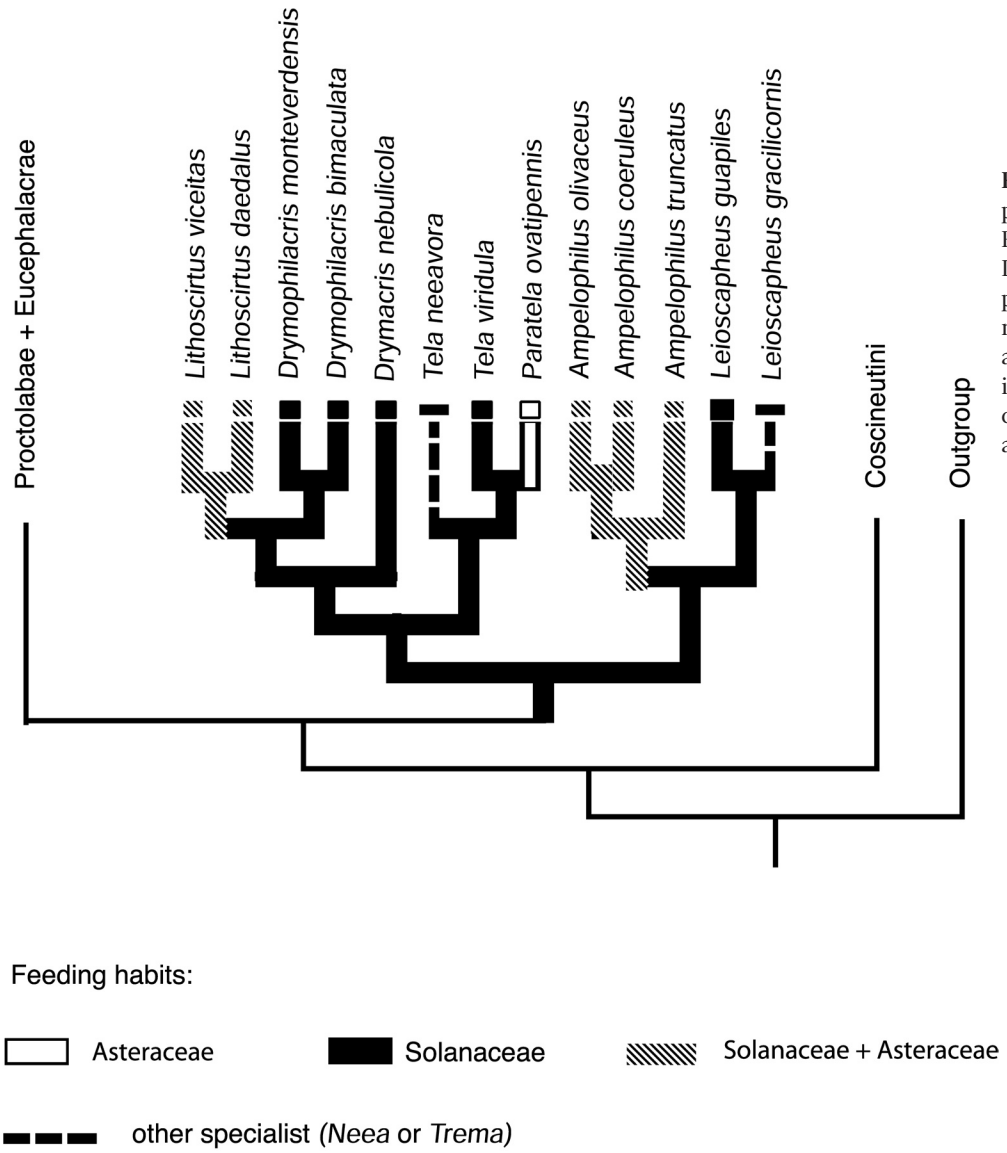


Fig. 6. Evolution of foodplant preference in the Proctolabinae. II. Foodplant preferences within the Lithoscirtae. The Lithoscirtae are primitively specialised on the Solanaceae, with subsequent exclusive or additional adoption of the Asteraceae in 3 independent cases, and of species of Nyctaginaceae and Ulmaceae on at least one occasion each.

likelihood, differing only in the divergence order of the poorly resolved *Lithoscirtus*/*Drymophilacris* species: the strict consensus is shown in Fig. 4. The topology of the Proctolabinae is the same as that found by normal ML methods (Fig. 1C). Taking the divergence of the Oedipodinae from the rest of the Acrididae as occurring 97 Mya (Gaunt & Miles 2002), the tree can be calibrated against geological time as shown (Fig. 4). The following timing of events is suggested by these data.

Apart from the Oedipodinae and a few other early-branching taxa, most of the remaining subfamilies of the Acrididae appear to have experienced a "star-burst" radiation over a relatively short period of time; the phylogenetic tree obtained shows a large unresolvable polychotomy at this point (Flook & Rowell 1977a, Rowell & Flook 1998). In the present data-set, this radiation can be equated with the split between the Proctolabinae and the Melanoplinae, here estimated at 60 Mya, *i.e.*, at the Cretaceous/Tertiary boundary. For comparison, the first undoubted fossil Acrididae are from the early Tertiary, about 50 Mya (Carpenter 1992). These palaeontological dates fit the molecular estimates well.

Within the Proctolabinae, the Coscineuti apparently diverged from the Proctolabini at around 53 Mya, and within the latter the Lithoscirtae and Proctolabae diverged at about 48 Mya. The modern genera within the Proctolabae are estimated to have diverged between 46 and 35 Mya; the genus *Adelotettix* (of which 2 different species were sequenced) is minimally 32 My old. Within the Lithoscirtae, the split between the 2 main clades (*i.e.*, the Lithoscirtus/Tela and the Leioscapheus/Ampelophilus clades) is estimated at 38 Mya. Both these clades divided again, at around 30 Mya; the modern genera *Leioscapheus, Ampelophilus*, (*Tela* + *Paratela*) and (*Lithoscirtus* + *Drymophilacris* + *Drymacris*) are minimally 20 to 30 My old. The 3 sequenced species of *Ampelophilus*, on the other hand, had a common ancestor only 8 Mya.

Within the Melanoplinae, the South American group Jivari split from the remaining (Northern Hemisphere) melanoplines some 50 Mya (see also Litzenbeger & Chapco 2003, Amédégnato *et al* 2003), and the 2 sequenced species of *Jivarus* diverged from each other 21 Mya; the remaining melanopline genera have divergence times between 31 and 20 Mya. Within the Oedipodinae, the band-winged clade diverged from the basal forms some 60 Mya, and split into Old World and New World lineages about 56 Mya; the sequenced genera have divergence times of 30 to 50 Mya.

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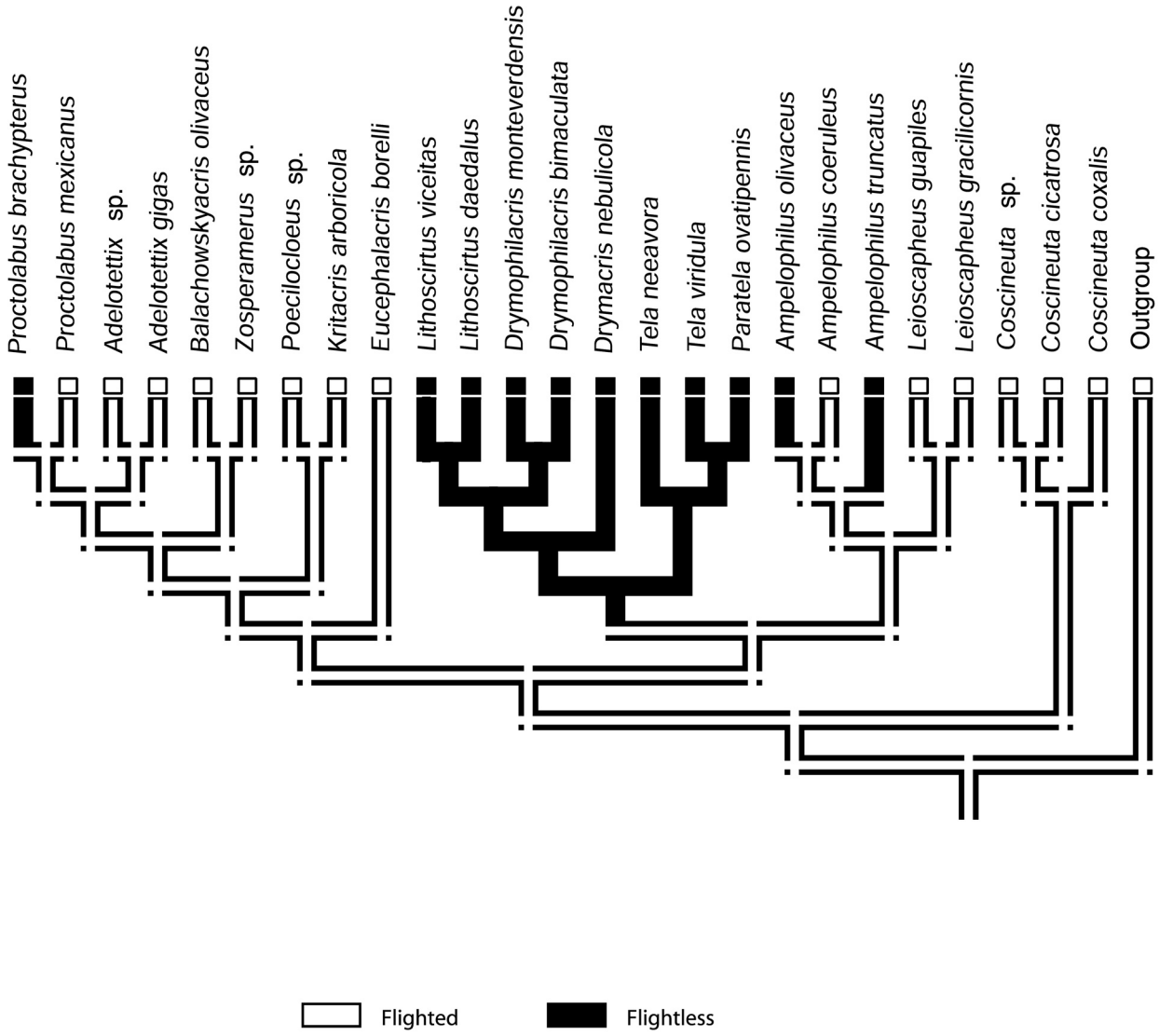


Fig. 7. Evolution of flightlessness in the Proctolabinae. The transition to flightlessness is here taken to be irreversible (see text). Under this assumption there are no equivocal states. The power of flight has been lost on at least 4 independent occasions.

3. Phylogenetic distribution of adaptive characters.

The phylogeny adopted here for purposes of character tracing is that shown in Fig. 3. The topology is that recovered by the Bayesian and Minimum Evolution analyses (see Fig. 1), chosen because their placement of *Eucephalacris* is in accordance with morphology. The following modifications and additions have been made:

a) *Proctolabus brachypterus* has been added to the tree as the sister of *P. mexicanus*. It was not sequenced. Morphology suggests that the 2 species are congeneric.

b) *Lithoscirtus viceitas* and *Drymophilacris bimaculata* have each been grouped with the other member of their genus. This can be readily justified on their morphological characteristics; see Rowell (2000) for a full description of the latter.

c) The 2 sequenced species of *Leioscapheus* have been made monophyletic, also on morphological grounds (see Descamps 1976).

A. Food plant specialisation.

The genera of Central American proctolabines and their known food plants are shown in Table 3. The corresponding data for South American proctolabine genera, insofar as these are known (Descamps 1980, Popov *et al*. 1994, Amédégnato 1997, and pers. com. 1998), are shown in Table 4.

Fig. 5 shows the distribution of generalist and specialist feeders mapped onto the phylogeny. From this it can be seen that the ancestral state of the Lithoscirtae is specialist, that of the Proctolabae and of the Proctolabini ambiguous, but quite possibly specialist too. The Coscineutini (containing only the single genus *Coscineuta*) are all wide-range polyphages. Whether this state is apomorphic or plesiomorphic within the subfamily depends on the coding of the outgroup. Our data do not bear on the ancestral state of the Proctolabinae. This would require knowing the sister group of the subfamily and its feeding habits. Unfortunately, the branching order of the acridid subfamilies cannot currently be resolved; the acridid radiation at the subfamily level appears to have been very sudden (see previous section).

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Table 5. The earliest macrofossil records (from Benton 1993) and fossil pollen records (from Muller 1981) of the angiosperm families known to be eaten by Proctolabinae.

Family	Earliest possible date (Mya)	Earliest certain date (Mya)	Earliest pollen record (Mya)
Asteraceae	53.2	37	32
Euphorbiaceae	87.6	69.5	60
Flacourtiaceae	62.7	58.5	30
Lauraceae		93.7	60
Melastomataceae	93.7	53.2	no data
Nyctaginaceae	93.7	3.4	53
Solanaceae	53.2	37	no data
Ulmaceae	143.2	69.5	92
Vochysiaceae	0.8	0.01	no data

Dates are the midpoint of the indicated geological stage, as given by Harland *et al.* 1990. "Earliest possible dates" are based on uncertain material.

Fig. 6 shows the use of the individual plant families by the specialist feeders within the Lithoscirtae. The most parsimonious reconstructions indicate that the ancestral specialisation of the Lithoscirtae was for the Solanaceae. The distribution of the ability to eat Asteraceae is also shown. This is found as a facultative property in *Ampelophilus* and in some species of both *Lithoscirtus* and *Drymophilacris*, and as a complete switch in *Paratela ovatipennis*, suggesting it is an extension of range from the Solanaceae, which has occurred convergently and independently within each of the 3 Lithoscirtae clades. In *Ampelophilus* and *Paratela* it may have been associated with genus formation. Two other Lithoscirtae species have abandoned the primitive Solanaceae hostplant for unrelated secondary succession trees (Table 3): *Tela neeavora* is a monophag on *Neea laetivirens* (Nyctaginaceae) and *Leioscapheus gracilicornis* is known to eat only *Trema micrantha* (Ulmaceae), like some other members of its genus (not shown), although *T. viridula* and *L. guapiles* still eat Solanaceae. Neither of these 2 shifts has been associated with larger morphological changes giving generic status.

Within the Proctolabae, we have no food plant data for *Adelotettix* or *Eucephalacris*. The remaining 5 genera shown on our trees are all food plant specialists, as far as is known. Both *Kritacris* and *Zosperamerus* eat *Trema*, but as they are never resolved as sister genera this habit has probably evolved independently in the 2 lines (and also a 3rd time in the Lithoscirtan genus *Leioscapheus*, see above). The alternative hypothesis, that *Trema*-specialisation evolved in the ancestor of the clade of which *Kritacris* is the most basal member, requires a subsequent loss of this character in at least 3 different lines. These data must however be treated with caution. Not only are there few Proctolabae genera represented in our analysis, but also *Balachowskyacris* and *Poecilocloeus* are both speciose genera (Table 1), and the food plants of only single species of each are known. These belong to the Euphorbiaceae and Flacourtiaceae respectively, but it is not clear how typical of the respective genera these plants are. All 3 species of *Proctolabus* for which data are available eat Solanaceae however, being in this as in other respects convergent with the Lithoscirtae. The ancestral specialisation of the Proctolabae is obscure, due to lack of data for this group.

B. Flight and wing morphology.

Fig. 7 shows the distribution of the capability of flight within the subfamily. Most flightless taxa are found within the Lithoscirtae. However, the flighted or partly flighted genera *Leioscapheus* and *Ampelophilus* are apparently not basal, but instead derived. The power of flight is usually considered unlikely to be regained in a brachypterous clade, due to the profound changes in morphology and physiology associated with this condition (*i.e.*, the character is irreversible — see Roff (1990) for discussion); acceptance of this hypothesis attributes the power of flight to the common ancestor of both *A. coeruleus* and *A. truncatus*, and this in turn has the formal effect of making the flighted condition primitive for the entire Lithoscirtae, again in accordance with the principle that flight loss is irreversible. This scheme implies that flight has been lost at least 3 times independently within the Lithoscirtae (once in the common ancestor of the Lithoscirtus and Tela clades, and at least twice within the genus *Ampelophilus*).

Contrary to the conventional view depicted above, Whiting *et al.* (2003) have recently proposed that the morphology and physiology of the flight system can be turned on or off in a unitary manner by the silencing or re-expression of hypothetical "master genes" in the pathway leading to flight, and have presented a molecular phylogeny of the Phasmida (considered by the present authors (1999) to be the sister-group to the Orthoptera) which supports this contention. If this hypothesis is accepted, 3 changes in flight expression are still required within the Lithoscirtae. For example, a loss at the base of the Lithoscirtus + Tela clade, and either one loss and one gain or 2 losses within *Ampelophilus*. An alternative scheme involving loss at the base of the Lithoscirtae and subsequent gain at the base of *Leioscapheus* and within *Ampelophilus* is equally parsimonious.

The plesiomorphic state of the remaining subtribes and of the Coscineutini is clearly to have functional wings. Interestingly, there has been at least one independent loss within the Proctolabae, within the genus *Proctolabus*, which has 6 flighted and 2 flightless (*P. cerciatus* and *P. brachypterus*) species. (The species we have sequenced, *P. mexicanus*, is flighted). Again, this is convergent with the state in the Lithoscirtae, as seen above in respect to food plant. *Azotocerus* is also brachypterous, but its phylogenetic position is not known.

Many proctolabines have what Descamps (1976) termed "cycloid" wings (Figs 8B, 8D-I). In these the hind wing is shortened along the axis that runs from the wing base to the tip of the remigium, but left unchanged along the axis running from the anterior to the posterior edge. In the unmodified condition (*Coscineuta*, Fig. 8A) the wing is longer than wide, and the remigium projects beyond the vannal area of the wing. In *Adelotettix* (Fig. 8C) the remigium is somewhat shortened but the wing otherwise unchanged. In *Eucephalacris, Balachowskyacris* and *Proctolabus* (Figs 8B, D, E) the remigium is as short or shorter than the vannal area, and in the latter 2 taxa there is the beginning of a reduction in the remigial venation, with the loss of either Rs, the posterior branch of the radius vein, or MP, the posterior medial vein, respectively. In some genera (*Zosperamerus, Leioscapheus*, Figs 8F & H), both of these veins are lost, leaving both M and R unbranched, and the remigium is very small in relation to the vannal area; the further reduction in venation in these genera may however merely reflect the small size of the insects. Parallel to these changes, the surface of the cycloid wing when expanded is modified from a plane surface to a dorsally convex one. In many genera the hind wing cannot be completely flattened for examination without causing splitting of the membrane along the distal parts of the radial veins, as shown by arrows in Fig. 8. The aerodynamic consequences of this change of shape are unknown.

Fig. 9 shows the phylogenetic distribution of the different modifications of the wings. There is a conflict between the phylogenetically derived position of *Adelotettix* and its wing morphology. It is

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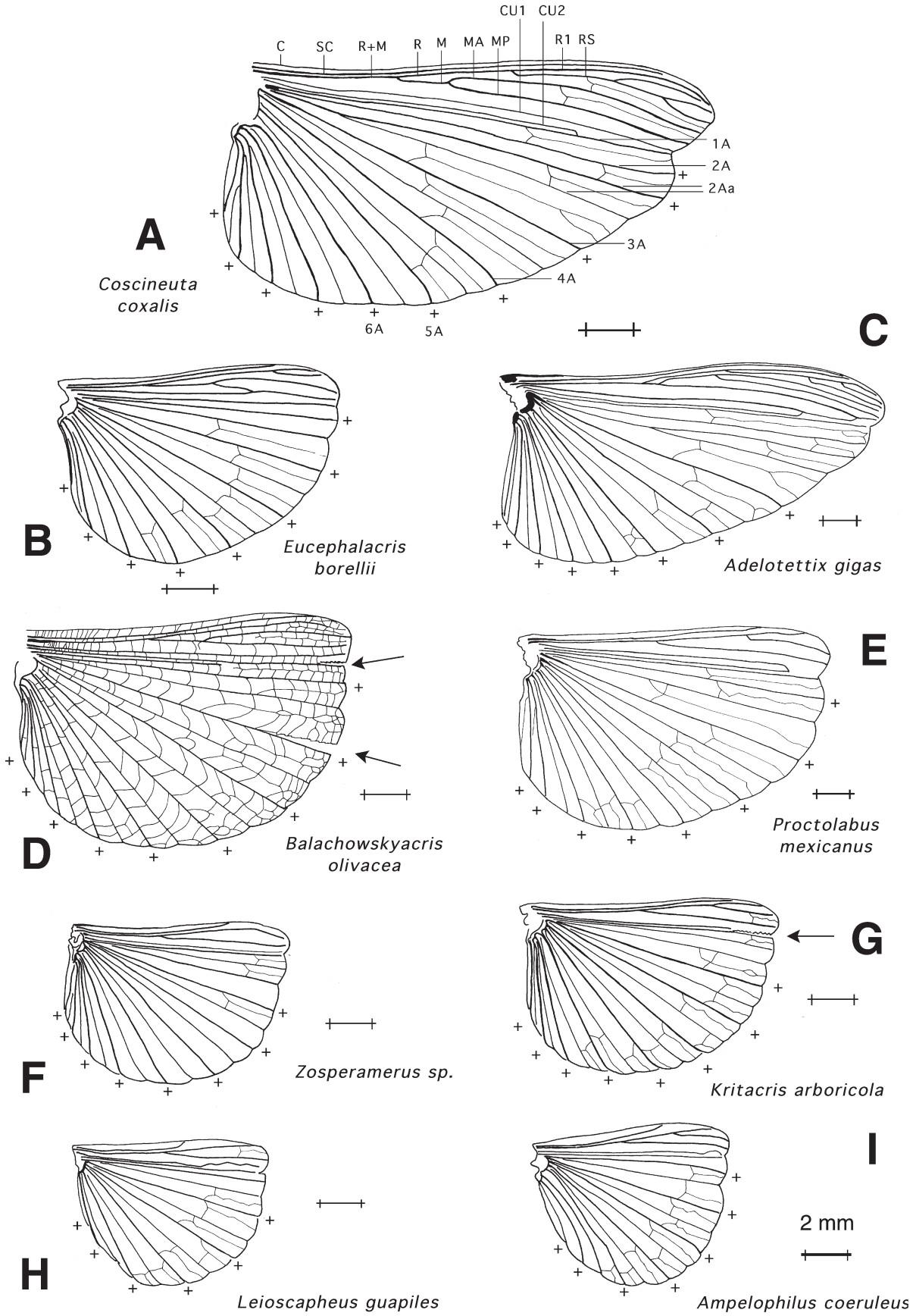


Fig. 8. Wing shape in the Proctolabinae. Arrows indicate splitting caused by flattening the naturally convex wing.

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the only member of the Proctolabini to have almost unmodified macropterous wings, similar to those of the Coscineutini and most other flighted Acrididae. Like flightlessness, the change from the primitive morphology may be irreversible. Applying this assumption to the present phylogeny makes the unmodified wing the primitive condition for the Proctolabae + Eucephalacrae. This in turn implies its independent loss on at least 4 occasions in the several lines of the Proctolabini. Were *Adelotettix* basal within the Proctolabae, or the loss of the primitive wing shape not irreversible (following the argument of Whiting *et al.* 2003), the phylogeny would necessitate fewer independent losses of normal wing morphology (see caption to Fig. 9).

Within the Lithoscirtae most taxa are brachypterous. The initial change happened in the common ancestor of the Tela and Lithoscirtus clades, and independently at least twice within the genus *Ampelophilus*. The most basal member of the Lithoscirtus clade, *Drymacris*, is still brachypterous, but there was been a further reduction to microptery in the common ancestor of the sister genera *Drymophilacris* and *Lithoscirtus*. The taxa which retain flight (*Leioscapheus, Ampelophilus coeruleus*) have typical cycloid wings (Figs 8 H, I), which must represent an independent acquisition of this trait, regardless of the correct position of *Adelotettix* within the Proctolabini (see above).

C. Ovipositor morphology.

In most Caelifera oviposition takes place in the soil, the eggs being protected by proteinaceous foam. In some taxa, however this habit has been lost and the eggs are placed either on or between leaves (epiphyllic oviposition) or inside the tissues of a plant (endophytic oviposition). These modifications are usually associated with food-plant specialisation, as they allow the female to place the eggs directly on the food plant, which in turn spares the larvae the dangers of having to seek a suitable host. Examples are found within *e.g.*, the acridid subfamilies Leptysminae, Copiocerinae, Oxyinae, Ommatolampinae and also in the Proctolabinae. Ideally, oviposition habits are determined by direct observation in the wild. Where these data are lacking, as is so for most species of Proctolabinae, a proxy can be found in the structure of the ovipositor. Ovipositor valves which are used to dig a hole in the soil or similar substrate are typically robust, relatively wide, often concave on their exterior dorsal and ventral faces — *i.e.*, spoon- or shovel-shaped — and either lack teeth totally or have only blunt serrations. Epiphyllic oviposition is associated with weak, often narrow and elongated ovipositor valves, tending towards a circular cross-section; in some cases the dorsal valves are spatulate, compressed dorsoventrally (pre-

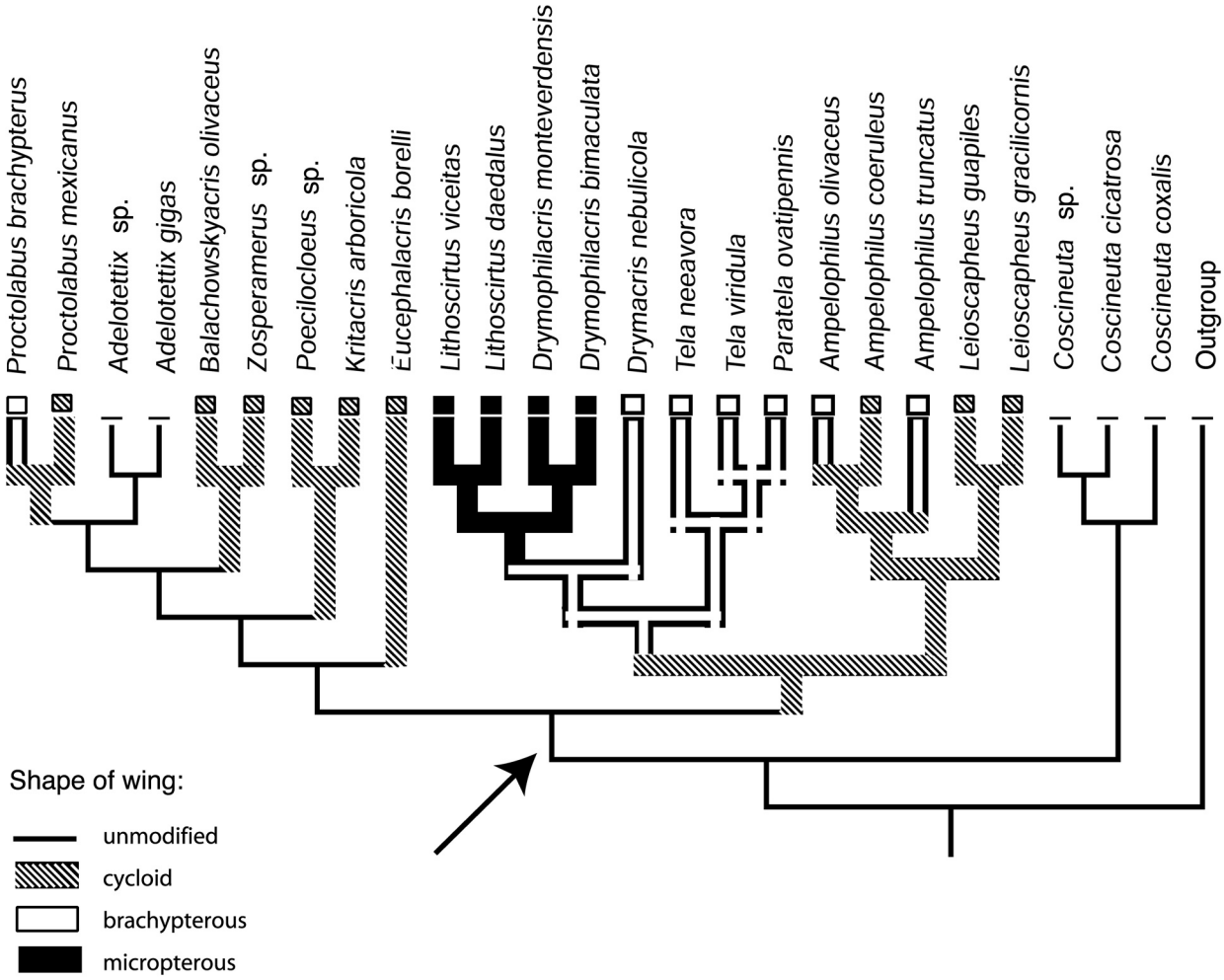


Fig. 9. Evolution of wing shape in the Proctolabinae. It is assumed that, once lost, an unmodified wing cannot be regained; further, that brachyptery and microptery are also irreversible. Under these assumptions, there are no equivocal states. Cycloid wings have evolved once in the Lithoscirtae, and, given the derived position of *Adelotettix*, at least 4 times within the Proctolabae and Eucephalacrae. If wings can be regained (see text), then cycloid wings may have evolved only once, in the common ancestor of the Proctolabini (arrow).

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sumably to manipulate the foam in which the eggs are embedded, and often divergent. Endophytic ovipositors usually have sharply pointed, hooked valves, with well developed sharp teeth arranged along saw-like outer edges (Braker 1989b); however, some animals with ovipositors of this type are known to lay in soil, rather than in plants, indicating that morphology alone is not adequate for a firm diagnosis of endophytic oviposition. Moreover, some species (*e.g.*, *Microtylopteryx hebardi*, Ommatolampinae, Braker 1989a) bite a preliminary hole in the stem or petiole of the food plant with the mandibles, and then insert the ovipositor to lay the eggs in the pith; this shows that the endophytic ovipositor must not necessarily be either sharp or saw-like.

When the measures relative length, breadth and span of the valves of proctolabine ovipositors are treated in isolation, they are not very illuminating. More can be gained from integrating these measurements (Fig. 10):

— The ovipositors of the generalist Coscineutini fit the description of typical soil-ovipositing grasshoppers as detailed above, and Coscineuta is indeed known to oviposit in the ground (Popov *et al.* 1994). Those of the Proctolabini are more varied.

— The ovipositors of most of the predominantly specialist Proctolabae are longer and more slender than those of *Coscineuta*, and the ventral valves are laterally compressed, fitting between the dorsal ones. They may be adapted to oviposition in clumps of arboreal humus. The exceptions among the Proctolabae are *Proctolabus* and *Adelotettix*. *Proctolabus* has long, thin valves edged with small sharp teeth. Its oviposition habit is unknown, but the structure suggests that it may be endophytic. On the other hand, the ovipositor of *Adelotettix* has the typical form of a soil-ovipositing species, not very different from *Coscineuta*.

— There is yet more diversity among the ovipositors of the Lithoscirtae. *Ampelophilus* species have relatively the longest valves of any, and they are narrow and saw-toothed, resembling those of *Proctolabus* in form. They too probably indicate an endophytic habit. The

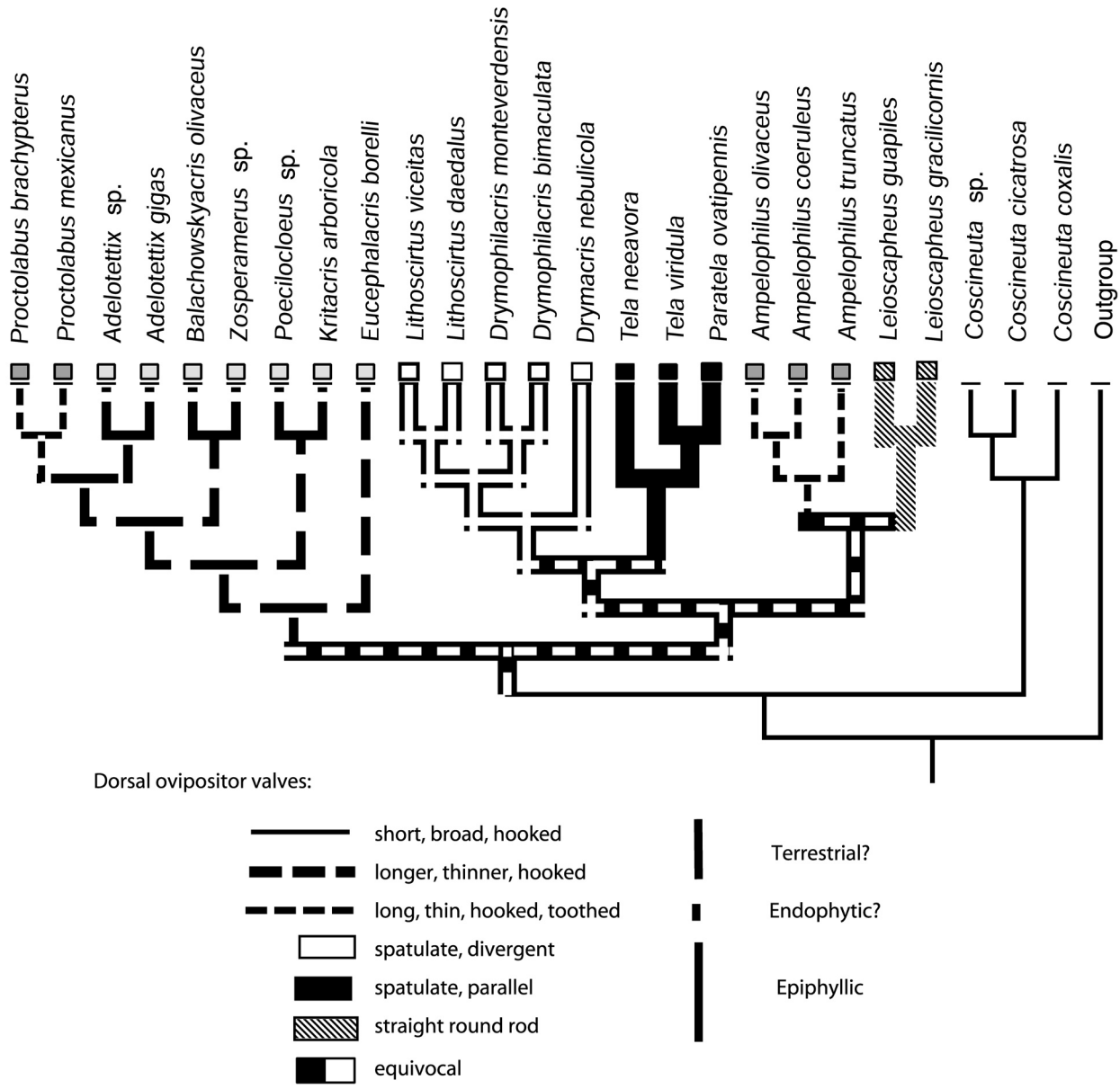


Fig. 10. Evolution of form of the dorsal ovipositor valve in the Proctolabinae. The situation for the ventral valves is similar (not shown).

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remaining Lithoscirtae genera have ovipositors suitable for epiphyllic laying, as first noted and postulated by Descamps (1976), and *Drymophilacris bimaculata* and *Leioscapheus guapiles* have indeed now been observed to do this in nature (Rowell, unpub. obs.). There are however marked differences between the clades. The Lithoscirtus clade has short, spatulate (= dorsoventrally flattened), divergent dorsal valves, and rod-like ventral valves, which are markedly shorter than the dorsal ones. Within this clade, the ovipositor of *Drymacris* is the least derived (in agreement with its basal phylogenetic position in its clade): it shows traces of marginal teeth, the upper surface of the dorsal valves is still slightly grooved, and the ventral valves are laterally compressed and forceps-like, similar to those of most Proctolabae. The Tela clade also has flattened dorsal valves, but they are parallel, pointed and blade-like; the ventral valves are rods and equal in length to the dorsal ones. In *Leioscapheus* both dorsal and ventral valves are reduced to cylindrical subequal rods. *L. guapiles* appears more derived in this respect than *L. gracilicornis*, in which the upper valves are somewhat thicker and still slightly grooved at their dorsal tips; *L. gracilicornis* is also usually resolved in the molecular phylogenies as being more basal than *L. guapiles* (Figs 1, 4). Whether these generic differences among the epiphyllic Lithoscirtae correspond to differences in oviposition technique remains to be determined.

Discussion

A. Systematics.

Within the limits of our sample, our molecular phylogeny is essentially concordant with the morphological one derived by previous authors, greatly reinforcing the credibility of both (for discussion, see *e.g.*, DeSalle & Grimaldi (1991) on phylogenetic congruence of morphology and molecular sequences in the Drosophilidae). Molecular data from a larger sample of the Amazonian species, especially the subtribe Saltonacrae, would be needed to extend our comparison of the 2 methods to the entire subfamily. It seems likely that the genus *Tela* is paraphyletic with respect to *Paratela*, suggesting that the latter genus may be superfluous.

The application of molecular clock technique for dating the tree presented here indicates that the major radiation of acridid families occurred at the Cretaceous/Tertiary boundary. This is an interesting finding as it suggests that the profound change in ecological conditions thought to have occurred at that time may have been the trigger of the previously demonstrated (Flook & Rowell 1997a) rapid radiation of the subfamilies. It is also striking that in all 3 subfamilies represented on the tree, the major phase of generic divergence was between 20 and 45 Mya.

B. Evolutionary history.

The ages we derive tentatively for the nodes of the molecular phylogeny have implications for both the historical biogeography of the Proctolabinae and the food-plant specialisation seen within it.

i. Biogeography and phylogeny.

The present day distribution of the subfamily, with its concentrations of genera in the southern half of Central America and in the Amazon, readily leads to biogeographical speculation. Amédégnato (especially 1977, but see also Amédégnato & Descamps 1983, Amédégnato & Poulain 1987 and Amédégnato 1990) has repeatedly suggested that the subfamily has its origin in the southern part of Central America, and from there has more recently invaded the northern part of Central America and Amazonia and subsequently other parts of South America. This hypothesis is based on a) the relatively primitive morphology of the Central American taxa (Coscineutini, Lithoscirtae and the Central American Proctolabae), and b) on the postulate (based on genital similarity) that the Proctolabinae are related to the Melanoplinae, which are usually considered a northern (in this case Holarctic) group, which has more recently extended its range to Southern America (see *e.g.*, Carbonell 1977). Recently, however, Amédégnato(2003) and coauthors have adopted the hypothesis that the Melanoplinae are in fact of South American origin, based on molecular evidence showing that the most basal modern branches are of South American taxa (a finding incidentally confirmed by our analysis(see our Fig. 4), though our estimated dates are slightly more modern than theirs). This makes a close relationship between the 2 subfamilies more plausible, but rather detracts from a Central American origin of the Proctolabinae, suggesting instead a South American one.

We have no new data bearing on the closeness of the relationship between the Proctolabinae and the Melanoplinae. However, Amédégnato's original hypothesis seems to ignore the complex questions of when there was geographical continuity between the various parts of Central and South America, and of the geological origins of modern southern Central America. This is especially relevant because only a few modern proctolabine genera (*Coscineuta, Adelotettix*) appear capable of long distance flight, and our analyses indicate that loss of flight, at least within the Lithoscirtus/Tela clade of the Lithoscirtae, is of the order of 30 My old. (Flightless animals do of course disperse over water barriers, but with much lower probability.) Our results indicate that both the Proctolabinae as a whole and its modern lineages are of considerable age, with the origin of the subfamily and the subsequent split between the 2 modern tribes taking place between 50 and 60 Mya. Even the modern clades within the Central American Lithoscirtae are probably 20 to 35 My old. The most recent connection of Central and South America, due to the formation of the Panamanian Isthmus, commencing about 12 Mya and completed about 3 Mya (review in Coates *et al.* 1992) is therefore probably not relevant to the evolutionary history of the group. Similarly, the Central American archipelago postulated by Duque-Caro (1990b, Fig. 7) from 13 Mya onwards is also too late to be relevant. Where were the Proctolabinae during their period of differentiation?

The geological and plate-tectonic history of southern Central America not well constrained [see *e.g.*, the various contributions in Dengo & Case 1990, Meschede *et al.* 1998, Hauff *et.al* (2000)], but no scenario envisages large exposed land masses south of the Chortis block (which extends roughly from central Guatemala to southern Nicaragua) and north of the South American craton between 50 and 25 Mya, though transitory volcanic island arcs are often invoked. Further, the Pangaean connection between the northern and southern parts of continent was broken *ca* 130 Mya, long before the origin of the Proctolabinae.

Alvarado and coworkers (Alvarado 1988, Lucas & Alvarado 1994) have cogently summarized the history of land vertebrate dispersal between the North and South American continents over geological time, and it may be assumed that where terrestrial vertebrates can go, grasshoppers can go too. These authors indicate that after the Pangean breakup the Greater Antillean arc could have formed a highly discontinuous island arc between the 2 continents, start-

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ing about 90 Mya, but there is no evidence that this was used for dispersal of the terrestrial fauna. A major faunal exchange, however, took place in the late Cretaceous and earliest Palaeocene when the Greater Antillean arc formed a continuous landbridge east of the present position of Central America. This date fits fairly well the original diversification of the Proctolabinae as suggested here, and offers a way to derive the original stock from either the northern or the southern continent. After *ca* 55 Mya, however, and until the formation of the present landbridge in Pliocene-Pleistocene, the only possible means of dispersal between the continents was by rafting or island hopping, either along the Lesser Antillean arc or along the Central American arc. Rafting cannot be dismissed as a serious possibility. The modern tropical South American rivers, especially the Amazon, discharge immense quantities of floating vegetation into the Atlantic, and prior to the creation of the present coastal mountains of northern Venezuela similar rivers drained into the Caribbean. This could have readily allowed South American insects to colonize Caribbean territories.

It therefore seems likely that the original diversification of the Proctolabinae took place on either the Chortis block or the South American craton [see Carbonell (1977) for an essentially similar opinion]. A third, but less likely, alternative is to invoke an originally separate terrain which later joined the South American continent. This is apparently the nature of *e.g.*, the Chocó block lying west of the Colombian Atrato or Uramita fault zones, thought to have first abutted the craton in the Miocene (see Pindell and Barrett 1990, who also emphasize that "the Caribbean region is composed largely of a collection of allochthonous terranes"; Duque-Caro (1990a), who describes Palaeocene foraminiferal assemblages in the Chocó suggesting an origin near Mexico or North Guatemala, and who documents the "mélange" nature of the block; and Hoernle *et al.* 2002, who show many of the terrains currently making up the Pacific coasts of Panama and Costa Rica as originating offshore from the Galapagos hot-spot). The difficulty with that hypothesis is in accounting for the original colonization of the off-shore land mass. The mid-Tertiary positions of the Chorotega and Chocó blocks, which together account for modern Costa Rica, Panama, and the Pacific fringe of Colombia, are not certainly known. Their mid-Tertiary rocks are mostly of marine or volcanic origin, neither obviously conducive to grasshopper faunas, but also include turbidites (terrestrial deposits). Eocene turbidites have been found recently in NW Costa Rica (T. Vogel, pers. com. 2003); this indicates that at least there was habitat available for colonization at this time. In view of all this, the distribution of the modern taxa of Proctolabinae may well have little correlation with the original evolutionary history of the group.

ii. Food plant specialisation, plant evolution and taxon formation.

The simplest interpretation of our data is that the ancestral Lithoscirtae were specialised on the Solanaceae from their inception (around 38 Mya) onwards, and that the modern specialisations of other Lithoscirtae on Asteraceae, Nyctaginaceae and Ulmaceae date from 20 to 30 Mya. [Jolivet and Petitpierre (1976), Bourdonnet and Doguet (1991) and Farrell (1998) have previously argued that herbivorous leaf beetle clades too may remain faithful to their original food plant taxa for long periods of geological time.] The ages of the known specialisations of individual species of Proctolabae on Vochysiaceae, Euphorbiaceae, Melastomataceae, Ulmaceae, Flacourtiaceae and Lauraceae are not known, but are probably of at least comparable age. How does this relate to the known evolution of these plant families?

The palynological record of the different plant families was reviewed by Muller (1981) and data on plant macrofossils are summarized in Benton (1993). The earliest dates for the relevant families are shown in Table 5. These fossil dates are of course minimum estimates of the age of the taxa; the macrofossil values for the Nyctaginaceae and the Vochysiaceae are obviously too recent, and simply reflect a sparse fossil record. In a (highly controversial!) attempt to gauge the age of families with poor fossil records, Sporne (1980, 1982) produced an Advancement Index for the dicotyledenous plants, based on morphological characters and roughly dated by reference to the palynological fossil record. This Index suggests that the Nyctaginaceae should be only slightly older than the Asteraceae and Solanaceae, an estimate supported by the pollen record, and that the Vochysiaceae should be slightly younger than the Melastomataceae.

The earliest certain fossil date for Solanaceae (37 Mya) coincides exactly with our estimate of the adoption of this plant family by the Lithoscirtae, and their secondary extensions from Solanaceae to Asteraceae, Nyctaginaceae and Ulmaceae between 25 and 33 Mya also present no historical conflict. The food plant families of the Proctolabae, excepting the Solanaceous food plant of *Proctolabus* itself (estimated origin 40 Mya), are all moderately old (Palaeogene) or very old (Cretaceous) families, as are most of the tropical tree families eaten by the ancient and polyphagous Coscineuti. Once again, the modern food-plant spectrum does not clash with our phylogenetic argument.

Recent findings on the origin of the Solanaceae and Asteraceae (Bremer 1993, Bremer *et al.* 1997, DeVore & Stuessy 1995, Olmstead *et al.* 1992, Olmstead & Palmer 1992, Olmstead *et al.* 1999, Olmstead pers. com.) are relevant to this discussion. Both families apparently originated in South America. The Asteraceae and Solanaceae are estimated to have split from their sister-groups, respectively the Calyceraceae and the Convolvulaceae, between 38 and 48 Mya. Rapid colonisation of other continents followed, for asteraceous pollen is widely distributed in the Oligocene, and all modern lineages of these families were established by 20 Mya.

A shift to a new plant family seems to be often associated with the morphological changes that are recognized as a higher taxon in the Proctolabinae (*e.g.*, with the formation of the subtribe Lithoscirtae, or of genera such as *Ampelophilus* within it). Inspection of the species of the modern Lithoscirtae genera clearly shows however that most cases of speciation within a genus are NOT associated with host plant shifts, but rather with geographical separation, leaving the host plant preference unchanged (there are only 2 exceptions, within *Tela*/*Paratela* and *Leioscapheus* respectively). In contrast, different proctolabine genera often eat different plants, suggesting that speciation events that *do* include a food plant shift may ultimately lead to the morphological changes which result in genus status. Presumably this is because the ecological isolation caused by food plant shift is followed by genetic change associated either with drift or with adaptation to the new host plant.

A final interesting question concerns the evolutionary choice of food plant. In the case of the Lithoscirtae, it seems clear that the modern spectrum of the subtribe is neither based on chemical resemblance nor on close phylogenetic relationships between the plant families selected. These are admittedly all eudicots, but belong to 4 different orders (Judd *et al.* 2002). Rather, it seems likely that evolution has favored extension from the original Solanaceae (Solanales) to other, unrelated plants which are commonly found in the same ecological habitat. Those Asteraceae (Asterales) which are eaten, share the preference of the Solanaceae for light-gap or

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forest edge situations, and the only members of the Nyctaginaceae (Caryophyllales) and Ulmaceae (Rosales) which are eaten (respectively *Neea* and *Trema*) are both typical secondary succession trees and also characteristic of these habitats. A similar radiation onto an ecological guild of unrelated plants has been postulated for the chrysomeline leaf-beetles of northtemperate marshlands (Pasteels & Rowell-Rahier 1991) and sub-alpine meadows (Dobler *et al.* 1996; Hsiao & Pasteels 1999).

iii. Parallel evolution of cycloid wings.

If our data are taken at face value, it seems that cycloid wings, found in the majority of flighted proctolabines, have been repeatedly and independently evolved. Two sorts of explanation for such parallelism suggest themselves: one is that there are selection pressures which strongly favor the trait, and the other that the genetic changes responsible occur frequently by chance. As far as is known, visual or acoustical signaling via the wings are, respectively, very rare or completely absent in the Proctolabinae, and it is hard to imagine another selective advantage for this sort of modification of the wings. The 2nd mechanism was explored in detail by DeSalle and Carew (1992), who suggested that most morphological traits are controlled by 1 or 2 main genes with many modifiers, rather than by the additive effects of many genes. Such a situation would allow for common homoplasy in structure due to repeated similar mutations.

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