

**CLADISTIC ANALYSIS OF THE NEARCTIC CHECKERED
BEETLE GENUS *AULICUS* SPINOLA
(COLEOPTERA: CLERIDAE: CLERINAE)**

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Abstract.—The results of a computerized cladistic analysis of the Nearctic checkered beetle genus *Aulicus* Spinola (Coleoptera: Cleridae: Clerinae) are presented. Seventeen adult morphological characters (7 multistate, 10 binary) were used to investigate the cladistic relationships of the fifteen valid species of *Aulicus*. Two Nearctic species of the genus *Trichodes* Herbst were used as outgroup taxa. Cladistic analysis with the parsimony computer program NONA yielded three equally parsimonious trees, each with thirteen nodes supported by unambiguous character optimizations, and having length 64, consistency index 50, and retention index 52. The strict consensus of these three trees has eleven resolved nodes.

The Nearctic checkered beetle genus *Aulicus* Spinola contains fifteen brightly colored species generally distributed throughout the deserts of the southwestern United States and western Mexico. Adults of these beetles are found on the flowers of herbaceous plants, on the foliage of shrubs and trees, and may also be encountered crawling on the ground or flying in desert habitats (Barr and Foster, 1979; Mawdsley, unpubl. obs.). The larvae of *A. terrestris* Linsley are known to feed on grasshopper egg masses (Linsley, 1936), and it is possible that larvae of other species also feed on these egg masses (Barr and Foster, 1979). From a taxonomic perspective, *Aulicus* is unique among genera of Cleridae in having been either summarized, reviewed, or revised four times, first by A. B. Wolcott (1910), then by C. Schaeffer (1921), again by E. G. Linsley (1936), and most recently by W. F. Barr and D. E. Foster (1979).

Barr and Foster were the first of these authors to discuss the putative phylogenetic relationships of *Aulicus* species. After studying variation in adult morphological characters in species of *Aulicus*, Barr and Foster (1979) concluded that “. . . features which usually would be regarded as important indicators of relationships have been found to be unreliable and present an inconsistent picture of phylogeny. The selection and use of one set of characters will indicate certain relationships, whereas the selection and use of another set of characters will result in a different expression of relationships.” Clearly, Barr and Foster were dealing with a more complex situation than that presented by clerid genera such as *Perilypus* Spinola or *Colyphus* Spinola, for which synapomorphy schemes were readily constructed by Ekis (1977a, b) without resorting to computerized methods. Because of the conflicts among the characters they studied, Barr and Foster did not present a phylogenetic hypothesis for the species of *Aulicus*, nor did they propose an informal species–group or formal subgeneric classification for this genus.

To test the assertion of Barr and Foster (1979) that adult morphological characters do not present a clear picture of the pattern of relationships among *Aulicus* species, I coded a set of adult morphological characters, which had been mentioned by these

authors in their discussions of relationships within *Aulicus*, for use in standard computerized parsimony analysis.

DESCRIPTION OF ADULT MORPHOLOGICAL CHARACTERS

The following seventeen characters were derived from the revision of *Aulicus* by Barr and Foster (1979). Character state numbers, which follow the descriptions of individual character states in parentheses, have been assigned arbitrarily, except in those few multistate characters that could be ordered as logical transformation series. For these characters, the states are arranged such that their numerical progression mirrors the ordering of the transformation series. Those multistate characters that could not be ordered as transformation series were analyzed as unordered. Terminals with multiple character states and terminals for which a particular character was inapplicable received the standard ambiguous/polymorphism coding “?”

- 1.) Head capsule uniformly black or blue (0), with red coloration (1).
- 2.) Antennal club abrupt, 3-segmented (0), gradual, 4–7 segmented (1).
- 3.) Antennal club compact, segments wider than long (0), loose, segments approximately as long as wide (1).
- 4.) Antennae dark brownish-black in both sexes (0), antennae pale brownish basally with intermediate segments darker, club pale in male and darkened in female (1), antennae pale in both sexes (2), antennal coloration variable (?) (unordered).
- 5.) Pronotal midsection only slightly expanded, not strongly globose (0), strongly globose (1).
- 6.) Pronotum uniformly black or blue (0), with red coloration (1).
- 7.) Abdominal sternites black in both sexes (0), black with red margins in both sexes (1), male sternites black, female reddish (2), male sternites reddish, female black (3), male sternites reddish, female bicolored (4), sternites reddish in both sexes, rarely darkened apically (5), variable (?) (unordered).
- 8.) Thoracic sternites black (0), red (1), both forms present in the same species (?).
- 9.) Legs black (0), with red markings or entirely reddish (1).
- 10.) Elytral punctures dense and distinct (0), elytra sparsely, moderately punctate (1), elytra nearly impunctate (2) (ordered).
- 11.) Male pretarsal claws without small, secondary tooth (0), with a small tooth on inner claw (1), with a large tooth on both claws not extending to apex of claw (2), with a large tooth on inner claw extending to or past apex of claws (3) (unordered).
- 12.) Apex of tegmen of male genitalia not distinctly narrowed in dorsal view (0), apex distinctly and abruptly narrowed in dorsal view (1).
- 13.) Male tegmen without (0), with (1) a lateral longitudinal carina.
- 14.) Male tegmen with zero (0), one (1), or two (2) lateral grooves (ordered).
- 15.) Groove(s) on male tegmen parallel-sided and of uniform depth (0), medially constricted (1), abruptly widened apically (2), abruptly widened basally (3), becoming obsolete apically (4), very shallow (5), character not applicable because grooves absent (?) (unordered).
- 16.) Apices of parameres of male tegmen gradually convergent (0), abruptly hooked inwards (1), straight (2), slightly divergent (3) (unordered).
- 17.) Apices of parameres of male tegmen rounded (0) or pointed (1) in lateral view.

Table 1. Taxon-character matrix for species of *Aulicus* Spinola plus outgroups.

<i>Trichodes nutalli</i> (Kirby)	000?0000010000?30
<i>Trichodes simulator</i> Horn	000?0000000000?20
<i>A. antennatus</i> Schaeffer	01101030021001100
<i>A. apachei</i> Barr and Foster	00101040001001100
<i>A. bicinctus</i> Linsley	00111000020011020
<i>A. coffini</i> (White)	1010111?000002020
<i>A. dentipes</i> Schaeffer	001110?0002001400
<i>A. edwardsii</i> (Horn)	01121010020101211
<i>A. femoralis</i> Schaeffer	10101151101001000
<i>A. fissipes</i> Schaeffer	00101040103001300
<i>A. humeralis</i> Linsley	00101040001001300
<i>A. linsleyi</i> Barr	00101040001001400
<i>A. monticola</i> Gorham	10101110000001030
<i>A. nero</i> Spinola	01101020002010?01
<i>A. nigriventris</i> Schaeffer	00111000010001501
<i>A. terrestris</i> Linsley	00101010010011001
<i>A. thoracicus</i> Schenkling	00101000003001501

METHODS OF ANALYSIS

A taxon-character matrix (Table 1) was constructed by coding each of the seventeen characters listed above for each of the fifteen species of *Aulicus*. In addition to the descriptions and illustrations in the revision of Barr and Foster (1979), I also examined adult specimens of all species of *Aulicus* to verify the character codings. The following institutional and private collections were examined: The Natural History Museum, London; Cornell University Insect Collection; J. R. Mawdsley (private collection); Museum of Comparative Zoology, Harvard University; Muséum National d'Histoire Naturelle, Paris; National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Snow Entomological Museum, University of Kansas. Specimens that had not been identified and labeled by Barr and Foster were identified by the present author using the keys, descriptions, and illustrations in Barr and Foster (1979).

Barr and Foster (1979) had difficulty in identifying a possible sister-taxon for the genus *Aulicus*. After considering several genera related to *Enoclerus* Gahan, they finally decided to place *Aulicus* "next to *Trichodes* [Herbst] awaiting comprehensive studies on its generic placement" (Barr and Foster, 1979). I agree with Barr and Foster that *Aulicus* probably belongs to a group of genera allied to *Trichodes*, whose species are united by similar dorsal color patterns and elytral surface sculpturing and very similar male genitalia. Other clerid genera that appear to belong to this group include the Australian *Eleale* Newman, the Madagascan *Eburiphora* Spinola, the Chilean *Calendyma* Lacordaire, and the central African *Dieropsis* Gahan. Barr and Foster (1979) note that similarities in the biologies of species of *Aulicus* and *Trichodes* also suggest a link between these two genera. Several species of *Trichodes* and *Aulicus* are the only clerids known to prey on grasshopper egg masses (Linsley, 1936; Corporaal, 1950; Foster, 1976). Given this morphological and biological evidence, a close relationship between *Trichodes* and *Aulicus* appears plausible. Two

Nearctic *Trichodes* species, *T. simulator* Horn and *T. nutalli* (Kirby), were therefore chosen as outgroup taxa for this analysis, and all 17 characters were coded for these two species.

Cladistic analysis of the matrix in Table 1 was performed using the computer program NONA (Goloboff, 1993). Although NONA can be used to implement a variety of weighting schemes, there is no clear rationale to apply *a priori* weighting to the adult morphological characters described above, and therefore all of these characters were analyzed as having equal weight. The complete sequence of commands used in analyzing this matrix is provided in Appendix 1.

Twenty replicates of the "mult" tree-search command were performed. For each "mult" run, taxon order is randomized, a Wagner tree (Farris, 1970) is constructed, tree bisection and reconnection (TBR) branch-swapping is performed on this Wagner tree, and the resulting tree(s) having shortest length are retained (Goloboff, 1993). Additional branch-swapping was performed on the trees found by "mult" using the "jump" command, which is designed to search among suboptimal trees for any indications of the existence of additional islands of most parsimonious trees (Goloboff, 1993). For this analysis, the "jump" command was used to investigate all trees up to ten steps longer than the most parsimonious trees. A strict consensus tree was calculated for all of the most parsimonious trees found in the "mult" and "jump" analyses, and both the strict consensus tree and all of the most parsimonious trees were saved in tree files for further examination.

NONA, like earlier computerized parsimony analysis programs, performs all of its internal calculations on unrooted Wagner networks (Farris, 1970), then reports trees by rooting these networks between the first taxon listed in the matrix (or another specified outgroup) and the remaining taxa. Thus, no polarization of characters is necessary prior to analysis, and the polarities of character transformations can be read directly from a cladogram to which all transformations between character states have been mapped.

Unlike the earlier program Hennig86 (Farris, 1988), NONA only retains those nodes in the most parsimonious trees that are supported by unambiguous character transformations. Thus, NONA may report fewer most parsimonious trees than Hennig86, which will report topologies that are only supported under certain optimizations.

The tree topologies from this analysis were examined and printed using WINCLADA (Nixon, 1999), an updated version of CLADOS (Nixon, 1993) for the Windows computer environment. WINCLADA optimizes characters onto cladograms using standard parsimony optimization methods: those of Farris (1970) for binary and ordered multistate characters; those of Fitch (1971) for unordered multistate characters.

RESULTS

Analysis of the matrix in Table 1 with NONA as described above yielded three equally parsimonious trees. Each of these trees has length 64, consistency index 50, and retention index 52. Although the branches in these trees are not well supported by unambiguously optimized characters, the trees are nevertheless well resolved, with 13 of 16 possible nodes supported by unambiguously optimized characters. The

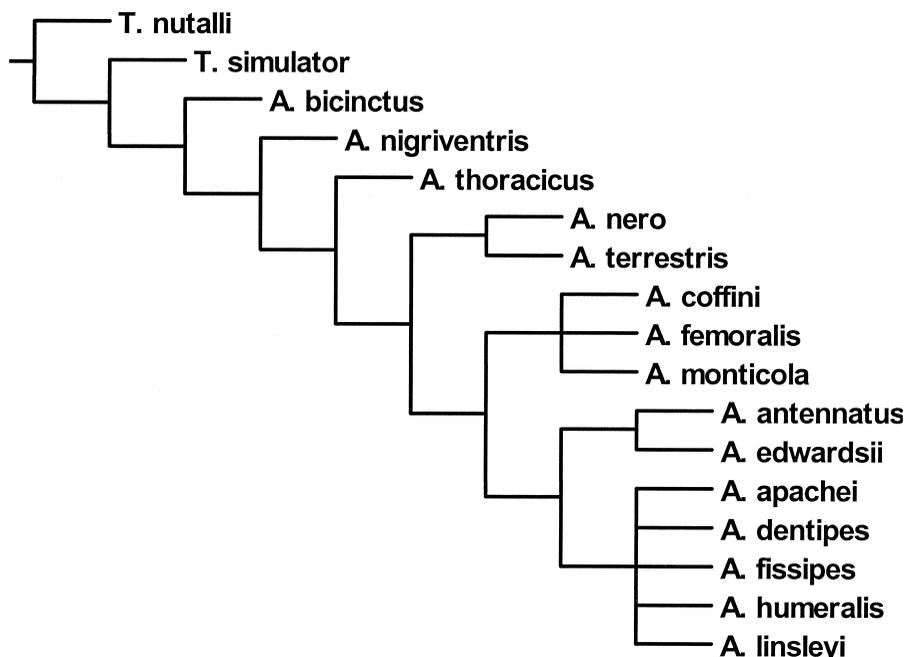


Fig. 1. Strict consensus topology of the three most parsimonious cladograms for species of the genus *Aulicus* Spinola. *Trichodes nutalli* and *T. simulator* are outgroups; the remaining terminals are species of *Aulicus*.

most ambiguous portion of these trees is the clade containing the species *A. apachei*, *A. fissipes*, *A. dentipes*, *A. humeralis*, and *A. linsleyi*, which has a different resolution in each of the three most parsimonious topologies.

The strict consensus of the three most parsimonious trees (Fig. 1) has eleven resolved nodes. The clade containing *A. apachei*, *A. fissipes*, *A. dentipes*, *A. humeralis*, and *A. linsleyi* collapses to a complete polytomy in this consensus tree.

DISCUSSION AND CONCLUSIONS

A majority of the unambiguous character transformations in the three most parsimonious trees for the data set analyzed here are homoplasious. The high levels of homoplasy in these trees, indicated by the relatively low consistency and retention indices, confirm Barr and Foster's contention that the morphological characters studied to date in *Aulicus* exhibit considerable conflict. However, these characters nevertheless support a set of most parsimonious topologies whose strict consensus is well resolved. The results presented here clearly demonstrate the value of computerized parsimony analyses for recovering patterns of relationships in groups where conflicts among characters cannot be easily resolved using traditional taxonomic methods.

It is interesting to note that the pattern of relationships found for the species of

Aulicus in this study contradicts many of the brief statements scattered throughout Barr and Foster's revision discussing the relationships of individual species of *Aulicus*. These statements can generally be found in the "Discussion" sections at the ends of the individual species treatments (Barr and Foster, 1979). Several of these statements are not directly supported by any character data, but rather appear to be intuitively based. Those statements that are based on character data often rely on characters (such as simple pretarsal claws in males) that are plesiomorphic in the context of the cladograms presented here. On the one hand, the conflict between these statements and the cladograms reported in the present study can be interpreted as a strong caution against proposing hypotheses of relationships in the absence of a comprehensive cladistic analysis. On the other hand, it is quite possible that some of the relationships postulated by Barr and Foster are valid and will be recovered when additional sources of cladistic data become available for the species of *Aulicus*.

My own studies of adult specimens of species of *Aulicus* have convinced me that most species of this genus exhibit considerable homogeneity in their external anatomical features. The characters listed above probably represent most of the adult external morphological characters that are phylogenetically informative in this genus. Future studies of the cladistic relationships of species of *Aulicus* will therefore have to rely on additional lines of evidence. Larvae have yet to be described for any of the species of *Aulicus*, but larval characters are known to separate species in other genera of the subfamily Clerinae (Böving and Champlain, 1920). The adult alimentary canal provides important characters for separating subfamilies and other major lineages of Cleridae (Ekis and Gupta, 1971; Crowson, 1972), while structures of the male internal reproductive system have been used to diagnose major lineages in the genus *Enoclerus* Gahan (Ekis, 1978). These and other internal anatomical character systems have yet to be systematically investigated in species of *Aulicus*. Molecular sequence data may also prove to be useful in developing a well-supported, robust hypothesis of relationships for *Aulicus* species.

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APPENDIX 1

The following string of commands was used to analyze the matrix in Table 1 with the computer program NONA, and to save the most parsimonious cladograms and strict consensus tree resulting from this analysis:

```
pack report hold100 hold/20 mult*20 hold* jump*10 ksv*aulicus.ss sv/ ne o/  
sv=aulicus.nel in sv/
```

The most parsimonious trees resulting from this analysis were saved in the file *aulicus.ss*; their strict consensus tree was saved in the file *aulicus.nel*. Complete descriptions of all commands are provided in the NONA documentation of Goloboff (1993).

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