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Phylogenetic relationships of genus *Pelophila* Dejean to other basal grade Carabidae (Coleoptera)

David H. Kavanaugh

Kavanaugh, D. H., Department of Entomology, California Academy of Sciences, San Francisco, California 94118, USA

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Traditionally, genus *Pelophila* Dejean has been placed in the tribe Nebriini, along with *Nebria* Latreille and *Leistus* Frölich. A phylogenetic analysis of basal grade caraboid lineages, based on 244 characters of adult morphology, suggests that this classification does not reflect accurately the phylogenetic relationships of *Pelophila*. A clade including the Notiokasiini (*Notiokasis* Kavanaugh & Nègre), Notiophilini (*Notiophilus* Dumeril), and Opisthiini (*Opisthius* Kirby and *Paropisthius* Casey) is more closely related to a clade including *Nebria* and *Leistus* than either clade is to *Pelophila*. Within supertribe Nebriitae, a new tribe, the Pelophilini, is proposed to include the two known species of *Pelophila*.

1. Introduction

Dejean described *Pelophila* in 1821, with *Carabus borealis* Paykull (1790) as the only included species (= type species by monotypy). Subsequently, fourteen additional names have been proposed, thirteen of which are synonyms of *P. borealis* (Dejean 1826, Lindroth 1961). Only *Pelophila rudis* (LeConte) (1863), originally described in genus *Nebria*, represents a second, distinct species of *Pelophila*. This genus is northern Holarctic in distribution, as is *P. borealis* itself. *Pelophila rudis* is restricted to the Nearctic Region, where its distribution is northern Transamerican (Kavanaugh 1980). Lindroth (1961) described the hygrophilous habits and the habitats of both species.

Adults of both *Pelophila* species differ from all other basal grade carabids by the presence of a complete scutellar striole, extended from the base to near the apex, on each elytron. Otherwise, *Pelophila* adults could easily be mistaken for adults of some *Nebria* species with exceptionally short, broad, and shiny bodies and short appendages.

Historically, different systematists have suggested affinities for *Pelophila* with *Blethisa* and other Elaphrini, with *Nebria* and other Nebriini, or, in a few cases, as an intermediate form related to both of these groups. Latreille (1802) recognized three "families" of basal carabids: the "Carabiques", including genera now placed in the tribes Carabini and Cychrini; the "Barbus", including *Omophron*, *Pogonophorus* (= *Leistus*), *Loricera*, and *Nebria* (which was described in that paper); and the "Elaphriens", including *Elaphrus* and *Bembidion*. In 1804 (and 1810), Latreille did not consider *Carabus borealis*, but he placed *Carabus multipunctatus* Linnaeus in *Nebria*. Gyllenhal (1810) included both *C. borealis* and *C. multipunctatus* in *Nebria*. Bonelli (1810) included both of these species in his new genus, *Blethisa*, which he did not place with *Nebria* and *Leistus* among the genera in his section "Simplicimani" of family "Carabici". Dejean (1826) listed *Pelophila* between *Nebria* and *Leistus* in the catalog of his collection, but in later works (e.g. Dejean & Boiduval 1829, 1830), grouped *Pelophila* instead with *Blethisa* and *Elaphrus*. Curtis (1824) considered *Pelophila* to be intermediate between *Nebria* and *Blethisa*.

Closer affinities between *Pelophila* and the other genera presently included in the tribe Nebriini (i.e. *Nebria* and *Leistus*) than with the elaphrines (including *Blethisa*) were firmly established in classifications by the middle 1850's. Lacordaire (1854) placed *Pelophila* in his "Carabides", along with *Nebria*, *Leistus*, *Metrius*, and several other genera now in the tribe Carabini, and excluded *Blethisa* from this group. Jacquelin du Val (1857), Gemminger and Harold (1868), Redtenbacher (1874), and Horn (1881) included *Pelophila* in a group with *Nebria*, *Leistus*, and one or more additional genera that are now placed in other tribes, but not in the Elaphrini. A tribe Nebriini that included only *Nebria*, *Leistus*, and *Pelophila* was recognized by Thomson (1859), Seidlitz (1891a, 1891b), Ganglbauer (1892), Reitter (1908), and Schaufuss (1916). This arrangement is consistent with the currently accepted classification (Ball 1960, Lindroth 1961, Kryzhanovsky 1976, Bousquet & Larochelle 1993), although various authors have described additional new nebriine genera, e.g. *Archastes* Jedlicka (1935) and *Archileistobrius* Shilenkov and Kryzhanovsky (1983), or removed species or groups of species from *Nebria* and classified these as separate genera, e.g. *Eurynebria* (Csiki 1927) and *Nipponconsole* (Habu 1958).

Recently, the close phylogenetic relationship between *Pelophila* and the other nebriine genera, which has been assumed, or at least implied, for the last 140 years, has begun to be questioned. Kavanaugh (1978) suggested closer phylogenetic relationship between *Notiophilus* and *Nebria* and *Leistus* than between *Pelophila* and the last two genera, based on both adult and larval features, and used this set of relationships (see fig. 369 in that paper) as an outgroup assumption in his phylogenetic analysis of Nearctic *Nebria* species. Kavanaugh and Nègre (1982) discussed incongruence in the distributions of apomorphic (derived) character states of different adult and larval characters among the genera included in supertribe Nebriitae (Kryzhanovsky 1976) (i.e. *Nebria*, *Leistus*, *Pelophila*, *Opisthius*, *Paropisthius*, *Notiophilus*, and *Notiokasis*) and noted the absence of synapomorphies supporting the monophyly of a group including only *Pelophila*, *Leistus*, and *Nebria*. Based mainly on features of larval morphology, Bousquet & Smetana (1991) and Bousquet & Larochelle (1993) doubted the monophyly of Nebriini including *Pelophila*, but noted that several synapomorphies support the monophyly of Notiophilini + Nebriini without *Pelophila*.

Since 1978, I have continued to investigate phylogenetic relationships among the Nebriini and recently completed a new and more comprehensive phylogenetic analysis of Nearctic and closely related Palaearctic *Nebria* species using computer-based analytical methods. Species representing all of the described subgenera of *Nebria* and all the genera of Nebriitae were including in the analysis, along with representatives of a few more distantly related carabid and other adephagan taxa, to provide a broad, yet detailed, outgroup context for the analysis of *Nebria* species. Results of the anaylsis will be presented in detail in a monograph on the Nearctic Nebriini now in preparation. However, it is the relationships among outgroup taxa suggested by the analysis, particularly those of *Pelophila* in relation to other nebriite genera, that I wish to address here.

2. Materials and methods

The phylogenetic analysis upon which this contribution is based was done in two steps: the first step using a large number of taxa to establish ground plan exemplars for the diverse outgroup genera, and the second step using these exemplars with *Pelophila* to establish the latter's relationships to the other taxa.

In the absence of any specific background assumption about character evolution (*sensu* Maddison 1993), the phylogenetic analyses undertaken were based on parsimony methods. The computer program, PAUP version 3.1 (Swofford & Begle 1991) was used to search for the most parsimonious (shortest length) trees. Comparisons among trees and the examination of character state distributions on trees were facilitated by use of the computer program, MacClade version 3.0 (Maddison & Maddison 1992). Tree lengths and retention indices noted below were calculated using MacClade algorithms.

The database upon which analyses were based recorded the state distributions of 244 characters in 103 taxa. Taxa included were: (1) all Nearctic *Nebria* species, (2) all closely related Palaearctic *Nebria* species, and representatives of (3) all subgenera of *Nebria* described prior to 1984, (4) all other genera of supertribe Nebriitae, and (5) a few more distantly related carabid and other adephagan genera. All characters examined were of adult external morphology or of adult internal genitalic morphology. Limitations placed on contributions for this symposium publication do not permit presentation of a listing of the names of the taxa represented, characters examined, or character states recorded. These will be provided in the monograph on Nearctic Nebriini now in preparation.

Initial analyses used the entire database (i.e. all taxa and all characters were considered). Because of the large number of taxa involved, all searches were conducted using PAUP's heuristic search option. However, different searches employed different weighting schemes (equal weighting, subjective differential weighting, and successive weighting) and different character types (unordered, ordered, and user-defined character state trees). Most importantly, no assumptions were made *a priori* about relationships among the included genera (i.e. no structure was imposed on the outgroup, non-*Nebria*, portions of the trees), so near outgroup relationships (i.e. relationships among the nebriite genera) could also be resolved by the analyses.

Character state distributions on the most parsimonous tree found by PAUP, where characters were equally weighted and unordered, were used to establish the states of each character on the stem branches for *Nebria*, *Nippononebria,* and *Leistus*. Establishment of ground plan lists of attributes for these three taxa permitted reduction of the total number of taxa included in the derivative analysis from 103 to 18 (Table 1). All 244 characters were used again and all were assigned equal weight and unordered. The search, again using PAUP's heuristic search option, involved 30 different random addition sequences and subsequent tree-bissection-reconnection (TBR) branch rearrangements, with MAXTREES set to 700, MULTIPARS turned on and STEEPEST DESCENT off, and zero-length branches collapsed.

3. Results and discussion

Initial PAUP searches, using the full database with 103 taxa and a variety of different combinations of weighting schemes and character types, found most parsimonious trees of slightly different topology. However, differences among these trees are confined almost exclusively to relatively minor rearrangements within a clade corresponding to genus *Nebria* in the broadest sense. Suggested relationships among the other genera are essentially the same in all of these shortest trees.

In the derivative analysis, using only 18 taxa, including ground plan exemplars for *Leistus*, *Nebria*, and *Nippononebria*, and with characters equally weighted and unordered, a single most parsimonious (shortest) tree (length = 1 412 steps, consistency index (CI) = 0.68, and retention index (RI) = 0.53) was found in all 30 random addition sequence replicates. This tree (Fig. 1A) has the same topology (except truncated for each of the taxa represented only by ground plan exemplars) as the shortest trees found in the initial searches. Again, space limitations preclude presentation of detailed results of these analyses, particularly discussions of the characters and character state distributions that give significance to the trees found. These details will be presented elsewhere and only a summary of findings is provided here.

Each node on the most parsimonious tree, but especially those that are critical for the placement of *Pelophila* among the included taxa, is well supported by synapomorphies (unambiguous changes). The only exception to this is at the base of the tree, where there should be a basal trichotomy. According to this analysis, it is equally parsimonious to place trachypachines as the sister group of either the dytiscoid hydradephagans, represented here by *Amphizoa*, or of the Carabidae. I chose to resolve the trichotomy (arbitrarily placing trachypachines as the sister group of carabids) so as to facilitate the calculation of tree lengths and other statistics, which are not calculated fully for trees with polychotomies (Maddison & Maddison 1992). Monophyly of a clade including all the genera of the traditional Nebriitae (i.e. node "a" in Fig. 1A) is supported by 10 synapomorphies. The monophyly of genus *Pelophila* itself is supported by 33 synapomorphies. Monophyly of a clade of nebriites minus only *Pelophila* (i.e. node "b" in Fig. 1A) is supported by 11 synapomorphies, and that of a clade including the traditional Nebriini without *Pelophila* (node "c") is supported by 12 synapomorphies. Perhaps most surprisingly, 12 synapomorphies support the monophyly of the clade, *Notiokasis* + *Notiophilus* + *Opisthius* + *Paropisthius* (node "d" in Fig. 1A).

As facilitated by MacClade, comparisons between this most parsimonious tree and trees of other topology were informative. A tree which retains the traditional Nebriini (Fig. 1B), including *Pelophila* with *Leistus* and *Nebria* in the broadest sense, requires seven extra steps (length = 1 419 steps, CI = 0.67, RI = 0.52). Monophyly of the traditional Nebriini is supported by only 4 synapomorphies, and these include at least three characters (e.g. depth of impression of elytral microsculpture) that may be particularly sensitive to choice of exemplars. As noted by Kavanaugh (1978) and Bousquet and Larochelle (1993), larval morphological features do not appear to support the monophyly of the traditional Nebriini, and so the inclusion of larval features in future analyses probably will provide no additional support for such a clade. A cursory review of gross larval features (e.g. shape of the base and nasale of the head capsule) suggests that a clade including *Notiophilus* with *Leistus* and *Nebria*, but excluding *Pelophila*, may be monophyletic (see Bousquet & Larochelle, 1993). Based on adult features alone, however, a tree with such a clade (Fig. 1C) requires 16 steps more than the most parsimonious tree if *Notiokasis* is included as the sister group of *Notiophilus* (length = 1 428 steps, CI = 0.67, RI = 0.52), at least 21 steps more if *Notiokasis* is placed anywhere else outside of this clade. Larvae of *Notiokasis* remain unknown, so it is difficult to assess just how the inclusion of larval characters might affect the results of future phylogenetic analyses. It appears likely, however, that larval features may provide more additional support for this tree than for the most parsimonious tree (Fig. 1A). Even if this were to occur, the core finding of the present analysis would be confirmed — namely, that taxa presently placed in two or more other tribes are more closely related to the *Leistus, Nebria*, and other closely related genera (or subgenera) than is *Pelophila*.

Table 1. List of taxa used as exemplars for analysis of phylogenetic relationships of *Pelophila* Dejean.

AMPHIZOIDAE
        Amphizoa LeConte: *A. insolens* LeConte
CARABIDAE
    Trachypachini
        Trachypachus Motschulsky: *T. gibbsi* LeConte
        Systolosoma Solier: *S. breve* Solier
    Pelophilini
        Pelophila Dejean: *P. borealis* (Paykull), *P. rudis* (LeConte)
    Opisthiini
        Opisthius Kirby: *O. richardsoni* Kirby
        Paropisthius Casey: *P. indicus* (Chaudoir)
    Notiokasiini
        Notiokasis Kavanaugh & Nègre: *N. chaudoiri* Kavanaugh & Nègre
    Notiophilini
        Notiophilus Duméril: *N. borealis* Harris
    Nebriini
        Archastes Jedlicka: *A. berezovskii* Shilenkov
        Leistus Frölich[1)]
        Nebria Latreille[1)]
        Nipponebria Habu[1)]
        Oreonebria K. Daniel: *O. castanea* (Bonelli)
        Orientonebria Shilenkov: *O. coreica* (Solsky)
    Carabini
        Carabus Linnaeus: *C. chamissonis* Fischer von Waldheim
    Elaphrini
        Blethisa Bonelli: *B. multipunctata* (Linnaeus)
    Platynini
        Calathus Bonelli: *C. advena* (LeConte)

[1)] Taxon represented by a ground plan exemplar, with character states of all characters established through an initial phylogenetic analysis involving two or more terminal taxa (*Nipponebria*, 5 spp.; *Leistus*, 2 spp.; *Nebria*, 81 spp.).

4. Conclusions

Based on results of the phylogenetic analyses conducted, it is clear that monophyly of the traditional tribe Nebriini is poorly supported, whereas that of a clade corresponding to the supertribe Nebriitae is well supported. For *Pelophila*, there is more support for a sister group relationship with a clade including all other nebriites (i.e. opisthiines + notiokasiines + notiophilines + remaining nebriines) than for any other placement.

Although this analysis strongly suggests that a clade including opisthiines + notiokasiines + notiophilines is the sister group of the nebriines (without *Pelophila*), the inclusion of characters of larval morphology in future analyses has the potential to support a slightly different set of relationships among these taxa. Consequently, I prefer to suggest a conservative change in classification at this time. Placing *Pelophila* in a higher taxon of its own, at the same rank as (if not higher than) opisthiines, notiophilines, notiokasiines and the remaining nebriines, seems justified. However, two alternatives present themselves. First, all of these taxa could be included as subtribes of a single tribe. In this case, the tribal name would be Nebriini, based on the priority of Nebriidae Laporte (1834) over Notiophili Motschulsky (1850), Opisthiinae Dupuis (1912), and Notiokasiini Kavanaugh and Nègre (1982) (see Madge 1989). Second, all could be ranked as tribes. I prefer the latter alternative, at least at present, for several reasons: 1) a supertribal name, Nebriitae, is already in wide use, and it would become synonymous with an expanded tribe Nebriini; 2) placing *Pelophila* in a tribe of its own requires only one nomenclatural change, whereas ranking *Pelophila* and all the present nebriite tribes as subtribes would require five nomenclatural changes, with no offsetting advantage except to reduce the number of tribes of Carabidae; and 3) placing these five tribes in a single expanded tribe would ignore both the antiquity and diversity of form and lifestyle of these ancient, independent lineages, at least in relation to other taxa currently ranked as distinct tribes in Carabidae. Hence, I propose the following interim classification of supertribe Nebriitae:

— Tribe Pelophilini (*Pelophila)*
— Tribe Opisthiini (*Opisthius*, *Paropisthius*)
— Tribe Notiophilini (*Notiophilus*)
— Tribe Notiokasiini (*Notiokasis*)
— Tribe Nebriini (*Archastes, Leistus*, *Nebria*, *Nippononebria*, etc.)

The following designation of type-genus and brief description is presented to insure that the new tribal name, Pelophilini, is available according to provisions of the International Code of Zoological Nomenclature (Articles 11f and 13a) for family-group names.

Pelophilini, new tribe

Type genus: *Pelophila* Dejean (1821: 7), by monotypy.

Description: Head large and very broad, with genae and occiput slightly inflated, elytra relatively short, legs and antennae relatively short; body and appendages black or piceous, frons without frontal pale spots; dorsum without metallic reflection; dorsal forebody shiny with microsculpture effaced. Head with apical margins of labrum and clypeus moderately to markedly concave; one pair of supraoribtal setae present; labium with paraglossae adnate, fused with ligular sclerite, posteroapical seta absent from penultimate labial palpomere; mentum with M1 setae subapical, slightly lateral of mental tooth; gula with a single pair of lateral setae, medial gular setae absent. Pronotum cordate but broad basally; prosternal intercoxal process markedly lanceolate; procoxal cavities open posteriorly, incompletely bridged internally. Elytron with scutellar striole long, extended to near elytral apex, interval 3 markedly catenate, not tuberculate, internal plica absent or present only as a slight rise; ventral pterothoracic sclerites smooth or nearly so; mesocoxal cavities disjunct; metacoxal closure complete. Legs with apical margin of fourth tarsomere of hind tarsus distinctly lobate lateroventrally. Abdomen with elytral-lock flange absent from sternum 6 laterally. Male genitalia with median lobe long and slender, cylindrical (in cross-section), only slightly arcuate (angle of logitudinal axis greater than 135° in lateral aspect), basal bulb quadrate, closed dorsally and broadly open basally; dorsobasal piece present as a small, vertical, mid-sagital fin; parameres asymmetrical, left paramere long and slender, right paramere very long and slender. Female genitalia with paraprocts sparsely setose, paraproct and valvifer moderately continuous basally, valvifer with dense setae on both membraneous and sclerotized medial portions; gonocoxa and gonostylus fused medially, widely separate laterally, both densely setose medi-

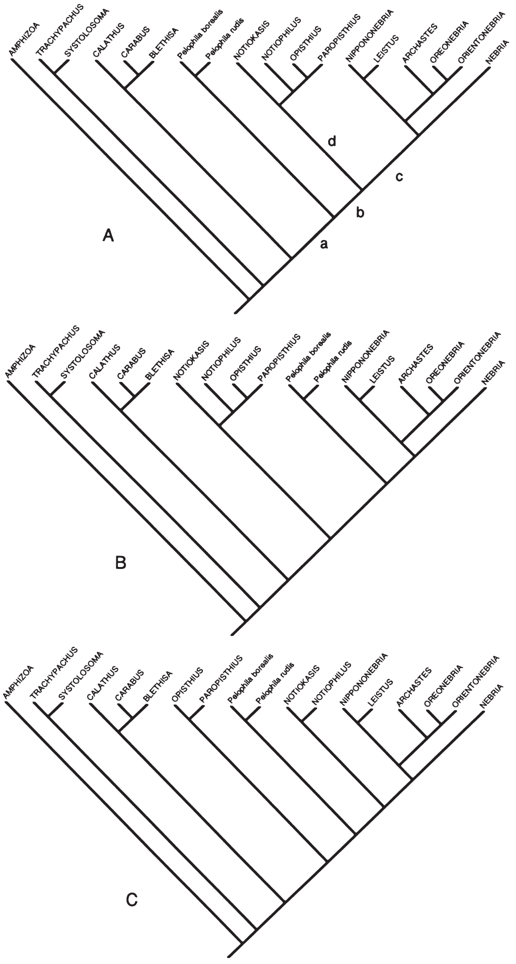

Fig. 1A–C. Cladograms illustrating alternative sets of relationships among *Pelophila* and other nebriite lineages. — A. Most parsimonious (shortest length) tree as determined using PAUP, version 3.1 algorithms, under the heuristic search option, with characters equally weighted and unordered (length = 1 412 steps, CI = 0.68, RI = 0.53). Branch segments (nodes) discussed in the text are identified by lower case letters (a through d). — B. Tree with tribe Nebriini, as traditionally conceived, intact (length = 1 419 steps, CI = 0.67, RI = 0.52). — C. Tree with a clade including *Notiophilus* and *Notiokasis* more closely related to *Leistus* and *Nebria* than is *Pelophila* (length = 1 428 steps, CI = 0.67, RI = 0.52).

ally and ventrally; gonostylus long, straight, slender, apically rounded (in both ventral and lateral aspects), ventral diagonal setal row with 6 or more long, setiform setae, mediodorsal setal row with 4 or more long, setiform setae.

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