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A phylogenetic review of the species groups of *Phylocentropus* Banks (Trichoptera: Dipseudopsidae)

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ABSTRACT

A phylogenetic review of the three species groups of the caddisfly genus *Phylocentropus* Banks, proposed by Ross (1965), is provided. The *Phylocentropus auriceps* Species Group contains 9 species: †*P. antiquus, P. auriceps,* †*P. cretaceous,* †*P. gelhausi,* †*P. ligulatus,* †*P. simplex,* †*P. spiniger,* †*P. succinolebanensis*, and †*P. swolenskyi,*; the *P. placidus* Species Group, 4 species: *P. carolinus*, *P. harrisi, P. lucidus,* and *P. placidus*; and the *P. orientalis* Species Group, 7 species: *P. anas, P. narumonae, P. ngoclinh, P. orientalis, P. shigae, P. tohoku,* and *P. vietnamellus.* A hypothetical phylogenetic tree of the genus is presented along with its historic biogeography.

Keywords: Trichoptera, Dipseudopsidae, *Phylocentropus*, amber, systematics, phylogeny, biogeography, Cretaceous, Eocene

Ross (1965) proposed three species groups for the genus *Phylocentropus* which at the time contained 10 species: 6 extant species (4 from eastern North America and 2 from eastern Asia) and 4 extinct species from Baltic amber. Since then 10 additional species of *Phylocentropus* have been discovered: 6 extant species (1 from southeastern North America and 5 from Southeast Asia) and 4 fossil species from New Jersey and Lebanese amber. These new contributions to our knowledge necessitate a review of Ross's classification of the genus. In this work the species of *Phylocentropus* unknown to Ross (1965) are assigned to species groups and a revised phylogeny is hypothesized.

Phylogenetic relationships below are based on examinations of specimens of *P. auriceps. P. carolinus, P. lucidus, P. placidus,* and the type of *P orientalis,* and species descriptions of all of the other species of the genus. Terminology by Schmid (1983, 1998) is used in this work.

A cladistic analysis is used to construct a tentative phylogenetic tree of *Phylocentropus* (Fig. 24). The analysis is based on morphological characters and inferred mentally with Hennigian logic (Hennig 1966). In the text, * = synapomorphies (numbered 1–16) that support corresponding branches in the phylogeny.

Dipseudopsidae Ulmer 1904

The family Dipseudopsidae includes six genera: *Dipseudopsis* Walker, *Limnoecetis* Marlier, *Protodipseudopsis* Ulmer, *Hyalopsyche* Ulmer, *Phylocentropus* Banks, and *Taymyrodipseudon* Ivanov & Melnitsky. Suppression of the subfamily Hyalopsychinae was suggested by Wells and Cartwright (1993) based on their observations of the larva of *Hyalopsyche disjuncta* Neboiss and the phylogenic analysis of Dipseudopsidae that was undertaken by Weaver & Malicky (1994). Adult dipseudopsids can be recognized quite easily by having antennae thick, straight and robust, with cavities of antennal scapes contiguous or very narrowly separated (Figs. 1–3). (The antennae of some Polycentropodidae can be similar, having scapes narrowly separated, as in Fig. 2, but their flagella are usually curved.) Larval characteristics also support monophyly of the family. Keys to extant genera for larvae and adults were provided by Weaver & Malicky (1994).

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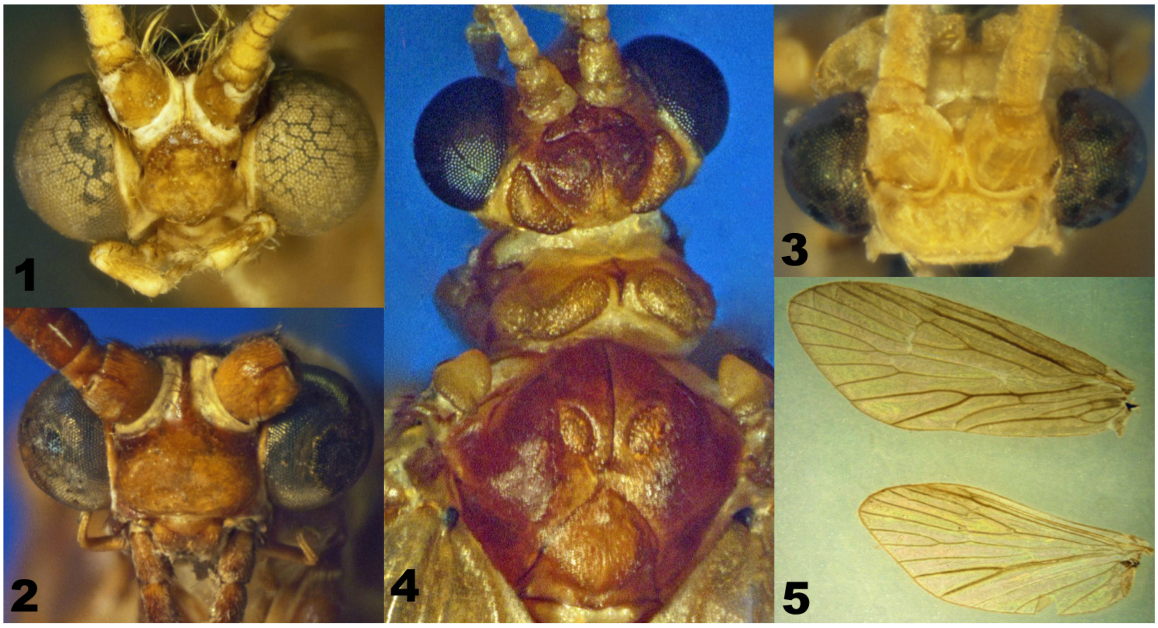
Phylocentropus Banks 1907

The known world fauna of the genus *Phylocentropus* includes 20 species (8 extinct, 12 extant). The extinct species include 4 in Baltic amber (Ulmer 1912) and 3 in New Jersey amber (Botosaneanu *et al*. 1998; Wichard & Bölling 2000; Wichard & Lüer 2003), and 1 from Lebanese amber (Wichard & Azar 2017). The present distribution of extant species is disjointed, having 5 in eastern North America and 7 in eastern Asia. Taxonomic works on the genus were provided by Schuster & Hamilton (1984) for the North American species and by Schmid (1983) for the Canadian species.



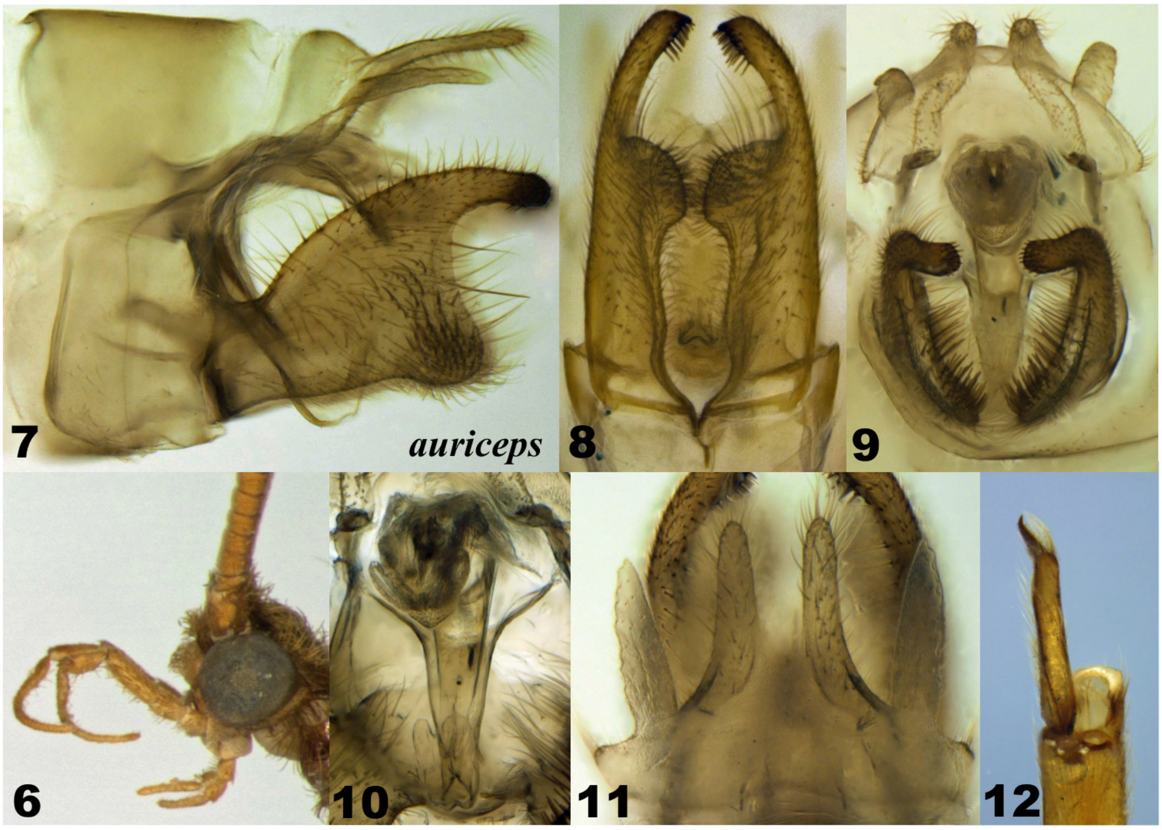
FIGURES 1–5. 1, *Phylocentropus placidus* Banks 1905b, male head, frontal. 2, *Dipseudopsis benardi* Navás 1930, male head, frontal. 3, *Limnoecetis tanganicae* (Marlier 1955), male head, frontal. 4, *P. placidus*, female head, pronotum and mesonotum, dorsal. 5, *Phylocentropus orientalis* Banks 1931, MCZ Type, male, left wings, dorsal.

Description: Wing venation (Fig. 5) almost complete with forks I and II originating at sectorial crossveins in both fore and hind wings of males and females. Forewings with all forks (I, II, III, IV, and V) present, forks I, II, IV sessile or nearly so; forks III and V petiolate; and discoidal, medial, and thyridial cells closed. Hind wings similar, except fork IV absent and medial cell open. Mesoscutal warts elliptical with long axis diagonal to median line and convergent posteriorly (Fig. 4). Spur formula: 3/4/4; apicomesal spur of each male hind leg usually unmodified.

Male genitalia, *tergite IX* usually broadly attached to *segment X*, but suture between them weak and inconspicuous. *Preanal appendages* variable, sometimes slender, triangular, spatulate or reduced, and attached to, and articulated with, posterolateral ventral sides of tergite IX just above point of its articulation with segment X. *Intermediate appendages* highly variable, their bases originating near posterior dorsomesal processes of inferior appendages and extending dorsoposterad; often attached to ventrolateral margins of segment X and then emerging on dorsal surface, sometimes as apicodorsal points, apicolateral patches of spiniform setae, or as separate arms, and in many of these variations bearing spiniform setae apically. *Inferior appendages* variable, short and rectangular or long and slender; sometimes with basodorsal processes, or other kinds of lobes; each often with group of short spines (or spiniform setae) mesally; and always one-segmented (without an articulated second article). *Phallic apparatus* variable, either relatively straight, curved, or C-shaped.

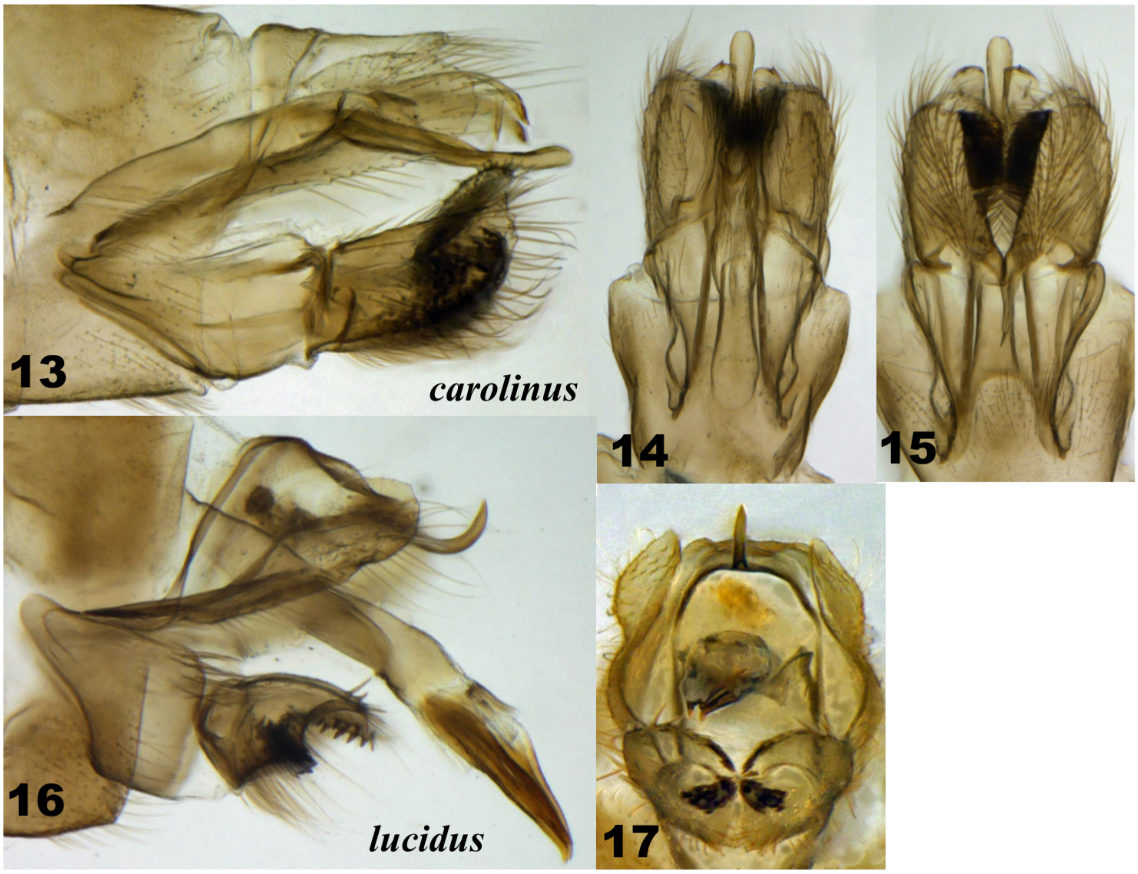
***Phylocentropus auriceps* Species Group**

P. auriceps (Banks 1905a), Figs. 6–12
† *P. antiquus* Ulmer 1912
† *P. cretaceous* Wichard & Bölling 2000
† *P. gelhausi* (Botosaneanu *et al*. 1998)
† *P. ligulatus* Ulmer 1912
† *P. simplex* Ulmer 1912
† *P. spiniger* Ulmer 1912
† *P. succinolebanensis* Wichard & Azar 2017
† *P. swolenskyi* Wichard & Lüer 2003



FIGURES 6–12. *Phylocentropus auriceps* Banks 1905a, male: 6, head, left lateral;7, genitalia, left lateral; 8, inferior appendages, ventral; 9, genitalia, caudal; 10, phallic apparatus, caudoventral; 11, segment X, dorsal; 12, mesoapical spur of right hind leg, ventral.

In *Phylocentropus*, all of the amber species have male genitalia with long slender appendages, and among the extant species this characteristic is shared by only one species, *P. auriceps.* For practical reasons, all of the fossil species are included in the *P. auriceps* Species Group, which is defined entirely by plesiomorphic characteristics. The *P. auriceps* Species Group was recognized by Ross as including *P. auriceps* and †*P. spiniger*. Ross noted that *1) the phallic apparatus of †*P. spiniger*, in the description by Ulmer (1912: fig. 66), has a chelate profile similar to that of *P. auriceps* (Ross 1965: fig. 1a); and this character is synapomorphic. The ventral portion of the chelate process in *P. auriceps* (Figs. 7 & 10) comprises two processes: 1) the *ventral prong,* heavily sclerotized ventral extension of the phallobase, and 2) the *internal harness,* heavily sclerotized part of the phallocrypt extending downward (further than the ventral margins of the inferior appendages) and then recurving, forming a receptacle for the ventral prong; the dorsolateral straps of the harness extend toward the bases of the intermediate appendages, near the areas of articulation between the tergite and sternite of segment IX. The internal harness appears to function in tandem with the ventral prong, much like a "flag harness" is used by a person to carry a flag in a parade.



FIGURES 13–17. *Phylocentropus* spp., male genitalia. 13–15, *P. carolinus* Carpenter 1933: 13, left lateral; 14, dorsal; 15, ventral. 16–17, *P. lucidus* (Hagen 1861): 16, left lateral; 17, caudal.

Based on other characters however, *P. auriceps* appears to be very archaic. It exhibits three plesiomorphic characteristics that are absent (or have not been observed yet) in other extant species of *Phylocentropus*. First, the inferior appendages are long. This characteristic is exhibited in all the species in amber and it was considered to be ancestral by Ross (1965). Second, labial palps are relatively long, being nearly equal to the length of maxillary palpomeres 1–3 combined. This character appears to be present in the following amber species (based on original species descriptions): †*P. cretaceous,* †*P. gelhausi*, †*P. spiniger*, and †*P. succinolebanensis*.

Third, the apicomesal spur of each male hind leg is modified. Because this character is present for the genus *Dipseudopsis* Walker (1852), (Weaver & Malicky 1994), and a similar characteristic is exhibited in some species of *Xiphocentron* (Brauer 1870) although the apical spurs are single in the latter (Schmid 1982a: figs. 177–183, 283–298) it might be an underlying synapomorphy (Saether 1979) of the superfamily Psychomyioidea, but has been lost in various subsequently evolved separate lineages. Possibly other species of the *P. auriceps* Species Group may have similar modified spurs, because they can be easily overlooked. For example, the knowledge of *P. auriceps* having modified spurs was unknown for nearly eight decades, until it was observed by Shuster & Hamilton (1984: figs. 17a, b). The presence or absence of these three characters cannot be determined for all of the extinct species of the *P. auriceps* Species Group due to the state of preservation of the individual fossils that are known. However as modified male apicomesal spurs are present in some caddisflies that are not closely related to Psychomyioidea: *Platycentropus raiatus* (Say 1838) and *Neophylax consimilis* Betten (1934), (Betten 1934: 27, figs 6c, d); *Glossosoma intermedium* (Klapalek 1892), *G. lividum* (Hagen 1861), *G. nigrior* Banks (1911), *G. verdona* Ross (1938), (Schmid 1982b: figs. 21–24); and single subapical spurs are modified in *Agapetus ungulatus* (Mosely 1939: 35, fig. 105), it would appear that this character may have evolved as the result of homoplasy rather than homology. As these modified spurs are sexually dimorphic, I wonder if they might be indicative of caddisflies with similar courtship behavior. Another possible plesiomorphic character of *P. auriceps* might be in the structure of its female genitalia, which Shuster & Hamilton (1984: figs. 11a–d) described. They noted that the female of *P. auriceps* differs from those of all species of the *P. placidus* Species Group by having female genitalia with segment X reduced and membranous, and cerci and lateral papillae large and prominent. Knowledge of the female genitalia of other species of *Phylocentropus* in the *P. auriceps* and *P. orientalis* Species Groups could be very useful for future phylogenetic analysis.

Branch of *P. placidus* + *P. orientalis* groups

A common lineage of the *P. placidus* Species Group + *P. orientalis* Species Group is supported by the synapomorphy that *2) inferior appendages and other appendages of male genitalia are much shorter and wider than in the *P. auriceps* Species Group. In species of the *P. auriceps* Species Group, each inferior appendage in ventral view is over 4X as long as its basal width, whereas in the *P. placidus* and *P. orientalis* Species Groups each inferior appendage is usually less than 2.5X as long. The inferior appendages in this branch are each usually somewhat rectangular or triangular in ventral view. The characteristic of the intermediate appendages joining segment X and then reemerging in one form or another, appears to be convergent within different groups. This characteristic has been observed by Ross (1965), Schuster & Hamilton (1984), and Schmid (1983), and was especially well illustrated in caudal view by the latter.

For synapormorphy *3) labial palps are reduced. In *P. placidus* labial palps are approximately 1.3X longer than the first two segments of the maxillary palps (Schmid 1983: fig. 1). This character has also been observed in *P. carolinus*, *P. lucidus*, and *P. orientalis*, and is assumed to be present in other species of this branch.

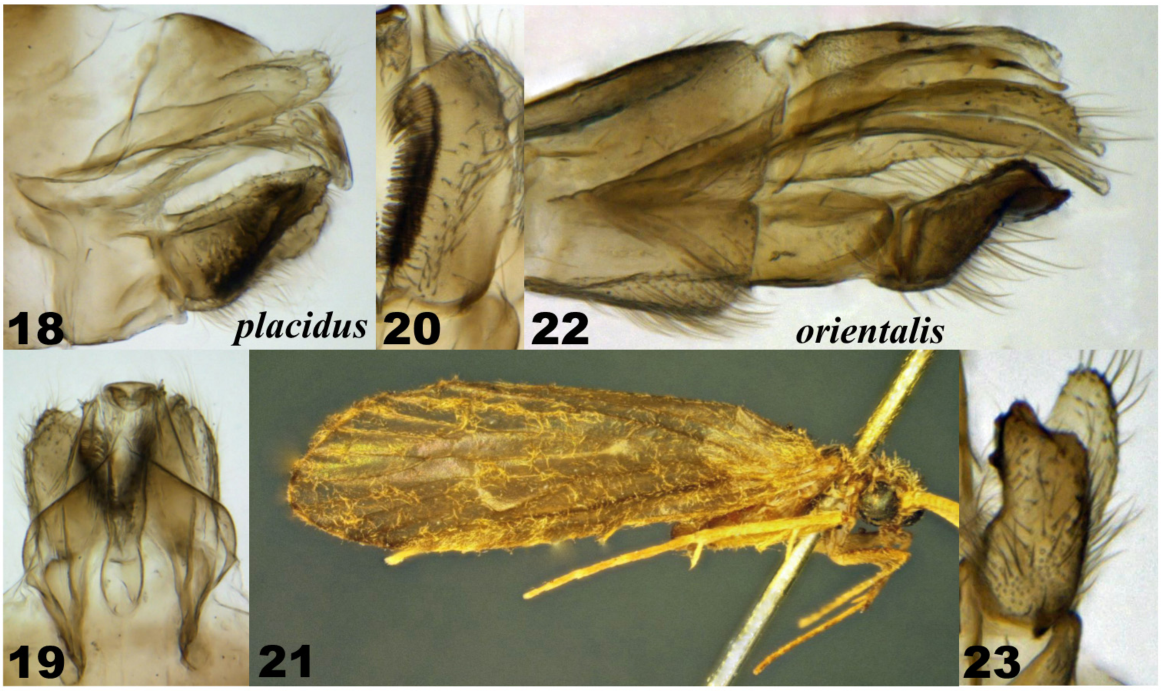
Phylocentropus placidus Species Group

P. carolinus Carpenter 1933, Figs. 13–15
P. harrisi Schuster & Hamilton 1984
P. lucidus (Hagen 1861), Fig. 16–17
P. placidus (Banks 1905b), Fig. 18–20

Ross (1965) recognized this group as including three species, *P. carolinus*, *P. lucidus*, and *P. placidus*; I add one more-recently-described species, *P. harrisi*. Monophyly of the *P. placidus* Species Group is indicated by the following: *4) each inferior appendage bears a large patch of spinose setae along the mesal margin (Figs. 15, 20) and *5) the phallus has a pair of apicolateral extensions (possibly a phallicata). The Branch of *P. placidus* + *P. harrisi* + *P. lucidus* shared the following synapomorphy: *6) intermediate appendages merge with the ventrolateral margins of segment X. The Branch of *P. placidus* + *P. harrisi* shared the following synapomorphies: *7) the apex of the phallus is curved ventrad and *8) intermediate appendages join segment X and then emerge on its dorsoapical surface as a pair of patches of spinose setae (Figs. 18, 19). In *P. lucidus* the intermediate appendages join segment X and then merge together and form a single apicomesal upturned spine (Figs. 16, 17). In *P. carolinus* the intermediate appendages remain separate, extend dorsoposterad, and then become bifid apically (Figs. 13–15).

Phylocentropus orientalis Species Group

P. anas Arefina-Armitage & Armitage 2011
P. narumonae Malicky & Chantaramongkol 1997
P. ngoclinh Arefina-Armitage & Armitage 2011
P. orientalis Banks, Figs. 5, 21–23
P. shigae Tsuda 1942
P. tohoku Arefina-Armitage & Armitage 2011
P. vietnamellus Mey 1995



FIGURES 18–23. *Phylocentropus* spp., males. 18–20, *P. placidus* Banks 1905b, genitalia: 18, left lateral; 19, dorsal; 20, right inferior appendage, ventral. 21–23, *P. orientalis* Banks 1931, MCZ Type: 21, habitus, right lateral; 22, genitalia, left lateral; 23, right inferior appendage, ventral.

Ross (1965) recognized this group as including one species*, P. orientalis* (Figs. 5, 21–23). The pair of long slender *subaedeagal lobes* described by Ross (1965: fig. 1A, *sl*) that form a glide below the aedeagus, are intermediate appendages. Six additional species from Asia have been added to this group: *P. shigae*, *P. vietnamellus*, *P. narumonae*, *P. anas, P. ngoclinh*, and *P. tohoku*. An excellent redescription of *P. shigae*, was provided by Nozaki *et al*. (2016).

Monophyly of the *P. orientalis* Species Group is implied by the following: *9) the ventral margin of the phallic apparatus has an obtuse angle in the middle of its ventral profile, similar to that of *P. orientalis*. The Branch of *P. shigae* + *P. tohoku* + *P. narumonae* + *P. ngoclinh* + *P. vietnamellus* + *P. anas* share the following synapomorphy: *10) the phallic apparatus has a long slender apicomeasal process. Monophyly for the Branch of *P. shigae* + *P. tohoku* + *P. narumonae* is implied by the following synaopmorphies: *11) the male genitalia have a large internal process which appears to be a hood-like extension of sternite IX; and *12) the intermediate appendages join segment X and emerge as apicodorsal points (but are reduced in *P. shigae*). The Branch of *P. shigae* + *P. tohoku* share the following synapomorphies: *13) the endotheca has an apical spine; and *14) inferior appendage with basodorsal process. The Branch of *P. ngoclinh* + *P. vietnamellus* + *P. anas* share the following synapomorphy: *15) segment X has a pair of long apicolateral arms, and the preanal appendages are slender. Monophyly for the Branch of *P. vietnamellus* + *P. anas* is inferred by the following: *16) the inferior appendages are tapered apically.

Phylogeny and Dispersal (Fig. 24)

Ross (1965) hypothesized that the three species groups of *Phylocentropus* "had all differentiated before the time of Baltic amber deposits" of the Eocene Epoch, approximately 40 *Mega anum* (Ma), but discoveries made since 1965 suggest that this occurred much earlier. Three species of *Phylocentropus* discovered in New Jersey amber, 90–95 *Ma*, (Botosaneanu *et al.* 1998; Wichard & Bölling 2000; Wichard & Lüer 2003) show similarities with the four species in Baltic amber described by Ulmer (1912). All of these fossil species have male genitalia with long appendages, a characteristic that Ross recognized as being primitive, and he also noted that one

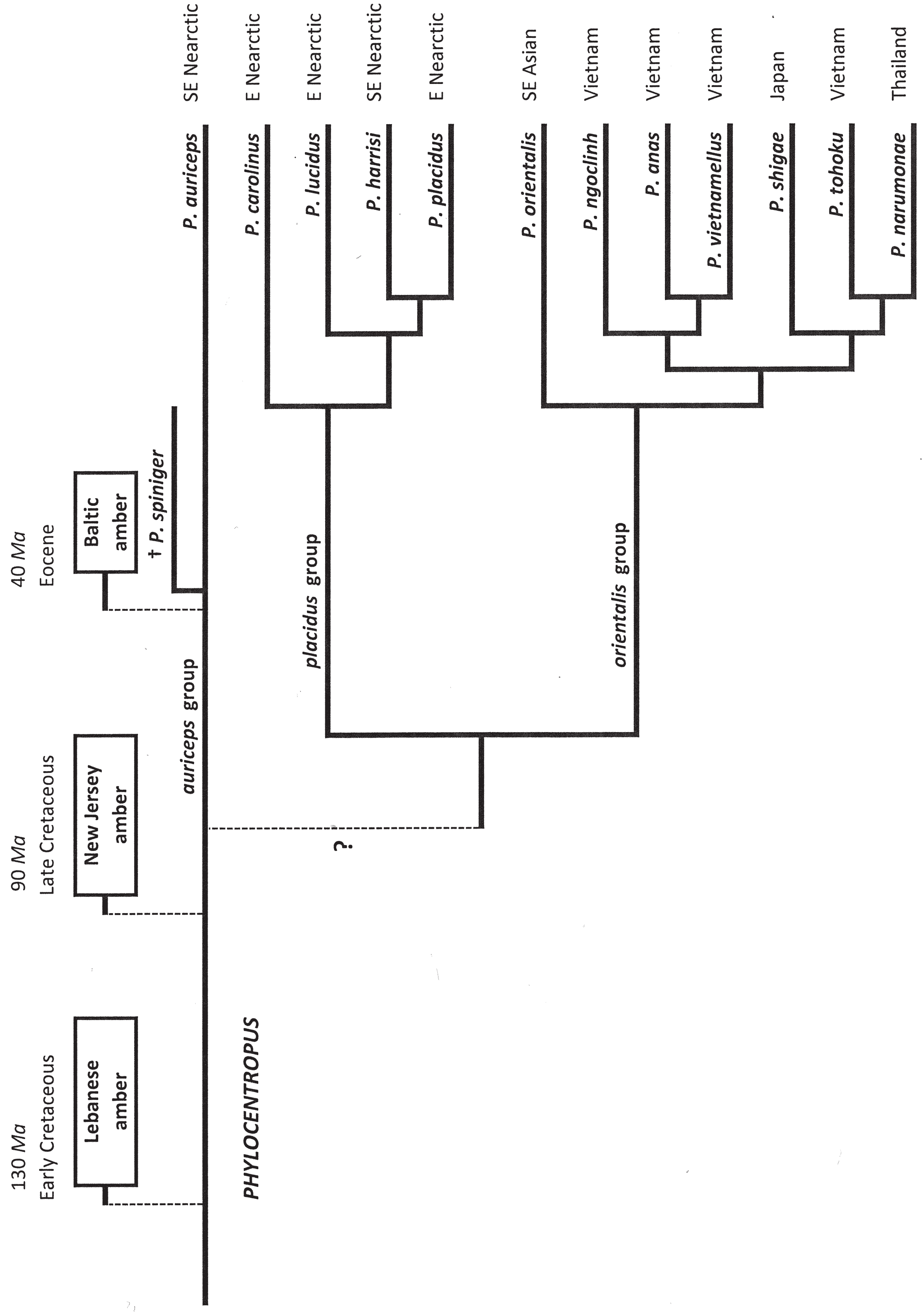


FIGURE 24. Hypothetical phylogenetic tree of *Phylocentropus* species.

extant species shares this characteristic, *P. auriceps* from the southern Appalachian Mts. Therefore, our current knowledge of the fossil fauna of *Phylocentropus*, suggests that the *P. auriceps* Species Group existed in both eastern North America and Europe, at least by 90 Ma.

I wonder if †*Taymyrodipseudon protopegasus* Ivanov & Melnitsky 2017, from Taymyr amber of northern Asia (85 Ma) might be a species of *Phylocentropus*? Based on the original description, it appears to have male genitalia with inferior appendages and hood-like internal process that are consistent with characteristics of the *P. orientalis* Species Group. If this is so, then *Phylocentropus* would have evolved into three groups by the Late Cretaceous. At this time the genus probably had a nearly contiguous Holarctic distribution, with the *P. orientalis* Species Group in the East (Asia) and the other two groups in the West (eastern North America and Europe). Later, the European fauna became extinct, probably during the Ice Ages that occurred later in the Tertiary, leaving survivors of the *P. auriceps* and *P. placidus* Species Groups in eastern North America and the *P. orientalis* Species Group in Asia. This scenario would explain the disjointed distribution of the extant species of *Phylocentropus*.

The most recently discovered fossil of *Phylocentropus* by Wichard & Azar (2017) is also the most remarkable: †*Phylocentropus succinolebanensis* from Lebanese amber is the oldest fossil of *Phylocentropus* yet known to science, being approximately 130 Ma from the Barremain Age, and the only known species of *Phylocentropus* from Gondwana, as Lebanon was in the northeastern peninsula of Gondwana in the Early Cretaceous. Therefore, it is hypothetically possible that the ancestor of *Phylocentropus* was Gondwanan, and this is supported by the fact that among its extant fauna, Africa has greatest number of dipseudopsid genera in the world, including *Dipseudopsis*, *Hyalopsyche, Limnoecetis*, and *Protodipseudopsis*, of which the latter two are endemic. This also lends support to the scenario hypothesized by Ross & Gibbs (1973), that a pre-Baltic amber ancestor of Dipseudopsidae may have evolved in Africa and dispersed to Eurasia, and that the evolution of the family "occurred in connection with a possible complex pattern of dispersal between Africa and Eurasia."

Basic weaknesses in this phylogenetic analysis (Fig. 24) are that no morphological synapomorphies are known for the genus *Phylocentropus* or the *P. auriceps* Species Group. One possible synapomorphy for the genus is that the hind wing medial cell is open, but this character is also present in *Hyalopsyche.* Therefore, monophyly of the genus is unsubstantiated. However, I suspect that the genus *Hyalopsyche* may represent a fourth group within *Phylocentropus.*

This genus deserves a more rigorous analysis than the one presented here. Such an analysis would require the examination of additional species of the *P. auriceps* and *P. orientalis* Species Groups. There are many intriguing characters (especially of the male genitalia) that could be useful, but I cannot understand them fully based merely on species descriptions that are available at this time.

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