

A phylogenetic analysis of the dung beetle genus *Phanaeus* (Coleoptera: Scarabaeidae) based on morphological data

DANA L. PRICE

Insect Syst. Evol. Price, D. L.: A phylogenetic analysis of the dung beetle genus *Phanaeus* (Coleoptera: Scarabaeidae) based on morphological data. *Insect Syst. Evol.* 38: 1-18. Copenhagen, April, 2007. ISSN 1399-560X.



The genus *Phanaeus* (Scarabaeidae: Scarabaeinae) forms an important part of the dung beetle fauna in much of the Western Hemisphere. Here a phylogeny for *Phanaeus*, including 49 *Phanaeus* sp., and 12 outgroup taxa, is proposed. Parsimony analysis of 67 morphological characters, and one biogeographical character produced 629 equally parsimonious trees of 276 steps. *Oxysternon*, the putative sister taxon is nested well within the subgenus *Notiophanaeus*, implying that *Oxysternon* might ultimately need to be synonymized with *Phanaeus*. Species groups of Edmonds (1994) recovered as monophyletic are *paleano*, *endymion*, *chalconelas*, *tridens*, *triangularis*, and *quadridens*. An 'unscaled' equal weighting analysis yielded 57,149 equally parsimonious trees of 372 steps. The strict consensus of these trees yielded a monophyletic *Phanaeus* with the inclusion of *Oxysternon*. Bootstrap values are relatively low and some clades are unresolved.

Dana L. Price, Graduate Program of Ecology and Evolution, Rutgers University, DEENR, 1st Floor, 14 College Farm Road, New Brunswick, NJ 08901 (dprice@eden.rutgers.edu).

Introduction

The genus *Phanaeus* is a group of tunneling dung beetles that are well known for their bright metallic colors and striking sexual dimorphism (Edmonds 1979). Despite numerous studies on biology and behavior of *Phanaeus* dung beetles, there has been no systematic research on the evolutionary relationships among the species. However, a detailed study of the skeletal morphology of *Phanaeus vindex* Macleay (Edmonds 1972), and a revision of the genus (Edmonds 1994) have provided essential taxonomic information about this group. Edmonds (1994) revision split *Phanaeus* into two subgenera: *Notiophanaeus* and *Phanaeus* s. str.. *Notiophanaeus* comprises five species groups including 15 mostly South American species. *Phanaeus* s. str., includes 27 species (+ four subspecies) arranged in eight species groups, mostly in Middle America. Since 1994, nine new species have been described. The principal aim of this study is to investigate, using

morphological characters and cladistic methods, the phylogeny of this clade. Hence, the monophyly of the genus, as well as relationships among *Phanaeus*, with special attention to previously proposed species groups, are also examined.

While most species delineations within *Phanaeus* are generally accepted, much controversy surrounds the number of subspecies. Edmonds (1994) four subspecies have since been increased to 26 subspecies. Subspecies descriptions from the literature are poor, type specimens would be needed in order to determine the differences, and obtaining type specimens can be quite difficult for studies not involving revisionary work. In addition, for several subspecies the only defining characteristic was color. Coloration is an important aspect of the morphology of these beetles, but its high intraspecific variation seriously limits its taxonomic usefulness (Edmonds 1994). For these reasons the subspecific nomenclature of Edmonds (1994) was used in this study.

Material and methods

Specimens used in this study were generously lent by the following institutions and people: David Furth and Nancy Adams, The National Museum of Natural History, Washington, D.C., U.S.A. (NMNH); Francois Genier, Canadian Museum of Nature, Ottawa, Ontario, Canada (CMN); Weiping Xie, The Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A. (NHMLAC); Sacha Spector, The American Museum of Natural History, New York, U.S.A. (AMNH); W.D. Edmonds, Marfa, Texas, U.S.A.; Trond Larsen, Princeton University, Princeton, New Jersey, U.S.A.; Kevina Vulinec, Delaware State University, Dover, Delaware, U.S.A.; Barney Streit, Tucson, Arizona, U.S.A.; and M.C. Thomas, Florida Department of Agriculture and Consumer Services, Gainesville, Florida, U.S.A.

Taxa

Forty-nine of fifty-one species total and two subspecies of *Phanaeus* were examined (following the nomenclature of Edmonds 1994). *Coprophanaeus pluto* (Harold, 1863), *C. telamon* (Erichson, 1847), *Oxysternon conspicuatum* (Weber, 1801), *O. lautum* (Macleay, 1819), *O. palaemon* Laporte, 1840, *O. silenus* Laporte, 1840, *O. spiniferum* Laporte, 1840, *Sulcophanaeus auricollis* (Harold, 1880), *S. favnus* (Fabricius, 1771), and *S. imperator* (Chevrolat, 1844) are included as outgroup taxa. Additional outgroup taxa from the tribe Eucraniini were *Anomiopsoides heteroclyta* (Blanchard, 1845), and *Glyphoderus sterquilinus* (Westwood, 1837). Outgroup representatives were chosen according to a recent phylogenetic analysis of the tribe Phanaeini (Philips et al. 2004).

Character selection

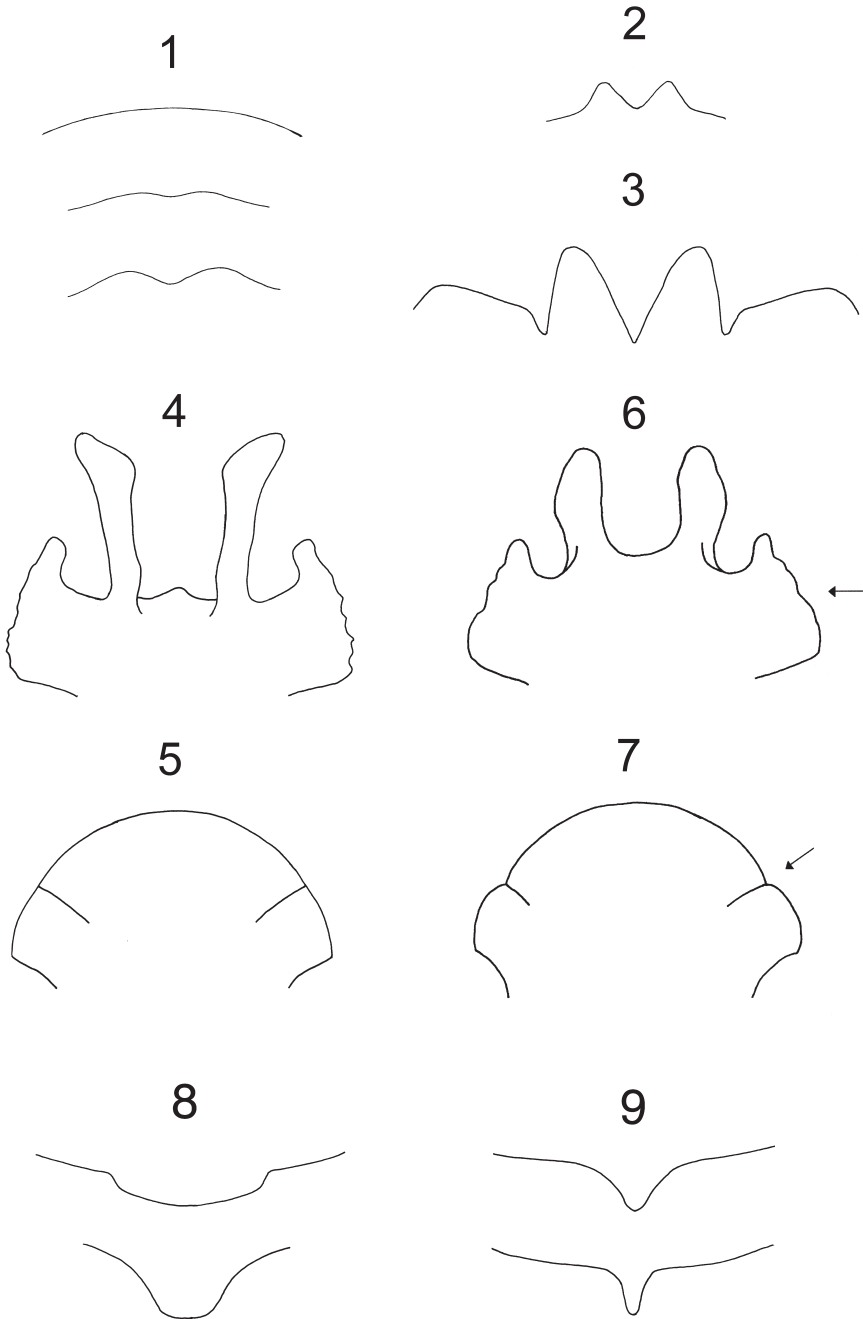
Sixty-seven morphological characters and one biogeographical character were scored (Appendix 1). Terminology and nomenclature follows Edmonds (1972; 1994). Several external morphological characters from Edmonds (1994) have been re-evaluated and coded. New characters include those of the antennae, legs, labrum, pygidium, and genitalia. Emphasis is placed on large male secondary sexual characters. For a number of species, some characters could not be scored due to lack of material, although in a few cases information was supplemented from the literature. Dissections of the labrum (male and female), male genitalia (phal-

lobase and parameres), and pygidium were followed by standard treatment with 10% KOH. Specimens were stored in 75% ethanol. Only dissected characters that showed no intraspecific variation were used in this study. *P. chalcomelas*, a species for which many individuals were available, was used as a model for character choice. One to four individuals of all other species were examined. Line drawings were made using a Wild Heerbrugg stereomicroscope equipped with a camera lucida. Additional characters were photographed using a Nikon 995 Coolpix digital camera with a digital adapter lens.

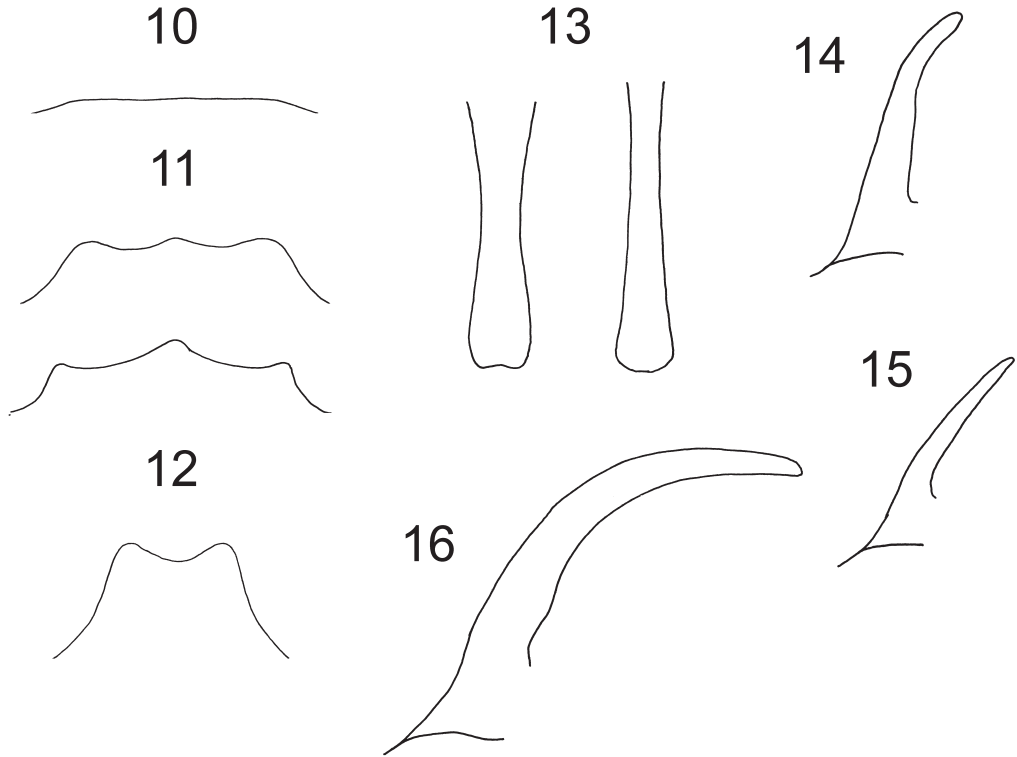
Analysis

Phylogenetic analyses based on maximum parsimony were carried out in PAUP 4.0b10 (Swofford 1999) using heuristic searches of 10,000 randomized replicates, TBR branch swapping, and ACC-TRAN character-state optimization. Because of the large numbers of equally parsimonious trees, the number of trees saved per replicate was limited to 100 during the first search. Another single heuristic search was then performed, starting with the trees saved from the initial analysis. Each character was weighted equally regardless of character type and the number of states ('scaled' equal weighting). Because some characters have multiple states, state transitions were, in effect, down-weighted in proportion to the number of states for these characters relative to binary characters (May 2002). In a second analysis, also using 'scaled', equally weighted characters, *Phanaeus* was constrained as monophyletic using the "constraints" command in PAUP, with *Oxysternon* as an outgroup (Outgroups+*Oxysternon* (*Phanaeus*)).

Additional weighting schemes examined include equal weighting for each state change ("unscaled equal weighting") (May 2002) and pseudoreplicate reweighting (Kjer 2001; 2002). The unscaled analysis was performed using the same methods as described for the scaled analysis. The pseudoreplicate weighting scheme was accomplished by conducting a bootstrap analysis with 100,000 replicates, using "Fast" stepwise-addition, including groups compatible with the 50% majority rule and saving the 100,000 trees to a tree file. Each character was then reweighted according to the rescaled consistency index, using the 'best fit' option in PAUP to all starting trees. A heuristic search of 1,000 replicates (saving no more than 100 trees) was then conducted using the rescaled



Figs 1-9. Clypeus of *Phanaeus* spp. 1-4. Anterior margin of clypeus: 1. rounded clypeus of *P. furiosus* (top), slightly bidentate clypeus of *P. splendidulus* (middle) and *P. melibaeus* (bottom); 2. Strongly bidentate clypeus of *P. paleano*; 3. *Coprophanaeus telamon*; 4. *Anomiopsoides heteroclyta*. 5-6. Lateral margin of the clypeus and the parietal area: 5. *P. vindex*; 6. *Anomiopsoides heteroclyta* female. 7. Outer margin of *P. palliatus* clypeus and parietal area. 8-9. Frontal view of clypeal process: 8. transverse process of *P. eximius* (top), and toothlike process of *P. haroldi* (bottom); 9. spiniform process of *P. dejeani* (top), and *P. paleano* (bottom).



Figs 10-16. Head capsule structures in *Phanaeus* spp. 10-12. Cephalic carina of large female in frontal view: 10. simple carina of *P. splendidulus*; 11. trituberculate carina of *P. bispinus* (top), and *P. mexicanus* (bottom); 12. bituberculate carina of *P. vindex*. 13. Male horn in dorsal view: *P. dejeani* (left), and *P. bispinus* (right). 14-16. Male horn shape in lateral view: 14. *P. splendidulus*; 15. *P. igneus*; 16. *P. a. amethystinus*.

data. The advantage of pseudoreplicate reweighting over successive weighting (Farris 1969) is that the large number of diverse but potentially near optimal starting trees breaks the circularity that can result from calculating weights from a single initial resolved tree (Kjer 2002).

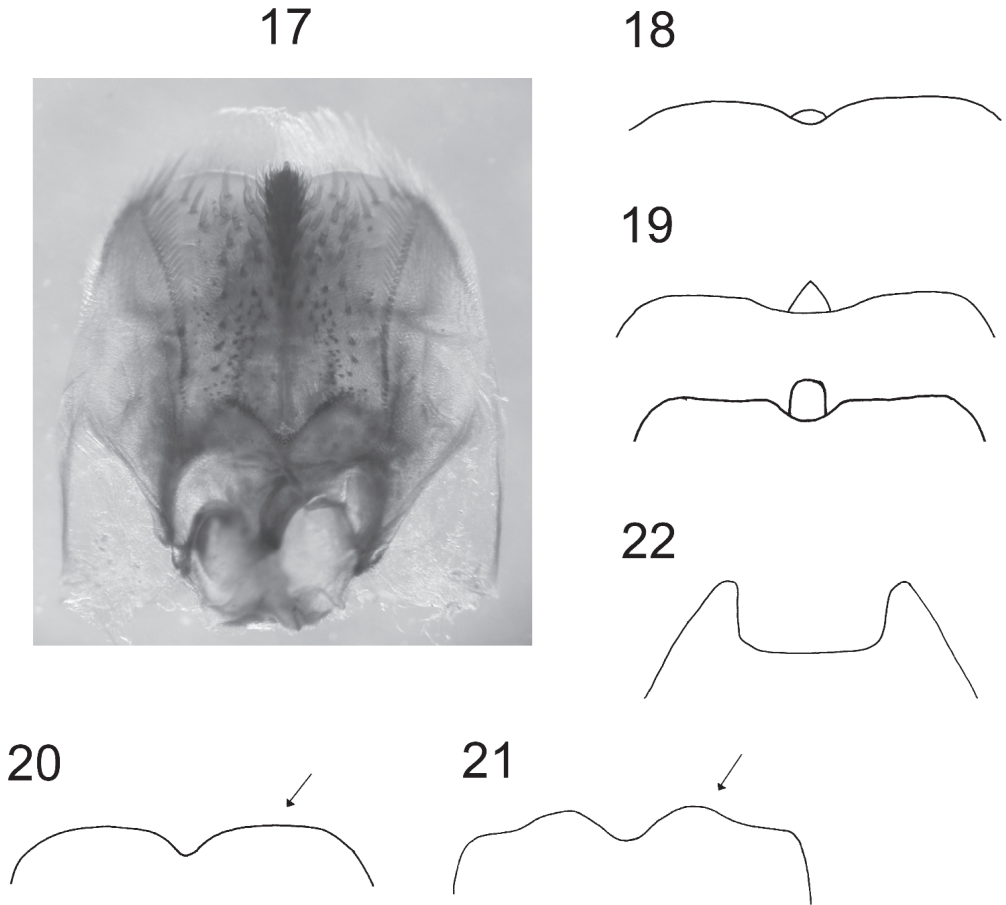
All characters were considered unordered, i.e. change was equally likely between any pair of states. Characters considered not applicable to a particular species were scored with a "?". In each analysis, trees were rooted using only *Anomiospodes heteroclyta* and *Glyphoderus sterquilinus* as outgroups. Support at each node was assessed using bootstrap values (Felsenstein 1985). Five hundred replicates were implemented, with 5 random addition sequences per replicate and no more than 500 trees saved per replicate.

Characters and character states

Morphological terms are based on Edmond's (1972) examination of the skeletal morphology of *Phanaeus vindex*. Note that character state designations have no significance with respect to polarity.

Cranium

1. Anterior margin of clypeus: (0) rounded to weakly bidentate (Fig. 1); (1) strongly bidentate (Fig. 2); (2) with deep, acute emarginations setting off two elongate, narrow teeth beneath which extends a strong, anteriorly directed, U-shaped carina (*Coprophanaeus*) (Fig. 3); (3) with four anterior processes, median processes larger (Figs 4, 6).
2. Lateral margin of clypeus and parietal area: (0) with external margin rounded and smooth (Fig.



Figs 17-22. Labrum of *Phanaeus* spp. 17. Digital photo of the labrum of *P. chalconelas* in dorsal view. 18-19. Apex of median process of the labrum in ventral view: 18. *P. chalconelas*; 19. *P. melibaeus* (top), and *Oxysternon conspicillatum* (bottom). 20-22. Apex of labrum in ventral view: 20. *P. chalconelas*; 21. *Sulcophanaeus favnus*; 22. *Glyphoderus sterquilinus*.

- 5); (1) with external margin dentate or irregular (Figs 6, 4).
- Edmonds (1972) suggests that the spatial relationship between the antennal sockets and the fronto-clypeal sulcus (frontal region) has been much reduced or eliminated by anterior and/or posterior expansion of other cephalic areas (e.g. the clypeus). Consequently, a vertex and gena are not distinguishable. Edmonds (1972) further describes this region as the parietal area, or parietals.
- 3. Outer margin of clypeus and parietal area: (0) distinctly notched laterally (Fig. 7); (1) not notched laterally (Fig. 5).
- 4. Clypeal process: (0) rounded or transverse to toothlike (Fig. 8); (1) spiniform (Fig. 9).
- 5. Cephalic carina of large female: (0) with horn or a central tubercle present; (1) with horn absent.
- 6. Cephalic carina of large females in frontal view: (0) simple (Fig. 10); (1) trituberculate (Fig. 11); (2) bituberculate (= corniform) (Fig. 12).
- 7. Cephalic carina of females: (0) even with or in line with anterior portion of eyes; (1) anterior to the eyes.
- 8. Cephalic carina of large males: (0) with horn present; (1) with horn absent.

9. Distal end of large male horn: (0) dorso-ventrally flattened, not expanded laterally; (1) dorso-ventrally flattened and expanded laterally (Fig. 13); (2) not compressed or expanded laterally.
10. Large male horn shape: (0) straight and perpendicular to head; (1) straight with distal 1/3rd bent back towards the pronotum (Fig. 14); (2) straight, bent backwards at base (Fig. 15); (3) curving backwards over the pronotum (Fig. 16).
11. Occipital ridge: (0) complete; (1) incomplete.

Labium

12. Premental sclerites: (0) completely sclerotized; (1) not completely sclerotized.

Labrum (= epipharynx)

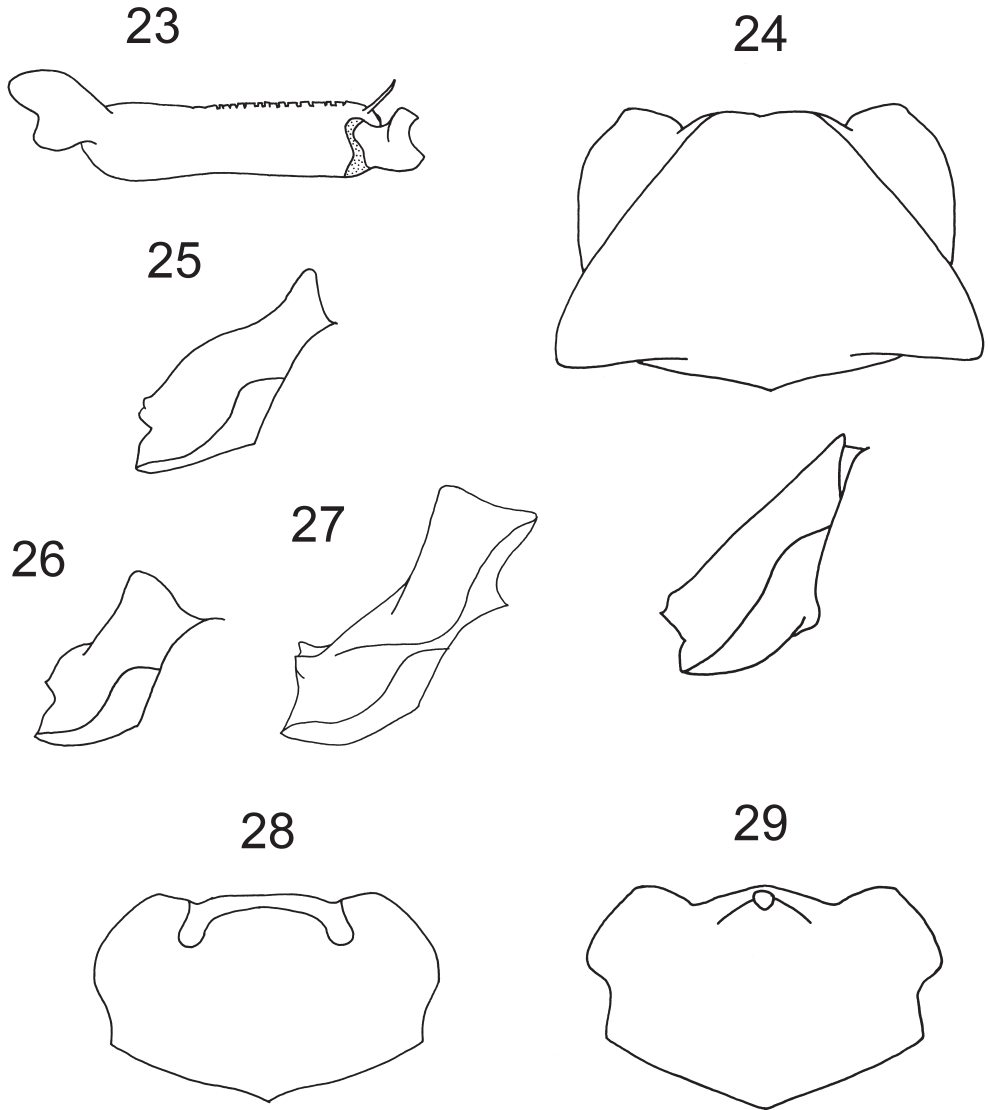
13. Length of apical fringe in relation to size of labrum: (0) \geq 1/3 length of labrum; (1) $<$ 1/3 length of labrum.
The labrum was measured from the apex of the anterior margin to a posterior point between the tormal process and the posterior median process of the labral suspensorium. In addition, the longest setae of the apical fringe were measured.
14. Number of setae present on one side of (right or left) dorsal (oral) surface of labrum (Fig. 17): (0) fewer than 30, short and stubby; (1) more than 30 to 70, not short and stubby; (2) more than 70, not short and stubby.
15. Dorsal surface: (0) with median brush of setae (Fig. 17); (1) with median sclerotized carina.
16. Length of median brush of labrum in lateral view: (0) uniformly short to medium length; (1) some setae markedly longer than other setae.
17. Setae of median brush: (0) of uniform width; (1) with wider setae at anterior end of brush than elsewhere.
18. Apex of median process: (0) slightly (Fig. 18) or not at all extending beyond anterior edge; (1) extending far beyond anterior edge (Fig. 19).
19. Apex of labrum (ventral view): (0) straight with shallow notch in center (Fig. 20); (1) with raised areas on both sides of the apex (appearing as bumps) (Fig. 21); (2) U-shaped (Fig. 22).

Antennae

20. Antennal scape: (0) partially laterally flattened; (1) cylindrical along entire length.
21. Antennal club: (0) spherical; (1) elongate.
22. Distal end of antennal scape: (0) with single long seta (Fig. 23); (1) without single long seta.
23. Scape: (0) dentate (Fig. 23); (1) more or less smooth.

Pronotum

24. Head-prothorax: (0) without interlocking mechanism; (1) with interlocking mechanism. The interlocking mechanism described by Edmonds (1972) is as follows: anterior margin of circumnotal ridge distinctly interrupted by emarginations receiving postocular lobes of parietals. This character represents a synapomorphy of *Phanaeus*.
25. Anterior pronotal sculpturing of large horned males consisting of: (0) two antero-lateral tubercles; (1) three or four tubercles or two antero-lateral tubercles with a central carina; (2) central conical tubercle or slightly raised portion (carina) extending into pronotum, or no tubercles.
26. Postero-medial margin of large male pronotum: (0) with two distinct tubercles; (1) with one central tubercle; (2) without tubercles.
27. Pronotum of large male: (0) with two medial spiniform processes directed toward the head; (1) without such processes.
28. Pronotal disk shape of large male: (0) centrally concave with two shallow bilateral depressions; (1) centrally concave lacking two shallow bilateral depressions; (2) not centrally concave.
29. Pronotal disk of large males: (0) centrally concave with median tubercle or fin-like carina; (1) centrally concave with bifurcated median carina; (2) without concavity and median carina.
30. Pronotal disk of large males: (0) with lateral spiniform processes directed dorsally or inward; (1) with lateral spiniform processes directed toward the head; (2) with lateral processes absent or not spiniform.
31. Postero-lateral margin of pronotal disk of large males: (0) projecting backwards or outwards such that the disk is almost triangular (Fig. 24); (1) produced laterally and outer margins narrowly upturned (Fig. 25); (2) curving



Figs 23-29. Antennal and pronotal structures in *Phanaeus* spp. 23. Left antennal scape in dorsal view of *P. daphnis*. Both dentition and distal seta of the scape are shown. 24-27. Postero-lateral margin of male pronotal disk: 24. dorsal view (top) and lateral view (bottom) of *P. meliagris*; 25. *P. eximius*; 26. *P. kirbyi*; 27. *P. demon*. 28-29. Female pronotum: 29. *P. mexicanus*; 30. *P. splendidulus*.

- upwards into a point (Fig. 26); (3) curving upwards or back into thick processes (Fig. 27); (4) not as described above.
- 32. Texture of female pronotum to unaided eye: (0) smooth or minutely punctate; (1) strongly punctate/punctatorugose, rugose, or granulate/granulorugose; (2) with large irregularly shaped black rugosities.
- 33. Pronotum of large female: (0) with antero-medial carinate prominence flanked on each side by elongate depression toward eye (Fig. 28); (1) with narrow carina, sometimes tuber-

culate, in shape of a line or inverted U and followed by oval concavity (Fig. 29); (2) evenly convex bearing three or four tubercles; (3) with two dorsal projections and an anterior, median concavity.

34. Postero-median pronotal fossae: (0) present in at least one sex; (1) absent in both sexes or only punctiform.
 35. Posteromedian angle of pronotum: (0) acutely produced between basal angles of elytra; (1) not acutely produced.

Legs

36. Foretibia: (0) tridentate (Fig. 30) or barely quadridentate (Fig. 31); (1) distinctly quadridentate (Fig. 32).
 37. Third tooth of foretibia: (0) not carinate (Fig. 30); (1) weakly or distinctly carinate (Figs 31, 32).
 Whether an individual has a carinate third tooth does not depend on whether they have quadridentate or tridentate foretibia.
 38. Front tibia with fourth basal tooth: (0) separated from third by narrow, slit-like notch (Fig. 33); (1) not separated from third tooth by narrow, slit-like notch.
 39. Foretibial spur: (0) truncate or bending inward at apex toward the head (Figs 31, 34); (1) not truncate, straight or medially curving downward (Fig. 35).
 40. Female foretarsi: (0) present; (1) absent.
 41. Female foretarsi: (0) without setae on segments 1 - 4; (1) with setae on segments 1 - 4.
 42. Longer spur of female mesotibia: (0) not distinctly dilated (Fig. 36); (1) distinctly dilated (Fig. 37).
 43. Basal segment of female meso-basitarsus: (0) >.25mm longer than wide; (1) <.25mm longer than wide.
 44. Modal number of setae on 5th segment of metatarsus: (0) <= 7; (1) 8 - 10; (2) 11 - 13; (3) > 14.

In addition to intraspecific variation, the number of setae present on one individual varied from the right to the left metatarsus. Size of the species was not a factor (i.e. a large species could have 9 and fewer setae on their 5th metatarsus, and small species could have more than 9). A sample size of at least 15 individuals was examined in order to determine the mode for each species. Species in which fewer than 15 individuals were available were coded with

question marks.

45. Fifth tarsal segment: (0) with brush (setae clumped at distal end) (Fig. 38); (1) with brush absent, setae not clumped together (Fig. 39).

Metasternum

46. Anteromedian angle of metasternum (ventral view): (0) drawn out as large, upwardly curved spine projecting between apices of forecoxae; (1) not as above.

Oxysternon, a genus whose members are often confused with certain *Phanaeus*, are immediately distinguished from all other phanaeines by a long spiniform extension of the anterior angle of the metasternum (Edmonds 1972; Edmonds and Zidek 2004). This character (above 46:0) gives the group its name.

47. Anteromedian angle of metasternum (ventral view): (0) coming to a point; (1) with raised lobate portion (Fig. 40); (2) with raised portion in the shape an arrow-head or a "V" (Fig. 41); (3) with anterior median angle straight, not raised.

In the phanaeines the metasternal region between the mesocoxae is strongly and abruptly depressed medially as a vertical angulate prominence. Since this region is often viewed from below, the metasternum is often described as "raised" (Edmonds 1972). Hence, character 47:3 above, represents two outgroup genera, *Anomiopsoides* and *Glyphoderus*.

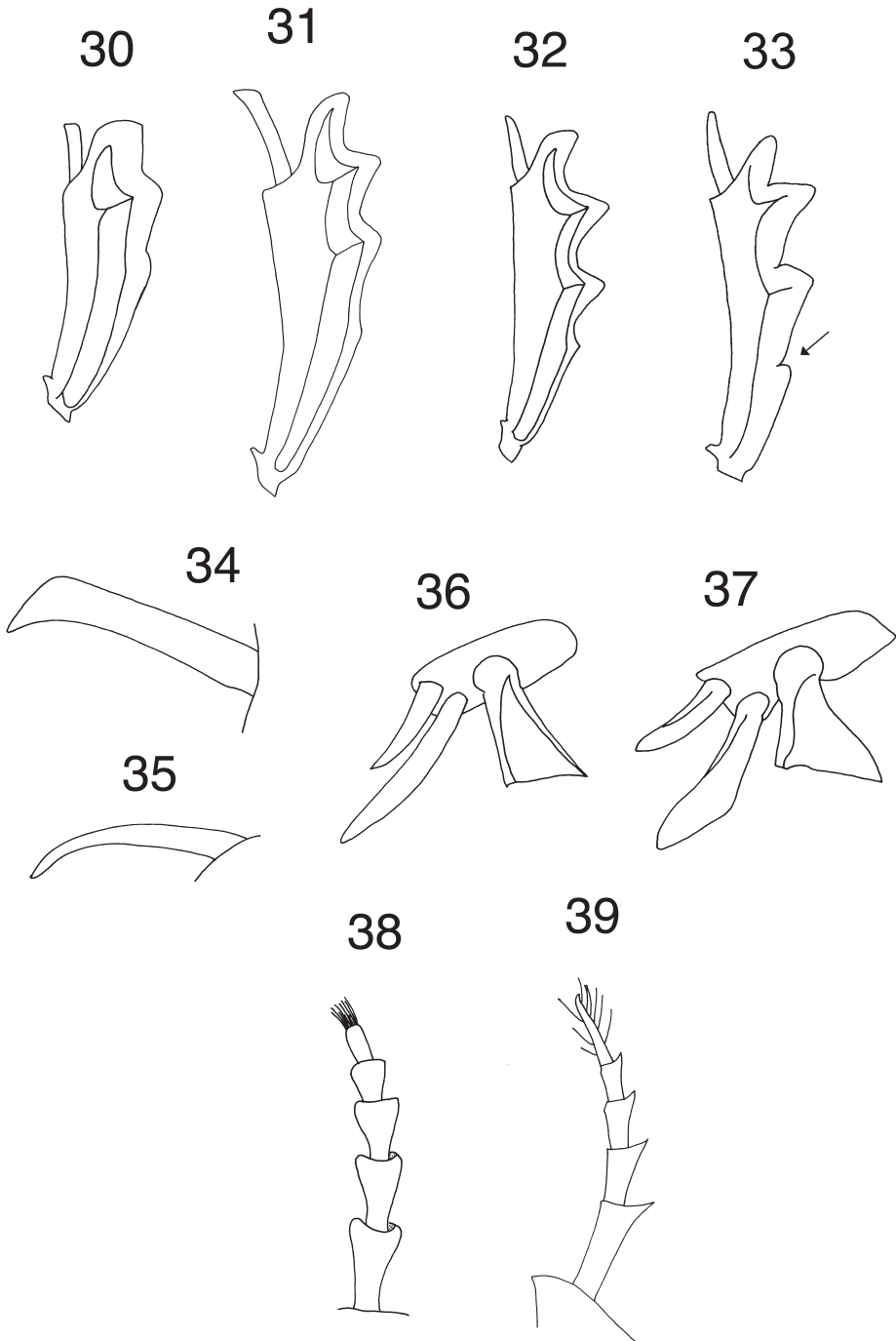
48. Pteuropleura and sides of metasternum: (0) clothed with dense pile of long white or yellow setae; (1) not clothed with long white or yellow setae.

Abdomen

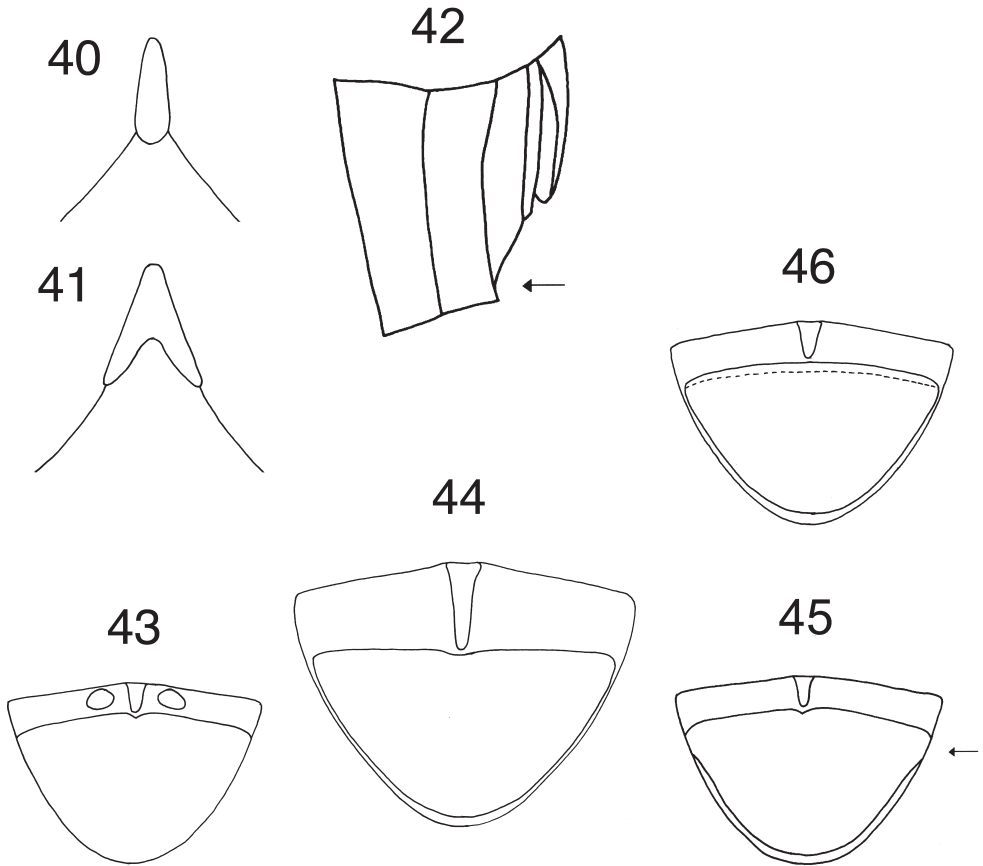
49. Middle of the anterior margin of 5th abdominal sternum: (0) impressed, causing posterior margin of 4th sternum to form a lip-like ledge below it (Fig. 42); (1) not impressed, thus 4th sternum not forming lip-like ledge.

Wings

50. Elytral striae: (0) carinulate (with small elevated, longitudinal carinae); (1) not carinulate.
 51. Elytral striae: (0) smooth to minutely punctate; (1) coarsely punctate, visible with unaided eye.
 52. Elytral interstriae: (0) appearing smooth to unaided eye; (1) visibly punctate or rugose.
 53. Body shape: (0) sides of elytra more or less



Figs 30-39. Leg structures in *Phanaeus* spp. 30-33. Foretibia in dorsal view: 30. *P. mexicanus*; 31. *P. haroldi*; 32. *P. difformis*; 33. notch indicated with an arrow (*P. endymion*). 34-35. Foretibial spur: 34. *P. haroldi* (dorsal view); 35. *Phanaeus* sp. (frontal view). 36-37. Longer spur of female mesotibia in ventral view: 36. *P. paleano*; 37. *P. demon*. 38-39. Hind tarsal segments: 38. brush of *Anomiopsoides heteroclyta*; 39. *P. quadridens*.



Figs 40-46. Abdominal structures of *Phanaeus* spp. 40-41. Antero-medial angle of metasternum in ventral view: 40. *P. howdeni*; 41. *P. t. triangularis*. 42. Impressed 5th abdominal sternum of *Oxytetrone conspicillatum* in lateral view. 43-46. Pygidium: 43. propygidium of *P. paleano*; 44. *P. amithaon*; 45. effaced anterior margin of the pygidium of *P. paleano*; 46. propygidial groove of *Oxytetrone palaemon*.

straight; (1) globose, sides rounded.

54. Hindwings: (0) present; (1) obsolete.

Outgroup genera *Animospodes*, and *Glyphoderus* are flightless, a trait typical of most species of the tribe Eucraniini (Ocampo 2005).

Pygidium

55. Propygidium: (0) with two circular depressions, one on each side of the pygidial slit (Fig. 43); (1) without circular depressions.

56. Medial length of propygidium; (0) about as long as lateral edge; (1) distinctly longer than at lateral edge (Fig. 44).

Estimated visually, measurements of the me-

dian and lateral edge were not recorded.

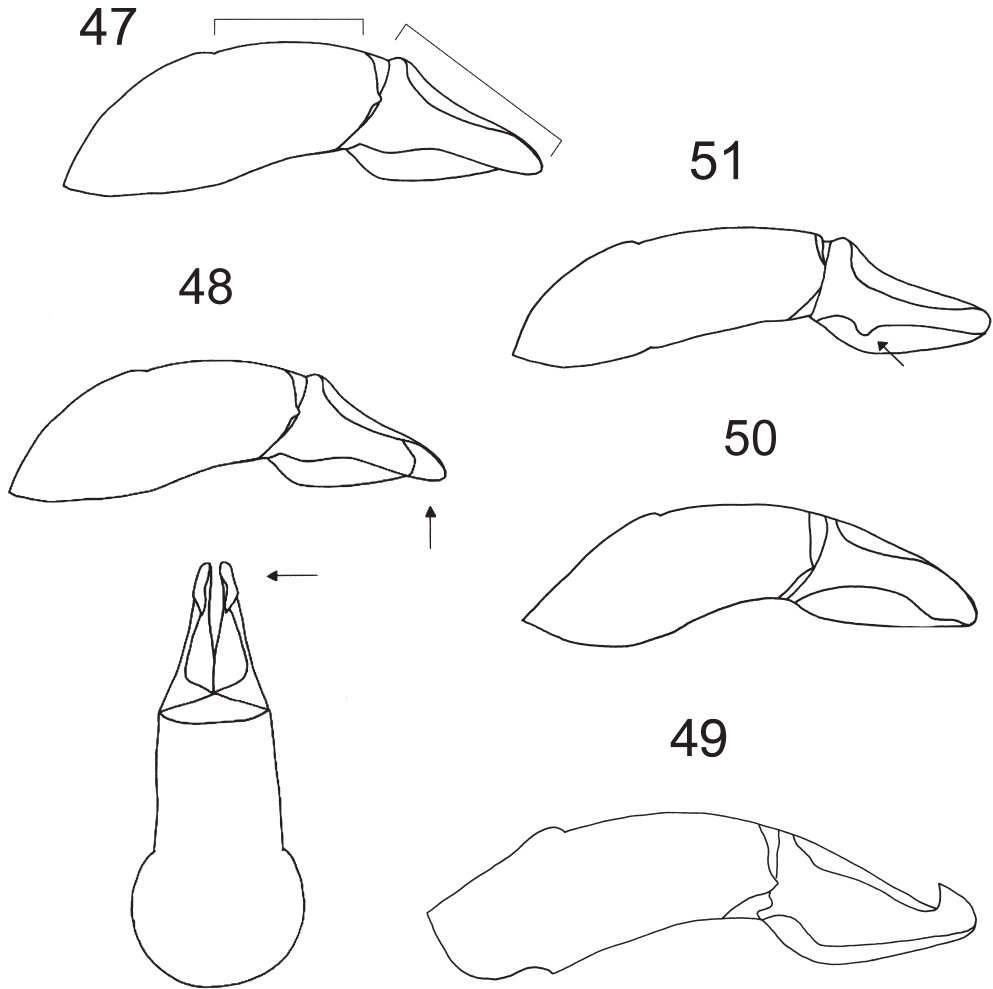
57. Raised outer margin of pygidium: (0) effaced anteriorly or not complete (Fig. 45); (1) complete.

58. Distinct groove below the transverse carina of the posterior propygidium: (0) present (Fig. 46); (1) absent.

59. Pygidial slit: (0) present; (1) absent.

Male Genitalia

60. Length of parameres: (0) > .25 mm shorter than phallobase; (1) within .25 mm length of phallobase; (2) > .25 mm longer than phallobase.



Figs 47-51. Male genitalia of *Phanaeus* spp. 47. Paramere and phallobase of a *Phanaeus* sp. showing measurements used for characters 60:0-2. 48. Paramere and phallobase of *P. haroldi*: lateral view (top); ventral view (bottom). 49-51. Paramere and phallobase: 49. Hooked paramere of *Coprophanaeus telaemon*; 50. lateral sclerotization of *Oxysternon spiniferum* paramere; 51. lateral sclerotization of *P. amithaon* paramere.

- The sclerotized portion of the phallobase was measured in lateral view from the anterior portion of the phallobase to the phallobase lip (Fig. 47).
- 61. Distal portion of parameres: (0) with a thickened region appearing as a slight flange (Fig. 48); (1) lacking thickened region (Figs 47, 50, 51).
 - 62. Paramere: (0) with hook (Fig. 49); (1) without hook.
 - 63. Distal end of paramere: (0) dorso-ventrally flattened; (1) not flattened.
 - 64. Lateral portion of paramere: (0) completely sclerotized; (1) not completely sclerotized.
 - 65. Lateral sclerotization of paramere: (0) arching downward (Fig. 50); (1) straight or curving upward.
 - 66. Lateral sclerotization of paramere: (0) with a lower knob (Fig. 51); (1) without lower knob.

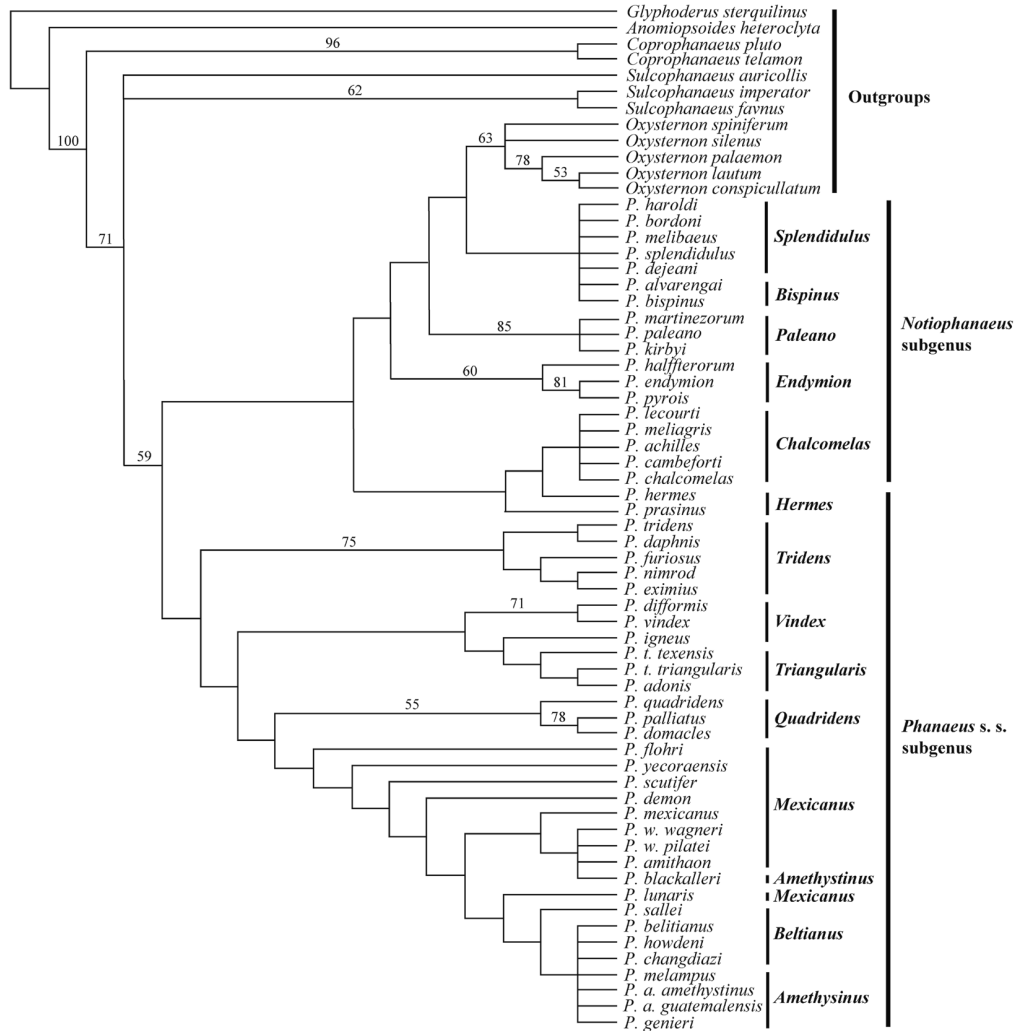


Fig. 52. The strict consensus tree of 629 equally parsimonious trees (276 steps, CI = 0.50, RI = 0.72) using 'scaled', equally weighted characters. The numbers above the branches are bootstrap values (>50%).

Individual Size

67. Body size of largest individuals: (0) \leq 25 mm; (1) $>$ 25 mm.

Biogeography

68. Locality: (0) South America; (1) Central and North America.

The data used for characters 67 and 68 were taken from the literature.

Results

The analysis of 67 morphological characters and one biogeographical character yielded 629 equally most parsimonious trees of 276 steps (CI = 0.50, RI = 0.72). All characters were parsimony informative. The strict consensus of these trees is given in Fig. 52. *Oxystemon* is nested well within the subgenus *Notiophanaeus*, implying that *Oxystemon* may be an apotypic derivative of *Phanaeus* that perhaps should eventually be sunk into *Phanaeus*.

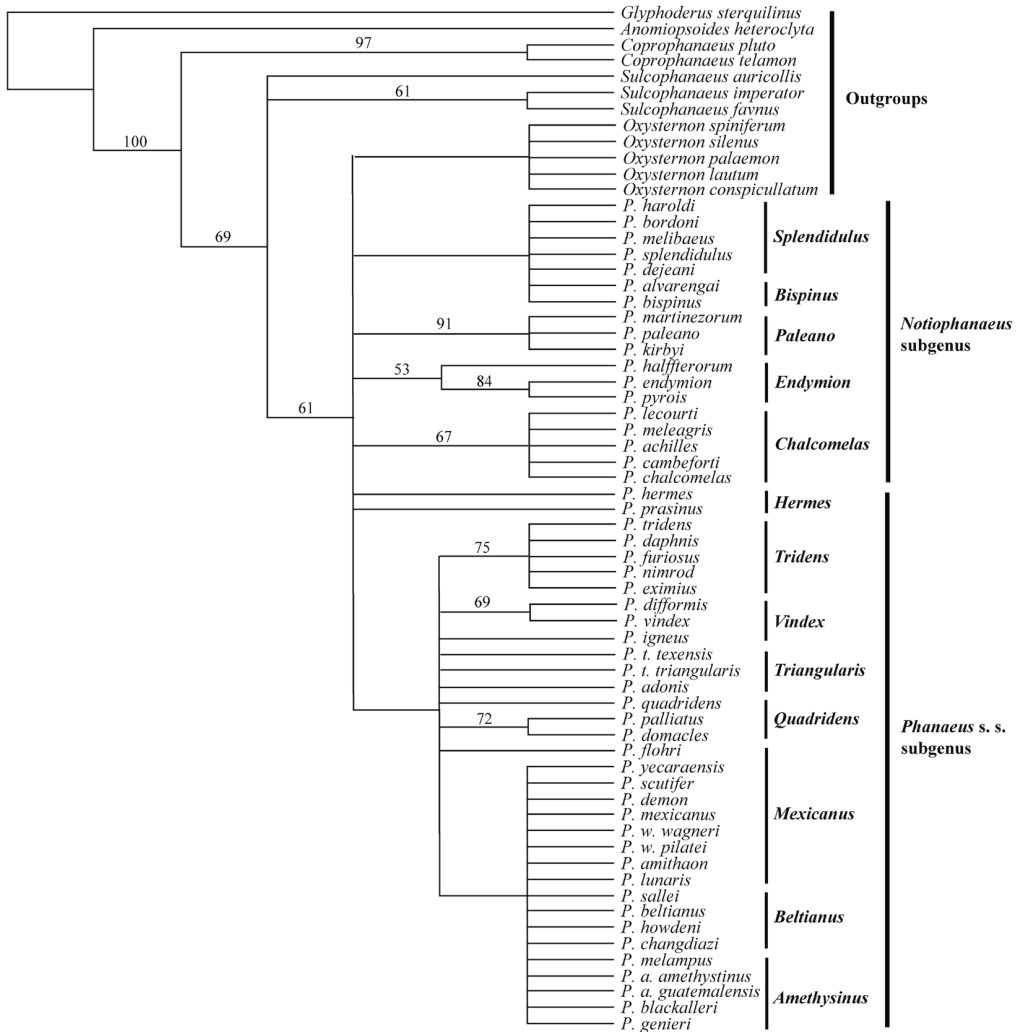


Fig. 53. The strict consensus of 57,149 equally parsimonious trees (372 steps, CI = 0.49, RI = 0.70) using unscaled, equally weighted parsimony. Numbers above the branches are bootstrap values (>50%).

The *Notiophanaeus* subgenus is recovered as monophyletic with the inclusion of the *hermes* species group and *Oxysternon*, as is *Phanaeus* s. str. if the *hermes* group is excluded. Six of Edmonds' (1994) species groups are recovered as monophyletic: *paleano*, *endymion*, *chalcomelas*, *tridens*, *triangularis*, and *quadridens*. Few clades are supported with bootstrap values greater than 50%. The constraint analysis yielded 251 equally most parsimonious trees of 279 steps (CI=0.50, RI=0.72).

The 'unscaled' equal weighting analysis recovered neither subgenus, and yielded a strict consensus with poor resolution and relatively low bootstrap values (Fig. 53). Species groups recovered as monophyletic include *paleano*, *endymion*, *chalcomelas*, and *tridens*, and all are supported with bootstrap values above 50%. The strict consensus of trees generated by pseudoreplicate reweighting (Fig. 54) supports a monophyletic *Phanaeus* with *Oxysternon* included. The subgenus *Phanaeus* s.

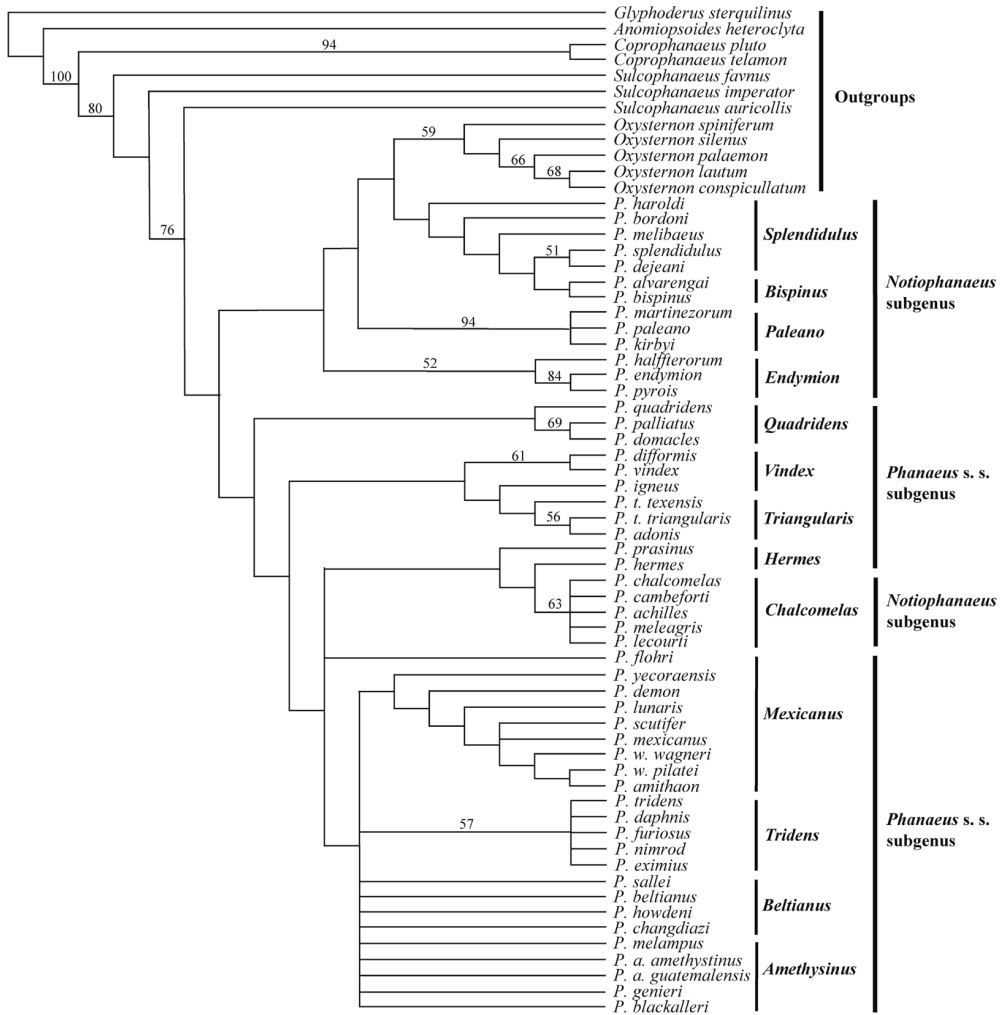


Fig. 54. The strict consensus of 3,830 equally parsimonious trees (380 steps, CI = .48, RI = 0.69), using pseudoreplicate reweighting of Kjer (2001, 2002). See text for description of analysis. The numbers above the branches are bootstrap values (>50%).

str. was recovered as monophyletic except that the *chalcomelas* species group nested within it.

Discussion

The overall findings from this study suggest that *Phanaeus*, with the inclusion of *Oxysternon*, is monophyletic (Figs 52, 54). Edmonds (1972) presumed a sister relationship between *Phanaeus* and *Oxysternon* based on three characters, the first two

being unique to *Phanaeus* and *Oxysternon*: a complete occipital ridge (char. 11), completely sclerotized premental sclerite (char. 12), and bipodal cephalic brachia (not used in this study). Characters 11 and 12 are uncontroverted in these analyses. Philips et al. (2004) further confirmed this close relationship between *Phanaeus* and *Oxysternon* in a phylogenetic analysis of the Phanaeini using morphological data. These latter authors reported nine controverted synapomorphies

among *Phanaeus* and *Oxysternon*, but each genus was only represented by one species.

The phylogenies presented here place *Oxysternon* within *Notiophanaeus* as the sister group to the *splendidulus* or *bispinus* species groups, but character 61 (distal portion of the paramere) is the only synapomorphy supporting this relationship. *Notiophanaeus* and *Phanaeus* s. str. share two uncontroverted synapomorphies of the head (11) and labium (12), as noted above. Five controverted synapomorphies shared by the subgenera include those of the head (1), pronotum (24, 31, 37), and legs (44). Additional controverted synapomorphies of *Phanaeus* s. str. include those of the head (6), antennae (22), and biogeography (68). Because the constraint tree was only three steps longer than the original scaled analysis, I suggest that *Oxysternon* not be sunk within *Phanaeus*, without additional supporting evidence.

Notiophanaeus and *Phanaeus* s. str. are monophyletic if slightly redefined. In the 'scaled' analysis the *hermes* group is nested within *Notiophanaeus* and appears to be the sister taxon to the *chalcomelas* group. The pseudoreplicate phylogeny also suggests that *hermes* is the sister taxon to the *chalcomelas* group, but nested them both well within *Phanaeus* s. str. Edmonds (1994) suggests that the primary distinction between the *Notiophanaeus* and *Phanaeus* s. str. is the nature of the pronotal sculpturing. The pronota of *Notiophanaeus* is described as having a glassy smooth appearance to the unaided eye. In *Phanaeus* s. str. the pronotum is always rugose to some degree. However, the blister-like rugosities on their pronota, coupled with the triangular shape of the pronotal disk, makes placement of the *chalcomelas* group in the *Phanaeus* phylogenies unstable.

Many of the species groups of Edmonds (1994) are recovered (especially in the scaled search). Species groups that were consistently recovered in all three analyses are: *paleano*, *endymion*, *chalcomelas*, and *tridens*. However, bootstrap values were low, and resolution of the unscaled analysis (Fig. 53) is poor, suggesting that more data is needed.

New species not described in Edmonds (1994) revision, but that were included in these analyses, are *P. bordoni* Arnaud, 1996 (presumed *splendidulus* species group), *P. lecourti* Arnaud, 2000 (presumed *chalcomelas* species group), *P. martinezorum* Arnaud, 2000 (presumed *paleano* species group), *P. yecoraensis* Edmonds, 2004 (presumed

mexicanus species group), *P. changdiazii* Kohlman and Solis, 2001 (presumed *beltianus* species group), *P. blackalleri* Degado-Castillo, 1991 and *P. genieri* Arnaud, 2001 (presumed *amethystinus* species group) (species group assignments were given by the describing authors). The phylogenetic conclusions presented in the scaled equal weighting analysis support the species groups given above, with the exception of *P. blackalleri*. This species appears to be a sister taxon to either *P. wagneri* or *P. amithaon* in the *mexicanus* group.

Edmonds (1994) placed *P. igneus* in the *vindex* species group based on the sculpturing of the elytra and pronotum, but he also stated that the sculpturing of the *vindex* species group is most closely approached by *P. triangularis texensis*. In both the scaled and pseudoreplicate analyses, *P. igneus* is recovered as more closely related to the *triangularis* group.

The difficulty of scoring several male characters was problematic for this research. As Edmonds (1994) noted, characters having an irregular distribution of character states, and continuous variation of some characters makes the taxonomy of some groups difficult, mostly within *Phanaeus* s. str. Also difficult was examination of characters of the clypeus and front tibia, which are subject to wear and can often lead to assessment errors. The lack of availability of large males and females, as well as specimens for dissection also complicated this research.

Several characters also have numerous possible states, notably male pronotal sculpturing, shape of the postero-lateral margin of the male pronotal disk, and shape of the female pronotum. These could be resolved into binary characters, but the result would be to weight these potentially non-independent characters very highly (May 2002). For this reason, I suggest the equally weighted tree using 'scaled' characters as most likely to reflect the true phylogeny, though additional weighting schemes should not be disregarded.

Future work on the evolution and phylogeny of *Phanaeus* should include an examination of biogeography and molecular data. Studies of the latter using cytochrome oxidase one (COI) and 28S rRNA (D2) are in progress. Furthermore, an examination of intraspecific genetic variation for several species of *Phanaeus*, may help to resolve issues dealing with subspecies nomenclature.

Acknowledgements

I am grateful to my advisers Michael May and Karl Kjer for their discussion of this manuscript and to W. D. Edmonds for his help along the way as well as for the numerous specimens he has sent to me over the past few years. I would also like to thank David Furth and Nancy Adams (National Museum of Natural History), Francois Genier (Canadian Museum of Nature) and Weiping Xie (Natural History Museum of Los Angeles County) for assistance in allowing me to examine the collections and for the loan of specimens. Special thanks are due to Sacha Spector (AMNH), Trond Larsen (Princeton University), Kevina Vulinec (Delaware State University), and Barney Streit for providing me with numerous *Phanaeus* specimens for examination and dissection. Lastly, I would like to thank John LaPolla and Jessica Ware for their help and encouragement over the years.

References

- Arnaud, P. (1997) Description d'une nouvelle espèce de *Phanaeus* (Col. Scarabaeidae). *Besoiro* 3: 6-7.
- Arnaud, P. (2000) Description de nouvelles espèces de *Phanaeides* (Col. Scarabaeidae). *Besoiro* 5: 6-8.
- Arnaud, P. (2001) Description de nouvelles espèces de *Phanaeides*. *Besoiro* 6: 2-8.
- Delgado-Castillo, L. (1991) A new Mexican species of *Phanaeus* (Coleoptera: Scarabaeidae). *Opuscula Zoologica Fluminensia* 69:1-6.
- Edmonds, W. D. (1972) Comparative skeletal morphology, systematics, and evolution of the Phanaeine dung beetles (Coleoptera: Scarabaeidae). *The University of Kansas Bulletin* XLIX: 731-874.
- Edmonds, W. D. (1979) A new species of *Phanaeus* from Mexico (Coleoptera: Scarabaeidae). *Pan-Pacific Entomologist* 55: 99-105.
- Edmonds, W. D. (1994) Revision of *Phanaeus* Macleay, a new world genus of scarabaeine dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Contributions in Science*, Natural History Museum of Los Angeles County 443: 1-5.
- Edmonds, W. D. (2004) A new species of *Phanaeus* Macleay (Coleoptera: Scarabaeidae, Scarabaeinae) from Sonora, Mexico. *Coleopterists Bulletin* 58: 119-124.
- Edmonds, W. D., & Zidek, J. (2004) Revision of the Neotropical dung beetle genus *Oxysternon* (Scarabaeidae: Scarabaeinae: Phanaeini). *Folia Heyrovkyana Supplementum* 11: 1-58.
- Felsenstein, J. (1985) Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783-791.
- Kjer, K. M., Blahnik, R. J., & Holzenthal, R. W. (2001) Phylogeny of Trichoptera (Caddisflies): characterization of signal and noise within multiple datasets. *Systematic Biology* 50: 781-816.
- Kjer, K. M., Blahnik, R. J., & Holzenthal, R. W. (2002) Phylogeny of caddisflies (Insecta, Trichoptera). *Zoologica Scripta* 31: 83-91.
- Kohlman, B. & Solis, A. (2001) A new species of *Phanaeus* Macleay (Coleoptera: Scarabaeidae, Scarabaeinae) from Costa Rica and Panama. *Besoiro* 6: 9-15.
- May, M. L. (2002) Phylogeny and taxonomy of the damselfly genus *Enallagma* and related taxa (Odonata: Zygoptera: Coenagrionidae). *Systematic Entomology* 27: 387-408.
- Ocampo, F. C. (2005) Revision of the southern South America endemic genus *Anomiopsoides* Blackwelder, 1944 (Coleoptera: Scarabaeidae: Scarabaeinae: Eucraniini) and description of its food relocation behavior. *Journal of Natural History* 39: 2537-2557.
- Philips, T. K., Edmonds, W. D., & Scholtz, C. H. (2004) A phylogenetic analysis of the New World tribe Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae): Hypotheses on relationships and origins. *Insect Systematics & Evolution* 35: 43-63.
- Swofford, D. L. (1999) *PAUP: Phylogenetic analysis using parsimony, Version 4*. Computer Program distributed by Sinauer.

Accepted for publication October 2006

Appendix 1. Data matrix for analyses. Fifty-one characters are binary and 17 are multistate. Multistate characters are coded as follows: (01) = A; (12) = B.

	1	1111111112	2222222223	3333333334	4444444445	5555555556	666666666
Species	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Phanaeus splendidulus</i>	0010101011	0011001100	0111221020	4011100100	1001110111	0000101001	110111100
<i>P. dejani</i>	001111011	00???.???	0111221020	4011100100	1001110111	0000???.???	???.???.???
<i>P. haroldi</i>	0010111000	0012001100	0111221021	4031111100	A000110111	0000101002	011111100
<i>P. melibaenus</i>	0010111000	0011001100	0111221020	4010111100	100?110111	0000???.???	011111100
<i>P. bordoni</i>	00101110?0	00???.???	0111221021	4010100100	000?110110	0000???.???	???.???.???
<i>P. chatcomelas</i>	0010101003	0011001000	0111021222	0220100100	0A01112111	1000100101	111110000
<i>P. achilles</i>	0010101023	0011001000	0111021222	0220100110	0001110111	1000100101	111110000
<i>P. cambeforti</i>	0010101003	0011001000	0111021222	0221100110	A001110111	1000100101	111111000
<i>P. meleagris</i>	001A101003	0011001000	0111021222	0220100110	1000110111	1000100001	111101000
<i>P. lecourti</i>	00101??003	00???.???	0111021222	0?20100110	???.?110111	1000???.???	01???.???
<i>P. avarengai</i>	10101111??	0011001100	0011220?22	40?01A11A0	???.?110110	000010110?	011111100
<i>P. bispinus</i>	0010111011	0010101100	0111220?22	403010A100	10?1110110	1000101001	011111100
<i>P. kirbyi</i>	101111022	0010101000	0111221222	1011111110	1000111010	0000000101	010111100
<i>P. paleano</i>	101111023	0001010000	0111221222	2011111110	100011A010	0000000101	010111100
<i>P. martinazorum</i>	10111100??	00???.???	0111?1222	2011101110	100?11A010	0000???.???	???.???.???
<i>P. halfterorum</i>	101011?023	00???.???	0111221222	0?1?1101010	???.?110111	0000???.???	???.???.???
<i>P. endymion</i>	101011003	0011001000	0101221222	0011111010	000011B111	0000100100	111111010
<i>P. pyrois</i>	101011003	0011011000	0101221222	0011111010	0000111111	0000100100	1111110A
<i>P. hermes</i>	001010123	00???.???	0111021222	21101101A0	1000111111	1000???.???	???.???.???
<i>P. prasinus</i>	001010123	0011001000	0111021222	2110110100	000112111	0000100101	111101000
<i>P. nimrod</i>	001111123	00???.???	0001021102	21101101A0	100011B111	0000???.???	???.???.???
<i>P. tridens</i>	000AA023	0011001010	0001121112	21101101A0	100011B111	0000111101	011111101
<i>P. eximius</i>	001011A023	00???.???	0001021102	2110110110	1000112111	0000???.???	???.???.???
<i>P. furtosus</i>	001011A023	0011001000	0001021112	4110110110	100011B111	0000111101	111111101
<i>P. daphnis</i>	0010111023	0011001000	0001221112	21101A01A0	100011B111	0000111101	011111101
<i>P. adonis</i>	0010111003	0011001000	0101221222	0110100110	000112111	0000111101	111110001
<i>P. t. triangularis</i>	0010111003	0011001000	0A01221222	0110100100	A001112111	0000111101	111110001
<i>P. t. texensis</i>	0010111003	0011001010	0A01221222	0110101100	0001112111	0100111101	111111010
<i>P. flohri</i>	0010111023	00???.???	0011021222	2100100100	0AA?112111	0000???.???	???.???.???
<i>P. demon</i>	0000120023	0011001000	0001021222	3101AA01A0	110111B111	0000101101	011111101
<i>P. scutifer</i>	0000121023	00???.???	0A01121222	21011001A0	01A?11B111	0000???.???	???.???.???

