TAXONOMIC STUDIES ON PALEOZOIC AND MESOZOIC BEETLES, WITH PHYLOGENETIC INTERPRETATION BASED ON ELYTRAL VENATION AND STRUCTURE

A Dissertation
Presented to the Faculty of the Graduate School
of Cornell University
In Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy

by
Sara Harriet Lubkin
August 2007

TAXONOMIC STUDIES ON PALEOZOIC AND MESOZOIC BEETLES, WITH PHYLOGENETIC INTERPRETATION BASED ON ELYTRAL VENATION AND STRUCTURE

Sara Harriet Lubkin, Ph. D.

Cornell University 2007

Although the Coleoptera are the largest order of animals and make up about 25% of all species currently living on Earth, there have been very few specialists working on early fossil Coleoptera, so despite the group's importance, the early evolutionary history of the beetles is poorly understood.

There is a substantial fossil record of Coleoptera originating in the early Permian. The majority of these fossils are preserved as isolated elytra, the hardened front wings of beetles. In most cases, fossil elytra are not useful for taxonomic identification; however, the very ornate elytra of the earliest Coleoptera include scales, setae, punctures, spines, and rudimentary venation - features that are potentially meaningful in phylogenetic studies.

In this first cladistic analysis of Permian and Mesozoic Coleoptera and coleopteroids, elytral characters are used to produce a character matrix which is phylogenetically analyzed using WinClada. The resultant trees show that many of the traditional family arrangements of the early Coleoptera and coleopteroids are not supported by a cladistic analysis of elytral characters and are poly- or paraphyletic. A revised classification system is proposed.

The family Tshekardocoleidae is redefined to include only *Tshekardocoleus* ROHDENDORF*, Afrocupes* GEERSTEMA AND VAN DER HEEVER and *Brochocoleus* HONG (in part). Two new families,

Moravocoleidae (*Moravocoleus* KUKALOVÁ *,* *Permocoleus* LUBKIN AND ENGEL, *Prosperocoleus* KUKALOVÁ) and Sylvacoleidae (*Boscoleus* KUKALOVÁ, *Sylvacoleus* PONOMARENKO, *Umoricoleus* KUKALOVÁ) are created to include some former members of Tshekardocoleidae. Further taxonomic revision, of the families Permocupedidae, Ommatidae and Cupedidae is still needed, but this study provides a framework for further study of the earliest beetles.

Because, fossil beetles are most commonly known only from elytral remains, a key to Paleozoic and Mesozoic elytra resembling Archostemata is constructed using only elytral characters to aid in the identification of fossil beetles.

Two significant fossil Coleoptera are described. *Paracupes svitkoi* LUBKIN from a remarkably preserved ninety-million year old beetle head from New Jersey, and *Permocoleus wellingtonensis* LUBKIN AND ENGEL, the earliest known beetle from the Western Hemisphere.

These studies show that on the family level, the diversity of early Coleoptera and Coleopteroids is far greater than previously thought.

BIOGRAPHICAL SKETCH

Sara Lubkin received her Bachelors of Science degree in Geology with a paleobiology emphasis from the University of California in Santa Barbara, where she completed an Honors thesis, *Fossil Insects and Other Invertebrates from the Middle Miocene Barstow Formation of the Calico Mountains, Mojave Desert, California*. This research focused on the middle-Miocene Barstow Formation in the Calico Mountains of the Mojave Desert in California. Her project included the removal of the insects and other arthropods from the nodules where they were preserved and the identification of the fossilized organisms. She then used the fossil assemblage to hypothesize about the climate of the lake and environment of deposition.

Since coming to Cornell in 1999, Sara's research has focused on fossil Coleoptera. She began by studying extant beetles belonging to the suborder Archostemata and has used that knowledge to reanalyze Permian and Mesozoic fossils in order to better understand the early diversification of the Coleoptera and the relationships among the earliest Coleoptera and Coleoptera-like fossils. She has also collaborated with Dr. Robert Nelson and Peter Nestor on a study of Pleistocene beetles associated with the Hyde Park mastodon site.

.

Dedicated to my children, Merlin, Elspeth, Arielle and Linnea,

and to my husband, Frank. Thank you!

ACKNOWLEDGMENTS

In alphabetical order, not order of importance: Warren Allmon, Sande Burr, John Cisne, David Grimaldi, Jon Hendricks, Liz Hermsen, John Hermanson, Conrad Labandera, Tom Langen, Jim Liebherr, Kelly Miller, Tam Nguyen, Alexander Ponomarenko, Andrew Ross, James Schulte, David Steere, Jennifer Svitko, Elena Welch, Quentin Wheeler, The American Museum of Natural History, The British Museum of Natural History, The National Science Foundation, The Virginia Museum of Natural History, Yale Peabody Museum, and the Free2B Moms.

Funding: U.S. National Science Foundation Graduate Research Fellowship; Geological Society of America Student Research Grant; American Museum of Natural History; Einaudi Center, Cornell University; Department of Earth and Atmospheric Sciences, Cornell University

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

A CLADISTIC ANALYSIS AND CLASSIFICATION OF EARLY FOSSIL COLEOPTERA BASED ON ELYTRA

Abstract

Insects comprise approximately 80 percent of the identified animal species on Earth, and the Coleoptera or beetles are the largest order of insects. By some estimates the Coleoptera make up as much as 30% of animal species, with over 360,000 described species of modern beetles. The majority of fossil Coleoptera are preserved as isolated elytra, which are the hardened front wings of beetles. In most cases, fossil elytra are not useful for taxonomic identification, and are listed as “family uncertain”. However, early fossil Coleoptera have very ornate elytra that may include scales, setae, punctures, spines, and rudimentary venation, features that are potentially meaningful in phylogenetic studies.

In this first cladistic analysis of Permian and Mesozoic Coleoptera and coleopteroids, elytral characters were used to produce a character matrix that was phylogenetically analyzed using WinClada. The resultant trees show that many of the traditional family arrangements of the early Coleoptera and coleopteroids are not supported by a cladistic analysis of elytral characters and are poly- or paraphyletic. A revised classification system is proposed.

The family Tshekardocoleidae is redefined to include only *Tshekardocoleus* ROHDENDORF 1944*, Afrocupes* GEERSTEMA AND VAN DER HEEVER 1996, and *Brochocoleus* HONG 1982 (in part). Two new families, Moravocoleidae (*Moravocoleus* KUKALOVÁ 1969*, Permocoleus*

LUBKIN AND ENGEL 2005, *Prosperocoleus* KUKALOVÁ 1969) and Sylvacoleidae (*Boscoleus* KUKALOVÁ 1969, *Sylvacoleus* PONOMARENKO 1963, *Umoricoleus* KUKALOVÁ 1969) are created to include some former members of Tshekardocoleidae. Further taxonomic revision, of the families Permocupedidae, Ommatidae and Cupedidae is still needed, but this study provides a framework for further study of the earliest beetles.

THE STRUCTURE AND venation of the hind wings of modern Coleoptera have been the subject of numerous studies (FORBES 1922, 1926; HAAS AND BEUTEL 2001; HAMMOND 1979; HORNSCHEMEYER 1998; KUKALOVÁ-PECK 2004; KUKALOVÁ-PECK AND LAWRENCE 1993; PONOMARENKO 1969B; WALLACE AND FOX 1975, 1980; WARD 1979; WHITING 1996). This makes sense, as hind wing venation and wing folding mechanisms have been particularly useful for providing phylogenetic information about relationships within beetle groups (BEUTEL AND HAAS 2000; HAMMOND 1979; WALLACE AND FOX 1980), and may be useful for determining the placement of Coleoptera within the Holometabola (BEUTEL AND HAAS 2000; HAAS AND KUKALOVÁ-PECK 2001; HORNSCHEMEYER 1998; KUKALOVÁ-PECK AND LAWRENCE 1993; WHITING, ET AL. 1997). However, hind wings are only rarely preserved in fossil beetles; the fossil record of Coleoptera is predominantly a record of elytra.

Fossil elytra have been extremely helpful in the identification of Pleistocene beetles, especially when microsculpture and patterns or metallic coloration are preserved, since many fossils younger than 4 MA can be matched to extant species (COOPE 1959, 1962, 1987 and others; ELIAS

1994, LINDROTH 1948; MATTHEWS 1979). However, their usefulness varies greatly from family to family and genus to genus, and identifications based only on elytra can be misleading (ELIAS 1994). Many fossil elytra are indistinguishable from one another or are distinguishable only on the basis of size, shape, and punctation or other ornamentation that may be altered by taphonomy and preservation. But more often, elytra cannot be conclusively identified and elytra-shaped fossils are commonly labeled as “Coleoptera?” with no further identification (e.g. CARPENTER 1992: 327-337). Identification is further confused because elytra-like forewings have evolved independently in many other groups of insects. An elytrous wing may in fact belong to the orders Psocoptera, Blattodea, Protoelytroptera or Heteroptera (Plataspidae, Naucoridae and others). However, these are generally very distinguishable from the elytra of beetles.

A.G. Ponomarenko of the Russian Paleontological Institute in Moscow is the world’s most prolific researcher on Permian and Mesozoic Coleoptera. Since 1963, he has described and named hundreds of fossil beetles. Yet, even PONOMARENKO (2002) has chosen to place Permian and Mesozoic Coleoptera and coleopteroids in explicitly artificial classification systems that are not reflective of phylogenetic relationships because there is the potential that very similar elytra might belong to groups that are not closely related.

In contrast to the elytra of most modern Coleoptera, which at most contain only the vestiges of wing veins, many of the more primitive Permian and Early Mesozoic elytra have detailed venation, which can be and at times has been used for both identification and classification purposes (KUKALOVÁ 1969; LUBKIN AND ENGEL 2005; MARTYNOV 1932, 1937; PONOMARENKO 1963, 2000, 2002; ROHDENDORF 1944, 1961). But, inconsistent naming of these veins has made deciphering these classifications difficult and has complicated the gathering of phylogenetic information. These multiple systems of vein nomenclature and of classification have obscured an understanding of the evolution of the early Coleoptera and their relatives.

Several classification systems for the early Coleoptera and coleopteroid fossils have been proposed. The oldest known fossil beetles were described from Early Permian (Lower Artinskian, ca. 268 MA) deposits in Obora, Czech Republic (KUKALOVÁ 1969), and from the Wellington Formation (Artinskian, 269-260 MA) of Midco, Oklahoma (LUBKIN AND ENGEL 2005), and from slightly younger deposits of Tshekarda, in the Ural Mountains of Russia (ROHDENDORF 1944; PONOMARENKO 1963). Most of these fossils have been placed in the family Tshekardocoleidae and have been considered true beetles based on their mesothoracic structure (KUKALOVÁ 1969). On the other hand, CROWSON (1975) placed all early Permian fossils in his suborder “Protocoleoptera” (a name also used by TILLYARD [1924] to refer to an order of non-coleopterous insects now considered to be closely related to the Dermaptera [SHCHERBAKOV AND YU 2002]), and PONOMARENKO (1969B, 2002) chose to place all Permian Coleoptera and Coleoptera-like fossils (coleopteroids) in the modern beetle suborder Archostemata despite some significant morphological differences. Some of the earliest Coleoptera possessed 13 antennomeres (compared to 11 in all modern Coleoptera), long elytra with cross venation that extended far beyond the tip of the abdomen, and a protruding ovipositor (KUKALOVÁ 1969; CROWSON 1975). These states are absent in modern beetles, hence the term coleopteroid (GRIMALDI AND ENGEL 2005) is used for these stem-group Coleoptera.

Elytra representing the family Oborocoleidae are also recorded from Obora, but unlike the “Tshekardocoleidae” only elytra are preserved. Because other body parts are unknown for this group, the Oborocoleidae have not yet been conclusively identified as beetles.

Late Permian beetles are classified in the families Permocupedidae, Asiocoleidae, Rhombocoleidae, Schizocoleidae, and Taldycupedidae. These are known from South America (PINTO 1987), southern Africa (GEERTSEMA AND VAN DER HEEVER 1996), Australia (TILLYARD 1924), and Eastern Europe (KUKALOVÁ 1969; MARTYNOV 1932, 1937; PONOMARENKO 1963, 2000, 2003; ROHDENDORF 1944, 1961). Although far more diverse and common than in the Early Permian, beetles and their relatives are still quite rare, comprising less than 1% of the total diversity in Late Permian insect assemblages (PONOMARENKO 1995). For these fossils, CROWSON (1975) created an additional suborder, Archecoleoptera, in which he included all Late Permian Coleoptera, although the morphological features of the group strongly suggests that Archecoleoptera is paraphyletic (CROWSON 1975; LAWRENCE 1982). Because some of these fossils strongly resemble modern Cupedidae, PONOMARENKO (1969B, 2002) included all Permian Coleoptera along with several Mesozoic families and the modern families Cupedidae, Ommatidae, Micromalthidae and Crowsonellidae in the suborder Archostemata. However, while some of these fossils do indeed resemble modern Cupedidae, the arrangement says little about phylogenetic relationships as the other suborders probably originated within this group (BEUTEL 1997; EUTEL AND HAAS 2000; CROWSON 1981; LAWRENCE AND NEWTON 1995). Because of the significant morphological differences within the group, Permian Coleoptera and coleopteroids are almost certainly a loosely related assemblage of taxa that are paraphyletic stem groups of extant Coleoptera.

Early Triassic Coleoptera are known only from the elytra of putatively aquatic beetles of the families Schizophoridae and Permosynidae from Russia (SINITSHENKOVA 2002). Unfortunately, insects from the Early Triassic are very rare in general. However, later Triassic (240-220 MA) Coleoptera are far more diverse and include several hundred species from more than 50 localities located on every continent except Antarctica (PONOMARENKO 1995). By the Late Triassic, beetles are quite common and comprise about 20% of the total diversity of fossil insect assemblages (CROWSON 1975). The majority of these fossils has been placed in Archostemata and includes the first beetles to be attributed to the extant families Cupedidae and Ommatidae (PONOMARENKO 1966). However, early members of the suborders Adephaga and Polyphaga are present as well. Triaplidae and Trachypachidae, both families of semi-aquatic Adephaga, are described from the late Triassic of Eurasia (PONAMARENKO 1977). The earliest known Polyphaga are Staphylinidae from the Carnian aged Cow Branch Formation of Virginia (225-230 MA) (FRASER, ET AL. 1996). While some beetles are very similar to their modern relatives, other families (Ademosynidae, Schizophoridae and Catiniidae) are extinct and have ambiguous phylogenetic placements (PONOMARENKO 1969B).

This study uses cladistic methods to analyze elytral characters in order to clarify early coleopteran and coleopteroid relationships. Veins are reinterpreted and homologized using a single system of vein nomenclature. The results of this analysis are used to construct a phylogeny-based classification system to better understand the evolution of the early Coleoptera and coleopteroids.

Materials and Methods

Study Taxa

Significant collections of Coleoptera from the Permian and Mesozoic are stored in museums in Russia, the United Kingdom, the United States, Czech Republic, South Africa, Australia and China. Smaller, yet very significant, collections exist in Brazil and Canada. Many of these specimens are both unique and very fragile. Because of both the world-wide distribution of these fossils and their fragile nature, direct study of this material was not possible. Instead, for all taxa except *Permocoleus wellingtonensis*, morphological information was obtained using illustrations from the primary literature rather than from actual specimens. Elytral venation is relatively simple compared to the more complex venation in the wings of insects belonging to other orders. Because patterns of venation are the defining characters for many fossil elytra, elytral venation is usually very carefully illustrated, thus information gathered from illustrations of fossil elytra is unlikely to be inaccurate. The main criterion for inclusion in this study was a clear illustration of at least one complete or near-complete elytron.

52 taxa were included in the study. These taxa include fossil Coleoptera and coleopteroids, modern Cupedidae, and outgroups.

Fossil Taxa

1. *Afrocupes firmae* (Figure 1.1a) GEERSTEMA AND VAN DER HEEVER 1996 (Permian, South Africa)

2. *Archicupes jacobsoni* (Figure 1.1b) ROHDENDORF 1961 (Lower Permian, Russia)

3. *Asiocoleus novojilovi* (Figure 1.1c) ROHDENDORF 1961 (Lower Permian, Russia)

4. *Boscoleus blandus* (Figure 1.1d) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

5. *Brochocoleus alatus* (Figure1.1e) PONOMARENKO 1994 (Lower Cretaceous, Mongolia)

6. *Brochocoleus punctatus* (Figure 1.1f) HONG 1982 (Upper Jurassic, China)

7. *Cytocupes angustus* (Figure 1.1g) ROHDENDORF 1961 (Upper Permian, Russia)

8. *Eocoleus scaber* (Figure 1.1h) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

9. *Forticupes laiyangensis* (Figure 1.1i) HONG 1990 (Lower Cretaceous, China)

10. *Kaltanicupes acutus* (Figure 1.1j) PONOMARENKO 1963 (Middle Permian, Russia)

11. *Kaltanicupes kitjakensis* (Figure 1.1k) PONOMARENKO 1963 (Middle Permian, Russia)

12. *Kaltanicupes major* (Figure 1.1l) PONOMARENKO 1963 (Middle Permian, Russia)

13. *Kaltanicupes ponomarenkoi* (Figure 1.1m) PINTO 1987 (Upper Permian, Brazil)

14. *Kaltanocoleus pospelovi* (Figure1.1n) ROHDENDORF 1961 (Lower Permian, Russia)

15. *Labradorocoleus carpenteri* (Figure 1.1o) PONOMARENKO 1969A (Cretaceous, Labrador)

16. *Liberocoleus intactus* (Figure 1.1p) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

17. *Longxianocupes tristichus* (Figure 1.1q) HONG, ET AL. 1985 (Lower Cretaceous, China)

18. *Magnocoleus huangjiapuensis* (Figure 1.1r) HONG 1998 (Lower Cretaceous, China)

19. *Moravocoleus fractus* (Figure1.1s) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

20. *Moravocoleus neglegens* (Figure 1.1t) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

21. *Moravocoleus perditus* (Figure 1.1u) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

22. *Moravocoleus permianus* (Figure 1.1v) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

23. *Notocupes brachycephalus* (Figure 1.1w) PONOMARENKO 1994 (Jurassic, Mongolia)

24. *Notocupes elegans* (Figure 1.1x) PONOMARENKO 1994 (Lower Cretaceous, Mongolia)

25. *Notocupes mongolicus* (Figure 1.1y) PONOMARENKO 1994 (Lower Cretaceous, Mongolia)

26. *Notocupes sp.* (Figure 1.1z) PONOMARENKO 1966 (Lower Cretaceous, Russia)

27. *Oborocoleus rohdendorfi* (Figure 1.1aa) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

28. *Permocoleus wellingtonensis* (Figure 1.1bb) LUBKIN AND ENGEL 2005 (Lower Permian, United States)

29. *Permocupes distinctus* (Figure 1.1cc) MARTYNOV 1933 (Permian, Russia)

30. *Permocupes semenovi* (Figure 1.1dd) MARTYNOV 1933 (Permian, Russia)

31. *Permocupoides skoki* (Figure 1.1ee) ROHDENDORF 1956 (Lower Permian, Russia)

32. *Prosperocoleus prosperus* (Figure 1.1ff) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

33. *Sogdelytron latum* (Figure 1.1gg) PONOMARENKO 1969B (Triassic, Asia)

34. *Sojanocoleus reticulatus* (Figure 1.1hh) MARTYNOV 1932 (Permian, Russia)

35. *Sylvacoleus richteri* (Figure 1.1ii) PONOMARENKO 1963 (Lower Permian, Russia)

36. *Synodus changmaensis* (Figure1.1jj) HONG 1982 (Jurassic, China)

37. *Tomiocupes carinatus* (Figure 1.1kk) ROHDENDORF 1961 (Upper Permian, Russia)

38. *Triassocupes yaochaensis* (Figure 1.1ll) HONG ET AL.. 1985 (Triassic, China)

39. *Tricoleodes acutus* (Figure 1.1mm) PONOMARENKO 1969B (Triassic, Asia)

40. *Tricoleus punctatus* (Figure 1.1nn) PONOMARENKO 1969B (Jurassic, Kazakhstan)

41. *Tricupes acer* (Figure 1.1oo) ROHDENDORF 1961 (Upper Permian, Russia)

42. *Tshekardocoleus magnus* (Figure 1.1pp) ROHDENDORF 1944 (Lower Permian, Russia)

43. *Tshekardocoleus minor* (Figure 1.13qq) PONOMARENKO 1963 (Lower Permian, Russia)

44. *Tychticupes radtschenkoi* (Figure 1.1rr) ROHDENDORF 1961 (Upper Permian, Russia)

45. *Umoricoleus perplex* (Figure 1.1ss) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

46. *Votocoleus submissus* (Figure 1.1tt) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

Extant Taxa

Among extant taxa, elytral venation is only present in modern Archostemata belonging to the families Cupedidae and Ommatidae, and museum specimens of both of these families were examined. All members of Cupedidae that were examined exhibited the same venation pattern (Figure 1.2a). These species included *Cupes capitatus* FABRICIUS (1801), *Priacma serrata* LECONTE (1874), *Prolixocupes lobiceps* LECONTE (1874), *Tenomerga anguliscutis* KOLBE (1886), *Tenomerga concolor* WESTWOOD (1835) *Tenomerga favella* NEBOISS (1984), *Tenomerga kapnodes* NEBOISS (1984), and *Tenomerga mucida* CHEVROLAT (1829). The Ommatidae examined (museum specimens of *Omma stanleyi* NEWMAN [1839] and *Tetraphalerus bruchi* HELLER [1913]) had a slightly different venation pattern (Figure 1.2b) from the Cupedidae, but that pattern was also consistent within the family. Therefore, only one species was chosen to represent each family.

Figure 1.1. Venation diagrams for study taxa
(left elytron, figures not drawn to scale)

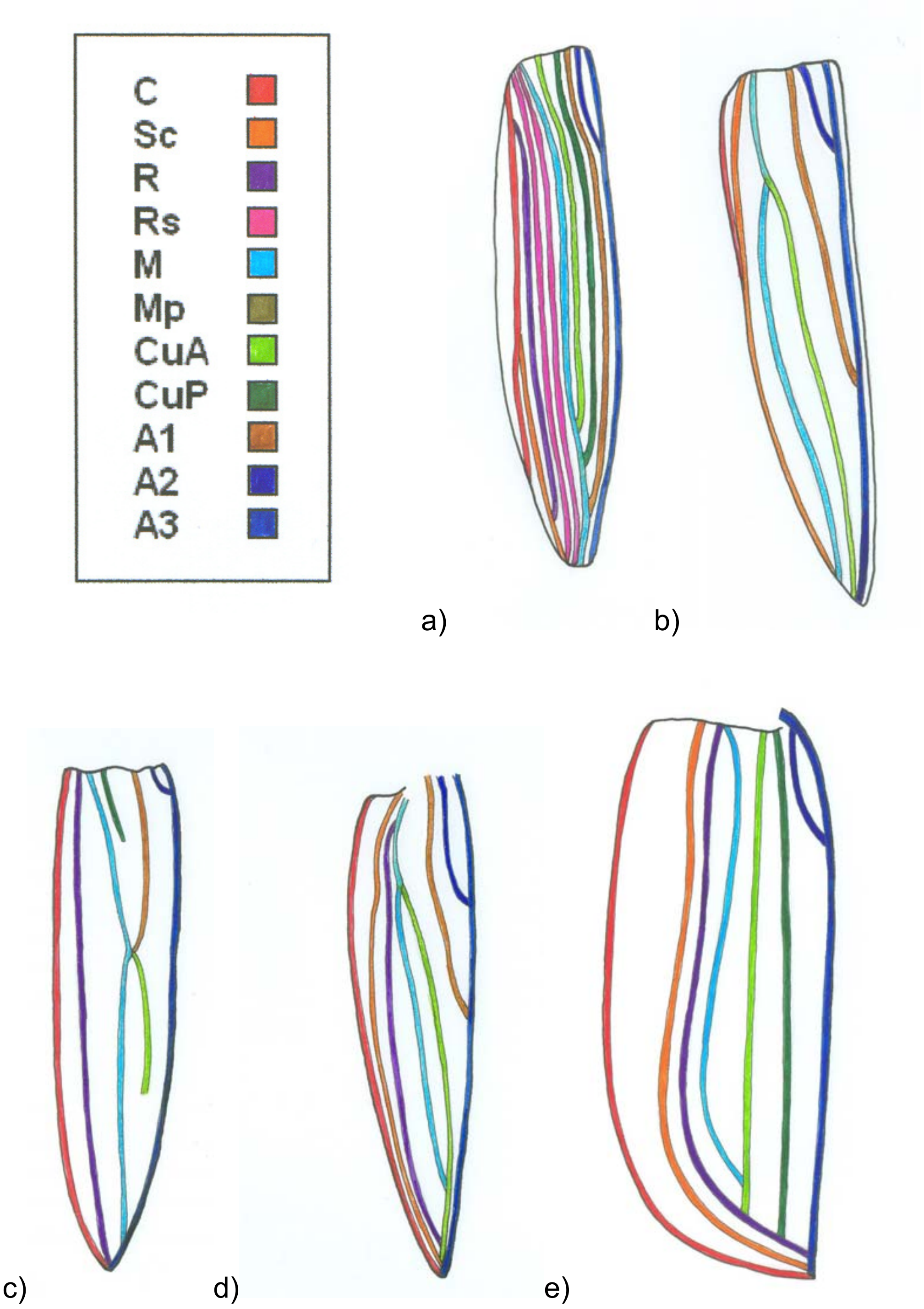
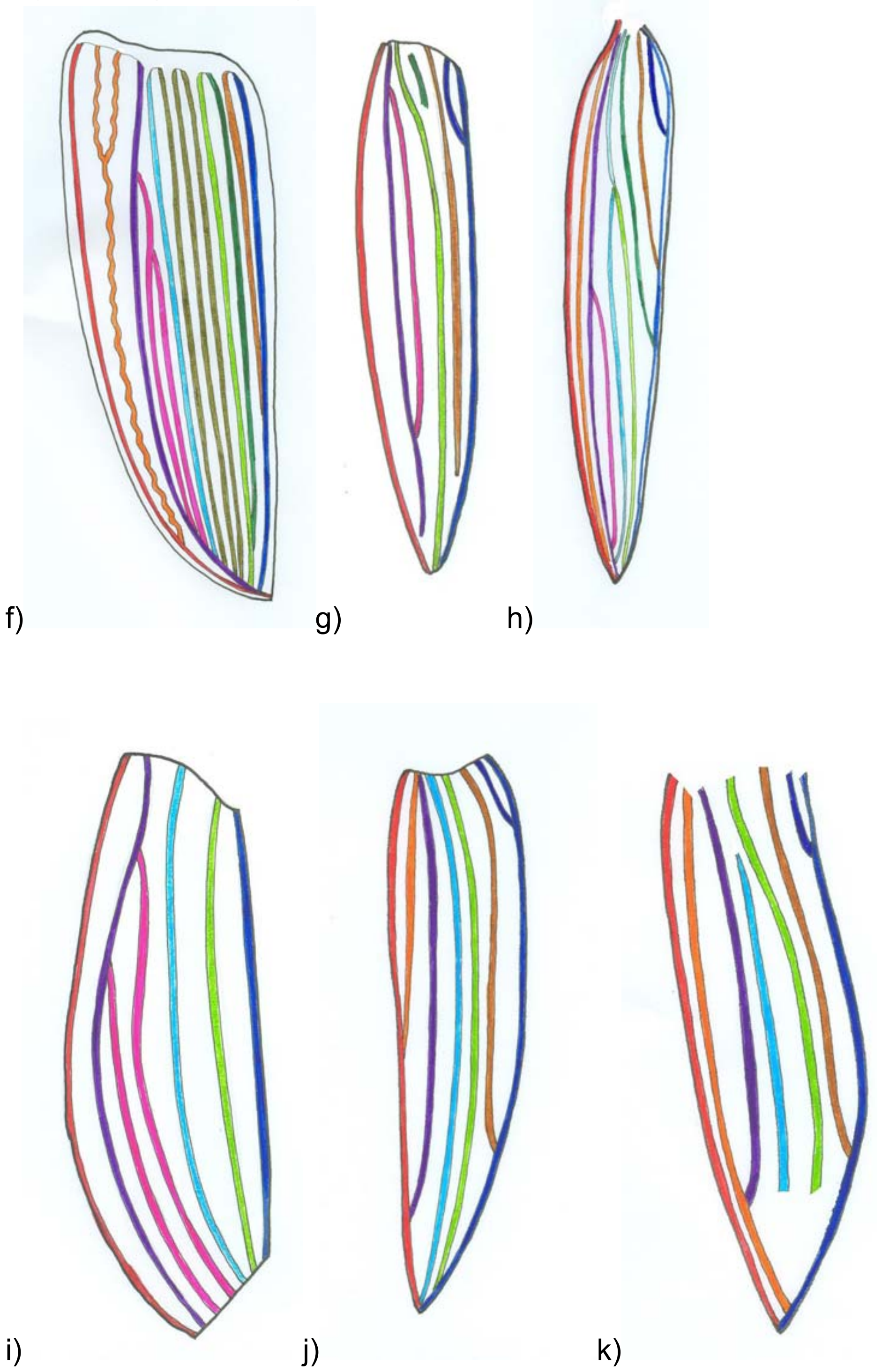
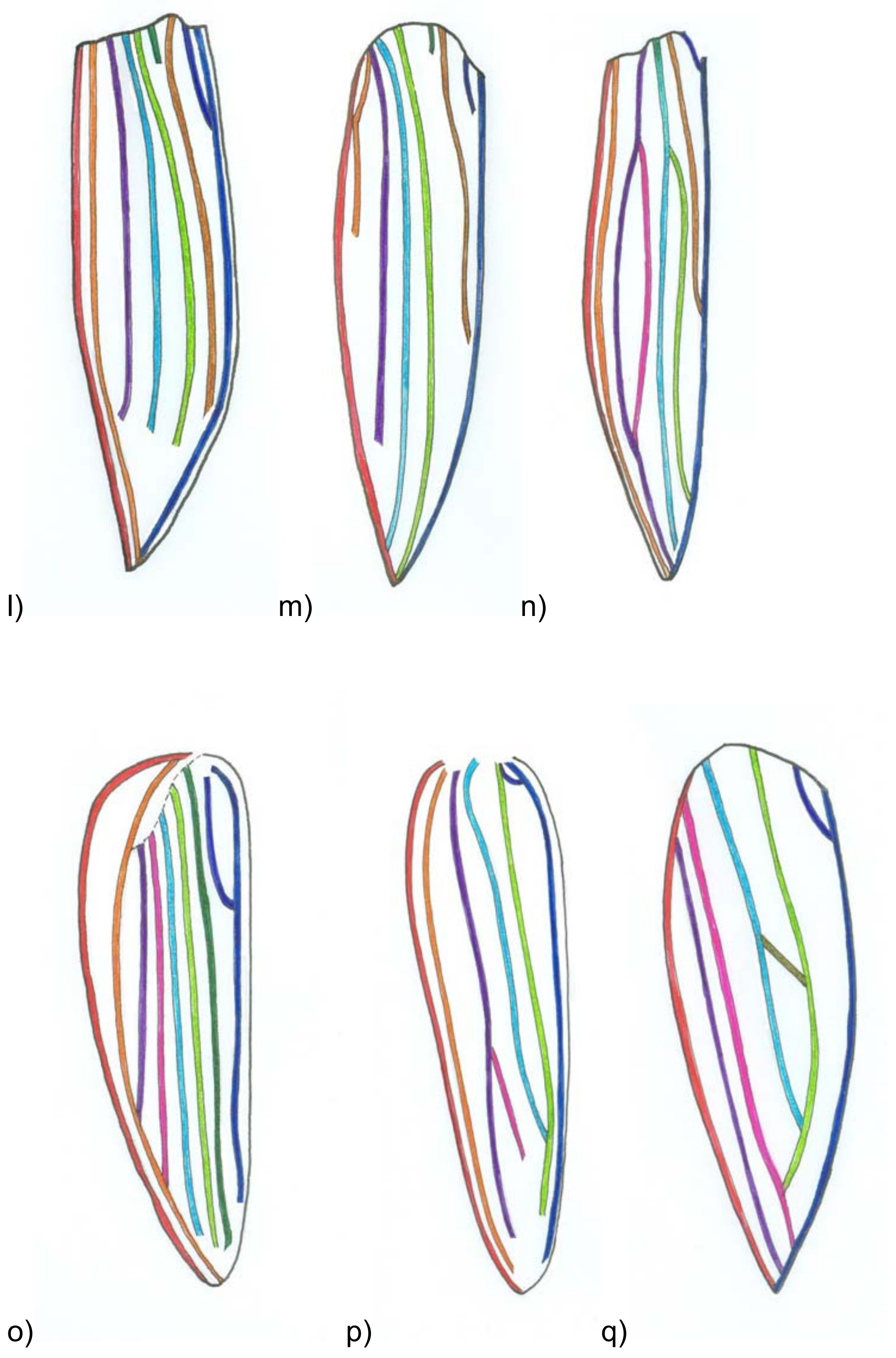

C 🟥
Sc 🟧
R 🟪
Rs ■
M 🟦
Mp 🟫
CuA 🟩
CuP 🟩
A1 🟫
A2 🟦
A3 🟦
a)
b)
c)
d)
e)

Figure 1.1 (Continued)


f) g) h)

i) j) k)

Figure 1.1 (Continued)



l) m) n)

o) p) q)

Figure 1.1 (Continued)

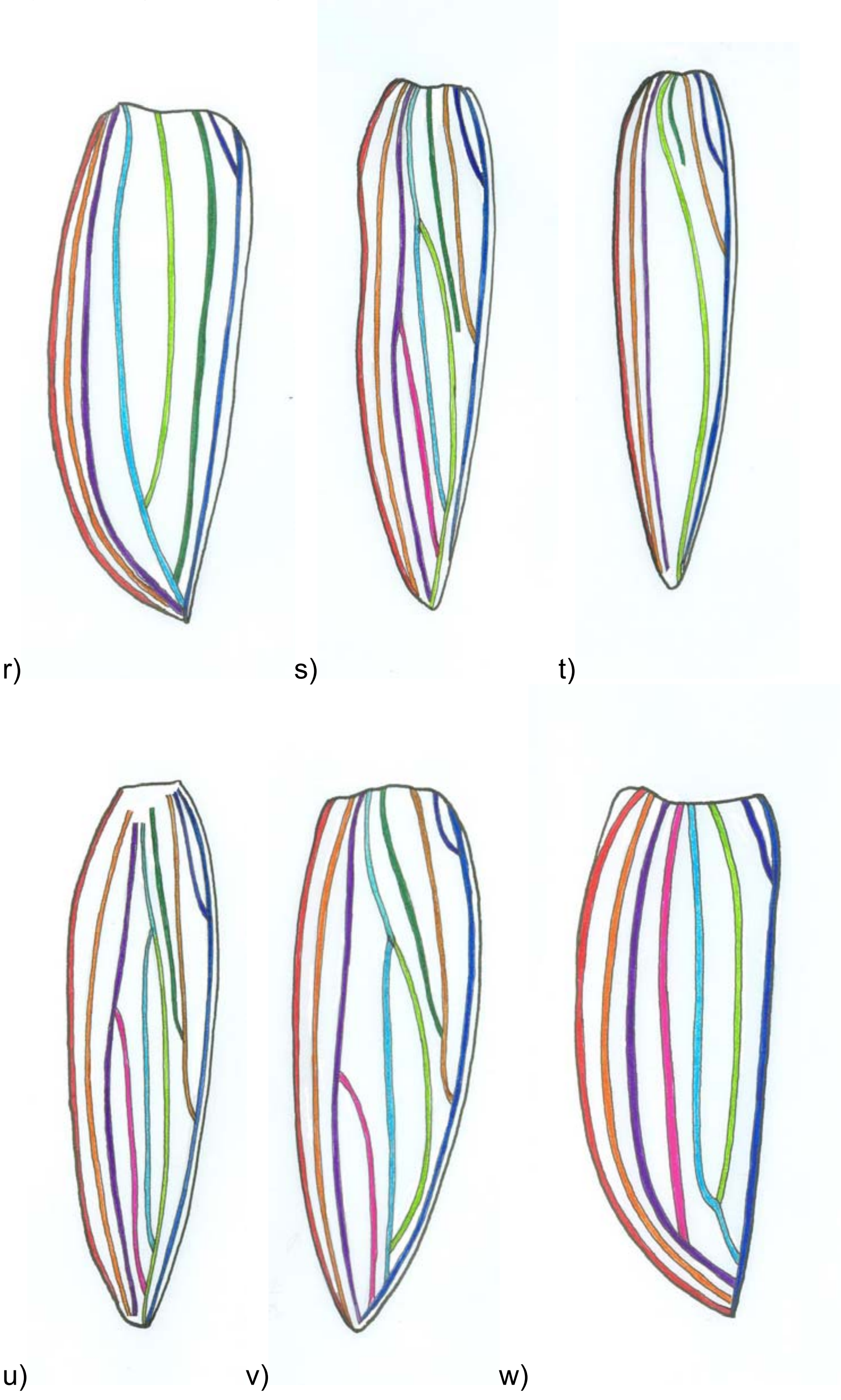
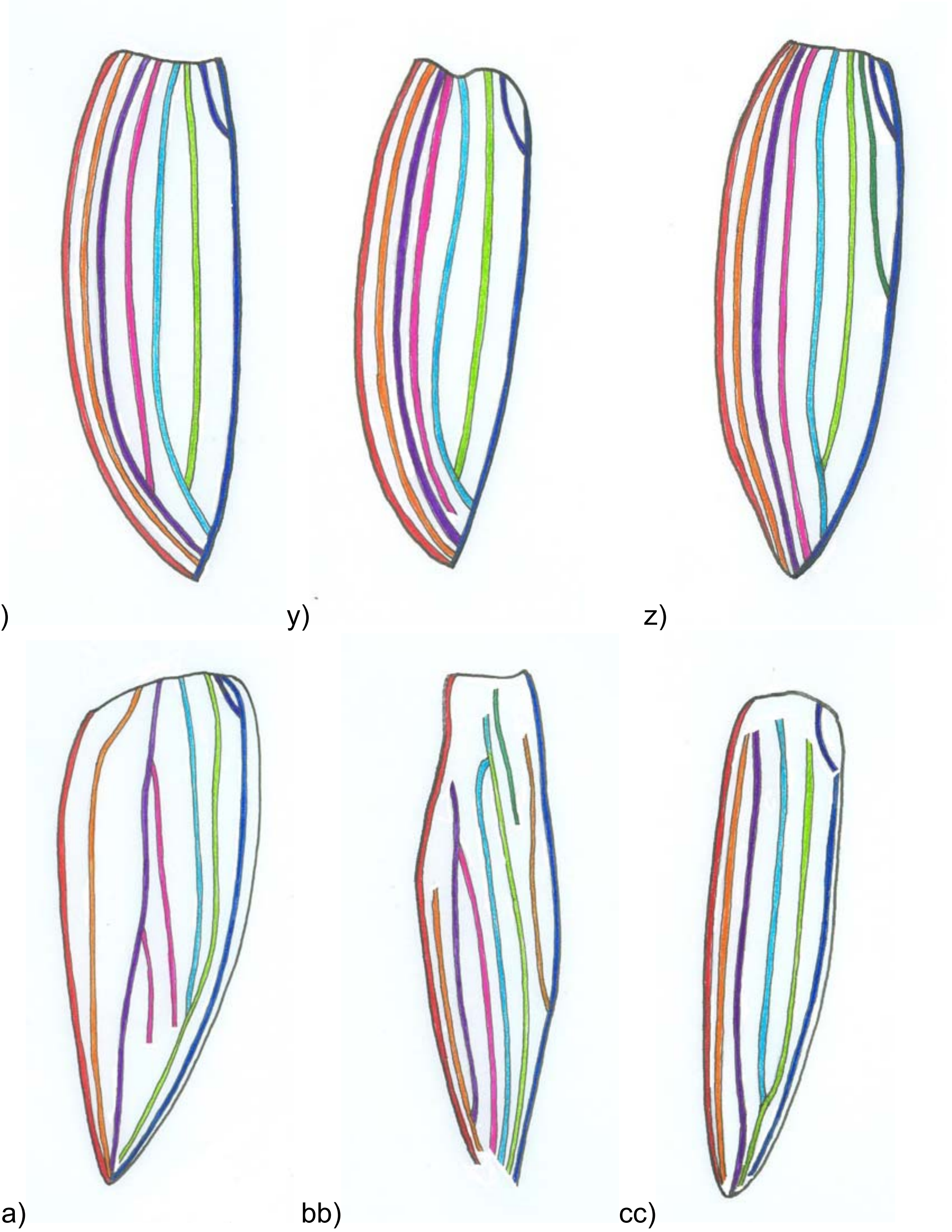


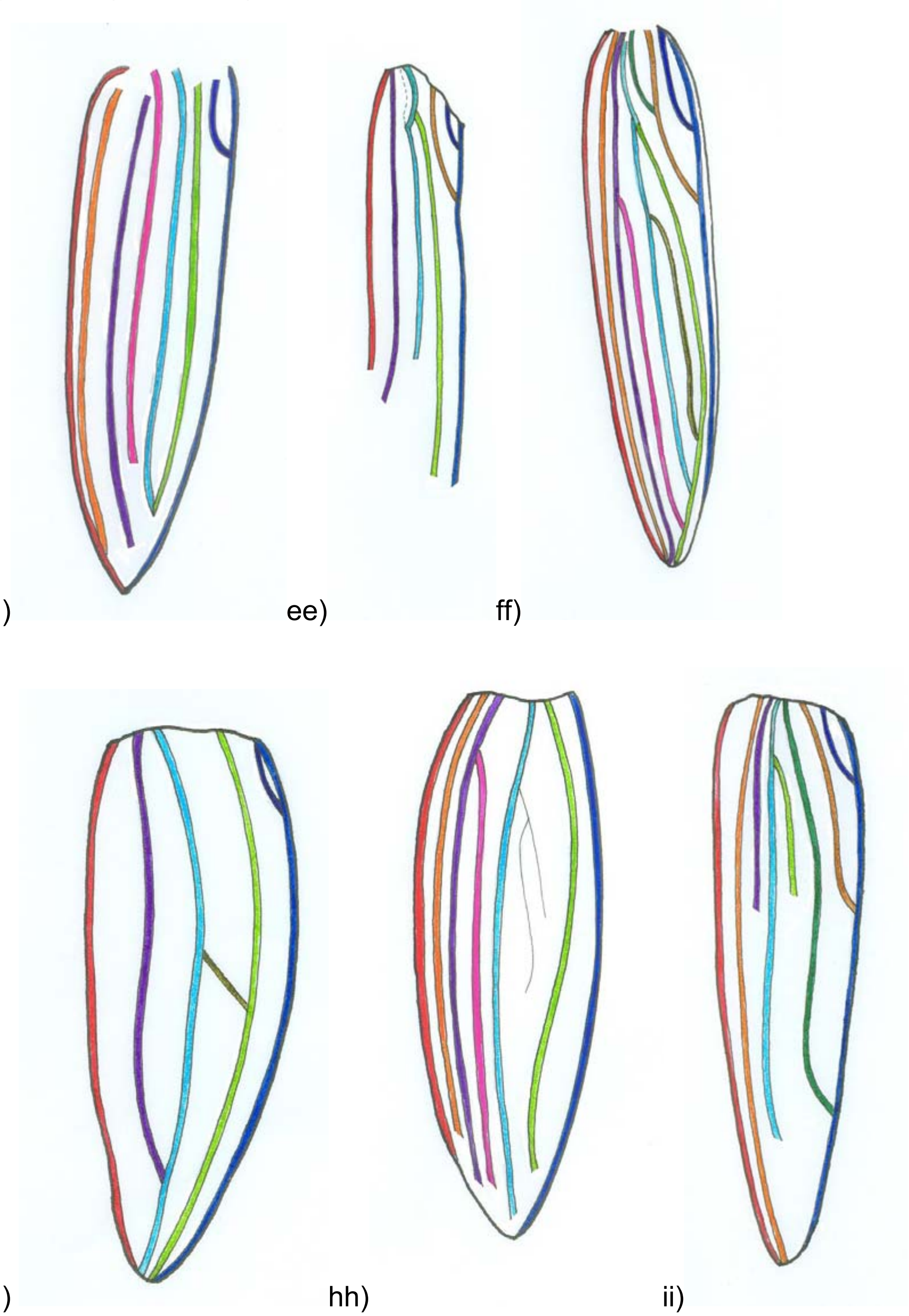
Figure 1.1 (Continued)



x) y) z)

aa) bb) cc)

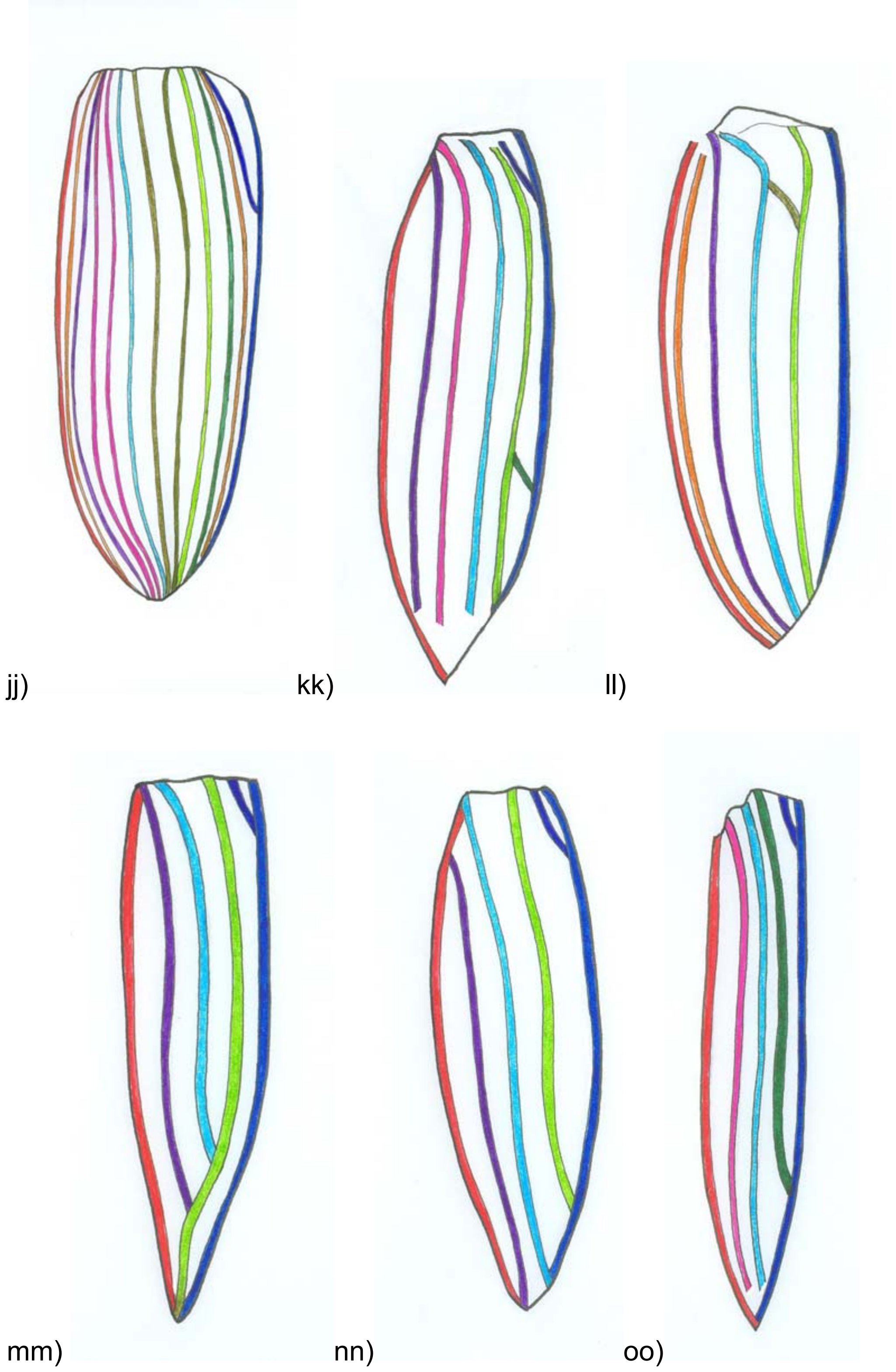
Figure 1.1 (Continued)



dd) ee) ff)

gg) hh) ii)

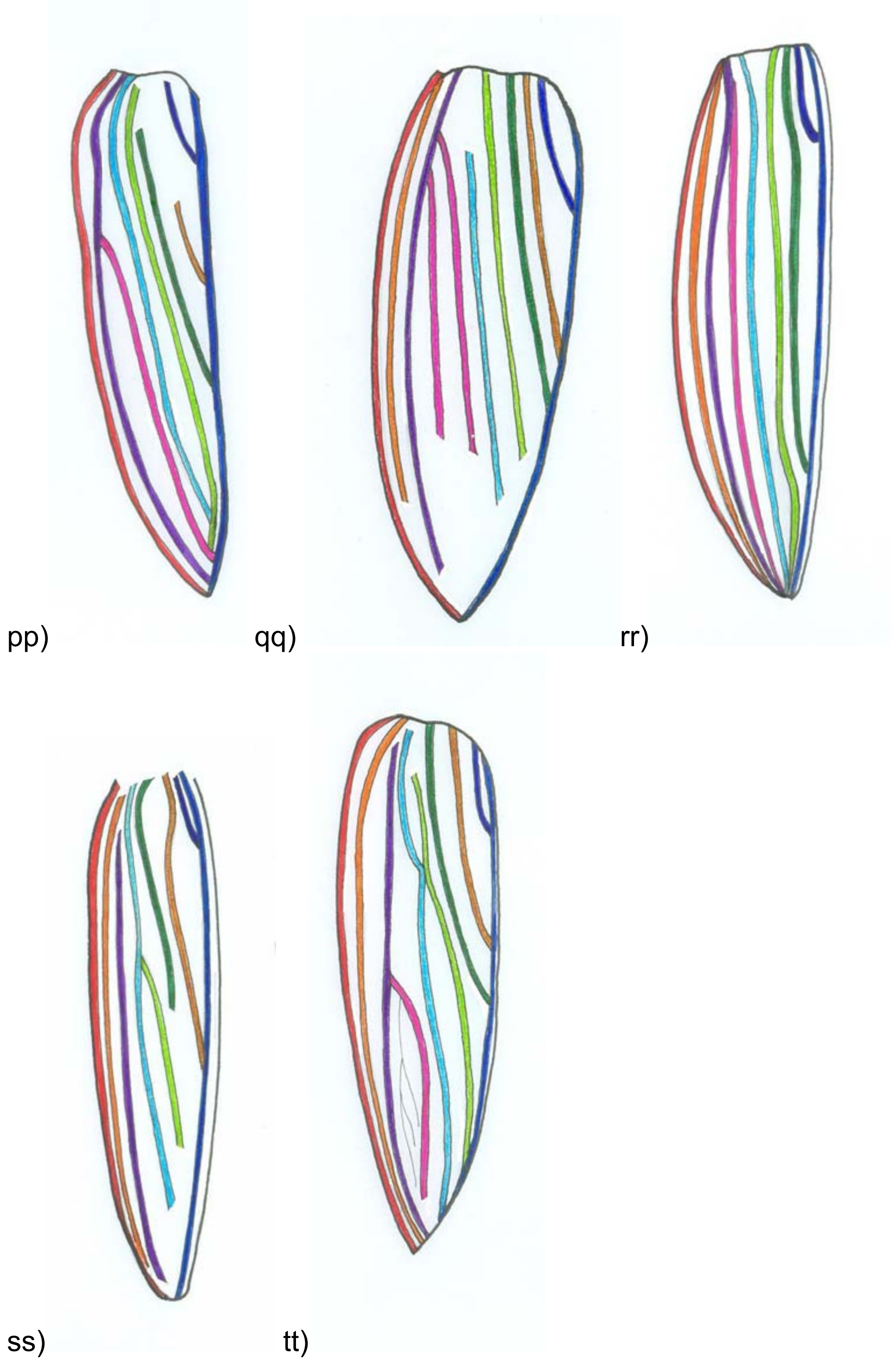
Figure 1.1 (Continued)



jj) kk) ll)

mm) nn) oo)

Figure 1.1 (Continued)

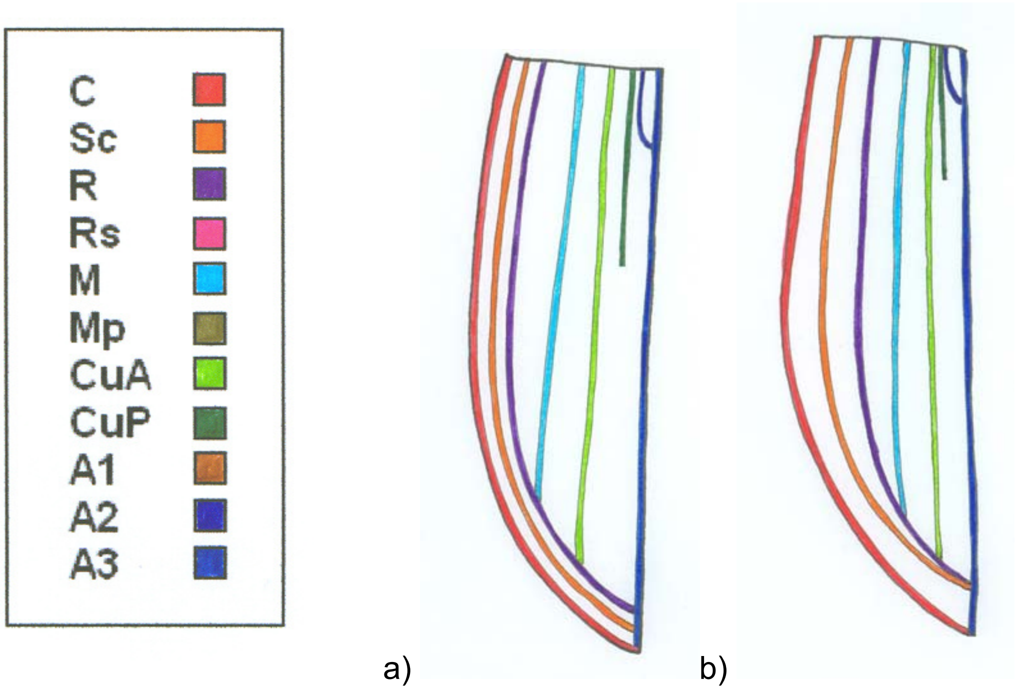


pp) qq) rr)

ss) tt)

47. *Tenomerga concolor* (Cupedidae)

48. *Omma stanleyi* (Ommatidae)



a) b)

Figure 1.2. Venation diagrams for modern taxa included in the study: a. *Tenomerga concolor* b. *Omma stanleyi* (left elytron, figures not drawn to scale)

Outgroups

Four taxa were used as outgroups. Both extant and extinct groups of Neuroptera were chosen. Neuroptera have been considered the most likely living relatives of Coleoptera (AFZELIUS AND DALLAI 1994; CROWSON 1981; HENNIG 1969; HORNSCHEMEYER 1998; KRISTENSEN 1975; LAWRENCE 1982; LAWRENCE AND NEWTON 1995; MICKOLEIT 1973; WHITING AND KATHIRITHAMBY 1997) because of similarities in the morphology and structure of mouthparts, forewing attachments, metathoracic wing bases, ovipositors, stemmata, sperm axonemes, legs, and 18s and 28s ribosomal DNA sequences. Two species of Megaloptera were chosen as the order Megaloptera is more generalized than other Neuropteran orders. In addition, a species of Raphidioptera was also used as outgroup.

The Glosselytrodea are an extinct order of insects thought to be related to the Neuroptera (CARPENTER AND KUKALOVÁ 1964). The family Permoberothidae is the most generalized of the Glosselytrodean families (CARPENTER 1992), so a species of *Permoberotha* was chosen as an outgroup.

49. Agulla (snakefly, extant, Raphidioptera)
50. Nigronia (dobsonfly, extant, Megaloptera)
51. Sialis (alderfly, extant, Megaloptera)
52. *Permoberotha villosa* TILLYARD 1932 (extinct, family Permoberothidae, order Glosselytrodea MARTYNOV 1938)

Characters

Criteria for choosing characters

Because Coleoptera are generally preserved only as isolated fossil elytra, only elytral characters were used, albeit in some cases other morphological characters were available such as antennal or thoracic structures. The characters used include elytral venation, shape and ornamentation. Although elytral venation has been lost in most modern Coleoptera, the veins of fossil elytra can be homologized with the venation in the front wings of related orders such as Neuroptera and fossil groups such as

Glosselytrodea. These groups were chosen as outgroups. Veins were identified as homologous based on vein position, path and neighboring veins.

Stratigraphic range was not used as a character, as stratigraphic range is not an intrinsic character of an organism, nor was it used to weigh characters as more or less primitive, because if stratigraphic-clade rank correlations are to be examined, stratigraphic position must remain separate from cladistic analysis.

Veins were named using a modification of the Comstock-Needham system of nomenclature (COMSTOCK AND NEEDHAM 1898A, 1898B): costa (C), subcosta (Sc), radius (R), radial sector (Rs_{1-4}), media (M), media posterior (MP), anterior cubitus (CuA), posterior cubitus (CuP), and anal veins (A_1, A_2, A_3). The identities of the veins were determined based on relative position, branching, paths and comparison with other taxa.

Although not always preserved or illustrated, puncture shape was included, as WIENS (1988) found that adding characters even with missing data still significantly increased the phylogenetic accuracy of a simulated data set. Kevin NIXON (Personal communication) argues that since missing data is treated by WinClada as having all character states present, large amounts of missing data may create “wild card” taxa that are not fixed in the cladogram and thus may reduce resolution. However, for most of the taxa examined in this study, there was very little missing data; although, in several cases, all character states were inapplicable.

Elytron shape was also included. Because shape may be influenced by taphonomy, and thus may be based on depositional and not phylogenetic history, only the side with greatest concavity was used as a character rather than morphometric measurements such as wing tip angle and concavity.

Intraspecific variation was not considered. In most instances, there is only one illustration (and often only one specimen) per species; thus, it was not possible to determine the extent of intraspecific variation. However, in the extant taxa (belonging to families Ommatidae and Cupedidae) there was no intraspecific variation in the characters included. Moreover, the characters states applied not only to the genus, but to the entire family.

Table 1.1: Characters and character states.
All characters are non-additive and unordered.

0. **Vein Sc:**
    0) Sc is present.
    1) Sc is absent.

1. **Length of Sc:**
    0) Full length; Sc reaches the edge or tip of the elytron.
    1) Shortened; Sc terminates before reaching elytron tip or edge.
    2) Very short; the length of Sc is less than one quarter the length of the elytron.
    3) Absent; length is zero.

2. **Veins C and Sc:**
    0) Merge at edge of elytron.
    1) Merge at tip of elytron.
    2) Merge before tip, but not at edge.
    3) Do not merge.

3. **Enlarged area between bases of C and Sc:**
    0) Absent.
    1) Slight enlargement.
    2) Definitely enlarged; at least twice the width separating the remainder of C and Sc.

4. **Vein R:**
    0) Present.
    1) Absent.

5. **Number of Rs veins:**
    0) Several.
    1) Two.
    2) One.
    3) None.

6. **Rs_1 is:**
    0) Attached to R about halfway down the elytron.
    1) Attached to R less than one-quarter of the distance from the base.
    2) Attached to R at base.
    3) Not attached to R.
    4) Absent.

Table 1.1 (Continued)

7. **R length:**
    0) Full length; reaches edge or tip
    1) Shortened; terminates before reaching edge or tip
    2) Very short; R is less than half the length of the elytron.
    3) R vein is absent; length is zero.

8. **Veins R and Sc:**
    0) Do not merge.
    1) Merge before tip.
    2) Merge at tip.

9. **R and Sc share a stem:**
    0) No.
    1) Yes.

10. **R and Rs_1 merge:**
    0) No.
    1) Yes.

11. **Vein M:**
    0) Present.
    1) Absent.

12. **MP branching:**
    0) Present.
    1) Absent.

13. **Veins M and R:**
    0) Do not merge.
    1) Merge.

14. **Vein CuA:**
    0) Present.
    1) Absent.

15. **CuA branching:**
    0) Present.
    1) Absent.

16. **CuA and M:**
    0) Share a stem.
    1) Originate separately near wing base

Table 1.1 (Continued)

17. **Veins CuA and M and A1 intersect to form an x-shape:**
    0) No.
    1) Yes.

18. **Posterior part of CuA:**
    0) Is approximately parallel to other veins (Figure 1.3a).
    1) Is deeply concave and approximately parallels the curve of the lower anal edge of the elytron (Figure 1.3b).
    2) Dips sharply toward anal edge of elytron (Figure 1.3c).
    3) Gradually angles down to anal edge (Figure 1.3d).
    4) CuA is too short to tell (Figure 1.3e).
    5) Entire vein is slightly concave (Figure 1.3f).
    6) Merges with vein M and then is straight to elytron tip (Figure 1.3g).

19. **Veins CuA and M:**
    0) Do not merge.
    1) Merge.

20. **Veins CuA and R:**
    0) Do not merge.
    1) Merge.

21. **Veins CuA and Rs_1:**
    0) Do not merge.
    1) Merge

22. **CuA length:**
    0) Full length; vein reaches the tip or edge of elytron.
    1) Full length after merging with vein M.
    2) Shortened; vein terminates before tip or edge.
    3) Quite short; vein length is equal to or less than one-quarter the length of the elytron
    4) CuA is absent, length is zero.

23. **Vein CuP:**
    0) Present.
    1) Absent.

24. **CuP and M and CuA:**
    0) Share a stem.
    1) Do not share a stem.

Table 1.1 (Continued)

25. **Length of CuP:**
    0) CuP reaches the tip of elytron.
    1) CuP reaches the anal edge of elytron.
    2) Short; CuP terminates before the edge or tip of the elytron.
    3) CuP is absent; length is zero.

26. **CuP and M:**
    0) Do not merge.
    1) Merge.

27. **CuP and A_1:**
    0) Do not intersect.
    1) Intersect.

28. **CuP and R:**
    0) Do not intersect.
    1) Intersect.

29. **CuP and CuA:**
    0) Do not intersect.
    1) Intersect.

30. **A_1:**
    0) Present.
    1) Absent.

31. **A_1 length:**
    0) Extends to tip.
    1) Reaches edge more than halfway between the base and tip.
    2) Reaches edge halfway or less than halfway between the base and tip.
    3) Shortened; vein terminates before tip or edge.
    4) Very short; vein length is less than one-eighth the length of the elytron
    5) A_1 is absent; length is zero.

32. **A_1 and CuA:**
    0) Do not merge.
    1) Merge.
    2) Not applicable.

33. **Vein A_2:**
    0) Present.
    1) Absent.

Table 1.1 (Continued)

34. **Additional A veins:**
    0) Present.
    1) Absent.

35. **Fold or line between Sc and R:**
    0) Absent.
    1) Present.

36. **Puncture shape:**
    0) Punctures absent.
    1) Round.
    2) Irregular, somewhat round, lumpy.
    3) Oval.
    4) Oval, but irregular.
    5) Rectangular.
    6) Quadrate.
    7) Irregular four-sided.
    8) Five-sided.
    9) Six-sided.
    10) Very irregular.

37. **Sc with divided stem:**
    0) Absent.
    1) Present.

38. **M length:**
    0) Full length; extends to tip
    1) Shortened; greater than or equal to one-half the length of the elytron
    2) Very short; less than one-half the length of the elytron
    3) Merges with CuA, then extends to full length.
    4) M is absent; length is zero.

39. **Elytron shape:**
    0) No elytron.
    1) Costal side of elytron is more concave.
    2) Anal side of elytron is more concave.
    3) Both sides of elytron are approximately equally concave; elytron has a leaf or blade shape.

40. **A_1 and CuA:**
    0) Do not share stem.
    1) Share stem.

Table 1.1 (Continued)

41. **Cross-vein between M and CuA:**
    0) Absent.
    1) Present.

42. **Rs_2 is:**
    0) Attached to Rs_1.
    1) Attached to R about half way from base.
    2) Attached at base of R.
    3) Not attached to R or Rs_1.
    4) Absent.

43. **Short vein from base of M to M/CuA attachment:**
    0) Absent.
    1) Present.

44. **Curvature of vein R:**
    0) R does not curve to meet anal edge.
    1) R curves to meet anal edge.

45. **Curvature of vein Sc:**
    0) Sc does not curve to meet anal edge.
    1) Sc curves to meet anal edge.

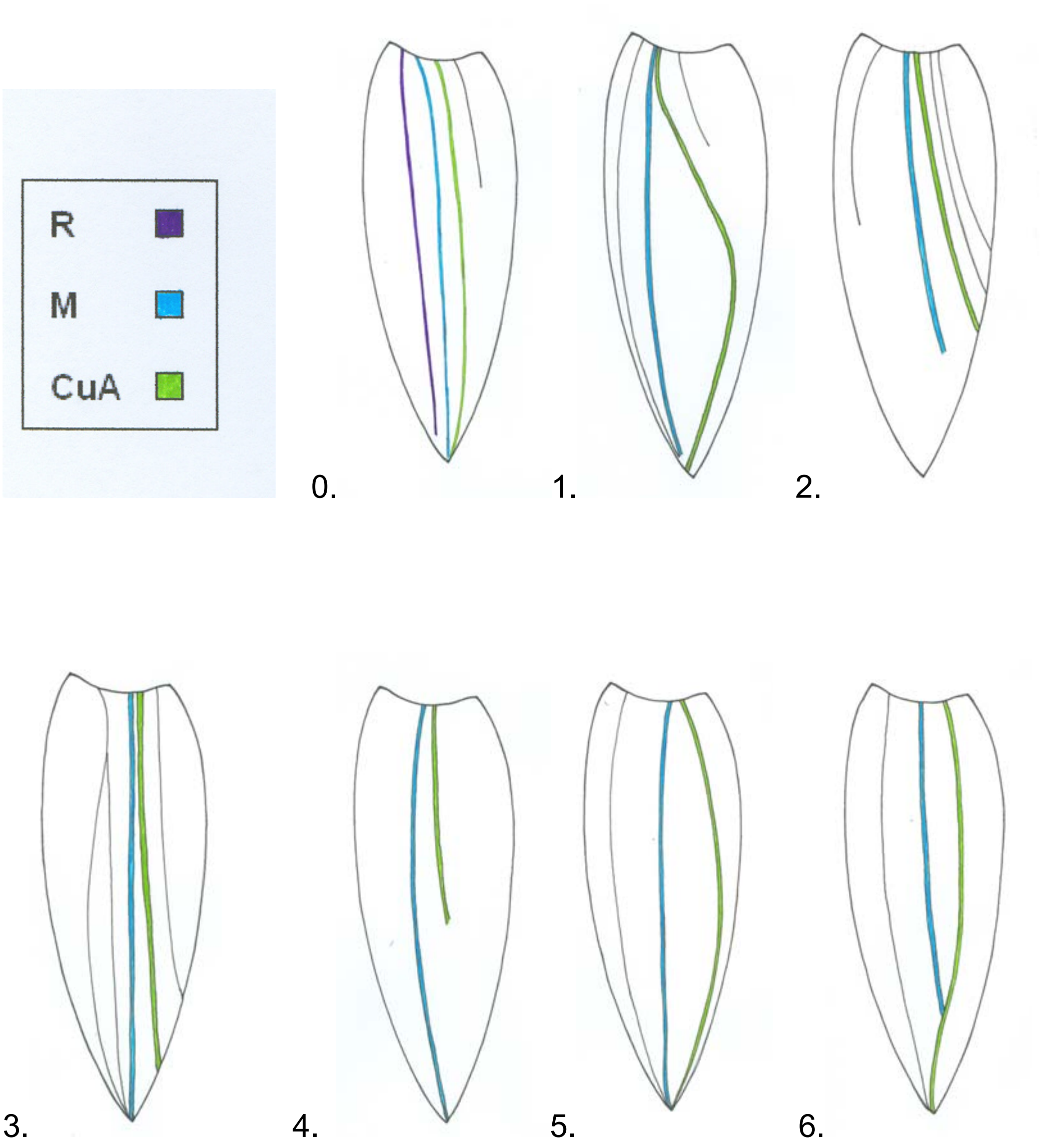


Figure 1.3. Character states for Character 18

Path of the posterior part of vein CuA (left elytron is shown, not real taxa)

0) Is approximately parallel to other veins (Figure 1.3a).
1) Is deeply concave and approximately parallels the curve of the lower anal edge of the elytron (Figure 1.3b).
2) Dips sharply toward anal edge of elytron (Figure 1.3c).
3) Gradually angles down to anal edge (Figure 1.3d).
4) CuA is too short to tell (Figure 1.3e).
5) Entire vein is slightly concave (Figure 1.3f).
6) Merges with vein M and then is straight to elytron tip (Figure 1.1g).

Changes from original descriptions

In some cases, coding of characters varied from that of the original description. Commonly, this was because different systems of naming veins were used. These changes are described below.

Afrocupes firmae (FIGURE 1.1a) GEERSTEMA AND VAN DER HEEVER 1996. Sc is present, but not marked in original drawing. Rs_1 and Rs_2 are present and not labeled. MP has been renamed M; A_3 as A_2; and A_2 as A_3 in order to homologize vein identity with those in other taxa based on vein shape and position. No other changes.

Archicupes jacobsoni (Figure 1.1b) ROHDENDORF 1961. Sc as in original; R identified as M, M identified as CuA as the path and location are very similar to that of M and CuA in several early Permian taxa, and there are no other cases of R and M sharing a stem. Cu is named CuP based on path and termination on anal edge of elytron. R and Rs are absent. A_2 and A_3 are present.

Asiocoleus novojilovi (Figure 1.1c) ROHDENDORF 1961. CuP, $A_{1,}$ A_2 labeled; no other changes.

Boscoleus blandus (Figure 1.1d) KUKALOVÁ 1969. Very short CuP present, but not labeled in original illustration. No changes.

Brochocoleus alatus (Figure 1.1e) PONOMARENKO 1994. Veins were not labeled in original description; veins were named based on position and path.

Brochocoleus punctatus (Figure 1.1f) HONG 1982. A_2 relabeled as A_3 in order to homologize with other taxa; A_2 is missing; based on path

Cytocupes angustus (Figure 1.1g) ROHDENDORF 1961. A_2 identified. No other changes.

Eocoleus scaber (Figure 1.1h) KUKALOVÁ 1969. No changes.

Forticupes laiyangensis (Figure 1.1i) HONG 1990. Description is in Chinese, veins were named based on position and path.

Kaltanicupes acutus (Figure 1.1j) PONOMARENKO 1963. Description is in Russian, illustration is unlabeled. Veins were named based on position and path.

Kaltanicupes kitjakensis (Figure 1.1k) PONOMARENKO 1963. Description is in Russian, illustration is unlabeled. Veins were named based on position and path.

Kaltanicupes major (Figure 1.1l) PONOMARENKO 1963. Description is in Russian, illustration is unlabeled. Veins were named based on position and path.

Kaltanicupes ponomarenkoi (Figure 1.1m) PINTO 1987. Vein labeled Rs is identified as M based on location and path in order to homologize with other Kaltanicupes. Rs_1 is absent. M is relabeled as CuA. CuP is very short and not labeled. Cu_2 is relabeled as A_1; A as A_2. No other changes.

Kaltanocoleus pospelovi (Figure 1.1n) ROHDENDORF 1961. No changes.

Labradorocoleus carpenteri (Figure 1.1o) PONOMARENKO 1969A. C, Sc as in original description, RS_1 renamed R, Rs_2 as Rs_1, A_2 as CuP based on vein shape and length. A_3 renamed A_2 and A_4 renamed A_3 to homologize with other taxa.

Liberocoleus intactus (Figure 1.1p) KUKALOVÁ 1969. CuP is identified as M, A_1 as CuA based on path of CuA and position of CuA similarity to other beetles from Moravia. KUKALOVÁ (1969) mentions the similarity of the paths to those of M and CuA in other taxa and considers it convergence, but does not explain her reasoning. No CuP, No A_1.

Longxianocupes tristichus (Figure 1.1q) HONG, ET AL. 1985. CuA shares a stem with M, Cu relabeled CuP; A is named A_2 based on position and path.

Magnocoleus huangjiapuensis (Figure 1.1r) HONG 1998. M_2 is named CuA based on position and path, Cu as CuP, A_1 absent, A_1 is renamed A_2, A_2 renamed A_3 based on the position and path of vein.

Moravocoleus fractus (Figure 1.1s) KUKALOVÁ 1969. No changes.

Moravocoleus neglegens (Figure 113t) KUKALOVÁ 1969. No changes.

Moravocoleus perditus (Figure 1.1u) KUKALOVÁ 1969. No changes.

Moravocoleus permianus (Figure 1.1v) KUKALOVÁ 1969. No changes.

Notocupes brachycephalus (Figure 1.1w) PONOMARENKO 1994. Veins not labeled in original description; veins were named based on position and path.

Notocupes elegans (Figure 1.1x) PONOMARENKO 1994. Veins not labeled in original description; veins were named based on position and path.

Notocupes mongolicus (Figure 1.1) PONOMARENKO 1994. Veins not labeled in original description; veins were named based on position and path.

Notocupes sp. (Figure 1.1z) PONOMARENKO 1966. Veins not labeled in original description; veins were named based on position and path.

Oborocoleus rohdendorfi (Figure 1.1aa) KUKALOVÁ 1969. C, Sc, R, Rs_1 as in original. Changes: CuP identified as M, A_1 as CuA based on similarities of curvature and path of vein to that in other specimens from the Lower Permian of Moravia. KUKALOVÁ (1969) mentions the similarity of the paths to those of M and CuA in other taxa and considers it convergence in both Oborocoleus and Liberocoleus, but does not explain her reasoning. No CuP, No A_1.

Permocoleus wellingtonensis (Figure 1.1bb) LUBKIN 2005. CuP not labeled in original illustration. R mislabeled as Rs.

Permocupes distinctus (Figure 1.1cc) MARTYNOV 1933. Sc, A_2, A_3 not labeled in original illustration. No changes.

Permocupes semenovi (Figure 1.1dd) MARTYNOV 1933. No changes.

Permocupoides skoki (Figure 1.1ee) ROHDENDORF 1956, 1961. M_2 is relabeled CuA to homologize with other taxa, Cu is A_1 based on path, A_2 present but not labeled in original illustration.

Prosperocoleus prosperus (Figure 1.1ff) KUKALOVÁ 1969. No changes.

Sogdelytron latum (Figure 1.1gg) PONOMARENKO 1969B. Original description in Russian. Veins were not labeled in original description; veins were named based on position and path.

Sojanocoleus reticulatus (Figure 1.1hh) MARTYNOV 1932. No changes.

Sylvacoleus richteri (Figure 1.1ii) PONOMARENKO 1963. Original description in Russian. Veins were not labeled in original illustration; veins were named based on position and path.

Synodus changmaensis (Figure 1.1jj) HONG 1982. Description is in Chinese, veins were named based on position and path. *Brochocoleus punctatus* was used as a reference.

Tomiocupes carinatus (Figure 1.1kk) ROHDENDORF 1961. No changes.

Triassocupes yaochaensis (Figure 1.1ll) HONG, ET AL.1985. Sc labeled (by position), Rs=R. Cross-vein present between M and CuA.

Tricoleodes acutus (Figure 1.1mm) PONOMARENKO 1969B. Original description in Russian. Veins were not labeled in original illustration; veins were named based on position and path.

Tricoleus punctatus (Figure 1.1nn) PONOMARENKO 1969B. Original description in Russian. Veins were not labeled in original illustration; veins were named based on position and path.

Tricupes acer (Figure 1.1oo) ROHDENDORF 1961. Cu renamed CuP based on path and termination on anal side of elytron. No other changes.

Tshekardocoleus magnus (Figure 1.1pp) ROHDENDORF 1944. Sc, R, Rs_1, Rs_2, and M, no changes. MP is identified as CuA based on vein position and similarity of vein curvature to CuA in other Permian fossils, Cu as CuP, A_3 labeled A_2 for homology purposes, A_2 labeled as extra anal vein.

Tshekardocoleus minor (Figure 1.1qq) PONOMARENKO 1963. Sc, R, Rs_1, no changes; M_1 is M; M_2 is CuA based on position. Cu_1 is CuP, Cu_2 is A_1, A is A_2 based on position.

Tychticupes radtschenkoi (Figure 1.1rr) ROHDENDORF 1961 (upper Permian, Russia). Veins not labeled in original description; veins were named based on position and path.

Umoricoleus perplex (Figure 1.1ss) KUKALOVÁ 1969. No changes.

Votocoleus submissus (Figure 1.1tt) KUKALOVÁ 1969. No changes.

Character weighting

Three analyses were completed. The character matrices used were identical except for character weights (Table 1.2). In Matrix 1, all characters were given equal weight. The resulting consensus tree (Figure 1.4) of 366 steps (CI 21, RI 29) showed very little resolution.

The use of parsimony is based on Dollo's Law (DOLLO 1890) which states that evolution is not reversible; structures lost in evolution are very unlikely to re-evolve in the same way (CROWSON 1970; MAYR 1982). As such, it is improbable that major veins would disappear and then reappear. So, in matrix 2 a weight of 25 was given to characters 0, 4, 5, 11, 12, 14, 15, 23, 31, 34 and 35, which express the presence of veins. This gave the presence of a vein greater importance than other characters such as the merging of two veins, and this greatly down-weighted the reappearance of lost veins. The resulting consensus tree (Figure 1.5, 4782 steps, CI 33, RI 72) showed greater resolution and fewer character reversals. Character reversals were still present, and are often due to multiple losses of the same vein. In an attempt to further deal with the problem of lack of resolution and character reversals due to multiple losses of the same vein, in matrix three, a baseline weight of two was given to all characters. Characters denoting the presence of veins (0, 4, 5, 11, 12, 14, 15, 23, 31, 34 and 35) were given a much higher weighting. Characters 37 (elytral concavity) and 40 (puncture shape) were very slightly down-weighted (weight=1) in order to emphasize venation. Puncture shape data was not available for most taxa and was coded as missing data when not available. Character 39, elytron shape based on the side of greatest elytral concavity, displayed several reversals seemed to have no relation to wing venation in consensus tree two. It is very likely that side of greatest concavity is a homoplasious character which has changed numerous times in response to body shape or lifestyle. However, deactivating this character made no significant difference in the results. Characters 6 and 44

(Rs1 and Rs_2 attachments) were given an increased weight of 50 as these characters seemed less likely to experience reversals than other characters because of the consistency within taxa.   Although this system of weighting did produce a better-resolved tree than when no weights were used, the consensus tree (Figure 1.6, 4782 steps, CI 33, RI 72) was less resolved than the consensus tree from analysis 2. A summary of character weights for each matrix is shown in Table 1.3.

In all analyses, all characters were treated as non-additive and unordered.

Table 1.2: Character matrix

Character states: 0, 1, 2, 3, 4, 5, 6
Inapplicable character: -
Unknown or missing data: ?

Taxon/Character	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Agulla sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Nigronia sp.	0	0	0	0	0	0	0	0	2	0	0	0	0
Sialis sp.	0	0	0	0	0	0	0	0	1	0	0	0	0
Permoberotha villosa	0	0	0	0	0	0	0	0	0	0	0	0	0
Afrocupes firmae	0	0	1	0	0	1	2	0	2	1	0	0	1
Archicupes jacobsoni	0	0	1	0	1	3	5	3	-	-	-	0	1
Asiocoleus novojilovi	1	3	-	-	0	3	4	0	-	-	-	0	1
Boscoleus blandus	0	0	1	2	0	3	4	0	2	1	-	0	1
Brochocoleus alatus	0	0	3	1	0	3	4	0	0	0	-	0	1
Brochocoleus punctatus	0	0	1	0	0	1	0	0	0	0	1	0	0
Cytocupes angustus	1	3	-	-	0	2	1	0	-	-	1	0	0
Eocoleus scaber	0	0	1	1	0	2	0	0	0	0	0	0	1
Forticupes laiyangensis	1	3	-	-	0	1	0	0	-	-	0	0	1
Kaltanicupes acutus	0	1	0	2	0	3	4	1	1	0	-	0	1
Kaltanicupes kitjakensis	0	0	3	1	0	3	4	1	1	0	-	0	1
Kaltanicupes major	0	0	3	0	0	3	4	1	1	0	-	0	1
Kaltanicupes ponomarenkoi	0	1	3	0	0	3	4	1	0	0	-	0	1
Kaltanocoleus pospelovi	0	0	1	0	0	2	0	0	0	0	1	0	1
Labradorocoleus carpenteri	0	0	3	2	0	2	3	1	1	0	0	0	1
Liberocoleus intactus	0	0	1	1	0	2	0	0	0	0	0	0	1
Longxianocupes tristichus	1	3	-	-	0	2	3	0	-	-	0	0	1
Magnocoleus huangjiapuensis	0	0	1	0	0	3	4	0	2	0	-	0	1
Moravocoleus fractus	0	0	1	1	0	2	0	0	0	0	0	0	1

Table 1.2 (Continued)

Taxon/Character	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Moravocoleus neglegens	0	0	1	1	0	3	4	0	0	0	-	1	1
Moravocoleus perditus	0	0	1	1	0	2	0	0	0	0	0	0	1
Moravocoleus permianus	0	0	1	1	0	2	0	0	0	0	0	0	1
Notocupes brachycephalus	0	0	3	0	0	2	3	0	0	0	1	0	1
Notocupes elegans	0	0	3	0	0	2	3	0	0	0	1	0	1
Notocupes mongolicus	0	0	3	0	0	2	1	0	0	0	0	0	1
Notocupes sp.	0	?	?	1	0	2	1	0	0	1	0	0	1
Oborocoleus rohdendorfi	0	0	1	1	0	1	0	0	2	0	0	0	1
Permocoleus wellingtonensis	0	0	1	1	0	2	0	0	1	0	0	0	1
Permocupes distinctus	0	0	1	0	0	3	4	0	0	0	-	0	1
Permocupes semenovi	0	0	1	0	0	2	2	1	0	0	0	0	1
Permocupoides skoki	1	3	-	-	0	3	4	?	-	-	-	0	1
Prosperocoleus prosperus	0	0	1	0	0	2	0	0	0	0	0	0	0
Sogdelytron latum	1	3	-	-	0	3	4	1	-	-	-	0	1
Sojanocoleus reticulatus	0	0	1	0	0	2	1	0	0	0	0	0	?
Sylvacoleus richteri	0	0	1	2	0	3	4	2	0	1	-	0	1
Synodus changmaensis	0	0	1	0	0	0	1	0	0	0	0	0	1
Tomiocupes carinatus	1	3	-	-	0	2	2	0	-	-	0	0	1
Triassocupes yaochaensis	0	0	3	0	0	3	4	0	0	0	-	0	1
Tricoleodes acutus	1	3	-	-	0	3	4	1	-	-	-	0	1
Tricoleus punctatus	1	3	-	-	0	3	4	0	-	-	-	0	1
Tricupes acer	1	3	-	-	1	2	3	3	-	-	-	0	1
Tshekardocoleus magnus	1	3	-	-	0	1	0	0	-	-	0	0	1
Tshekardocoleus minor	0	0	1	0	0	1	0	0	2	0	0	0	1
Tychticupes radtschenkoi	0	0	1	0	0	2	2	0	0	0	0	0	1
Umoricoleus perplex	0	0	1	1	0	3	4	0	2	0	-	0	1
Votocoleus submissus	0	0	1	1	0	0	0	0	2	0	0	0	1
Tenomerga concolor	0	0	3	0	0	3	4	0	0	0	-	0	1
Omma stanleyi	0	0	3	0	0	3	4	0	1	0	-	0	1

Table 1,2 (Continued)

Taxon/Character	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Agulla sp.	0	0	0	0	0	0	0	0	0	0	0	0
Nigronia sp.	0	0	0	1	0	0	0	0	0	0	0	0
Sialis sp.	0	0	0	0	0	0	0	0	0	0	0	0
Permoberotha sp.	0	0	1	0	0	0	0	0	0	0	0	0
Afrocupes firmae	0	0	1	1	0	0	1	0	0	1	0	1
Archicupes jacobsoni	-	0	1	0	0	1	0	-	-	0	0	1
Asiocoleus novojilovi	0	0	1	1	1	5	0	0	-	2	0	1
Boscoleus blandus	0	0	1	0	0	5	1	0	-	1	0	1
Brochocoleus alatus	0	0	1	1	0	0	1	1	-	2	0	1
Brochocoleus punctatus	1	0	1	1	0	0	0	1	0	0	0	1
Cytocupes angustus	0	0	1	1	0	0	0	0	0	0	1	-
Eocoleus scaber	0	0	1	0	0	1	0	0	0	0	0	1
Forticupes laiyangensis	0	0	1	1	0	0	0	0	0	0	1	-
Kaltanicupes acutus	0	0	1	1	0	5	0	0	-	0	1	-
Kaltanicupes kitjakensis	0	0	1	1	0	5	0	0	-	?	1	-
Kaltanicupes major	0	0	1	1	0	5	0	0	-	?	0	1
Kaltanicupes ponomarenkoi	0	0	1	1	0	5	0	0	-	0	0	1
Kaltanocoleus pospelovi	0	0	1	0	0	1	0	0	0	0	1	-
Labradorocoleus carpenteri	0	0	1	1	0	0	0	0	0	0	0	1
Liberocoleus intactus	0	0	1	1	0	1	1	?	?	0	1	-
Longxianocupes tristichus	0	0	1	1	0	1	1	0	1	2	1	-
Magnocoleus huangjiapuensis	0	0	1	1	0	0	1	0	-	1	0	1
Moravocoleus fractus	0	0	1	0	0	1	1	1	1	0	0	1
Moravocoleus neglegens	-	0	1	-	-	1	-	0	-	0	1	-
Moravocoleus perditus	0	0	1	0	0	1	1	1	1	0	0	1
Moravocoleus permianus	0	0	1	0	0	1	0	0	0	0	0	1
Notocupes brachycephalus	0	0	1	1	0	6	1	0	0	1	1	-
Notocupes elegans	0	0	1	1	0	6	1	0	0	1	1	-
Notocupes mongolicus	0	0	1	1	0	5	1	0	-	2	1	-
Notocupes sp.	0	0	1	1	0	6	1	0	0	1	0	1

Table 1.2 (Continued)

Taxon/Character	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Oborocoleus rohdendorfi	0	0	1	1	0	1	1	0	1	0	1	-
Permocoleus wellingtonensis	0	0	1	0	0	1	0	0	0	0	0	1
Permocupes distinctus	0	0	1	1	0	6	1	0	-	1	1	-
Permocupes semenovi	0	0	1	1	0	5	1	0	0	2	1	-
Permocupoides skoki	0	0	1	0	0	0	0	0	-	0	1	-
Prosperocoleus prosperus	0	0	1	0	0	1	1	1	1	0	0	1
Sogdelytron latum	1	0	1	1	0	1	0	0	-	0	1	-
Sojanocoleus reticulatus	0	0	1	0	0	1	0	0	0	0	1	-
Sylvacoleus richteri	0	0	1	0	0	1	0	0	-	3	0	1
Synodus changmaensis	0	0	1	1	0	0	0	0	0	0	0	1
Tomiocupes carinatus	0	0	1	0	0	1	0	0	0	0	1	1
Triassocupes yaochaensis	0	0	1	1	0	0	0	0	-	0	1	-
Tricoleodes acutus	0	0	1	1	0	1	1	1	-	0	1	-
Tricoleus punctatus	0	0	1	1	0	0	0	0	-	0	1	-
Tricupes acer	-	1	1	-	-	-	-	-	-	4	0	-
Tshekardocoleus magnus	0	0	1	1	0	1	1	0	1	2	0	1
Tshekardocoleus minor	0	0	1	1	0	0	0	0	0	0	0	1
Tychticupes radtschenkoi	0	0	1	1	0	3	0	0	0	0	0	1
Umoricoleus perplex	0	0	1	0	0	1	0	0	-	0	0	1
Votocoleus submissus	0	0	1	0	0	1	0	0	0	0	0	1
Tenomerga concolor	1	0	1	1	0	0	0	1	-	2	0	1
Omma stanleyi	1	0	1	1	0	0	0	1	-	2	0	1

Table 1,2 (Continued)

Taxon/Character	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**
Agulla sp.	0	0	0	0	0	0	0	0	0	0	0
Nigronia sp.	0	0	0	0	0	0	0	0	0	0	0
Sialis sp.	0	0	0	0	0	0	0	0	0	0	0
Permoberotha sp.	0	0	0	0	0	0	0	0	0	0	0
Afrocupes firmae	2	1	0	0	1	0	1	0	0	1	0
Archicupes jacobsoni	3	-	-	-	-	0	1	0	0	1	0
Asiocoleus novojilovi	2	0	0	0	0	0	3	1	0	1	0
Boscoleus blandus	2	0	0	0	0	0	2	0	0	1	0
Brochocoleus alatus	2	0	0	1	0	1	5	-	0	1	0
Brochocoleus punctatus	0	0	0	1	0	0	0	0	0	1	0
Cytocupes angustus	3	-	-	-	-	1	5	-	0	1	0
Eocoleus scaber	1	0	0	0	0	0	2	0	0	1	0
Forticupes laiyangensis	3	-	-	-	-	1	5	-	0	1	0
Kaltanicupes acutus	3	-	-	-	-	0	1	0	0	1	0
Kaltanicupes kitjakensis	3	-	-	-	-	0	1	0	0	1	0
Kaltanicupes major	2	0	0	0	0	0	1	0	0	1	0
Kaltanicupes ponomarenkoi	2	0	0	0	0	0	1	0	0	1	0
Kaltanocoleus pospelovi	3	-	-	-	-	0	1	0	0	1	0
Labradorocoleus carpenteri	0	0	-	0	0	1	5	-	0	1	?
Liberocoleus intactus	3	-	-	-	-	1	5	-	0	1	0
Longxianocupes tristichus	3	-	-	-	-	1	5	-	0	1	0
Magnocoleus huangjiapuensis	0	1	-	0	1	1	5	-	0	1	0
Moravocoleus fractus	2	0	0	0	0	0	2	0	0	1	0
Moravocoleus neglegens	3	-	-	-	-	0	2	0	0	1	0
Moravocoleus perditus	2	0	1	0	0	0	2	0	0	1	0
Moravocoleus permianus	2	0	1	0	0	0	2	0	0	1	0
Notocupes brachycephalus	3	-	-	-	-	1	5	-	0	1	0
Notocupes elegans	3	-	-	-	-	1	5	-	0	1	0
Notocupes mongolicus	3	-	-	-	-	1	5	-	0	1	0
Notocupes sp.	2	0	-	0	1	1	5	-	0	1	?
Oborocoleus rohdendorfi	3	-	-	-	-	1	5	-	0	1	0
Permocoleus wellingtonensis	2	0	0	0	0	0	1	0	0	1	0
Permocupes distinctus	3	-	-	-	-	1	5	-	0	1	0
Permocupes semenovi	3	-	-	-	-	1	5	-	0	1	0
Permocupoides skoki	3	-	-	-	-	0	2	0	0	1	0
Prosperocoleus prosperus	2	0	1	0	0	0	2	0	0	1	0
Sogdelytron latum	3	-	-	-	-	1	5	-	0	1	0

Table 1.2 (Continued)

Taxon/Character	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Sojanocoleus reticulatus	3	-	-	-	-	1	5	-	1	1	0
Sylvacoleus richteri	1	0	0	0	0	0	2	0	0	1	1
Synodus changmaensis	0	0	0	0	0	0	0	0	0	0	0
Tomiocupes carinatus	2	0	-	0	1	1	5	-	0	1	0
Triassocupes yaochaensis	3	-	-	-	-	1	5	-	1	1	0
Tricoleodes acutus	3	-	-	-	-	1	5	-	0	1	0
Tricoleus punctatus	3	-	-	-	-	1	5	-	0	1	0
Tricupes acer	1	0	-	-	-	1	5	-	0	1	0
Tshekardocoleus magnus	1	0	0	0	0	0	2	0	0	1	0
Tshekardocoleus minor	1	0	0	0	0	0	2	0	0	1	0
Tychticupes radtschenkoi	1	0	-	0	0	1	5	-	1	1	0
Umoricoleus perplex	2	0	0	0	0	0	2	0	0	1	0
Votocoleus submissus	1	0	0	0	0	0	2	0	0	1	1
Tenomerga concolor	2	0	0	0	0	1	5	-	0	1	0
Omma stanleyi	2	0	0	0	0	1	5	-	0	1	0

Table 1,2 (Continued)

Taxon/Character	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**
Agulla sp.	0	0	0	0	0	0	0	0	0	0
Nigronia sp.	0	0	0	0	0	0	0	0	0	0
Sialis sp.	0	0	0	0	0	0	0	0	0	0
Permoberotha sp.	0	0	0	0	0	0	0	0	0	0
Afrocupes firmae	?	0	0	1	0	0	2	0	0	0
Archicupes jacobsoni	8	0	0	1	0	0	4	0	-	0
Asiocoleus novojilovi	?	0	0	1	-	0	4	0	0	-
Boscoleus blandus	8	0	3	1	0	0	4	0	0	0
Brochocoleus alatus	?	0	3	1	0	0	4	0	1	1
Brochocoleus punctatus	3	1	0	1	0	0	0	0	1	1
Cytocupes angustus	?	0	0	1	-	0	4	0	0	-
Eocoleus scaber	?	0	0	1	0	0	4	0	0	0
Forticupes laiyangensis	6	0	0	1	-	0	1	0	1	-
Kaltanicupes acutus	?	0	0	2	0	0	4	0	0	0
Kaltanicupes kitjakensis	?	0	?	2	0	0	4	0	0	0
Kaltanicupes major	?	0	1	4	0	0	4	0	0	0
Kaltanicupes ponomarenkoi	?	0	0	1	0	0	4	0	0	0
Kaltanocoleus pospelovi	?	0	0	1	0	0	4	0	0	0
Labradorocoleus carpenteri	?	0	0	1	-	0	4	0	0	0
Liberocoleus intactus	?	0	3	3	-	0	4	0	0	0
Longxianocupes tristichus	7	0	3	2	-	1	4	0	0	-
Magnocoleus huangjiapuensis	1	0	3	1	-	0	4	0	1	1
Moravocoleus fractus	?	0	3	1	0	0	4	0	0	0
Moravocoleus neglegens	?	0	-	2	0	0	4	0	0	0
Moravocoleus perditus	?	0	3	1	0	0	4	0	0	0
Moravocoleus permianus	6	0	0	2	0	0	4	1	0	0
Notocupes brachycephalus	?	0	3	1	-	0	4	0	1	1
Notocupes elegans	?	0	3	1	-	0	4	0	1	1
Notocupes mongolicus	?	0	3	1	-	0	4	0	1	1

Table 1.2 (Continued)

Taxon/Character	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Notocupes sp.	?	0	3	1	-	0	4	0	0	0
Oborocoleus rohdendorfi	3	0	3	4	-	0	1	0	0	0
Permocoleus wellingtonensis	5,6	0	0	4	0	0	4	0	0	0
Permocupes distinctus	8	0	3	2	-	0	4	0	0	0
Permocupes semenovi	?	0	1	2	-	0	4	0	0	-
Permocupoides skoki	8	0	1	?	0	0	4	0	0	-
Prosperocoleus prosperus	1,3	0	3	2	0	0	4	0	0	0
Sogdelytron latum	?	0	0	2	-	1	4	0	0	-
Sojanocoleus reticulatus	?	0	0	2	-	0	4	0	0	0
Sylvacoleus richteri	2	0	1	2	0	0	4	0	0	0
Synodus changmaensis	2	0	0	3	0	0	3	0	0	0
Tomiocupes carinatus	8	0	0	2	1	0	4	0	0	-
Triassocupes yaochaensis	?	0	0	2	-	1	4	0	0	0
Tricoleodes acutus	?	0	3	2	-	0	4	0	0	0
Tricoleus punctatus	?	0	0	2	-	0	4	0	0	-
Tricupes acer	3,5	0	0	1	-	0	4	0	-	-
Tshekardocoleus magnus	7	0	3	1	0	0	1	0	0	-
Tshekardocoleus minor	?	0	0	2	0	0	1	0	0	0
Tychticupes radtschenkoi	?	0	0	1	-	0	4	0	0	0
Umoricoleus perplex	?	0	0	1	0	0	4	0	0	0
Votocoleus submissus	?	0	0	2	0	0	0	1	0	0
Tenomerga concolor	6	0	1	1	-	0	4	0	1	1
Omma stanleyi	6	0	1	1	-	0	4	0	1	1

Table 1.3: Character Weights

Matrix # **Character #**	1	2	3
0	1	25	100
1	1	1	2
2	1	1	2
3	1	1	2
4	1	25	100
5	1	25	100
6	1	1	50
7	1	1	2
8	1	1	2
9	1	1	2
10	1	1	2
11	1	25	100
12	1	25	100
13	1	1	2
14	1	25	100
15	1	25	100
16	1	1	2
17	1	1	2
18	1	1	2
19	1	1	2
20	1	1	2
21	1	1	2
22	1	1	2
23	1	25	100
24	1	1	2
25	1	1	2
26	1	1	2

Table 1.3 (continued)

Matrix # **Character #**	**1**	**2**	**3**
27	1	1	2
28	1	1	2
29	1	1	2
30	1	25	100
31	1	1	2
32	1	1	2
33	1	25	100
34	1	25	100
35	1	1	2
36	1	1	2
37	1	1	1
38	1	1	2
39	1	1	2
40	1	1	1
41	1	1	2
42	1	1	50
43	1	1	2
44	1	1	2
45	1	1	2
46	1	1	2

Tree Search

The character matrices (47 characters, 52 terminals) were constructed using WinClada (NIXON 2002). Both WinClada's (NIXON 2002) Island Hopper and NONA (GOLOBOFF 1999) were used for the tree search.

Results

The analysis of matrix 1 resulted in 602 most parsimonious trees of 230 steps. Thirty-six nodes were collapsed to form the strict consensus tree of 366 steps (CI 21, RI 29) shown in Figure 1.4. Matrix 2 yielded 313 most parsimonious trees of 886 steps. Eleven nodes were collapsed to produce the strict consensus tree of 1,017 steps (CI 33, RI 74) (Figure 1.5). Analysis of matrix 3 resulted in 515 most parsimonious trees with a length of 3,898 steps. The strict consensus of 4,782 steps (CI 33, RI 72) resulting from the collapse of nine nodes is shown in (Figure 1.6). The dramatic increase in steps is due to character weighting. Although a fully resolved tree was not obtained, some groupings were consistent across all trees. These are discussed below.

Table 1.4: Summary of Tree Search results

	Number of MPTs	**Length of MPTs**	**Length of consensus tree**	**CI/RI**
Matrix 1	602	230	366	21/29
Matrix 2	313	886	1,017	33/74
Matrix 3	515	3,898	4,782	33/72

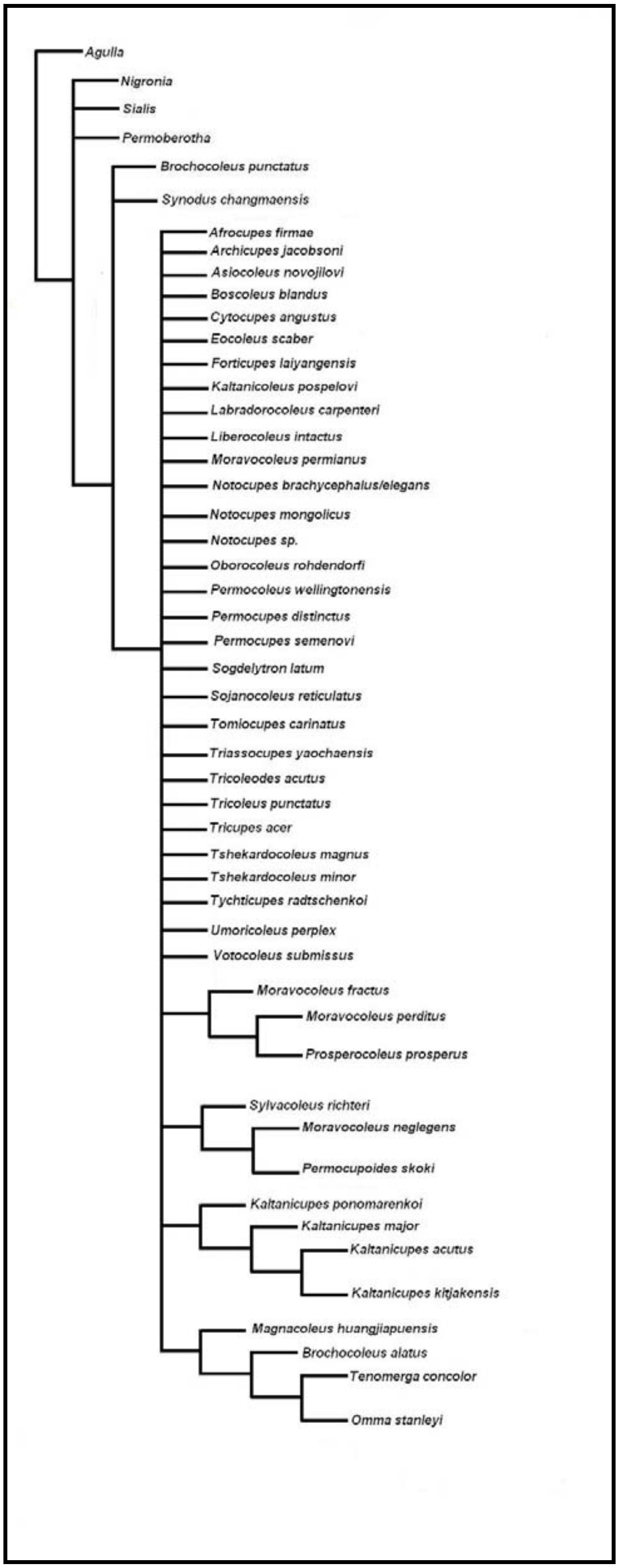


Figure 1.4: Consensus tree for Matrix 1

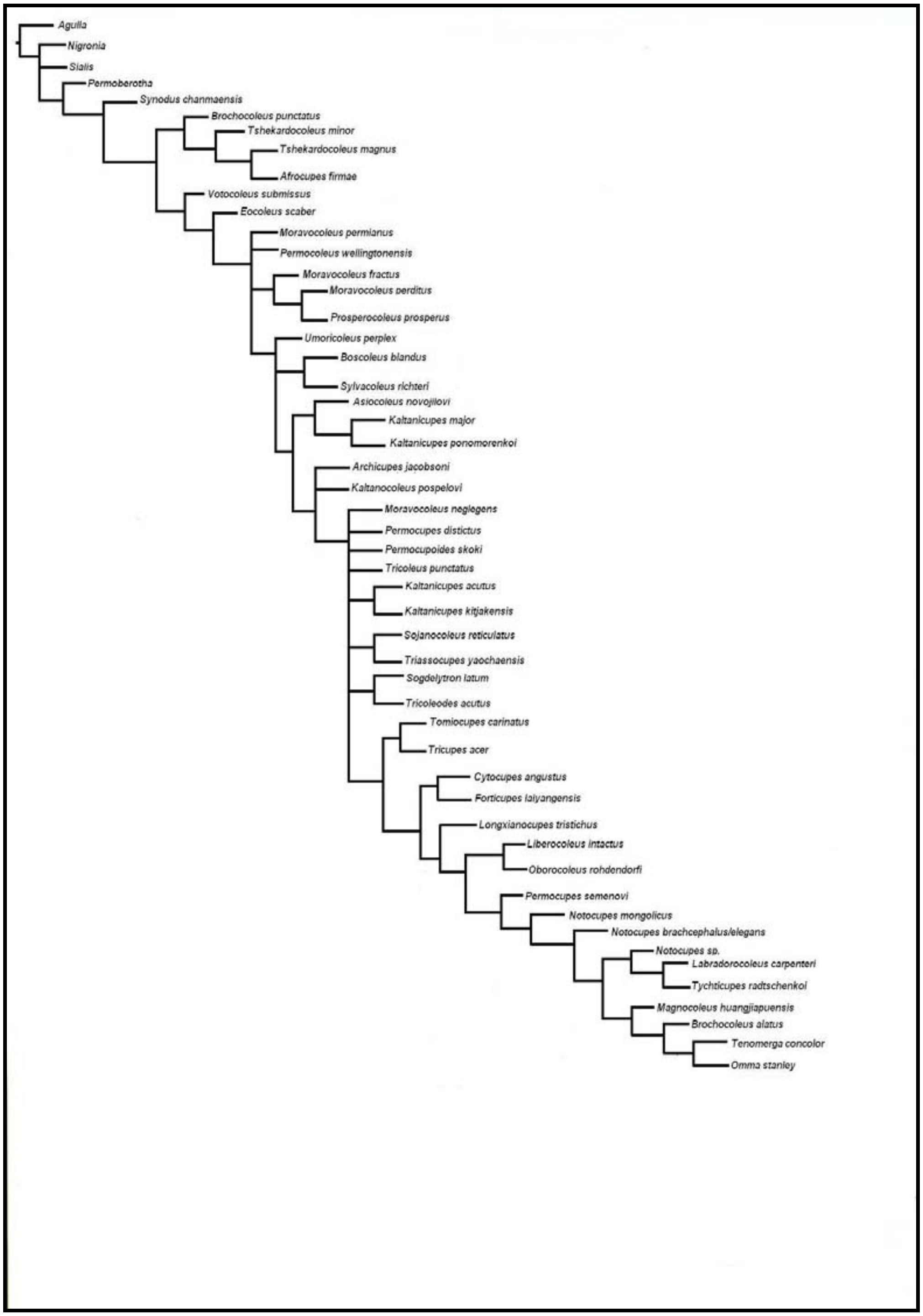


Figure 1.5: Consensus tree for Matrix 1

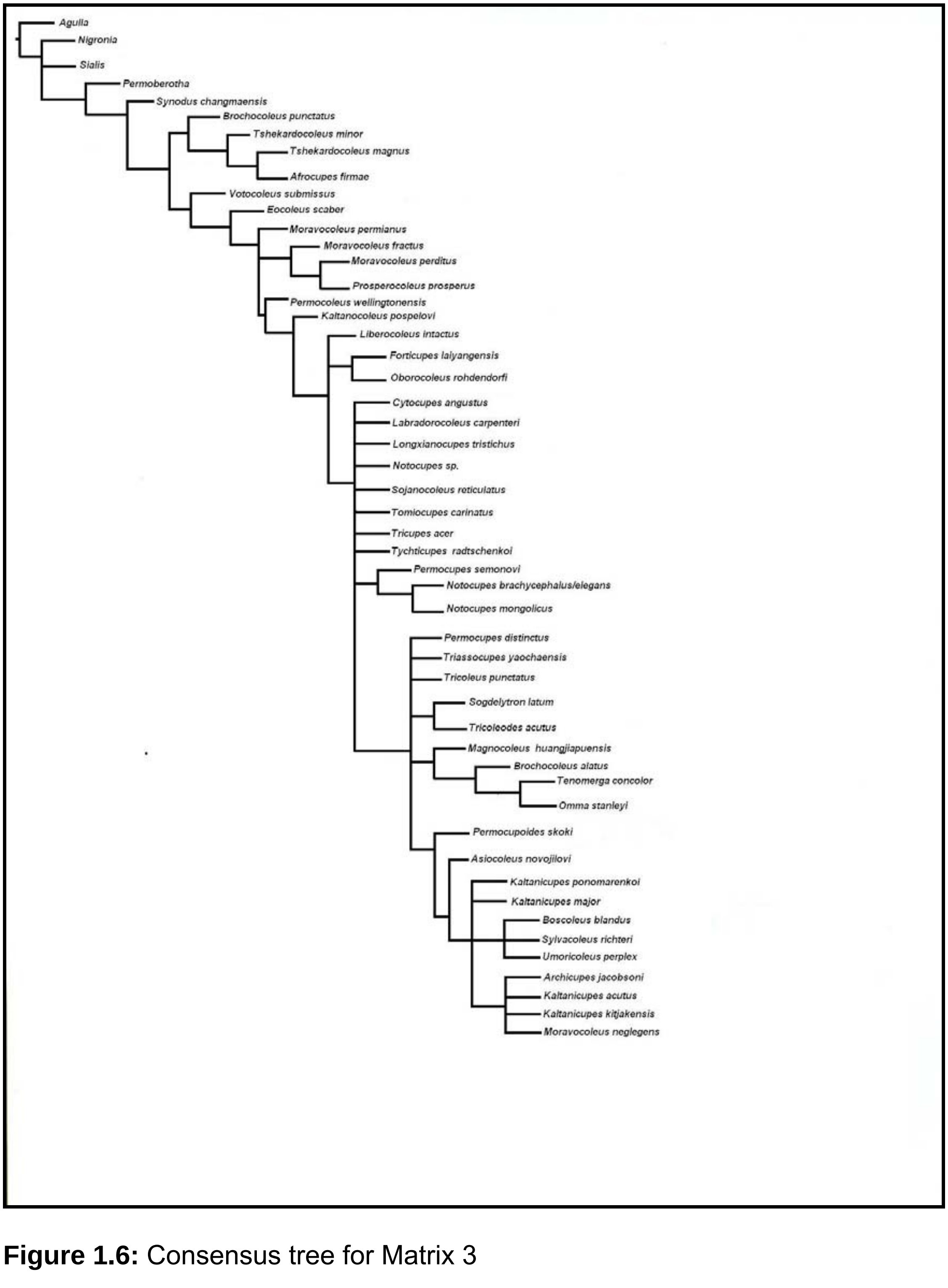


Figure 1.6: Consensus tree for Matrix 3

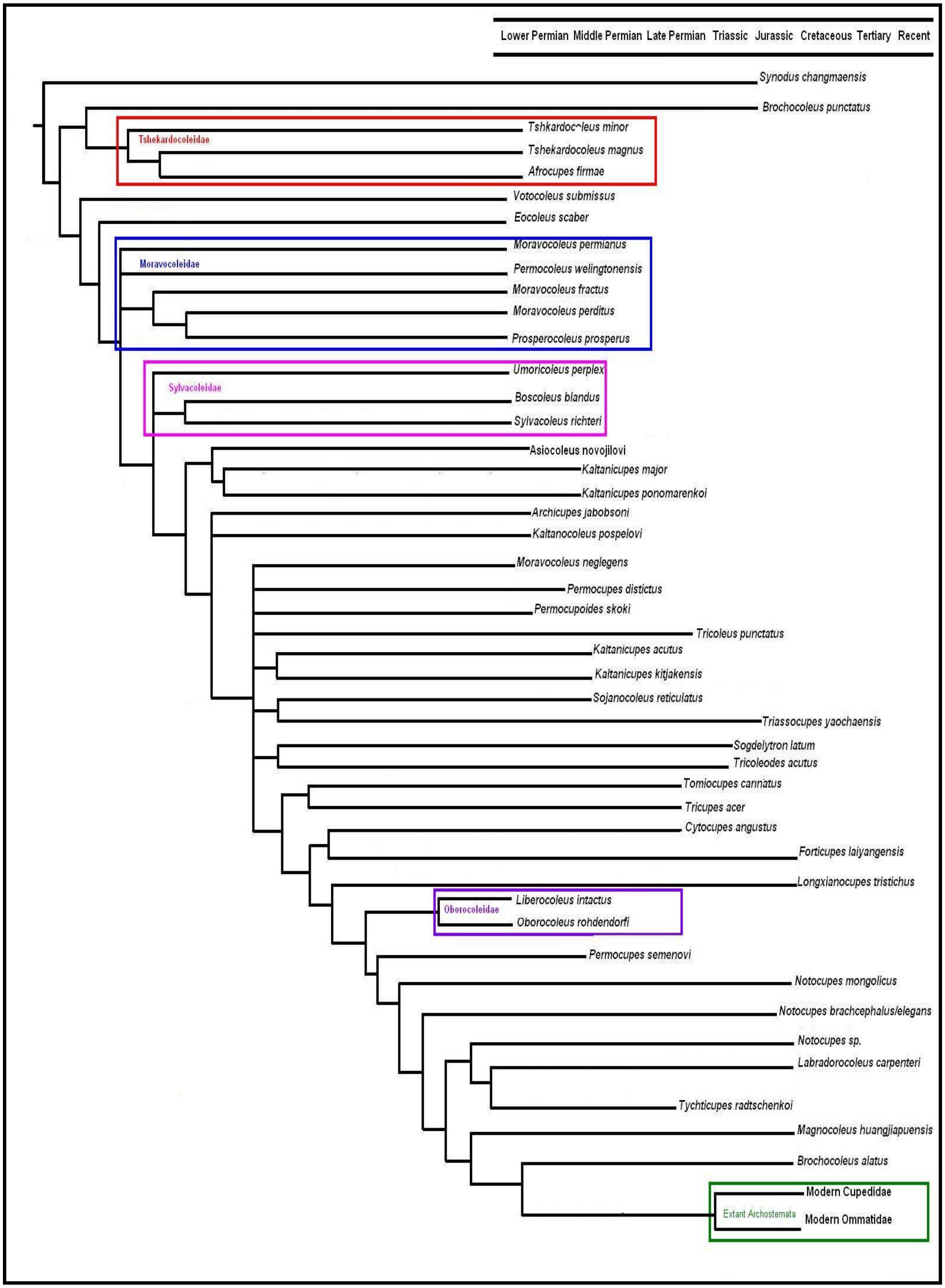


Figure 1.7: Consensus tree from Analysis 2 (with timescale) showing the family affiliations of early Coleoptera and coleopteroids.

The obtaining of a resolved tree was complicated by multiple homoplasious losses of veins. Because it is impossible to homologize losses, when there was a loss, the tree resolution was dependent on the presence of other characters. However, since characters were not independent, a loss sometimes affected other characters such as vein length or vein path, where it was coded as an inapplicable state (-). Inapplicable states are treated by NONA (GOLOBOFF 1998) as having all states present. When too many veins were lost in a taxon, the result was an abundance of most parsimonious placements which resulted in polytomies in the consensus tree. There is in Coleoptera a simplification of elytral venation with time, and this trend of vein loss was expressed as a loss of resolution in the lower part of the tree. Nonetheless, while not fully resolved, these trees provide plenty of interesting and consistent information.

In all analyses, the Coleoptera/coleopteroids formed a monophyletic group with the non-Coleoptera as sister taxa.

In all the consensus trees, the most primitive coleopteroids included *Brochocoleus punctatus* and *Synodus changmaensis.* In consensus trees two and three, they also included *Afrocupes firmae, Eocoleus scaber*, *Oborocoleus rohdendorfi, Tshekardocoleus magnus, Tshekardocoleus minor* and *Votocoleus submissus. Afrocupes, Eocoleus, Oborocoleus*, *Tshekardocoleus,* and *Votocoleus* are fossils of Permian age. *Brochocoleus punctatus* and *Synodus changmaensis* are Chinese fossils of Upper Jurassic age and may represent remnants of separate coleopteroid lineages that are sister groups to the sub-order Coleoptera. Perhaps the history of these lineages will be unearthed as more beetle fossils are described from China. The elytral venation of *Brochocoleus punctatus* (Figure 1.1f) is significantly different from that of the Lower Cretaceous *Brochocoleus alatus* (Figure 1.1e), and the two species do not appear to be related; these differences will be discussed later.

As interpreted, *Synodus changmaensis* (Figure1.1jj) is the most primitive of the Coleoptera and coleopteroids. The venation differs from the rest of the group in that MP branching is present and there are additional veins that are not present in other members of the Coleoptera. In addition, RS_2 arises independently from the elytral base.

The “Tshekardocoleidae” (ROHDENDORF 1944) are traditionally considered the most primitive of the Coleoptera (CARPENTER 1992; PONOMARENKO 1969, 2000). This large and diverse group is defined as small or medium-sized beetles with antennae of 13 monofiliform antennomeres, antennae slightly longer than head and thorax combined, small, rounded, well-separated fore-coxae, mesothorax almost as long as metathorax, abdomen with five visible sternites, elytra much longer than abdomen, all main elytral veins usually present, Rs with one or two branches directed posteriorly, hind wing with C and Sc close together and folds present between M and CuA and CuA and Cu (ROHDENDORF 1944; CARPENTER 1992). The “family” traditionally includes the genera *Tshekardocoleus*, *Avocoleus*, *Boscoleus*, *Dictyocoleus*, *Eocoleus*, *Moravocoleus*, *Prosperocoleus*, *Retelytron*, *Sylvacoleodes*, *Sylvacoleus*, *Umoricoleus*, *Uralocoleus*, and *Votocoleus* (CARPENTER 1992; PONOMARENKO personal correspondence). However, with the exception of *Boscoleus*, *Moravocoleus*, *Sylvacoleus* and *Tshekardocoleus*, these taxa are only known from fossil elytra. In the cladistic analysis of elytral characters, the Tshekardocoleidae formed a polyphyletic group, and even the genus *Tshekardocoleus* was not monophyletic. This is not surprising as the venation of *Tshekardocoleus minor*

(Figure 1.1qq) differs from that of *Tshekardocoleus magnus* (Figure1.1pp) in that Sc is absent and there is only a single Rs vein.

Afrocupes firmae (Figure 1.1a) is a Late Paleozoic coleopteroid from the Whitehill Formation of South Africa (GEERSTEMA AND VAN DER HEEVER 1996). It has been placed in Permocupedidae although the number of veins and their placement is more similar to that of *Tshekardocoleus*. Unfortunately the abdomen and antennae are only partially preserved, thus the similarity of its non-elytral morphology to the "Tshekardocoleidae" is uncertain.

In Consensus Trees Two and Three, *Tshekardocoleus* is part of a monophyletic group that includes *Afrocupes firmae* (Figure 1.1a) and *Brochocoleus punctatus* (Figure 1.1f). Members of this group have two Rs veins and only three anal veins. In *Brochocoleus punctatus* Rs_2 arises from Rs_1, and it is the sister taxon to the group containing *Tshekardocoleidae* and *Afrocupes* in which Rs_2 arises from R. The family Tshekardocoleidae is revised to be restricted to this monophyletic grouping, and new families are constructed for some of the other genera.

Family Tshekardocoleidae ROHDENDORF, 1944

Tshekardocoleidae ROHDENDORF, 1944, p.252 (type genus *Tshekardocoleus* Rohdendorf, 1944).

Included genera. *Tshekardocoleus* ROHDENDORF 1944*, Afrocupes* GEERSTEMA AND VAN DER HEEVER 1996*, Brochocoleus* HONG 1982 (in part).

***Diagnosis*.** Elytra with all major veins (C, Sc, R, M, CuA, CuP) present. Rs with one or two branches directed posteriorly. Veins A_1, A_2, A_3 present.

The genus *Moravocoleus* is part of a monophyletic group that consists of *Moravocoleus permianus* (Figure 1.1v), *Moravocoleus fractus* (Figure1.1s) , *Prosperocoleus prosperus* (Figure1.1ff), and *Moravocoleus perditus* (Figure 1.1u) (and sometimes *Permocoleus wellingtonensis* [Figure 1.1bb]). *Moravocoleus neglegens* (Figure 1.1t) was not included in this group. However, its absence can be attributed to multiple losses of veins (Rs, M and CuP are absent) rather than similarities in the veins that are present. *Moravocoleus* species differ from other Tshekardocoleidae and primitive coleopteroids in that based on body fossils of *Moravocoleus permianus* and *Moravocoleus perditus,* they possess short antennae with 11 antennomeres and short ovipositors (KUKALOVÁ 1969). The elytra are much simplified with a single Rs vein, CuA and M share a stem, and the posterior portion of CuA is deeply concave. For this reason the genera *Moravocoleus* and *Prosperocoleus* are removed from the Tshekardocoleidae, and are placed in a new family, the Moravocoleidae with *Permocoleus.*

Moravocoleidae, new family

Type genus*. Moravocoleus* KUKALOVÁ 1969.

Included genera. *Moravocoleus* KUKALOVÁ 1969*, Permocoleus* LUBKIN AND ENGEL 2005, *Prosperocoleus* KUKALOVÁ 1969.

Diagnosis. Antennae with eleven segments. Ovipositor short. Elytra with veins C, Sc, R, Rs, M, CuA, CuP, A_1, A_2, A_3 present. Single Rs vein attached near midpoint of R. Veins M and CuA share stem. CuP short, terminates at or near A_1. Posterior portion of CuA deeply concave.

Stratigraphic and geographic distribution: Lower Permian of North America and Europe.

When characters are weighted, the species *Umoricoleus perplex* (Figure 1.1ss), *Boscoleus blandus* (Figure 1.1d), and *Sylvacoleus richteri* (Figure 1.1ii) form a monophyletic group separate from the other "Tshekardocoleidae". These species have no Rs vein, but the posterior portion of CuA is deeply concave as it is in *Moravocoleus*. The actual position of the group may be most similar to its placement in consensus tree two, but the position is uncertain and is not consistent with morphology as *Sylvacoleus richteri* has 13 antennal segments.

Sylvacoleidae, new family

Type genus. *Sylvacoleu*s PONOMARENKO 1963

***Included genera*.** *Boscoleus* KUKALOVÁ 1969, *Sylvacoleus* PONOMARENKO 1963, *Umoricoleus* KUKALOVÁ 1969.

Diagnosis. Elytra with veins C, Sc, R, M, CuA, CuP, A_1, A_2, A_3 present, RS absent. M and CuA share stem. CuP missing in *Boscoleus.*
Stratigraphic and geographic distribution: Lower Permian of Czech Republic and Russia.

The Oborocoleidae (KUKALOVÁ 1969) includes *Oborocoleus rohdendorfi* and *Liberocoleus intactus.* The family is described as similar to Tshekardocoleidae, but with M and CuA reduced and A_1 long (KUKALOVÁ 1969, CARPENTER 1992). The monophyly of Oborocoleidae was supported in the slightly-weighted analysis (consensus tree two), but when weighted *Oborocoleus rohdendorfi* (Figure 1.1aa) was grouped with *Forticupes* *laiyangensis* (Figure1.1i) (lower Cretaceous, China), with *Liberocoleus intactus* (Figure 1.1p) as the sister taxon. All three taxa are missing veins A_1 and CuP, although the loss could be convergent. The problem of multiple vein losses is further compounded In *Forticupes* as Sc and A_2 are reduced to the point of being absent (Figure1.1p). These multiple losses may well have influenced *Forticupes'* placement in that tree.

The placement of Oborocoleidae within the Coleoptera has been considered uncertain because no body fossils are known (KUKALOVÁ, 1969). However, based on elytral venation, the Oborocoleidae are comfortably nested within the earliest beetles.

. The Permocupedidae (MARTYNOV 1933) is a relatively large family that includes abundant later Permian Coleoptera that are somewhat vaguely defined as being small to medium sized beetles with reticulate elytra which have most veins present. In this large group of beetles Rs is absent, CuA and M do not share a stem, and CuP is usually, but not always, present (MARTYNOV 1933). Permocupedidae included in this analysis are *Archicupes jacobsoni*, *Afrocupes firmae*, *Cytocupes angustus*, *Kaltanicupes acutus, Kaltanicupes kitjakensis*, *Kaltanicupes major*, *Kaltanicupes ponomarenkoi*, *Kaltanocoleus pospelovi*, *Permocupes distinctus* and *Permocupes semenovi.* The Permocupedidae did not form a monophyletic group and are sprinkled throughout the resulting trees. Because of the size of this diverse family and the lack of resolution in this part of the consensus trees, a revision of Permocupedidae is a project for the future.

The genus *Kaltanicupes* (*Kaltanicupes acutus, Kaltanicupes kitjakensis*, *Kaltanicupes major*, and *Kaltanicupes ponomarenkoi*) form a monophyletic group when no characters are weighted. This group has a short R, no Rs veins, CuA is slightly concave and A_1 is present and reaches the edge of the lower half of the elytron. However, when characters are weighted, the genus is separated into groups: *Kaltanicupes major* and *Kaltanicupes ponomarenkoi,* and *Kaltanicupes acutus* and *Kaltanicupes kitjakensis.* Vein CuP is present in *Kaltanicupes major* (Figure 1.1l) and *Kaltanicupes ponomarenkoi* (FIGURE 1.3 m) and absent in *Kaltanicupes acutus* (Figure1.1j) and *Kaltanicupes kitjakensis* (Figure 1.1k) and this accounts for their separation from the rest of the genus. The genus *Kaltanicupes* is probably a monophyletic group with the loss of CuP defining the smaller clade of *Kaltanicupes acutus* and *Kaltanicupes kitjakensis.*

The Canadian fossil *Labradorocoleus carpenteri* (Figure 1.1o) is the sole member of the Cretaceous family Labradorocoleidae. In analysis 2, it is grouped with the late Permian species *Tychticupes radtschenkoi* (Figure 1.1rr), a member of the family Taldycupedidae. Because clear illustrations of other Taldycupedidae were not available, *Tychticupes radtschenkoi* is the only Taldycupedid included in the study. Although the shape of the elytron differs, the elytra of both families have nine thick, almost parallel veins.

The family Tricoleidae includes the genera *Sogdelytron*, *Tricoleodes*, *Tricoleus*, and *Willcoxia* (DUNSTAN 1923). In consensus trees two and three, *Sogdelytron latum* (Figure 1.1gg) and *Tricoleodes acutus* (Figure 1.1 mm) form a monophyletic group. *Tricoleus punctatus* (Figure 1.1nn) was part of a polytomy which included the *Sogdelytron* -*Tricoleodes* group as well as other “Permocupedidae” and non-“Permocupedidae”.

Notocupes is an extinct genus belonging to the extant family Cupedidae. Four species of *Notocupes* were included in the analysis: *Notocupes brachycephalus*, *Notocupes elegans*, *Notocupes mongolicus* and an unnamed *Notocupes sp.* *Notocupes brachycephalus* (Figure 1.1w) and *Notocupes elegans* (Figure 1.3x) showed identical venation patterns and, therefore, were combined for the analysis. When characters were weighted, they placed near or with *Notocupes mongolicus* (Figure 1.3y). In consensus tree three, these three species form a monophyletic group that is defined by the merger of C with Sc, and the curving of Sc and R to the anal edge of the elytron. Most of the veins in *Notocupes sp.* (Figure 1.3z). are the same as in the other *Notocupes*, but CuP is present in *Notocupes sp.,* while it is absent in *Notocupes brachycephalus*, *Notocupes elegans* and *Notocupes mongolicus.* In addition, Sc and R do not curve to the anal edge, and end at the tip of the elytron. Additionally, the shape of the elytron of *Notocupes sp.* is quite different. The anal edge is almost straight in *Notocupes brachycephalus*, *Notocupes elegans* and *Notocupes mongolicus*, but it is concave in *Notocupes sp.* Thus, *Notocupes sp.* is very likely not a *Notocupes*, but a member of another, yet undetermined, genus.

In all trees, *Magnocoleus huangjiapuensis* (Lower Cretaceous, China) and *Brochocoleus alatus* (Lower Cretaceous, Mongolia) formed a monophyletic group with the modern species *Omma stanleyi* (Ommatidae) and *Tenomerga concolor* (Cupedidae). In this group veins Sc and R curve to intersect with the anal edge of the elytron as they do in *Notocupes,* CuP is present and short, M intersects with CuA, and there are no Rs veins. It is interesting that the closest fossil relatives to the extant Cupedidae are found in Asia, as a number of modern species of Cupedidae are also known from Asia.

Magnocoleus huangjiapuensis (Figure 1.3r) is the single member of the family Magnocoleidae. PONOMARENKO (1994 and personal correspondence) considers *Brochocoleus* to belong to Ommatinae which he considers a subfamily of Cupedidae rather than an independent family. However, only *Brochocoleus alatus* fit in this grouping. *Brochocoleus punctatus* did not. In *Brochocoleus alatus*, both Sc and R curve to intersect with the anal edge of the elytron, but in *Brochocoleus punctatus* this is only true for R. Sc terminates on C and is distinguished by being divided anteriorly. In addition, all major veins and Rs branching are present, while in *Brochocoleus alatus* there is no Rs branching and A_1 is absent. The genus requires revision, but there are other Chinese taxa to consider.

Interestingly, neither *Notocupes* nor *Synodus* (both are also attributed to Cupedidae) fit into this grouping, although the elytra of *Notocupes* have a similar shape, and both Sc and R curve to terminate on the anal edge. This arrangement calls for the redefinition and restriction the family Cupedidae as it applies to fossils. The extant Cupedidae (Figure 1,2a) and Ommatidae (Figure1.2b) differ from each other only in that Sc and R merge in Ommatidae and do not in Cupedidae. If modern Ommatidae and Cupedidae are to be considered separate families, then Cupedidae must be restricted to those taxa exhibiting the "*Cupes*" venation pattern.

While elytra of extant Cupedidae share features such as venation and punctation with many Permian and Mesozoic fossil elytra, these characters are primitive and cannot be used as criterion for placement in Cupedidae. Modern genera of Cupedidae are known from as early as the Cretaceous (*Paracupes svitkoi*, LUBKIN 2002), but it seems that the extant Archostemata are indeed a monophyletic relict of a far greater diversity of reticulated beetles.

Conclusions

This is the first cladistic analysis of the early Coleoptera and Coleopteroids. This study found that many of the long-accepted family groupings of the early Coleoptera and coleopteroids are not supported by cladistic analysis of elytral venation, and that these groups are poly- or paraphyletic. The family Tshekardocoleidae is redefined and two new families Moravocoleidae and Sylvacoleidae are created to include some former members of Tshekardocoleidae. The family Permocupedidae still requires revision and it is proposed that Cupedidae and Ommatidae are restricted to taxa showing the modern pattern of elytral venation. The proposed changes are summarized in Table 1.5.

The elytra of the earliest Coleoptera (*Moravocoleus permianus, Moravocoleus neglegens, Moravocoleus fractus, Moravocoleus perditus, Eocoleus scaber, Umoricoleus perplex, Boscoleus blandus, Prosperocoleus prosperus, Oborocoleus rohdendorfi, Liberocoleus intactus* (KUKALOVÁ 1969) and *Permocoleus wellingtonensis* (LUBKIN AND ENGEL 2005) are not the most primitive. *Permocoleus wellingtonensis* is the earliest new world beetle and is very similar to the Moravocoleidae from Obora. This suggests that by the Artinskian (269 MA), both Coleoptera and coleopteroids were present and the Moravocoleidae, at least, were widely distributed implying an earlier origin for the Coleoptera. The earliest Coleopteroids are younger and known from Tshekarda (Kungurian 260-256 MA) (PONOMARYOVA 1998), and this signifies that there are more fossils to be found and that our knowledge of the earliest beetles and their relatives is still incomplete.

More puzzling is the age of the suborder Archostemata. Without body fossils, it is difficult to determine what fossil taxa belong in the suborder.

Table 1.5: Proposed changes to the classification of the basal Coleoptera and Coleopteroids

Family	**Type Genus**	**Included Genera**	**Elytral Diagnosis**
Coleopteroids			
Tshekardocoleidae	*Tshekardocoleidae*	*Tshekardocoleus* , *Afrocupes,* *Brochocoleus* (in part)	Elytra with all major veins present, Rs with two branches directed posteriorly, A_1, A_2, A_3 present
Coleoptera			
Moravocoleidae n.f.	*Moravocoleus*	*Moravocoleus,* *Permocoleus,* *Prosperocoleus*	Elytra with veins C, Sc, R, Rs, M, CuA, CuP, A_1, A_2, A_3 present, single Rs vein attached near midpoint of R. M and CuA share stem. CuP short, terminates at or near A_1. Posterior portion of CuA deeply concave.
Sylvacoleidae n.f.	*Sylvacoleus*	*Boscoleus,* *Sylvacoleus,* *Umoricoleus*	Elytra with veins C, Sc, R, M CuA, CuP, A_1, A_2, A_3 present, Rs absent/ M and CuA share stem.

Table 1.5 (Continued)

Permocupedidae	*Permocupes*		Requires significant revision
Oborocoleidae	*Oborocoleus*	*Oborocoleus*, *Liberocoleus*	Elytra with veins C, SC, R, M, CuA present. Rs attached below midpoint of R. M and CuA merge. A_1 and CuP absent.
Ommatidae	*Omma*	*Omma, Tetraphalerus*	Elytra with veins C, Sc, R, M, CuA, CuP and A_2 present. Sc and R curve to terminate on anal edge. CuP short. Rs absent. Sc and R merge.
Cupedidae	*Cupes*	*Cupes, Tenomerga, Distocupes, Adinolepis, Ascioplaga, Rhipsideignea, Prolixocupes, Priacma*	Elytra with veins C, Sc, R, M, CuA, CuP and A_2 present. Sc and R curve to terminate on anal edge. CuP short. Rs absent. Sc and R parallel; do not merge.

Modern Archostemata are identified by a suite of morphological characters including both primitive features such as reticulated elytra, scales, the absence of cervical sclerites, and movable hind coxae, and more derived characters such as the fusion of the adult labrum to the head capsule and larval characters – characters that are not often fossilized. Modern Cupedidae and Ommatidae form a monophyletic clade and they are certainly Archostemata. The Oborocoleidae very likely are not, but are an Archostematan-like stem group. Thus, Archostemata would probably encompass a group at the lower end of the cladogram and would have originated by the late Permian. This would be consistent with the earliest appearance of the other suborders.

Because of the monophyly of modern Cupedidae and Ommatidae, extinct taxa previously placed in these families need to be reexamined and new families need to be constructed. This study has shown that, on the family level, the diversity of early Coleoptera and Coleopteroids is far greater than previously thought. The basal Coleoptera had complex patterns of elytral venation which can be used for determining phylogenetic relationships. However, in more derived beetles, the venation is simplified and major veins are lost. Diagnosing the relationships among the early Coleoptera is complicated by convergent losses of veins. Since, in most cases, all that is available for study of these taxa are isolated fossil elytra, this analysis accentuates the need for a consistent naming system for elytral venation and for less ambiguity in taxon definitions. Further taxonomic revision, of the families Permocupedidae and Cupedidae is still needed. It would be most interesting to see if the resultant trees from this study withstand the addition of morphological characters. However, this cannot be done without actual examination of specimens

REFERENCES

AFZELIUS, B.A. AND DALLAI, R. 1994. Characteristics of the flagellar axoneme in Neuroptera, Coleoptera and Strepsiptera. Journal of Morphology 219: 15-20.

BEUTEL, R. G. 1997. Über Phylogenese und Evolution der Coleoptera (Insecta), insbesondere der Adephaga. Abhandlungen des Naturwissenshaftlichen Vereins, Hamburg, 31:1-164.

BEUTEL, R.G. AND HAAS, F 2000. Phylogenetic relationships of the suborders of Coleoptera (Insecta). Cladistics 16: 103-141.

CARPENTER, F.M. 1992. Superclass Hexapoda. Pp. 1-655, *in* Kaesler, R.L. (Ed.) Treatise on Invertebrate Paleontology, Part R, Arthropoda 3-4. Geological Society of America; Boulder, Colorado; xxii + 655 pp.

CARPENTER, F. M. AND KUKALOVA, J. 1964. The structure of the Protoelytroptera, with description of a new genus from Permian strata of Moravia. Psyche 71: 183-197.

CHEVROLAT, A. 1829. Pp. 58, i*n* Guérin-Méneville. Iconographie du Régne Animal de G. Cuvier. Volume 3. Paris; xvi + 756pp.

COMSTOCK, J.H., AND NEEDHAM, J.G. 1898A. The wings of insects. Chapter 1. An introduction to the study of the homologies of the wing-veins. The American Naturalist 32: 43-48.

COMSTOCK, J.H., AND NEEDHAM, J.G. 1898B. The wings of insects. Chapter 2. The venation of the typical insect wing. The American Naturalist 32: 81-89.

COOPE, G.R. 1959. A Late Pleistocene Chelford, Cheshire. Proceedings of the Royal Society of London B 151: 70-86.

COOPE, G.R. 1962. A Pleistocene coleopterous fauna with arctic affinities from Flatbury, Worcestershire. Quarterly Journal of the Geological Society of London 118: 103-123.

COOPE, G.R. 1987. Fossil beetle assemblages as evidence for sudden and intense climatic changes in the British Isles. Pp. 147-150, *in* W.H. Berger and L.D. Labeyrie (Eds.), Abrupt Climate Change. Reidel, Dordrecht, the Netherlands; 452 pp.

CROWSON, R.A. 1970. Classification and Biology. Aldine Publishing Company, Chicago; 350 pp.

CROWSON, R.A. 1975. The evolutionary history of Coleoptera as documented by fossil and comparative evidence. Atti del X Congresso Nazionale Italiano de Entomologia, Sassari: 47-90.

CROWSON, R.A. 1981. The biology of the Coleoptera. Academic Press, London; 802 pp.

DOLLO, L. 1890. Première note sur les mosasauriens de Maestricht. Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie 4:151–169.

DUNSTAN, B. 1923. Mesozoic insects of Queensland. Part I. Introduction to Coleoptera. Geological Survey of Queensland, Publication 273: 1-74.

ELIAS, S.A. 1994. Quaternary Insects and Their Environments. Smithsonian Institution Press, Washington, DC; xiii + 284pp.

FABRICIUS, J. C. 1801. Systema elevtheratorvm secvndvm ordines, genera, species adiectis synonymis, locis, observationibvs, descriptionibvs. Tomvs II. Kiliae. (Bibliopoli Academici); pp. 1-687, I-IV [= 1-4], 1-93, [1].

FORBES, W.T.M. 1922. The wing-venation of the Coleoptera. Annals of the Entomological Society of America 15: 328-345, pls. XXIX-XXXV.

FORBES, W.T.M. 1926. The wing-folding patterns of the Coleoptera. Journal of the New York Entomological Society 34: 42-68, 91-139.

FRASER, N.C., GRIMALDI, P.E., OLSEN, P.E. AND AXSMITH, B. 1996. A Triassic Lagerstätte from Eastern North America. Nature 380: 615-619.

GOLOBOFF, P. 1999. NONA (NO NAME) ver. 2 Published by the author, Tucumán, Argentina.

GEERTSEMA, H. AND VAN DER HEEVER, J.A. 1996. A new beetle, *Afrocupes firmae* gen. et sp. nov. (Permocupedidae) from the Late Paleozoic Whitehill Formation of South Africa. South African Journal of Science 92: 497-499.

GRIMALDI, D. AND ENGEL, M.S. 2005. Evolution of the Insects. Cambridge University Press, Cambridge, United Kingdom. 755p.

HAAS, F AND BEUTEL, R.G. 2001. *W*ing folding and the functional morphology of the wing base in Coleoptera. Zoology (Jena) 104: 123-141.

HAAS, F. AND KUKALOVÁ-PECK, J. 2001. Dermaptera hindwing structure and folding: New evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). European Journal of Entomology 98: 445-509.

HAMMOND, P.M. 1979. Wing-folding mechanisms of beetles, with special reference to investigations of Adephagan phylogeny. Pp. 113-180, *in* Erwin, T.L., G.E. Ball, D.R. Whitehead and A.L. Halpern (Eds.), Carabid Beetles: Their Evolution, Natural History, and Classification. W. Junk, The Hague; the Netherlands 646 pp.

HELLER, K. M. 1913. Ein neuer Cupedidae: Wiener Entomologische Zeitung 32: 235-236.

HENNIG W. 1969. Die Stammesgeschichte der Insekten. Kramer, Frankfurt am Main, Germany; 436 pp.

HONG, Y.-C. 1982. Discovery of new Lower Cretaceous insects, at Xishan, Beijing. Bulletin of the Tianjin Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences 1982(4): 87-96.

HONG Y.-C., LIU, Z. AND LUI, S. 1985. Discovery and studying of the Triassic fauna and flora of the Niangniangmiao in Longxian, Shaanxi. Bulletin of the Xi'an Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences 10: 105-120.

HONG, Y-C. 1990. Fossil insects from the Laiyang Basin, Shandong Province. Pp. 44-189 *in* Regional Surveying Team, Shandong Bureau of Geology and Mineral Resources (Eds.), The stratigraphy and palaeontology of Laiyang Basin, Shandong Province; 189pp.

HONG, Y-C. 1998. Magnocoleidae fam. nov. (Insecta: Coleoptera). Geoscience (China) 12: 40-48.

HORNSCHEMEYER, T. H. 1998. Morphologie und Evolution der Flugelgelenks der Coleoptera und Neuropterida. [Morphology and evolution of the wing base of Coleoptera and Neuropterida.] Bonner Zoologische Monographien 43: 1-126.

KOLBE, H. J., 1898. Eine neue gattung der Cupesiden: Entomologische Nachrichten 24: 179-180.

KRISTENSEN N. P. 1975. The phylogeny of hexapod “orders.” A critical review of recent accounts. Zeitschrift für Zoologisches Systematisches Evolutionforschungen. 13:1–44.

KUKALOVÁ, J. 1969. On the systematic position of the supposed Permian beetles, Tshecardocoleidae, with a description of a new collection from Moravia. Sbornik Geologickych Ved, Paleontology 11: 139-162.

KUKALOVÁ-PECK, J. AND LAWRENCE, J. F. 1993. Evolution of the hind wing in Coleoptera. The Canadian Entomologist 125(2): 181-258

KUKALOVA-PECK, J. 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. European Journal of Entomology 101: 95 144.

LAWRENCE, J.F. 1982. Coleoptera. Pp. 482-553, *in*: Parker, S.P. (Ed.). Synopsis and Classification of Living Organisms. McGraw-Hill: New York, New York; 1119 pp.

LAWRENCE, J.F. AND NEWTON, A. F. 1992. Evolution and Classification of Beetles. Annual Review of Ecology and Systematics 13: 261-290

LAWRENCE J.F. AND NEWTON A.F. 1995 Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names) II. Pp. 779-1006, *in* J. Pakaluk and S.A. Ślipiński (eds.), Biology, Phylogeny and Classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson. Museum I Instytut Zoologii PAN, Warsaw, Poland; xii + 1006 pp.

LECONTE, J. L. 1847. On the Cupesidae of North America: Transactions of the American Entomological Society 5: 87-88.

LINDROTH, C.H. 1948. Interglacial insect remains from Sweden. Arbosk Sveriges Geologiska Undersoekning Series C 42: 1-29.

LUBKIN, S.H. 2003. *Paracupes svitkoi* (Coleoptera: Archostemata: Cupedidae: Cupedini), a new species from the Cretaceous of New Jersey. Acta Zoologica Cracoviensia, 46 (suppl. – Fossil Insects): 189-194.

LUBKIN, S.H. AND ENGEL, M. 2005. *Permocoleus*, new genus, the first Permian Beetle (Coleoptera) from North America. Annals of the Entomological Society of America 98: 73-77.

MARTYNOV, A.V. 1932. Permian fossil insects from the Arkhangelsk District. Transactions of the Paleontologicheskogo Institut Akademii Nauk SSSR 2: 83-96.

MARTYNOV, A.V. 1933. Permskie iskopaemye nasekomye arkhangel’skogo kraya. Chast’ II. Setchatokrylye, vislokrylye i zhuki, s prilozheniem opisaniya dvukh novykh zhukov iz tikhikh gor [Permian fossil insects from the Arkhangelsk District. Part II. Neuroptera, Megaloptera, and Coleoptera, with descriptions of two new beetles from Tikhie Gory]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 2: 63-69.

MARTYNOV, A.V. 1937. Permian fossil insects from Kargala and their relationships. Transactions of the Paleontologicheskogo Institut Akademii Nauk SSSR 7: 1-92.

MARTYNOV, A.V. 1938. Ocherki geologicheskoj istorii I filogenii otryadov nasekomykh (Pterygota). 1. Paleoptera I Neoptera-Polyneoptera [Essays on the geologic history and phylogeny of insect orders. 1. Paleoptera and Neoptera-Polyneoptera]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 7: 1-150.

MATTHEWS, J.V., Jr. 1979. Late Tertiary Carabid fossils from Alaska and the Canadian Arctic Archipelago. Pp. 425-445, *in* T. L. Erwin, G. E. Ball, D. R. Whitehead and A. L. Halpern (eds.), Carabid Beetles: Their Evolution, Natural History, and Classification. Dr. W. Junk, The Hague, The Netherlands; 646 pp.

MAYR, E. 1982. The growth of biological thought. Belknap Press of Harvard University Press, Cambridge, Massachusetts; 974pp.

MICKOLEIT, G. 1973. Zur Anatomie und Funktion des Raphidiopteren-Ovipositors (Insecta, Neuropteroidea). Zeitschrift fur Morphologie der Tiere 76: 145-171.

NEBOISS, A. 1984. Reclassification of *Cupes* Fabricius (s. lat), with descriptions of new genera and species (Cupedidae: Coleoptera). Systematic Entomology 9: 433-477.

NEWMAN, E. 1839. Supplementary notes on the synonymy of *Passandra.* Annals and Magazine of Natural History 3: 303-304.

NIXON, K. C. 1999-2002. WinClada version 1.0000 Published by the author, Ithaca, NY.

PINTO, I.D. 1987. Permian Insects from Paraná Basin, South Brazil IV Coleoptera. Pesquisas 19: 5-12.

PONOMARENKO, A. G. 1963. Paleozojskie zhuki Cupedidea evroplskoj [Paleozoic Cupedid beetles from the European part of the USSR]. Paleontologichskij Zhurnal 1963(1): 70-85.

PONOMARENKO, A.G. 1966. Zhuki semeystva Cupedidae iz nizhnego triasa Sredney Azii [Beetles of the family Cupedidae from the lower Triassic of Central Asia]. Paleontologichskij Zhurnal 1966(4): 47-68.

PONOMARENKO, A.G. 1969A. Cretaceous insects from Labrador. 4. A new family of beetles (Coleoptera: Archostemata). Psyche 76: 306-310.

PONOMARENKO, A.G. 1969B. Istoricheskoe razvitie zhestkokrylykh-arkhostemat [Historical development of the Coleoptera-Archostemata]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 125: 1-240.

PONOMARENKO, A.G. 1977. Mezozoiskiye zhestkokrylyye [Mesozoic Coleoptera]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 161: 1-204.

PONOMARENKO, A.G. 1994. New Mesozoic cupedid beetles from Mongolia; Brochocoleini and Notocupedini. Paleontological Journal 28: 102-155.

PONOMARENKO, A.G. 1995. The geological history of beetles. Pp. 155-17, *in* J. Pakaluk and S.A. Ślipiński (eds.), Biology, Phylogeny and Classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson. Museum I Instytut Zoologii PAN, Warsaw, Poland; xii + 558 pp.

PONOMARENKO, A.G. 2000. New beetles from the Permian of European Russia. Paleontological Journal Supplement. 34: 312-316.

PONOMARENKO, A.G. 2002. Superorder Scarabaeidea Laicharting, 1781. Order Coleoptera Linné, 1758. The Beetles. Pp. 164-176, *in* A.P. Rasnitsyn and D.L.J. Quicke (eds.), History of insects. Kluwer Academic Publishers, Dordrecht, the Netherlands; xii+517 pp.

PONOMARENKO, A.G. 2003. Ecological evolution of beetles (Insecta: Coleoptera). Acta Zoologica Cracoveinsia 46 (Supplement): 319-32.

ROHDENDORF, B. B. 1944. A new family of Coleoptera from the Permian of the Urals. Comptes rendus (Doklady) de l' Akademie des sciences de l'URSS. 44: 252-253.

ROHDENDORF, B. B. 1956. Paleozojskie nasekomye Yuzhnoj Sibiri [Paleozoic insects from southern Siberia]. Entomologicheskogo Obozrenie 35: 111-119.

ROHDENDORF, B. B. 1961. Nadotrayad Coleopteroidea. Zhestkokryloobraznye [Superorder Coleoptera]. Pp. 393-469, *in* B.B. Rohdendorf, E. Eh. Becker-Migdisova, O.M. Martynova, and A.G. sharov, Paleozoiske nasekomye kuznetkogo basseina [Paleozoic insects of the Kuznetsk basin]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 85.

SHCHERBAKOV, D.E. AND YU, A. 2002. Superorder Cimicidea Laichartring, 1781. The bugs, cicadas, plant lice, scale insects, etc. (=Cimicida Laichartring, 1781, =Homoptera Leach, 1815 + Heteroptera Latreille, 1810). Pp.143-156, *in* A.P. Rasnitsyn and D.L.J. Quicke (eds.), History of insects. Kluwer Academic Publishers, Dordrecht, the Netherlands; xii+517 pp.

SINITSHENKOVA, N.D., 2002. Superorder Dictyoneuridea Handlirsch, 1906 (= Palaeodictyopteroidea). Pp. 115-124, *in* A.P. Rasnitsyn and D.L.J. Quicke (eds.), History of insects. Kluwer Academic Publishers, Dordrecht, the Netherlands; xii+517 pp.

TILLYARD, R.J. 1924. Upper Permian Coleoptera and a new order from the Belmont Beds, New South Wales. Proceedings of the Linnean Society of New South Wales 49: 492-435.

TILLYARD, R.J. 1932. Kansas Permian Insects. Part 14: The order Neuroptera. American Journal of Science 23: 1-30.

WALLACE, F.L. AND FOX, R.C. 1975. A comparative morphological study of the hind wing venation of the order Coleoptera, Part I. Proceedings of the Entomological Society of Washington 77(3): 329-354.

WALLACE, F.L. AND FOX, R.C. 1980. A comparative morphological study of the hind wing venation of the order Coleoptera, Part II. Proceedings of the Entomological Society of Washington 82(4): 609-654.

WARD, R. D. 1979. Metathoracic wing structures as phylogenetic indicators in the Adephaga (Coleoptera). Pp. 181–191, *in* T. L. Erwin, G. E. Ball, D. R. Whitehead and A. L. Halpern (eds.), Carabid Beetles: Their Evolution, Natural History, and Classification. Dr. W. Junk, The Hague, The Netherlands; 646 pp.

WIENS, J.J. 1988. Phylogenetic analysis of morphological data. Smithsonian Institution Press, Washington D.C.; 220 pp.

WESTWOOD, J. O. 1835. Insectorum arachnoidumque novorum dacades duo. Zoological Journal 5: 440-453.

WHITING, M.F. AND KATHIRITHAMBY, J, 1996. Strepsiptera do not share hind wing venational synapomorphies with Coleoptera: a reply to Kukalova-Peck and Lawrence. Journal of the New York Entomological Society 103: 1-14.

WHITING, M.F., CARPENTER, J.C., WHEELER, Q.D., AND WHEELER, W.C. 1997. The strepsiptera problem: Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. Systematic Biology 46: 1-68.

CHAPTER 2

KEY FOR THE IDENTIFICATION OF PERMIAN AND MESOZOIC COLEOPTERA BASED ON CLADISTIC ANALYSIS OF WING VENATION

Abstract

Because, fossil beetles are most commonly known only from elytral remains, a key to Paleozoic and Mesozoic elytra resembling Archostemata is constructed using only elytral characters to aid in the identification of fossil beetles.

UNLIKE THE ELYTRA of most modern Coleoptera, which at most possess only traces of wing venation, Permian and Early Mesozoic elytra have conspicuous and sometimes elaborate venation, which can be and is used for both identification and classification (LUBKIN 2005; MARTYNOV 1932, 1933; KUKALOVÁ 1969; PONOMARENKO 1963, 1969A, 1969B, 1994; ROHDENDORF 1944, 1961). But, the use of several different systems of vein nomenclature has made deciphering these classifications difficult and can complicate the identification of fossil elytra.

In addition, descriptions of fossil elytra are often vague or contradictory as illustrated by these examples from the Treatise on Invertebrate Paleontology (CARPENTER 1992):

> *Tshekardocoleus* ROHDENDORF 1944.
>
> > *“Elytron with M and CuA without a common stem, or at most with a short stem…..”*
>
> *Kaltanocoleus* ROHDENDORF 1961
>
> > *“Little known genus, similar to Kaltanicupes.”*

Perhaps, more complete descriptions can be obtained from the primary literature; however, these descriptions are often in Chinese or in Russian, and can be difficult to obtain, even from excellent libraries such as those at Cornell University and at the Smithsonian Institution. When describing a new species, it is difficult to determine out affiliations without a thorough cladistic analysis (see Chapter 1), however this is time consuming. These difficulties have contributed to the misidentification and misclassification of fossil Coleoptera. Hence, an easy to understand key is a useful starting point for the identification of fossil Coleoptera.

As most fossil Coleoptera are known only from fossil elytra, the key is constructed using only elytral characters, primarily elytral venation. Veins are named using the modified Comstock-Needham nomenclature (COMSTOCK AND NEEDHAM 1898A, 1898B): Costa (C), Subcosta (Sc), Radius (R), Radial sector ($Rs_{1\text{-}4}$), Media (M), Media posterior (MP), Anterior cubitus (CuA), Posterior cubitus (CuP), and Anal veins (A_1, A_2, A_3).

Not every fossil elytron is included in the key. Because morphological information was obtained using illustrations from the primary literature rather than from actual specimens, the main criterion for inclusion in the key was a clear illustration of at least one complete or near complete elytron. However, the key is a practical starting point for the identification of any fossil elytron with venation.

Taxa included:

1. *Afrocupes firmae* GEERSTEMA AND VAN DER HEEVER 1996 (Permian, South Africa)
2. *Archicupes jacobsoni* ROHDENDORF 1961 (lower Permian, Russia)
3. *Asiocoleus novojilovi* ROHDENDORF 1961 (lower Permian, Russia)

4. *Boscoleus blandus* KUKALOVÁ 1969 (lower Permian, Czech Republic)

5. *Brochocoleus alatus* PONOMARENKO 1994 (lower Cretaceous, Mongolia)

6. *Brochocoleus punctatus* HONG 1982 (upper Jurassic, China)

7. *Cytocupes angustus* ROHDENDORF 1961 (upper Permian, Russia)

8. *Eocoleus scaber* KUKALOVÁ 1969 (lower Permian, Czech Republic)

9. *Forticupes laiyangensis* HONG 1990 (lower Cretaceous, China)

10. *Kaltanicupes acutus* PONOMARENKO 1963 (middle Permian, Russia)

11. *Kaltanicupes kitjakensis* PONOMARENKO 1963 (middle Permian, Russia)

12. *Kaltanicupes major* PONOMARENKO 1963 (middle Permian, Russia)

13. *Kaltanicupes ponomarenkoi* PINTO 1987 (upper Permian, Brazil)

14. *Kaltanocoleus pospelovi* ROHDENDORF 1961 (lower Permian, Russia)

15. *Labradorocoleus carpenteri* PONOMARENKO 1969A (Cretaceous, Labrador)

16. *Liberocoleus intactus* KUKALOVÁ 1969 (lower Permian, Czech Republic)

17. *Longxianocupes tristichus* HONG, ET AL. 1985 (lower Cretaceous, China)

18. *Magnocoleus huangjiapuensis* HONG 1998 (lower Cretaceous, China)

19. *Moravocoleus fractus* KUKALOVÁ 1969 (lower Permian, Czech Republic)

20. *Moravocoleus neglegens* KUKALOVÁ 1969 (lower Permian, Czech Republic)

21. *Moravocoleus perditus* KUKALOVÁ 1969 (lower Permian, Czech Republic)

22. *Moravocoleus permianus* KUKALOVÁ 1969 (lower Permian, Czech Republic)

23. *Notocupes brachycephalus* PONOMARENKO 1994 (Jurassic, Mongolia)

24. *Notocupes elegans* PONOMARENKO 1994 (lower Cretaceous, Mongolia)

25. *Notocupes mongolicus* PONOMARENKO 1994 (lower Cretaceous, Mongolia)

26. *Notocupes sp.* PONOMARENKO 1966 (lower Cretaceous, Russia)

27. *Oborocoleus rohdendorfi* KUKALOVÁ 1969 (lower Permian, Czech Republic)

28. *Permocoleus wellingtonensis* LUBKIN AND ENGEL 2005 (lower Permian, United States)

29. *Permocupes distinctus* MARTYNOV 1933 (Permian, Russia)

30. *Permocupes semenovi* MARTYNOV 1933 (Permian, Russia)

31. *Permocupoides skoki* ROHDENDORF 1956 (lower Permian, Russia)

32. *Prosperocoleus prosperus* KUKALOVÁ 1969 (lower Permian, Czech Republic)

33. *Sogdelytron latum* PONOMARENKO 1969B (Triassic, Asia)

34. *Sojanocoleus reticulatus* MARTYNOV 1932 (Permian, Russia)

35. *Sylvacoleus richteri* PONOMARENKO 1963 (lower Permian, Russia)

36. *Synodus changmaensis* HONG 1982 (Jurassic, China)

37. *Tomiocupes carinatus* ROHDENDORF 1961 (upper Permian, Russia)

38. *Triassocupes yaochaensis* HONG, ET AL. 1985 (Triassic, China)

39. *Tricoleodes acutus* PONOMARENKO 1969B (Triassic, Asia)

40. *Tricoleus punctatus* PONOMARENKO 1969B (Jurassic, Kazakhstan)

41. *Tricupes acer* ROHDENDORF 1961 (upper Permian, Russia)

42. *Tshekardocoleus magnus* ROHDENDORF 1944 (lower Permian, Russia)

43. *Tshekardocoleus minor* PONOMARENKO 1963 (lower Permian, Russia)

44. *Tychticupes radtschenkoi* ROHDENDORF 1961 (upper Permian, Russia)

45. *Umoricoleus perplex* KUKALOVÁ 1969 (lower Permian, Czech Republic)

46. *Votocoleus submissus* KUKALOVÁ 1969 (lower Permian, Czech Republic)

47. Family Cupedidae (extant and fossil)

48. Family Ommatidae (extant and fossil)

Key to fossil elytra:

1a. Elytra with veins C, SC, R, Rs, M,
CuA, CuP, A_1 and A_2 present ……………….……….…………………..….2

1b. Elytra with any of veins C, SC, R, Rs, M,
CuA, CuP, A_1 and A_2 not present ……………...……………...……..…12

2a. Sc with divided stem …………..…………..………*Brochocoleus punctatus*

2b. Sc without divided stem …..……..……………….……………………...3

3a. Elytron with 11 approximately parallel veins
that converge near tip ……..…..…………..……...*Synodus changmaensis*

3b. Elytron with fewer than 12 veins. Not all veins parallel.…..........……….4

4a. Single Rs present..……………………………………………………..………6

4b. Two Rs veins present …………………TSHKARDOCOLEIDAE (in part)..5

5a. R merges with Sc; M and CuA merge,
M and CuP merge, M and A_1 merge,
Rs_1 and Rs_2 attached at base ……..............................*Afrocupes firmae*

5b. R and Sc do not merge; Veins M, CuA,
CuP,A_1 approximately parallel,
Rs_1 and Rs_2 arise from R..…………………...…..*Tshekardocoleus minor*

6a. M and CuA do not share a stem, but briefly touch
approximately ¼ distance from base...................*Votocoleus submissus*

6b. M and CuA share a stem.………………………..……… ………………….7

7a. M and CuA merge ……………….……………….....MORAVOCOLEIDAE..8

7b. M and CuA do not merge ………..…………………………….……………11

8a. Rs and CuA merge ………………………..……………………….…………9

8b. Rs and CuA do not merge.………...……………....*Moravocoleus permianus*

9a. MP branching present ……………..……..…….*Prosperocoleus prosperus*

9b. MP branch absent..………….………………………………..……………10

10a. CuP terminates before reaching A_1……….……..……..*Moravocoleus fractus*

10b. CuP short, terminates on A1..……………..……..….*Moravocoleus perditus*

11a. CuP terminates on anal edge …………………………..*Eocoleus scaber*

11b. CuP short, does not

terminate on anal edge …………………....*Permocoleus wellingtonensis*

12a. Vein M absent ………….…………………………………………………….13

12b. Vein M present …….…………….…………..…………………………………14

13a. Sc present; Rs absent ………...…...……….……*Moravocoleus neglegens*

13b. Sc absent; Rs present,

Rs merges with R..……………………………....………*Cytocupes angustus*

14a. Short cross-vein present between M and CuA ……………..……………15

14b. Short cross-vein not present between M and CuA..…………………..…17

15a. Sc present ……………….…………………….*Triassocupes yaochaensis*

15b. Sc absent ……………………..……………………………………………16

16a. Rs present, R merges with M ………………….………*Sogdelytron latum*

16b. Rs present, R does not merge with M …..……*Longxianocupes tristichus*

17a. Sc present ...……..…………………………………………………………18

17b. Sc absent ……………………..…………………………………………….40

18a. Rs absent ……………....………………………………….….…………..19

18b. Rs present.……..…………………………………………………….. ...31

19a. A_1 present..……………………....…………….……….…….…….……24

19b. A_1 absent………………………………………………………..………..…20

20a. M and CuA merge, CuP present.…………………………...………………..21

20b. M and CuA parallel and do not merge; CuP present,

but may be quite short ………………………… modern Archostemata..23

21a. CuP present ……………………………………………………………..22

21b. CuP absent ….…………………………………………..*Permocupes distinctus*

22a. M curves like Sc and R; M terminates on CuP

CuA and CuP intersect with R ….……………...……*Brochocoleus alatus*

22b. M curves and merges with CuP, CuA and CuP

do not intersect with R ……………………*Magnocoleus huangjiapuensis*

23a. Sc and R merge near tip.……………..…..…………….………..Ommatidae

23b. Sc and R do not merge.………..……………………………………Cupedidae

24a. M and CuA share stem.……….…………………………………...….25

24b. M and CuA do not share a stem …………..………………*Kaltanicupes*..28

25a. R present …….………………………………………SYLVACOLEIDAE…24

25b. R absent ..…………………………………………………*Archicupes jacobsoni*

26a CuP present …...………………………………………………………27

26b. CuP absent ….………………………………………………*Boscoleus blandus*

27a. CuP full length, reaches edge of elytron......……….....*Sylvacoleus richteri*

27b. CuP short ……………………………………..………*Umoricoleus perplex*

28a. Sc short, R does not merge with Sc ……………………………………..29

28b. Sc long, R merges with Sc ……..…...……………………………………..30

29a. CuP absent, Sc terminates on C …………..….……*Kaltanicupes acutus*

29b. CuP very short, Sc briefly merges

with C about 1/8 distance from base ………*Kaltanicupes ponomarenkoi*

30a. CuP very short …………………………................……*Kaltanicupes major*

30b. CuP absent..……………………………..……….*Kaltanicupes kitjakensis*

31a. One Rs branch present..…………………………………………………..32

31b. Two Rs branches present...………………….………*Oborocoleus rohdendorfi*

32a. Rs branches from R ……..…………………………………….…………33

32b. Rs separate from R …..…………………………………….……….….36

33a. CuP present, C, Sc, Rs,

M, CuA approximately parallel ………...……*Tychticupes radtschenkoi*

33b. CuP absent, C, Sc, Rs, M,

CuA not parallel ………………………………………………..…………34

34a. M and CuA do not share stem...……………………………………….35

34b. M and CuA share stem ……………………………*Kaltanocoleus pospelovi*

35a. Rs branches in lower half or R;

M and CuA merge …………………………………..…*Liberocoleus intactus*

35b. Rs branches in upper half of R;

M and CuA do not merge ……….…………........*Sojanocoleus reticulatus*

36a. R and Rs merge ...………………...…………………………………37

36b. R and Rs do not merge ...…………………………………..……38

37a. M and CuA merge,

CuP absent ………...….*Notocupes brachycephalus, Notocupes elegans*

37b. M and CuA do not merge,

CuP present ………………….………………*Labradorocoleus carpenteri*

38a. CuP absent ……………….…………………………………………..39

38b. CuP present ……..……………………………………………*Notocupes sp.*

39a. Sc merges with C at edge of elytron;

M and CuA merge ……………………….……..…*Permocupes semenovi*

39b. Sc and C do not merge, M and CuA merge ………..*Notocupes mongolicus*

40a. Rs present ….....…..……………………………………….………….……….41

40b. Rs absent..…………………………………………………….…………….…44

41a. R with 2 Rs branches.……………..………………..*Forticupes laiyangensis*

41b. R with 1 Rs branch ……………………..……………………………….42

42a. R present, CuA present ……..…………………………………………43

42b. R absent; CuA absent …...………………………..………...…...….*Tricupes acer*

43a. R and Rs share stem, M and CuA merge.

A$_1$ present ……….………………….……...........*Tshekardocoleus magnus*

43b. R and Rs do not share stem, M and CuA do not merge,

A$_1$ absent ………………………….……….............*Tomiocupes carinatus*

44a. CuP long, does not form X-shape with

M and CuA ……………………..……………………..……………….……45

44b. CuP short, does not reach edge or tip,

does not merge with another vein;   M, CuA

and A$_2$ merge in center of M to form X-shape ...….*Asiocoleus novojilovi*

45a. A$_1$ present ………………...…………………………....*Permocupoides skoki*

45b. A$_1$ absent ……………………...…………………..………………………46

46a. R and M merge with CuA……….………………….…..….*Tricoleodes acutus*

46b. R and M and CuA approximately parallel

and reach edge or tip ………………………………..*Tricoleus punctatus*

REFERENCES

CARPENTER, F.M. 1992. Superclass Hexapoda. Pp. 1-655, *in* Kaesler, R.L. (Ed.) Treatise on Invertebrate Paleontology, Part R, Arthropoda 3-4. Geological Society of America; Boulder, Colorado; xxii + 655 pp.

COMSTOCK, J.H., AND NEEDHAM, J.G. 1898A. The wings of insects. Chapter 1. An introduction to the study of the homologies of the wing-veins. The American Naturalist 32: 43-48.

COMSTOCK, J.H., AND NEEDHAM, J.G. 1898B. The wings of insects. Chapter 2. The venation of the typical insect wing. The American Naturalist 32: 81-89.

GEERTSEMA, H. AND VAN DER HEEVER, J.A. 1996. A new beetle, *Afrocupes firmae* gen. et sp. nov. (Permocupedidae) from the Late Paleozoic Whitehill Formation of South Africa. South African Journal of Science 92: 497-499.

HONG Y.-C., LIU, Z. AND LUI, S. 1985. Discovery and studying of the Triassic fauna and flora of the Niangniangmiao in Longxian, Shaanxi. Bulletin of the Xi'an Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences 10: 105-120.

HONG, Y-C. 1990. Fossil insects from the Laiyang Basin, Shandong Province. Pp. 44-189, *in* Regional Surveying Team, Shandong Bureau of Geology and Mineral Resources (Eds.), The stratigraphy and palaeontology of Laiyang Basin, Shandong Province; 189pp.

HONG, Y-C. 1998. Magnocoleidae fam. nov. (Insecta: Coleoptera). Geoscience (China) 12: 40-48.

KUKALOVÁ, J. 1969. On the systematic position of the supposed Permian beetles, Tshecardocoleidae, with a description of a new collection from Moravia. Sbornik Geologickych Ved, Paleontology 11: 139-162.

LUBKIN, S.H. AND ENGEL, M. 2005. *Permocoleus*, new genus, the first Permian Beetle (Coleoptera) from North America. Annals of the Entomological Society of America 98: 73-77.

MARTYNOV, A.V. 1932. Permian fossil insects from the Arkhangelsk District. Transactions of the Paleontologicheskogo Institut Akademii Nauk SSSR 2: 83-96.

MARTYNOV, A.V. 1933. Permskie iskopaemye nasekomye arkhangel’skogo kraya. Chast’ II. Setchatokrylye, vislokrylye i zhuki, s prilozheniem opisaniya dvukh novykh zhukov iz tikhikh gor [Permian fossil insects from the Arkhangelsk District. Part II. Neuroptera, Megaloptera, and Coleoptera, with descriptions of two new beetles from Tikhie Gory]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 2: 63-69.

PINTO, I.D. 1987. Permian Insects from Paraná Basin, South Brazil IV Coleoptera. Pesquisas 19: 5-12.

PONOMARENKO, A. G. 1963. Paleozojskie zhuki Cupedidea evroplskoj [Paleozoic Cupedid beetles from the European part of the USSR]. Paleontologichskij Zhurnal 1963(1): 70-85.

PONOMARENKO, A.G. 1966. Zhuki semeystva Cupedidae iz nizhnego triasa Sredney Azii [Beetles of the family Cupedidae from the lower Triassic of Central Asia]. Paleontologichskij Zhurnal 1966(4): 47-68.

PONOMARENKO, A.G. 1969A. Cretaceous insects from Labrador. 4. A new family of beetles (Coleoptera: Archostemata). Psyche 76: 306-310.

PONOMARENKO, A.G. 1969B. Istoricheskoe razvitie zhestkokrylykh-arkhostemat [Historical development of the Coleoptera-Archostemata]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 125: 1-240.

PONOMARENKO, A.G. 1994. New Mesozoic Cupedid beetles from Mongolia; Brochocoleini and Notocupedini. Paleontological Journal 28: 102-155.

ROHDENDORF, B. B. 1944. A new family of Coleoptera from the Permian of the Urals. Comptes rendus (Doklady) de l’ Akademie des sciences de l’URSS. 44: 252-253.

ROHDENDORF, B. B. 1956. Paleozojskie nasekomye Yuzhnoj Sibiri [Paleozoic insects from southern Siberia]. Entomologicheskogo Obozrenie 35: 111-119.

ROHDENDORF, B. B. 1961. Nadotrayad Coleopteroidea. Zhestkokryloobraznye [Superorder Coleoptera]. Pp. 393-469, *in* B.B. Rohdendorf, E. Eh. Becker-Migdisova, O.M. Martynova, and A.G. sharov, Paleozoiske nasekomye kuznetkogo basseina [Paleozoic insects of the Kuznetsk basin]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 85.

[*]CHAPTER 3

PERMOCOLEUS, NEW GENUS, THE FIRST PERMIAN BEETLE (COLEOPTERA) FROM NORTH AMERICA

Abstract

Permocoleus wellingtonensis, new genus and new species, is based on an elytron from the Permian Wellington Formation of Oklahoma, and is the only Paleozoic record of the order Coleoptera from North America and the oldest record for the New World. Until now, Permian Coleoptera were known only from Europe, Australia, Southern Africa and South America, but were conspicuously absent from North America, despite the Wellington Formation being among the most diverse deposits of Permian insects. *Permocoleus* provides evidence that early beetles were globally distributed.

THE ORDER COLEOPTERA is not just the largest group of insects, but with over 360,000 described species of modern beetles (ERWIN 1991; LIEBHERR, ET AL.. 2003), it is also the most diverse order of animals, with representatives in almost every plausible non-marine habitat. Coleoptera is extremely rare in Paleozoic insect deposits (PONOMARENKO 2000). The oldest known fossil beetles were described from Early Permian (Lower Artinskian, ca. 268 MA) deposits in Obora, Czech Republic (KUKALOVÁ 1969) and slightly younger deposits of Tshekarda, Russia (ROHDENDORF 1944; PONOMARENKO 1963). These belong to the family Tshekardocoleidae and

---

[*] LUBKIN, S.H. AND M. ENGEL 2005. "*Permocoleus*, new genus, the first Permian Beetle (Coleoptera) from North America." Annals of the Entomological Society of America 98: 73-77.

are considered true beetles based on their mesothoracic structure (KUKALOVÁ 1969). Elytra representing the family Oborocoleidae are also recorded from Obora, but because no other structures are preserved, the oborocoleids cannot be conclusively identified as beetles, although such a placement seems likely.

Late Permian beetles are classified in the families Permocupedidae, Asiocoleidae, Rhombocoleidae and Schizocoleidae, and these are known from South America (PINTO 1987), southern Africa (GEERTSEMA AND VAN DER HEEVER 1996), Australia (TILLYARD 1924), and eastern Europe (KUKALOVÁ 1969; MARTYNOV 1932, 1937; PONOMARENKO 1963, 2000, 2003; ROHDENDORF 1944, 1961). This distribution of early fossil Coleoptera has been anomalous. The Early Permian deposits of Elmo, Kansas and Midco, Oklahoma are among the most prolific of all Permian deposits for insects (CARPENTER 1992; GRIMALDI AND ENGEL 2005; RASNITSYN AND QUICKE 2002), but Paleozoic beetles were absent from North America. The oldest previously known North American Coleoptera are those from the Late Triassic (Carnian, ca. 230 MA) of the eastern United States (FRASER, ET AL.1996).

Herein, a single elytron from the Wellington Formation of Noble County, Oklahoma is described and figured. The specimen is the earliest occurrence of Coleoptera in the Western Hemisphere and is the only Permian beetle known from North America.

Geology/Stratigraphy

The Wellington Formation (CRAGIN 1896) is of Artinskian age (269-260 MA), and extends from south-central Kansas to northern Okalahoma. The formation is well known for a rich fossil insect fauna that was extensively described by the late F.M. Carpenter mostly from the Elmo deposits in Kansas, but also from the Midco locality in Oklahoma (e.g., CARPENTER 1947, 1979). The evenly bedded shales and dolomites, and the gray to green lenticular sandstones of the Wellington Formation in Oklahoma have been interpreted as a saline tidal flat environment with interdispersed channels, lakes and ponds (OLSON 1970; SCHULTZE 1985; SHELTON 1979). Although in general the shales and sandstones of the Wellington Formation are not fossiliferous (RAASCH 1946), a remarkable assemblage of fossil insects is present (CARPENTER 1947, 1979; TASCH, 1961; TASCH AND ZIMMERMAN 1959, 1962).

Systematic Paleontology

Order COLEOPTERA LINNAEUS, 1758

Permocoleus, **n. gen.**

***Diagnosis*.** Elytron long and narrow with rows of semi-quadrate cells between veins. Five major veins (C, Sc, Rs, M and CuA) distinguishable and roughly parallel to elytral margins. Vein Rs branches posteriorly. Two rows of cells are present between veins C and Rs, between branches of vein Rs, and between veins M and CuA. Two complete rows and one partial row of cells are present between veins Rs and M. Cell rows coalesce between Rs-M and M-CuA into a single row near wing apex. Vein A_1 present. One vein meets C near apex.

Permocoleus differs from members of Permocupedidae primarily in that in the former vein Rs is present and branches, while in Permocupedidae vein

Rs is absent. *Permocoleus* differs from Tshekardocoleidae and Oborocoleidae in that the venation is not as complete and Rs is the only radial vein present. Body is unknown.

Stratigraphical and geographic distribution: Lower Permian (Artinskian) of Oklahoma, United States.

Type species**.** *Permocoleus wellingtonensis* n. sp.

Permocoleus wellingtonensis Lubkin & Engel, **new species**

Figures 3.1 – 3.2

Diagnosis**.** As for the genus with the following additions: Total length as preserved 4.5 mm; maximal width as preserved 1.15 mm (length/width ratio of elytron approximately 4.0). Small elytron with vein 1A incomplete. Several partial rows of cells present on distal edge of elytron. Veins M and CuA almost touching at posterior end.

Type Material*.* HOLOTYPE: MCZ 31136, single elytron from Oklahoma: Noble County: Section 23 (TASCH NOBLE V; TASCH 1961). Wellington Formation, Lower Permian (Lower Artinskian, 269-260 MA). The specimen resided among unsorted Permian material in Harvard's Museum of Comparative Zoology for over 30 years. Carpenter never referred to the specimen, and it is labeled "Coleoptera?" indicating a one-time uncertainty about its identity.

Etymology*.* The generic name refers to the Permian age of the specimen, whereas the specific epithet is for the Wellington Formation.

Figure 3.1. Photograph of holotype of *Permocoleus wellingtonensis*, n. gen. *et* n. sp. Elytron length is 4.5 mm.

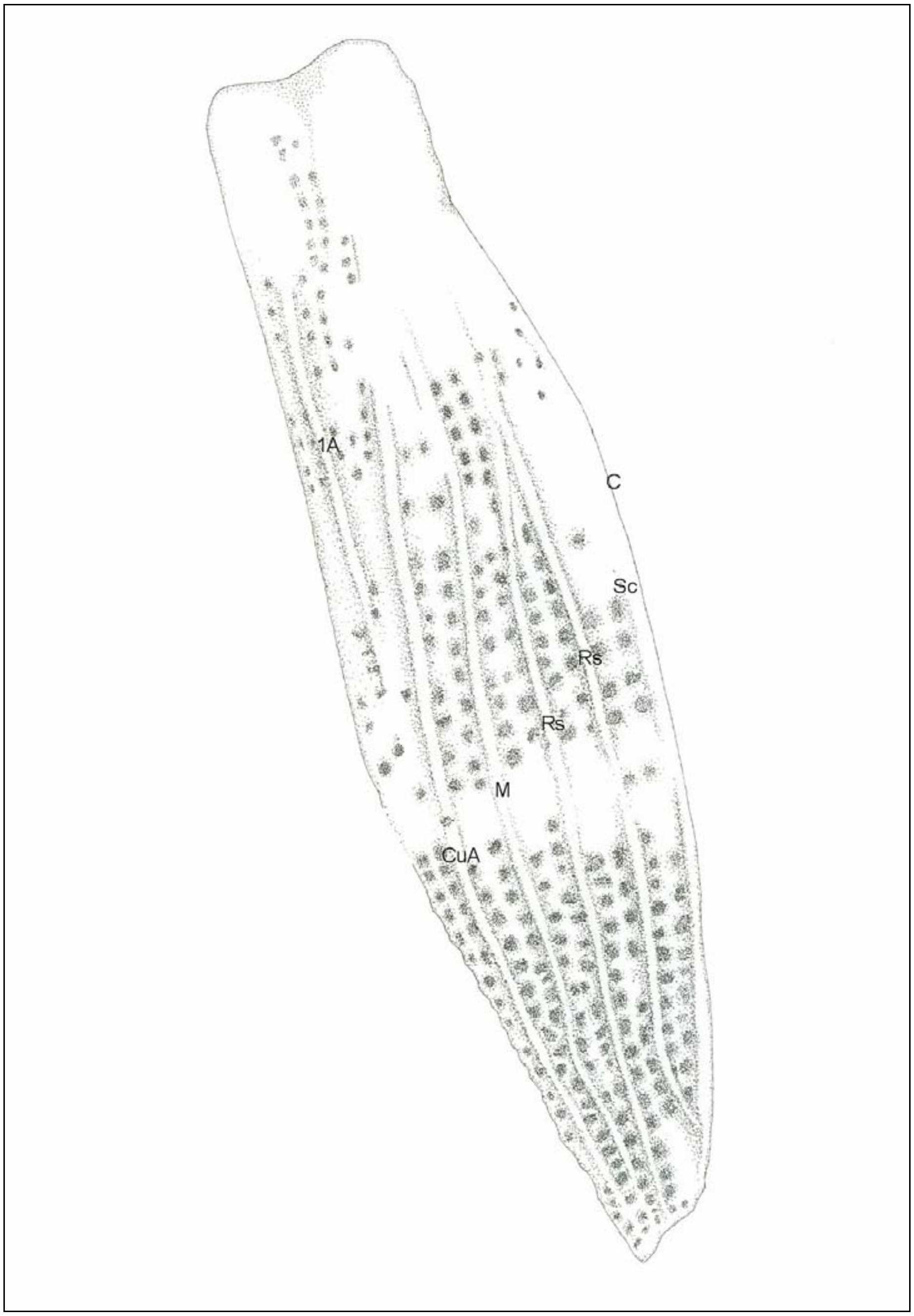


Figure 3.2. Line illustration of holotype of *Permocoleus wellingtonensis,* n. gen. *et* n. sp.

Discussion

The specimen is more similar to the elytra of later Permian Coleoptera than it is to the more elaborate elytra of the coleopteroids from Obora; therefore, it is tentatively placed in Coleoptera proper. Of the Permian Coleoptera, this species most resembles members of Permocupedidae, especially the South American species *Kaltanicupes ponomarenkoi* (PINTO 1987). However, the unique pattern of venation distinguishes this specimen from Permocupedidae and all other known Permian beetle families. Given that the specimen is among the oldest of the Coleoptera, it is perhaps surprising that it appears to more closely resemble the reduced venation of typical beetles rather than the elaborate venation of Protocoleoptera. Given the incompleteness of the material at hand, it is impossible to place the specimen definitively and, therefore, to draw conclusions concerning vein evolution. Hopefully, continued exploration of the Paleozoic of North America will reveal more completely preserved specimens and a greater diversity of early beetles and beetle-like relatives. Despite the incomplete preservation, however, *Permocoleus wellingtonensis* represents an important geological and biogeographical record for understanding early beetle evolution and provides us with a small glimpse into the beginnings of Nature's “inordinate fondness.”

ACKNOWLEDGEMENTS

The authors express their appreciation to David A. Grimaldi of the American Museum of Natural History for comments and for support of this study; to Tam C. Nguyen, also of the American Museum of Natural History for assistance with photography; and to Phil Perkins of Harvard's Museum of Comparative Zoology for arranging the loan. Partial support was provided by a graduate research fellowship from the National Science Foundation to SHL, and by a Kansas Technology Corporation-NSF EPSCoR grant (KAN29503) and NSF EF-0341724 to MSE. This is contribution #3396 of the Division of Entomology, Natural History Museum and Biodiversity Research Center, University of Kansas.

REFERENCES

CARPENTER, F.M. 1947. Lower Permian insects from Oklahoma, Part I. Introductions and the Orders of Mecoptera, Protodonata and Odonata. Proceedings of the American Academy of Arts and Sciences 76: 25-53.

CARPENTER, F.M. 1979. Lower Permian insects from Oklahoma, Part II. Orders Ephemeroptera and Palaeodictyoptera. Psyche 86: 261-290.

CARPENTER, F.M. 1992. Superclass Hexapoda. Pp. 1-655, *in* Kaesler, R.L. (Ed.) Treatise on Invertebrate Paleontology, Part R, Arthropoda 3-4. Geological Society of America; Boulder, Colorado; xxii + 655 pp.

CRAGIN, F.W. 1896. The Permian system in Kansas. Colorado College Studies 6: 1-48.

CROWSON, R.A. 1975. The evolutionary history of beetles as documented by fossil and comparative evidence. Atti del Congresso Nazionale Italiano de Entomologia 10: 47-90.

ERWIN, T.L. 1991. How many species are there?: Revisited. Conservation Biology 5: 330-333.

FRASER, N.C., D.A. GRIMALDI, AND P.E. OLSEN. 1996. A Triassic Lagerstatte from eastern North America. Nature (London) 380: 615-619.

GEERTSEMA, H. AND VAN DER HEEVER, J.A. 1996. A new beetle, *Afrocupes firmae* gen. et sp. nov. (Permocupedidae) from the Late Paleozoic Whitehill Formation of South Africa. South African Journal of Science 92: 497-499.

GRIMALDI, D. AND ENGEL, M.S. 2005. Evolution of the Insects. Cambridge University Press, Cambridge, United Kingdom. 755p.

KUKALOVÁ, J. 1969. On the systematic position of the supposed Permian beetles, Tshecardocoleidae, with a description of a new collection from Moravia. Sbornik Geologickych Ved, Paleontology 11: 139-162.

LIEBHERR, J.K. AND J.V. MCHUGH. 2003. Coleoptera (beetles, weevils, fireflies) Pp. 209-203, *in* V.H. Resh and R.T. Cardé (eds.), Encyclopedia of insects. Academic Press, San Diego, CA; 900pp.

MARTYNOV, A.V. 1932. Permian fossil insects from the Arkhangelsk District. Transactions of the Paleontologicheskogo Institut Akademii Nauk SSSR 2: 83-96.

MARTYNOV, A.V. 1937. Permian fossil insects from Kargala and their relationships. Transactions of the Paleontologicheskogo Institut Akademii Nauk SSSR 7: 1-92.

OLSON, E.C. 1970. New and little known genera and species of vertebrates from the Lower Permian of Oklahoma. Fieldiana Geology 18: 359-434.

PINTO, I.D. 1987. Permian insects from Paraná Basin, South Brazil IV Coleoptera. Pesquitas 19: 5-12.

PONOMARENKO, A. G. 1963. Paleozojskie zhuki Cupedidea evroplskoj [Paleozoic Cupedid beetles from the European part of the USSR]. Paleontologichskij Zhurnal 1963(1): 70-85.

PONOMARENKO, A.G. 2000. New beetles from the Permian of European Russia. Paleontological Journal Supplement. 34: 312-316

PONOMARENKO, A.G. 2002. Superorder Scarabaeidea Laicharting, 1781. Order Coleoptera Linné, 1758. The Beetles. Pp. 164-176, *in* A.P. Rasnitsyn and D.L.J. Quicke (eds.), History of insects. Kluwer Academic Publishers, Dordrecht, the Netherlands; xii+517 pp.

PONOMARENKO, A.G. 2003. Ecological evolution of beetles (Insecta: Coleoptera). Acta Zoologica Cracoveinsia 46 (Supplement): 319-32.

RAASCH, G.O. 1946. The Wellington Formation in Oklahoma. PhD dissertation, University of Wisconsin, Madison.

RASNITSYN, A.P. AND D.L.J. QUICKE. 2002. History of insects. Kluwer Academic Publishers, Dordrecht, the Netherlands; xii+517 pp.

ROHDENDORF, B. B. 1944. A new family of Coleoptera from the Permian of the Urals. Comptes rendus (Doklady) de l' Akademie des sciences de l'URSS. 44: 252-253.

ROHDENDORF, B. B. 1961. Nadotrayad Coleopteroidea. Zhestkokryloobraznye [Superorder Coleoptera]. Pp. 393-469, *in* B.B. Rohdendorf, E. Eh. Becker-Migdisova, O.M. Martynova, and A.G. sharov, Paleozoiske nasekomye kuznetkogo basseina [Paleozoic insects of the Kuznetsk basin]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 85.

SCHULTZE, H.P. 1985. Marine to onshore vertebrates in the Lower Permian of Kansas, and their paleoenvironmental implications. Paleontological Contributions 113: 1-18.

SHELTON, J.W. 1979. Geology and mineral resources of Noble County, Oklahoma. Oklahoma Geological Survey Bulletin 128.

TASCH, P. 1961**.** Vertical extension of mid-Continent Leonardian insect occurrences. Science (Washington DC) 135: 378-379.

TASCH, P. AND J.R. ZIMMERMAN. 1959. New Permian insects discovered in Kansas and Oklahoma. Science (Washington DC) 130: 1656.

TASCH, P. AND J.R. ZIMMERMAN. 1962. The *Asthenohymen-Delopterum* bed – a new Leonardian insect horizon in the Wellington of Kansas and Oklahoma. Journal of Paleontology 36: 1319-1333.

TILLYARD, R.J. 1924. Kansas Permian insects. Part 1. The geologic occurrence and environment of the insects. American Journal of Science, Fifth Series 7: 171-209.

[*]CHAPTER 4

***PARACUPES SVITKOI* (*COLEOPTERA: ARCHOSTEMATA: CUPEDIDAE: CUPEDINI*), A NEW SPECIES FROM THE CRETACEOUS OF NEW JERSEY**

Abstract

Paracupes svitkoi is a new species based on a single specimen from the Raritan Formation of the Cretaceous of New Jersey. The fossil, a well-preserved, fusainized head, is the first fossil member of the genus *Paracupes*. It is very similar to the modern species in the genus.

THE OLD CROSSMAN'S clay pits of Sayreville, Middlesex County, New Jersey, one of the more prolific sites for New Jersey amber (GRIMALDI 2000), is also the source of an unusual flora of fusainized (charcoalified) plants and insects. This outcrop of the Raritan Formation of New Jersey contains more than 100 taxa of fossil flowers, fruits, seeds, cones and wood (GANDOLFO, ET AL. 1998) including the first fossil evidence of many angiosperm groups such as Hamamelidaceae (ZHOU, ET AL. 2001), Capparales (GANDOLFO, ET AL. 1998) and the earliest known monocot flower (Tiuridaceae) (GANDOLFO, ET AL. 1997). The insect remains include elytra, legs, mandibles and other parts mainly of Coleoptera, and Neuroptera. This is the

---

[*] LUBKIN, S.H. 2003. "*Paracupes svitkoi* (Coleoptera: Archostemata: Cupedidae: Cupedini), a new species from the Cretaceous of New Jersey". Acta Zoologica Cracoviensia, 46 (suppl. – Fossil Insects): 189-194.

first description of a fossil insect from the site and this is the first fossil *Paracupes*, a genus that until now was known only from two extant South American species.

Geology

THE RARITAN FORMATION of the Atlantic Coastal Plain is a series of interbedded gravels, sands and silty clays deposited in fluvial channels and as overbank flood deposits (JENGO 1995). The South Amboy Fire Clay is the uppermost of the five members of the Raritan Formation, and is conformably overlain by the Old Bridge Sand member of the Magothy Formation. It is a fine-grained, light gray sandy silty clay with mica, lignite, marcasite and traces of white feldspar (JENGO 1995). At its base, the South Amboy Fire Clay is interbedded with the Sayreville Sand member of the Raritan Formation (JENGO 1995). The specimen described here was collected from an exposure of the Amboy Fire Clay at Old Crossman's Clay Pit near Sayreville, New Jersey.

Based on pollen analysis (GROOT, ET AL. 1961), the age of the South Amboy Fire Clay is proposed to be Turonian. Fossil flowers collected from the Old Crossman's Clay pits suggest a tropical or subtropical climate (GANDOLFO, ET AL. 2001) based on comparison of these fossil flowers to modern tropical angiosperms.

Materials and Methods

The fossil is a single, three-dimensional fusainized (charcoalified) head of a beetle. Although, the cause of the fusainization is unknown, FRIIS (1988) proposes that the charcoalification may be due to rapid heating during forest fires. New Jersey amber sometimes contains bits of fire-damaged wood and heat-produced bubbles, which may be evidence of forest fire (GRIMALDI 2000). In addition, GRIMALDI (2000) suggests the amber could be the result of fire-induced sap flow. While only the heavily sclerotized parts of the insects remain: legs, elytra, mandibles, and some heads, the fusainization allows minute details such as eye facets, scales, and setae to be preserved. Although many of the fragments cannot be easily identified, this specimen was readily recognized as a cupedid.

The specimen was found in sample collected from the Old Crossman's Clay Pit in Sayreville, New Jersey.   The unconsolidated sediments were first dissolved in warm water and sieved through a series of progressively finer screens. The remaining material was washed with a strong detergent in order to remove any excess clay. The material was swirled in water to suspend the fossils and the suspended organic material was decanted to remove any sand. Other minerals were removed by treating with hydrofluoric acid (HF 49%) followed by several rinses in distilled water. Fossils were air dried and then sorted under a Zeiss SV-8 stereomicroscope.

The specimen was mounted on an aluminum stub and sputter coated with gold palladium. The micrographs were produced using the Hitachi 4500 scanning electron microscope at Cornell's Integrated Microscopy Center.

Systematic Paleontology

Order COLEOPTERA LINNAEUS, 1758
Suborder ARCHOSTEMATA KOLBE, 1908
Family CUPEDIDAE LACORDAIRE, 1857
Tribe CUPEDINI CROWSON, 1962

Genus PARACUPES KOLBE, 1898

Paracupes svitkoi Lubkin, sp. Nov.

Figures 4.1 – 4.2

Diagnosis. The specimen belongs in *Paracupes* and is diagnosable from all other genera of Cupedidae by the lack of posterior tubercles (KOLBE, 1908). *Paracupes* have only a single pair of conical tubercles that is located at the base of antennae. It was compared with a specimen of *P. brasiliensis* from the Canadian National Insect Collection and with the original description of *P. asicus* (NEBOISS 1989). It is similar to the extant *Paracupes* species *P. brasiliensis* KOLBE (1908) and *P. asicus* NEBOISS (1989), but can be distinguished from those species by the shape of the head and by the strongly serrated mandibular teeth. The head is somewhat similar to that of *P. asicus* in that the head is abruptly marginate behind the eyes with a ridge that extends posteriorly; however, in *P. svitkoi* the posterio-lateral angles of the head are flattened and project slightly beyond the eye. In *P. brasiliensis* the head rises gradually above the eyes and the posterio-lateral angles are rounded. However, the scales on the dorsal surface of the head are slender and tapering like those on *P. brasiliensis*. On *P. ascius*, the scales are stout and widen distally.

***Type Material*.** The holotype, a fossil head, CUPC#1339.

Type Locality. Old Crossman's Clay Pit, Middlesex County, New Jersey.

Figure 4.1. Scanning electron micrograph - dorsal view of *Paracupes svitkoi.* Scale bar = 500 µm. Imaging by J.L. Svitko.

Figure 4.2. Scanning electron micrograph – anterior view of *Paracupes svitkoi*. Scale bar = 500 µm. Imaging by J.L. Svitko. (500 µm). Eyes large, diameter 1/3 width of head (~.38 mm).

Age and Stratigraphy. Late Cretaceous; South Amboy Fire Clay, Raritan Formation. Deposited in the Cornell University Paleobotanical Collection at Bailey Hortorium, Cornell University.

Description. Length of head is ~1.15 mm. Greatest width ~1.35 mm. Neck-like constriction behind eyes wider than long, about half width of head Entire surface of head covered with small tubercles and remains of scales.

Antennal insertions located dorsally, separated by much less than diameter of eyes. Antennae missing. Single pair of conical tubercles located behind antennal insertions.

Mandibles large (~20% total length of head), three distinct mandibular teeth. Mandibles covered with tubercles except near teeth. Labrum easily visible, appears semi-rectangular from above, but triangular at tip. Gula short, almost as wide as long.

Etymology. Named for Jennifer Svitko, of the Bailey Hortorium, who prepared and photographed the specimen.

Other material. Isolated Cupedoid elytra are also present in the New Jersey sediments (Figures 4.3 and 4.4); however, it is not possible to determine if they belong to the same species.

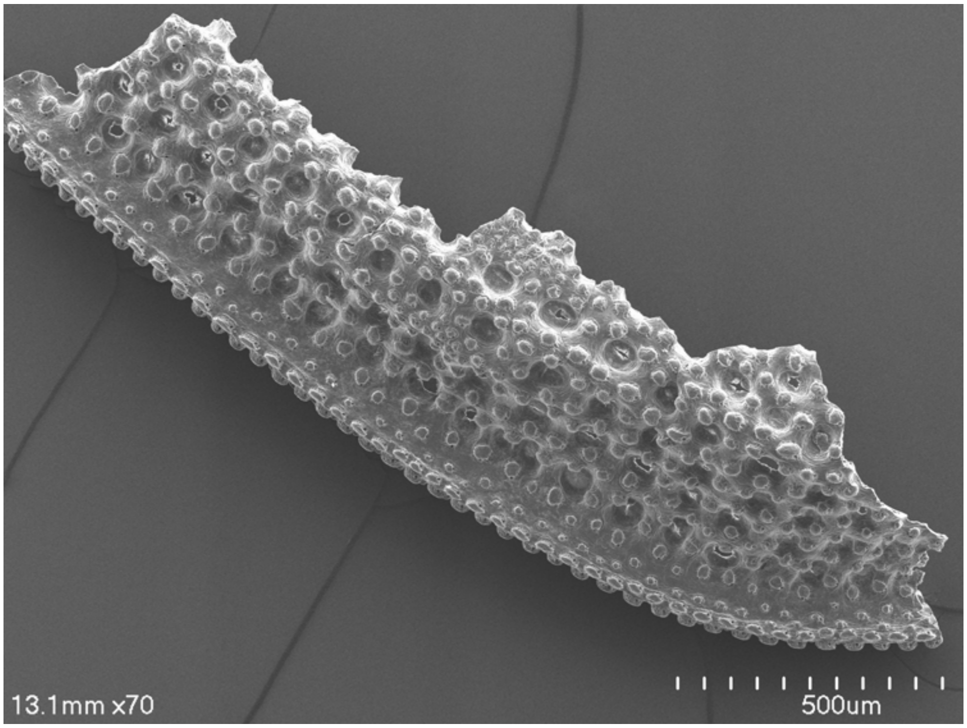


Figure 4.3. Scanning electron micrograph showing a fragment of a fusainized elytron from the Turonian of New Jersey. Imaging by S.H. Lubkin.

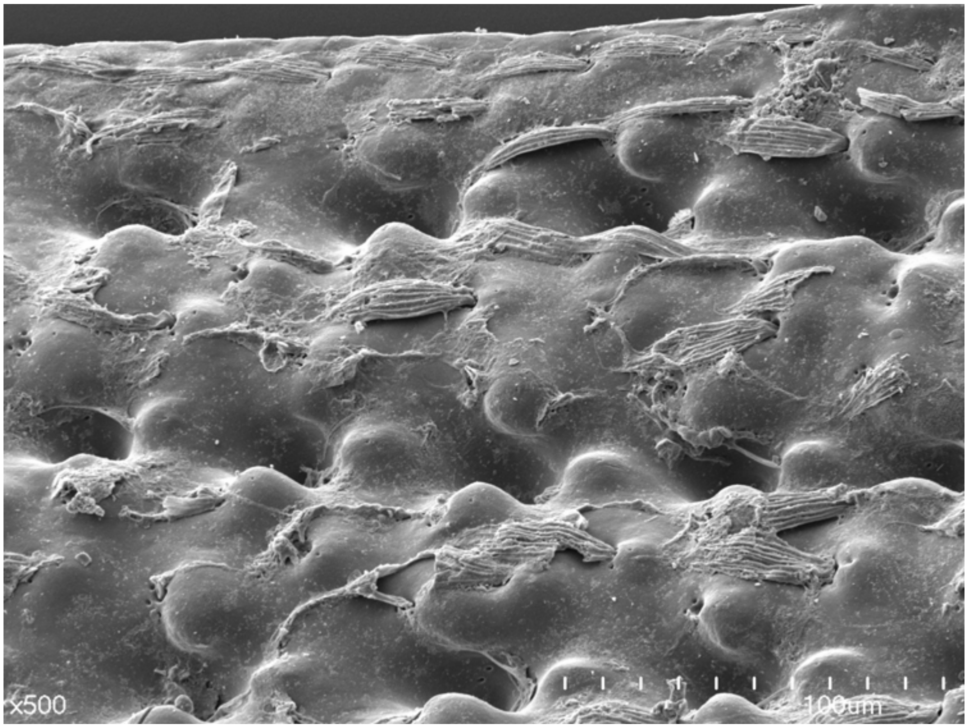


Figure 4.4. Scanning electron micrograph of another charcoalified elytron showing the scales and punctures that are characteristic of Cupedoid elytra. Imaging by S.H. Lubkin.

Discussion

The family Cupedidae includes some of the earliest known fossil beetles (Permian, LABANDEIRA 1994) and some of the most primitive living beetles (LAWRENCE 1999). Although the group was quite diverse in the Permian and early Mesozoic (PONOMARENKO 1995), there are only about 25 extant species and nine extant genera.

Four of the nine genera have a fossil record. *Cupes* is known from Eocene aged Baltic amber (IABLOKOFF-KHNZORIAN 1960), and from the Pliocene of northern Germany (GERSDORF 1976). *Tenomerga* (NEBOISS 1984) is described from German sediments of Eocene age (TROSTER 1993), and *Priacma* is known both from Baltic amber (MOTSCHOULSKY 1856) and from the Cretaceous of Mongolia (PONOMARENKO 1986, 1997). With the specimen described here, *Paracupes svitkoi* makes the fourth.

ACKNOWLEDGMENTS

The fossil was obtained by W. L. Crepet and K.C. Nixon using funds from NSF Grant # DEV-0108369. Processing and imaging of the specimen was done by J. L. Svitko, Bailey Hortorium, Cornell University. I would also like to thank D.A. Grimaldi for bringing the fossil to my attention.

REFERENCES

FRIIS, E. M., CRANE, P.P., AND PEDERSON, K.R. 1988. Reproductive structures of Cretaceous Platanaceae. Biologiske Skrifter, Det Kongelige Danske Videnskabernes Selskap, 31: 1-55.

GANDOLFO, M.A., NIXON, K.C., ET AL.. 1998. Oldest known fossils of monocotyledon. Nature 394: 532-533.

GANDOLFO, M.A., NIXON, K.C., CREPET, W.L. 1997. The oldest known fossil flower of monocotyledons with affinities to the modern family Triuridaceae. American Journal of Botany 84(6 suppl.): 196.

GANDOLFO, M.A., NIXON, K.C., AND CREPET, W.L. 2001. Turonian Pinaceae of the Raritan Formation, New Jersey. Plant Systematics and Evolution. 226: 187-203.

GERSDORF, E. 1976. Dritter Beitrag uber Kafer (Coleoptera) aus dem Jungtertiar von Willershausen, Bl. Northeim 4226. Geologisches Jahrbuch, A 36: 103-145.

GRIMALDI, D.A. 2000. Studies on fossils in amber with particular reference to the Cretaceous of New Jersey. Backbuys Publishers. Leiden, the Netherlands; viii + 498 pp.

GROOT, J.J., PENNY, J.S., GROOT, C.R. 1961. Plant microfossils and age of the Raritan, Tuscaloosa and Magothy Formations of the eastern United States. Palaeontographica B 108: 16- 140.

IABLOKOFF-KHNZORIAN. 1960. New beetles from Baltic amber (Insecta, Coleoptera). Comptes Rendus de L'Academie des Sciences de L'URSS 136: 209-210.

JENGO, J.W. 1995. Stratigraphic framework and sequence stratigraphy of sections of the cretaceous age Raritan-Magothy Formations, Middlesex County, New Jersey. Northeastern Geology and Environmental Science 17: 223-246.

KOLBE, H. J. 1908. Mein System der Coleopteren: Zeitschrift fur wissenchaftliche Insektenbiologie 4: 246-251.

LABANDEIRA, C.C. 1994. A compendium of fossil insect families. Milwaukee Public Museum Contrubutions to Biology and Geology 88, 1-71.

LACORDAIRE,T. 1857. Cupesidae. Pp. 505-507, *in* Lacordaire, T and Chapuis, F. (eds.) Histoire Naturelle des Insectes: Genera des Coléoptères ou expose méthodique et critique des tous les genres proposés jusqu'ici dans cet ordre d'insectes. Paris, Librairie Encyclopedique de Roret.

LAWRENCE, J.F. 1999. The Australian Ommatidae (Coleoptera: Archostemata): New species, larva and discussion of relationships. Invertebrate Taxonomy 13: 369-390.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, sononymis, locis ed. 10; 823 pp.

MOTSCHOULSKY, V. 1856. Études Entomologiques. Helsingfors, France.

NEBOISS, A. 1984. Reclassification of Cupes Fabricius (s.lat.) with descriptions of new genera and species (Cupedidae: Coleoptera). Systematic Entomology 9: 443-447..

NEBOISS, A. 1989. New species of Archostemata (Coleoptera, Ommatidae, Cupedidae). Revue Française d'Entomologie 11: 109-115.

PONOMARENKO, A.G. 1995. The geological history of beetles. Pp. 155-171, *in* J. Pakaluk and S.A. Ślipiński (eds.), Biology, Phylogeny and Classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson. Museum I Instytut Zoologii PAN, Warsaw, Poland; xii + 558 pp.

PONOMARENKO, A.G. 1986. Coleoptera. Pp. 84-107, *in* The Joint Soviet Mongolian Palaeontological Expedition. Insects in the early Cretaceous ecosystems of the West Mongolia. Nakua, Moscow; 107pp.

PONOMARENKO, A.G. 1997. New beetles of the family Cupedidae from the Mesozoic of Mongolia. Ommatini, Mesocupedini, Priacmini: Paleontological Journal 31: 389-399.

TRÖSTER, G. 1993. Zwei neue mitteleuropaische Arten der Gattung Tenomerga Neboiss 1984 aus dem Mitteleozan der Grube Messel und des Eckfelder Maares (Coleoptera: Archostemata: Cupedidae). Mainzer Naturwissenschaftliches – Archives 31: 169-176.

ZHOU, Z.K., CREPET, W.L., NIXON, K.C. 2001. The earliest fossil evidence of the Hamamelidaceae: Late Cretaceous (Turonian) inflorescences and Fruits of Altingioidae. American Journal of Botany 88: 753-766.

CHAPTER 5

DISSERTATION SUMMARY

INSECTS COMPRISE APPROXIMATELY eighty percent of the identified animal species (ERWIN 1988; MAY 1988) on Earth, and the Coleoptera or beetles are the largest order of insects. By some estimates the Coleoptera make up as much as 30% of animal species, with over 360,000 described species of modern beetles (ERWIN 1991; LIEBHERR AND MCHUGH 2003). Beetles live in every possible non-marine habitat including on crops, on flowers, on fruits and seeds, on leaves, in leaf litter, under tree bark, in rotten wood, in soil, under rocks, on decaying carcasses, in flour bins, in our homes and in every type of freshwater habitat from puddles and ponds to lakes and streams to swamps and even beaches.

Considering the diversity and abundance of beetle species, the Coleoptera are easily the most successful group of terrestrial animals to ever inhabit the Earth. Therefore, to understand animal life on Earth, it is important to understand beetles. Beetles have held the position of most diverse insect group since the early Jurassic (PONOMARENKO 1969, PONOMARENKO 2000), but very little is known about earliest beetles and the origins of this great diversity.

The earliest identified fossil Coleoptera are described from Early Permian (Lower Artinskian, ca. 268 MA) deposits in Obora, Czech Republic (KUKALOVÁ 1969), and from the Wellington Formation (Artinskian, 269-260 MA) of Midco, Oklahoma (LUBKIN AND ENGEL 2005), and from slightly younger deposits of Tshekarda, in the Ural Mountains of Russia (PONOMARENKO 1963; ROHDENDORF 1944).

Fossil beetles are only generally known only from isolated elytra. Elytra are the hardened front wings of beetles. These hardened wings serve to protect the abdomen and hind wings of Coleoptera and allow beetles to live in a variety of habitats while still retaining the ability to fly.

Fossil elytra have been extremely helpful in the identification of Pleistocene beetles used in paleoclimate studies (COOPE 1959, 1962, 1987 and others; ELIAS 1994; LINDROTH 1948). In fossils younger than 4 MA, microsculpture and patterns or metallic coloration are often preserved, and many elytra can be matched to those of extant species (MATTHEWS 1979). However, the usefulness of elytra in identification varies greatly from family to family and genus to genus, and identifications based only on elytra can be misleading (ELIAS 1994), especially for older fossil elytra. Often times, fossil elytra are distinguishable from one another only on the basis of size, shape, and punctation or other ornamentation that may have been altered by taphonomy and preservation. Very frequently, elytra cannot be conclusively identified and elytra-shaped fossils are commonly labeled as “Coleoptera?” with no further identification (e.g. CARPENTER 1992: 327-337).

Although in most cases, fossil elytra are not useful for taxonomic identification, the earliest fossil Coleoptera and their near-Coleoptera relatives, the coleopteroids, have very ornate elytra that may include scales, setae, punctures, spines, and even venation, features that are potentially meaningful in phylogenetic studies (KUKALOVÁ 1969; LUBKIN AND ENGEL 2005; MARTYNOV 1932, 1937; PONOMARENKO 1963, 2000, 2002; ROHDENDORF 1944, 1961). Venation may be especially helpful for taxonomic studies as venation in the hind wings of modern Coleoptera has provided an abundance of phylogenetic information about relationships within beetle groups (BEUTEL AND HAAS 2000; HAMMOND 1979; WALLACE AND FOX 1980), and possibly the placement of Coleoptera within the Holometabola (BEUTEL AND HAAS 2000; HAAS AND BETEL 2001; HORNSCHEMEYER 1998; KUKALOVÁ-PECK AND LAWRENCE 1993; WHITING, ET AL. 1997).

However, since hind wings are only rarely preserved in fossil beetles, and the fossil record of Coleoptera is predominantly a record of elytra, these remnants of wing venation are often the only morphological characters that are available for phylogenetic studies. However, in the past, conflicting systems have been used for naming these veins. This has made the gathering of phylogenetic information difficult and has obscured an understanding of the evolution of the early Coleoptera and their relatives.

In the first cladistic analysis of Permian and Mesozoic Coleoptera and coleopteroids, elytral characters were used to produce a character matrix that was phylogenetically analyzed using WinClada (NIXON 1999-2002) AND nona (GOLOBOFF 1999). The resultant trees showed that many of the traditional family arrangements of the early Coleoptera and coleopteroids are not supported by a cladistic analysis of elytral characters and are poly- or paraphyletic. A revised classification system is proposed.

Materials and Methods

Study Taxa

Significant collections of Coleoptera from the Permian and Mesozoic are stored in museums worldwide. Many of these specimens are both unique and very fragile, so direct study of this material was not possible. Instead, for all taxa except *Permocoleus wellingtonensis*, morphological information was obtained using illustrations from the primary literature rather than from actual specimens. The main criterion for inclusion in this study was a clear illustration of at least one complete or near-complete elytron.

52 taxa were included in the study. These included taxa are listed in the appendix and include fossil Coleoptera and coleopteroids, modern Cupedidae, and outgroups.

Four taxa, including extant and extinct groups, of Neuroptera were chosen as outgroups. Neuroptera have been considered the most likely living relatives of Coleoptera (AFZELIUS AND DALLAI 1994; CROWSON 1981; HENNIG 1969; HORNSCHEMEYER 1998; KRISTENSEN 1975; LAWRENCE 1982; LAWRENCE AND NEWTON 1995; MICKOLEIT 1973; WHITING, ET AL. 1997) because of similarities in the morphology and structure of mouthparts, forewing attachments, metathoracic wing bases, ovipositors, stemmata, sperm axonemes, legs, and 18s and 28s ribosomal DNA sequences.

Characters and Character States

Because Coleoptera are generally preserved only as isolated fossil elytra, only elytral characters were used to create the character matrix, although in a few instances morphological characters such as antennal or thoracic structures were available. Elytral venation has been lost in most modern Coleoptera, but the veins of fossil elytra can be homologized with the venation in the front wings of related orders such as Neuroptera and fossil groups such as Glosselytrodea. These groups were chosen as outgroups. The forty-six characters (listed in the appendix) include elytral venation, shape and ornamentation. All characters were non-additive and unordered.

The venation patterns were traced and veins were color-coded based on vein position, path and neighboring veins. The color-coded veins were then named using a modification of the Comstock-Needham system of nomenclature (COMSTOCK AND NEEDHAM 1898A, 1898B): costa (C), subcosta (Sc), radius (R), radial sector (Rs_{1-4}), media (M), media posterior (MP), anterior cubitus (CuA), posterior cubitus (CuP), and anal veins (A_1, A_2, A_3).

Originally all characters were given the same weight, but obtaining a resolved tree was complicated by multiple homoplasious losses of veins. It is impossible to homologize losses, and when there is a character loss, the tree resolution is dependent on the presence of other characters. However, as many of the characters were not independent, a loss also affected other characters such as vein length or vein path, where absence is coded as an inapplicable state (-). Inapplicable states are treated by NONA (GOLOBOFF 1998) as having all states present. When too many veins were lost in a taxon, the result was an abundance of most parsimonious placements which resulted in polytomies in the consensus tree. Two weighting schemes were created in an attempt to deal with this problem. In the second and third analyses, characters denoting the presence of veins were given a higher weighting. A summary of character weights for each matrix is shown in the appendix.

The character matrices (Appendix 4; 47 characters, 52 terminals) were constructed using WinClada (NIXON 2002). Both WinClada's (NIXON 2002) Island Hopper and NONA (GOLOBOFF 1999) were used for the tree search.

Results

The analysis of matrix 1 resulted in 602 most parsimonious trees of 230 steps. Matrix 2 yielded 313 most parsimonious trees of 886 steps. Analysis of matrix 3 resulted in 515 most parsimonious trees with a length of 3,898 steps. The consensus trees are shown in Appendix 5. The dramatic increase in steps is due to character weighting. The results of the tree search are summarized in Table 5.1.

Table 5.1: Summary of Tree Search results

	Number of MPTs	**Length of MPTs**	**Length of consensus tree**	**CI/RI**
Matrix 1	602	230	366	21/29
Matrix 2	313	886	1,017	33/74
Matrix 3	515	3,898	4,782	33/72

Most of the trends in beetle evolution have to do with the ability to live in small, tight spaces (elytra, increased sclerotization, hind wings that fold both lengthwise and crosswise to fit under the elytra, reduced venation in the hind wings, a shield like pronotum, flattened body shape, internal genitalia, and a reduced ovipositor). In elytra, there is a simplification of elytral venation with time, and this trend of vein loss was expressed as a loss of resolution in the lower part of the tree. Nonetheless, while not fully resolved, these trees provide plenty of interesting and consistent information.

The family Tshekardocoleidae was found to be paraphyletic and was redefined to include only *Tshekardocoleus* ROHDENDORF 1944*, Afrocupes* GEERSTEMA AND VAN DER HEEVER 1996 and *Brochocoleus* HONG 1982 (in part). Two new families, Moravocoleidae (*Moravocoleus* KUKALOVÁ 1969*, Permocoleus* LUBKIN AND ENGEL 2005, *Prosperocoleus* KUKALOVÁ 1969) and Sylvacoleidae (*Boscoleus* KUKALOVÁ 1969, *Sylvacoleus* PONOMARENKO 1963, *Umoricoleus* KUKALOVÁ 1969) were created to include some of the former members of the “Tshekardocoleidae”. Further taxonomic revision, of the families Permocupedidae, Ommatidae and Cupedidae is still needed, but this study provides a framework for further study of the earliest beetles. A consensus tree with the new and revised families is shown in Figure 5.1.

In addition, a key for identifying fossil elytra based only on venation and other elytral characters was created. This is especially important because the fossil record of beetles is primarily a record of elytra. While the conspicuous and often elaborate venation of Permian and Mesozoic elytra has proved to be useful for classification, descriptions based only on venation can be vague, contradictory, or confusing, as new species are not necessarily described by specialists in Coleoptera. And while the most complete descriptions can be obtained from the primary literature, these are often in Russian or Chinese and can be difficult to obtain.

When describing a new species, it is difficult to figure out the phylogenetic affiliations of an elytron without a thorough cladistic analysis. When LUBKIN AND ENGEL (2004) described *Permocoleus wellingtonensis*, a single elytron of lower Permian age from Wellington Formation of Oklahoma, Lubkin searched through the primary literature and thought the elytron most resembled *Kaltanicupes Ponomarenkoi* a Late Permian beetle from South America (PINTO 1987). However, the analysis showed that *Permocoleus* is most similar to the older Moravocoleidae from Obora. The purpose of the key

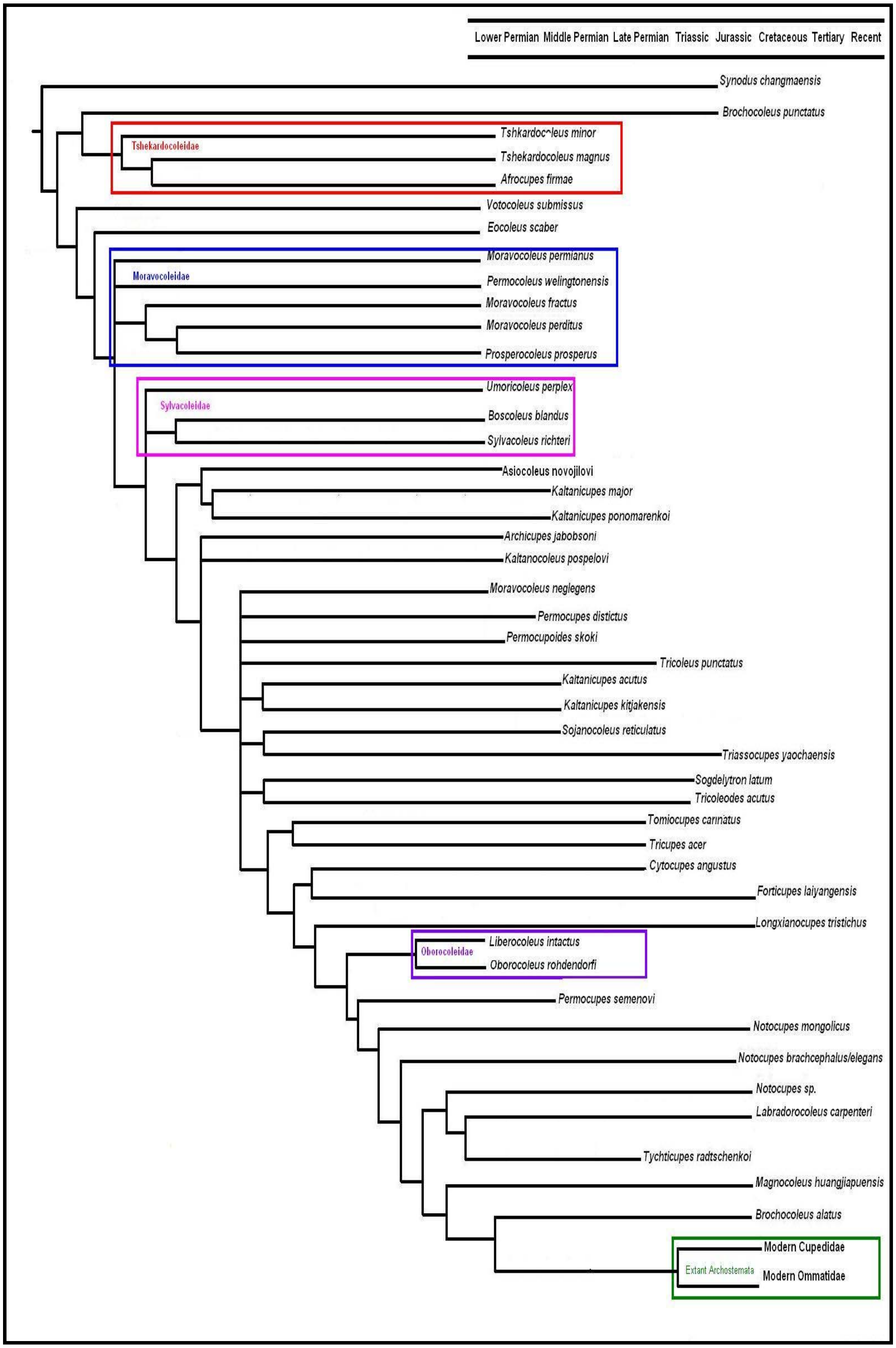


Figure 5.1: Consensus tree from Analysis 2 showing the family affiliations of early Coleoptera and coleopteroids.

is to prevent such mistakes that could lead to erroneous conclusions about beetles diversity and biogeography.

Discussion

Identifying the phylogenetic relationships among living beetles can be difficult and often depends of larval or internal characters (PONOMARENKO 2002), information that is not usually preserved in the fossil record. Because the fossil record of beetles is essentially a record of elytra, we are dependent on elytral characters to discover the relationships among the earliest Coleoptera. Fortunately the earliest fossil elytra possess the remnants of wing venation, and these remnants are helping to clarify the relationships among the earliest Coleoptera and Coleopteroids.

Our knowledge of the relationships among the earliest Coleoptera and coleopteroids has been obscured by multiple systems of classification and inconsistent nomenclature of elytral veins. When structure is added in the forms of homologization of wing veins and cladistic analysis, the relationships among these first beetles become easier to understand. This is the first cladistic analysis of the early Coleoptera and Coleopteroids. This study found that many of the long-accepted family groupings of the early Coleoptera and coleopteroids are not supported by cladistic analysis of elytral venation, and that these groups are poly- or paraphyletic.

The family Tshekardocoleidae was redefined and two new families Moravocoleidae and Sylvacoleidae were created to include some former members of Tshekardocoleidae. The family Permocupedidae still requires revision and it is proposed that Cupedidae and Ommatidae be restricted to taxa showing the modern pattern of elytral venation

The earliest fossil elytra are known from deposits in Obora, Czech Republic (KUKALOVÁ 1969). Members of three families Moravocoleidae, Oborocoleidae and Sylvacoleidae are present as well as the genera *Eocoleus* and *Votocoleus*. Surprisingly, the elytra of the earliest Coleoptera are not the most primitive. *Permocoleus wellingtonensis* is the earliest new world beetle (from Midco, Oklahoma) and is very similar to the Moravocoleidae from Obora. This suggests that by the Artinskian (269 MA), both Coleoptera and coleopteroids were present, and the Moravocoleidae, at least, were widely distributed. The earliest known Coleopteroids are younger than the earliest Coleoptera and known from Tshekarda (Kungurian 260-256 MA) (PONOMARYOVA 1998). This signifies both an earlier origin for the Coleoptera-Coleopteroid lineage and that our knowledge of the earliest beetles and their relatives is still incomplete.

Both the Obora and Midco sites are the remains of lacustrine environments. Obora is comprised of a lacustrine mudstone (KUKALOVA-PECK AND WILLMANN 1990) and Midco (TASCH 1962, 1963; TASCH AND ZIMMERMAN 1959) is a preserved coastal region containing both freshwater and playa lakes.

SMITH's (2000) study on beetle taphonomy in an ephemeral lake in southeastern Arizona proposes that in lakes there is a bias towards the preservation of ground dwelling and plant dwelling beetles. Modern Archostemata tend to be specialized wood borers, and are considered the most primitive of modern beetles (BEUTEL AND HAAS 2000; CATERINO, ET AL. 2002; CROWSON 1981; LAWRENCE AND NEWTON 1995; SHULL, ET AL. 2001), so it has been assumed that early beetles may perhaps also be wood-borers. However, wood or fungi eaters were absent in Smith's sample.

It is quite possible that the earliest beetles were instead ground dwelling. However, it is equally possible, that early Coleoptera are rare because they are wood-boring and, therefore, not easily preserved.

The extant Archostemata may in fact be quite derived. In Figure 5.1, the extant Archostemata fit very neatly on a monophyletic branch of the consensus tree. This monophyly was consistent in all analyses. Obviously modern Archostemata are a relict of a far greater diversity of reticulated beetles and the definition of Cupedidae needs to be narrowed. As it is currently used for classifying fossils, Cupedidae is a paraphyletic assemblage of Coleoptera.

In all the consensus trees, the most primitive coleopteroids included *Brochocoleus punctatus* and *Synodus changmaensis.* Both are Chinese fossils of Upper Jurassic age and may represent remnants of separate coleopteroid lineages that are sister groups to the sub-order Coleoptera. Perhaps the history of these lineages will be unearthed as more beetle fossils are described from China.

Conclusions

Beetles are the largest group of animals living on Earth and this study provided a starting point for researching the earliest Coleoptera and the relationships among the beetles and coleopteroids. Still to be understood are the origins of the modern suborders and relationships among them. There have been few molecular studies of the beetle suborders (CATERINO, ET AL. 2002; MADDISON, ET AL. 1999; SHULL, ET AL. 2001), and these have been based only on limited sequences of 18S rDNA. Although morphological studies show (BEUTEL AND HAAS 2000; CROWSON 1981) that the

Archostemata are the sister group to the rest of the Coleoptera, wing venation is not present in all other Coleoptera (although punctures and striations may, in fact, be remnants) and so the remaining suborders can not be fit in the resulting tree. Both the earliest Adephaga and Polyphaga known from Triassic of Virginia (Grimaldi personal communication, 2005) and their placement in the tree will require morphological data.

Morphological data will also valuable for testing the resultant trees from this study. However, this cannot be done without actual examination of specimens. Future plans include the addition of morphological data to the study, reanalysis and revision of the Permocupedidae and fossil Cupedidae, and the addition of more elytral data. With a phylogenetic framework for studying the earliest Coleoptera and their relatives, it will be possible to better understand patterns of beetle diversification and extinction and to understand how the beetles became the most diverse and successful group of animals on Earth.

REFERENCES

AFZELIUS, B.A. AND DALLAI, R. 1994. Characteristics of the flagellar axoneme in Neuroptera, Coleoptera and Strepsiptera. Journal of Morphology 219: 15-20.

BEUTEL, R.G. AND HAAS, F 2000. Phylogenetic relationships of the suborders of Coleoptera (Insecta). Cladistics 16: 103-141.

CARPENTER, F.M. 1992. Superclass Hexapoda. Pp. 1-655, *in* Kaesler, R.L. (Ed.) Treatise on Invertebrate Paleontology, Part R, Arthropoda 3-4. Geological Society of America; Boulder, Colorado; xxii + 655 pp.

CATERINO, M.S., SHULL, V.L., HAMMOND, P.M. AND VOLGER, A.P. 2002. Basal relationships of Coleoptera inferred from 18S rDNA sequences. Zoological Scripta 31: 41-49.

COMSTOCK, J.H., AND NEEDHAM, J.G. 1898A. The wings of insects. Chapter 1. An introduction to the study of the homologies of the wing-veins. The American Naturalist 32: 43-48.

COMSTOCK, J.H., AND NEEDHAM, J.G. 1898B. The wings of insects. Chapter 2. The venation of the typical insect wing. The American Naturalist 32: 81-89.

COOPE, G.R. 1959. A Late Pleistocene Chelford, Cheshire. Proceedings of the Royal Society of London B 151: 70-86.

COOPE, G.R. 1962. A Pleistocene coleopterous fauna with arctic affinities from Flatbury, Worcestershire. Quarterly Journal of the Geological Society of London 118: 103-123.

COOPE, G.R. 1987. Fossil beetle assemblages as evidence for sudden and intense climatic changes in the British Isles. Pp. 147-150, *in* W.H. Berger and L.D. Labeyrie (Eds.), Abrupt Climate Change. Reidel, Dordrecht, the Netherlands; 452 pp.

CROWSON, R.A. 1981. The biology of the Coleoptera. Academic Press, London; 802 pp.

ELIAS, S.A. 1994. Quaternary Insects and Their Environments. Smithsonian Institution Press, Washington, DC; xiii + 284pp.

ERWIN, T.L. 1988. The tropical forest canopy: the heart of biotic diversity. Pp 123-129 *in* Wilson E.O. and Peter F.M. (eds.) Biodiversity. National Academy Press. Washington DC; 521pp.

ERWIN, T.L. 1991. How many species are there?: Revisited. Conservation Biology 5: 330-333.

GOLOBOFF, P. 1999. NONA (NO NAME) ver. 2 Published by the author, Tucumán, Argentina.

GEERTSEMA, H. AND VAN DER HEEVER, J.A. 1996. A new beetle, *Afrocupes firmae* gen. et sp. nov. (Permocupedidae) from the Late Paleozoic Whitehill Formation of South Africa. South African Journal of Science 92: 497-499.

HAAS, F AND BEUTEL, R.G. 2001. *W*ing folding and the functional morphology of the wing base in Coleoptera. Zoology (Jena) 104: 123-141.

HAMMOND, P.M. 1979. Wing-folding mechanisms of beetles, with special reference to investigations of Adephagan phylogeny. Pp. 113-180, *in* Erwin, T.L., G.E. Ball, D.R. Whitehead and A.L. Halpern (Eds.), Carabid Beetles: Their Evolution, Natural History, and Classification. W. Junk, The Hague; the Netherlands 646 pp.

HENNIG W. 1969. Die Stammesgeschichte der Insekten. Kramer, Frankfurt am Main, Germany; 436 pp.

HONG, Y.-C. 1982. Discovery of new Lower Cretaceous insects, at Xishan, Beijing. Bulletin of the Tianjin Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences 1982(4): 87-96.

HONG Y.-C., LIU, Z. AND LUI, S. 1985. Discovery and studying of the Triassic fauna and flora of the Niangniangmiao in Longxian, Shaanxi. Bulletin of the Xi'an Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences 10: 105-120.

HONG, Y-C. 1990. Fossil insects from the Laiyang Basin, Shandong Province. Pp. 44-189, *in* Regional Surveying Team, Shandong Bureau of Geology and Mineral Resources (Eds.), The stratigraphy and palaeontology of Laiyang Basin, Shandong Province; 189pp.

HONG, Y-C. 1998. Magnocoleidae fam. nov. (Insecta: Coleoptera). Geoscience (China) 12: 40-48.

HORNSCHEMEYER, T. H. 1998. Morphologie und Evolution der Flugelgelenks der Coleoptera und Neuropterida. [Morphology and evolution of the wing base of Coleoptera and Neuropterida.] Bonner Zoologische Monographien 43: 1-126.

KRISTENSEN N. P. 1975. The phylogeny of hexapod "orders." A critical review of recent accounts. Zeitschrift für Zoologisches Systematisches Evolutionforschungen. 13:1–44.

KUKALOVÁ, J. 1969. On the systematic position of the supposed Permian beetles, Tshecardocoleidae, with a description of a new collection from Moravia. Sbornik Geologickych Ved, Paleontology 11: 139-162.

KUKALOVA-PECK, J. 2004. Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. European Journal of Entomology 101: 95 144.

KUKALOVÁ-PECK, J. AND LAWRENCE, J. F. 1993. Evolution of the hind wing in Coleoptera. The Canadian Entomologist 125(2): 181-258

KUKALOVÁ-PECK, J. AND WILLMANN, R. 1990. Lower Permian mecopteroid-like insects from Central Europe (Insecta: Endopterygota). Canadian Journal of Earth Sciences 27: 459-468.

LAWRENCE, J.F. 1982. Coleoptera. Pp. 482-553, *in*: Parker, S.P. (Ed.). Synopsis and Classification of Living Organisms. McGraw-Hill: New York, New York; 1119 pp.

LAWRENCE J.F. AND NEWTON A.F. 1995 Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names) II. Pp. 779-1006 *in* J. Pakaluk and S.A. Ślipiński (eds.), Biology, Phylogeny and Classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson. Museum I Instytut Zoologii PAN, Warsaw, Poland; xii + 1006 pp.

LIEBHERR, J.K. AND J.V. MCHUGH. 2003. Coleoptera (beetles, weevils, fireflies), pp. 209-203, *in* V.H. Resh and R.T. Cardé (eds.), Encyclopedia of insects. Academic Press, San Diego, CA; 900pp.

LINDROTH, C.H. 1948. Interglacial insect remains from Sweden. Arbosk Sveriges Geologiska Undersoekning Series C 42: 1-29.

LUBKIN, S.H. AND ENGEL, M. 2005. *Permocoleus*, new genus, the first Permian Beetle (Coleoptera) from North America. Annals of the Entomological Society of America 98: 73-77.

MADDISON, D.R., BAKER, M.D., AND OBER K.A. 1999. Phylogeny of Carabid beetles as inferred from 18s ribosomal DNA (Coleoptera: Carabidae). Systematic Entomology 24: 103-138.

MARTYNOV, A.V. 1932. Permian fossil insects from the Arkhangelsk District. Transactions of the Paleontologicheskogo Institut Akademii Nauk SSSR 2: 83-96.

MARTYNOV, A.V. 1933. Permskie iskopaemye nasekomye arkhangel'skogo kraya. Chast' II. Setchatokrylye, vislokrylye i zhuki, s prilozheniem opisaniya dvukh novykh zhukov iz tikhikh gor [Permian fossil insects from the Arkhangelsk District. Part II. Neuroptera, Megaloptera, and Coleoptera, with descriptions of two new beetles from Tikhie Gory]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 2: 63-69.

MARTYNOV, A.V. 1937. Permian fossil insects from Kargala and their relationships. Transactions of the Paleontologicheskogo Institut Akademii Nauk SSSR 7: 1-92.

MARTYNOV, A.V. 1938. Ocherki geologicheskoj istorii I filogenii otryadov nasekomykh (Pterygota). 1. Paleoptera I Neoptera-Polyneoptera [Essays on the geologic history and phylogeny of insect orders. 1. Paleoptera and Neoptera-Polyneoptera]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 7: 1-150.

MATTHEWS, J.V., Jr. 1979. Late Tertiary Carabid fossils from Alaska and the Canadian Arctic Archipelago. Pp. 425-445, *in* T. L. Erwin, G. E. Ball, D. R. Whitehead and A. L. Halpern (eds.), Carabid Beetles: Their Evolution, Natural History, and Classification. Dr. W. Junk, The Hague, The Netherlands; 646 pp.

MAY, R.M. 1988. How many species are there on earth? *Science* 241: 1441–1449.

MICKOLEIT, G. 1973. Zur Anatomie und Funktion des Raphidiopteren-Ovipositors (Insecta, Neuropteroidea). Zeitschrift fur Morphologie der Tiere 76: 145-171.

NIXON, K. C. 1999-2002. WinClada version 1.0000 Published by the author, Ithaca, NY.

PINTO, I.D. 1987. Permian Insects from Paraná Basin, South Brazil IV Coleoptera. Pesquisas 19: 5-12.

PONOMARENKO, A. G. 1963. Paleozojskie zhuki Cupedidea evroplskoj [Paleozoic Cupedid beetles from the European part of the USSR]. Paleontologichskij Zhurnal 1963(1): 70-85.

PONOMARENKO, A.G. 1966. Zhuki semeystva Cupedidae iz nizhnego triasa Sredney Azii [Beetles of the family Cupedidae from the lower Triassic of Central Asia]. Paleontologichskij Zhurnal 1966(4): 47-68.

PONOMARENKO, A.G. 1969A. Cretaceous insects from Labrador. 4. A new family of beetles (Coleoptera: Archostemata). Psyche 76: 306-310.

PONOMARENKO, A.G. 1969B. Istoricheskoe razvitie zhestkokrylykh-arkhostemat [Historical development of the Coleoptera-Archostemata]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 125: 1-240.

PONOMARENKO, A.G. 1977. Mezozoiskiye zhestkokrylyye [Mesozoic Coleoptera]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 161: 1-204.

PONOMARENKO, A.G. 1994. New Mesozoic cupedid beetles from Mongolia; Brochocoleini and Notocupedini. Paleontological Journal 28: 102-155.

PONOMARENKO, A.G. 1995. The geological history of beetles. Pp. 155-171, *in* J. Pakaluk and S.A. Ślipiński (eds.), Biology, Phylogeny and Classification of Coleoptera: Papers celebrating the 80th birthday of Roy A. Crowson. Museum I Instytut Zoologii PAN, Warsaw, Poland; xii + 558 pp.

PONOMARENKO, A.G. 2000. New beetles from the Permian of European Russia. Paleontological Journal Supplement. 34: 312-316.

PONOMARENKO, A.G. 2002. Superorder Scarabaeidea Laicharting, 1781. Order Coleoptera Linné, 1758. The Beetles. Pp. 164-176, *in* A.P. Rasnitsyn and D.L.J. Quicke (eds.), History of insects. Kluwer Academic Publishers, Dordrecht, the Netherlands; xii+517 pp.

PONOMARENKO, A.G. 2003. Ecological evolution of beetles (Insecta: Coleoptera). Acta Zoologica Cracoveinsia 46 (Supplement): 319-32.

PONOMARYOVA, G. U., NOVOKSHONOV V.G., AND NAUGOLNYKH, S.V. 1998. Tshekarda – A Locality of Permian Fossil Plants and Insects. Perm University: Perm, Russia; 92 pp.

ROHDENDORF, B. B. 1944. A new family of Coleoptera from the Permian of the Urals. Comptes rendus (Doklady) de l' Akademie des sciences de l'URSS. 44: 252-253.

ROHDENDORF, B. B. 1956. Paleozojskie nasekomye Yuzhnoj Sibiri [Paleozoic insects from southern Siberia]. Entomologicheskogo Obozrenie 35: 111-119.

ROHDENDORF, B. B. 1961. Nadotrayad Coleopteroidea. Zhestkokryloobraznye [Superorder Coleoptera]. Pp. 393-469, *in* B.B. Rohdendorf, E. Eh. Becker-Migdisova, O.M. Martynova, and A.G. sharov, Paleozoiske nasekomye kuznetkogo basseina [Paleozoic insects of the Kuznetsk basin]. Trudy Paleontologicheskogo Institut Akademii Nauk SSSR 85.

SMITH, D.M. 2000. Beetle taphonomy in a Recent ephemeral lake, Southeastern Arizona. Palaios 15: 152-160.

SHULL, V.L., VOLGER, A. P., BAKER, M.D., MADDISON, D.R. AND HAMMOND, P.M. 2001. Sequence alignment of 18S ribosomal RNA and the basal relationship of adephagan beetles: Evidence for monophyly of aquatic families and the placement of Trachypachidae. Systematic Biology 50: 945-969.

TASCH, P. 1961**.** Vertical extension of mid-Continent Leonardian insect occurrences. Science (Washington DC). 135: 378-379.

TASCH, P. AND J.R. ZIMMERMAN. 1959. New Permian insects discovered in Kansas and Oklahoma. Science (Washington DC). 130: 1656.

TASCH, P. AND J.R. ZIMMERMAN. 1962. The *Asthenohymen-Delopterum* bed – a new Leonardian insect horizon in the Wellington of Kansas and Oklahoma. Journal of Paleontology 36: 1319-1333.

WALLACE, F.L. AND FOX, R.C. 1980. A comparative morphological study of the hind wing venation of the order Coleoptera, Part II. Proceedings of the Entomological Society of Washington 82(4): 609-654.

WHITING, M.F., CARPENTER, J.C., WHEELER, Q.D., AND WHEELER, W.C. 1997. The strepsiptera problem: Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. Systematic Biology 46: 1-68.

APPENDIX

SUPPLEMENTAL MATERIALS

List of taxa included in the study

1. *Afrocupes firmae* (FIGURE 1.3a) GEERSTEMA AND VAN DER HEEVER 1996 (Permian, South Africa)

2. *Archicupes jacobsoni* (FIGURE 1.3b) ROHDENDORF 1961 (Lower Permian, Russia)

3. *Asiocoleus novojilovi* (FIGURE 1.3c) ROHDENDORF 1961 (Lower Permian, Russia)

4. *Boscoleus blandus* (FIGURE 1.3d) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

5. *Brochocoleus alatus* (FIGURE 1.3e) PONOMARENKO 1994 (Lower Cretaceous, Mongolia)

6. *Brochocoleus punctatus* (Figure 1.3f) HONG 1982 (Upper Jurassic, China)

7. *Cytocupes angustus* (FIGURE 1.3g) ROHDENDORF 1961 (Upper Permian, Russia)

8. *Eocoleus scaber* (FIGURE 1.3h) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

9. *Forticupes laiyangensis* (FIGURE 1.3i) HONG 1990 (Lower Cretaceous, China)

10. *Kaltanicupes acutus* (FIGURE 1.3j) PONOMARENKO 1963 (Middle Permian, Russia)

11. *Kaltanicupes kitjakensis* (FIGURE 1.3k) PONOMARENKO 1963 (Middle Permian, Russia)

12. *Kaltanicupes major* (FIGURE 1.3l) PONOMARENKO 1963 (Middle Permian, Russia)

13. *Kaltanicupes ponomarenkoi* (FIGURE 1.3m) PINTO 1987 (Upper Permian, Brazil)

14. *Kaltanocoleus pospelovi* (FIGURE 1.3n) ROHDENDORF 1961 (Lower Permian, Russia)

15. *Labradorocoleus carpenteri* (FIGURE 1.3o) PONOMARENKO 1969A (Cretaceous, Labrador)

16. *Liberocoleus intactus* (FIGURE 1.3p) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

17. *Longxianocupes tristichus* (FIGURE 1.3q) HONG, ET AL.. 1985 (Lower Cretaceous, China)

18. *Magnocoleus huangjiapuensis* (FIGURE 1.3r) HONG 1998 (Lower Cretaceous, China)

19. *Moravocoleus fractus* (FIGURE 1.3s) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

20. *Moravocoleus neglegens* (FIGURE 1.3t) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

21. *Moravocoleus perditus* (FIGURE 1.3u) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

22. *Moravocoleus permianus* (FIGURE 1.3v) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

23. *Notocupes brachycephalus* (FIGURE 1.3w) PONOMARENKO 1994 (Jurassic, Mongolia)

24. *Notocupes elegans* (FIGURE 1.3x) PONOMARENKO 1994 (Lower Cretaceous, Mongolia)

25. *Notocupes mongolicus* (FIGURE 1.3y) PONOMARENKO 1994 (Lower Cretaceous, Mongolia)

26. *Notocupes sp.* (FIGURE 1.3z) PONOMARENKO 1966 (Lower Cretaceous, Russia)

27. *Oborocoleus rohdendorfi* (FIGURE 1.3aa) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

28. *Permocoleus wellingtonensis* (FIGURE 1.3bb) LUBKIN AND ENGEL 2005 (Lower Permian, United States)

29. *Permocupes distinctus* (FIGURE 1.3cc) MARTYNOV 1933 (Permian, Russia)

30. *Permocupes semenovi* (FIGURE 1.3dd) MARTYNOV 1933 (Permian, Russia)

31. *Permocupoides skoki* (FIGURE 1.3ee) ROHDENDORF 1956 (Lower Permian, Russia)

32. *Prosperocoleus prosperus* (FIGURE 1.3ff) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

33. *Sogdelytron latum* (FIGURE 1.3gg) PONOMARENKO 1969B (Triassic, Asia)

34. *Sojanocoleus reticulatus* (FIGURE 1.3hh) MARTYNOV 1932 (Permian, Russia)

35. *Sylvacoleus richteri* (FIGURE 1.3ii) PONOMARENKO 1963 (Lower Permian, Russia)

36. *Synodus changmaensis* (FIGURE 1.3jj) HONG 1982 (Jurassic, China)

37. *Tomiocupes carinatus* (FIGURE 1.3kk) ROHDENDORF 1961 (Upper Permian, Russia)

38. *Triassocupes yaochaensis* (FIGURE 1.3ll) HONG, ET AL. 1985 (Triassic, China)

39. *Tricoleodes acutus* (FIGURE 1.3mm) PONOMARENKO 1969B (Triassic, Asia)

40. *Tricoleus punctatus* (FIGURE 1.3nn) PONOMARENKO 1969B (Jurassic, Kazakhstan)

41. *Tricupes acer* (FIGURE 1.3oo) ROHDENDORF 1961 (Upper Permian, Russia)

42. *Tshekardocoleus magnus* (FIGURE 1.3pp) ROHDENDORF 1944 (Lower Permian, Russia)

43. *Tshekardocoleus minor* (FIGURE 1.3qq) PONOMARENKO 1963 (Lower Permian, Russia)

44. *Tychticupes radtschenkoi* (FIGURE 1.3rr) ROHDENDORF 1961 (Upper Permian, Russia)

45. *Umoricoleus perplex* (FIGURE 1.3ss) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

46. *Votocoleus submissus* (FIGURE 1.3tt) KUKALOVÁ 1969 (Lower Permian, Czech Republic)

47. *Tenomerga concolor* (Cupedidae)

48. *Omma stanleyi* (Ommatidae)

49. Agulla (snakefly, extant, Raphidioptera)

50. Nigronia (dobsonfly, extant, Megaloptera)

51. Sialis (alderfly, extant, Megaloptera)

52. *Permoberotha villosa* TILLYARD 1932 (extinct, family Permoberothidae, order Glosselytrodea MARTYNOV 1938)

Characters and character states

All characters are non-additive and unordered.

0. **Vein Sc:**
    0) Sc is present.
    1) Sc is absent.

1. **Length of Sc:**
    0) Full length; Sc reaches the edge or tip of the elytron.
    1) Shortened; Sc terminates before reaching elytron tip or edge.
    2) Very short; the length of Sc is less than one quarter the length of the elytron.
    3) Absent; length is zero.

2. **Veins C and Sc:**
    0) Merge at edge of elytron.
    1) Merge at tip of elytron.
    2) Merge before tip, but not at edge.
    3) Do not merge.

3. **Enlarged area between bases of C and Sc:**
    0) Absent.
    1) Slight enlargement.
    2) Definitely enlarged; at least twice the width separating the remainder of C and Sc.

4. **Vein R:**
    0) Present.
    1) Absent.

5. **Number of Rs veins:**
    0) Several.
    1) Two.
    2) One.
    3) None.

6. **Rs_1 is:**
    0) Attached to R about halfway down the elytron.
    1) Attached to R less than one-quarter of the distance from the base.
    2) Attached to R at base.
    3) Not attached to R.
    4) Absent.

7. **R length:**
    0) Full length; reaches edge or tip
    1) Shortened; terminates before reaching edge or tip
    2) Very short; R is less than half the length of the elytron.
    3) R vein is absent; length is zero.

8. **Veins R and Sc:**
    0) Do not merge.
    1) Merge before tip.
    2) Merge at tip.

9. **R and Sc share a stem:**
    0) No.
    1) Yes.

10. **R and Rs_1 merge:**
    0) No.
    1) Yes.

11. **Vein M:**
    0) Present.
    1) Absent.

12. **MP branching:**
    0) Present.
    1) Absent.

13. **Veins M and R:**
    0) Do not merge.
    1) Merge.

14. **Vein CuA:**
    0) Present.
    1) Absent.

15. **CuA branching:**
    0) Present.
    1) Absent.

16. **CuA and M:**
    0) Share a stem.
    1) Originate separately near wing base.

17. **Veins CuA and M and A1 intersect to form an x-shape:**
    0) No.
    1) Yes.

18. **Posterior part of CuA:**
    0) Is approximately parallel to other veins (Fig. 1.1a).
    1) Is deeply concave and approximately parallels the curve of the lower anal edge of the elytron (Fig. 1.1b).
    2) Dips sharply toward anal edge of elytron (Fig. 1.1c).
    3) Gradually angles down to anal edge (Fig. 1.1d).
    4) CuA is too short to tell (Fig. 1.1e).
    5) Entire vein is slightly concave (Fig. 1.1f).
    6) Merges with vein M and then is straight to elytron tip (Fig. 1.1g).

19. **Veins CuA and M:**
    0) Do not merge.
    1) Merge.

20. **Veins CuA and R:**
    0) Do not merge.
    1) Merge.

21. **Veins CuA and Rs_1:**
    0) Do not merge.
    1) Merge

22. **CuA length:**
    0) Full length; vein reaches the tip or edge of elytron.
    1) Full length after merging with vein M.
    2) Shortened; vein terminates before tip or edge.
    3) Quite short; vein length is equal to or less than one-quarter the length of the elytron
    4) CuA is absent, length is zero.

23. **Vein CuP:**
    0) Present.
    1) Absent.

24. **CuP and M and CuA:**
    0) Share a stem.
    1) Do not share a stem.

25. **Length of CuP:**
    0) CuP reaches the tip of elytron.
    1) CuP reaches the anal edge of elytron.
    2) Short; CuP terminates before the edge or tip of the elytron.
    3) CuP is absent; length is zero.

26. **CuP and M:**
    0) Do not merge.
    1) Merge.

27. **CuP and A_1:**
    0) Do not intersect.
    1) Intersect.

28. **CuP and R:**
    0) Do not intersect.
    1) Intersect.

29. **CuP and CuA:**
    0) Do not intersect.
    1) Intersect.

30. **A_1:**
    0) Present.
    1) Absent.

31. **A_1 length:**
    0) Extends to tip.
    1) Reaches edge more than halfway between the base and tip.
    2) Reaches edge halfway or less than halfway between the base and tip.
    3) Shortened; vein terminates before tip or edge.
    4) Very short; vein length is less than one-eighth the length of the elytron
    5) A_1 is absent; length is zero.

32. **A_1 and CuA:**
    0) Do not merge.
    1) Merge.
    2) Not applicable.

33. **Vein A_2:**
    0) Present.
    1) Absent.

34. **Additional A veins:**
   0) Present.
   1) Absent.

35. **Fold or line between Sc and R:**
   0) Absent.
   1) Present.

36. **Puncture shape:**
   0) Punctures absent.
   1) Round.
   2) Irregular, somewhat round, lumpy.
   3) Oval.
   4) Oval, but irregular.
   5) Rectangular.
   6) Quadrate.
   7) Irregular four-sided.
   8) Five-sided.
   9) Six-sided.
   10) Very irregular.

37. **Sc with divided stem:**
   0) Absent.
   1) Present.

38. **M length:**
   0) Full length; extends to tip
   1) Shortened; greater than or equal to one-half the length of the elytron
   2) Very short; less than one-half the length of the elytron
   3) Merges with CuA, then extends to full length.
   4) M is absent; length is zero.

39. **Elytron shape:**
   0) No elytron.
   1) Costal side of elytron is more concave.
   2) Anal side of elytron is more concave.
   3) Both sides of elytron are approximately equally concave; elytron has a leaf or blade shape.

40. **A_1 and CuA:**
   0) Do not share stem.
   1) Share stem.

41. **Cross-vein between M and CuA:**
    0) Absent.
    1) Present.

42. **Rs_2 is:**
    0) Attached to Rs_1.
    1) Attached to R about half way from base.
    2) Attached at base of R.
    3) Not attached to R or Rs_1.
    4) Absent.

43. **Short vein from base of M to M/CuA attachment:**
    0) Absent.
    1) Present.

44. **Curvature of vein R:**
    0) R does not curve to meet anal edge.
    1) R curves to meet anal edge.

45. **Curvature of vein Sc:**
    0) Sc does not curve to meet anal edge.
    1) Sc curves to meet anal edge.

Character Matrix

Character states: 0, 1, 2, 3, 4, 5, 6
Inapplicable character: -
Unknown or missing data: ?

Taxon/Character	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Agulla sp.	0	0	0	0	0	0	0	0	0	0	0	0	0
Nigronia sp.	0	0	0	0	0	0	0	0	2	0	0	0	0
Sialis sp.	0	0	0	0	0	0	0	0	1	0	0	0	0
Permoberotha villosa	0	0	0	0	0	0	0	0	0	0	0	0	0
Afrocupes firmae	0	0	1	0	0	1	2	0	2	1	0	0	1
Archicupes jacobsoni	0	0	1	0	1	3	5	3	-	-	-	0	1
Asiocoleus novojilovi	1	3	-	-	0	3	4	0	-	-	-	0	1
Boscoleus blandus	0	0	1	2	0	3	4	0	2	1	-	0	1
Brochocoleus alatus	0	0	3	1	0	3	4	0	0	0	-	0	1
Brochocoleus punctatus	0	0	1	0	0	1	0	0	0	0	1	0	0
Cytocupes angustus	1	3	-	-	0	2	1	0	-	-	1	0	0
Eocoleus scaber	0	0	1	1	0	2	0	0	0	0	0	0	1
Forticupes laiyangensis	1	3	-	-	0	1	0	0	-	-	0	0	1
Kaltanicupes acutus	0	1	0	2	0	3	4	1	1	0	-	0	1
Kaltanicupes kitjakensis	0	0	3	1	0	3	4	1	1	0	-	0	1
Kaltanicupes major	0	0	3	0	0	3	4	1	1	0	-	0	1
Kaltanicupes ponomarenkoi	0	1	3	0	0	3	4	1	0	0	-	0	1
Kaltanocoleus pospelovi	0	0	1	0	0	2	0	0	0	0	1	0	1
Labradorocoleus carpenteri	0	0	3	2	0	2	3	1	1	0	0	0	1
Liberocoleus intactus	0	0	1	1	0	2	0	0	0	0	0	0	1
Longxianocupes tristichus	1	3	-	-	0	2	3	0	-	-	0	0	1
Magnocoleus huangjiapuensis	0	0	1	0	0	3	4	0	2	0	-	0	1
Moravocoleus fractus	0	0	1	1	0	2	0	0	0	0	0	0	1
Moravocoleus neglegens	0	0	1	1	0	3	4	0	0	0	-	1	1
Moravocoleus perditus	0	0	1	1	0	2	0	0	0	0	0	0	1
Moravocoleus permianus	0	0	1	1	0	2	0	0	0	0	0	0	1
Notocupes brachycephalus	0	0	3	0	0	2	3	0	0	0	1	0	1
Notocupes elegans	0	0	3	0	0	2	3	0	0	0	1	0	1
Notocupes mongolicus	0	0	3	0	0	2	1	0	0	0	0	0	1
Notocupes sp.	0	?	?	1	0	2	1	0	0	1	0	0	1
Oborocoleus rohdendorfi	0	0	1	1	0	1	0	0	2	0	0	0	1
Permocoleus wellingtonensis	0	0	1	1	0	2	0	0	1	0	0	0	1

Permocupes distinctus	0	0	1	0	0	3	4	0	0	0	-	0	1
Permocupes semenovi	0	0	1	0	0	2	2	1	0	0	0	0	1
Permocupoides skoki	1	3	-	-	0	3	4	?	-	-	-	0	1
Prosperocoleus prosperus	0	0	1	0	0	2	0	0	0	0	0	0	0
Sogdelytron latum	1	3	-	-	0	3	4	1	-	-	-	0	1
Sojanocoleus reticulatus	0	0	1	0	0	2	1	0	0	0	0	0	?
Sylvacoleus richteri	0	0	1	2	0	3	4	2	0	1	-	0	1
Synodus changmaensis	0	0	1	0	0	0	1	0	0	0	0	0	1
Tomiocupes carinatus	1	3	-	-	0	2	2	0	-	-	0	0	1
Triassocupes yaochaensis	0	0	3	0	0	3	4	0	0	0	-	0	1
Tricoleodes acutus	1	3	-	-	0	3	4	1	-	-	-	0	1
Tricoleus punctatus	1	3	-	-	0	3	4	0	-	-	-	0	1
Tricupes acer	1	3	-	-	1	2	3	3	-	-	-	0	1
Tshekardocoleus magnus	1	3	-	-	0	1	0	0	-	-	0	0	1
Tshekardocoleus minor	0	0	1	0	0	1	0	0	2	0	0	0	1
Tychticupes radtschenkoi	0	0	1	0	0	2	2	0	0	0	0	0	1
Umoricoleus perplex	0	0	1	1	0	3	4	0	2	0	-	0	1
Votocoleus submissus	0	0	1	1	0	0	0	0	2	0	0	0	1
Tenomerga concolor	0	0	3	0	0	3	4	0	0	0	-	0	1
Omma stanleyi	0	0	3	0	0	3	4	0	1	0	-	0	1

Taxon/Character	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**
Agulla sp.	0	0	0	0	0	0	0	0	0	0	0	0
Nigronia sp.	0	0	0	1	0	0	0	0	0	0	0	0
Sialis sp.	0	0	0	0	0	0	0	0	0	0	0	0
Permoberotha sp.	0	0	1	0	0	0	0	0	0	0	0	0
Afrocupes firmae	0	0	1	1	0	0	1	0	0	1	0	1
Archicupes jacobsoni	-	0	1	0	0	1	0	-	-	0	0	1
Asiocoleus novojilovi	0	0	1	1	1	5	0	0	-	2	0	1
Boscoleus blandus	0	0	1	0	0	5	1	0	-	1	0	1
Brochocoleus alatus	0	0	1	1	0	0	1	1	-	2	0	1
Brochocoleus punctatus	1	0	1	1	0	0	0	1	0	0	0	1
Cytocupes angustus	0	0	1	1	0	0	0	0	0	0	1	-
Eocoleus scaber	0	0	1	0	0	1	0	0	0	0	0	1
Forticupes laiyangensis	0	0	1	1	0	0	0	0	0	0	1	-
Kaltanicupes acutus	0	0	1	1	0	5	0	0	-	0	1	-
Kaltanicupes kitjakensis	0	0	1	1	0	5	0	0	-	?	1	-
Kaltanicupes major	0	0	1	1	0	5	0	0	-	?	0	1
Kaltanicupes ponomarenkoi	0	0	1	1	0	5	0	0	-	0	0	1
Kaltanocoleus pospelovi	0	0	1	0	0	1	0	0	0	0	1	-
Labradorocoleus carpenteri	0	0	1	1	0	0	0	0	0	0	0	1
Liberocoleus intactus	0	0	1	1	0	1	1	?	?	0	1	-
Longxianocupes tristichus	0	0	1	1	0	1	1	0	1	2	1	-
Magnocoleus huangjiapuensis	0	0	1	1	0	0	1	0	-	1	0	1
Moravocoleus fractus	0	0	1	0	0	1	1	1	1	0	0	1
Moravocoleus neglegens	-	0	1	-	-	1	-	0	-	0	1	-
Moravocoleus perditus	0	0	1	0	0	1	1	1	1	0	0	1
Moravocoleus permianus	0	0	1	0	0	1	0	0	0	0	0	1
Notocupes brachycephalus	0	0	1	1	0	6	1	0	0	1	1	-
Notocupes elegans	0	0	1	1	0	6	1	0	0	1	1	-
Notocupes mongolicus	0	0	1	1	0	5	1	0	-	2	1	-
Notocupes sp.	0	0	1	1	0	6	1	0	0	1	0	1
Oborocoleus rohdendorfi	0	0	1	1	0	1	1	0	1	0	1	-
Permocoleus	0	0	1	0	0	1	0	0	0	0	0	1

wellingtonensis												
Permocupes distinctus	0	0	1	1	0	6	1	0	-	1	1	-
Permocupes semenovi	0	0	1	1	0	5	1	0	0	2	1	-
Permocupoides skoki	0	0	1	0	0	0	0	0	-	0	1	-
Prosperocoleus prosperus	0	0	1	0	0	1	1	1	1	0	0	1
Sogdelytron latum	1	0	1	1	0	1	0	0	-	0	1	-
Sojanocoleus reticulatus	0	0	1	0	0	1	0	0	0	0	1	-
Sylvacoleus richteri	0	0	1	0	0	1	0	0	-	3	0	1
Synodus changmaensis	0	0	1	1	0	0	0	0	0	0	0	1
Tomiocupes carinatus	0	0	1	0	0	1	0	0	0	0	1	1
Triassocupes yaochaensis	0	0	1	1	0	0	0	0	-	0	1	-
Tricoleodes acutus	0	0	1	1	0	1	1	1	-	0	1	-
Tricoleus punctatus	0	0	1	1	0	0	0	0	-	0	1	-
Tricupes acer	-	1	1	-	-	-	-	-	-	4	0	-
Tshekardocoleus magnus	0	0	1	1	0	1	1	0	1	2	0	1
Tshekardocoleus minor	0	0	1	1	0	0	0	0	0	0	0	1
Tychticupes radtschenkoi	0	0	1	1	0	3	0	0	0	0	0	1
Umoricoleus perplex	0	0	1	0	0	1	0	0	-	0	0	1
Votocoleus submissus	0	0	1	0	0	1	0	0	0	0	0	1
Tenomerga concolor	1	0	1	1	0	0	0	1	-	2	0	1
Omma stanleyi	1	0	1	1	0	0	0	1	-	2	0	1

Taxon/Character	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**
Agulla sp.	0	0	0	0	0	0	0	0	0	0	0
Nigronia sp.	0	0	0	0	0	0	0	0	0	0	0
Sialis sp.	0	0	0	0	0	0	0	0	0	0	0
Permoberotha sp.	0	0	0	0	0	0	0	0	0	0	0
Afrocupes firmae	2	1	0	0	1	0	1	0	0	1	0
Archicupes jacobsoni	3	-	-	-	-	0	1	0	0	1	0
Asiocoleus novojilovi	2	0	0	0	0	0	3	1	0	1	0
Boscoleus blandus	2	0	0	0	0	0	2	0	0	1	0
Brochocoleus alatus	2	0	0	1	0	1	5	-	0	1	0
Brochocoleus punctatus	0	0	0	1	0	0	0	0	0	1	0
Cytocupes angustus	3	-	-	-	-	1	5	-	0	1	0
Eocoleus scaber	1	0	0	0	0	0	2	0	0	1	0
Forticupes laiyangensis	3	-	-	-	-	1	5	-	0	1	0
Kaltanicupes acutus	3	-	-	-	-	0	1	0	0	1	0
Kaltanicupes kitjakensis	3	-	-	-	-	0	1	0	0	1	0
Kaltanicupes major	2	0	0	0	0	0	1	0	0	1	0
Kaltanicupes ponomarenkoi	2	0	0	0	0	0	1	0	0	1	0
Kaltanocoleus pospelovi	3	-	-	-	-	0	1	0	0	1	0
Labradorocoleus carpenteri	0	0	-	0	0	1	5	-	0	1	?
Liberocoleus intactus	3	-	-	-	-	1	5	-	0	1	0
Longxianocupes tristichus	3	-	-	-	-	1	5	-	0	1	0
Magnocoleus huangjiapuensis	0	1	-	0	1	1	5	-	0	1	0
Moravocoleus fractus	2	0	0	0	0	0	2	0	0	1	0
Moravocoleus neglegens	3	-	-	-	-	0	2	0	0	1	0
Moravocoleus perditus	2	0	1	0	0	0	2	0	0	1	0
Moravocoleus permianus	2	0	1	0	0	0	2	0	0	1	0
Notocupes brachycephalus	3	-	-	-	-	1	5	-	0	1	0
Notocupes elegans	3	-	-	-	-	1	5	-	0	1	0
Notocupes mongolicus	3	-	-	-	-	1	5	-	0	1	0
Notocupes sp.	2	0	-	0	1	1	5	-	0	1	?
Oborocoleus rohdendorfi	3	-	-	-	-	1	5	-	0	1	0
Permocoleus wellingtonensis	2	0	0	0	0	0	1	0	0	1	0
Permocupes distinctus	3	-	-	-	-	1	5	-	0	1	0
Permocupes semenovi	3	-	-	-	-	1	5	-	0	1	0
Permocupoides skoki	3	-	-	-	-	0	2	0	0	1	0
Prosperocoleus prosperus	2	0	1	0	0	0	2	0	0	1	0
Sogdelytron latum	3	-	-	-	-	1	5	-	0	1	0
Sojanocoleus reticulatus	3	-	-	-	-	1	5	-	1	1	0
Sylvacoleus richteri	1	0	0	0	0	0	2	0	0	1	1

Synodus changmaensis	0	0	0	0	0	0	0	0	0	0	0
Tomiocupes carinatus	2	0	-	0	1	1	5	-	0	1	0
Triassocupes yaochaensis	3	-	-	-	-	1	5	-	1	1	0
Tricoleodes acutus	3	-	-	-	-	1	5	-	0	1	0
Tricoleus punctatus	3	-	-	-	-	1	5	-	0	1	0
Tricupes acer	1	0	-	-	-	1	5	-	0	1	0
Tshekardocoleus magnus	1	0	0	0	0	0	2	0	0	1	0
Tshekardocoleus minor	1	0	0	0	0	0	2	0	0	1	0
Tychticupes radtschenkoi	1	0	-	0	0	1	5	-	1	1	0
Umoricoleus perplex	2	0	0	0	0	0	2	0	0	1	0
Votocoleus submissus	1	0	0	0	0	0	2	0	0	1	1
Tenomerga concolor	2	0	0	0	0	1	5	-	0	1	0
Omma stanleyi	2	0	0	0	0	1	5	-	0	1	0

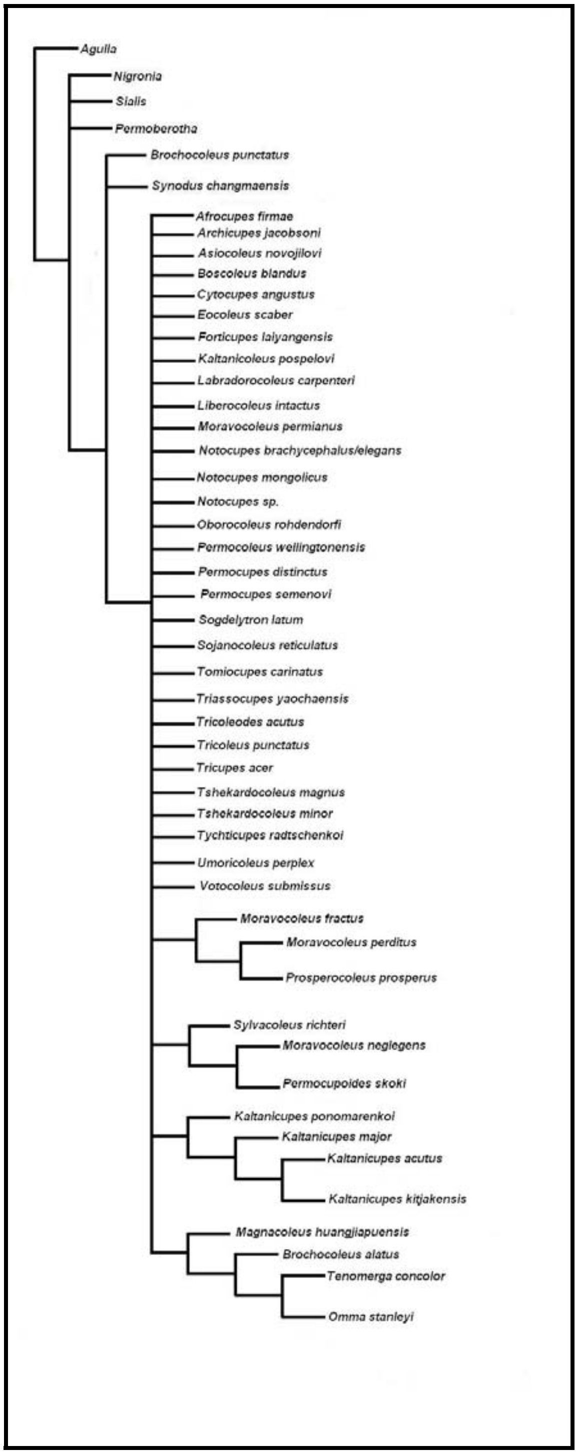
Character Weights

Matrix # **Character #**	1	2	3
0	1	25	100
1	1	1	2
2	1	1	2
3	1	1	2
4	1	25	100
5	1	25	100
6	1	1	50
7	1	1	2
8	1	1	2
9	1	1	2
10	1	1	2
11	1	25	100
12	1	25	100
13	1	1	2
14	1	25	100
15	1	25	100
16	1	1	2
17	1	1	2
18	1	1	2
19	1	1	2
20	1	1	2
21	1	1	2
22	1	1	2
23	1	25	100
24	1	1	2
25	1	1	2
26	1	1	2

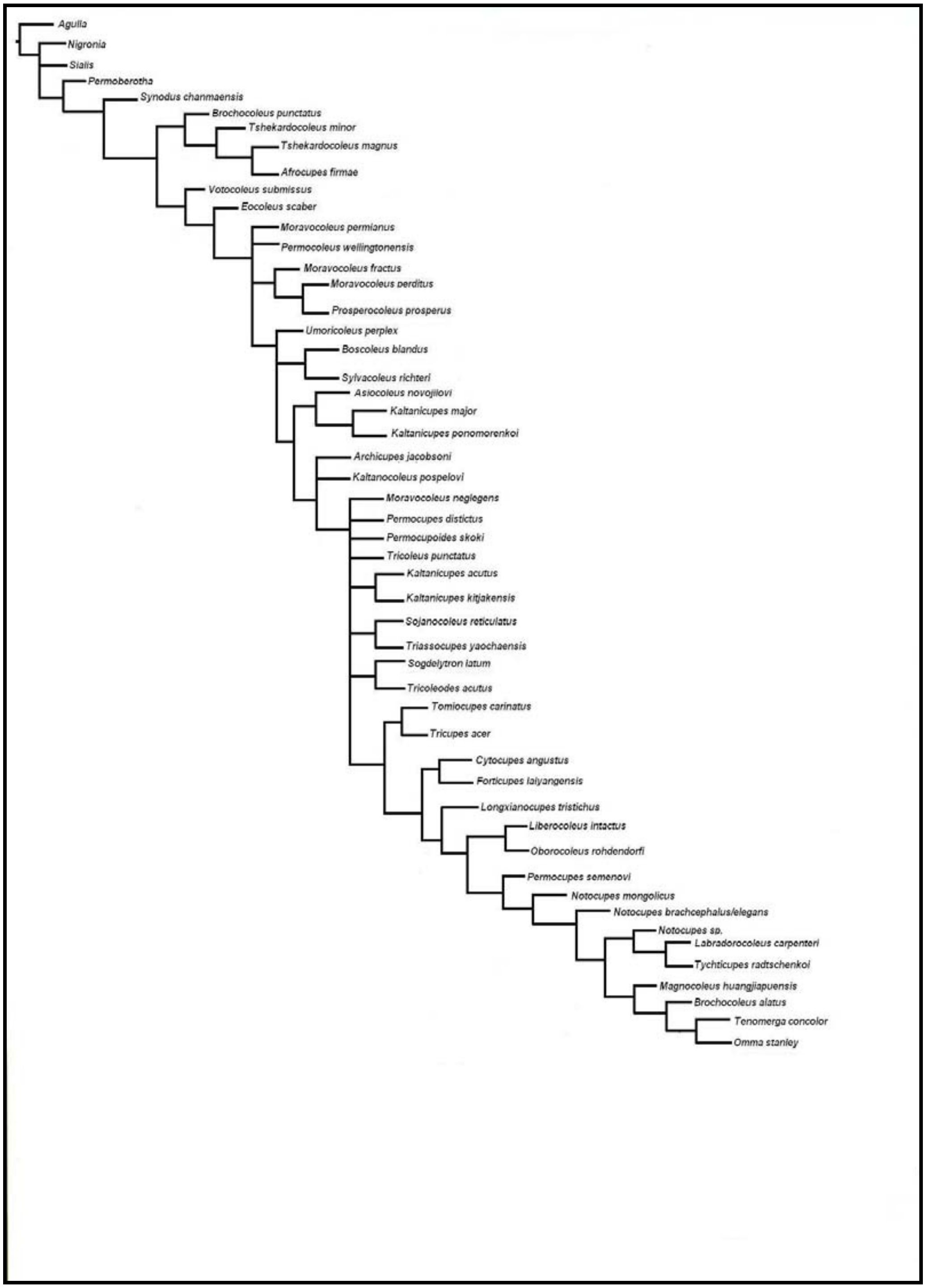
27	1	1	2
28	1	1	2
29	1	1	2
30	1	25	100
31	1	1	2
32	1	1	2
33	1	25	100
34	1	25	100
35	1	1	2
36	1	1	2
37	1	1	1
38	1	1	2
39	1	1	2
40	1	1	1
41	1	1	2
42	1	1	50
43	1	1	2
44	1	1	2
45	1	1	2
46	1	1	2

Consensus Trees

Consensus tree for Matrix 1



Consensus tree for Matrix 2



Consensus tree for Matrix 3