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## Family-Group Names for Bees (Hymenoptera: Apoidea)

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## ABSTRACT

The 173 family-group names for bees (Apoidea: Anthophila) are cataloged in chronological order. For each name the correct author, date, type genus, and combining stem are provided. The following names are considered *nomina nuda*: Phenacolletini, Ctenioschelini, †Chalicodomopsini, Liphanthini, Austropanurgini, and Hoplitini. The authorship of three names (Tapinotaspini, Hexepeolini, and Ancyloscelidina) is corrected as each was a *nomen nudum* when first proposed, but has been subsequently made available by other authors. The following new names are proposed herein: **Scraptrinae** Ascher and Engel, new subfamily (Colletidae); **Nef-fapini** Ascher, new tribe (Andrenidae: Panurginae); **Afrodasyopodini** Engel, new tribe (Melittidae: Dasypodainae), **Afrodasyopoda** Engel, new genus; **Hesperapina** Ascher and Engel, new subtribe (Melittidae: Dasypodainae); **Macrogaleina** Engel, new subtribe (Apidae: Xylocopinae); and **Ancyloscelidina** Engel and Michener, new subtribe (Apidae: Apinae). A hierarchical outline of Apoidea classification (inclusive of the digger wasps), indicating the suggested current usage of all available family-group names is appended. The name Anthophila, as proposed by Latreille, is adopted for the bees as a whole.

## INTRODUCTION

Increased phylogenetic scrutiny on the hierarchical structure of life has resulted in numerous reclassifications of organisms. Such alterations to the classification of life at all levels require the application of names for these groupings. Often such alterations result in relatively minor changes to reflect the increased understanding of organismal affinities. Whether minor or major, the application of names to these groups must follow sets of procedural rules so as to minimize nomenclatural instability, allowing the maximal retrieval of information from the vast biological literature, particularly older references with valuable data but obviously employing classificatory systems reflective of their era. Zoological nomenclature strictly regulates names in only three classes: the species-group (species and subspecies), the genus-group (genera and subgenera), and the family-group (names from superfamily to infratribe) (table 1). Many authors have attempted to catalog the correct application of names in the genus-group and every revision or monograph concerns itself with those of the species-group. Relatively little attention is paid, however, to names in the family-group and, as a result, tremendous confusion abounds about the history of such names, their correct form and authorship, and their accurate application in more modern systems.

The bees (Apoidea: Anthophila) are among the most intensely studied of aculeate Hymenoptera and have, perhaps, one of the more stable higher nomenclatures. This is in

TABLE 1  
Categorical Ranks in the Family-Group

Hyperfamily (-oides) <sup>a</sup>
<b>Superfamily</b> (-oidea)
Epifamily (-oidae) <sup>a</sup>
<b>Family</b> (-idae)
<b>Subfamily</b> (-inae)
<b>Supertribe</b> (-iti) <sup>b</sup>
<b>Tribe</b> (-ini)
<b>Subtribe</b> (-ina)
Infratribe (-ita) <sup>a</sup>
Clan (-itoi) <sup>a,c</sup>
Subclan (-iloi) <sup>a,c</sup>
Infraclan (-isoi) <sup>a,c</sup>
Chaste (-isoa) <sup>a,c</sup>

*Note:* Ranks and suffixes are modified from those proposed by Bour and Dubois (1984) and McKenna and Bell (1997); ranks in boldface employed herein.

<sup>a</sup> Rank not employed herein, but could be used to enrich the hierarchical classification at a later date (I cannot at present envision any utility, however, for recognizing family-group ranks below infratribe in the Apoidea).

<sup>b</sup> Bour and Dubois (1984) suggested the suffix -inoi for the rank of supertribe; however, I have used the more commonly employed suffix -iti.

<sup>c</sup> The ranks can only be loosely classified in the family group and names proposed for these ranks should perhaps not be considered coordinate with those of the higher, more traditional family-group categories.

large part due to the number of excellent monographic and phylogenetic treatments of generic and suprageneric taxa in the group (e.g., Michener, 1944, 1965, 1981; Ruz, 1987; Roig-Alsina and Michener, 1993; Alexander and Michener, 1995; Ascher, 2004).

The family-group names of bees were the subject of scrutiny by Michener (1986a); however, nearly 40 additional names have been proposed in the intervening years, several overlooked, older names have been discovered, and subsequent corrections have been identified, necessitating the current treatment.

The bees are included in the superfamily Apoidea along with a grade of wasps, the so-called “Sphecidae”, spheciform wasps, “digger” wasps, or more aptly apoid wasps. Family-group names for the apoid wasps were recently cataloged by Menke (1997), with additions and emendations by Antropov (2000) and Menke and Pulawski (2002). Although members of the Apoidea, these names are not cataloged herein for two reasons: (1) they have recently received the aforementioned taxonomic treatment and (2) they are, simply put, not bees. However, the classification of apoid wasps has recently been altered (e.g., Ohl, 1996; Prentice, 1998; Melo, 1999). Therefore, these names are included in the hierarchical outline of the superfamily (*vide* appendix 1) for the sake of completeness and to reflect the current usage of family-group names (and their synonyms) in a revised, multi-family system of Apoidea.

Numerous names have been proposed for bees or to denote suprageneric groups of bees, but are not based on an available genus-group name. Examples of such names include: Platiglossata Latreille, Nemoglossata Latreille, Mellifera Latreille (this name was even emended at one time to have a family-group suffix, as Melliferidae), Pepalephora Billberg, Archiapidae Friese, Proapidae Friese, Pygidalia Robertson, Apygidalia Robertson, Corbiculata Engel, Melissomorpha Engel, Paramelitturgini Patiny, etc. None of these, or other such names, are available in zoological nomenclature (ICZN, 1999a: Art. 11.7.1.1) and are, therefore, not considered herein. The various divisional names proposed by Rayment (1935)—i.e., Colletiformes (p. 16), Andreniformes (p. 226), Megachiliformes (p. 394), Xylocopiformes (p. 452), and Apiformes (p. 490)—could be considered family-group names since they are based on available genus-group names. Fortunately, family-group names based on all of these genera had previously been proposed

and thus Rayment’s names can be considered merely superfluous emendations (i.e., as *nomina vana*).

Instead, below I have considered only those names based on a genus-group name, regardless of the status of the generic name (i.e., whether or not the generic name has proved to be preoccupied, unavailable, invalid, etc.). This has resulted in a compilation of 173 family-group names for bees.

#### A NAME FOR THE BEES

Since the rightful unification of the apoid wasps and the bees into a single superfamily, many melittologists have lamented that the bees, themselves, now lack a formal rank. This desire to have the bees singled out with an official rank and name has led some to demote them all to a single family, Apidae. Given the diversity of bees and the tremendous utility of a multi-familial classification for this lineage, I believe it is worthwhile to retain the current classification rather than demote each taxon. However, I disagree that the bees as a whole require a formal rank. As I have noted previously (Engel, 2001: 35), the rank of epifamily could be applied and the bees would be known as “Apoidae” (i.e., basing the name on the oldest, available family-group name: *vide infra*). This would only serve to confuse issues as this name is nearly identical to superfamily Apoidea (i.e., the currently employed suffix for the rank of epifamily is unfortunate and serious consideration should be given to changing it). I believe it most prudent to not employ the rank of epifamily and to instead use a non-ranked name for the bees. The utility of the name Aculeata, long used without a formal rank, is an excellent example of a significant lineage to which a non-ranked name has been applied successfully. Indeed, some recent authors have chosen to use the non-ranked name Apiformes for the bees. Apiformes was first introduced by Rayment (1935) for what is effectively the corbiculate apines of today and was later expanded to include all bees by Brothers (1975: 640). This name has, fortunately, not achieved universal usage and for myriad reasons I suggest that it not be adopted. Perhaps the longest used name for the bees has been Anthophila as proposed by

Latreille (1804: originally in the plural as *Anthophili*, but subsequently emended: *vide etiam* Latreille, 1805, 1807). This name was used for the bees as a whole by numerous authors throughout much of the 19th and early 20th centuries (e.g., Westwood, 1840; Smith, 1853, 1855; Cresson, 1887; Dalla Torre, 1896; Handlirsch, 1925). To the best of my knowledge, this is the oldest, formalized name applied to the bees as a whole and it is, moreover, quite descriptive (meaning “lovers of flowers”). I, therefore, recommend that this name be readopted for the bees, without formal rank (*vide* appendix 1).

#### FORMAT

The format for entries generally follows that employed in similar family-group name treatments (e.g., Engel and Krishna, 2004). Daggers (†) indicate names proposed for fossil lineages. When the author originally used an incorrect spelling for the stem (*nomen imperfectum*) I have provided the name as it first appeared, followed by how the name should have appeared with a corrected stem. For example, Cockerell and Atkins (1902) proposed the name *Ericrocinae* based on the type genus *Ericrocis*; however, the stem is incorrectly formed and should have been *Ericrocidinae*. Such incorrect original stems are denoted by “*recte* *Ericrocidinae*” and simply indicate how the name *should* have appeared. If the author simply employed a non standard suffix I have not considered these as incorrectly formed and therefore did not provide such corrections. For example, Lepeletier de Saint Fargeau (1841) proposed *Rhathymites*, based on *Rhathymus*, which has as its stem *Rhathym-* and the family-group name is therefore not corrected simply because he used a different suffix for the rank of family. Alternatively, in the same paper Lepeletier de Saint Fargeau (1841) proposed *Eulemites* based on *Eulaema*, which is corrected to *Eulaemites*, denoted as “*recte* *Eulaemites*”, since the stem is *Eulaem-*. The correct combining stem for any family-group name based on the name today is provided in each entry.

I have included in the list six *nomina nuda* that are based on available genus-group names. These names were not subsequently

made available in later publications (unlike some other family-group *nomina nuda*), appearing only as *nomina nuda*. Unlike some of the other names, there is no reason to validate these names, as they would be best considered synonyms of already available names (*vide* appendix 1).

As in my other papers, I have placed as the first date for each name and article the date as it is printed in publication. If the date for nomenclatorial purposes differs from the printed date (e.g., the publication appeared later than as printed, or the name is attributed to a different date by the ICZN for purposes of priority), then this date appears in brackets following the printed date. This format is also employed in the bibliography.

#### FAMILY-GROUP NAMES

1. *Andrenetae* Latreille, 1802a: 422. Type genus: *Andrena* Fabricius, 1775. Combining stem: *Andren-*. Note: *vide etiam* *Apiariae* (*vide infra*).

2. *Nomades* Latreille, 1802a: 425. Type genus: *Nomada* Scopoli, 1770. Combining stem: *Nomad-*. Note: *vide etiam* *Apiariae* (*vide infra*).

3. *Apiariae* Latreille, 1802a: 425. Type genus: *Apis* Linnaeus, 1758. Combining stem: *Ap-*. Notes: Although the family-group names based on *Andrena* and *Nomada* have page priority (or, in the case of *Nomades*, which appears on the same page, priority in position on the printed page itself) over that based on *Apis*, it is up to the first reviser to select which name is to be given nomenclatorial priority. Such priority has been universally given to the name based on *Apis* by entomologists since the earliest days of zoological nomenclature. As to competitions of priority between *Nomadidae* and *Andrenidae*, this seems to be of little concern, but I believe priority would be owed to *Andrenidae* should any such question arise owing to the usage of *Andrenidae* and *Apidae* as the main divisions of bees in many 19th century classifications.

There had been confusion in the past as to whether the name based on *Sphex* or on *Apis* had priority and should be used to form the superfamilial name encompassing both bees and digger wasps. Unlike the preceding

names (i.e., Andrenetae and Nomades), Sphegimae Latreille (1802b: 331) did not appear until a subsequent publication in the same year (November 1802, *vide* Dupuis, 1986) and is automatically junior to the three family-group names provided in Latreille (1802a), which appeared prior to April 1802. Apoidea takes priority over Sphecoidea (as would Andrenoidea and Nomadoidea) (*vide etiam* Michener, 1986a, and Menke, 1997).

4. Eucerae Latreille, 1802b: 376. Type genus: *Eucera* Scopoli, 1770. Combining stem: Eucer-.

5. Podalirii Latreille, 1802b: 377. Type genus: *Podalirius* Latreille, 1802a. Combining stem: Podaliri-.

6. Xylocopae Latreille, 1802b: 379. Type genus: *Xylocopa* Latreille, 1802b. Combining stem: Xylocop-.

7. Ceratinae Latreille, 1802b: 380. Type genus: *Ceratina* Latreille, 1802b. Combining stem: Ceratin-.

8. Megachiles Latreille, 1802b: 381. Type genus: *Megachile* Latreille, 1802a. Combining stem: Megachil-.

9. Euglossae Latreille, 1802b: 384. Type genus: *Euglossa* Latreille, 1802a. Combining stem: Eugloss-.

10. Bombi Latreille, 1802b: 385. Type genus: *Bombus* Latreille, 1802a. Combining stem: Bomb-.

11. Prosopiariae Fallén, 1813: 32. Type genus: *Prosopis* Fabricius, 1804 (*nec Prosopis* Jurine *In* Panzer, 1801, *nomen rejiciendum* [ICZN, 1939]). Combining stem: Propid-.

12. Panurgida Leach, 1815: 156. Type genus: *Panurgus* Panzer, 1806. Combining stem: Panurg-.

13. Anthrenoides Burmeister, 1829: 30, *nomen imperfectum* [*recte* Anthrenides]. Type genus: *Anthrena* Illiger, 1801, *nomen vanum*. Combining stem: Anthren-. Note: This name should not be confused with the genus-group name *Anthrenoides* Ducke.

14. Melliturgites Newman, 1834: 379, *nomen imperfectum* [*recte* Melitturgites]. Type genus: *Melitturga* Latreille, 1809. Combining stem: Melitturg-.

15. Lithurgites Newman, 1834: 379. Type genus: *Lithurgus* Berthold, 1827. Combining stem: Lithurg-.

16. Apathites Newman, 1834: 379. Type

genus: *Apathus* Newman, 1834. Combining stem: Apath-.

17. Osmiites Newman, 1834: 401. Type genus: *Osmia* Panzer, 1806. Combining stem: Osmi-.

18. Anthophorini Dahlbom, 1835: 5. Type genus: *Anthophora* Latreille, 1803. Combining stem: Anthophor-.

19. Meliponites Lepeletier de Saint Fargeau, 1836: 407. Type genus: *Melipona* Illiger, 1806. Combining stem: Melipon-.

20. Chelostomidae Kirby, 1837: 270. Type genus: *Chelostoma* Latreille, 1809. Combining stem: Chelostom-.

21. Melectides Westwood, 1840 [1839]: 270. Type genus: *Melecta* Latreille, 1802a. Combining stem: Melect-.

22. Eulemites Lepeletier de Saint Fargeau, 1841: 218, *nomen imperfectum* [*recte* Eulaemites]. Type genus: *Eulaema* Lepeletier de Saint Fargeau, 1841. Combining stem: Eulaem-.

23. Colletides Lepeletier de Saint Fargeau, 1841: 295. Type genus: *Colletes* Latreille, 1802a. Combining stem: Collet-. Note: Although employed by Lepeletier de Saint Fargeau (1841) as a French vernacular, the name was adopted by later authors in latinized form and considered valid. Lepeletier de Saint Fargeau's name is, therefore, available as a family-group name, dating from the first publication employing it as a vernacular (ICZN, 1999a: Art. 11.7.2). The same condition holds true for other family-group names proposed by this author.

24. Psithyrides Lepeletier de Saint Fargeau, 1841: 423. Type genus: *Psithyrus* Lepeletier de Saint Fargeau, 1832. Combining stem: Psithyr-.

25. Phileremides Lepeletier de Saint Fargeau, 1841: 510. Type genus: *Phileremus* Latreille, 1809. Combining stem: Philerem-.

26. Rhathymites Lepeletier de Saint Fargeau, 1841: 539. Type genus: *Rhathymus* Lepeletier de Saint Fargeau and Audinet-Serville, 1828. Combining stem: Rhathym-.

27. Melittidae Schenck, 1860: 136. Type genus: *Melitta* Kirby, 1802. Combining stem: Melitt-.

28. Stelidae Schenck, 1860: 141, *nomen imperfectum* [*recte* Stelididae]. Type genus: *Stelis* Panzer, 1806. Combining stem: Stelid-.

29. Rhophitidae Schenck, 1866 [1867]:



322, *nomen imperfectum* [recte Rophitidae]. Type genus: *Rophites* Spinola, 1808. Combining stem: Rophit-.

30. Sphecodidae Schenck, 1868 [1869]: 316. Type genus: *Sphecodes* Latreille, 1804. Combining stem: Sphecod-.

31. Megillina Thomson, 1869: 7. Type genus: *Megilla* Fabricius, 1804. Combining stem: Megill-.

32. Halictina Thomson, 1869: 8. Type genus: *Halictus* Latreille, 1804. Combining stem: Halict-.

33. Coelioxynae Dalla Torre and Friese, 1894: 35. Type genus: *Coelioxys* Latreille, 1809. Combining stem: Coeliox-.

34. Neolarrini Fox, 1894 [1895]: 302. Type genus: *Neolarra* Ashmead, 1890. Combining stem: Neolarr-.

35. Oxaeinae Ashmead, 1899a: 70. Type genus: *Oxaea* Klug, 1807a. Combining stem: Oxae-.

36. Anthidiinae Ashmead, 1899a: 72. Type genus: *Anthidium* Fabricius, 1804. Combining stem: Anthidi-.

37. Centrini Cockerell and Cockerell, 1901: 47, *nomen imperfectum* [recte Centridini]. Type genus: *Centris* Fabricius, 1804. Combining stem: Centrid-.

38. Melissodinae Robertson, 1901: 231. Type genus: *Melissodes* Latreille, 1829. Combining stem: Melissod-. Note: This name has been overlooked by most bee systematists. It was first noticed by M. G. Rightmyer and I am grateful that she has brought it to my attention.

39. Ericrocinae Cockerell and Atkins, 1902: 46, *nomen imperfectum* [recte Ericrocidae]. Type genus: *Ericrocis* Cresson, 1887. Combining stem: Ericrocid-.

40. Dioxinae Cockerell, 1902: 233, *nomen imperfectum* [recte Dioxyinae]. Type genus: *Dioxys* Lapeletier de Saint Fargeau and Audinet-Serville, 1825. Combining stem: Dioxy-.

41. Allodapinae Cockerell, 1902: 233. Type genus: *Allodape* Lapeletier de Saint Fargeau and Audinet-Serville, 1825. Combining stem: Allodap-.

42. Trypetini Robertson, 1903a: 164. *Nomen praeoccupatum* (nec Trypetidae Loew, 1861 [Diptera: Tephritidae]). Type genus: *Trypetes* Schenck, 1859 [1861], *nomen praeoccupatum* (nec *Trypetes* Schönherr,

1836 [Coleoptera: Curculionidae]). Combining stem: Trypet-. Note: The family-group name is also homonymous with a family-group name based on *Trypetes* Schönherr, 1836; i.e., Trypetinae Lacordaire, 1866 (originally spelled Trypetides by Lacordaire, but given a standard family-group suffix by Pascoe, 1870). The coleopterous taxon was emended to Trypetidinae (Pierce, 1919; ICZN, 1974), preserving Trypetinae for a lineage of flies based on the genus *Trypeta* Meigen, 1803. The family-group name based on *Trypetes* Robertson, 1903a cannot be conserved since its type genus is also a junior homonym (ICZN, 1999a: Art. 39).

43. Epeolinae Robertson, 1903b: 284. Type genus: *Epeolus* Latreille, 1802a. Combining stem: Epeol-.

44. Trachusinae Robertson, 1904: 37. Type genus: *Trachusa* Panzer, 1804b. Combining stem: Trachus-.

45. Exoneuridae Robertson, 1904: 37. Type genus: *Exoneura* Smith, 1854. Combining stem: Exoneur-.

46. Protandreninae Robertson, 1904: 38. Type genus: *Protandrena* Cockerell, 1896. Combining stem: Protandren-.

47. Dufoureae Robertson, 1904: 42. Type genus: *Dufourea* Lapeletier de Saint Fargeau, 1841. Combining stem: Dufourea-.

48. Nomiidae Robertson, 1904: 42. Type genus: *Nomia* Latreille, 1804. Combining stem: Nomi-.

49. Macropididae Robertson, 1904: 42. Type genus: *Macropis* Panzer, 1809. Combining stem: Macropid-.

50. Emphoridae Robertson, 1904: 43. Type genus: *Emphor* Patton, 1879. Combining stem: Emphor-.

51. Entechniini Cockerell, 1906: 99. Type genus: *Entechnia* Patton, 1879. Combining stem: Entechni-.

52. Palaeorhizidae Perkins, 1908: 29. Type genus: *Palaeorhiza* Perkins, 1908. Combining stem: Palaeorhiz-.

53. Meroglossidae Perkins, 1908: 29. Type genus: *Meroglossa* Smith, 1853. Combining stem: Merogloss-. Note: Although proposed tentatively by Perkins (1908) the name dates from that publication since prior to 1931 the simple formation of any family-group name based on an available genus-group name is

to be considered available (ICZN, 1999a: Art. 12.2.4).

**54.** Exaeretinae Cockerell, 1908: 41. Type genus: *Exaerete* Hoffmannsegg, 1817. Combining stem: Exaeret-.

**55.** Exomalopses Vachal, 1909: 7. Type genus: *Exomalopsis* Spinola, 1853. Combining stem: Exomalops-.

**56.** Melitomatae Vachal, 1909: 7. Type genus: *Melitoma* Lepeletier de Saint Fargeau and Audinet-Serville, 1828. Combining stem: Melitom-.

**57.** Diphaglossinae Vachal, 1909: 33. Type genus: *Diphaglossa* Spinola, 1851. Combining stem: Diphagloss-.

**58.** †Glyptapinae Cockerell, 1909b: 13. Type genus: *Glyptapis* Cockerell, 1909a. Combining stem: Glyptap-.

**59.** Oxystoglossini Schrottky, 1909a: 482. Type genus: *Oxystoglossa* Smith, 1853. Combining stem: Oxystogloss-.

**60.** Eucondylopsinae Friese, 1909: 99. Type genus: *Eucondylops* Brauns, 1902. Combining stem: Eucondylops-.

**61.** Hemisiinae Cockerell and Robbins, 1910: 183. Type genus: *Hemisia* Klug, 1807b. Combining stem: Hemisi-.

**62.** Gastrohalictinae Schrottky, 1911: 84. Type genus: *Gastrohalictus* Ducke, 1902. Combining stem: Gastrohalict-.

**63.** Epicharitina Schrottky, 1913: 259. Type genus: *Epicharis* Klug, 1807b. Combining stem: Epicharit-.

**64.** Tetraloniinae Schrottky, 1913: 263. Type genus: *Tetralonia* Spinola, 1838. Combining stem: Tetraloni-.

**65.** Hylaeidae Viereck, 1916: 737. Type genus: *Hylaeus* Fabricius, 1793. Combining stem: Hylae-. Note: The name *Prosopiaridae* Fallén, 1813 has priority over Hylaeidae; however, the family-group name based on *Hylaeus* has been conserved over that based on *Prosopis* (ICZN, 1993).

**66.** Dasypodinae Börner, 1919: 180 (Dasypodainae, *nomen emendatum* [ICZN, 1999b]). Type genus: *Dasyпода* Latreille, 1802a. Combining stem: Dasyпода-. Note: The stem of the family-group name based on *Dasyпода* Latreille, 1802a was altered from Dasyпод- to Dasyпода- by ICZN (1999b).

**67.** Halictoidinae Börner, 1919: 181. Type genus: *Halictoides* Nylander, 1848. Combining stem: Halictoid-.

**68.** Nomioidini Börner, 1919: 181. Type genus: *Nomioides* Schenck, 1866 [1867]. Combining stem: Nomioid-.

**69.** Bremidae Frison, 1919: 157. Type genus: *Bremus* Panzer, 1804a (*nec Prosopis* Jurine in Panzer, 1801, *nomen rejiciendum* [ICZN 1939: Op. 135]). Combining stem: Brem-.

**70.** Perditinae Robertson, 1922: 160. Type genus: *Perdita* Smith, 1853. Combining stem: Perdit-.

**71.** Calliopsinae Robertson, 1922: 160. Type genus: *Calliopsis* Smith, 1853. Combining stem: Calliops-.

**72.** Anthemurginae Robertson, 1922: 160. Type genus: *Anthemurgus* Robertson, 1902a. Combining stem: Anthemurg-.

**73.** Systrophini Handlirsch, 1925: 819. Type genus: *Systropha* Illiger, 1806. Combining stem: Systroph-.

**74.** Odyneropsini Handlirsch, 1925: 821. Type genus: *Odyneropsis* Schrottky, 1902. Combining stem: Odynerops-.

**75.** Osirini Handlirsch, 1925: 821. Type genus: *Osiris* Smith, 1854. Combining stem: Osir-.

**76.** Ammobatini Handlirsch, 1925: 821. Type genus: *Ammobates* Latreille, 1809. Combining stem: Ammobat-.

**77.** Melanempidini Handlirsch, 1925: 821. Type genus: *Melanempis* Saussure, 1890 [1892]. Combining stem: Melanempid-.

**78.** Chrysanthedinae Handlirsch, 1925: 821. Type genus: *Chrysantheda* Perty, 1833. Combining stem: Chrysanthed-.

**79.** Aglainae Handlirsch, 1925: 822. Type genus: *Aglae* Lepeletier de Saint Fargeau and Audinet-Serville, 1825. Combining stem: Agla-.

**80.** Augochloridae Beebe, 1925: 102. Type genus: *Augochlora* Smith, 1853. Combining stem: Augochlor-. Note: This name is widely indicated to date from Moure (1943). However, as noted by Engel (1999a, 2000), the correct author and date is Beebe (1925).

**81.** Lasioglossinae Robertson, 1926: 117. Type genus: *Lasioglossum* Curtis, 1833. Combining stem: Lasiogloss-.

**82.** Chloralictini Robertson, 1926: 117. Type genus: *Chloralictus* Robertson, 1902b. Combining stem: Chloralict-.

**83.** Pasititidae Robertson, 1926: 118, *nomen imperfectum* [recte Pasitidae]. Type ge-

nus: *Pasites* Jurine, 1807. Combining stem: Pasit-.

**84.** Xeromelissinae Cockerell, 1926: 222. Type genus: *Xeromelissa* Cockerell, 1926. Combining stem: Xeromeliss-.

**85.** Hylaeoidinae Cockerell, 1930a: 148, *nomen imperfectum* [recte Hyleoidinae]. Type genus: *Hyleoides* Smith, 1853. Combining stem: Hyleoid-.

**86.** Neopasiphaeinae Cockerell, 1930a: 148. Type genus: *Neopasiphae* Perkins, 1912. Combining stem: Neopasiphae-.

**87.** Ctenoplectridae Cockerell, 1930a: 148. Type genus: *Ctenoplectra* Kirby in Kirby and Spence, 1826. Combining stem: Ctenoplectr-.

**88.** Fideliidae Cockerell, 1932: 358. Type genus: *Fidelia* Friese, 1899. Combining stem: Fideli-.

**89.** Stenotritini Cockerell, 1934: 6. Type genus: *Stenotritus* Smith, 1853. Combining stem: Stenotrit-. Note: The family-group names established by Cockerell in this account of Australian bees (namely, Stenotritini, Phenacolletini, and Paracolletini) are quite problematic, although the solution to the nomenclatorial dilemma proves to be merely academic as it does not alter their usage. None of the three family-group names proposed in this article are provided with a description and therefore fail one of the criteria for availability of such names established after 1930 (ICZN, 1999a: Art. 13.1). Cockerell merely notes at the top of page 6 in his article, "The genera may be divided into three tribes, Stenotritini, Phenacolletini and Paracolletini", and then later includes them as headers for sections considering the species in further detail (but again, does not accompany the tribal headings with any characters purported to differentiate them from each other or from other such suprageneric groups). Thus, Stenotritini, Phenacolletini, and Paracolletini should be considered *nomina nuda*. However, while Cockerell's names fail Article 13.1, two of them (i.e., Stenotritini and Paracolletini) satisfy the provision to 13.1 provided by 13.2.1 (ICZN, 1999a) whereby a name proposed after 1930 and before 1961 that lacks a description is to be considered available from its original publication *only* if it was employed as valid before 2000 and was not rejected by any author applying Article 13.1 between 1960 and

2000. Thus, the usage of Stenotritini and Paracolletini by subsequent authors (e.g., Michener, 1944, 1965) and the fact that no author rejected the names as *nomina nuda* between 1960 and 2000 permits these two names to be considered available from Cockerell (1934). This is not the case for Phenacolletini (*vide infra*).

**90.** Phenacolletini Cockerell, 1934: 7, *nomen nudum*. Type genus: *Phenacolletes* Cockerell, 1905. Combining stem: Phenacollet-. Note: As discussed under Stenotritini (*vide supra*), Phenacolletini was technically a *nomen nudum* in Cockerell (1934). Unlike Stenotritini and Paracolletini, which are conserved by the provisions of Article 13.2.1 (ICZN, 1999a), Phenacolletini was not employed as valid by later authors and thus remains unavailable. While it might be argued that Rayment (1935, p. 186) subsequently employed the name Phenacolletini, I cannot consider this to be true since Rayment is merely quoting the line from Cockerell (1934). I cannot see any reason why Phenacolletini should be made available herein as it is clearly a synonym.

**91.** Paracolletini Cockerell, 1934: 8. Type genus: *Paracolletes* Smith, 1853. Combining stem: Paracollet-. Note: Refer to discussion under Stenotritini (*vide supra*).

**92.** Biastini Linsley and Michener, 1939: 272. Type genus: *Biastes* Panzer, 1806. Combining stem: Biast-.

**93.** Neopasitini Linsley and Michener, 1939: 274. Type genus: *Neopasites* Ashmead, 1898. Combining stem: Neopasit-.

**94.** Epeoloidini Linsley and Michener, 1939: 294. Type genus: *Epeoloides* Giraud, 1863. Combining stem: Epeoloid-.

**95.** Protepeolini Linsley and Michener, 1939: 301. Type genus: *Protepeolus* Linsley and Michener, 1937. Combining stem: Protepeol-.

**96.** Heriadini Michener, 1941: 152. Type genus: *Heriades* Spinola, 1808. Combining stem: Heriad-.

**97.** Augochloropsini Moure, 1943: 462. Type genus: *Augochloropsis* Cockerell, 1897. Combining stem: Augochlorops-. Note: Although a character description is not provided for this tribe, Moure's statement that it is proposed for Vachal's (1911) "*Halicti vibrissati*" can be considered biblio-



graphic reference to a description, therefore making the name available in this publication by indication.

**98.** Megaloptinae Moure, 1943: 479. Type genus: *Megalopta* Smith, 1853. Combining stem: Megalopt-.

**99.** Caupolicanini Michener, 1944: 238. Type genus: *Caupolicana* Spinola, 1851. Combining stem: Caupolican-.

**100.** Euryglossinae Michener, 1944: 238. Type genus: *Euryglossa* Smith, 1853. Combining stem: Eurygloss-.

**101.** Chilicolinae Michener, 1944: 240. Type genus: *Chilicola* Spinola, 1851. Combining stem: Chilicol-.

**102.** Ancylini Michener, 1944: 273. Type genus: *Ancyla* Lepeletier de Saint Fargeau, 1841. Combining stem: Ancy-.

**103.** Caenoprosopidini Michener, 1944: 275. Type genus: *Caenoprosopis* Holmberg, 1886. Combining stem: Caenoprosopid-.

**104.** Townsendiellini Michener, 1944: 277. Type genus: *Townsendiella* Crawford, 1916. Combining stem: Townsendiell-.

**105.** Ammobatoidini Michener, 1944: 277. Type genus: *Ammobatoides* Radoszkowski, 1868 [1867]. Combining stem: Ammobatoid-.

**106.** Eufrieseini Moure, 1944: 12. Type genus: *Eufriesea* Cockerell, 1908a. Combining stem: Eufriese-.

**107.** Eulonchopriinae Moure, 1945: 140. Type genus: *Eulonchopria* Brèthes, 1909. Combining stem: Eulonchopri-.

**108.** Lonchopriinae Moure, 1945: 141. Type genus: *Lonchopria* Vachal, 1905b. Combining stem: Lonchopri-.

**109.** Dissoglottini Moure, 1945: 142. Type genus: *Dissoglotta* Moure, 1945. Combining stem: Dissoglott-.

**110.** Trigonini Moure, 1946: 611. Type genus: *Trigona* Jurine, 1807. Combining stem: Trigon-.

**111.** Lestrimelittini Moure, 1946: 611. Type genus: *Lestrimelitta* Friese, 1903b. Combining stem: Lestrimelitt-.

**112.** Dianthidiini Moure, 1947: 15. Type genus: *Dianthidium* Cockerell, 1900. Combining stem: Dianthidi-.

**113.** Trichothurgini Moure, 1949: 268. Type genus: *Trichothurgus* Moure, 1949. Combining stem: Trichothurg-.

**114.** Pararhophitini Popov, 1949: 507.

Type genus: *Pararhophites* Friese, 1898. Combining stem: Pararhophit-.

**115.** Euerbstiinae Moure, 1950: 303. Type genus: *Euerbstia* Friese, 1925. Combining stem: Euerbsti-.

**116.** Ptiloglossidiini Moure, 1953: 71. Type genus: *Ptiloglossidia* Moure, 1953. Combining stem: Ptiloglossidi-.

**117.** Caenohalictinae Michener, 1954: 97. Type genus: *Caenohalictus* Cameron, 1903. Combining stem: Caenohalict-.

**118.** Canephorulini Michener, LaBerge, and Moure, 1955: 207. Type genus: *Canephorula* Jörgensen, 1909. Combining stem: Canephorul-.

**119.** Eucerinodini Michener and Moure, 1957: 444. Type genus: *Eucerinoda* Michener and Moure, 1957. Combining stem: Eucerinod-.

**120.** Tetrapediini Michener and Moure, 1957: 442. Type genus: *Tetrapedia* Klug, 1810. Combining stem: Tetrapedi-.

**121.** Ctenioschelini Michener, 1965a: 10, *nomen nudum*. Type genus: *Ctenioschelus* Romand, 1840. Combining stem: Ctenioschel-. Note: This name is not available from this publication since it was merely included in a list of tribes but not accompanied by a description as required for family-group names after 1930 (ICZN, 1999a: Arts. 13.1, 13.2). It has not been subsequently made available and I do not believe it is necessary to do so now as it is assuredly a synonym of Ericrocidini.

**122.** Mydrosomini Michener, 1966: 719, *nomen imperfectum* [*recte* Mydrosomatini]. Type genus: *Mydrosoma* Smith, 1879. Combining stem: Mydrosomat-.

**123.** Holcopasitini Rozen, 1966: 30. Type genus: *Holcopasites* Ashmead, 1899a. Combining stem: Holcopasit-.

**124.** Pachyanthidiini Pasteels, 1969: 6. Type genus: *Pachyanthidium* Friese, 1905. Combining stem: Pachyanthidi-.

**125.** Icteranthidiini Pasteels, 1969: 7. Type genus: *Icteranthidium* Michener, 1948. Combining stem: Icteranthidi-.

**126.** Euaspini Pasteels, 1969: 7. Type genus: *Euaspis* Gerstäcker, 1857. Combining stem: Euasp-.

**127.** Thrinchostomini Sakagami, 1974: 258, *nomen imperfectum* [*recte* Thrinchostomatini]. Type genus: *Thrinchostoma* Saus-

sure, 1890 [1892]. Combining stem: Thrinchostomat-.

**128.** Habropodini Marikovskaya, 1976: 688. Type genus: *Habropoda* Smith, 1854. Combining stem: Habropod-.

**129.** Isepeolini Rozen, Eickwort, and Eickwort, 1978: 18. Type genus: *Isepeolus* Cockerell, 1907. Combining stem: Isepeol-.

**130.** Meganomiinae Michener, 1981: 18. Type genus: *Meganomia* Cockerell, 1909c. Combining stem: Meganomi-.

**131.** Promelittini Michener, 1981: 60. Type genus: *Promelitta* Warncke, 1977. Combining stem: Promelitt-.

**132.** Sambini Michener, 1981: 60. Type genus: *Samba* Friese, 1908. Combining stem: Samb-.

**133.** Manueliini Sakagami and Michener, 1987: 439. Type genus: *Manuelia* Vachal, 1905a. Combining stem: Manueli-.

**134.** Protomeliturgini Ruz, 1991: 215. Type genus: *Protomeliturga* Ducke, 1912. Combining stem: Protomeliturg-.

**135.** Brachynomadini Roig-Alsina and Michener, 1993: 157. Type genus: *Brachynomada* Holmberg, 1886. Combining stem: Brachynomad-. Note: Descriptions, which are required after 1930 (ICZN, 1999a: Arts. 13.1., 13.2, “must be accompanied by a description that states in words characters that are purported to differentiate the taxon”; and were also required by the edition of the Code that was applicable in 1993; namely, ICZN, 1985: Art. 13a), of new family-group taxa are difficult to discern in this publication and I do not believe that the extraction of characters mapped from their numerous cladograms can be considered diagnoses since no unique tree or suite of characters are explicitly cited for defining their new taxa. However, family-group names can be made available by reference, and in the case of Brachynomadini these authors explicitly refer to the definition of the “melanomadine complex of Alexander (1990)”. I, therefore, believe them to have satisfactorily met the criteria for availability by bibliographic reference to a description.

**136.** Tapinotaspidini Moure, 1992 [1994]: 306. Type genus: *Tapinotaspis* Holmberg, 1903. Combining stem: Tapinotaspid-. Note: This name was first mentioned in Roig-Alsina and Michener (1993: 159), as Tapino-

taspini Roig-Alsina and Michener, 1993, *nomen imperfectum* [recte Tapinotaspidini] and is widely held to be available from that publication (e.g., Michener, 1997). For the same reasons described for Hexepeolini (*vide infra*) I believe that Tapinotaspidini was a *nomen nudum* in 1993 as no description was provided as clearly required by the Code (ICZN, 1999a: Arts. 13.1, 13.2; and was also required by the edition of the Code which was applicable in 1993; namely, ICZN, 1985: Art. 13a). It might be believed that the statement, “These genera are those of sections 1, 2, and 5 of Exomalopsini as understood by Michener and Moure (1957)”, could qualify as a bibliographic reference, but there are no diagnostic traits given to unite groups 1, 2, and 5 together in the cited paper (which would, therefore, represent characters of Tapinotaspidini). As such, the reference fails to validate the name by indication. However, Moure’s (1992: NB; this paper dates for nomenclatorial purposes from 1994) subsequent account of the tribe includes a description and employs a family-group name based on an available genus-group name. I, therefore, consider the name as having been first made available in the latter paper, despite Michener’s (1997) comments to the contrary (Roig-Alsina, 1997, also includes what can be considered a description of the tribe). Since both Tapinotaspidini and Paratetrapediini date from the same paper and are synonyms, I here select the former name for the tribe following current taxonomic usage.

**137.** Paratetrapediini Moure, 1992 [1994]: 306. Type genus: *Paratetrapedia* Moure, 1941. Combining stem: Paratetrapedi-.

**138.** Hexepeolini Rozen, 1996: 188. Type genus: *Hexepeolus* Linsley and Michener, 1937. Combining stem: Hexepeol-. Note: This name suffers the same problem as described for Brachynomadini and Tapinotaspidini (*vide supra*). The name was first mentioned in Roig-Alsina and Michener (1993: 157) as Hexepeolini Roig-Alsina and Michener, 1993, and is widely held to be available from that publication. However, I believe that Hexepeolini was a *nomen nudum* in 1993. I cannot conscientiously consider it as available from Roig-Alsina and Michener (1993) despite the inclusion of only *Hexepeolus* since

no description or bibliographic reference to such a description is provided (as explicitly required by the Code [ICZN, 1999a: Arts. 13.1, 13.2] and was also required by the edition of the Code that was applicable in 1993; namely, ICZN, 1985: Art. 13a). Inclusion of a single genus does not validate the name, as such an indication is not valid after 1930. Thus, I consider Hexepeolini Roig-Alsina and Michener, 1993 a *nomen nudum* and unavailable from that work. The next paper providing a clear description that can loosely be attributed to the tribe (i.e., providing in words characters that purport to differentiate the taxon from others), albeit based on larval characters, is that of Rozen (1996) who, prior to his description, states, “was assigned to its own monotypic tribe, the Hexepeolini” (NB: prior to 1999 it was not necessary to explicitly state that a family-group name was new). Since Rozen (1996) uses a family-group name based on an available genus-group name and provides a differential diagnosis that can be loosely attributed to the tribe, I consider the name Hexepeolini to have been made available in that work.

**139.** Teratognathini Silveira, 1995: 449. Type genus: *Teratognatha* Ogloblin, 1956. Teratognath-.

**140.** †Electrapina Engel, 1998a: 99. Type genus: †*Electrapis* Cockerell, 1908b. Combining stem: Electrap-.

**141.** Camptopoeumini Patiny, 1999: 270, *nomen imperfectum* [recte Camptopoeini]. Type genus: *Camptopoeum* Spinola, 1843. Combining stem: Camptopoe-. Note: *Camptopoeum* is a combination of the Greek words *kampto* (meaning “bend”) and *poieo* (meaning “make”). The latter word, when latinized, has as its stem *poe-* and, as such, the spelling of the family-group name is corrected herein.

**142.** Mermiglossini Patiny, 1999: 270. Type genus: *Mermiglossa* Friese, 1912. Combining stem: Mermigloss-.

**143.** Panurginini Patiny, 1999: 271. Type genus: *Panurginus* Nylander, 1848. Combining stem: Panurgin-.

**144.** †Chalicodomopsini Engel, 1999b: 4, *nomen nudum*. Type genus: †*Chalicodomopsis* Engel, 1999b. Combining stem: Chalicodomops-. Note: This family-group name is unavailable, since after 1930 all fam-

ily-group names require a formal description (ICZN, 1999a: Art. 13.2). There is no reason to validate it herein.

**145.** Corynurina Engel, 2000: 51. Type genus: *Corynura* Spinola, 1851. Combining stem: Corynur-.

**146.** Ischnomelissiti Engel, 2000: 66. Type genus: *Ischnomelissa* Engel, 1997. Combining stem: Ischnomeliss-.

**147.** Thectochloriti Engel, 2000: 66. Type genus: *Thectochlora* Moure, 1940. Combining stem: Thectochlor-.

**148.** Megaloptidiiti Engel, 2000: 66. Type genus: *Megaloptidia* Cockerell, 1900. Combining stem: Megaloptidi-.

**149.** Agapostemonina Engel, 2000: 67. Type genus: *Agapostemon* Guérin-Ménéville, 1844. Combining stem: Agapostemon-.

**150.** Alocandreninae Michener, 2000: 228. Type genus: *Alocandrena* Michener, 1986b. Combining stem: Alocandren-.

**151.** Liphanthini Michener, 2000: 262, *nomen nudum*. Type genus: *Liphanthus* Reed, 1894. Combining stem: Liphanth-. Note: This name was first used in an unpublished doctoral dissertation by Ruz (1987) and was thus unavailable. Its subsequent usage has not made it available and there seems little reason to do so since it would merely be a synonym of Protandrenini.

**152.** Austropanurgini Michener, 2000: 262, *nomen nudum*. Type genus: *Austropanurgus* Toro, 1980. Combining stem: Austropanurg-. Note: This name suffers the same problems as Liphanthini; see note for Liphanthini (*vide supra*).

**153.** Hoplitini Nobile and Tomarchio, 2000: 46, *nomen nudum*. Type genus: *Hoplitis* Klug, 1807b. Combining stem: Hoplit-.

**154.** Penapini Engel, 2001: 37. Type genus: *Penapis* Michener, 1965b. Combining stem: Penap-.

**155.** †Paleomelittidae Engel, 2001: 41. Type genus: †*Paleomelitta* Engel, 2001. Combining stem: Paleomelitt-.

**156.** Redivivini Engel, 2001: 45. Type genus: *Rediviva* Friese, 1911. Combining stem: Rediviv-.

**157.** †Eomacropidini Engel, 2001: 46. Type genus: †*Eomacropis* Engel, 2001. Combining stem: Eomacropid-.

**158.** †Protolithurgini Engel, 2001: 51.

Type genus: †*Protolithurgus* Engel, 2001.  
Combining stem: Protolithurg-.

**159.** †*Ctenoplectrellina* Engel, 2001: 54.  
Type genus: †*Ctenoplectrella* Cockerell,  
1909a. Combining stem: Ctenoplectrell-.

**160.** †*Boreallodapini* Engel, 2001: 77.  
Type genus: †*Boreallodape* Engel, 2001.  
Combining stem: Boreallodap-.

**161.** †*Electrobombini* Engel, 2001: 88.  
Type genus: †*Electrobombus* Engel, 2001.  
Combining stem: Electrobomb-.

**162.** †*Melikertini* Engel, 2001: 112. Type  
genus: †*Melikertes* Engel, 1998a. Combining  
stem: Melikert-.

**163.** *Meliturgulini* Engel, 2001: 179. Type  
genus: *Meliturgula* Friese, 1903a. Combining  
stem: Meliturgul-. Note: *Meliturgulini* re-  
places the name *Paramelitturgini* Patiny,  
1999: 272, *nomen illegitimum*, the latter of  
which was not based on an available genus-  
group name (and is, therefore, excluded from  
the list presented here).

**164.** *Nolanomelissini* Rozen and Ascher *in*  
Rozen, 2003: 102. Type genus: *Nolanomelis-*  
*sa* Rozen, 2003. Combining stem: Nolanom-  
meliss-.

**165.** *Rhogepeolina* Rightmyer, 2004: 15.  
Type genus: *Rhogepeolus* Moure, 1955.  
Combining stem: Rhogepeol-.

**166.** *Thalestriina* Rightmyer, 2004: 17.  
Type genus: *Thalestria* Smith, 1854. Comb-  
ining stem: Thalestri-.

**167.** *Neofideliina* Engel, 2004: 826. Type  
genus: *Neofidelia* Moure and Michener,  
1955. Combining stem: Neofideli-.

**168.** *Scraptrinae* Ascher and Engel, herein  
(*vide infra*). Type genus: *Scrapter* Lepeletier  
de Saint Fargeau and Audinet-Serville, 1828.  
Combining stem: Scraptr-.

**169.** *Neffapini* Ascher, herein (*vide infra*).  
Type genus: *Neffapis* Ruz *in* Rozen and Ruz,  
1995. Combining stem: Neffap-.

**170.** *Afrodasyopodini* Engel, herein (*vide*  
*infra*). Type genus: *Afrodasyopoda* Engel,  
herein (*vide infra*). Combining stem: Afrod-  
asyopod-.

**171.** *Hesperapina* Ascher and Engel, herein  
(*vide infra*). Type genus: *Hesperapis* Cock-  
erell, 1898. Combining stem: Hesperap-.

**172.** *Macrogaleina* Engel, herein (*vide in-*  
*fra*). Type genus: *Macrogalea* Cockerell,  
1930b. Combining stem: Macrogale-.

**173.** *Ancyloscelidina* Engel and Michener,

herein (*vide infra*). Type genus: *Ancyloscelis*  
Latreille, 1829. Combining stem: Ancylos-  
celid-. Note: The name was first mentioned  
in Roig-Alsina and Michener (1993: 159), as  
*Ancyloscelina* Roig-Alsina and Michener,  
1993, *nomen imperfectum* [*recte* *Ancyloscel-*  
*idina*]. However, this name suffers the same  
problem as described for *Brachynomadini*  
and I believe that *Ancyloscelidina* was a *no-*  
*men nudum* in 1993. I cannot conscionably  
consider it as available from Roig-Alsina and  
Michener (1993) despite the inclusion of  
only *Ancyloscelis* since no description or bib-  
liographic reference to such a description is  
provided (as explicitly required by the Code  
[ICZN, 1999a: Arts. 13.1, 13.2] and was also  
required by the edition of the Code that was  
applicable in 1993; namely, ICZN, 1985:  
Art. 13a). Indeed, the subtribe is “diag-  
nosed” by its exclusion from the subtribe  
*Emphorina*, which is not explicitly diagnosed  
therein either and thus one cannot extrapolate  
the characters purported to differentiate An-  
cyloscelidina. Inclusion of a single genus  
does not validate the name, as such an indi-  
cation is not valid after 1930. Thus, I con-  
sider *Ancyloscelidina* Roig-Alsina and Mich-  
ener, 1993 a *nomen nudum* and unavailable  
from that work. Unfortunately, no paper be-  
tween 1993 and the publication of the most  
recent edition of the Code (ICZN, 1999a) has  
made the name available. While Michener  
(2000) also employed the subtribal name,  
post 1999 a family-group name must explic-  
itly state that it is proposed as new, cite a  
type genus, and be accompanied by a de-  
scription purporting characters that diagnose  
the taxon (ICZN, 1999a: Art. 16), the first  
two of which are not included therein. No  
such account for *Ancyloscelidina* has ap-  
peared and the name is, therefore, newly  
made available herein (*vide infra*).

## SYSTEMATICS

Below are provided descriptions for six  
new family-group taxa. The placement of the  
new taxa among other bee lineages can be  
determined from the outline provided in ap-  
pendix 1 as well as under the comments pro-  
vided for each. In the diagnoses, the concepts  
of the various higher taxa of Apoidea are  
those as outlined in appendix 1 (e.g., Hyla-



einae herein is used in a broader sense to encompass the former subfamilies Euryglossinae and Xeromelissinae as tribes).

**SCRAPTRINAE** Ascher and Engel,  
new subfamily

TYPE GENUS: *Scapter* Lepeletier de Saint Fargeau and Audinet-Serville, 1828 (*nec Scapter* Lepeletier de Saint Fargeau, 1841).

DIAGNOSIS: Body form of adults elongate as in many Xeromelissini; nonmetallic; vestiture sparse in most species. Premental fovea present (as in Xeromelissini and Hylaeini: homologous foveae are less well defined in Euryglossini; absent in true Paracolletinae, Colletinae *s. str.*, and Diphaglossinae); galeal comb reduced, usually to 3–4 small bristles. Facial foveae a narrow groove in many species, relatively broad in certain species but never densely setose and confined to a broad band between the compound eye and the lateral ocellus as in Colletinae *s. str.* and Diphaglossinae. Metabasitibial plate present (in many species carinate margin is interrupted, and in some species distinct lobes or tubercles are found resembling the tubercles characteristic of Euryglossini; absence of metabasitibial plates in Xeromelissini and Hylaeini may be correlated with cavity-nesting habits characteristic of these tribes; ground nesting in certain members of these tribes is likely secondary). Inner metatibial spur of female straight, tapering, ciliate; scopa of hind legs well developed; hind legs of males of certain species modified, with metafemur swollen and metabasitarsus expanded posteriorly towards apex (this modification is closely paralleled in many xeromelissine males: compare illustrations of *Scapter* in Eardley, 1996, with those of xeromelissines in Toro and Moldenke, 1979). Forewing with two submarginal cells; second submarginal cell more than two-thirds as long as first (much shorter in most Hylaeinae *s. lato*, excepting, e.g., *Hyleoides*); pterostigma usually large, receiving r-rs towards middle. Pygidial and prepygidial fimbria of female present. Male S7 with apical lobes reduced or absent; if present, lobes small, aetose, laterally directed (Eardley, 1996: 37, twice erroneously referred to S8 of *Scapter* as “seventh sternite”); his diagnosis on the following page is

correct), elongate and with apex protruding externally in dorsal view, superficially resembling a pygidial plate, which is absent in *Scapter* males (S8 internal in most other colletids). Mature larva with genal area laterally expanded; hypostomal ridge forming right angle with posterior thickening of head capsule; epistomal ridge arching dorsally to level of antennae; anterior tentorial pit extremely low in position (low anterior tentorial pits may be partially correlated with a strongly arched epistomal ridge); inner apical surface of maxilla rounded; salivary lips absent; integument of body not spiculate (McGinley, 1981); furthermore, all *Scapter* species possess characters general to colletids that do not spin cocoons and lack many other distinctive larval and adult apomorphies unique to Diphaglossinae, Colletinae *s. str.*, Hylaeini, and Xeromelissini (e.g., McGinley, 1981; Michener, 2000; Ascher, 2004).

DISTRIBUTION: The 31 species of Scaptrinae are endemic to southern Africa (South Africa, Namibia, and Zimbabwe). Most are found in the semiarid Nama-Karoo and Succulent Karoo biomes (Eardley, 1996). True Paracolletinae are absent from Africa. Most species of the latter subfamily occur in temperate South America and Australia but a few derived taxa extend to adjacent areas such as North America north to southeastern Arizona and various islands near Australia such as Misoöl, New Guinea, Lord Howe, New Zealand, and New Caledonia (Michener, 2000).

COMMENTS: Presently the type genus is the only genus recognized in the subfamily. However, *Scapter* is notably diverse and groups of its species differ by characters often used to delimit bee genera and subgenera (e.g., Michener, 2000). Once a cladistic study of the genus has been undertaken segregation of the species into subgenera would certainly appear warranted.

*Scapter* has traditionally been placed in the Colletinae: Paracolletini (e.g., Michener, 1944), but neither the subfamilial nor the tribal placement has ever been supported by any substantial apomorphic characters, and Paracolletini has long been recognized as an exceptionally plesiomorphic and probably paraphyletic bee group (e.g., Michener, 1944,



1989). McGinley (1981: cladogram F) mapped his larval characters onto Michener's (1944) phylogenetic hypothesis. These supported the clade of Hylaeinae *s. lato* but otherwise provided little support for the traditional higher classification of the Colletidae. McGinley's (1981) preferred cladogram (cladogram D) for the paraphyletic Paracolletini demonstrated great divergence between *Scapter* and all other paracolletines, including the superficially similar *Callomelitta*. Cladograms including additional colletid lineages (e.g., his cladogram J) showed that *Scapter* is misplaced in Paracolletinae and demonstrated cladistic relationships among *Scapter*, *Colletes*, and Hylaeinae *s. lato*, excluding all paracolletines. Unfortunately, he did not propose a new classification based on his larval data.

Michener (2000) suggested that *Scapter* and *Callomelitta* are distinctive enough to warrant tribal status if separated from the old Paracolletini, but he presented far more compelling evidence demonstrating distinctiveness of the former as compared to the latter, and did not justify retaining *Scapter* at any rank within any existing subfamily. Michener (op. cit.) may be correct to interpret the tuberculate margin of the metabasitibial plate in certain *Scapter* and certain euryglossines as independently derived, but this parallelism is unusual and therefore suggestive of rather close relationship. His interpretation of similarities between the facial foveae of *Scapter* and those of *Callomelitta* and *Eulonchopria* proper as convergent is also likely correct, but similarity to the fovea of Hylaeini and Euryglossini may be truly homologous (e.g., Ascher, 2004). Silveira et al. (2002) recognized that *Scapter* did not belong in Paracolletinae, which they recognized as distinct from Colletinae *s. str.*, but did not propose a new subfamily for this taxon, which was extralimital to their study. Ascher (2004) presented support for a sister relationship between *Scapter* and the clade (Xeromelissini + (Euryglossini + Hylaeini)) (= Hylaeinae *s. lato* in the current classification: *vide* appendix 1) exclusive of Stenotritinae, Diphaglossinae, Paracolletinae, and Colletinae *s. str.*, in an analysis including adult and larval characters (notably those of McGinley, 1981).

Scaptrinae is one of six recognized subfamilies of Colletidae along with Stenotritinae, Diphaglossinae, Colletinae *s. str.* (including only *Colletes* and *Mourecotelles*), Paracolletinae (*sensu* Silveira et al., 2002, with *Scapter* formally excluded), and Hylaeinae (*sensu novum*, with the traditional subfamilies Euryglossinae and Xeromelissinae classified as tribes therein). Monophyly of each of the subfamilies Stenotritinae, Diphaglossinae, Colletinae *s. str.*, and Hylaeinae *s. lato* is supported by strong apomorphies (e.g., Michener, 2000), as is the monophyly of the tribes Hylaeini and Xeromelissini. Stenotritines lack colletid glossal synapomorphies and associated cellophane-like cell linings, which suggests placement basal to the remaining colletids, a position supported by some molecular data (e.g., Brady and Danforth, 2004). If shown to be sister to Colletidae, recognition of this taxon as a family (Michener, 2000) or subfamily (Engel, 2001, and herein) would both be consistent with phylogeny. Apomorphic character support for Euryglossini is more limited, but paraphyly with respect to Hylaeini has not been proposed. The status of Paracolletinae excluding *Scapter* as a monophyletic group is equivocal; there is no compelling evidence demonstrating either monophyly or paraphyly with respect to other subfamilies. In the absence of the latter evidence it is appropriate to retain the group pending further study. *Callomelitta* possesses many unusual characters (e.g., McGinley, 1981; Michener, 2000), but no strong evidence suggests that it is related to a nonparacolletine lineage.

#### NEFFAPINI Ascher, new tribe

TYPE GENUS: *Neffapis* Ruz in Rozen and Ruz, 1995.

DIAGNOSIS: (based, in part, upon description and illustrations in Rozen and Ruz, 1995). Glossa greatly elongate, each approximately four times as long as prementum, reaching beyond middle of metasoma in repose; glossal apex attenuate; labial palpus greatly elongate, three-segmented, first segment short, less than half as long as second segment, third segment extremely elongate, nearly four times as long as second; maxillary palpus minute, two-segmented; parag-

lossa short, widened distally; mandible with basal projection. Labrum flat; clypeus of female maculated with yellow (as in many other Panurgini, unlike most protandrenines). Antennal sockets unusually low on face (as in the otherwise dissimilar Calliopsini). Facial foveae shallow, poorly delimited (well-defined in most protandrenines, but also weak in many Panurgini *sensu* Ascher, 2004). Forewing with two submarginal cells (three in some protandrenines, Melitturgina, and Meliturgulina). Fovea of second metasomal tergum almost invisible (usually evident in protandrenines). S6 of female with inner surface laterad straight basal margin on each side with short, longitudinal sclerotized ridge (as in *Panurginus* and some other Old World panurgines, ridge extending across sternum in most protandrenines). S6 of male quadrate, apex very slightly emarginate; S7 of male with bilobed apex exposed; with short, subtriangular apical lobes broadly joined to broad body of sternum; basal apodemal arms broadly joined to sternal body (as in many Panurgini such as *Camptopoeumina*, unlike most protandrenines, which have smaller sternal bodies, elongate slender basal apodemal arms, and well-defined, membranous apical lobes); S8 of male narrowed basally to form spiculum (as in many Panurgini). Penis valves and penis fused in basal half; gonostylus angled orthogonal to gonocoxites; gonostylus slender and well-differentiated from much broader gonocoxites by membrane; volsellae free mesally. Mature larva with median section of epistomal ridge present but weak; antennal prominences low; maxillary apex (except for palpus) approximately in line with labial apex as seen in lateral view, labium therefore not greatly recessed relative to maxilla as in true protandrenines (Rozen and Ruz, 1995); thoracic tubercles unmodified as in most Panurgini, not forming lateral pockets between the prothorax and mesothorax and between the mesothorax and metathorax as in true Protandrenini and *Melitturga* (Rozen and Ruz, 1995; Rozen and Yanega, 1999). Pupa with few tubercles; mesoscutum, tegula, and base of metatibia on outer surface lacking distinct tubercles; terminal spine short, apically rounded, and not sclerotized (Rozen and Ruz, 1995).

**DISTRIBUTION:** The single species of *Neffapis* is endemic to the Coquimban desert of central Chile (Region IV, the Coquimban Region) at the southern end of the Atacama Desert, where it occurs with another Coquimban endemic andrenid genus, *Euherbstia* (*vide* Rozen, 1993). The few published records of *Neffapis* are from the type locality, 6 km S. Vicuña in southern Elqui Province, and from Las Breas in northern Limarí Province (Rozen and Ruz, 1995). Additional collections at the AMNH are as follows: Chile: Elqui Province: 8 males, 7 km S of Vicuña, X-6-1997 (J. G. Rozen, Jr., H. Navarrete); 2 females, 3 males, same except on *Malesherbia humilis*; 1 male, 6 km S of Vicuña, XI-20-1991 (J. G. Rozen, Jr., L. E. Peña, A. Ugarte); 7 females, 2 males, same except X-30-2000 (J. G. Rozen, Jr.); 1 male, 22 km S of Vicuña, 30°; 10'27"S 70°30'54"W, X-31-2000 (J. G. Rozen, Jr.).

**COMMENTS:** This group was recognized as one of nine subtribes of an expanded tribe Panurgini by Ascher (2004), along with *Promelitturgina* (herein considered a tribe, *sensu* Engel), *Melitturgulina*, *Melitturgina*, *Mermiglossina* (herein considered a junior subjective synonym of *Melitturgina*, *sensu* Engel), *Camptopoeina*, *Panurginina*, *Panurgina*, and *Perditina*. The other three panurgine tribes recognized by Ascher (2004) were *Nolanomelissini*, *Calliopsini*, and *Protandrenini*.

*Neffapis* is apparently an oligolege of *Malesherbia humilis* Poeppig (Malesherbiaceae) (Rozen and Ruz, 1995) and the long tongue of *Neffapis* is probably an adaptation for collecting nectar from this plant. *Neffapis* flies in the austral spring; dates of collection range from 6 October–5 January.

#### **AFRODASYPODINI** Engel, new tribe

**TYPE GENUS:** *Afrodasyopoda* Engel, new genus.

**DIAGNOSIS:** Glossal apex attenuate; labrum less than four times as long as wide. F1 approximately 2.5 times as long as wide. Compound eyes diverging below. Metatibia lacking keirotichiae; primitively possesses projection on metabasitarsus (like *Promelittini* and some *Sambini*). Basal tergal bands only present on metasomal T2 and T3; median el-

evated area of pygidial plate absent (present in *Dasypodaini*).

COMMENTS: The single species, known only from South Africa, presently known of *Afrodasypodini* is interesting in its intermingling of some traits of the tribes *Dasypodaini* and *Sambini*.

*Afrodasyпода* Engel, new genus

TYPE SPECIES: *Rhinochaetula plumipes* Friese, 1912.

DIAGNOSIS: As for the tribe (*vide supra*).

ETYMOLOGY: The new genus-group name is a combination of Africa and the generic name *Dasyпода*, type genus for the subfamily. The name is feminine.

COMMENTS: The only included species is *Afrodasyпода plumipes* (Friese), **new combination**.

**HESPERAPINA** Ascher and Engel,  
new subtribe

TYPE GENUS: *Hesperapis* Cockerell, 1898.

DIAGNOSIS: Galeal comb present, albeit weak in the American clade of *Hesperapis* and apomorphically reduced to about five bristles in a species of *Eremaphanta* (*Popovapis*). Scopa largely confined to outer surface of metatibia and metabasitarsus; inner metatibial surface with longitudinal median band of keirotichia (scopal setae dense, long, minutely barbed, present on both inner and outer surfaces of metatibia and metabasitarsus, and keirotichia absent in *Dasyпода*); metabasitibial plate present in female and nearly all males (apomorphically absent in some male *Hesperapis*) (absent in *Dasypodaina*). Propodeal profile nearly horizontal at base (all more or less in same plane in *Dasyпода*). Male S1 with broad, transparent marginal zone with deep median cleft; latero-apical lobes of male S7 absent (present in other *dasypodaines*). Gonostylus usually short and broad, fully fused to gonocoxite (nearly always deeply bifid and well differentiated from gonocoxite by narrow, partly membranous area in *Dasypodaina*). Larva with extreme reduction of cephalic and mouthpart structures; maxilla and labium fused; prementum and postmentum fused (Rozen and McGinley, 1974; Rozen, 1978; however, larvae of *Eremaphanta* remain un-

discovered and so validity of larval traits await confirmation).

COMMENTS: *Hesperapina* is herein proposed for *Hesperapis* s.l. (i.e., *sensu* Michener, 2000, including subgenera *Capicola* and *Xeralictoides*; previously these taxa had been treated as separate genera, e.g., Michener, 1981) and *Eremaphanta*. The distribution of hesperapines is unique among bees and features remarkable disjunctions. Nearly all species occur in or near xeric or Mediterranean-climate areas. In the Old World *Eremaphanta* is restricted to xeric regions of Central Asia southwest to Iran (subgenus *Popovapis* to Baluchistan), while *Hesperapis* (*Capicola*) and its sister subgenus *Capicoloides* are restricted to xeric parts of South Africa and Namibia. The remaining subgenera of *Hesperapis* are restricted to North America. Most species are found in seasonally dry habitats in the western United States and northwestern Mexico; the overall range extends from Oregon, North Dakota, and Illinois south to the Gulf Coast of Alabama and northwestern Florida and to Baja California Sur and Morelos, Mexico (Michener, 2000). The only plausible explanation for the extreme disjunction between the three areas of hesperapine occurrence, which are not linked directly by geology, is extensive extinction of ancestral populations in intervening areas due to climatic deterioration (e.g., Engel, 2001). *Hesperapina* thus exhibits limited, relict distribution in three of Sclater's biogeographic regions, whereas its sister group *Dasypodaina* is widely distributed across the Palearctic Region but absent from North America and sub-Saharan Africa.

**MACROGALEINA** Engel, new subtribe

TYPE GENUS: *Macrogalea* Cockerell, 1930b.

DIAGNOSIS: Body robust and densely setose. Male compound eyes enlarged. Jugal lobe of hind wing greatly enlarged. Female with fasciae of appressed setae on T2–5. Body of mature larva with numerous short setae (some setae hooked at apices), lacking tubercles and elongate setae of subtribe *Allodapina*.

COMMENTS: Species of *Macrogalea* are unlike those of any other allodapine genera and

the segregation of the genus into its own subtribe highlights the structural as well as biological differences between it and other alodapines. This distinction is also supported by molecular studies (e.g., Schwarz et al., 2003). The subtribe occurs in Madagascar and Africa (Ethiopia south to Namibia).

**ANCYLOSCELIDINA** Engel and Michener,  
new subtribe

TYPE GENUS: *Ancyloscelis* Latreille, 1829.

DIAGNOSIS: Clypeus strongly protuberant; paraocular carina present along inner margin of compound eye; maxillary palpus with sparse, short setae; scopa on metatibia and metabasitarsus composed of elongate, coarsely plumose setae; cu-a in hind wing less than half as long as second abscissa M + Cu; second abscissa M + Cu in hind wing three-fourths as long as M; male T7 apically rounded; male hind leg greatly modified, metafemur dilated, at least twice as wide as mesofemur; male S7 with broad disc, with 2–4 small apical lobes, shorter than disc.

COMMENTS: This subtribe has been recognized in earlier studies of apine classification but the family-group name has not previously been made available. This minor nomenclatorial difficulty is corrected here.

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## APPENDIX

## HIERARCHICAL CLASSIFICATION OF SUPERFAMILY APOIDEA

Herein I provide a classificatory outline of the superfamily Apoidea. All names, including synonyms (italicized), are included in this listing. Names are provided with their corrected spelling and, therefore, may not appear with the same stem or suffix with which they were originally proposed. Those names for apoid wasps follow Menke (1997) and Menke and Pulawski (2002), with updates from Antropov (2000), but the hierarchical arrangement follows that of Ohl (1996), Prentice (1998), and Melo (1999) so as to reflect phylogenetic relationships relative to the bees. As is frequently done in apoid wasps, I have used subtribes throughout the bees. General references to

the classification of Recent and fossil bees include Michener (2000) and Engel (2001), with excellent accounts of the phylogeny of particular groups by Ascher (2003, 2004), Brady and Danforth (2004), Danforth et al. (2004), Roig-Alsina and Michener (1993), etc. The addition of infratribes or other intercalated ranks (*vide* table 1) could greatly enrich the classificatory hierarchy of bees, more intensely reflecting their presumed phylogenetic relationships. I have not presently felt it warranted to recognize such levels, instead employing only those ranks widely adopted across other insect lineages, particularly elsewhere in the Apoidea.

## Superfamily APOIDEA Latreille, 1802a

“**spheciforms**” [*apoid wasps; paraphyletic grade to Anthophila*]

Family †ANGAROSPHECIDAE Rasnitsyn, 1975

= †*Baissodidae* Rasnitsyn, 1975

Family HETEROGYNAIDAE Nagy, 1969, *nomen emendatum* (ICZN, 1987)

Family AMPULICIDAE Shuckard, 1840

Subfamily Ampulicinae Shuckard, 1840

Tribe †Apodolichurini Antropov, 2000

Tribe †Cretampulicini Antropov, 2000

Tribe †Mendampulicini Antropov, 2000

Tribe Dolichurini Lepeletier de Saint Fargeau, 1845

Tribe Ampulicini Shuckard, 1840

Family SPHECIDAE Latreille, 1802b

Subfamily Chloriontinae Fernald, 1905

Subfamily Sceliphrinae Ashmead, 1899b, *nomen conservandum* (ICZN, 1999a: Art. 40.2)

Tribe Sceliphriini Ashmead, 1899b, *nomen conservandum* (ICZN, 1999a: Art. 40.2)

= *Pelopoeini* Leach, 1815

Tribe Podiini de Sausurre, 1892

Subfamily Stangeellinae Bohart and Menke, 1976

Subfamily Sphecinae Latreille, 1802b

Tribe Sphecini Latreille, 1802b

Tribe Prionychini Bohart and Menke, 1963

Subfamily Ammophilinae André, 1886

Family CRABRONIDAE Latreille, 1802b

Subfamily †Burmastatinae Antropov, 2000 [*Or separate family?*]

Subfamily Astatinae Lepeletier de Saint Fargeau, 1845

Tribe Astatini Lepeletier de Saint Fargeau, 1845

= *Diploplectrini* Fox, 1894 [1895]

= *Dimorphini* Brues and Melander, 1932

Tribe Ammoplanini Evans, 1959

Tribe Eremiasphecini Menke, 1967

Subfamily Bembicinae Latreille, 1802b

Tribe Alyssontini Dalla Torre, 1897

Tribe Nyssonini Latreille, 1804, *nomen emendatum* (ICZN, 1979)

Tribe Bembicini Latreille, 1802b

Subtribe Heliocausina Handlirsch, 1925

Subtribe Exeirina Dalla Torre, 1897

= *Clitemnestrina* Nemkov and Lelej, 1996

= *Olgina* Nemkov and Lelej, 1996

Subtribe Gorytina Lepeletier de Saint Fargeau, 1845



- = *Arpactina* Turner, 1915
- = *Hoplisina* Rohwer, 1916
- = *Argogorytina* Nemkov and Lelej, 1996
- Subtribe Handlirschiina Nemkov and Lelej, 1996
- Subtribe Stizina Costa, 1859
- Subtribe Bembicina Latreille, 1802b
- Subtribe Stictiellina Bohart and Horning, 1971
- Subfamily Philanthinae Latreille, 1802b
  - Tribe Philanthini Latreille, 1802b
    - Subtribe Philanthina Latreille, 1802b
    - Subtribe Philanthinina Menke, 1967
  - Tribe Aphilanthopini Bohart, 1966
  - Tribe Pseudoscoliini Menke, 1967
  - Tribe Cercerini Lepeletier de Saint Fargeau, 1845
- Subfamily Pemphredoninae Dahlbom, 1835
  - Tribe Odontosphecini Menke, 1967
  - Tribe Entomosericini Dalla Torre, 1897
  - Tribe Psenini Costa, 1858
    - = *Mimesini* Cresson, 1887
    - = *Psenulini* Gittins, 1969
  - Tribe Pemphredonini Dahlbom, 1835
    - Subtribe Pemphredonina Dahlbom, 1835
    - Subtribe Spilomenina Menke, 1989
    - Subtribe Stigmata Bohart and Menke, 1976
- Subfamily Crabroninae Latreille, 1802b
  - Tribe Mellinini Latreille, 1802b
    - Subtribe Mellinina Latreille, 1802b
    - Subtribe Xenosphecina Parker, 1966
  - Tribe Dinetini Fox, 1894 [1895]
  - Tribe Laphyragogini Bohart and Menke, 1976
  - Tribe Palarini Schrottky, 1909b
  - Tribe Larrini Latreille, 1810
    - Subtribe Larrina Latreille, 1810
      - = *Larradina* de Saussure, 1890 [1892]
    - Subtribe Gastrosericina André, 1886
      - = *Tachytina* Bohart, 1951<sup>a</sup>
  - Tribe Miscophini Fox, 1894 [1895]
    - = *Lyrodini* Fox, 1894 [1895]
    - = *Sericophorini* Dalla Torre, 1897
    - = *Nitelini* Dalla Torre, 1897
    - = *Paranyssontini* Turner, 1914
  - Tribe Trypoxylini Lepeletier de Saint Fargeau, 1845
    - = *Pisini* Ashmead, 1899b
  - Tribe Bothynostethini Fox, 1894 [1895]
    - Subtribe Bothynostethina Fox, 1894 [1895]
    - Subtribe Scapheutina Menke, 1968
  - Tribe Oxybelini Leach, 1815
  - Tribe Crabronini Latreille, 1802b
    - Subtribe Anacrabronina Ashmead, 1899b
    - Subtribe Crabronina Latreille, 1802b
      - = *Lindeniina* Ashmead, 1899b
      - = *Thyreopodina* Ashmead, 1899b
      - = *Rhopalina* Ashmead, 1899b
      - = *Soleniina* Bradley, 1926
      - = *Pemphilidina* Pate, 1935
      - = *Karossiina* Pate, 1936
- Family Incertae Sedis
  - Subfamily †Cirrosphecinae Antropov, 2000 (*perhaps near Ampulicidae?*)
- Anthophila** Latreille, 1804 *vel* 1807 [*bees*]<sup>b</sup>
- Family COLLETIDAE Lepeletier de Saint Fargeau, 1841

- Subfamily Stenotritinae Cockerell, 1934
  - Subfamily Diphaglossinae Vachal, 1909
    - Supertribe Caupolicaniti Michener, 1944
      - Tribe Caupolicanini Michener, 1944
    - Supertribe Diphaglossiti Vachal, 1909
      - Tribe Diphaglossini Vachal, 1909
      - Tribe Dissoglottini Moure, 1945
        - = *Ptiloglossidiini* Moure, 1953
        - = *Mydrosomatini* Michener, 1966
  - Subfamily Paracolletinae Cockerell, 1934, *nomen protectum* (ICZN, 1993)
    - = *Neopasiphaeinae* Cockerell, 1930
    - = *Phenacolletinae* Cockerell, 1934, *nomen nudum*
    - = *Eulonchopriinae* Moure, 1945
    - = *Lonchopriinae* Moure, 1945
  - Subfamily Colletinae Lepeletier de Saint Fargeau, 1841
  - Subfamily Scraptrinae Ascher and Engel, *subfamilia novum*
  - Subfamily Hylaeinae Viereck, 1916, *nomen protectum* (ICZN, 1993)
    - Supertribe Hylaeiti Viereck, 1916, *nomen protectum* (ICZN, 1993)
      - Tribe Euryglossini Michener, 1944
      - Tribe Hylaeini Viereck, 1916, *nomen protectum* (ICZN, 1993)
        - = *Prosopidini* Fallén, 1813
        - = *Palaeorhizini* Perkins, 1908
        - = *Meroglossini* Perkins, 1908
        - = *Hyleoidini* Cockerell, 1930a
    - Supertribe Xeromelissiti Cockerell, 1926
      - Tribe Xeromelissini Cockerell, 1926
        - = *Chilicolini* Michener, 1944
  - Family HALICTIDAE Thomson, 1869, *nomen protectum* (ICZN, 1993)
    - Subfamily Rophitinae Schenck, 1866 [1867]
      - Tribe Rophitini Schenck, 1866 [1867]
        - = *Dufoureini* Robertson, 1904
        - = *Halictoidini* Börner, 1919
        - = *Systrophini* Handlirsch, 1925
      - Tribe Penapini Engel, 2001
    - Subfamily Nomiinae Robertson, 1904
    - Subfamily Halictinae Thomson, 1869, *nomen protectum* (ICZN, 1993)
      - Supertribe Nomioiditi Börner, 1919
        - Tribe Nomioidini Börner, 1919
      - Supertribe Halictiti Thomson, 1869, *nomen protectum* (ICZN, 1993)
        - Tribe Halictini Thomson, 1869, *nomen protectum* (ICZN, 1993)
          - Subtribe Sphecodina Schenck, 1868 [1869]
          - Subtribe Halictina Thomson, 1869
            - = *Gastrohalictina* Schrottky, 1911
            - = *Lasioglossina* Robertson, 1926
            - = *Chloralictina* Robertson, 1926
            - = *Thrinchostomatina* Sakagami, 1974
        - Tribe Caenohalictini Michener, 1954
          - Subtribe Agapostemonina Engel, 2000
          - Subtribe Caenohalictina Michener, 1954
      - Tribe Augochlorini Beebe, 1925, *nomen protectum* (ICZN, 2000)
        - Subtribe Corynurina Engel, 2000
        - Subtribe Augochlorina Beebe, 1925, *nomen protectum* (ICZN, 2000)
          - = *Oxystoglossina* Schrottky, 1909a
          - = *Augochloropsina* Moure, 1943
          - = *Megaloptina* Moure, 1943
          - = *Ischnomelissina* Engel, 2000
          - = *Thectochlorina* Engel, 2000
          - = *Megaloptidiina* Engel, 2000
- Family ANDRENIDAE Latreille, 1802a
  - Subfamily Euerbstiinae Moure, 1950

- Subfamily Andreninae Latreille, 1802a
  - = *Anthreninae* Burmeister, 1829
  - = *Alocandreninae* Michener, 2000
- Subfamily Oxaeinae Ashmead, 1899a
- Subfamily Panurginae Leach, 1815
  - Supertribe Nolanomelissiti Rozen and Ascher *In* Rozen, 2003
    - Tribe Nolanomelissini Rozen and Ascher *In* Rozen, 2003
  - Supertribe Panurgiti Leach, 1815
    - Tribe Calliopsini Robertson, 1922
    - Tribe Protandrenini Robertson, 1904
      - = *Liphanthini* Michener, 2000, *nomen nudum*
      - = *Austropanurgini* Michener, 2000, *nomen nudum*
    - Tribe Neffapini Ascher, *tribus novum*
    - Tribe Protomeliturgini Ruz, 1991
    - Tribe Meliturgulini Engel, 2001
    - Tribe Panurgini Leach, 1815
      - Subtribe Meliturgina Newman, 1834
        - = *Mermiglossina* Patiny, 1999
      - Subtribe Camptopoeina Patiny, 1999
      - Subtribe Panurginina Patiny, 1999
      - Subtribe Panurgina Leach, 1815
      - Subtribe Perditina Robertson, 1922
- Family †PALEOMELITTIDAE Engel, 2001
- Family MELITTIDAE Schenck, 1860
  - Subfamily Meganomiinae Michener, 1981
  - Subfamily Macropidinae Robertson, 1904
    - Tribe †Eomacropidini Engel, 2001
    - Tribe Macropidini Robertson, 1904
  - Subfamily Melittinae Schenck, 1860
    - Tribe Redivivini Engel, 2001
    - Tribe Melittini Schenck, 1860
  - Subfamily Dasypodainae Börner, 1919
    - Supertribe Promelittiti Michener, 1981
      - Tribe Promelittini Michener, 1981
    - Supertribe Dasypodaiti Börner, 1919
      - Tribe Afrodasypodini Engel, *tribus novum*
      - Tribe Sambini Michener, 1981
      - Tribe Dasypodaini Börner, 1919
        - Subtribe Dasypodaina Börner, 1919
        - Subtribe Hesperapina Ascher and Engel, *subtribus novum*
- Family MEGACHILIDAE Latreille, 1802b
  - Subfamily Pararhophitinae Popov, 1949
  - Subfamily Fideliinae Cockerell, 1932
    - Tribe Neofideliini Engel, 2004
    - Tribe Fideliini Cockerell, 1932
  - Subfamily Lithurginae Newman, 1834
    - Tribe †Protolithurgini Engel, 2001
    - Tribe Lithurgini Newman, 1834
      - = *Trichothurgini* Moure, 1949
  - Subfamily Megachilinae Latreille, 1802b
    - Tribe Anthidiini Ashmead, 1899a, *nomen protectum* (ICZN, 1993)
      - Subtribe Anthidiina Ashmead, 1899a, *nomen protectum* (ICZN, 1993)
        - = *Stelididina* Schenck, 1860
        - = *Trachusina* Robertson, 1904
        - = *Dianthidiina* Moure, 1947
        - = *Pachyanthidiina* Pasteels, 1969
        - = *Icteranthidiina* Pasteels, 1969
        - = *Euaspina* Pasteels, 1969
      - Subtribe Dioxyina Cockerell, 1902
      - Tribe †Glyptapini Cockerell, 1909b

- Tribe †Ctenoplectrellini Engel, 2001
- Tribe Osmiini Newman, 1834
  - Subtribe Heriadina Michener, 1941
    - = *Trypetina Robertson, 1903a, nomen praeoccupatum*
  - Subtribe Osmiina Newman, 1834
    - = *Chelostomina Kirby In Kirby and Spence, 1837*
    - = *Hoplitina Nobile and Tomarchio, 2000, nomen nudum*
- Tribe Megachilini Latreille, 1802b
  - = *Coelioxiyini Dalla Torre and Friese, 1894*
  - = †*Chalicodomopsini Engel, 1999b, nomen nudum*
- Family APIDAE Latreille, 1802a
  - Subfamily Xylocopinae Latreille, 1802b
    - Supertribe Xylocopiti Latreille, 1802b
      - Tribe Xylocopini Latreille, 1802b
        - Supertribe Manuelliiti Sakagami and Michener, 1987
          - Tribe Manuelliini Sakagami and Michener, 1987
      - Supertribe Ceratinitini Latreille, 1802b
        - Tribe Ceratinini Latreille, 1802b
        - Tribe †Boreallodapini Engel, 2001
        - Tribe Allodapini Cockerell, 1902
          - Subtribe Macrogaleina Engel, *subtribus novum*
          - Subtribe Allodapina Cockerell, 1902
            - = *Exoneurina Robertson, 1904*
            - = *Eucondylopsini Friese, 1909*
    - Subfamily Nomadinae Latreille, 1802a
      - Supertribe Neolarriti Fox, 1894 [1895]
        - Tribe Neolarrini Fox, 1894 [1895]
          - Tribe Ammobatini Handlirsch, 1925, *nomen protectum* (ICZN, 1993)
            - Subtribe Pasitina Robertson, 1926
              - Subtribe Ammobatina Handlirsch, 1925, *nomen protectum* (ICZN, 1993)
                - = *Phileremina Lepeletier de Saint Fargeau, 1841*
                - = *Melanempidina Handlirsch, 1925*
            - Tribe Caenoprosopidini Michener, 1944
        - Supertribe Nomaditi Latreille, 1802a
          - Tribe Townsendiellini Michener, 1944
          - Tribe Nomadini Latreille, 1802a
            - Tribe Biastini Linsley and Michener, 1939
              - = *Neopasitini Linsley and Michener, 1939*
          - Tribe Ammobatoidini Michener, 1944
            - = *Holcopasitini Rozen, 1966*
          - Tribe Hexepeolini Rozen, 1996
          - Tribe Brachynomadini Roig-Alsina and Michener, 1993
          - Tribe Epeolini Robertson, 1903b
            - Subtribe Odyneropsina Handlirsch, 1925
            - Subtribe Rhogepeolina Rightmyer, 2004
            - Subtribe Epeolina Robertson, 1903b
            - Subtribe Thalestriina Rightmyer, 2004
    - Subfamily Apinae Latreille, 1802a
      - Supertribe Euceriti Latreille, 1802b
        - Tribe Osirini Handlirsch, 1925 [*allied to Tapinotaspidini?; supertribal placement tentative*]
          - = *Epeoloidini Linsley and Michener, 1939*
        - Tribe Isepeolini Rozen, Eickwort, and Eickwort, 1978
        - Tribe Protepeolini Linsley and Michener, 1939
        - Tribe Exomalopsini Vachal, 1909
        - Tribe Ancylini Michener, 1944
        - Tribe Teratognathini Silveira, 1995
        - Tribe Eucerini Latreille, 1802b
          - Subtribe Eucerinodina Michener and Moure, 1957
          - Subtribe Eucerina Latreille, 1802b
            - = *Melissodina Robertson, 1901*



- = *Tetraloniina* Schrottky, 1913
- = *Canephorulina* Michener, LaBerge, and Moure, 1955
- Tribe Ctenoplectrini Cockerell, 1930a
- Tribe Emphorini Robertson, 1904
  - Subtribe Ancyloscelidina Engel and Michener, *subtribus novum*
  - Subtribe Emphorina Robertson, 1904
    - = *Melitomina* Vachal, 1909
    - = *Entechniina* Cockerell, 1906
- Tribe Tapinotaspidini Moure, 1992 [1994]
  - = *Paratetrapediini* Moure, 1992 [1994]
- Supertribe Apiti Latreille, 1802a
  - Tribe Tetrapediini Michener and Moure, 1957 [*supertribal placement tentative*]
  - Tribe Rhathymini Lepeletier de Saint Fargeau, 1841
  - Tribe Anthophorini Dahlbom, 1835
    - = *Podaliriini* Latreille, 1802b
    - = *Megillini* Thomson, 1869
    - = *Habropodini* Marikovskaya, 1976
  - Tribe Melectini Westwood, 1840 [1839]
  - Tribe Ericrocidini Cockerell and Atkins, 1902
    - = *Ctenioschelini* Michener, 1965a, *nomen nudum*
  - Tribe Centridini Cockerell and Cockerell, 1901
    - = *Hemisiini* Cockerell and Robbins, 1910
    - = *Epicharitini* Schrottky, 1913
  - Corbiculate apines* [*Corbiculata* Engel, 1998b<sup>c</sup>]—
  - Tribe Euglossini Latreille, 1802b
    - = *Eulaemini* Lepeletier de Saint Fargeau, 1841
    - = *Exaeretini* Cockerell, 1908a
    - = *Chrysanthedini* Handlirsch, 1925
    - = *Aglaini* Handlirsch, 1925
    - = *Eufrieseini* Moure, 1944
  - Tribe Bombini Latreille, 1802b
    - = *Apathini* Newman, 1834
    - = *Psithyrini* Lepeletier de Saint Fargeau, 1841
    - = *Bremini* Frison, 1919
  - Tribe †Electrobombini Engel, 2001
  - Tribe †Electrapini Engel, 1998a
  - Tribe Apini Latreille, 1802a
  - Tribe †Melikertini Engel, 2001
  - Tribe Meliponini Lepeletier de Saint Fargeau, 1836
    - = *Trigonini* Moure, 1946
    - = *Lestrimelittini* Moure, 1946

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† Fossil taxon.

<sup>a</sup> The availability of this name from Bohart (1951) should, perhaps, be reinvestigated as the few statements on p. 945 where the name is proposed can only marginally be considered to constitute a differential diagnosis. More likely, the name was truly made available in later papers. Given that Tachytini is a synonym it is merely an academic point.

<sup>b</sup> The name Anthophila may be dated from either its proposal as a plural (Latreille, 1804) or its later emendation (Latreille, 1807).

<sup>c</sup> I created the nonranked name “Corbiculata” for a 1998 symposium on corbiculate bee relationships (Engel, 1998b). Although it was picked up by some of the symposium attendants and organizers, I do not recommend its adoption and instead favor the informal terminology of simply “corbiculate bees” for this group.

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