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# FOSSIL RECORD OF THE RUBIACEAE

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## ABSTRACT

Fossils of 134 taxa attributed to the Rubiaceae are described or mentioned in 115 publications dating from 1850 and from deposits as old as the Cretaceous and Paleocene. Close scrutiny of these records indicates, however, that the oldest and most likely (accepted) representatives of the family are four genera, *Emmenopterys* Oliv. from the Middle Eocene of Oregon and Washington, U.S.A., *Fareamea* Aubl. from the Late Eocene of Panama, and *Guettarda* L. (cf. as †*Guettardidites*; †= fossil taxon) and *Canthium* Lam. (as †*Rubipollis oblatus*) from the Late Eocene of Australia, and a probable fifth genus, the alternate-leaved †*Paleorubiaceophyllum eocenicum* from the Middle Eocene of Tennessee/Kentucky, U.S.A. The record represents three subfamilies (Rubioidae, Ixoroideae, Cinchonoideae) from three widely separated geographic regions, implying an earlier origin in the Late Cretaceous or Paleocene. From the Oligocene, there are six accepted genera, *Coprosma* J. R. Forst. & G. Forst., *Coprosma-Opercularia*, *Fareamea* Aubl., *Macrosphyra* Hook. f. (as †*Triporetadites hoekeni*), *Mitragyna* Korth. (as †*Retitricolporites annulatus*), and *Pinckneya* Michx. from Africa (Cameroon), Australia and New Zealand, U.S.A. (Oregon), and Puerto Rico. The period of greatest diversification and radiation was in the Miocene, with 20 accepted genera reported from North America, Central America, South America, Southeast Pacific-Asia, Africa, and Europe. Stages in the evolution of three characters are further suggested by the fossil record. The relatively uncommon occurrence of alternate leaves among modern taxa is typical of advanced genera (e.g., *Didymochlamys* Hook. f., *Sabicea* Aubl., *Theligonum* L.), but this feature may have already developed by the Middle Eocene (†*Paleorubiaceophyllum*). Polyploidy is suggested in the Middle Eocene *P. eocenicum* var. *laurensis* by epidermal cells 32 µm in diameter or nearly twice the size of the other varieties. Pollen polymorphism, possibly coordinated with or as a prelude to heterostyly, is represented by the diporate pollen of *Fareamea* in the Late Eocene, and triporate and tetraporate forms in the Miocene and Pliocene. Currently, the principal needs are: (1) to clarify pending Paleocene records of †*Cinchonidium* (*Cinchona* L.), North Dakota, U.S.A.; *Galium* L., Greenland; and †*Psilatricolpites coprosmoides* (*Coprosma*, Chile); and (2) to examine the several large Cretaceous megafossil floras now under study (e.g., Anfiteatro de Ticó, Argentina; Crato, Brazil; Turonian-age floras, New Jersey and Sweden) for specimens with features that suggest a rubiaceous complex or with an aggregation of features suggesting presence of the family.

*Key words:* Fossils, Rubiaceae.

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Reconstructing the fossil history of plant families requires assembling reports often from widely scattered literature dating back centuries. For the Rubiaceae, there are approximately 134 taxa described or mentioned in 115 publications including the earliest ones of Unger (1850, *Canthidium* [Unger spelling], †*Cinchonidium*, Croatia), Wessel and Weber (1855, †*Rubiacites*, Germany), Heer (1868, *Galium* L., Greenland), and others from later in the 1800s and early 1900s. All are accounted for in the present summary, and none have been revised since the original publications. There are other reports in unpublished theses and dissertations, and there is casual, unconfirmed mention of the family as possibly present in some putative Late Cretaceous and older deposits in the literature of the 1800s that also are not included.

These reports must be filtered through at least a preliminary assessment to yield a database of plausible records. The procedure for evaluating the fossil pollen records of extant angiosperms used here is similar to that of Muller (1981). In this informal rating, “A” (accepted) means that: (1) the specimens have been reexamined and are considered to represent the Rubiaceae; or (2) the specimens are sufficiently diagnostic to allow recognition to genus or family from the illustrations and/or descriptions (e.g., the dimorphic pollen of *Fareamea* Aubl.); and (3) the identification does not pose improbable age, phylogenetic, paleoecologic, or biogeographic problems to the extent this context information is available for the taxon and the locality. “P” (pending) means additional information (e.g., more accurate age determination, better

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preserved or more complete specimens), and/or confirmation through reexamination of the material is needed. "NA" (not accepted) means: (1) only casual reference is made to family affinities (e.g., the fossil pollen named *Tricolporopollenites arnotiensis* that Scholtz [1985] compared to *Anthospermum* L., *Nenax* Gaertn., and *Rubia* L., as well as to the Euphorbiaceae and Bombacaceae); or (2) features are present that are not found in or characteristic of the family. These assessments are by the present author, unless otherwise indicated. The abbreviations are also explained the first time they are used in the Synopsis section.

Another step in reconstructing an accurate geologic history for a family is to identify the location of specimens presently rated as pending. Finally, reexamination of this material will eventually be necessary by those familiar with leaf, floral, seed/fruit, wood, and pollen morphology of extant species, and the phylogenetic and biogeographic implications of the reports. Such pending material for the Rubiaceae includes the leaf †*Cinchonidium ovale* from the Paleocene of North Dakota, U.S.A., the fruit *Galium* †*antiquum* from the Paleocene of Greenland, and the pollen †*Psilatricolpites coprosmoides* (*Coprosma* J. R. Forst. & G. Forst.) from the Oligocene to Recent of New Zealand (A) and reported from the Paleocene of Chile (P). In the following summary, abbreviations for the repositories of specimens (not *Index Herbariorum* abbreviations [Holmgren & Holmgren, 1998]), or author affiliation at the time of publication, are as follows: ASNU, Australian National University, Canberra, Australia; CNRS, Centre National Recherche Scientifique, Paris, France; FLMNH, Florida Museum of Natural History, Gainesville, Florida, U.S.A.; FSTS-J, Faculté Sciences Techniques St.-Jérôme, Marseille, France; GIL, Geological Institute, Leiden, The Netherlands; GSC, Geological Survey of Canada, Calgary, Canada; GSV, Geological Survey of Victoria, Victoria, Australia (as of 2004, GeoScience Victoria); JVG, Josephinum Vienna/Graz, Austria; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MO, Missouri Botanical Garden, St. Louis, Missouri, U.S.A. (the author's modern spore and pollen reference collection, fossil collection, literature collection, and associated materials are currently being transferred to the Smithsonian Tropical Research Institute, Panama); MPUC, Museum of Paleontology, University of California, Berkeley, California, U.S.A.; NIGP, Nanjing Institute of Geology and Paleontology, People's Republic of China; NMP, National Museum, Prague, Czech Republic; NTU, National Taiwan University, Taipei, Taiwan; NZGS, New Zealand Geological Survey, Lower Hunt, New Zealand; RN-D, Realgym-

nasium zu Neustadt-Dresden, Germany; RRNA, Robertson Research (North America), Calgary, Alberta, Canada; SAMC, South African Museum, Cape-town, South Africa; SM, Senckenberg Museum, Frankfurt am Main, Germany; SOCDH, Shell Oil Company, Den Hague, The Netherlands; SUPA, Stanford University, Palo Alto, California, U.S.A.; UA, University of Amsterdam, Amsterdam, The Netherlands; ULP, Université Louis Pasteur, Strasbourg, France; UPMC, Université Pierre et Marie Curie, Paris, France; USGS, U.S. Geological Survey, Denver, Colorado, U.S.A.; USNM, U.S. National Museum (Paleobiology Division), Washington, D.C., U.S.A.; UNSWK, University of New South Wales, Kensington, Australia; UVA, University of Vienna, Vienna, Austria; VGS, Vermont Geological Survey, Waterbury, Vermont, U.S.A.; ZOOZ, Zoological Museum, University of Zurich, Zurich, Switzerland; ZGIB, Zentrales Geologisches Institut, Berlin, Germany. Abbreviations for repositories are provided at the end of each summary, followed by abbreviations for status. Superscript numbers in text denote the following: 1, Early Miocene fide Berry (1938), Early Eocene fide Romero (1986: 454), age unsettled. 2, Rubiaceae affinities not cited by authors, only implied by the etymology of the generic names (see Andrews, 1970; Blazer, 1975; Watt, 1982). 3, *Anisomeris* C. Presl, *Chomelia*, *Guettarda*, *Terebraria* et al. type. 4, Eocene fide Romero (1986: 453), Paleocene fide Palma-Heldt (1980).

#### A SYNOPSIS OF REPORTS OF FOSSIL RUBIACEAE

##### CRETACEOUS

There are six fossil taxa from the Cretaceous referred to the Rubiaceae that represent four form genera and six species. None have been confirmed as belonging to the family.

1. †*Rubiaephyllum gaylussaciae* Bayer. **Leaf**, Bohemia, Bayer in Fritsch (1893: 131, fig. 192). According to Kvacek (pers. comm., 2006), the morphology and preservation of the specimens in this report make the family assignment uncertain. NMP. NA.
- 2–3. †*Tricolporopollenites arnotiensis* Scholtz (1985: 71, figs. 17d–h) and †*T. brinkiae* Scholtz (1985: 72, figs. 17a–c). **Pollen**, southwest Africa. The beds range in age from 71 Ma (Late Cretaceous) to 64 Ma (Early Paleocene), but because the samples came from the upper part of the section, they are probably Early Paleocene. The specimens are only informally compared by Scholtz (1985) to the Rubiaceae (*Anthospermum*,

*Nenax*, *Rubia*), as well as to the Euphorbiaceae and Bombacaceae. SAMC. NA.

4–5. †*Triorites aspidatus* and †*T. megaporus* (authors unknown, contact: G. Liu, pers. comm., 2006). **Pollen**, People's Republic of China. Both pollen records provided by G. Liu (pers. comm., 2006). Only informal reference is made to the family by Liu (possibly *Gardenia* J. Ellis). NIGP. NA.

6. †*Triporetetradites scabratus* van Hoeken-Klinkenberg (1964: 226, fig. 16). **Pollen**, Nigeria, attributed to *Gardenia* by Krutzsch (1970; as *Gardenia* type). According to Muller (1981), the specimens are too poorly preserved to be recognized as *Gardenia*. GIL. NA.

#### PALEOCENE

Six fossil taxa are mentioned for the family from the Paleocene, representing five form and modern genera and five species. None have been confirmed as belonging to the Rubiaceae. Three warrant reexamination: *Cinchonidium ovale* Lesq., *Galium antiquum* Heer, and *Psilatricolpites coprosmoides* Couper.

1. †*Cinchonidium ovale* Lesq. (1883: 229, pl. 48, figs. 8–10b). **Leaf**, North Dakota, U.S.A., cf. *Cinchona* L. USNM (the specimen cannot be located in the USNM collections; S. Wing, pers. comm., 2006). P.

2. *Galium* †*antiquum* Heer (1868: 119, pl. 17, figs. 8, 8b; Heer, 1883: 114). **Fruit**, Greenland. ZOOZ. P.

3. †*Psilatricolpites coprosmoides* Couper. **Pollen**, originally recognized as *Coprosma* J. R. Forst. & G. Forst. sp. by Couper (1953: 54, pl. 9, fig. 143, Late Miocene to Recent; 1960: 59, pl. 9, figs. 1–3, Middle Oligocene to Recent) from New Zealand. This pollen type was recognized by Doubling and Chotin (1975: 559–560, pl. 2, fig. 13) from the Paleocene of Chile, and was said to resemble certain *Coprosma*. There is only a very brief description for the Chile record. Couper, NZGS or SOCDH, Oligocene to Recent, A; Douginger, ULP, Paleocene, P.

4. †*Retistephanocolpites* Leidelmeyer sp. **Pollen**, tetracolpate, described by Scholtz (1985: 76, fig. 19e–g) from southwestern Africa. Scholtz (1985: 76) notes that “No positive suggestions can be made regarding the affinity of *Retistephanocolpites* sp. The pollen of *Rubia* (Rubiaceae) and *Catastemma* Benth. (Bombacaceae), amongst

others, appear superficially similar to this fossil species.” SAMC. NA.

5–6. †*Tricolporopollenites arnotiensis* and †*T. brinkiae* from the Arnot Pipe sediments of Late Cretaceous to Early Paleocene age have been mentioned earlier. SAMC. NA.

#### EOCENE

For the Eocene, 32 fossil taxa (including family reports for the Rubiaceae and the name †*Tricolporé reticulé*) representing 22 form and modern genera and 28 species are mentioned for the Rubiaceae.

1. *Cephalanathus* †*glabratifolius*<sup>1</sup> Berry (1938: 132–133, pl. 54, figs. 3–6). **Leaf**, Argentina. Berry (1938) compares the fossil to *Cephalanathus glabratus* (Spreng.) K. Schum. growing today in Paraguay, Uruguay, and northern Argentina. USNM. P.

2. *Coprosoma* †*incerta*<sup>1</sup> Berry. **Leaf**, Berry (1938: 133, pl. 47, fig. 1), Argentina. USNM. P.

3. *Coprosoma* †*spathulatifolia*<sup>1</sup> Berry. **Leaf**, Berry (1938: 133, pl. 52, figs. 4, 5), Argentina. USNM. P.

4. *Coussarea* †*tertiaria*<sup>1</sup> Berry. **Leaf**, Berry (1938: 131, pl. 53, fig. 5), Argentina. USNM. P.

5. †*Cricotriporites camerounensis* Sal.-Cheb. **Pollen**, Salard-Cheboldaeff (1978: 246, pl. 6, fig. 4), Late Eocene to Early Miocene, Cameroon. Salard-Cheboldaeff (1978) compared the fossil to *Randia uliginosa* DC., but this is regarded doubtful by Muller (1981). UPMC. NA.

6. cf. *Emmenopterys* Oliv. **Fruit**, Middle Eocene Republic flora (49–48 Ma), Washington, U.S.A. (Wehr & Manchester, 1996: 25, pl. 2, fig. 6). FLMNH. A.

7. *Emmenopterys* †*dilcheri* Manchester (Fig. 1A, B). **Infructescence and fruit**, Middle Eocene Clarno flora (44 Ma), Oregon, U.S.A. (Manchester, 1994: 80–81, pl. 36, figs. 1–11). The extant *Emmenopterys henryi* Oliv. of People's Republic of China is mentioned as similar by Manchester (1994) and Wehr and Manchester (1996). FLMNH. A.

8. *Exostema* †*pseudocaribaeum* Berry (1916: 349, pl. 106, fig. 3). **Leaf**, Middle Eocene, Tennessee/Kentucky, U.S.A. When originally described, Berry (1916) thought the Wilcox Formation was Early Eocene, but it is now considered Middle Eocene. Similarity is cited by Berry with

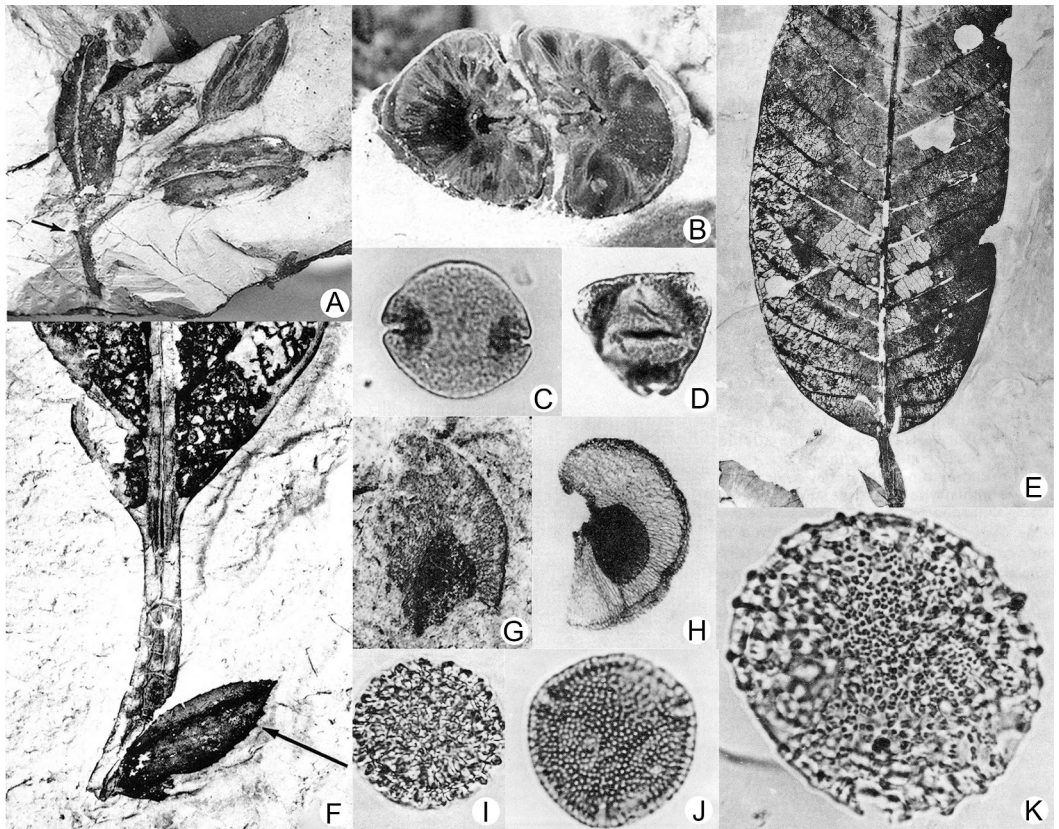


Figure 1. A, B. *Emmenopterys dilcheri* Manchester from the Middle Eocene Clarno flora, Oregon, U.S.A. —A. Inflorescence. —B. Fruit. A, B from Manchester (1994), used with permission of the Paleontological Research Institution, Ithaca, New York, U.S.A., and the author. —C. *Faramea* pollen, diporate form, from the Late Eocene Gatuncillo flora, Panama, from Graham (1985). —D. *Faramea* pollen, triporate form, from the Middle Pliocene Paraje Solo flora, Veracruz, Mexico, from Graham (1976). —E, F. *Paleorubiaceophyllum eocenicum* (Berry) Roth & Dilcher from the Middle Eocene Claiborne flora, Tennessee/Kentucky, U.S.A. Reprinted with permission from Roth and Dilcher (1979). —G. *Pinckneya dilcheri* Meyer & Manchester from the Oligocene Bridge Creek flora, John Day Formation, Oregon, U.S.A. —H. *Pinckneya pubens* Michx., modern seed, from Meyer and Manchester (1997). Images G, H used with permission of the University of California Press, Berkeley, California, U.S.A., and the author (Manchester). —I. *Chomelia* type pollen from the Late Miocene Gatun flora, Panama, from Graham (1991a). —J. *Posqueria* pollen from the Late Miocene Gatun flora, Panama, from Graham (1991a). —K. *Sabicea* pollen from the early Miocene Culebra flora, Panama, from Graham (1988).

the extant *Exostema caribaum* (Jacq.) Roem. & Schult. of the Caribbean region. USNM. P.

9. *Faramea* Aubl. Pollen, distinctive diporate form, Late Eocene Gatuncillo flora, Panama, Graham (1985: 9–520, figs. 64, 65; Fig. 1C). MO. A.

10. *Gardenia* type (as †*Tripоротetradites nachterstedtensis* Krutzsch (1970: 412, pl. 48, figs. 27–32). Pollen, Late Eocene of Germany. ZGIB. A (by Muller, 1981; here P, confirmation needed).

11. *Guettarda* †*ellipticifolia* Berry (1916: 348, pl. 106, figs. 1, 2). Leaf, Middle Eocene, Mis-

sissippi/Tennessee, U.S.A., Berry (1916) compared to the extant *Guettarda elliptica* Sw. from the Caribbean region. USNM. P.

12–13. cf. †*Guettardidites ivirensis* Khan (1976: 763, fig. 24). Pollen, *Guettardidites* sp., MacPhail (1999: 205, pl. 5, fig. 7); pollen, Late Eocene to Early Pliocene, Murray Basin, Australia, *Guettarda*. ASNU. A.

14. *Hoffmannia* †*protogaea*<sup>1</sup> Engelh. Leaf, Berry (1938: 131, pl. 53, figs. 1, 2), Argentina, P. Berry (1922: 86), Chile<sup>4</sup>. USNM (all). P.

15. †*Ixorophyllum anceps* Geyer (1887: 495, pl. 35, figs. 1, 2). **Leaf**, Eocene, Borneo. Repository unknown. P.
16. †*Paleorubiaceophyllum eocenicum* (Berry) Roth & Dilcher (1979: 1203–1205, figs. 1–2; Fig. 1E, F; *Paleorubiaceophyllum* sp., Dilcher & Lott, 2005: 17–18, fig. 9a, b). **Leaf**, Middle Eocene Claiborne flora of Tennessee/Kentucky, U.S.A. Additional fossil material (branches) has shown that the leaves are alternate (Manchester, pers. obs., 2006). FLMNH. A or P (because of alternate branching?).
17. *Psychotria* †*eogenica* Berry (1929b: 166–167, pl. 3, figs. 17–21). **Seed**, Eocene, Peru. USNM. P.
18. *Psychotria* †*grandifolia* Engelm. **Leaf**, Berry (1916: 349–350, pl. 105, fig. 1), Middle Eocene, Tennessee/Kentucky, U.S.A. Berry (1916) compared this with *Psychotria grandis* Sw. USNM. P. It is also listed (as *Psychotria grandifolia*?) by Berry (1941: 84) but not described or illustrated, **leaf**, Kentucky, U.S.A. USNM. NA.
19. *Psychotria* †*oregona* Chaney & Sanborn (1933: 96, pl. 33, fig. 4). **Leaf**, Eocene, Oregon, U.S.A. Chaney and Sanborn (1933) compared it to the extant *Psychotria undata* Jacq. of the Caribbean region, but the record has not been verified. MPUC. P.
- 20–21. †*Randiapollis microreticulatus* Ke & Shi. **Pollen**, *R. reticulatus* Ke & Shi. **Pollen**, Eocene, People's Republic of China (G. Liu, pers. comm., 2002). Only general affinity to the family suggested by Liu. NIGP. NA.
22. *Remijia* †*tenuiflorifolia*<sup>1</sup> Berry. **Leaf**, Berry (1938: 132, pl. 54, figs. 1, 2), Argentina, USNM. P.
23. *Rondeletia* †*longiflorifolia*<sup>1</sup> Berry. **Leaf**, Berry (1938: 132, pl. 54, figs. 7, 8), Argentina. USNM. P.
24. Rubiaceae type 1 (Graham, 1985: 520, figs. 66, 67). **Pollen**, type 2 (Graham, 1985: 520, figs. 68, 69); **pollen**, Late Eocene, Panama. MO. A (as family).
25. †*Rubiaceocarpum markgrafi* Kräusel (1939: 108, pl. 1, figs. 19–24). **Seed**, Eocene, Egypt. SM. P (as family).
26. †*Rubiacites chomeliifolia*<sup>1</sup> Berry. **Leaf**, Berry (1938: 133–134, pl. 55, figs. 1, 2), Argentina. USNM. P (as family).
27. †*Rubiacites? pellicieraformis* Berry (1930: 134, pl. 49, fig. 19). **Fruit**, Middle Eocene, Tennessee, U.S.A., family but no generic affinity mentioned by Berry (1930). USNM. P.
28. †*Rubiacites sphericus* Berry (1930: 133–134, pl. 45, figs. 9–11). **Fruit**, Middle Eocene, Tennessee/Kentucky, U.S.A., family but no generic affinity mentioned by Berry (1930). USNM. P.
29. †*Rubiacites wilcoxensis* Berry (1930: 133, pl. 45, fig. 8). **Fruit**, Middle Eocene, Tennessee/Kentucky, U.S.A., family but no generic affinity mentioned by Berry (1930). USNM. P.
30. †*Rubipollis oblatulus* (Pocknall & Mildenhall) Mildenhall & Pocknall. **Pollen**, MacPhail (1999: 205, pl. 11, figs. 26, 27), Late Eocene to Early Pliocene, Murray Basin, Australia. MacPhail (1999) associated this with *Canthium* Lam. NZGS. A.
31. †*Tricolporé reticulé*, without attribution in Gruas-Cavagnetto (1977). **Pollen**, from the late Eocene and Oligocene, France. This was listed as *Chomelia* Jacq. type in Gruas-Cavagnetto (1978). It is not clear if it can be distinguished from the pollen of other rubiaceous genera fide Muller (1981). UPMC. NA (as Rubiaceae or *Chomelia*).
- †*Triporettradites nachterstedtensis* (see *Gardenia*).
32. †*Uragoga tertiaria* Berry (1929b: 166, pl. 3, fig. 16). **Seed**, Eocene, Peru. USNM. P.

## OLIGOCENE

For the Oligocene, 16 fossil taxa representing 17 form and modern genera (including *Tricolporé reticulé*) and 13 species have been assigned or compared with the Rubiaceae.

1. †*Canthiumidites* aff. *bellus* (Stover & Partridge) Mildenhall & Pocknall. **Pollen**, Argentina (Barreda, 1997: 286, pl. 1, figs. 10, 11). Barreda (1997) compares the fossil to *Gardenia* (Old World tropics; see Miocene). MACN. NA.
2. †*Cinchonidium copeanum* (Lesq.) Ettingsh. (1883: 130; Ettingshausen, 1888: 49). **Leaf**, Nevada, U.S.A. Ettingshausen (1883, 1888) compares the fossil to *Cinchona* (Andes). USNM (Lesquereux material), JVG (Ettingshausen material). P.

3. †*Circotroporites camerounensis* (see Eocene).
  4. *Coprosma* type. **Pollen**, New Zealand (Couper, 1960: 59, pl. 9, figs. 1–3). Included in Mildenhall (1980: 215), NZGS. A (fide Mildenhall, 1980).
  5. *Faramea*. **Pollen** (triporate form), Puerto Rico (Graham & Jarzen, 1969: 328, fig. 21). *Faramea* presently grows in tropical America. MO. A.
  6. *Guettarda* †*intercalaris* Hollick (1928: 225, pl. 81, fig. 5b). Line drawing of leaf fragment, Puerto Rico. *Guettarda* presently grows in New Caledonia and tropical America. USNM. P.
  7. cf. †*Guettardidites* Khan (see Eocene).
- Macrosphyra* Hook. f. (see *Triporetetradites hoekeni*)
8. †*Mitragynaxylon gevinii* Koeniguer & Lemoigne in Gevin et al. (1971: 386–393, text-figs. 1, 2; pl. 23, figs. 1–8). **Wood**, Oligocene and Miocene, Algeria. Laboratoire Géologie Appliquée (Gevin), Laboratoire de Paléobotanique (Lemoigne), Université de Lyon (Université Claude-Bernard); Laboratoire de Paléobotanique, Université de Paris (Koeniguer). P.
  9. †*Naucleaphyllum ovale*<sup>2</sup> Louvet & Mouton (1970: 82–85, pl. 2). **Leaf**, Libya. Repository unknown. NA.
  10. †*Palaeocoprosmadites zelandiae* Pocknall. **Pollen**, MacPhail (1999: 205, pl. 9, figs. 16, 17), Late Oligocene to Pleistocene, Murray Basin, Australia. MacPhail (1999) compares the fossil to *Coprosma-Opercularia*. ASNU. A.
  11. *Pinckneya* †*dilcheri* Meyer & Manchester (1997: 149, pl. 63, figs. 8–10; Fig. 1G). **Seed**, Oregon, U.S.A. This is an extant genus in the Rubiaceae with one species (*Pinckneya pubens* Michx.; Fig. 1H) in the southeastern U.S.A. FLMNH. A.
  12. †*Psilatricolpites coprosmidis* (see Paleocene).
  13. †*Retitricolporites annulatus* Sal.-Cheb. (1978: 236–238, pl. 4, figs. 7–9). **Pollen**, Cameroon. Salard-Cheboldaeff (1978) compares the fossil to *Mitragyna inermis* (Willd.) Kuntze, which grows in Cameroon. UPMC. A (fide Muller, 1981).
  14. †*Rubioxylon naucleoides* E. Hofm. (1952: 172, pl. 13, fig. 3). **Wood**, Austria. Repository unknown (Vienna, Austria). P.
  15. †Tricolporé reticulé (see Eocene).
  16. †*Triporetetradites hoekeni* Sal.-Cheb. (1978: 252, pl. 7, fig. 3). **Pollen**, Cameroon. Salard-Cheboldaeff (1978) compares the fossil to the extant *Macrosphyra longistyla* (DC.) Hiern that grows in Cameroon. UPMC. A (fide Muller, 1981).
- MIocene
- Note that fossils described by Berry (1925, 1938) from Laguna del Hunco and Río Pichileufu, Argentina, and referred by him to the Miocene, are now regarded as Eocene (Romero, 1986; Wilf et al., 2005; Zamalao, pers. comm., 2008). For the Miocene, 58 fossil taxa representing 46 form and modern genera and 37 species have been assigned or compared with the Rubiaceae.
1. *Borreria* G. Mey. **Pollen**, Médus (1975: 576, pl. 10, fig. 3, pl. 11, figs. 30–32), Senegal. FSTS-J. A.
  2. *Bothriospora* †*twitii* Engelm. (1895: 30, pl. 6, fig. 6). **Leaf**, Colombia (also Pons, 1985: 241). Pons (1985) compares the fossil with the extant *Bothriospora corymbosa* (Benth.) Hook. f. growing today in Colombia, Ecuador, Guyana, and Peru. RN-D (Engelhardt material), UPMC (Pons material). P (both).
  3. *Canthidium* †*radobojanum* Unger (1850: 429). **Leaf**, Croatia. The genus occurs today in the Paleotropics. UVA. P.
  4. †*Canthiumidites bellus* (Stover & Partridge) Mildenhall & Pocknall. **Pollen**, MacPhail (1999: 205, pl. 5, figs. 5, 6), Early to Middle Miocene, Murray Basin, Australia; *Canthiumidites* cf. *bellus* Middle Miocene–Early Pliocene, Falkland Islands, MacPhail and Cantrill (2006: 610, table 1; 613, table 3; pl. III, figs. 39, 40); *Randia*. ASNU. A.
  5. *Chiococca* P. Browne. **Leaf**, Axelrod (1940; 1979: 32), Mint Canyon flora, southern California, U.S.A. The Mint Canyon flora is found on a terrane transported north from northwestern Mexico along the San Andreas Fault. MPUC. A.
  6. *Chomelia* Jacq. type. **Pollen**, Graham (1991a: 212–213, fig. 40; Fig. II; Graham, 1991b), Panama. MO. A (as the family).
  7. †*Cinchonidium racemosum* Unger. **Fruit**, Unger (1850: 430; Unger, 1865: 11, pl. 3, figs. 1, 2, 6), Croatia. UVA. P.

8. †*Condaminea grandifolia* Engelh. (1895: 34, pl. 7, fig. 2; pl. 9, fig. 1). **Leaf** (as Rutaceae), Colombia. RN-D. P; Berry (1919: 293–294, pl. 17), leaf, Peru. USNM. P.
9. *Coprosma* type. **Pollen**, Leopold (1969: 1180, pl. 311, fig. 37), Marshall Islands. USGS. A (as Rubiaceae; see also †*Psilatricolpites coprosmoides*, Paleocene, pollen).
10. *Cosmibuena* Ruiz & Pav. **Pollen**, Graham (1991a: 213, fig. 43; Graham, 1991b), Panama. MO. A.
11. *Coussarea* †*membranacea*<sup>1,4</sup> Engelh. **Leaf**, Chile (see Tertiary undifferentiated), Berry (1922: 86, listed only), Chile. RN-D (Engelhardt material). P.
12. †*Cricotriporites camerounensis* (see Eocene).
13. †*Elaeagnites campanulatus* Heer. **Calyx**, Heer (1876: 58, pl. 12, fig. 11), Spitsbergen. ZOOZ. P.
14. *Endlicheria rhamnoides* Engelh. **Leaf**, Engelhardt (1895: 12, pl. 1, figs. 7 [as 17 in Engelhardt, 1895 text], 19, 20), Colombia; Berry (1929a: 91, listed only), Ecuador, under Rubiaceae but genus belongs to the Lauraceae. RN-D (Engelhardt material). P.
15. *Exostema* †*precaribaeum* Berry. **Leaf**, Berry (1939a: 132–133, pl. 18, figs. 4, 5), Cuba. USNM. P.
16. *Faramea* types 1, 2, **pollen** (triporate, tetraporate forms), Graham (1991a: 213, figs. 41, 44, 45, 48; 1991b), Panama. MO. A.
17. *Faramea miocenica* Berry. **Leaf**, Berry (1925: 228–230, pl. 7, fig. 4), Argentina (Patagonia). USNM. P.
- Faramea* (see also †*Psilatriporites corstanjei*).
18. †*Favitricolporites magnus* without attribution in Mandaokar (2003: 190, no illustrations, description, referred to Rubiaceae), Mizoram region, northeastern India. Lucknow, India. NA.
19. *Galium* L. **Pollen**, White & Ager (1994: 51, pl. 4, fig. 22), Alaska, U.S.A. GSC, USGS. A.
- Gardenia* (see also †*Triporettradites letouzeyi*).
20. *Gardenia* cf. *grievei* Horne. **Pollen**, Leopold (1969: 1175, pl. 310, figs. 16, 17), Marshall Islands. USGS. A (fide Muller, 1981).
21. *Gardenia pterocalyx* Valetton type. **Pollen**, Anderson & Muller (1975: 307–308, listed only), Borneo. SOCDH. A.
22. †*Gardeniapites taiwanensis* Huang. **Pollen**, Huang (1978: 79, pl. 1, figs. 9, 10), Taiwan. NTU. A (fide Muller, 1981).
23. *Gouatteria* †*tenuinervis*<sup>4</sup> Engelh. **Leaf**, Engelhardt (1891: 656–657, pl. 5, fig. 6b), Chile, P; Berry (1922: 86, listed only), Chile, P. RN-D (Engelhardt material). P.
24. cf. *Guettarda* L. **Pollen**, Leopold (1969: 1175–1176, pl. 310, figs. 29, 30), Marshall Islands. USGS. A.
25. *Guettarda* †*cookei* Berry. **Leaf**, Berry (1921: 125–126, pl. 21, figs. 5, 6; Tertiary), Dominican Republic. USNM. P. Berry (1923a: 9), Haiti. USNM. P. Berry (1923b: 26), Oaxaca, Mexico (as ?, fragmentary). USNM. P.
26. cf. †*Guettardidites* Khan (see Eocene).
27. *Ixora* cf. *Ixora casei* Hance. **Pollen**, Leopold (1969: 1174, pl. 310, figs. 13–15), Marshall Islands. USGS. A (fide Muller, 1981).
28. *Macrosphyra* (see Oligocene).
29. †*Mitragynaxylon gevini* (see Oligocene).
30. *Mitragyna* Korth. type (see Oligocene).
31. *Morelia* A. Rich. ex DC. (see *Retitriporites boltenhagenii*).
32. †*Retitriporites boltenhagenii* Sal.-Cheb. (1978: 247–248, pl. 6, fig. 2). Salard-Cheboldaeff (1978) compares the fossil to *Morelia senegalensis* A. Rich. ex DC., Cameroon. UPMC. A (as *Morelia* type pollen; Muller, 1981).
33. cf. *Morinda citrifolia* L. **Pollen**, Leopold (1969: 1175, pl. 311, figs. 1, 2, 9, 10), Marshall Islands. USGS. A (fide Muller, 1981).
34. cf. *Mussaenda frondosa* L. **Pollen**, Leopold (1969: 1149, pl. 311, figs. 3, 4), Marshall Islands. USGS. A.
35. *Palaeocoprosmadites*. **Pollen**, Zamalao (2000), Middle Tertiary, Tierra del Fuego, Argentina. MACN. A (as family; see Oligocene).
36. *Posoqueria* Aubl. type. **Pollen**, Graham (1991a: 213, figs. 51–53; 1991b; Fig. 1J), Panama. MO. A.
37. *Posoqueria* †*colombiana* Engelh. **Leaf**, Engelhardt (1895: 40, pl. 7, fig. 8), Colombia. P;

- Berry (1945: 148, listed only), Ecuador. P. Berry (1936: 65–66, pl. 2, fig. 4, Colombia). RN-D (Engelhardt material). USNM (Berry material). P.
38. †*Psilatricolpites coprosmoides* (see Paleocene).
39. †*Psilatriporites corstanjei* Hoorn. **Pollen**, Hoorn (1994a: 102, pl. 4, fig. 35; see also Hoorn, 1994b, c), Colombia, compared to triporate form of *Faramea*. UA. A.
- Randia* (see also †*Triporopollenites bellus*).
40. *Randia* L. **Pollen**, Mildenhall (1980: 222), New Zealand. NZGS. A.
41. cf. *Randia cochinchinensis* (Lour.) Merr. **Pollen**, Leopold (1969: 1176–1177, pl. 310, figs. 31, 32), Marshall Islands. USGS. A (Muller, 1981, but wording may suggest that Leopold compares the fossil specifically to *R. chartacea* F. Muell.).
42. *Randia* †*mohavensis* Axelrod. **Leaf**, Axelrod (1950: 156), California, U.S.A. MPUC. P.
43. †*Retitricolporites crassicostatus* Hammen & Wijmstra. **Pollen**, Hoorn (1994a: 105, pl. 6, fig. 63a, b), Colombia. Compared to Rubiaceae. UA. A.
44. *Rondeletia* L. **Leaf**, Berry (1923b: 26, pl. 7, fig. 3), Oaxaca, Mexico. USNM. P.
45. *Rondeletia* †*goldmani* Berry. **Leaf**, Berry (1918: 42–43, pl. 18, fig. 3), Panama. USNM. P.
46. *Rubia*. **Pollen**, van Campo (1976), Spain. CNRS. A (fide Muller, 1981).
47. Rubiaceae<sup>3</sup>. **Pollen** types 1, 2, Graham (1989: 63, figs. 45, 46), Panama. MO. A.
48. †*Rubiacites asperuloides*<sup>2</sup> Weber. **Leaf**, Wessel and Weber (1855: 149, pl. 26, fig. 12), Germany. Repository unknown. P (as family).
49. †*Rubiacites ixoreoides* Berry. **Fruit**, Berry (1918: 43, 44, pl. 18, figs. 9–12). Panama. USNM. P (as family).
50. †*Ruboides lignita* Perkins. **Fruit**, Perkins (1905: 193, pl. 78, figs. 80, 84). Vermont, U.S.A. VGS (specimens not at VGS, location unknown). The Brandon Lignite was later studied by Traverse (1955: 74, 1994; pollen listed by Traverse [1955] as Rubiaceae?, and under Pollen Not Classified, ??Rubiaceae??) and Tiffney (1977 et seq.; fruits, seeds; see also Tiffney & Traverse, 1994; Rubiaceae not listed). P (fruit and pollen as family).
51. *Sabicea* Aubl. **Pollen**, Graham (1987; 1988: 1456, figs. 63, 64; Fig. 1K), Panama. MO. A.
52. *Sabicea* †*asperifolia* Engelh. **Leaf**, Engelhardt (1895: 40–41, pl. 5, fig. 6; pl. 8, fig. 6), Colombia. RN-D. P.
53. *Sabicea*? †*elliptica*<sup>4</sup> Engelh. (1891: 657, pl. 5, figs. 5, 7). **Leaf**, Chile. P; Berry (1922: 86, listed only), Chile. RN-D (Engelhardt material).
54. *Scyphiphora hydrophyllacea* Gaertn. type pollen. Leopold (1969: 1149, pl. 34, figs. 15, 16), Marshall Islands. USGS. A (fide Muller, 1981).
55. cf. *Timonius* DC. **Pollen**, Leopold (1969: 1176, pl. 310, figs. 21–23), Marshall Islands. USGS. A (fide Muller, 1981).
56. †*Triporopollenites bellus* Stover & Partridge. **Pollen**, Martin (1978: 191, figs. 7r, s), Australia, similar to *Randia chartacea*. UNSWK. A.
57. †*Triporotetradites letouzeyi* Sal.-Cheb. **Pollen**, Salard-Cheboldaeff (1978: 253, pl. 8, fig. 1), Cameroon. Salard-Cheboldaeff (1978) compares the fossil to *Gardenia*. UPMC. A (fide Muller, 1981).
58. †*Triporotetradites* sp. **Pollen**, MacPhail (1999: 205). Early to Middle Miocene, Murray Basin, Australia. MacPhail (1999) compares the fossil to *Gardenia*. ASNU. A.

PLIOCENE

For the Pliocene, 16 fossil taxa representing 14 form and modern genera and six species have been assigned or compared to the Rubiaceae.

1. cf. *Alibertia* A. Rich. ex DC. **Pollen**, Graham (1976: 813, figs. 196, 197, 200), Veracruz, Mexico. MO. A.
2. *Borreria* G. Mey. **Pollen**, Graham (1976: 813, fig. 195), Veracruz, Mexico. MO. A.
3. †*Canthiumidites reticulatus* Khan. **Pollen**, Khan (1976: 766, fig. 29), Papua New Guinea. Khan (1976) compares the fossil to *Canthium obovatum* Klotzsch ex Eckl. & Zeyh. RRNA. A (as *Canthium* type fide Muller, 1981).
4. *Cephalanthus occidentalis* L. **Leaf**, Hannibal (1911: 335, 339), California, U.S.A. SUPA (possibly consolidated with collections at the Museum, UC-Berkeley). P.



5. *Faramaea* Aubl. **Pollen** (triporate form), Graham (1976: 813, figs. 179, 180; Fig. 1D), Veracruz, Mexico. MO. A.
6. cf. *Galium* L. **Pollen**, Menke (1976: 65–66, text-fig. 4b, pl. 36, figs. 9–11), Germany. Geologisches Landesamt, Schleswig-Holstein. P (fide Muller, 1981, “Menke (1976) has tentatively identified *Galium* pollen from the Pliocene of northwest Germany.”).
7. cf. †*Guettardidites ivirensis* Khan (see Eocene).
8. *Hoffmannia* †*boliviana* Berry. **Leaf**, Berry (1939b: 63–64, pl. 4, fig. 11), Bolivia. USNM. P.
- Laugeria* L. (see *Terebraria* Kuntze).
9. *Nertera* Banks & Sol. ex Gaertn. **Pollen**, Mildenhall (1980: 215, 228); listed only; lower Pliocene? New Zealand. See also Mildenhall and Crosbie (1979).
10. †*Psilatricolpites coprosmoides* (see Paleocene).
11. *Psychotria* L. **Pollen**, Wijninga (1996: 152, pl. 4, fig. 40), Colombia. UA. A.
12. Rubiaceae. **Pollen**, Wijninga (1996: 152, pl. 4, fig. 39), Colombia. UA. A.
13. Rubiaceae. **Pollen**, stephanocolpate, Graham (1976, figs. 237, 238), Veracruz, Mexico. MO. A.
14. †*Rubiacites nummularioides* Berry. **Leaf**, Berry (1917: 161, pl. 18, fig. 15; Singewald & Berry, 1922: 42, 111–112, pl. 7, fig. 7), Bolivia. USNM. P (as family).
15. *Sabicea* Aubl. **Pollen**, Graham and Dilcher (1998: 1430, fig. 18), Costa Rica. MO. A.
16. *Terebraria* Kuntze in Post & Kuntze. **Pollen**, Graham (1976: 813, figs. 187, 188), Veracruz, Mexico. MO. A (as *Terebraria* type; now *Laugeria* L.).
- Coprosmaephyllum minus* Deane. **Leaf**, Deane (1904: 213, pl. 20, figs. 7, 8); *Coprosmaephyllum ovatum* Deane. **Leaf**, Deane (1904: 212, pl. 20, figs. 1–3), Australia. Deane (1904) compares the fossils to the extant *Coprosma*. GSV. A.
5. *Coussarea* †*membranacea* Engelm. **Leaf**, Engelhardt (1891: 656, pl. 5, fig. 2). Chile. RN-D. P.
6. *Gouatteria* †*tenuinervis* Engelm. **Leaf**, Engelhardt (1891: 656–657, pl. 5, fig. 6b). Chile. RN-D. P.
7. *Guettarda* †*cookei* Berry. **Leaf**, Berry (1921: 125–126, pl. 21, figs. 5, 6), Dominican Republic. USNM. P.
8. *Hoffmannia* †*protogaea* Engelm. **Leaf**, Engelhardt (1891: 657, pl. 5, fig. 1), Chile. RN-D. P.
9. *Psychotria* †*grandifolia* Engelm. **Leaf**, Engelhardt (1891: 656, pl. 11, fig. 4), Chile. RN-D. P.
10. †*Psychotriphyllum attenuatum* Deane. **Leaf**, Deane (1900: 60, pl. 15, fig. 2), Australia. Deane (1900) compares the fossil to *Psychotria*. GSV. A.
11. *Rondeletia* †*goldmani* Berry. **Leaf**, Berry (1937: 72, 79), Trinidad. USNM. P.
12. †*Rubiaceaecarpum multicarpellare* Menzel. **Fruit**, Menzel (1913: 10, pl. 1, figs. 20–24), Germany. Dresden. P (as family).
13. †*Rubiiphyllites linearis* Hector. **Leaf**, Hector (1880: 49; nom. nud. fide Andrews, 1970), New Zealand. Repository unknown. NA.
14. *Sabicea*? †*elliptica* Engelm. **Leaf**, Engelhardt (1891: 657, pl. 5, figs. 5, 7), Chile. RN-D. P.

## QUATERNARY

A number of Rubiaceae have been reported for the Quaternary, mostly Late Glacial and Holocene, representing taxa currently growing in the region of the fossil locality, in the modern (post 1975) literature, and used primarily for paleoenvironmental reconstructions. All are plausible and designated “A” (Accepted). Among examples of these records included here are 13 genera and 10 species:

- 1–4. †*Coprosmaephyllum angustifolium* Deane. **Leaf**, Deane (1904: 213, pl. 20, figs. 4–6); *Coprosmaephyllum attenuatum* Deane. **Leaf**, Deane (1904: 213, pl. 20, figs. 9, 10);

1. *Borreria* G. Mey. (Cuba: Moncana Ferrera et al., 1990–1991; Belize: Hansen, 1990; Panama: Bartlett & Barghoorn, 1973; Galápagos Islands: Colinvaux & Schofield, 1976; Colombia: Hooghiemstra, 1984; Brazil: Ledru et al., 2001; de

TERTIARY (UNDIFFERENTIATED; MOST NEOGENE,

PROBABLY MIOCENE)

For the Tertiary undifferentiated, 14 fossil taxa representing 11 forms and modern genera and 14 species have been assigned or compared to the Rubiaceae.

- Oliveira et al., 1999; Behling, 1997b; Bolivia: Paduano et al., 2003).
2. *Borreria anthospermoides* DC. (Colombia: Hooghiemstra, 1984).
  3. *Borreria laevis* (Lam.) Griseb. (Colombia: Hooghiemstra, 1984).
  4. *Borreria latifolia* (Aubl.) K. Schum. (Brazil: Behling, 1997b).
  5. *Canthium* Lam. (Borneo: Anderson & Muller, 1975).
  6. *Cephalanthus* L. (Louisiana, U.S.A.: Delcourt & Delcourt, 1977).
  7. *Cephalanthus occidentalis* L. (Tennessee, U.S.A.: Berry, 1924).
  8. *Faramea* Aubl. (Panama: Bartlett & Barghoorn, 1973).
  9. *Faramea occidentalis* (L.) A. Rich. (Cuba: Moncada Ferrera et al., 1990–1991).
  10. *Galium* L. (California, U.S.A.: Potbury, 1932; Washington, D.C., U.S.A.: Berry, 1924; Baja California, Mexico: Lozano-Garcia et al., 2002; Chile: Latorre et al., 2003; China, Late Pliocene to Quaternary: G. Liu, pers. comm., 2002; included in Mildenhall, 1980: 215, Late Quaternary, New Zealand).
  11. *Galium californicum* Hook. & Arn. (California, U.S.A.: Mason, 1934).
  12. *Galium palustre* L. (Germany: D. Mai, pers. comm., 2002; Mania & Mai, 1969).
  13. *Galium stellatum* Kellogg (Chihuahuan Desert, Mexico/U.S.A.: van Devender, 1990).
  14. *Guettarda calyptrata* A. Rich. (Cuba: Moncada Ferrera et al., 1990–1991).
  15. *Jackia* Wall. in Roxb. (Borneo: Anderson & Muller, 1975).
  16. *Machaonia* Bonpl. (Venezuela: Salgado-Labouriau, 1980).
  17. *Psychotria* L. (Brazil: Behling, 1997b).
  18. *Psychotria* cf. *alba* Ruiz & Pav. (Brazil: Behling, 1997b).
  19. *Randia* L. (Panama: Bartlett & Barghoorn, 1973).
  20. *Relbunium* (Endl.) Hook. f. (Brazil: Behling, 1997b; Colombia: Hooghiemstra, 1984).
  21. Rubiaceae (Argentina: Heusser, 1995; Mancini, 1998; Prieto, 2000; Quattrocchio & Borromei, 1998; Brazil: van der Hammen & Absy, 1994; Behling, 1997a; de Oliveira et al., 1999; Chile: Paduano et al., 2003; Heusser et al., 1999; Colombia: Hooghiemstra, 1984; Costa Rica: Hooghiemstra et al., 1992; Islebe & Hooghiemstra, 1997; Kesel, 1983; Guatemala: Islebe et al., 1996; Mexico: Brown & Jacobs, 1988; Lozano-Garcia et al., 2002; Panama: Bartlett & Barghoorn, 1973).
  22. *Timonius* DC. (Borneo: Anderson & Muller, 1975).
  23. *Warszewiczia* Klotzsch (Colombia: Hooghiemstra, 1984).

#### DISCUSSION

Based on the above synopsis, the accepted and pending records are summarized in Table 1, and the currently accepted records are arranged according to subfamilies, age, locality, and present distribution of the closest modern analogs in Table 2. From this summary, some generalizations emerge, as well as places where additional information would be especially useful. Regarding the origin of the family, the presently accepted fossils are too young to provide a clear indication. The oldest are cf. *Emmenopterys* from the 49–48 Ma Middle Eocene Republic flora of Washington, U.S.A. (Wehr & Manchester, 1996; subfamily Ixoroideae), and *E. dilcheri* from the 44 Ma Middle Eocene Clarno flora of Oregon, U.S.A. (Manchester, 1994). The genus is presently found in the People's Republic of China, where other genera similar to western American Tertiary plant fossils occur (e.g., *Metasequoia* Hu & W. C. Cheng, *Ailanthus* Desf., *Cercidium* Tul. complex, *Engelhardia* Lesch. ex Blume, *Platycarya* Siebold & Zucc., *Pterocarya* Kunth; Graham, 1999: 200–217). The next oldest fossils are from the Late Eocene and include *Canthium* (Australia, MacPhail, 1999; present distribution Old World tropics; subfamily Ixoroideae), *Faramea* (Panama, Graham, 1985; present distribution tropical America; subfamily Rubioideae), and *Guettarda* (Australia, MacPhail, 1999; present distribution New Caledonia and tropical America), in addition to the alternate-leaved †*Paleorubiaceophyllum* from the Middle Eocene of the southeastern U.S.A. Thus, in the Eocene, the family is represented by four or five genera, from all three subfamilies as presently circumscribed, in North America, Central

Table 1. Genera of accepted (A) and pending (P) Rubiaceae reported in the fossil record arranged according to subfamilies and tribes. The subfamilial classification follows that used in Dessein et al. (2005; see also Jalaluddin et al., 2008; Kahan et al., 2008; Martínez-Cabrera et al., 2008; Smedmark et al., 2008).

Taxon	Age	Locality <sup>1</sup>	Status
Subfamily Rubioideae			
Cousareeae			
<i>Coussarea</i>	Tertiary	Chile	P
	Eocene	Argentina	P
<i>Faramea</i>	Late Eocene	Panama	A
	Middle Oligocene	Puerto Rico	A
	Early Miocene	Panama	A
	Eocene	Argentina	P
	Pliocene	Panama	A
<i>Faramea</i> (as <i>Psilatriporites corstanjei</i> )	Miocene	Colombia	A
	Middle Pliocene	Veracruz, Mexico	A
Psychotriaceae			
<i>Psychotria</i>	Eocene	Peru	P
	Eocene	KY/TN	P
	Eocene	OR	P
	Pliocene	Colombia	A
	Tertiary	Chile	P
<i>Psychotria</i> (as <i>Psychotriphyllum attenuatum</i> )	Tertiary	Australia	A
Morindeae			
<i>Morinda</i>	Miocene	Marshall Islands	A
Spermacoaceae			
<i>Borreria</i>	Pliocene	Veracruz, Mexico	A
	Miocene	Senegal	A
Anthospermeae			
<i>Coprosma</i>	Eocene	Argentina	P
<i>Coprosma</i> (as <i>Coprosmaephyllum angustifolium</i> et al.)	Tertiary	Australia	A
<i>Coprosma</i> (as <i>Psilatricolpites coprosmoides</i> )	Paleocene	Chile	P
<i>Coprosma-Opercularia</i> (as <i>Palaeocoprosmadites zelandiae</i> )	Oligocene to Pleistocene	New Zealand	A
<i>Coprosma</i> type	Miocene	Marshall Islands	P
Rubiaceae			
<i>Galium</i>	Paleocene	Greenland	P
<i>Galium</i>	Miocene	AK	A
cf. <i>Galium</i>	Pliocene	Germany	P
<i>Rubia</i>	Miocene	Spain	A
Subfamily Ixoroideae			
Condamineae			
<i>Condaminea</i>	Miocene	Colombia, Peru	P
<i>Elaeagia</i> (as <i>Elaeagnites campanulatus</i> )	Miocene	Spitsbergen	P
<i>Emmenopterys</i>	Middle Eocene	WA, OR	A
<i>Pinckneya</i>	Oligocene	OR	A
Sabiceae			
<i>Sabicea</i>	Miocene	Panama	A
	Pliocene	Costa Rica	A
(as <i>Sabicea? elliptica</i> )	Tertiary	Chile	P
(as <i>Sabicea asperifolia</i> )	Miocene	Colombia	P
Ixoreae			
<i>Ixora</i>	Miocene	Marshall Islands	A
(as <i>Ixorophyllum anceps</i> )	Eocene	Borneo	P
<i>Scyphiphora</i>	Miocene	Marshall Islands	A
Vanguerieae			
<i>Canthium</i> (as <i>Rubipollis oblatius</i> )	Late Eocene to Early Pliocene	Australia	A
	Miocene	Croatia	P
<i>Canthium</i> (as <i>Canthiumidites reticulatus</i> )	Pliocene	Papua New Guinea	A

Table 1. Continued.

Taxon	Age	Locality <sup>1</sup>	Status
Gardenieae			
cf. <i>Alibertia</i>	Pliocene	Veracruz, Mexico	A
<i>Gardenia</i> type (as <i>Triporettradites nachterstedtensis</i> )	Late Eocene	Germany	P
<i>Gardenia</i>	Miocene	Borneo	A
	Miocene	Marshall Islands	A
(as <i>Gardeniapites taiwanensis</i> )	Miocene	Taiwan	A
(as <i>Triporettradites letouzeyi</i> )	Miocene	Cameroon	A
(as <i>Triporettradites</i> sp.)	Early to Middle Miocene	Australia	A
<i>Macrosphyra</i> (as <i>Triporettradites hoekei</i> )	Oligocene, Miocene	Cameroon	A
<i>Morelia</i> (as <i>Retitriporetites boltenhagenii</i> )	Miocene	Cameroon	A
Subfamily Cinchonoideae			
Cinchoneae			
<i>Cinchona</i> (as <i>Cinchonidium ovale</i> )	Paleocene	ND	P
<i>Cinchona</i> (as <i>Cinchonidium copeanum</i> )	Oligocene	NV	P
<i>Cinchona</i> (as <i>Cinchonidium racemosum</i> )	Miocene	Croatia	P
Portlandia–Exostema–Catesbaeae–Chiococceae (PECC) clade			
<i>Chiococca</i>	Miocene	CA	A
<i>Exostema</i>	Middle Eocene	TN/KY	P
(as <i>Exostema precaribaeum</i> )	Miocene	Cuba	P
<i>Remijia</i>	Eocene	Argentina	P
Naucleaeae			
<i>Cephalanthus</i>	Eocene	Argentina	P
	Pliocene	CA	P
<i>Mitragyna</i> (as <i>Retitricolporites annulatus</i> )	Oligocene	Cameroon	A
<i>Mitragyna</i> (as <i>Mitragynaxylon</i> )	Oligocene, Miocene	Algeria	P
Hilleae–Hamelieae			
<i>Cosmibuena</i>	Miocene	Panama	A
<i>Hoffmannia</i>	Eocene, Tertiary	Argentina, Chile	P
	Pliocene	Bolivia	P
Rondeletieae			
<i>Rondeletia</i>	Miocene	Oaxaca, Mexico	P
	Miocene	Panama	P
	Eocene	Argentina	P
	Tertiary	Trinidad	P
Guettardeae			
<i>Guettarda</i>	Eocene	MS/TN	P
(as cf. <i>Guettardidites</i> )	Oligocene	Puerto Rico	P
	Eocene to Pliocene	Australia	A
	Oligocene	Puerto Rico	P
cf. <i>Guettarda</i>	Miocene	Marshall Islands	A
	Tertiary	Dominican Republic	P
	Miocene	Haiti	P
	Miocene	Oaxaca, Mexico	P
<i>Terebraria</i> ( <i>Laugeria</i> ; as <i>Terebraria</i> type)	Pliocene	Veracruz, Mexico	P
cf. <i>Randia</i>	Miocene	Marshall Islands	A
<i>Randia</i>	Miocene	New Zealand	A
<i>Randia</i> (as <i>Canthiumidites bellus</i> )	Early to Middle Miocene	Australia	A
<i>Randia</i> (as <i>Triporopollenites bellus</i> )	Miocene	Australia	A
<i>Randia</i>	Miocene	CA	P
<i>Randia</i>	Miocene	Marshall Islands	A
cf. <i>Timonius</i>	Miocene	Marshall Islands	A
Uncertain position/incertae sedis			
<i>Bothriospora</i>	Miocene	Colombia	P
<i>Endlicheria</i> (Lauraceae?)	Miocene	Colombia, Ecuador	P
<i>Gouatteria</i>	Tertiary	Chile	P
cf. <i>Mussaenda</i>	Miocene	Marshall Islands	A

Table 1. Continued.

Taxon	Age	Locality <sup>1</sup>	Status
<i>Posoqueria</i> type	Miocene	Panama	A
		Colombia	P
		Ecuador	P
<i>Terebraria</i>	Pliocene	Veracruz, Mexico	A
<i>Uragoga tertiaria</i> (subfam.?)	Eocene	Peru	P
Rubiaceae (family only)			
<i>Chomelia</i> type	Miocene	Panama	A
	Rubiaceae	Eocene	Panama
	Miocene	Panama	A
	Pliocene	Colombia	A
	Pliocene	Veracruz, Mexico	A
(as <i>Retitricolporites crassicosatus</i> )	Miocene	Colombia	P
(as <i>Rubiacites asperuloides</i> )	Miocene	Germany	P
(as <i>Rubiacites chomeliifolia</i> )	Eocene	Argentina	P
(as <i>Rubiacites ixoreoides</i> )	Miocene	Panama	P
(as <i>Rubiacites nummularioides</i> )	Pliocene	Bolivia	P
(as <i>Rubiacites? pellicieraformis</i> )	Eocene	TN	P
(as <i>Rubiacites sphericus</i> )	Eocene	TN/KY	P
(as <i>Rubiacites wilcoxensis</i> )	Eocene	TN/KY	P
(as <i>Rubiaceocarpum markgrafi</i> )	Eocene	Egypt	P
(as <i>Rubiaceocarpum multicarpellare</i> )	Tertiary	Germany	P
(as <i>Rubioxylon naucleoides</i> )	Oligocene	Austria	P
(as <i>Ruboides lignita</i> )	Miocene	VT	P
Subfamily assignment uncertain			
<i>Paleorubiaceophyllum eocenicum</i>	Eocene	TN/KY	A

<sup>1</sup> Abbreviations for states (U.S.A.) are: AK, Alaska; CA, California; KY, Kentucky; MS, Mississippi; ND, North Dakota; NV, Nevada; OR, Oregon; TN, Tennessee; VT, Vermont; WA, Washington.

America, and Australia. This representation and distribution indicate an earlier Late Cretaceous or Paleocene origin and emphasize the need to: (1) further investigate the pending Paleocene material, and (2) devote special attention to Cretaceous megafossil deposits, such as the Early Cretaceous (Aptian) Anfiteatro de Ticó flora of Argentina, the Aptian-Albian Crato flora of Brazil, the late Middle Cretaceous (Turonian) flora of New Jersey, the Late Cretaceous (Senonian) flora of Sweden, and elsewhere for plants of rubiaceous-complex affinities.

After the Cretaceous and Paleocene, the numbers of accepted genera (form generic and modern names, including cf. identifications) in subsequent epochs are Eocene: four or five, Oligocene: six, Miocene: 20, and Pliocene: seven. Even allowing for some duplication of form-generic and modern names (†*Palaeocoprosmadites*, †*Psilatricolpites-Coprosma*; *Triporotetradites letouzeyi-Gardenia*; *Guettardidites-Guettarda*), and the different number and size of the floras studied for the various intervals, the figures suggest the Miocene (23.8–5.3 Ma) as a time of major diversification of the Rubiaceae.

The radiation of the family based on accepted records parallels the pattern of diversification. In the Eocene, fossils of Rubiaceae are known from

three regions: North America north of Mexico (Washington, Oregon, U.S.A., *Emmenopterys*; possibly the southeastern U.S.A., *Paleorubiaceophyllum*); Mexico–Central America–Caribbean region (Panama, *Faramea*); and the Southeast Pacific–Asia region (Australia, *Canthium*, *Guettarda*). In the Oligocene, they are found in four regions: North America north of Mexico (Oregon, *Pinckneya*); Mexico–Central America–Caribbean region (the Antilles, *Faramea*); the Southeast Pacific–Asia region (Australia, *Guettarda*; New Zealand, *Coprosma*, *Coprosma-Opercularia*); and Africa (Cameroon, *Macrosphyra*, *Mitragyna*). By the Miocene, accepted reports of Rubiaceae include six regions (with nine subregions): North America (California, U.S.A., *Chiococca*; Alaska, U.S.A., *Galium*), Mexico–Central America–Caribbean region (Panama, *Chomelia*, *Cosmibuena*, *Faramea*, *Posqueria* type, *Sabicea*), South America (Colombia, *Faramea*), Southeast Pacific–Asia region (Australia, *Gardenia*, *Guettarda*, *Randia*; New Zealand, and *Randia*; Borneo, *Gardenia*; Marshall Islands, *Gardenia*, *Guettarda*, *Ixora* L., *Morinda*, cf. *Mussaenda*, cf. *Randia*, cf. *Timonium*; Taiwan, *Gardenia*), Africa (Cameroon, *Macrosphyra*, *Mitragyna*, *Morelia*, *Gardenia*; Senegal, *Borreria*), and Europe (Spain, *Rubia*).

Table 2. Summary of the "A" (accepted) records of the Rubiaceae.

Taxon	Age	Fossil occurrence <sup>1</sup>	Modern distribution <sup>1</sup>
Subfamily Rubioideae <sup>2</sup>			
<i>Faramea</i>	Eocene	Panama	tropical America
	Middle Oligocene	Puerto Rico	
	Early Miocene	Panama	
	Miocene	Colombia	
	Pliocene	Veracruz, Mexico	
<i>Coprosma</i>	Oligocene to Pleistocene	New Zealand	Southeast Asia, Chile (Juan Fernandez Islands)
<i>Morinda</i>	Miocene	Marshall Islands	tropical
<i>Borreria</i>	Miocene	Senegal	warm regions of the world
	Pliocene	Veracruz, Mexico	
<i>Galium</i>	Miocene	AK	nearly cosmopolitan
<i>Rubia</i>	Miocene	Spain	warm regions of the world
<i>Psychotria</i>	Pliocene	Colombia	warm regions of the world
	Tertiary	Australia	
Subfamily Ixoroideae <sup>3</sup>			
<i>Emmenopterys</i>	Middle Eocene	WA/OR	People's Republic of China, Burma, Thailand
<i>Canthium</i>	Late Eocene to Early Pliocene	Australia	Old World tropics
	Pliocene	Papua/New Guinea	
	Pliocene	OR	
<i>Pinckneya</i>	Oligocene	OR	Southeastern U.S.A.
<i>Macrosphyra</i>	Oligocene to Miocene	Cameroon	tropical Africa
<i>Gardenia</i>	Early to Middle Miocene	Australia	Old World tropics
	Miocene	Borneo	
	Miocene	Marshall Islands	
	Miocene	Taiwan	
	Miocene	Cameroon	
<i>Ixora</i>	Miocene	Marshall Islands	New and Old World tropics
cf. <i>Posoqueria</i>	Miocene	Panama	New World tropics
<i>Morelia</i>	Miocene	Cameroon	tropical Africa
<i>Mussaenda</i>	Miocene	Marshall Islands	Old World tropics
<i>Sabicea</i>	Miocene	Panama	tropical America, Africa, Madagascar
	Pliocene	Costa Rica	
<i>Scyphiphora</i>	Miocene	Marshall Islands	Indomalaysian coasts, India, Sri Lanka, Australia
<i>Alibertia</i>	Pliocene	Veracruz, Mexico	tropical America, West Indies
Subfamily Cinchonoideae <sup>4</sup>			
<i>Chiococca</i>	Miocene	CA	FL; West Indies, tropical America
<i>Guettarda</i>	Eocene to Pliocene	Australia	New Caledonia, tropical America
	Miocene	Marshall Islands	
<i>Randia</i>	Miocene	Australia	New and Old World tropics (present-day definition, tropical America)
	Miocene	New Zealand	
	Miocene	Marshall Islands	
<i>Mitragyna</i>	Oligocene	Cameroon	tropical Africa, Asia
<i>Cosmibuena</i>	Miocene	Panama	tropical southern Mexico, Central and South America
	Miocene	Panama	
cf. <i>Timonius</i>	Miocene	Marshall Islands	Southeast Asia, Pacific islands

<sup>1</sup> Abbreviations for states (U.S.A.) are: AK, Alaska; CA, California; OR, Oregon; WA, Washington.

<sup>2</sup> Eight genera, seven accepted; oldest: Middle(?) to Late Eocene (*Faramea*), Panama.

<sup>3</sup> Twelve genera, 12 accepted; oldest: Middle Eocene (*Emmenopterys*), WA/OR; Late Eocene to Early Pliocene (*Canthium*), Australia.

<sup>4</sup> Thirteen genera, six accepted; 32; oldest: Late Eocene to Pliocene (*Guettarda*), Australia.

The earliest accepted appearance of modern Rubiaceae in the Eocene and its extensive diversification and radiation in the Miocene involve several factors. One is the length of the different epochs within the Tertiary Period: Paleocene (~65–54.8 Ma; 10.2 Ma duration), Oligocene (33.7–23.8 Ma; 9.9 Ma), and Pliocene (5.3–1.8 Ma; 3.5 Ma), compared to the Eocene (54.8–33.7 Ma; 21.1 Ma) and the Miocene (23.8–5.3 Ma; 18.5 Ma). However, during these longer epochs, fundamental changes took place in the climate and landscape at more specific times (Graham, 1999, 2008). In the Eocene, it was a significant change from the Paleocene–Eocene Thermal Maximum (PETM) or the Early Eocene Climatic Optimum (EECO), during which time temperatures were as warm or warmer than in all of the Phanerozoic (last 500 Ma), to cooler temperatures in the Middle and Late Eocene, representing the transition from hothouse to eventual icehouse conditions. This interval near the Middle to Late Eocene boundary also corresponds to the time when an increasing number of plant fossils can be referred to modern genera; viz., a principal period in the modernization of the Earth's vegetation.

The time spanning the Miocene involved both climatic and physical changes in the landscape. At the beginning of the Miocene (23.8 Ma), Arctic glaciers were present but not extensive, whereas by the end of the epoch (5.3 Ma) and in the Mio-Pliocene, there were both continental glaciers and sea ice that supplemented Antarctic glaciers in cooling the waters of the ocean basins. The effect, evident globally by the beginning of the Middle Miocene (~15 Ma), was another drop in temperature and a marked increase in seasonality. The vegetation responded with expanding versions of seasonally dry forests, caatingas, cerrado, steppe, savanna, grasslands, and near-deserts that would form communities modern in range and composition during the increasingly cold, dry intervals of the Pliocene and Quaternary.

Climate changes in the Miocene were paralleled by pronounced alterations in the landscape. For example, the Transvolcanic Belt of Mexico and the Central Andes Mountains of South America (Gregory-Wodzicki, 2000; Gregory-Wodzicki et al., 1998; Graham et al., 2001) attained most of their elevation, as did the Himalayas, during the 18 Ma interval of the Miocene.

The evolution of character traits is difficult to reconstruct from the fossil record presently available. However, the appearance of certain features can be documented by specific points in time. The typical leaf arrangement in the Rubiaceae is opposite, with alternate leaves found in a few, more advanced genera (e.g., *Didymochlamys*, *Sabicea*, *Theligonum*). However, if †*Paleorubiaceophyllum* is correctly assigned to

the family, as seems likely, this apomorphic character was present by the Middle Eocene (~45 Ma).

Pollen polymorphism is often associated with heterostyly, usually expressed by differences in pollen size, exine thickness, or occasionally pollen sculpture patterns in the different anther lengths (e.g., *Rudgea jasmminoides* (Cham.) Müll. Arg.; scabrate in pin flowers, echinate in thrum flowers; Baker, 1956). In *Faramea*, however, distinctly diporate, triporate, and occasional tetraporate pollen occurs on the same reference slides of modern pollen. In some species, almost all the grains are triporate (e.g., *F. talaman-carum* Standl., Panama, Kirkbride et al. 496, MO) and in others they are mostly diporate (*F. vaginata* Griseb., Cuba, Webster 3837, MO), while occasionally tetraporate pollen is abundant (*F. scalaris* Standl., Panama, Davidson 436, MO). If this pollen polymorphism, as opposed to random pollen variability or sterility in *Faramea*, is associated with heterostyly, then the feature, or its early development, was already present by the Late Eocene as shown by the diporate form in the Gatuncillo Formation of Panama. The presence of alternate leaves and pollen dimorphism in the Eocene, together with the diversity and distribution of Rubiaceae in that epoch, all suggest an earlier origin for the family.

#### CONCLUSION

The history of the Rubiaceae is based on assessments from the synopsis of all known reports. Tables 1 (accepted and pending reports) and 2 (accepted reports only) provide a more realistic statement of the current paleobotanical status of the family than implied by the older literature, and reveal stages in the evolution of the group after its origin. The oldest verified occurrences are in the Eocene, yet the number of likely taxa and their distribution, and the possible presence of apomorphic features such as alternate leaves and pollen polymorphism, suggest a pre-Eocene origin, probably in the Late Cretaceous or Early Paleocene. The climatic changes in the Miocene favoring the generation of novel genotypes and phenotypes, and pronounced landscape evolution providing an increased diversity of habitats, are compatible with the fossil record and further suggest the Miocene as a time of significant diversification and radiation of the family.

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