

# Mite-Plant Associations from the Eocene of Southern Australia

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Acarodomatia or "mite houses" are located on leaves of many present-day angiosperms and are inhabited by mites that may maintain leaf hygiene. Eocene deposits in southern Australia have yielded acarodomatia on fossil leaves of *Elaeocarpaceae* and *Lauraceae* and also contain oribatid mites with close affinities to those that inhabit the acarodomatia of the closest living relatives of the fossil plant taxa. The data indicate that mite-plant associations may have been widespread in southern Australia 40 million years ago.

**D**ATA ON THE EVOLUTIONARY HISTORY of beneficial associations between angiosperms and arthropods, apart from evidence that insect pollination developed early in the radiation of angiosperms (1), are scarce. For example, no fossils are reported for any of the plant structures important in the widespread and abundant symbioses between plants and ants (2). A century ago, Lundström (3) proposed that specialized chambers, which he termed acarodomatia ("little mite houses"), on leaves of angiosperms were sites for a protective mutualism with mites, an ancient and diverse group of arthropods (4). These morphogenetic structures, located in the vein axils on the leaf undersurface, are shelters for egg laying and development of mites. Because acarodomatia house fungivorous, lichenophagous, and predaceous mites, but rarely phytophagous ones, they may decrease fungal parasitism, epiphyll loads, and damage by phytophages on leaves (5, 6). Present-day associations are geographically widespread and taxonomically diverse, and domatia occur in over 80 plant families in both tropical and temperate regions (5). We describe acarodomatia and mites from Eocene leaf deposits in southern Australia and show that related mites inhabit domatia of the closest living relatives of the fossil plant taxa in structurally similar rain forest now restricted to northeastern Australia.

"Mummified" leaves (7) were extracted from clay lenses from the Alcoa Coal Mine in Anglesea (AN), Victoria (38°11'S, 144°25'E) and from the Monier East Yatala Sand Pit in Golden Grove (GG), South Australia (34°47'S, 138°43'E), sites separated by over 600 km. Biostratigraphic analyses place the ages of the lenses as late and middle

Eocene (37 to 42 million and 42 to 49 million years ago, respectively) (8). Leaf sizes and attributes in these Eocene deposits best match those of complex notophyll vine forest (CNVF) in northeastern Australia (9).

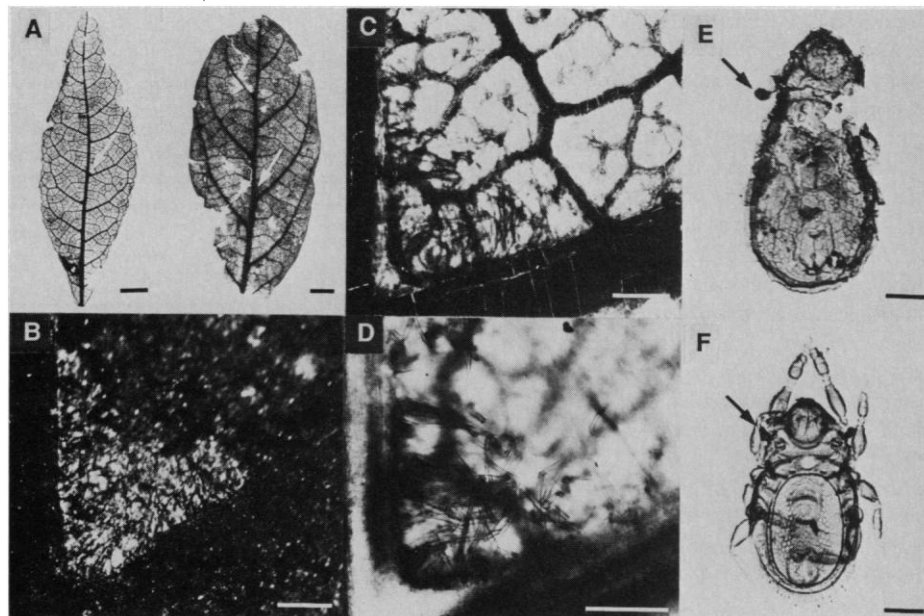
Acarodomatia are present on two leaf types at both sites (Fig. 1, A to C). Domatia-bearing leaves with serrate margins have affinities with *Sloanea/Elaeocarpus* (*Elaeocarpaceae*) and those with entire margins have been assigned to *Laurophyllum* (*Lauraceae*) (10). Both leaf types are common in both fossil deposits (each >10% of total leaves recovered) (8). At AN, 89% of *elaeocarpaceous* leaves examined bore domatia ( $n = 53$ ), and 74% had domatia at GG ( $n = 34$ ). However, domatia occur rarely on laura-

ceous leaves: of all leaves examined, only three at AN ( $n = 50$ ) and two at GG ( $n = 50$ ) had domatia. These *Laurophyllum* are rare, representing 2 of 14 lauraceous taxa (8).

For *Elaeocarpaceae* aff. *Sloanea/Elaeocarpus*, the domatium comprises a narrow flange along the midrib and primary lateral vein that tapers away from the vein juncture (Fig. 1C), and is comparable in size to the acarodomatia of extant Australian *Elaeocarpaceae* (5). The leaf lamina circumscribed by the flange is carpeted by trichomes arising from the nerves and lamina. The form of the fossil domatium suggests affinity with modern *Sloanea* and closely resembles the domatium structure of *S. australis* subsp. *parviflora* (Fig. 1D). Domatia number averages 10.4 per leaf (range, 5 to 22;  $n = 47$ ) and 7.4 (range, 1 to 14;  $n = 18$ ) at AN and GG, respectively, similar to domatia number on leaves of modern *Sloanea* (11).

The domatium of *Laurophyllum* is composed of trichomes arising from the nerves and restricted to the juncture of the midrib and primary lateral veins (Fig. 1B). They average 9 and 11 per leaf at AN and GG, respectively. The modern generic affinities of this lauraceous fossil taxon are unknown.

We also found mites in these Eocene deposits (Table 1). Only adults of oribatid mites were recovered, presumably because they are heavily sclerotized and more likely



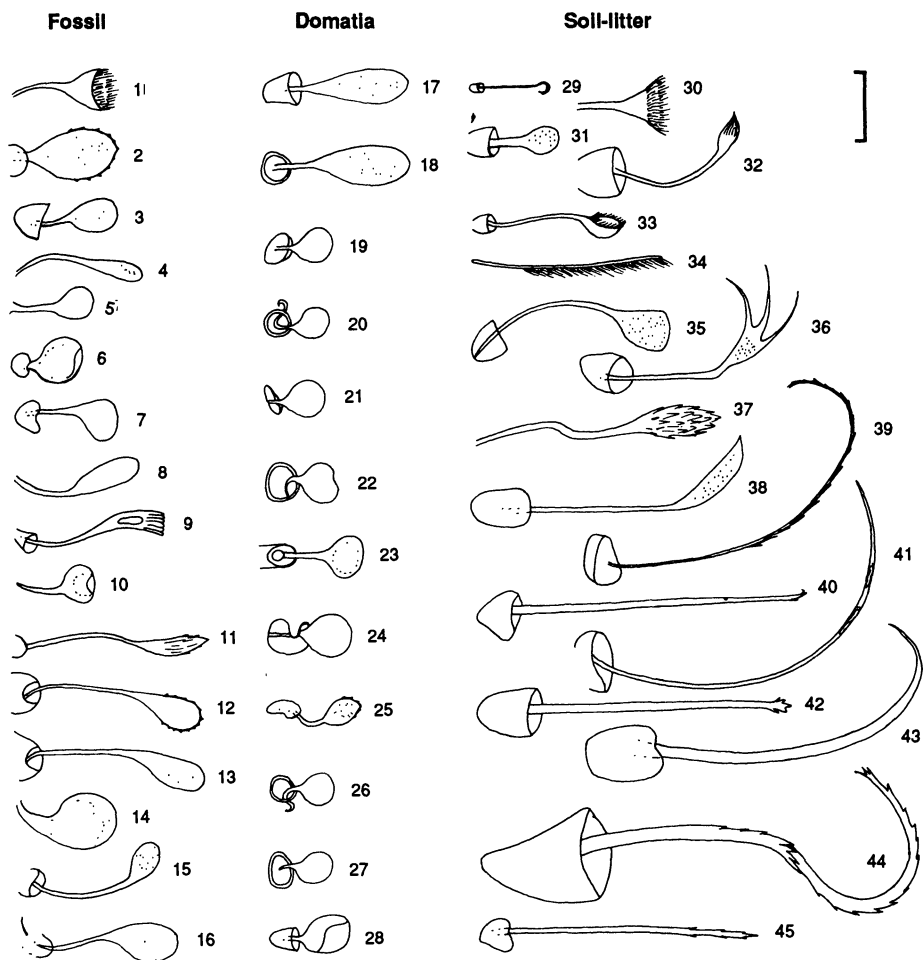
**Fig. 1.** (A) Domatia-bearing leaves of *Elaeocarpaceae* aff. *Sloanea/Elaeocarpus* (AN2158, left) and *Laurophyllum* (AN5150, right) from the Eocene deposits at Anglesea, Victoria, Australia. Arrows indicate domatia. Scale bars, 1 cm. Specimens are housed in the Adelaide University Paleobotanical Collection. (B) The domatium of *Laurophyllum* (*Lauraceae*) from Anglesea. Scale bar, 500  $\mu$ m. (C) The domatium of *Elaeocarpaceae* aff. *Sloanea/Elaeocarpus* from Anglesea. Scale bar, 500  $\mu$ m. (D) Skeletal preparation (28) of the leaf of *Sloanea australis* subsp. *parviflora* (*Elaeocarpaceae*) from State Forest Reserve 194, north Queensland (17°19'S, 145°24'E) showing the domatium. Scale bar, 500  $\mu$ m. (E) Fossil adult cymbaeremacid mite (*Scapheremaeus* sp.) from Golden Grove, South Australia. Scale bar, 50  $\mu$ m. Arrow indicates a bothridial sensillum. (F) Adult *Scapheremaeus* sp. from a leaf domatium of *Sloanea australis* subsp. *parviflora*. Scale bar, 50  $\mu$ m.

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**Fig. 2.** Bothridial sensilli of oribatid mites collected from the fossil deposits, from domatia of Elaeocarpaceae and Lauraceae in northeastern Australia, and from soil-litter below complex nophyll vine forest at Noah Creek, north Queensland (16°08'S, 145°26'E). Numbers in first two columns correspond to taxa in Table 1. For soil-litter mites, *Congocephus* (Carabodidae), 29; Cepheidae, 30; *Afronothrus* (Trhypochthoniidae), 31; *Suctobelbella* (Suctobelbidae), 32; *Rostrozetes* (Haplozetidae), 33; *Apophophora* (Mesoplophoridae), 34; *Trichogalumna* (Galumnidae), 35; *Acorppia* (Oppidae), 36; *Sadocephus* (Cepheidae), 37; *Zetorchestes* (Zetorchestidae), 38; *Eremobelba* (Eremobelbidae), 39; *Meristacarus* (Lohmanniidae), 40; *Galumnopsis* (Galumnellidae), 41; *Phyllhermannia* (Hermannidae), 42; *Setoppia* (Oppidae), 43; *Eremulus* (Eremulidae), 44; *Archegozetes* (Archegozetidae), 45. Scale bar, 25  $\mu$ m, except for 45, where it represents 50  $\mu$ m.



to be preserved than most other mites. Many were likely to be arboreal, feed on fungi and lichens, and occupy leaf domatia. Of ten families, the Cymbaeremacidae and Oripodidae are primarily arboreal and six others have some arboreal species (12). Further, most of the fossil mites have a shortened, globose or club-shaped bothridial sensillus (Fig. 2), a strong correlate with an arboreal habit (13). All of the fossil oribatids are from families or genera with lichen-feeding representatives (14), suggesting that they fed on epiphyllic or epiphytic lichens and fungi.

Oribatid mites also occupy domatia of extant rain forest trees with close affinities to the fossil leaves. For five species of Elaeocarpaceae and two of Lauraceae, most oribatids were in domatia (71%,  $n = 305$ ), and they made up 33% (range, 19 to 68%) of all mite occurrences in domatia (15). These oribatids overlap taxonomically with those from the fossil deposits, sharing four families (Table 1). At the generic level, *Scapheremaeus*, found in fossil deposits at both sites, also inhabit domatia of *Sloanea australis* subsp. *parviflora* (Table 1 and Fig. 1, E and F). Moreover, the shapes and sizes of the bothridial sensilli of mites from domatia overlap broadly with those of the fossil mites (Fig. 2).

The fossil leaf beds at AN and GG may have accumulated by the direct input of leaves from the canopy into ephemeral stream channels (8, 9). If so, mite deposition may have occurred directly from the forest canopy, largely bypassing mite fauna in soil and litter. This is supported by the taxonomic differences between the fossil and soil-litter oribatids, which share only 2 of 24 families, and the distinctive characteristics of the bothridial sensilli of each group (Fig. 2). A taphonomic filter favoring arboreal species is also suggested by the discovery of *Scapheremaeus* in submerged leaf packs con-

**Table 1.** Oribatid mites from the fossil deposits (AN, Anglesea; GG, Golden Grove) and in domatia of extant Elaeocarpaceae (SA, *Sloanea australis* subsp. *parviflora*; SL, *S. langii*; SW, *S. woollsii*; EC, *Elaeocarpus coorangooloo*; EL, *E. largiflorens*), and Lauraceae (CT, *Cryptocarya triplinervis*; ECo, *Endiandra cowleyana*) in northeastern Australia (27). Families and genera with known arboreal taxa (12, 13) are marked with an asterisk. Taxonomic assignments are shown by pluses; uncertain assignments are indicated by a question mark; nr = near. Numbers refer to sensilli in Fig. 2.

| Mites                      | Fossil deposits |         | Domatia                      |
|----------------------------|-----------------|---------|------------------------------|
|                            | AN              | GG      |                              |
| Cymbaeremacidae*           | ‡1              |         |                              |
| <i>Scapheremaeus</i> *     | +2              | +       | +SA, 17                      |
| nr. <i>Scapheremaeus</i> * |                 | +3      | +SA, 18                      |
| Ceratozetidae*             |                 | +4      | +CT, 19†                     |
| Oripodidae*                | +5              | ‡6      | +SA, SW, EC, EL, ECo; 20–22‡ |
| Oribatulidae*              |                 |         |                              |
| nr. <i>Phauloppia</i> *    |                 | +7      |                              |
| nr. <i>Decoribatula</i> *  |                 |         | +EL, 23                      |
| Carabodidae*               |                 |         |                              |
| <i>Carabodes</i> *         | ‡8              |         |                              |
| Plateremacidae*            |                 |         |                              |
| <i>Pedrocortesella</i>     |                 | ‡9      |                              |
| Scutoverticidae*           |                 | ‡10, 11 |                              |
| Oribatellidae              |                 |         |                              |
| nr. <i>Lamellobates</i>    |                 | +12     |                              |
| Tegoribatidae              | ‡13             | +14, 15 |                              |
| Galumnidae*                |                 | +16     |                              |
| Scheloriobatidae*          |                 |         | +EC, CT, 24, 25              |
| nr. <i>Domatorina</i> *    |                 |         | +SW, EC, EL, CT, 26          |
| gen. nov.                  |                 |         | +SL, 27                      |
| Symbioribatidae*           |                 |         |                              |
| nr. <i>Symbioribates</i> * |                 |         | +SA, 28                      |

†Immatures of Ceratozetoidea.

‡Immatures of Oripodoidea.

taining domatia-bearing leaves and in a leaf domatium of *Sarcopteryx* sp. aff. *martyana* (Sapindaceae) from stream channels under CNVF at Noah Creek.

The discovery of acarodomatia and mites from Eocene deposits separated by over 600 km suggests that mite-plant associations were widespread in rain forest across southern Australia over 40 million years ago. Both deposits contain fossil oribatids with arboreal features, the same domatia-bearing leaf taxa occur in similar frequencies, and leaf physiognomy and the frequency of domatia-bearing leaf types are comparable to present-day CNVF (9, 16). Acarodomatia and mites should also occur in Tertiary deposits in other regions (17). Up to 50% of present-day genera of woody plants in deciduous broadleaf forest have domatia (6, 18) and many, such as *Acer*, *Juglans*, *Quercus*, *Tilia*, and *Ulmus*, are important elements in Tertiary floras (19).

The radiation of epiphyllous and parasitic fungi (20) and phytophagous arthropods (21) that accompanied the diversification of angiosperms may help explain the occurrence of acarodomatia by the Eocene. At least seven taxa of epiphyllous fungi occur on Eocene leaves at AN and GG (22), and they are present in Tertiary floras elsewhere in Australia (23). Insects also mined *Elaeocarpaceae* leaves (24), and phytophagous mites are associated with Eocene leaves at a nearby site (25). These types of antagonistic interactions probably led to the early diversification of defenses among angiosperms (21, 26). Our results suggest that protective mutualism between arthropods and plants may be ancient.

#### REFERENCES AND NOTES

- W. Crepet, *Rev. Palaeobot. Palynol.* **27**, 213 (1979); J. Basinger and D. Dilcher, *Science* **224**, 511 (1984).
- A. Beattie, *The Evolutionary Ecology of Ant-Plant Mutualisms* (Cambridge Univ. Press, Cambridge, 1985), p. 8.
- A. Lundström, *Nova Acta Reg. Soc. Uppsala* **3**, XIII (1887).
- P. Kevan, W. Chaloner, D. Savile, *Paleontology* **18**, 391 (1975); W. Shear et al., *Science* **224**, 492 (1984); G. Krantz, *A Manual of Acarology* (Oregon State Univ. Press, Corvallis, 1986), p. 1.
- D. O'Dowd and M. Willson, *Biol. J. Linn. Soc.* **37**, 191 (1989).
- R. Pemberton and C. Turner, *Am. J. Bot.* **76**, 105 (1989).
- Mummified leaves are a rare form of fossilization in which the cuticular envelope of the leaf remains intact.
- D. Christophel, W. Harris, A. Syber, *Alcheringa* **11**, 303 (1987); D. Christophel and D. Greenwood, *Trans. R. Soc. S. Aust.* **111**, 155 (1987).
- D. Christophel and D. Greenwood, *Proc. Ecol. Soc. Aust.* **15**, 139 (1988). Notophyllous leaves are 7.5 to 12.5 cm in length [L. Webb, *J. Ecol.* **47**, 551 (1959)].
- No set of foliar characters distinguishes between *Elaeocarpus* and *Sloanea* species at the generic level. The entire margined taxon can be confidently placed with the Lauraceae [R. Hill, *Alcheringa* **10**, 327 (1986)].
- Domatia number per leaf averaged 8.8, 12.8, and 9.4 on *S. australis* subsp. *parviflora*, *S. langii*, and *S. woolsi*.
- J. Aoki, *Pacif. Sci.* **8**, 281 (1966); R. Norton, *Acarologia* **24**, 449 (1983); R. Norton and J. Palacios-Vargas, *ibid.* **28**, 75 (1987); C. Perez-Inigo, *Graellsia* **43**, 127 (1987); D. Lee and C. Birchby, *Trans. R. Soc. S. Aust.* **113**, 1 (1989).
- J. Aoki, *3rd Int. Congr. Acarol.* (1971), p. 59. The bothridial sensillum may be an air-current (rheotactic) receptor. The elaborate forms in the soil-litter environment may be unnecessary in an exposed environment where the sensillum is usually shortened and near globose [R. Norton and J. Palacios-Vargas, *Folia Entomol. Mex.* **52**, 61 (1982)].
- E. Seyd and M. Seaward, *Zool. J. Linn. Soc.* **80**, 369 (1984).
- A total of 2996 domatia, 547 leaves, and 102 shoots on 19 trees was sampled. Mites occupied 27 to 88% of the domatia of each species.
- At AN and GG, 2 of 18 and 2 of 25 leaf types have domatia, respectively. At Noah Creek, 2 of 27 leaf types in leaf litter on the forest floor had acarodomatia; in leaf litter packs from the stream channel, 3 of 30 and 4 of 32 had domatia.
- A. Lundström, *Bot. Zentblatt.* **14**, 246 (1890).
- Y. Brouwer and H. Clifford, *Notes Jodrell Lab.* **12**, 1 (1990); M. Willson, unpublished results.
- O. Ball, *Bull. Agric. Mech. Coll. Texas* **2**, 1 (1931); J. Wolfe, in *Paleobotany, Paleocology, and Evolution*, K. Niklas, Ed. (Praeger, New York, 1981), vol. 2, p. 79.
- D. Dilcher, *Paleontographica* **116**, 1 (1965); K. Pirozynski, *Annu. Rev. Phytopath.* **14**, 237 (1976).
- P. Ehrlich and P. Raven, *Evolution* **18**, 586 (1964).
- D. Christophel, unpublished results.
- R. Lange, *N. Jb. Geol. Palaont. Abh.* **151**, 142 (1976).
- A. Rozeffelds, *Alcheringa* **12**, 1 (1988).
- R. Southcott and R. Lange, *Rec. S. Aust. Mus.* **16**, 1 (1971).
- P. Regal, *Science* **196**, 622 (1977).
- Mites were extracted using the Na<sub>2</sub>CO<sub>3</sub> method [M. Brasier, *Microfossils* (Allen & Unwin, London, 1980), p. 164].
- D. Christophel and S. Lys, *Aust. J. Bot.* **34**, 649 (1986).
- A. Irvine, B. Gray, R. Halliday, D. Lee, S. Swann, M. Willson, and N. Wilson helped with the study. A. Beattie, B. Downes, R. Halliday, E. Lindquist, D. Walter, and M. Willson improved the manuscript. Supported by the Australian Research Council.

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## Strain Measurements and the Potential for a Great Subduction Earthquake Off the Coast of Washington

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Geodetic measurements of deformation in northwestern Washington indicate that strain is accumulating at a rate close to that predicted by a model of the Cascadia subduction zone in which the plate interface underlying the continental slope and outer continental shelf is currently locked but the remainder of the interface slips continuously. Presumably this locked segment will eventually rupture in a great thrust earthquake with a down-dip extent greater than 100 kilometers.

THE POTENTIAL FOR A GREAT THRUST earthquake in the Cascadia subduction zone along the coast of Washington (Fig. 1) has been a subject of controversy (1). The Juan de Fuca plate is being subducted beneath the North American plate in an east-northeastward direction. Subduction there may be aseismic, that is, incapable of producing a great earthquake. The absence of even small thrust earthquakes along the plate interface is the primary evidence for aseismic subduction (2). That evidence is supported to some extent by indications that the shallow regional stress field in northwestern Washington involves north-northeast compression (3) rather than the east-northeast compression expected from subduction. The relative youth (~8 million years) and the thick sediment cover of the oceanic plate at the deformation front imply high temperatures in the subducted plate and high pore pressures in the subducted sediments and overlying accretionary prism, conditions that favor aseismic subduction (4, 5). However, great earthquakes

do occur at other subduction zones where relatively young ocean crust is blanketed by a thick sediment cover (6), and geologic evidence (7, 8) indicates that large earthquakes have occurred along the coast of Washington at an average interval of about 600 years over the past several thousand years. Also, surveys of triangulation and trilateration networks (9) generally indicate an east-northeast contraction in northwestern Washington consistent with the accumulation of strain expected for seismic subduction.

To obtain an accurate measure of strain accumulation along the Cascadia subduction zone, we installed an eight-station trilateration network (Fig. 1) in the eastern core of the Olympic terrane, a post-Eocene accretionary prism. The network was surveyed in September 1982, 1983, 1986, and 1990. In each survey the same 21 distances between pairs of geodetic stations were measured with a Geodolite, a precise electro-optical distance-measuring instrument. The refractivity correction was determined from end-point pressure measurements and temperature and humidity profiles measured along the line from a small aircraft at the time of ranging (10). The measured distances range from 9 to 27 km, and the standard errors in

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