Family Coccidae

The soft scales or coccids are the third largest family of scale insects, including about 1,130 species in more than 160 genera (Ben-Dov 2002a). Soft scales occur in all zoogeographic regions on over 200 families of host plants, especially on trees and woody shrubs (Ben-Dov 1993). Females have two or three immature instars and males have four (Hodgson 1994). The wax covering varies across the family, but is relatively consistent within genera. Many genera produce an inconspicuous transparent wax, whereas others have an ornate waxy covering or mealy wax secretions (Hodgson and Henderson 2000); the wax is attached to the soft scale body. Eggs usually are laid in a filamentous waxy ovisac or in a cavity under the body of the female. Second-instar males produce an unusual test that frequently is diagnostic for the genus and/or species (Miller and Williams 1990).

There are surprisingly few gall-inducing soft scales. We can find records of only five species in three genera (Table 1), although there could be a few more reported in the literature. The only purported coccid that induces covering galls is Cissococcus fulleri Cockerell (Brain 1918, Hodgson 1994, Beardsley 1997). It is not clear if Cissococcus is properly placed in the family (Cockerell 1902, Hodgson 1994, Miller and Hodgson 1997). According to Brain (1918), the female of C. fulleri induces pear-shaped galls on the stems, tendrils, and leaf stalks of Cissus in South Africa. The galls are about 12 mm long, woody, with a truncate top where there is a large circular opening that leads into an outer gall chamber at the bottom of which is a minute orifice above the chamber housing the coccid. The anal plates of the adult female are modified to form a plug for the opening. Males do not induce galls but are believed to form a glassy puparium that is not divided into plates (as is typical of coccids), but has a fringe of glassy filaments plus two submarginal rows of extremely long white glassy filaments. Examination of the figure in Brain (1918) suggests that the puparium is more similar to the test produced by second-instar male eriococcids than to that of soft scales. The unusual morphology of the adult female, in which the dorsum is restricted to a small area and the bulk of the body is formed by the venter (Hodgson 1994), is presumably an adaptation to the gall habitat.

The large genus Coccus contains almost 90 species (Ben-Dov 1993), but only one is believed to be gallicolous. Coccus resinatum (Kieffer and Herbst 1909) is reported to induce galls on the stems of Baccharis in Chile (Ben-Dov 1993). Few details are available on the gall structure and there are no recent reports on this species. There are no obvious morphological adaptations to a gallicolous way of life.

Clenochiton currently has about 20 species (Ben-Dov 2002a) but only four New Zealand species truly belong there (Hodgson and Henderson 2000). Three of these, C. paraviridis Henderson and Hodgson, C. toru Henderson and Hodgson, and C. viridis Maskell, induce distortions on the leaves of their hosts (Hodgson and Henderson 2000, Maskell 1890). A depression formed under the female body on the undersides of leaves acts as a brood chamber for the eggs. Leaf distortion is not evident on the under surface of
the leaf until the body of the female is removed, but small bumps can be seen on the upper leaf surface.

Several species of ant-attended soft scales have been described as associated with some kind of host-plant deformation, but it is not always clear whether the scale is the cause of the deformity. For example, *Myzolecanium kibarae* Beccari, from Papua New Guinea, lives in ant tunnels in branches of *Kibara formicarum* Becc. (Monimiaceae) (Beccari 1877); swollen areas of the host apparently only occur when *M. kibarae* is present. In the description of *Cryptostigma secretus* Morrison (= *C. inquilina* (Newstead)), it was indicated that the adult female is sometimes found in depressions on the stems.

**Family Diaspididae**

The diaspidids or armored scales are the largest family of Coccoidea, comprising about 2,370 species in 378 genera (Y. Ben-Dov, personal communication, Miller and Gimpel 2002b). They occur in all zoogeographic regions and, based on an analysis of the host data presented in Borchsenius (1966), armored scales occur on about 180 families of host plants and nearly 1,400 host genera. Armored scales generally inhabit hosts that are long lived, such as trees and shrubs, but occasionally are found on annuals as well.

Female armored scales have two immature instars and the males have four (Danzig 1980). All species form some sort of wax cover that is not attached to the body of the insect and is domicile-like in its structure. In most instances, the exuviae of the first and second instar are incorporated into the scale cover of the adult female; the cover is molded from wax produced by glands that are scattered over the body and from anal secretions (Foldi 1990). Stylets of diaspidids are generally believed to penetrate the host intracellularly and the cell contents are used as food; the penetrated cells die and chlorotic feeding areas can often be observed around the feeding scale (Sadof and Neal 1993). Honeydew is not produced by armored scales because they do not feed in the phloem like most other scale insect groups (Beardsley and Gonzalez 1975).

Larew (1990), in a comprehensive review of gall-inducing diaspidids, mentioned 31 species in 20 genera that elicit some form of host deformation. He presented information on the anatomy of the gall of *Diaspidiotus liquidambaris* (Kotinsky), one of only two armored scales reported to induce galls in the USA. The gall is started when crawlers settle on the undersides of *Liquidambaris* leaves (Hamamelidaceae) causing a pit on the lower surface and a small yellow bump on the upper surface. The opening to the gall is covered by the scale cover (Stoetzel 1976). Galls are formed when leaf growth is nearly complete, suggesting that nonmeristematic leaf tissue is responsible for gall development. The predominant cell in the gall wall is an undifferentiated parenchyma cell. The epidermal cells on each gall surface enlarge, becoming thin and elongate, but the guard cells and stomata appear normal on the lower surface of the gall. The cells surrounding the stylets differ from other cells by having a prominent nucleus and nucleolus and a
less vacuolate cytoplasm. These cells resemble nutritive cells similar to those produced by some other gall-inducing insects. It is of interest that the male of this scale also causes galls (Stoetzel and Davidson 1974), but few details are available on the structure of its gall. The only other detailed treatment of the anatomy of an armored scale gall was presented by Goidanich (1960) for Carulaspis visci (Schrank). The gall is usually restricted to the surface on which the scale insect feeds and there is no swelling on the opposite surface. The plant tissues surrounding the scale enlarge, forming a circular raised area. The parenchyma cells nearest the insertion of the mouthparts are abnormally small. As in the previous species, the scale cover plugs the opening of the gall. There is no evidence of nutritive cells near the mouthparts; in fact, the stylets were found penetrating nearby vascular tissues. Males apparently do not induce galls. These two examples of armored scale galls seem to differ from asterolecaniid pit galls by lacking a lignified area under the body of the scale.

It appears that the primary mechanism of gall induction in armored scales is to induce the plant to develop a pit. In most instances, even covering galls start as pits and become enclosed primarily by continued growth of plant tissues that surround the insect body. Exceptions include leaf rolling by Dinaspis taiwana Takahashi, Leucaspis podocarpi Green, and Poliaspis media Maskell, and the witches'-brooms elicited by Maskellia globosa Fuller and by an undescribed diaspidid. Immature male scales induce galls in only five of the 22 gall-inducing species for which males have been observed. Gall-inducing armored scales seem to have few unusual morphological adaptations to their gall-inhabiting existence. This may be because gall and scale-cover environments are relatively similar. Larew (1990) even suggested the likelihood that diaspidids protected by scale covers may form nutrient sinks similar to those established by at least one diaspidid gallers. One unusual characteristic of gall-inducing armored scales is the scale cover. Nearly all non-galling diaspidids incorporate the shed skins of the immature stages in the scale cover (Stoetzel 1976, Foldi 1990), but this is rarely the case for armored scales that live in enclosing galls. Variation in these species includes: one or both of the exuviae block the gall opening and wax lines the inside of the gall cavity; the first-instar exuviae block the gall opening and no waxy secretion is produced; wax is used to block the gall opening and the shed skins remain inside the gall; a complete cover with exuviae and wax occurs inside the gall.

Although there is no definitive phylogeny of the diaspidids, it is fairly evident that the gall-inducing habit has evolved multiple times. This hypothesis is supported by the fact that gall-inducing species occur in 28 diaspidid genera in eight of the 14 tribes included in the Borchsenius (1966) classification system. Gall induction is rare in armored scales, occurring in only about 1.6 percent of the known world fauna.

Thirty-nine species (including one undescribed species discussed by Anthony (1974a), but not including those mentioned by Reyne (1954)) of gall-inducing diaspidids in 28 named genera are known (Table 1). Although Houard (1923) and Larew (1990) both reported Lepidosaphes espinosa Porter
as causing swollen stems on *Baccharis rosmarinifolia* Hook and Arn., we could find no evidence of this in Porter’s (1920) description. Nine species induce host deformation inconsistently (*Adiscodiopsis ericitola* (Marchal), *Aspidiotus excisus* Green, *Aspidiotus nerii* Bouché, *Chionaspis salicis* (L.), *Diaspidiotus ancylius* (Putnam), *Dynaspidiotus britannicus* (Newstead), *Epidiaspis leperii* (Signoret), *Lepidosaphes ulmi* (L.), and *Melanaspis obscura* (Comstock)) by occasionally inducing swelling of the stems or weak pitting of the leaves. Of the remaining 30 species, 10 produce pits or leaf pouch galls similar to the ones described above (*Abagrallaspis lirioidendri* Miller and Howard, *Adiscofiorina secreta* (Green), *Aspidiotus putarius* Green, *Carulaspis visci* (Schrank), *Chrysothamalus fodiens* (Maskell), *Diaspidiotus liquidambaris*, *Diaspidiotus nitrariae* (Marchal), *Diaspidiotus roseni* Danzig, *Emmereziaspis galliformens* (Charmoy), and *Thysanocoris nepheleii* (Maskell)), two produce pits on stems or twigs (*Anastomoderma palauensis* Beardsley and *Aonidia loranthi* Green), one produces twig swelling (*Diaspis manni* (Green)), and one produces pits on both leaves and twigs (*Aonidiella taorenisi* (Lindinger)). The remaining 16 species (including one undescribed species) induce galls that enclose the entire body of the adult female and are discussed in more detail below.

*Cryptophyllaspis* was treated by Borchsenius (1966) as a separate and distinct genus with four species from disparate localities. Although this genus has often been treated as a synonym of *Aspidiotus* (Williams and Watson 1988), we are treating it as valid to emphasize that all species in the genus induce galls. According to Green (1896), the gall of *Cryptophyllaspis occulta* (Green) begins as a pit on the underside of the leaf; by the time the adult female appears, the scale body is nearly completely enclosed in leaf tissue of the *Grewia* host (Malvaceae) and the gall protrudes from the upper leaf surface. The white scale cover blocks the narrow entrance to the gall, but the shed skins are not part of the cover and remain inside the gall. The immature male produces a shallow pit on the underside of the leaf. According to Green (1905b) the gall of *Cryptophyllaspis elongata* (Green) is similar and is produced on the same *Grewia* host. The galls are elongate, irregular tubes, slightly constricted at the base. Unlike the galls of *C. occulta*, these protrude from the lower surface of the leaf; the opening is on the upper surface. The gall of *Cryptophyllaspis ruhsaameni* Cockerell was described by Rübsaamen (1905) as a small hairless leaf gall that protrudes from the top surface of the *Cerbera* host (Apocynaceae). *Cryptophyllaspis bornmuelleri* Rübsaamen (1902) is described as merely being quite different from mite galls, conical, and occurring on the leaves of *Globularia* (*Globulariaceae*).

The genus *Diaspis* contains about 57 species (Miller and Gimpel 2002b) and only two of these induce galls (*D. cordiae* Rübsaamen and *D. manni* (Green)). In the description of *D. cordiae*, Rübsaamen (1906) indicated that its galls strongly resembled those formed by eriophyid mites, but he could never locate mites or find evidence of them in any of the numerous galls examined. The gall is apparently formed on the undersides of the leaves and protrudes on the upper surface. The cavity of the gall is filled with white hairs, and hairs cover the outer surface as well. The exuviae of the scale are obvious among the hairs in the cavity of the gall. *D. manni* only causes twig swelling (Green and Mann 1907).
Dinaspis contains 11 species worldwide (Miller and Gimpel 2002b), and only a single Taiwanese species, Dinaspis taiwana Takahashi, induces galls. This unusual armored scale induces leaf-roll galls on Actinodaphne pedicellata Hayata (Lauraceae) (Takahashi 1936). They are produced on the undersides of young leaves and roll only a small part of the outer edges of the leaf surface. The galls become yellow with age and may contain one to several females. At a distance, the host plant appears as if something has chewed small notches in the leaf margins.

Discodiaspis contains six species from Africa, Europe, and North America (Miller and Gimpel 2002b), and only the South African species D. gallamformans Ben-Dov induces galls. According to Ben-Dov (1974), it induces a covering gall on the twigs of an unidentified species of Zygocephym (Zygophyllaceae), generally near the branch nodes. The gall is oval and protrudes above the surface of the twig with the chamber invaginated into the bark. There is a small slit in the gall adjacent to the pygidium of the adult female.

Leucaspis contains 32 species (Miller and Gimpel 2002b) and only one induces galls. Leucaspis podocarpit Green induces leaf-roll galls in New Zealand on the podocarp Prumnopitys taxifolia (Solander ex D. Don) D.J. de Laubenfels (R.C. Henderson, personal communication). The leaf rolls occur on the portion of the lateral leaf where the scale insect settles on the underside. Galls of females usually cause the leaf to foreshorten and bend at the gall site. There may be a gall on both sides of a leaf. Males cause a lesser roll than females and the leaf remains straight beyond the male-induced roll. This species does not induce galls on its more favored host, Podocarpus totara D. Don (R.C. Henderson, personal communication).

The Australian genus Maskellia has a single described species, M. globosa Fuller, and is one of the most unusual gall-inducing diaspids. Although originally described from Eucalyptus gomphocephala DC. in southwest Western Australia (Fuller 1897), similar insects and galls occur on a range of species of Eucalyptus (Myrtaceae) in southeastern Australia and have been treated as conspecific (Froggatt 1915, Farrow 1996). The following description is based on Fuller (1897) and Froggatt (1915). Unlike most gallocous species of armored scales, both males and females induce galls and each is very different in appearance (Fig. 9). Galls of females develop on young twigs and often are so dense that they become coalesced, giving an aborted, uneven shape to the Eucalyptus twigs. Single galls of females vary from irregularly globular to pyriform with a definite pear-shaped internal chamber. A small hole is present at the narrow apex of the gall and is plugged by the sclerotized shed skin of the second-instar nymph. The body of the female is globular except for the narrow posterior apex; this body form allows the female to fit tightly into the pear-shaped internal chamber. Galls of males are produced on leaves and are cylindrical or horn-shaped. Although the gall protrudes from the upper leaf surface, the opening is on the lower surface and is closed with a ‘white wad’ or shed skin. The presence of galls can cause leaves of the affected foliage to be smaller and more crowded.
Fig. 9  *Maskellia globosa* (Diaspididae) on the foliage of *Eucalyptus gomphocephala* DC. from Western Australia. (a) Two twigs infested with mature galls of females and males; (b) adult female (enlarged); (c) adult female (enlarged) with second-instar exuviae capping abdomen; (d) transverse section of a gall of a female showing wall (w) and twig axis (ta); (e) galls of males on a leaf (enlarged). Scale bar = 10 mm for the galled twig. (Redrawn from Fuller (1897) by P.J.G.)

than normal, thus creating a witches'-broom. In southeastern Australia, where *M. globosa* is reported to have four generations annually, it is sometimes so abundant that numerous witches'-broom outgrowths infest the branches of its host trees causing dieback and even tree death (Farrow 1996, Elliott et al. 1998).
Mauritiaspis contains only two species, both of which are purported to induce galls. The original descriptions of the galls (Mamet 1939) are not very detailed, but the gall of *M. malloti* Mamet probably falls into the category of a pouch gall. It is described as being globose or truncate, occurring on the lower surface of the leaves with the opening on the upper surface. The scale cover, including the exuviae, is inside the gall. The gall of *M. minusopis* Mamet, on the other hand, may be more correctly categorized as a leaf pit gall since it is described as a globular protuberance on the lower surface of the leaf, with the larval exuviae set in a small depression in its center, and an ellipsoidal projection on the upper leaf surface.

Green (1899) described an unusual gall-living armored scale from Sri Lanka on the leaves and stems of *Loranthus* (Loranthaceae) as *Chionaspis fodiens* Green, and it was later placed in the monotypic genus *Nudachaspis*. The body of the adult female is completely buried in host tissue and no definite central chamber is formed (Fig. 10). The pygidium is normally oriented toward the gall opening on the host surface. This opening is covered by the shed skin of the first instar and is surrounded by a raised area that looks like a blister. The adult female does not form a scale cover, but is briefly enclosed inside the delicate second exuviae. As the female matures, the anterior portion of her body becomes unusually enlarged, causing the shed skin of the second instar to rupture and break into many pieces. Males apparently do not induce galls.

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**Fig. 10** Gall of females of *Nudachaspis fodiens* (Diaspididae) on a stem of *Loranthus*; enlargement shows cut-away view of two female armored scales embedded in stem tissue. Scale bar = 10 mm for the galled twig. (Redrawn from Green (1899) by G.L. Miller)
Parachionaspis is a monotypic genus described for the gallicolous species *P. galliformens* Green. The gall induced by this species is apparently formed similarly to pit galls, but the plant tissues that surround the insect's body eventually enclose all but a small dorsal opening (Green 1899). A hollow cell is formed beneath the insect body, suggesting that a depression is formed in the tissue. The gall opening is covered by the shed cuticles of the first two instars and a thin wax covering lines the walls of the gall. Males do not induce galls.

There are 10 species of *Poliaspis* (Miller and Gimpel 2002b), only one of which occurs in galls. The New Zealand species *P. media* induces leaf-roll galls on species of at least two genera of native plants, *Myrsine* (Myrsinaceae) and *Coprosma* (Rubiaceae); galling is apparently obligate only on two species of *Myrsine* (R.C. Henderson, personal communication). *M. australis* (A. Rich.) Allan has ovate leaves with undulate margins and the gall is a tightly rolled, leaf-tip curl, which becomes obviously chlorotic. Although the tip of the leaf is deformed, the rest is not stunted. *M. salicina* Heward has narrow leaves and both of the long edges of young leaves are rolled, but the galls do not become chlorotic. Large populations can build up inside both types of leaf rolls, as at least two generations of the scale inhabit a gall before the leaf senesces (the host plants are evergreen). Males probably are part of the aggregations found inside the galls. Leaf rosette galls on *Coprosma* species are induced when crawlers settle on new leaves and deform the host by stunting the shoot and curling the leaves. Female scales may be found on normal leaves as well (R.C. Henderson, personal communication).

*Protodiaspis* comprises 16 species (Miller and Gimpel 2002b), but includes only one possible gallicolous species. Only a brief description of the gall of *Protodiaspis cinchonae* McKenzie (1944) is available and it is not known whether the scale is the gall inducer or is an inquiline. The galls are very small tubular structures that occur on the leaves of *Cinchona calisaya* Wedd. (Rubiaceae) between the primary veins. Based on the illustration in the original description, it appears that the opening to the gall is on the lower leaf surface and the gall itself protrudes above the upper surface. It strongly resembles an eriophyid mite gall.

An unusual type of host deformation, described and illustrated by Anthony (1974a), is caused by an undescribed armored scale on *Lithocarpus sundaicus* (Bl.) Rehd. (Fagaceae) in Singapore. The first-instar nymphs settle in the axils of young leaves or lateral buds and cause shortening of the internodes, abnormal leaves that are tufted into a rosette, leaf axils that are enlarged basally, cessation of growth of the primary axis of the shoot, and formation of ancillary shoots. The end product is something that looks like a witches'-broom composed of rosettes of dwarfed, compound pinnate leaves. The scale insects occur at the base of the leaf or bud axils, which are swollen around the body of the insect.

Reyne (1954) mentioned several additional species of unidentified armored scales that induce galls. Some of these were figured in Doctors van Leeuwen-Reynvaan and Docters van Leeuwen (1926, 1941). Those of special
interest were from Indonesia on *Claoxylon indica*um Hassk. (Euphorbiaceae), *Homalanthus populneus* Pax (Euphorbiaceae), and *Santalum album* L. (Santalaceae). Each was hornlike in shape and occurred on the leaves of the host. They were induced by diaspidine armored scales that looked like members of the genus *Chionaspis* in the field.

**Family Eriococcidae**

The family Eriococcidae has about 550 described species and is the fourth largest family of Coccoidea. Eriococcids, also called felt scales, occur worldwide and have been collected on more than 45 plant families (Miller and Gimpel 2000). The most widely utilized family is the Myrtaceae from which about 140 described species have been recorded. Most gall-inducing eriococcids also feed on members of the Myrtaceae, which is a diverse family in the southern hemisphere where most gallicolous eriococcids occur.

The Eriococcidae is defined primarily on shared primitive features and the absence of features found in other families. and is not monophyletic (Cox and Williams 1987, Cook et al. 2002, Hodgson 2002). Eriococcids represent a grade or organization rather than a clade, however, the family is retained in the interest of nomenclatural stability and because the alternative is to divide the constituent taxa among a number of new families, many of which would be difficult to diagnose morphologically.

Eriococcids have two immature instars in the female and four in the male (Fig. 1). Females either live exposed on their host plant, in which case they are almost always covered by a waxy test, as for the majority of eriococcid species, or they live at least partially concealed by plant tissues in bark or in a gall of various kinds. Females feed in all stadia but males feed only during the early stadia after which they usually secrete a loose waxy test or cocoon, sometimes called a sac, in which they pupate. The males of gall-inducing species may pupate within their own gall, within the maternal gall, or on the foliage or bark outside the galls, depending on the genus.

At least 107 described species of eriococcids are gallicolous, about 85 of the latter are endemic to Australia, and only four occur in the northern hemisphere where the fauna is better known (Miller and Gimpel 2000). In addition, there is a considerable number of undescribed, gall-inducing eriococcids in Australia, as a result of limited taxonomic work on an extensive fauna (Beardsley 1974a, 1984) and the occurrence of cryptic or sibling species (e.g., Cook 2001b). Although there are only a few monotypic or species-poor genera of gallicolous eriococcids described from South America, this region's eriococcid fauna is poorly known and many more species may await discovery. New Zealand's eriococcid fauna is much better known due to Hoy's (1962) monograph, but even there a few undescribed species and genera of gall-inducing eriococcids have since been collected (R.C. Henderson, personal communication).

The galls of eriococcids are almost always covering galls, often are woody, and sometimes have complicated structure. The complexity of eriococcid galls is similar to or exceeds that of many cynipid wasp galls, which are
described as incredibly diverse, with each cynipid species inducing a highly characteristic and often highly complex gall structure (Ronquist and Liljeblad 2001, Stone et al. 2002). In most gall-inducing Coccoidea only the female induces a gall (Table 1) or the galls of the male and female are monomorphic; but in several genera of eriococcids the male and female nymphs each elicit a characteristic gall (e.g., Froggatt 1921a, b, Beardsley 1984, Gullan 1984a, b). As far as is known in the Eriococcidae, this phenomenon of sexually dimorphic galls occurs only in Apionomorpha, Cylindrococcus, Opisthoselis, Neotecococcus, Pseudotecococcus, and to a less developed degree in the pit- or blister-inducing species of Lachnodius and Sphaerococcopsis (reviewed under each genus below). In a few other eriococcid genera, such as Ascelis, Casuarinaloma, Cystococcus, and perhaps all species of Eremococcus, only females induce galls and males develop within this maternal domicile (Table 1). For several gall-inducing species and genera of eriococcids the habits of the males are not known. Galls of female eriococcids range from simple open-topped leaf or stem pits (e.g., a few Eriococcus species and some Lachnodius species), to simple, enclosed galls on stems, leaves, buds, or fruit (e.g., Aculeococcus species, Calycicoccus merwei Brain, and all Opisthoselis and Sphaerococcopsis species), to elaborate, sometimes woody, structures that may have a specialized inner layer or sometimes a camouflaged shape (e.g., all species of Apionomorpha, Casuarinaloma, Cylindrococcus, Cystococcus, and Eremococcus). Galls of the last two types always have a discrete orifice that is small in relation to the size of the gall and ranges from an elongate slit to a round hole.

For the purposes of this chapter, we mostly have not included eriococcids that cause simple plant distortion, such as leaf or stem curling or bending, as gallers. Such information is not consistently available but, more importantly, there are so many other eriococcid taxa with highly developed galling habits that discussion is devoted to these.

**Aculeococcus**

The females of the two described species of Aculeococcus, *A. morrisoni* Lepage and *A. yongpingensis* Tang and Hao, both induce enclosed galls on the leaves of their host plants. The female of the Brazilian species, *A. morrisoni*, was collected from elongate, conical galls on an undetermined wild host plant near São Paulo (Lepage 1941). *A. yongpingensis* was collected at Yungping in Yunnan, China, and its host was tentatively identified as *Cinnamomum* (Lauraceae) (Tang and Hao 1995). Each gall of *A. yongpingensis* is conical, 0.8–1.0 mm wide and 1.2 mm high, with a distinct circular orifice; many galls occur together on the underside of the host leaf. Lepage (1941) suggested that *Aculeococcus* is related to the South African gall-inducing genus *Calycicoccus* Brain, and Ferris (1957b) supported a relationship between these two taxa and the South American genus *Macracanthopyga*. Although the galls and insects of *Aculeococcus* and *Calycicoccus* share certain similarities, the gall of *A. morrisoni* is of a different growth form from those of *A. yongpingensis* and *C. merwei* Brain, and the shared turbinate body form and
sclerotized posterior abdomen of the adult females may be convergent, as suggested by Beardsley (1984). Males have not been described.

**Apionomorpha**

All species of *Apionomorpha* induce galls on *Eucalyptus* and are found throughout much of Australia and in a few localities in Papua New Guinea (Gullan 1984a). Galls are often morphologically elaborate (Figs 11 and 13) and have complex anatomy (Küster 1937, Gullan 1984a). They do not alter the shape of the organ (leaf, stem, or bud) on which they grow, for example, a gall developing on a eucalypt bud does not prevent that bud from maturing into a seed-bearing fruit (Fig. 15). Male and female insects of *Apionomorpha* induce galls that are morphologically distinct (Figs 11, 12 and 14), although often formed from apparently identical tissue on the same plant. Galls of females are large (one to several cm long), often woody structures produced on stems or more rarely on leaves and have a species-specific shape; there is always an apical orifice that is often plugged by necrotic tissue, covered by a cap of gall tissue, or otherwise hidden prior to maturity of the female (Beardsley 1984, Gullan 1984a, Gullan and Jones 1989). In contrast, galls of the males of the various species are generally similar to each other and consist of much smaller (no more than 1 cm long), tubular structures on leaves, stems or galls of females (Figs 12 and 14).

Currently there are 39 described species of *Apionomorpha* (Gullan 1984a, Gullan and Jones 1989), but we estimate that there are at least twice that number (L.G.C. and P.J.G., unpublished data). Adult females of *Apionomorpha* have a turbinate body (Fig. 1), 3–34 mm long and 1–15 mm wide, and lie within the gall with their sclerotized anal lobes directed towards the gall orifice. First-instar nymphs are sexually dimorphic only in species in which the males induce their galls on the galls of conspecific females (Cook et al. 2000). The life cycle of males is rarely more than 1 yr and adult males (Fig. 16) survive just a few days after leaving their galls. In contrast, the females of many *Apionomorpha* species are remarkably long-lived as adults (up to 5 yr), during which time they may produce thousands of crawlers (Cook and Gullan 2002). This longevity can result in the overlap of generations on one host tree. The long reproductive life of females also ensures survival of populations in the event of catastrophic disturbances such as wild fires. The survival of just one or a few females in patches of unburnt vegetation can provide a source of crawlers to allow colonization of regenerating eucalypts. The crawlers of some species of *Apionomorpha* appear to be well adapted for long distance dispersal (Cook et al. 2000) and can re-establish populations relatively rapidly after local extinction events (Gullan et al. 1997).

Most *Apionomorpha* species have been collected from more than one eucalypt species and most from five or more eucalypt species (Gullan 1984a), but there is considerable karyotypic variation (Cook 2000) and allozyme differentiation (Cook 2001a) within some morphological species of *Apionomorpha*, suggesting that cryptic species-complexes occur. A detailed study of *A. munita* (Schrader) has shown that each of its three subspecies is
Figs 11–16  Galls of four species of *Apliomorpha* (Eriococcidae) on *Eucalyptus* species from Australia (note the extreme dimorphism of galls of males and females). Fig. 11 Galls of females of *A. munita* (Schrader). Fig. 12 An aggregation of galls of males of *A. munita* on a gall of conspecific female. Fig. 13 Mature gall of female of *A. umalis* (Tepper). Fig. 14 A compound gall of males of *A. pharetrata* (Schrader) on a maternal gall attached to a leaf (the compound gall is cut in half to reveal the tubular chambers in which the males develop). Fig. 15 Gall of female of *A. malleacola* Gullan on eucalypt fruit. Fig. 16 Adult male of *A. pharetrata* copulating with adult female through orifice of gall. (Photographs by P.J.G. except Fig. 16 by L.G.C.)
restricted to discrete sections of the eucalypt subgenus *Symphyomyrtus* and that each subspecies exhibits considerable chromosomal variation (Cook 2001b). Furthermore, karyotypically differentiated populations of each subspecies are often restricted to only one or a few eucalypt species or series. These differences are sufficient to recognize the subspecies as distinct species. Thus, if the full extent of genetic variation within and among all *Apionomorpha* species was known, there may be much greater host specificity than is currently recognized.

The parasitoids of *Apionomorpha* and the inquilines of its galls include a range of chalcidoid and proctotrupoid wasps, weevils and even pyralid moths (Froggatt 1893, Gullan 1981). Females of *Apionomorpha* are parasitized by the bizarre dart-tailed wasps of the genus *Camerellona* (Hymenoptera: Pteromalidae). Adult female wasps have the apex of the gaster dilated into three leaf-like extensions, resembling the flute of a dart. Only one of these parasitoid wasps is reared from each adult female of *Apionomorpha*.

**Ascelis**

This Australian genus has four described species and only the females induce galls (Miller and Gimpel 2000). *Ascelis attenuata* Froggatt induces blister galls, about 1 mm in diameter, on *Eucalyptus piperata* Smith (Froggatt 1894). *A. praemollis* Schrader and *A. schraderi* Froggatt both induce leaf galls on *Corymbia gummifera* (Gaertner) K.D. Hill and L.A.S. Johnson (formerly *Eucalyptus corymbosa* Smith) (Myrtaceae) in coastal areas of New South Wales (Froggatt 1894, 1921a). Galls of *A. praemollis* are spherical, 12–20 mm in diameter, whereas those of *A. schraderi* are flattened blister galls similar to those of *A. attenuata* but larger (about 12 mm in diameter). *A. melaleucae* Fuller induces galls on the stems of its *Melaleuca* host in Western Australia (Fuller 1899). Unlike the galls of the other *Ascelis* species, those of *A. melaleucae* are divided into two chambers, with the insect occupying the lower chamber and a glassy filament from the abdomen projecting into the outer chamber and often protruding from the orifice at the conical apex of the gall.

Adult females of *Ascelis* are characterized by their lack of antennae and legs, and by their globular body with a somewhat prolonged abdomen that ends in a heavily sclerotized, buttonlike structure, which plugs the gall orifice. Males complete their development within the chamber of the maternal gall (Schrader 1863, Froggatt 1921b); in *A. melaleucae*, males live in the outer chamber (Fuller 1899). Although the life cycle of *Ascelis* has not been studied in detail, it is likely that male first-instar nymphs eclose well before their sisters and that female crawlers are unable to exit the gall until after the mother’s post-partum body has shrunk and allowed the gall orifice to be unplugged.

**Atriplica**

This genus has only one described species, *A. gallicola* Cockerell and Rohwer, known from leaf galls on *Atriplex* species (Chenopodiaceae) in western North America (Cockerell and Rohwer 1909, Ferris 1955, Gill 1993). The female causes a swelling of the base of the leaf and the sides of the leaf fold
upwards leaving an open slit above with the leaf margins curling outwards. The general morphology of the adult female closely resembles that of non-galling *Eriococcus* species and there are no special modifications related to living in a gall. The habits of the male are not known.

**Callococcus**

Currently, *Callococcus* has four described species, *C. acaciae* (Maskell), *C. leptospermi* Maskell, *C. neumannii* Foggatt, and the type species *C. pulchellus* (Maskell), and is placed in the Asterolecaniidae (Morrison and Morrison 1927, Coles et al. 1988, Miller et al. 1998). We here transfer *Callococcus* to the Eriococcidae based on molecular data from *C. acaciae* and *C. pulchellus* (L.G.C. and P.J.G., unpublished data), study of male morphology of *C. leptospermi* (C.J. Hodgson, unpublished data) and our re-examination of adult female and, where available, crawler morphology of all species.

Of the above species, only *C. leptospermi* induces galls; the other *Callococcus* species live exposed on the stems but remain covered by copious waxy secretions or within an elaborate waxy test (Fuller 1899, Foggatt 1921b). The gall and most female and male instars of *C. leptospermi* were described or redescribed and illustrated by Coles et al. (1988). Each gall consists of a woody swelling on a twig of *Leptospermum* (Myrtaceae), induced by the feeding of the female. Coles et al. (1988) made detailed observations of the life cycle of *C. leptospermi* and suggested that it took 2 yr. First-instar nymphs display sexual dimorphism, which is unusual for scale insects but occurs in several other gall-inducing taxa (Cook et al. 2000). First-instar females feed on maternal gall tissue and disperse from the gall as newly molted second-instar nymphs which migrate to new galling sites on the twigs. Males exhibit similar behavior but do not induce galls. During their first stadium and probably most of their second stadium, male nymphs feed in the maternal gall. Second-instar males then leave the gall and settle either in crevices on its outer surface or in nearby sites on the stem or bud of the twigs, where they form loose waxy cocoons and pupate. Nymphal development in *C. leptospermi* requires further study because a few of the determinations of the immature female and male instars made by Coles et al. (1988) are unusual. For example, Coles et al. described three immature instars for the female of *C. leptospermi* but all other eriococcids (and asterolecaniids) are believed to have only two female immature stages.

**Calycicoccus**

This monotypic genus was described by Brain (1918) for *C. merwei* Brain on *Apodytes dimidiata* E. Meyer ex Arn. (Icacinaceae), which is a small tree common along the southeastern coast of South Africa. *C. merwei* is unusual in being the only eriococcid native to South Africa. Females of *C. merwei* induce galls of two distinct forms on the leaves of the host plant. Galls of the most common form open on the underside of leaves and are about 3 mm in diameter and flatly conical; glassy filaments from the posterior of the female’s abdomen protrude from the orifice in the center of each gall’s cone. The second form of the gall, which occurs on the upper leaf surface, is about
4.5 mm in diameter and has a 5 mm-long tapering point curved to one side; Brain (1918) considered this gall to be an inverted form of the gall because the insects from the two types of gall appeared identical although differing in size. Males do not induce galls and probably feed on the lower leaf surface.

**Capulinia**

Of the four described species of *Capulinia*, only *C. crateriformis* Hempel induces obvious galls (Hempel 1900a), although the New Zealand species, *C. orbiculata* Hoy, develops in circular depressions in the bark (Hoy 1958). The crater-shaped galls of the female of *C. crateriformis* occur on the bark of branches and twigs of the fruit tree *Eugenia jaboticaba* Kiaersk. (Myrtaceae) in Brazil (Hempel 1900a). It is reported to cause considerable damage to its host. The adult female has reduced hind legs and no fore or mid legs. Males and crawlers are unknown. There has been no recent, detailed study of this species and it is not even certain whether it is congeneric with the type species, *C. sallet* Signoret.

**Carpochloroides**

This genus contains two species, *Carpochloroides viridis* Cockerell from Brazil and *C. mexicanus* Ferris from Mexico (Ferris 1957a). Both feed on *Eugenia* species (Myrtaceae), but only *C. mexicanus* induces galls on its hosts. The adult female of *C. mexicanus* has a membranous, rounded body less than 2 mm in diameter, highly reduced antennae and no legs. Its gall is almost globular, up to 2 cm long, and involves the petioles on small twigs; the gall orifice is obscure. Males and their habits are unknown.

**Casuarinaloma**

The single species, *Casuarinaloma leatii* (Fuller), was described from galls on an undetermined species of Casuarinaceae from near Perth, Australia (Fuller 1899), and later was reported from eastern Australia on both *Allocasuarina* and *Casuarina* (Froggatt 1933), but the latter specimens have not been compared with Fuller’s material and may represent a second species. Fuller (1899) described the adult female as pink, subglobose, and segmented, with short, stout legs, and the gall of the female as somewhat spherical with fluted sides and growing at the apex of branchlets. Froggatt (1921b, 1933) described the galls as occurring in clusters of three or four, or singly, at the tips of branchlets, each gall a flattened sphere, circular in cross section (about 6 mm across), flattened on top, and with 10–12 ridges running from apex to basal attachment. Froggatt (1933) described the adult female as broadly rounded, 1.5 mm long, red, and with well developed legs. Males develop within the maternal galls (Froggatt 1933).

**Cylindrococcus**

There are only two named species of *Cylindrococcus*, *C. casuarinae* Maskell, and *C. spiniferus* Maskell (Gullan 1984b), but at least one new Western Australian species has been recognized (P.J.G. and L.G.C., unpublished data).
All species induce galls on Allocasuarina species (Casuarinaceae) and galls of females, which can be up to 30 mm long, somewhat resemble seed cones (Fig. 17). Galls of males and females are similar in structure but those of males are smaller and more slender than the galls of their conspecific females (Fig. 18). Each gall is composed either of imbricating whirls of bladelike bracts or of thickened, coalesced bracts, and the only entrance to the gall chamber is where the bracts come together at the gall apex. The fore legs and antennae of adult females are reduced to coxal stumps, whereas the other two pairs of legs are lobelike and lack evidence of segmentation (Gullan 1984b). The dorsum of the posterior abdominal segments of C. casuarinae is sclerotized and anal lobes are lacking, whereas in C. spiniferus the anal lobes are modified into a pair of irregularly semicircular projecting plates bordered posteriorly by stout spines. The abdominal modifications of both species may serve to plug the entrance of the gall and perhaps deter parasitoids. The most amazing feature of adult males is their extremely elongate external genitalia, which just exceed the length of the abdomen and are more than half the length of the body. An elongate aedeagus and penial sheath presumably allow the male to penetrate the tightly imbricate bracts of the female’s gall to impregnate her (Gullan 1978).

**Figs 17–18**  Galls of *Cylindrococcus spiniferus* (Eriococcidae) on stems of Allocasuarina species from Victoria, Australia. **Fig. 17** Mature gall of female. **Fig. 18** Young gall of female (f) and galls of males (m). (Photographs by P.J.G.)

**Cystococcus**

This remarkable genus occurs only on the genus Corymbia (formerly part of Eucalyptus) in northern and central Australia. There are three species,
Cystococcus echiniformis Fuller, C. pomiformis (Froggatt), and an undescribed species (Froggatt 1893, Fuller 1899, Gullan and Cockburn 1986). The females induce woody, subspherical galls on the stems of their host tree (Fig. 19); the galls of C. pomiformis sometimes reach almost 9 cm in diameter although most galls are less than 5 cm in diameter (P.J.G., unpublished data). Males complete their development within the maternal gall, feeding from a layer of nutritive tissue lining the gall cavity (Figs 21 and 22). Galls of Cystococcus are called bloodwood apples or bush coconuts and are used as food by Australian Aborigines who consume the female raw and then scrape out and eat the edible, white nutritive tissue of the gall (Froggatt 1893, Latz 1995). This genus is notable for its highly sexually dimorphic first-instar nymphs, its sexual dichromism, in which male offspring are produced before female offspring, and its intersexual phoresy, in which adult males carry their first-instar sisters on their bodies when they leave the maternal gall (Gullan and Cockburn 1986). The adult male has a long slender abdomen that facilitates the transport of his tiny, tortoise-like sisters (Fig. 23). This phoresy is apparently an effective means of dispersal for female crawlers because their galls occur more evenly distributed among suitable host trees than do those of other gall-inducing eriococcids (Gullan and Cockburn 1986).

The mouth region of the adult female is firmly attached to the tissue at the base of the gall cavity and the gall orifice is plugged by her abdominal apex, which has a slight prolongation that ends in a highly sclerotized, black, buttonlike structure (Fig. 20). The mature female can attain a length of over 2 cm (P.J.G., unpublished data) and is globular prior to reproduction and then gradually changes to a cylindrical shape as her body shrinks after oviposition. This shrinkage eventually leads to the retraction of her abdominal apex from the gall orifice allowing the departure of her adult sons carrying their tiny sisters. It is not clear whether adult males mate with their mother inside the maternal gall or whether they impregnate virgin females in other galls as suggested by Breeden and Breeden (1972). When adult males land on the natal or nearby trees, their sisters alight and disperse over the foliage and initiate new galls on young stems.

Eremococcus

This genus contains four described Australian taxa (formerly in Sphaerococcus). They are Eremococcus pirogallis (Maskell) from eastern mainland Australia, E. rugosus rugosus (Maskell) and E. rugosus elongatus (Maskell) from southwestern Western Australia, and E. turbinata (Froggatt) from Tasmania (Maskell 1894, 1897, Froggatt 1921b, Miller et al. 1998). E. rugosus elongatus was described as a 'variety' of E. rugosus by Maskell (1897) but may not be distinct (Miller et al. 1998). Usually, Eremococcus is treated as a member of the Asteroelecaniidae (Morrison and Morrison 1922, Miller et al. 1998), but here we treat it as a member of the Eriococcidae (L.G.C. and P.J.G., unpublished data). All species induce structurally similar galls on the leaves or stems of species of Agonis and Leptospermum (Froggatt 1921b, P.J.G.,
unpublished data), which are two closely related genera of Myrtaceae. The record of *E. turbinata* from a *Melaleuca* species is believed to be erroneous (Miller et al. 1998).

The galls induced by females of all species in this genus somewhat resemble the fruit or flower buds of their host plants. Depending on species, mature galls range from 4–13 mm in height, are globular, subgobular, fusiform, turbinate or pear-shaped, and have either a rounded or a conically pointed apex (Maskell 1894, 1897, Froggatt 1921b) (Fig. 24). The gall orifice
is near the base of the gall on the stalked attachment except in *E. rugosus elongatus* in which the orifice is on the opposite side of the leaf to the body of the gall. In *E. pirogallis*, at the apex of the cavity in the gall of the female, there is a small saucer-shaped platform on which the female sits and feeds. According to Froggatt (1921b), the galls of *E. pirogallis* often cover the foliage on huge stands of *Leptospernum* plants growing in the vicinity of Sydney and in the Blue Mountains in New South Wales. The gall varies during the course of development from green, pink, and red, to light brown when mature. Adult females have no or reduced antennae and no legs (Maskell 1894, 1987). Males are unknown for *E. rugosus rugosus* and *E. turbinata*, however, for *E. rugosus elongatus* Maskell (1897) wrote: “Male pupae in galls similar to those of the females, but smaller, more cylindrical, yellowish or brownish, and somewhat less wrinkled”. Unfortunately it is not clear from this brief description whether each gall has a single male or several males. The distinction is important because if each gall has a single occupant then that insect is likely to have induced the gall, whereas the presence of multiple males in one chamber suggests male offspring developing in the maternal gall, as described in detail for *E. pirogallis* (Maskell 1894). Males of *E. pirogallis* pupate in the gall of the female embedded in white cottony material with each male occupying a cell in the cotton and all males lined up, pointing in the same direction. The adult male has an extremely long, slender and very elastic penis which Maskell assumed is used to impregnate the adult female which sits at considerable distance from the gall orifice. Maskell stated that the galls containing male pupae also each had an adult female gravid with eggs, which we believe is good evidence for sexual dichromism. Maskell, however, conjectured that the males could not be the offspring of that female and must have entered the gall cavity from other galls and then pupated, which is unnecessarily complicated and probably incorrect given our knowledge of several other eriococcids with similar habits.

**Eriococcus**

The large genus *Eriococcus* as currently defined (i.e., as treated tentatively by Miller and Gimpel 2000) was not monophyletic in a phylogenetic analysis based on SSU rDNA (18S rDNA) data (Cook et al. 2002). Very few of the species presently placed in *Eriococcus* (*Acanthococcus* in some literature) induce galls and, of those that do, most occur in New Zealand.

At least seven described New Zealand species of *Eriococcus* (*sensu lato*) are gallicolous (Hoy 1962, Miller and Gimpel 2000, R.C. Henderson, personal communication). These species are probably not closely related, because they differ in host-plant preferences and in female morphology. The species are *E. abditus* Hoy, *E. acutispinatus* Hoy, *E. arcanus* Hoy, *E. cavellii* (Maskell), *E. elytranthae* Hoy, *E. fessor* (Maskell), and *E. montanus* Hoy; each induces galls on the leaves, stems, or cladodes of a member of a different host-plant family (Maskell 1887, Hoy 1962, Miller and Gimpel 2000, R.C. Henderson, personal communication). *E. cavellii* is not listed as gallicolous in Hoy (1962) or any other literature because Maskell’s original description
was based on a mixed collection of *E. cavellii* and *E. nelsonensis* Hoy and the description of *E. nelsonensis* in life was given erroneously for *E. cavellii* (R.C. Henderson, personal communication). Hoy’s (1962) descriptions of the galls of these species are very brief, but the females live in leaf or stem pits in *E. acutispinatus* (stems at nodes) (R.C. Henderson, personal communication), *E. abditis*, *E. elytrantha*, *E. fossor*, and *E. montanus*; and are in enclosed cladode galls in *E. arcanus* (Fig. 25). The female of *E. cavellii* lives on a stem swelling at the leaf bud axil (R.C. Henderson, personal communication). In addition to these seven species, females of *E. fuligitectus* Hoy induce leaf fold galls when they feed on the main vein of *Carpodetus serratus* J.R. Forster and G. Forster; the affected leaf folds in half and curls along the main vein (R.C. Henderson, personal communication). Males are unknown for most New Zealand species, but in *E. abditis* the white, felted, cocoons of the males have been observed on the inside edges of old, open female galls, not completely filling the pit (R.C. Henderson, personal communication).

![Figs 24-25](image)

Figs 24–25  Galls of females of two genera of Eriococcidae. Fig. 24 *Eremococcus turbinata* on *Leptospermum nitidum* Hook. f. from Victoria, Australia (photograph by P.J.G.); scale bar = 10 mm. Fig. 25 *Eriococcus arcanus* on the cladode of *Phylocladus trichomanoides* D. Don from Auckland, New Zealand (photograph by R.C. Henderson); scale bar = 2 mm.

There is one species of gall-inducing *Eriococcus*, *E. orbiculus* (Matesova), from *Tamarix* species (Tamaricaceae) in Kazakhstan and Mongolia (Miller and Gimpel 2000). The adult female, its gall, and the life cycle were described by Matesova (1960); nymphaal feeding induces the growth of fleshy folds that close to form a gall, which is vacated by the female in autumn.
after the folds of the gall open. Apparently infestations with this galling eriococcid can be so heavy that growth of the plant is depressed (Matesova 1960). Eriococcus devoniensis (Green), from the Bristish Isles and continental Europe, so distorts the stem of its host Erica (Ericaceae) at the point of feeding that the stem may curl in a circle to enclose the insect (Williams 1985b).

Floracoccus

This genus was erected for a single species, F. elevans (Maskell), that induces galls on the bark of Eucalyptus dumosa Cunn. ex Oxley in Victoria, Australia (Beardsley 1974a). Only adult female insects are known. Their blisterlike galls, 4–7 mm in diameter, are similar to those of Sphaerococcopsis except that the minute central orifice is more irregular and the galls are shallower in Floracoccus. The female is globular with highly reduced antennae and legs and a distinctive central, approximately circular, raised and sclerotized boss composed of pouchlike invaginations. This peculiar structure presumably acts as a plug to occlude the gall orifice.

Gallacoccus

We consider this gall-inducing genus to belong in the Beesoniidae, as discussed under that family.

Kuwanina

This genus contains only the non-galling type species Kuwanina parva (Maskell) from the Palearctic and the gall-inducing K. obscurata (Maskell) from Australia, and they may not be congeneric (Miller et al. 1998). Females of K. obscurata live in blister galls on the bark of their host trees (Maskell 1896, Froggatt 1921b, Ferris 1919). They are globular, small (about 1 mm wide) and legless. Males are known only from their empty pupal tests and they either do not induce galls or they vacate their galls to pupate, as in at least one other Australian blister-gall-inducing genus. There is some confusion in the literature concerning whether the hosts belong to Acacia or Eucalyptus or both (compare Maskell 1896, Froggatt 1921b, Ferris 1919), but it is almost certain the true host is a eucalypt, given an annotation in Froggatt’s notebook and because no other eriococcid is known to induce galls on Acacia species.

Lachnodius

Only four species of Lachnodius, L. eucalypti (Maskell), L. hirsutus (Froggatt), L. hirtus Maskell, and L. leuctaris Maskell, have been described (Miller and Gimpel 2000), but about 18 more species have been recorded (J.W. Beardsley, unpublished data). All species of Lachnodius feed on Eucalyptus (Myrtaceae) (we regard Maskell’s (1896) record of an Acacia species as the host of L. hirtus as erroneous) and occur only in Australia. Adult females have ovoid bodies that are quite flattened dorsoventrally and bear a marginal row of often spinelike setae. Legs and antennae are usually well developed. Males have been described only for L. eucalypti (Maskell 1892) and are not known for most species.
At least 14 species of this genus induce pit galls or, more rarely, enclosed or partially enclosed galls. Most of these species develop in open-top leaf or twig galls; twig-galling species are the most common (J.W. Beardsley, unpublished data). Mature females of one species, *L. hirsutus*, have been collected from partially enclosed, woody twig galls that had irregular wedges of plant tissue surrounding the gall opening. It appears that the galls of *L. hirsutus* and related species may split open about the time of female maturity because enclosed globular twig galls of nymphs have been collected in association with empty galls, similar to those of *L. hirsutus* (J.W. Beardsley and P.J.G., unpublished data). The immature stages of a few undescribed *Lachmodius* species appear to feed under bark, rather than induce galls, and the habits of several other new species are not known. Collection of adult females under bark does not mean that nymphal development occurs there. Life cycle observations have been made for only two species, *L. eucalypti* and *L. lectularius* (J.W. Beardsley, unpublished data). Nymphs develop in pit galls until the adult stage for females and the second instar for males and then vacate their galls and migrate to the bark of the trunks and branches of their host tree. Females oviposit there and males form pupal cocoons in protected locations, usually under loose bark. The place or timing of copulation is not known, but ovipositing females have been found during spring and summer.

**Macracanthopyga**

This genus is known only from the type species, *M. verganiina* Lizer y Trelles, from Argentina (Lizer y Trelles 1955). Ferris (1957b) considered it to be gallicolous and closely related to *Aculeococcus* and *Calycicoccus*; Beardsley (1984) also included it in his list of gall-inducing Coccoidea. However, it is clear from reading the original description in French, that the female of *M. verganiina* forms a hard wax cover that is firmly attached to the host-plant branch and does *not* induce a plant gall.

**Madarococcus**

There are six described species of *Madarococcus*, all from New Zealand, and only *M. cunicularius* Hoy induces enclosed galls (Hoy 1962). Five of the species feed exclusively on *Nothofagus* (Fagaceae), mostly on the underside of leaves. The adult female of *M. cunicularius* is less than 1 mm long and lives in a small gall that opens on the leaf underside. Feeding by the females of *M. viridulus* Hoy causes curling and distortion of the host-plant leaf (Hoy 1962). Males pulate in white felted cocoons, sometimes in close proximity to a group of females, and do not cause noticeable deformations of their own (R.C. Henderson, personal communication). There are at least three undescribed species of *Madarococcus* in southeastern Australia and the females of one species from Tasmania inhabit small leaf galls (P.J.G. and L.G.C., unpublished data).
**Neotectococcus**

This monotypic genus was erected for *N. lectularius* Hempel, which induces galls on the leaves of an unknown host plant in Itatinga, Brazil (Hempel 1937). Galls are sexually dimorphic. The gall of the female is lenticular, 3 mm in diameter, and much lighter in color than the rest of the leaf. The gall of the male is tubular, more protruding, and smaller in diameter than the gall of the female.

**Opisthoscelsis**

There are 16 described species of *Opisthoscelsis*, but *O. prosopidis* Kieffer and Jorgensen, from a leguminous host in Argentina, is not considered to belong to this genus (Miller and Gimpel 2000). All other species of *Opisthoscelsis* induce covering galls on *Eucalyptus* in Australia (Froggatt 1921a, Miller and Gimpel 2000). In addition to the 15 named Australian species, there are about another 10 undescribed species (P.J.G., unpublished data). Adult females of all *Opisthoscelsis* species are characterized by extremely reduced fore and mid legs and greatly elongated hind legs, which accounts for the generic name (Greek: ‘opisth’—‘hind’, ‘scelis’—‘leg’); in a few species the hind leg length of mature females exceeds the body length. Galls of females occur on twigs or leaves, are usually conical, spherical, mammiform, or thorn-shaped, and up to 14 mm high in *O. maskelli* Froggatt but usually much less than 10 mm high in other species (P.J.G., unpublished data). Galls on twigs are woodier than those on leaves but the gall wall becomes lignified with age in all species. In leaf-galling species, the gall orifice can be on the upper or lower surface and it may be at the top of the main gall protuberance or on the opposite leaf surface to the body of the gall. Galls of males are smaller than galls of females (2–6 mm high), tubular and occur on leaves in most species (Froggatt 1921b, P.J.G., unpublished data).

The species fall into two distinct groups that differ in female and male morphology, reproductive mode, and use of the gall chamber. The first group includes the type species, *O. subrotunda* Schrader, and is characterized by an adult male with a short, broad abdomen bearing glandular pouch setae apically, and a globular adult female that completely fills the gall chamber; the female is ovoviviparous, retaining eggs in her body until they hatch. Species in the second group, such as *O. fibularis* Froggatt, *O. mammularis* Froggatt, and *O. maskelli* Froggatt, have an adult male with a long, attenuate abdomen lacking glandular pouch setae (as illustrated by Therion 1968), and a pyriform or ovoid adult female that occupies only the lower part of the gall cavity; the female is oviparous, laying her eggs into the spacious gall chamber. Presumably the modified abdomen of the adult male allows impregnation of a female whose vulva is at considerable distance from the gall orifice (Gullan 1984c).

**Pseudotectococcus**

There is only one species, *P. anonae* Hempel, which induces small galls on the upper leaf surface of cultivated *Annona* (Annonaceae) and has been
collected only at Viçosa, Brazil (Hempel 1935). The galls are about 3 mm high, 1.5 mm in basal diameter, and open on the lower leaf surface. Galls are sexually dimorphic; those of females are conical, whereas those of males are approximately cylindrical. Eggs are reported to be numerous in the gall chamber of females. The adult female is fusiform, about 2 mm long and has a heavily sclerotized pair of large anal lobes (Hempel 1937, Miller and Gimpel 2000). *Pseudotectococcus* may be related to *Tectococcus* as suggested by Hempel (1935). Some recent research reported chemical changes in leaf tissue of *Rollinia laurifolia* Schlecht. (Annonaceae) galled by *P. anonae* (Soares et al. 2000).

**Sphaerococcopsis**

The four described species of *Sphaerococcopsis*, *S. inflatipes* (Maskell), *S. platynotum* Beardsley, *S. simplicior* (Maskell), and *S. uniblicus* Beardsley, all induce blister-like galls on the bark of *Eucalyptus* species in southeastern Australia (Beardsley 1974b). Adult females of all *Sphaerococcopsis* species have a globular body, 1–2 mm long, and the hind legs are conspicuously larger than the first two pairs (Beardsley 1974b). Second-instar females have highly reduced appendages and regain their legs at the imaginal molt. Mature galls of *Sphaerococcopsis* consist of a small swelling covering a shallow, circular cavity beneath a thin layer of eucalypt tissue (Beardsley 1974b). Very young nymphs are completely enclosed but older galls have a dorsal orifice (approximately 0.5 mm in diameter in mature galls), which is plugged by exuviae and waxy secretions in galls of nymphs, and later is occluded by the sclerotized shield that forms a central disc on the dorsum of the female. Beardsley (1974b) reported that *S. simplicior* is probably univoltine because oviposition was observed in early summer, fully grown first-instar nymphs were present in completely enclosed bark galls in June and July (midwinter), second-instar nymphs appeared in August and September, and adult females were first observed in October. Male nymphs deserted their galls in September (spring) and formed loose waxy cocoons under the bark or in crevices.

**'Sphaerococcus' species**

*Sphaerococcus* Maskell used to be a 'dumping ground' for scale insects of uncertain taxonomic placement, although the type species is a mealybug (Pseudococcidae) and *Sphaerococcus* (*sensu stricto*) has been redefined (Williams 1985a, Ben-Dov 1994) and a number of other *Sphaerococcus* species have been transferred to other genera (Miller et al. 1998). However, a number of Australian gall-inducing eriococcid species, originally described as species of *Sphaerococcus*, have been retained as 'Sphaerococcus' until their relationships can be elucidated and new genera described. These species are: 'S.' *ferrugineus* Froggatt (currently listed under the Beesonidae in Ben-Dov et al. 2003), 'S.' *froggatti* Maskell, 'S.' *morrisoni* morrisoni Fuller, 'S.' *morrisoni elongatus* Fuller, 'S.' *pustulans* Green, 'S.' *socialis* Maskell, and 'S.' *tepperi* Fuller (Maskell 1894, 1897, Froggatt 1898, Fuller 1899, Green 1905a, Miller et al. 1998).
Females of 'S.' *pustulans* live beneath flattish, circular, blisterlike swellings, 4–5 mm in diameter, on eucalypt bark (Green 1905a). The adult female is about 2 mm long, legless, and has highly reduced antennae. Males are unknown. We concur with Beardsley's (1974a) suggestion that 'S.' *pustulans* is closely related to, but not congeneric with, *Floracoccus* and *Sphaerococcopsis*, based on our assessment of the original description of the adult female and its gall (Green 1905a) and the erioccid features discussed by Miller et al. (1998). Beardsley (1974a) also stated that he had collected an undescribed species related to 'S.' *pustulans*.

The other six *Sphaerococcus* taxa listed above induce complex galls on paperbarks, *Melaleuca* species (Myrtaceae) (Maskell 1894, 1897, Froggatt 1898, Fuller 1899), although 'S.' *tepperi* may have been collected on either *Melaleuca* or the related genus *Kunzea* (Fuller 1899). The galls of these species are mostly 10–30 mm in diameter, globular or elongate-obovoid and covered by bracts that either are filamentous ('S.' *ferrugineus*, Fig. 26), curling and cylindrical ('S.' *foggattii*), sheathing ('S.' *morrisoni morrisoni* and 'S.' *morrisoni elongatus*), or imbricating ('S.' *socialis* and 'S.' *tepperi*) (Figs 27 and 28). Males

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**Figs 26–28** Mature galls of *Sphaerococcus* (Eriococcidae) on *Melaleuca* species from Australia. **Fig. 26** 'S.' *ferrugineus* from northern New South Wales. **Fig. 27** Gall of 'S.' *socialis* cut open to reveal male pupae in their cocoons. **Fig. 28** A group of galls of 'S.' *socialis* from southwest Western Australia. (Photographs by P.J.G.)
develop amongst the bract bases within the maternal gall in 'S. socialis (Maskell 1897) (Fig. 27); males are unknown or poorly known for the other species, although a single live adult male has been collected with an adult female inside a gall of 'S. morrisoni elongatus (P.J.G., unpublished data). In some galls of 'S. socialis there are multiple adult females (Maskell 1897) and these appear to belong to more than one generation (L.G.C. and P.J.G., unpublished data). There are several undescribed, gall-inducing species of this group on Melaleuca in southeastern and southwestern Australia (P.J.G. and L.G.C., unpublished data).

**Stegococcus**

This New Zealand genus was described for *S. oleariae* Hoy, the females of which induce leaf galls on *Olearia* (Compositae) (Hoy 1962). The galls open on the upper leaf surface but protrude as a swelling on both leaf surfaces. The adult female is only about 1 mm long and presumably the gall is very small as well. Hoy (1962) believed that *Stegococcus* was closely related to *Eriococcus*, several New Zealand species of which also induce galls; the adult females can be distinguished by the lack of large tubular ducts on the dorsum in *Stegococcus*. Males and their habits are unknown. Another, undescribed, species of *Stegococcus* from New Zealand lives enclosed in flask-shaped stem galls on *Olearia* species (R.C. Henderson, personal communication).

**Tectococcus**

This monotypic South American genus was erected for the Brazilian species *T. ovatus* Hempel, whose female induces circular galls, up to 8 mm in diameter, on the leaves of its host plants (Hempel 1900b, 1901). Hempel stated that the galls protruded on both leaf surfaces but opened on the underside. A more recent study (Vitorino et al. 2000) described the galls as convex on one side of the leaf and acuminate on the other, up to 8.5 mm deep, and with the gall orifice on the acuminate side, which was usually the upper leaf surface. Hempel described the host as a shrub belonging to the Myrtaceae, but later Hoy (1963) reported the hosts as *Psidium variabile* Berg. (Myrtaceae) and *Daphnopsis racemosa* Griseb. (Thymelaeaceae). Hoy's citations are unlikely to be correct given the results of recent host specificity testing and field observations by Vitorino et al. (2000), who studied the biology of *T. ovatus* around Curitiba, Paraná, Brazil. Galls of *T. ovatus* developed only on *Psidium cattleyanum* Sabine and *P. spathulatum* Mattos and not on the commonly cultivated species *P. guajava* L. Vitorino et al. (2000) also described the female and male insects, their life cycle and behavior, their galls and the growth of the galls, and the natural enemies. Galls of males are narrower and more acuminate than galls of females. Reproduction is believed to be facultatively parthenogenetic; males appear in spring and sometimes in late fall. Females lay up to about 600 yellow eggs into the gall chamber between late fall and early winter and to a lesser extent oviposit again in midsummer. One of the host plants of *T. ovatus*, the Brazilian endemic known as strawberry guava, *P. cattleyanum*, has become an invasive weed in places
outside its native range, especially in Hawaii. *T. ovatus* is considered a suitable agent for biological control of strawberry guava because heavy gall infestations result in leaf fall and subsequent weakening of the trees, and populations of the insect can be cultured successfully (Vitorino et al. 2000).

Ferris (1957a) redescribed the adult female, described the first-instar nymph and illustrated both stages. The adult female appears to display no special adaptations for gall existence and resembles a typical eriococcid except that the anal ring is small, lightly sclerotized and bears no setae. Hempel (1935) suggested that *T. ovatus* may be related to *Pseudotectococcus monae* and Ferris (1957a) indicated that it may be closely related to, or even congeneric with, *Neotectococcus lectularius*.

**Family Kermesidae**

The kermesids or gall-like scales include 91 species in 10 genera. They occur primarily in the northern temperate areas and are unknown from the Australasian and Neotropical regions. Based on an analysis of the host data presented in Miller and Gimpel (2002a), kermesids are found primarily on *Quercus* (Fagaceae). Females typically have three immature instars and males have four (Miller 1991, Bullington and Kosztarab 1985). Most species of *Kermes* and *Allokermes* become quite rotund, have a mottled external color pattern, and look like plant galls or plant buds. Most kermesids lack conspicuous wax on their bodies, but *Kermes nudus* Bullington and Kosztarab and *K. shastensis* Ehrhorn are exceptions, with a white wax covering.

There are only three species of kermesids that induce galls (Table 1), or about 3 percent of the total kermesid fauna. The galls associated with two (*Fulbrightia gallicola* Ferris and *Reynvaenia gallicola* Reyne) of the three species are bud-like, and may arise because the internodes fail to elongate, coupled with malformation of leaves and/or bud scales. It is possible that these two species are related because they are similar morphologically and induce similar galls.

*Fulbrightia* is a monotypic genus including the Chinese species *F. gallicola* that induces galls on *Quercus delavayi* Franch. (Ferris 1950). The female apparently attaches itself to the base of a twig bud and the developing twig becomes distorted in such a manner that the lateral twigs arising beyond the point of attachment are greatly shortened, the leaves are reduced in size, and each twig with its leaves forms a gall that looks like a cone (Fig. 29). The area shared by the bases of several of these cones becomes swollen. The scale insect that induced the deformation is buried in the swollen base of the cone. Ferris (1950) noted that male insects were developing in a ‘cottony case’ in the galls he studied but that no adult males were present. There are nymphal males among the bracts of the galls in the type collection of Ferris (P.J.G., unpublished data).

*Olliffiella* is considered to be a monotypic genus, but see the discussion below concerning the status of a second species, *O. secunda* Ferris. *O. cristicola* Cockerell induces woody galls (Fig. 30) on the undersides of leaves of *Quercus emoryi* Torr. and *Q. hypoleucoides* A. Camus in Arizona, New Mexico, and
Figs 29–30 Mature galls of female gall-like scales (Kermesidae). Fig. 29 Fulbrightia gallicola on Quercus devalayi from Yunnan Province, China (after Ferris 1950). Fig. 30 Oliffiella cristicola on a leaf of Quercus emoryi from Arizona, USA. (drawing by G.L. Miller) Scale bars = 10 mm.

Mature galls of female gall-like scales (Kermesidae). Fig. 29 Fulbrightia gallicola on Quercus devalayi from Yunnan Province, China (after Ferris 1950). Fig. 30 Oliffiella cristicola on a leaf of Quercus emoryi from Arizona, USA. (drawing by G.L. Miller) Scale bars = 10 mm.

Mexico. Galls develop along the midribs of leaves and are thorn-shaped, with the narrow apex pointing down away from the lower leaf surface (Cockerell 1896, Kosztarab 1982). The adult female occupies about a third of the gall chamber at the narrow end, and her dorsal body surface is sclerotized and faces the gall opening. The kermesid’s styles are inserted in the narrow end of the gall and an opening to the gall is located on the upper leaf surface. Males of this species have not been reported. The thrips Torovithrips kosztarabi Johansen is a common inhabitant of the galls of O. cristicola (Kosztarab 1982). O. secunda Ferris has been mentioned as a second species of gall-inducing North American kermesid, but Bullington and Kosztarab (1985) indicated that the original description was based on a third-instar female and most probably is a synonym of O. cristicola. The process of gall development apparently is similar in both ‘species’.

Reynvaania gallicola is the only species in Reynvaania and induces thick cottony or fluffy galls on the twigs of Quercus lineata Blume in Indonesia (Reyne 1954). Globular galls are usually formed on the terminals of young twigs, but sometimes are subterminal, with the young twig running through the gall. The gall consists of a cluster of radially arranged buds that are covered with numerous long, flat, red hairs. Sometimes full-grown leaves are attached to the galls. A chamber is formed inside the gall where a single adult female resides. Crawlers were found among the hairs on the outside of the galls; males were not mentioned in the original description.

**Family Lecanodiapiidae**

The lecanodiapiids, or false pit scales, contain 11 genera and 78 species and occur in every zoogeographic region (Ben-Dov and German 2002). Most described species are in the Oriental region (25), but there are many in the Australasian (19) and the Afrotropical regions (13). The Nearctic, Neotropical, and Palearctic regions each have fewer than 10 species. The family occurs on a diverse array of host plants encompassing about 67
different plant families, but nearly twice as many species occur on hosts in the Fabaceae than on species in any other host family. Little biological information is available on lecanodiaspids, but what is known indicates that females have two immature instars and males have four (Miller 1991). Males have been reported for most species and they pupate in a test that resembles the test of the female but is smaller. The female test is often rather ornate and is formed of felted wax produced in the second instar (Howell and Kosztarab 1972).

Thirteen species (17 percent) in five genera of lecanodiaspids induce galls or some form of host deformation (Table 1). Eight of these species are from relatively dry areas of Australia and the remaining five are dispersed around the world. Like asterolecaniids, several species of lecanodiaspids induce pits on the host. In the genus Lecanodiaspis, Anthony (1974a) described the process of pit formation associated with an unknown species from Singapore on Xylophila malayana Hook.f. and Thoms. (Annonaceae). Apparently the area under the body of the insect collapses and becomes fissured and the area surrounding this area grows rapidly and forms a fusiform swelling. This account is virtually identical with the observations made by Parr (1940) for the pit induced by the asterolecaniid Asterodiaspis variolosa.

Brookesiella is a monotypic Australian genus described for B. tuberans Lambdin and Kosztarab. It apparently does not elicit a pit on its acacia host but does induce a swelling at the feeding site with associated gum accumulation (Lambdin and Kosztarab 1974).

Gallinococcus leptospermi (Morrison and Morrison) is the only species in Gallinococcus (formerly in Amorphococcus) and has a complicated taxonomic history (Miller et al. 1998). Ferris (1919), Morrison and Morrison (1927), and Lambdin and Kosztarab (1973) consider this species to induce enclosed galls and, although we do not have definitive information to counter this observation, we suggest that it is incorrect. The galls of G. leptospermi have been assumed to be the same as those described and illustrated by Froggatt (1921b) for Sphaerococcus leptospermi Maskell because the type specimen of the lecanodiapid was said to come from galls determined to be S. leptospermi by Froggatt (Ferris 1919). The galls illustrated by Froggatt (1921b) undoubtedly belong to S. leptospermi (Maskell 1894), now Callicoccus leptospermi (Maskell) (Coles et al. 1988)—discussed in the Eriococcidae in this chapter. Thus the known specimens of the lecanodiapid, G. leptospermi, either must have come from galls that Froggatt mistakenly identified as those of S. leptospermi or they settled in the opened galls of C. leptospermi rather than eliciting the gall on their own. The galls of both species are described as woody swellings on the branches of Leptospermum and both apparently occur in the same areas of New South Wales. No other lecanodiapid induces enclosed galls and thus it is most likely that G. leptospermi does not induce galls.
Of the 52 species treated in the revision of *Lecanodiaspis* by Howell and Kosztarab (1972) only eight are reported to cause some form of host deformation. They are: *L. acaciae* (Maskell), *L. convexa* Froggatt, *L. dilatata* Froggatt, *L. distincta* Howell and Kosztarab, *L. eucalypti* (Maskell), *L. mirocribraria* Froggatt, *L. partihenii* Howell and Kosztarab, and *L. rugosa* Hempel (Table 1). The general nature of the gall is basically the same in most species, although in *L. acaciae*, *L. dilatata*, and *L. distincta* the body of the insect is not only set in a pit, but the twig also is abnormally swollen where the insect rests. Some species induce deep pits whereas others live in shallow ones. In *L. mirocribraria* there is no pit or definite gall, but its host (*Eucalyptus impressa* Labill., *Eucalyptaceae*) is abnormally twisted where the feeding lecanodiaspidids are located. The galls of *L. eucalypti* are shallow pits, but they are unusual because pits form on both leaves and stems. In all other cases, the pits are limited to either the stems or twigs of the host. No mention has been made of galls being induced by male nymphs. Although it is likely that a few other species of *Lecanodiaspis* cause host deformation, this phenomenon does not appear to be common. In several instances an explicit observation was made that certain species, e.g., *L. quercus* Cockerell, *L. asterospermae* (Maskell), and *L. sardo* Targioni Tozzetti do not induce pits or host deformation (Howell and Kosztarab 1972).

*Prosopophora* has five species, all from the Oriental region (Ben-Dov and German 2002), but only *Prosopophora circularis* Borchsenius has been reported to cause pits on the stems of its unknown host plant (Borchsenius 1960).

*Sticticanthus* is a monotypic genus from the Oriental region. The single included species, *S. azadirachtae* (Green), induces shallow pits on the young stems of *Azadirachta indica* A. Juss. (Meliaceae) and several species of *Derris* (Fabaceae) (Green 1909, Lambdin and Kosztarab 1973).

Family Margarodidae

The margarodids, sometimes called giant scales because of the large size of the females of many groups, comprise over 400 species in more than 70 genera (Foldi 2001) and are the only group of archaeococcoids with gall-inducing species. The Margarodidae is very diverse morphologically (Morrison 1928) and contains some extremely ancient lineages sometimes recognized as family-level taxa (Koteja 1974, 1990, Gullan and Sjarda 2001). Host-plant use is diverse (Morrison 1928), but no catalog is available. They exhibit an amazing diversity of life cycle types and habits, including free-living with or without copious wax coverings, bark dwelling, cyst forming on plant roots and, rarely, gall inducing. They have two or three immature female instars and four immature male instars. Males generally have habits similar to their conspecific females but are absent in a number of taxa and poorly known in others.

Only three species in three genera of margarodids induce galls and all are restricted to conifers (Table 1). One genus, *Matsucoccus*, is Holarctic and feeds on Pinaceae, whereas the other two genera, *Araucaricoccus* and *Coniferococcus*, occur only in southeastern Queensland, Australia, on host
trees of the Araucariaceae. *Araucaricoecus* has one described species, *A. queenslandicus* Brimblecombe, and *Coniferococcus* has three described species, of which only *C. agathidis* Brimblecombe induces galls (Brimblecombe 1960, Brimblecombe and Heather 1965). *A. queenslandicus* is found only on hoop pine, *Araucaria cunninghamii* Sweet, and occurs in practically all rainforest areas that contain hoop pine in southeast Queensland as well as in nearby plantations (Brimblecombe 1959). *C. agathidis* infests Queensland kauri pines, species of *Agathis*, and can cause severe defoliation of plantation trees, which die if attacked heavily over several years (Brimblecombe and Heather 1965, Heather and Schauberg 1966).

The adult female of *A. queenslandicus* is elongate-oval, up to 22 mm long, with a constriction in the anterior abdomen; the antennae and legs are well developed but the mouthparts and anus are atrophied (Brimblecombe 1960). Mature galls are large (up to 2–3 cm in diameter) and consist of a rounded swelling of the stem often covered with needles and, if formed near the apex of a twig, sprout miniature twigs, producing a witches'-broom appearance on the tree (Fig. 31). Galls are initiated by young nymphs that settle mainly on actively growing, small branches in the spring. The second-instar nymph is legless and cystlike; its body enlarges as it feeds during the summer and autumn. In September (early spring), the adult female emerges from the heavily sclerotized second-instar cuticle, that is retained within the gall, by squeezing through a small, posterior hole in the second-instar exuviae (Brimblecombe 1959). During oviposition, almost the whole of the female's abdomen becomes invaginated to form a marsupium and the cuticle then becomes hard and brittle (Brimblecombe 1959, 1960). It seems that eggs are retained in this protective body cavity, although Brimblecombe is not explicit concerning this aspect of the life cycle. Males are not known and it is possible that *A. queenslandicus* is parthenogenetic, although this has not been suggested previously.

The adult female of *C. agathidis* is similar to *A. queenslandicus* but much smaller, about 3 mm long (Brimblecombe 1960). The life cycle and biology have been well documented by Brimblecombe and Heather (1965) and Heather and Schauberg (1966). First-instar nymphs settle on very young leaves and, after 9–14 d, molt to legless, encysted second-instar nymphs (cysts). Feeding induces tiny pimplelike blister galls (Fig. 32) that form by death of the pallasade parenchyma cells, so that the cyst sinks below the leaf surface, and is enclosed by raised and discolored tissue. As in *Araucaricoecus*, the flaccid adult female emerges posterior end first from the cyst, although many females never fully emerge but oviposit by extruding just their posterior abdomen. Males metamorphose to adults about 5 d after they leave the cyst. Each female lays only one batch of 150–200 eggs in a secreted mealy eggsac, which is deposited in a sheltered location on the host plant. The complete life cycle takes 4–6 wk in the spring and there are several generations per year, the population peak coinciding with the spring growth flush of the kauri pines. Brimblecombe and Heather (1965) suggested that *C. agathidis* was facultatively parthenogenetic, presumably based on
observation of egg-laying by unmated females, but they did not provide evidence nor any experimental details.

All the approximately 35 named species of Matsucoccus feed on Pinus species in the northern hemisphere (Ray and Williams 1984, Mendel 1998, Foldi 2001). Only M. gallicolus Morrison, the gall pine scale, is gallicolous; the immature females live in small pustule galls on the young twigs of several Pinus species (Parr 1939, Morrison 1939). Adult females emerge from the galls in summer and move to the trunk or main branches where they each lay about 300 eggs in an ovisac under the bark scales. Eggs overwinter under the bark and hatch in spring when the crawlers seek out new twigs on which to initiate their galls. Feeding by the young nymph leads to collapse of the plant cells below its body while at the same time host tissues grow over and almost enclose the nymph which sinks into the enlarging hole in the stem. During the second stadium, the gall entrance is blocked by the first-instar exuviae. After the final molt, the adult female squeezes her flexible body out through the small gall orifice and migrates to an oviposition site. The adult female is elongate, 2.0–4.5 mm long, and morphologically similar to C. agathidis. Males are extremely rare and may not be necessary for reproduction. M. gallicolus is widespread in pine forest areas of the eastern states of the USA, where heavy infestations kill branches and sometimes even mature trees (Parr 1939).
Family Pseudococcidae

The mealybugs or pseudococcids are the second largest family of scale insects, including about 1,990 species in more than 270 genera (Ben-Dov 2002b). Mealybugs occur in all zoogeographic regions and, based on an analysis of the host information in the mealybug catalogue by Ben-Dov (1994), occur on about 250 families of plants. The most important hosts are herbaceous plants, such as grasses (585 mealybug species utilize Poaceae) and composites (250 species occur on Asteraceae).

Female mealybugs have three immature instars and males have four (Miller 1991). Adult females are characterized by a white mealy wax secretion that covers most or all of the body. Mealybugs that occur in confined situations, such as grass sheaths or under bark, usually have reduced amounts of this mealy secretion. Marginal areas of the body often have a series of protruding lateral wax filaments and the number, size, and distribution of these structures vary among species. A filamentous wax secretion that encloses the eggs and part of the adult female is produced by species that lay eggs. Ooviviparous species usually lack this filamentous secretion.

Gall induction is relatively rare in the family, reported in 17 species and 12 genera (Williams and Miller 1999) comprising less than 1 percent of the world pseudococcid fauna. More than half of all gall-inducing pseudococcid species occur in Hawaii. Mealybug galls generally develop on the leaves of their hosts (14 species), but are on the stems or twigs in three species. The predominant type of gall (nine species) is a leaf roll involving either the edge of the leaf or the entire leaf. Five mealybug gallers induce pits that remain relatively flat or become distended into pockets or even fingerlike deformations. The galls on twigs and stems in two cases are covering galls; in the third case the structure of the gall is unknown. None of the males of gall-inducing mealybugs species is known to induce separate galls. We suspect that most gall-inducing mealybugs are unrelated and developed their gallicolorous behavior independently. However, it is likely that the congeneric Hawaiian gall inducers in Nesopedronia, Neotriarumus, and Pseudococcus are closely related to each other.

Cataenococcus contains nearly 25 species but only one is reported to induce galls. Cataenococcus gallicolus (Mamet 1954) is presumed to have induced the galls in which it was originally collected, but there is so little information that this is uncertain. Mamet (1954) described the female as “In gall on twig of an undetermined creeper ...”.

Euerycoccus includes 14 species but only E. sternlichti Williams may induce galls. This Israeli species occurs in the hollow stems of oak branches in colonies of two to five individuals. The mealybugs live in galls up to 8 cm long and 2–3 mm wide and are associated with Crematogaster ants that carry the mealybugs into their nests during times of danger (Williams 1958).

Galltalacoccus contains only G. tenoriori Beardsley, an Hawaiian species that induces pocket galls on the leaves of its myrtleaceous host, a species of Metrosideros (Beardsley 1971b).
The only described gall-inhabiting mealybug from South Africa is in the monotypic genus *Grewiacoccus*. *Grewiacoccus gregalis* Brain induces finger-shaped pouch galls that protrude through the upper leaf surface and are located near the leaf margins of its *Grewia* host (Malvaceae) (Brain 1918). The gall is about 6 mm long, broadly inflated apically, and tapers to an opening on the underside of the leaf. Two dense white wax filaments and a small amount of fine cottony wax protrude through the opening. A single leaf may have one to 12 galls and individual galls can have one to three adult females inside. Adult males have not been collected, but a smaller gall was illustrated and described. The small galls lacked inhabitants so it is unknown whether they were galls that did not develop because of female mortality or were induced by males that had emerged and were never collected (Brain 1918). Lenticular-shaped leaf galls containing mealybugs that probably belong to a second species of *Grewiacoccus* are known from a *Grewia* species in Zimbabwe; these mealybugs were ant-attended (P.J.G., unpublished data).

The only gall-eliciting mealybug from the Caribbean Islands is *Lantanacoccus sauroides* Williams and Granara de Willink, the single described species of *Lantanacoccus*. The species apparently induces a pit gall on the leaves of the *Lantana* host (Verbenaceae). It is assumed that the sclerotization and enlarged setae on the dorsum on the adult female afford some protection from natural enemies (Williams and Granara de Willink 1992).

The gall of *Miconicoccus ruebsaamenii* Williams and Miller was described in detail by Rübsaamen (1906), but the monotypic genus and species were not described until 1999 by Williams and Miller. The gall encloses the body of the adult female and there is a small opening that is barely visible. The gall causes an obvious swelling in the host branch of *Miconia* (Melastomataceae) and sometimes causes abnormal bending of the affected branch. It is interesting that a wax tube protrudes from this opening, is apparently attached to the anal opening of the adult female, and serves as the vehicle for eliminating the honeydew outside the gall. Rübsaamen compared it with the anal wax tube of the margarodid *Xylococcus filifer* Löw.

The largest group of gallicolous mealybugs is in *Nesopedonia*, which contains five species. Four species induce galls on the pinnules of ferns belonging to *Dicranopteris*. These vary from a rosette-like coil of several pinnules to rolled single pinnules, or just the rolled apex of a pinnule (Beardsley 1957, 1959). A fifth species forms galls on ferns of *Cibotium chamissoi* Kaulf. by rolling just the margin of individual pinnules. The males of most *Nesopedonia* species produce waxy cocoons on infested leaves without any deformation. Cocoons of *N. dura* (Beardsley) were present inside female galls.

*Phyllococcus oahuensis* (Ehrhorn) is the only member of *Phyllococcus*. It induces pointed, erect galls on the leaves of its urticaceous host, *Ureia sandwicensis* Wedd. The unusual sclerotized portion of the posterior abdomen of the adult female forms a plug that blocks the entrance to the gall (Zimmerman 1948).
Pseudococcus encompasses more than 150 species and is worldwide in its distribution. Two species of Pseudococcus induce leaf galls on Santalum (Santalaceae) in Hawaii. They seem to have no gall-adapted morphological modifications that would set them apart from other species in the genus. Pseudococcus antiricolen Ferris elicits deep, fingerlike pouch galls that protrude from the upper surface of the leaf. Zimmerman (1948) suggested that several generations developed in a single gall. Leaves become very distorted and notched when several galls are on a single leaf. The gall of P. gallicola Ehrhorn is a deep pouch that usually protrudes on the upper surface of the leaf (Zimmerman 1948).

Pseudoripersia turgipes (Maskell) is one of two species in Pseudoripersia. It causes distortion and curling of the slender branches of Casuarina and perhaps Allocasuarina species (Casuarinaceae). Sometimes the branches become so contorted that they cover significant portions of the insect, but no consistently shaped enclosing gall develops (Proggatt 1921a, Williams 1985a).

The only two species of the Hawaiian Pseudotrionymus both induce leaf deformation on their myrtaceous hosts (Beardsley 1959). P. multiductus Beardsley rolls the entire leaf, whereas in P. refer tus (Ferris) only the leaf margins are rolled.

Quadragalicoccus lauracearum Williams and Miller is the only representative of this mealybug genus. Although Williams and Miller (1999) indicated that the gall was on leaf petioles of the two lauraceous hosts, it appears that galls occur only on stems (Paul Hanson, personal communication). The ecology of the species was studied by Blackmer and Hanson (1997). Males were collected in the galls of Q. lauracearum but it is unknown if they developed there.

Several pseudococcid species have been collected from galls that were not induced by them; for example, Cataenococcus custralensis (Cockerell), C. hispidus (Morrison), Chorizococcus wilsoni McKenzie, Conulicoccus beardsleyi Williams, C. pholeter Williams, and Phenacoccus arthrophyti Archangelskaya. Conulicoccus beardsleyi and C. pholeter have a narrow apex of their abdomens, which may be a morphological adaptation to live in galls; they have often been collected in deserted galls of various sorts. Other species of mealybugs sometimes elicit host deformation, but are not obligately gallicolous. These include: Hypoecoccus festerianus (Lizer y Treles), H. pungens Granara de Willink, Macronellicoccus australiensis (Green and Lidgett), M. hirsutus (Green), Paracoccus marginatus Williams and Granara de Willink, Nipaecoccus viridis (Newstead), Phenacoccus herreni Cox and Williams, P. manihoti Matile-Ferrero, P. parvus Morrison and Planococcus lilacinus (Cockerell).

**CONCLUDING REMARKS**

**Morphological Specializations of Gall-inducing Coccoidea**

Certain morphological features are common among gall-inducing coccoid taxa due to adaptive specialization for gall life (Beardsley 1984). The shared possession of these features may indicate a close relationship of the taxa,
but convergent similarity can also confuse estimates of relationships that are based on morphology. An example of similar morphology that may or may not be due to common ancestry is found in the South African species *Calycococcus merwei* and the two species of *Aculeococcus*, one from China and the other from Brazil. Molecular data would provide an independent source of information for determining the relationships of such species.

Different instars have different adaptations for gall habituation, but those of the adult female are best known because the taxonomy of scale insects is based on this long-lived stage. The adult females of gall-inducing taxa frequently have reduced or no eyes, legs, or antennae compared with closely related non-galling taxa. Compared with non-galling relatives, the external coverings are either lost or reduced. The feeding styles of gall-inducing coccoids are often much shorter than those of many non-galling taxa, presumably because gallicolous species can feed from cells in the gall wall. In addition, the adult females may possess modifications of various body parts that act as a plug for the gall orifice. The opercular structures involved vary among genera but are usually heavily sclerotized and include modified anal lobes or anal plates (as in *Apliomorpha*, *Calycococcus*, *Cissococcus*, *Cylindrococcus*, *Miconicoccus*, and *Phylococcus*) or a pluglike termination of the abdomen (as in *Ascelis*, *Frenchia*, and *Cystococcus*) in those groups in which the end of the abdomen is directed towards the gall opening, or some kind of dorsal patch or shield in those species which plug the orifice with part of their dorsum (as in *Floracoccus*, *Sphaerococcus*, and *Lantanacoccus*). Although there is a trend to leg reduction among the females of most gall-inducing coccoids, the long hind legs of adult females of *Opisthoscelis* and *Sphaerococcopsis* may serve to clasp and guide the male's abdomen prior to copulation (Beardsley 1974b, 1984).

The abdomen and external genitalia of adult males of a few gall-inducing taxa are greatly elongated (Gullan 1984c). In *Ascelis*, *Cystococcus*, and some species of *Opisthoscelis* the male's abdomen is long and tapered (Froggatt 1894, Theron 1968, Gullan and Cockburn 1986). In *Cylindrococcus*, the abdomen of the adult male is not especially elongate, but his penis and penial sheath are extremely long, slender and sclerotized (Gullan 1978), whereas in *Eremococcus pirogallis* the male has an extremely long, slender, and very elastic penis (Maskell 1894). Presumably, the elongation evolved to assist copulation with a female whose vulva was positioned some distance from the gall orifice. The use of the abdomen for transporting nympha! female siblings in *Cystococcus* could be a secondarily derived function.

In first-instar nymphs, little or no specialization is associated with the galling habit compared with other instars, probably because crawlers are the dispersal agents. However, sexual dimorphism occurs among crawlers of taxa in which first-instar females disperse but males develop in, or on, the maternal gall (Cook et al. 2000). Examples include the first-instar nymphs of *Cystococcus*, some *Apliomorpha* species, and species of Beesoniidae. The dimorphism involves reductions in male crawlers of features involved in dispersal, and thus male nymphs have reduced legs, less sclerotization of the cuticle, and reduced or no marginal and dorsal spinedike setae.
Male Habits and Sexual Dimorphism of Coccoid Galls

The males of a number of gall-inducing taxa are unknown or have not been studied. In most gall-inducing coccoids for which both sexes have been studied, only the female induces a gall or the galls of the two sexes are similar in appearance and usually simple in structure. For example, in Sphaerococcus and some species of Lachnoides, the young galls of males and females are relatively similar and the male nymphs vacate their galls to pupate. However, the life cycle has not been studied and males have not been observed for most species of Lachnoides. In those gall-inducing taxa for which males are known and do not induce galls, the males either have habits similar to their non-galling relatives (e.g., living under a scale or under waxy secretions) or they feed and develop as young nymphs in the maternal gall. The latter behavior is exhibited by males in one pseudococcid genus and in six eriococcid groups, although males may sometimes pupate in the leaf-roll galls induced by female mealybugs of Nesopodra. In the diaspidid Potiaspis media, males probably develop along with females inside a communal leaf-roll gall. Male development in a complex maternal gall occurs only in the mealybug Quadrigallicoccus and, in the Eriococidae, in all species of Ascelis, Casuarinaloma, Cystococcus, and a group of Melaleuca-feeding 'Sphaerococcus' species, in at least one species of Eremococcus, and in Calloglossus leptospermi. In the first five of these eriococcid taxa, the males also pupate in the chamber of the maternal gall.

Sexually dimorphic galls occur in at least one species of Frenchia (Asterozoonidae), in Maskellia globosa (Diaspididae), and in Apionorma, Cylindrococcus, Opisthotis, Neotectococcus, Pseudotectococcus, and Tectococcus (Eriococidae). A few other examples may exist because the habits of males of several gall-inducing eriococcid taxa are still unknown. The occurrence of sexually dimorphic galls indicates that the stimulus for gall induction differs between the sexes. That is, the expression of gall-inducing chemicals or the feeding behavior of the sexes must differ. It is not generally due to a differential response of different plant parts, such as leaves versus stems, because the dimorphic galls of Frenchia, Apionorma, Neotectococcus, Opisthotis, Pseudotectococcus, and Tectococcus can be produced by the two sexes on the same plant part. This is also true for mature galls of Cylindrococcus species, but in this genus the differences may be size related: the females live in much larger, more robust galls than do the smaller males (Fig. 18).

Geographic Distribution of Gall-inducing Coccoids

About 200 species of gall-inducing scale insects are known from the southern hemisphere, whereas only about 80 species are known from the northern hemisphere (Table 1). Very few taxa occur in both hemispheres and therefore some 70 percent of all gallcolous coccoid species occur exclusively in the southern hemisphere. The species count for the southern hemisphere is heavily biased by Australia, which hosts the largest proportion of gall-inducing taxa with approximately 160 endemic species from 24 genera
representing five families. Of these species, more than 85 percent are currently placed in the Eriococcidae. The non-Australian, southern hemisphere gallicolous taxa are mostly from New Zealand (about 15 species, six genera, three families) and South America (about 12 described species, 12 genera, five families). Southern Africa is very species-poor, with just six gallicolous species known. Eriococcidae contribute the largest proportion of gall-inducing species in both New Zealand and South America. Elsewhere in the world, including Africa, the Eriococcidae do not represent a majority of gallicolous taxa. Thus, although the majority of gall-inducing scale insect species occur in the southern hemisphere, they are heavily skewed towards eriococcids in Australia.

In the northern hemisphere, no single family is numerically dominant, although members of the Diaspididae and Astereolecaniidae are the most common gall-inducing taxa. However, in some regions, particular scale insect groups are more prevalent as gallers. The Pseudococcidae are the sole gallicolous family in Hawaii and Beesoniidae are predominant in South East Asia.

Host-plant Affiliations of Gall-inducing Coccoids

All polyphagous (more than one host family) gallicolous coccoid species induce shallow pits whereas those that induce covering galls are restricted to only one host family and, typically, a single host genus. Gallicolous diaspidids induce galls on the most angiosperm families (more than 24) (Table 1). This may be because most gallicolous diaspidids induce simple galls (pits, folds and deformations) and because gall-inducing Diaspididae are more geographically widespread than other groups.

Only five coccoid taxa (three margarodids, one eriococcid, and a diaspidid) induce galls on conifers. All other gallicolous scale insects feed only on angiosperms. Myrtaceous hosts support the greatest number of gall-inducing coccoids, with more than 130 species found on this plant family. Other than one species of Diaspididae, three species of Lecanodiapidae and three species of Pseudococcidae, all coccoids that induce galls on Myrtaceae belong to the Eriococcidae. Within the Myrtaceae, *Eucalyptus* is galled by the highest number of scale insect species (10 genera, three families). Thus, the prevalence of galling on Myrtaceae reflects the numerical dominance of gall-inducing eriococcids in Australia. However, gallicolous eriococcids in general appear to have an association with Myrtaceae, since species in four countries (Australia, Brazil, New Zealand, and Mexico) gall this host.

The family Fagaceae hosts the broadest range of gall-inducing scale insects with five families (Astereolecaniidae, Beesoniidae, Diaspididae, Kermesidae, and Pseudococcidae) (Table 1). It is clear that the host preferences of the gall-inducing scale insect guild do not reflect the species richness and abundance of plant families. For example, the speciose and widespread families Fabaceae (= Leguminosae), Poaceae, and Rubiaceae are host to very few gallicolous coccoids, although the family Fabaceae is the most common host family of non-galling coccoids in the families Coccidae,
Diaspididae, Lecanodiidae and Pseudococcidae, and Poaceae and Rubiaceae also are widely utilized by certain coccoid families (Ben-Dov et al. 2002). Fabaceae is very diverse in Australia, where the majority of gall-inducing scale insects occur, but it is galled by only two species there.

At lower taxonomic levels, such as genus, gallicolous coccoid species richness may be a reflection of species richness of the host. All but one gallicolous species of Beesoniidae feed on the species-rich Dipterocarpaceae, and there may be a large radiation of undescribed beesonids on dipterocarps in tropical Asia and tropical Africa (Anthony 1980, Jenkins 1992, Takagi 2001). In Australia, the speciose genera *Apionomorpha*, *Lachnodius* and *Opithoscelis* all occur on the diverse host genus *Eucalyptus*. Species of each of these three coccoid genera are relatively host-species specific and therefore host diversity may be playing a role in generating insect species richness through host specialization.

**Evolution of the Gall ing Habit**

The gall-inducing habit has probably evolved many times among scale insects, as suggested by its sporadic occurrence in at least nine families. The number of origins cannot be tested without robust phylogenetic hypotheses for each of the families concerned and, at this stage, even monophyly of some families (such as the Margarodidae and Eriococcidae) is in dispute. However, in most families with multiple gall-inducing taxa, the habit appears in apparently disparate groups, suggesting that it has arisen independently in separate lineages.

One striking pattern, noted above in the discussion on geographic distribution and host affiliations, is the radiation of galling taxa among the Australian Eriococcidae associated with Myrtaceae. To answer the question of why Australia has so many more gall-inducing eriococcids than other regions, we need to determine the number of origins of the galling habit among the Australian eriococcids. Many independent origins would support an adaptive (environmental) explanation, whereas if only a few lineages have radiated extensively, this would suggest phylogenetic constraint and a possible host effect. Adaptive hypotheses attempt to explain the abundance of galling species as a response to the environment, such as (1) the advantage of gall living to insects in unpredictably dry environments or (2) Koteja’s (1987) hypothesis that woody coccoid galls act as protection in a fire-prone environment, like occurs in much of Australia. Alternatively, if host effects and evolutionary constraints are important, then two scenarios can be envisaged. In the first, the ancestors of the extant gallicolous eriococcids may have evolved an intimate association with myrtaceous host plants that subsequently underwent repeated vicariant speciation, carrying their specialist herbivores along with them. If this idea is correct, then there should be some evidence for co-speciation of galling eriococcids and their myrtaceous hosts. In the second scenario, there might have been an adaptive radiation in the myrtaceous-galling group so that once myrtaceous gall ing evolved, the eriococcids transferred onto unrelated myrtaceous taxa and
then radiated. In this scenario, we would expect only closely related eriococcids on closely related host plants, but not necessarily a match of phylogenies of eriococcid genera to host genera, and the eriococcids should be younger than the hosts.

Unfortunately, there is a dearth of robust phylogenetic knowledge of *Eucalyptus* and related genera, although molecular phylogenetic data will shortly be available on Australian gall-inducing eriococcids (L.G.C. and P.J.G., unpublished). The gall-inducing habit has probably arisen at least four times amongst this group: once in a clade comprising *Lachnodius, Opisthostecelis*, and most other Myrtaceae-feeding eriococcids; another time in *Cylindrococcus* (Casuarinaceae feeding); another amongst a *Nothofagus*-feeding group; and another in *Apicomorpha* (*Eucalyptus* feeding). Multiple origins of gall induction, rather than multiple losses, are implicated because each of these groups has non-gall-inducing sister taxa with adult female morphology of the plesiomorphic eriococcid type. In contrast, each of the galling taxa has a different adult female morphology. If the galling habit was ancestral for Australian eriococcids and had been frequently lost, then adult females of the sister taxa of galling groups would be expected to have morphologies reflecting their galling past; this is not so in any of the above four lineages.

It is possible that many covering galls have evolved from pit-type galls. A few coccoid groups have gallicolous taxa that induce pits and related taxa that are fully enclosed in covering galls. Examples occur in the Asterolecaniidae, Diaspididae, and in the eriococcid genus *Lachnodius*. Knowledge of the phylogenetic relationships of species of *Lachnodius* may assist in understanding the evolution of pit and covering gall complexity because of the diversity of habits displayed by different species. A few *Lachnodius* species live in woody enclosed galls, others in open-topped pits, and still others appear not to induce galls at all. More broadly, the Myrtaceae-feeding, gall-inducing eriococcid clade also may provide insights into gall evolution. This group, which includes *Lachnodius*, comprises taxa that induce a variety of gall types including pits, enclosed galls, and bractlike (budlike) galls.

**Directions for Future Research**

Much remains to be learned about the mechanism of gall induction among scale insects. For example, the nature of the signal is not known for any scale insect or any other insect (Stone and Schönrogge 2003), although Parr (1939, 1940) showed that salivary secretions induced the gall-like response in two unrelated scale insects (*A. variolosa* and *M. gallicolus*) that induce simple galls. Parr (1940) suggested that enzymes or similar substances were the active agents in gall induction because heat denaturation of the salivary extract eliminated the plant-gall response in his experiments. However, at least in complex covering galls, it is possible that gall initiation may be mediated by genetic information that is ultimately extraneous to both the plant and the insect, in that it might involve injection of a symbiotic virus, plasmid, or other genetic material into the plant in the saliva of the galling insect. Such a mechanism has been considered for gall induction by gall
wasps, Cynipidae (Ronquist and Liljeblad 2001). We suggest that progress in understanding gall induction may be made by the molecular biochemical study of a gall system in which the insect induces sexually dimorphic galls. Determination of any gender-based differences in DNA expression or microorganisms (e.g., endosymbionts) of the insect may provide clues to the active agent(s) of gall induction. The Apionomphra–Eucalyptus interaction would be an ideal system because of the large size of the insects, their ease of rearing and the strikingly different galls induced by males and females.

Gall induction clearly has evolved multiple times in scale insects. A full understanding of the evolution of behavior and life history requires a robust phylogeny. Unfortunately, the relationships of many gall-inducing scale insects are either not known or poorly known and future studies should address this problem. In addition, there are many gallicolous species yet to be formally named and described, and the faunas of certain regions, such as South America, are poorly represented in collections. This is especially true of the family Eriococcidae, which contains the largest group of scale insects with complex galls.

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