Biological Journal of the Linnean Society, 2007, **90**, 153–172. With 6 figures

Biology of *Rhoophilus loewi* (Hymenoptera: Cynipoidea: Cynipidae), with implications for the evolution of inquilinism in gall wasps

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Received 26 April 2005; accepted for publication 1 March 2006

The sole described indigenous afrotropical cynipid, the South African endemic *Rhoophilus loewi*, was originally described as a gall inducer. As predicted by phylogenetic relationships, we confirm that *R. loewi* is instead an inquiline wasp. Although all other cynipid inquilines develop in galls induced by cynipid wasps, or very rarely cecidomyiid midges, *R. loewi* is the only cynipid inquiline of a lepidopteran gall, inducing secondary inquiline cells in galls induced by a cecidosid moth genus *Scyrotis* on *Rhus* species (Anacardiaceae). *Rhoophilus* is a lethal inquiline; its larval cells expand into the hollow interior of the host gall resulting in death of the gall inducer. *Rhoophilus loewi* is redescribed and the final-instar larva described for the first time. We describe host-plant associations, the morphology and phenology of gall formation, and the suite of parasitoid Hymenoptera associated with these galls. The community centred on *Scyrotis* galls is compared with those observed in other hosts of inquiline cynipids. Elucidation of the life history of *R. loewi* has fundamental implications for understanding the evolution of cynipid wasps. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **90**, 153–172.

ADDITIONAL KEYWORDS: Cecidosidae – community ecology – inquiline – *Rhus* – *Scyrotis*.

INTRODUCTION

The Gall wasps (Cynipinae; Cynipidae) are a species-rich group of herbivorous insects that either induce galls on plants or develop as obligate inhabitants (termed inquilines) in the galls induced by other insects. Gall-inducing cynipids belong to five tribes, each associated with different sets of plant hosts: the Cynipini gall oaks and their relatives, the Pediaspidini gall southern beech (*Nothofagus*) and *Acer*, the Diplolepidini gall roses, the Eschatocerini gall *Acacia* and *Prosopis*, and the Aylacini gall a range of herbaceous plants. The inquiline gall wasps are currently classified as members of a single tribe, the Synergini, although recent DNA sequence data suggests that inquilines may have evolved from gall-inducing ancestors several times (Ronquist, 1994; Ronquist & Liljeblad, 2001; Nylander *et al*., 2004a). All of the inquilines whose biology has been studied in detail are incapable of inducing their own galls, but develop in specialized larval cells within galls induced by other insects (Ronquist, 1994; Stone *et al*., 2002). The majority of inquilines develop in galls induced by other gall wasps, predominantly on oaks and roses. Similar to gall-inducing cynipids, inquilines are obligate herbivores, feeding on specialized nutritive tissues lining the larval cell.

The Cynipinae are predominately a northern Hemisphere group, and most of the 1300 described species are Holarctic. The exceptions are eight species that occur in South America, and the endemic South

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African genus *Rhoophilus* Mayr (Ritchie, 1993). *Rhoophilus* was described towards the end of the 19th Century (Mayr, 1881) to accommodate *Rhoophilus loewi* Mayr, the only indigenous cynipid species described from the Afrotropical region. The specimens originated from the Novara expedition to the Cape of Good Hope (South Africa) and were given to Mayr by Mr Jelinek. There are eight adult specimens and four galls in the Mayr collection in Vienna, from where the type material was recently examined (Melika & Bechtold, 2001). *Rhoophilus loewi* was originally described as a gall inducer. However, adult morphology clearly indicated a close phylogenetic relationship with inquiline cynipids (Weld, 1952; Ronquist, 1994; Melika & Bechtold, 2001; Ronquist & Liljeblad, 2001). Mayr's original description of *R. loewi* is inadequate in detailing characters diagnosing the species among the other inquiline cynipids, necessitating the redescription of the species. Nevertheless, both phylogenetic reconstructions based on morphology (Ronquist, 1999; Ronquist & Liljeblad, 2001; Vårdal, Sahlén & Ronquist, 2003; Nieves-Aldrey, Vårdal & Ronquist, 2005) and DNA sequence data (Nylander *et al*., 2004b) group *Rhoophilus* with the *Synergus* group of inquiline genera (which also includes *Synophrus* and *Saphonecrus*). With the exception of *Rhoophilus*, all other members of this group develop as inquilines in galls induced on oaks (*Quercus*). With very few exceptions (Askew, 1999), the host galls are induced by cynipids in the tribe Cynipini.

Rhoophilus loewi was originally reared from galls on a woody shrub, *Rhus lucida* L. (Mayr, 1881; Kieffer, 1910). Although its phylogenetic placement strongly suggests that *Rhoophilus* is an inquiline, this ecological role has not been confirmed, and the host gall inducer has remained unknown. *Rhoophilus* is intriguing because there are no known native gall-inducing cynipids (and hence potential hosts) associated with *Rhus* species: the only other cynipids recorded from subsaharan Africa are an undescribed genus of gall inducer, with closest affinities to Pediaspidini, reared from galls on the indigenous Red Pear tree *Scolopia mundii* (Eckl. & Zeyh.) Warb. (Flacourtiaceae) (F. Ronquist and G. Melika, pers comm.), and an introduced aylacine cynipid (*Phanacis hypochoeridis* Kieffer) recorded from galls on a herbaceous plant, *Hypochoeris radicata* L. (Asteraceae). Potential hosts must thus be sought among other insects inducing galls on *Rhus*, a feature that makes the biology of *Rhoophilus* highly unusual among cynipid inquilines, and thus of considerable interest.

At the turn of the 20th Century a moth, *Scyrotis athleta* Meyrick (Cecidosidae), was described from specimens reared from 'jumping beans' that form within the leaves and young stems of *Rhus glauca* Thunberg on Table Mountain, Cape Province, South Africa (Meyrick, 1909). The 'bean' of *S. athleta* is a regular oval case, *c*. 6×4 mm in diameter, with a hard, finely vermiculated (bearing wavy, wormlike lines) surface (apparently not of plant origin), that separates from the surrounding plant tissue when the larva is fully grown. The plant tissue ruptures irregularly and the 'bean' drops to the ground where it jumps around for 6 weeks or more (Meyrick, 1909). *Scyrotis* was originally placed in the Tineidae by Meyrick, and subsequently included in the Incurvariidae (Scoble, 1980). However, its true taxonomic position is within the Cecidosidae (Incurvarioidea) (Davis, 1999). All species within this superfamily have a piercing ovipositor that can be extended to insert eggs into plant tissue. The larvae are univoltine, developing within galls on *Rhus* (South Africa) and *Schinus* species (South America) (Anacardiaceae) (Davis, 1999). The Cecidosidae are a southern Hemisphere family with seven species in six genera: *Cecidoses*, *Dicranoses*, *Eucecidoses*, and *Oliera* in southern South America, and *Ptisanora* and *Scyrotis* from South Africa (Davis, 1999). The larva of *Cecidoses* and *Eucecidoses* form hard, woody, spherical, thick-walled nondehiscent galls, 18 mm in diameter, on woody terminal branches of *Schinus*; the galls have an operculum that forms independently of larval development, allowing the adult moth to emerge (Wille, 1926; Davis, 1999).

Here, we redescribe the adult morphology of *R. loewi*, and provide the first description of the final instar larva. We emphasize those traits shared by closely related inquilines, and also those that distinguish *Rhoophilus*. We provide evidence that *R. loewi* develops as an inquiline within galls induced by a *Scyrotis* species, and describe the impact of *Rhoophilus* on host gall structure. The assemblage of chalcid parasitoid wasps associated with both *Scyrotis* and *Rhoophilus* is described and the community ecology compared with what is known of the other communities occupied by cynipid inquilines. We discuss the evolutionary implications of the unravelling of a unique life history for cynipid wasps.

MATERIAL AND METHODS

Thirteen species of *Rhus* were visually surveyed for galls. *Scyrotis* galls and *Rhoophilus* modified galls were hand-collected and taken back to the laboratory where ranges of different sized galls were dissected to observe their development. Presence of parasitoids were recorded in dissected galls associated with two *Rhus* species to determine percentage parasitism of *Scyrotis* larva. Wasps were reared from intact galls kept in plastic containers with netting lids. Galls on *R. lucida* were enclosed in cotton bags in the field to collect the 'jumping beans' as they fell. Adult *R. loewi* specimens were placed on cuttings of *R. lucida* in the laboratory and their behavioural responses to galls of different sizes were observed.

Adult *Rhoophilus* were dissected in 70% ethanol, air-dried, mounted on a stub and coated with gold, and micrographs were taken with a scanning electron microscope Fei Quanta 200 (high vacuum technique) for several standardized views. Forewings were mounted in euparal on slides, and later examined under a stereomicroscope. Larvae were transferred directly from absolute alcohol onto a standard electron microscopy stub and into the microscope at low vacuum, without prior fixation or coating. However, mandibles were dissected, mounted, and observed in the same manner as for adult morphological parts.

Specimens are deposited in the Museo Nacional de Ciencias Naturales (Madrid) and Iziko South African Museum (Cape Town).

RESULTS

REDESCRIPTION OF *R. LOEWI* MAYR (1881)

Material examined

The redescription of *R. loewi* was based on the following material: South Africa, Western Cape: near Hermanus, 19 January 2003, emerged during April 2003, J. L. Nieves-Aldrey, ex leaf galls on *R. lucida*; Robertson, J. H. Giliomee, ex twig galls on *Rhus undulata*.

Additional material examined: South Africa, Western Cape: Onrust River, River Side Lane, 34°24.965′S, 19°10.550′E, V. B. Whitehead, 28 December 1999, emerged May to June 2000, Dune thicket, ex leaf petiole galls on *R. lucida*; Onrust River, corner Beach & Erica roads, 34°24.965′S, 19°10.550′E, V. B. Whitehead, 29 December 1999, emerged May to June 2000, Dune thicket, ex leaf petiole galls on *R. lucida*; Vermont, 34°24.90′S, 19°10.00′E, V. B. Whitehead, 28 December 1999, emerged April to June 2000, ex stem gall on *R. lucida*; Karwyderskraal Farm, 34°17.805′S, 19°10.620′E, V. B. Whitehead, 28 December 1999, emerged April to July 2000, ex leaf petiole galls on *R. lucida*; Bot River – Karwyderskraal road, 34°20′S, 19°11′E, V. B. Whitehead, 28 December 1999, emerged April to July 2000, ex leaf petiole galls on *R. lucida*; Afdaks River, 34°20.894′S, 19°08.342′E, V. B. Whitehead, 28 December 1999, emerged April to July 2000, ex leaf petiole galls on *R. lucida*; Onrust River, 34°24.99′S, 19°10.49′E, 9 June 2000, V. B. Whitehead, ex leaf gall on *R. lucida*; Good Hope Nursery, south of Scarborough, 34°12′S, 18°22′E, V. B. Whitehead, 31 December 2000, ex leaf petiole gall on *R. lucida*; 1 km E of Scarborough, 34°12′S, 18°22′E, V. B. Whitehead, 31 December 2000, ex leaf petiole gall on *R. lucida*; De Hoek, 33°56′S, 18°45′E, 20 September 2000, emerged June 2001, V. B. Whitehead, ex leaf galls on *R. undulata*; Het Kruis, Groenrivier, 32°36′S, 18°45′E, V. B. Whitehead, 27 September 2000, emerged June to July 2001, Dry Mountain Fynbos, ex leaf petiole gall on *R. undulata*; Malmesbury, 33°27′S, 18°44′E, V. B. Whitehead, 27 September 2000, ex leaf petiole galls on *R. undulata*; Karwyderskraal Farm, 34°21′S, 19°13′E, V. B. Whitehead, 14 September 2000, ex stem galls on *Rhus laevigata*; Betty's Bay, 34°22′S, 18°56′E, V. B. Whitehead, 30 August 2000, ex leaf petiole galls on *R. lucida*; 22 km north of Matjiesfontein, 33°02.44′S, 20°35.18′E, 12 October 2000, emerged June to July 2001, V. B. Whitehead, ex leaf galls on *R. undulata*; Arabella Country Estate, 34°18.45′S, 19°07.70′E, S. van Noort, 17 June 2000, ex leaf petiole galls on *R. lucida*; Lamloch, 34°19.80′S, 19°04.91′E, emerged 3–25 July 2000, S. van Noort, ex leaf gall on *R. lucida*; Cederberg, Stadsaal Grotte, 32°31.41′S, 19°19.05′E, 10 July 2000, S. van Noort, CE00-R01, ex leaf gall on *R. undulata*; Wingfield, 33°53.44′S, 18°32.22′E, S. van Noort, 26 August 2000, Sand Plains Fynbos, ex leaf petiole galls on *R. lucida*; Kogelberg Nature Reserve, 34°19.523′S, 18°57.986′E, S. van Noort & P. M. Huntly, 1 May 2002, emerged May to July 2002, Mesic Mountain Fynbos, KB02-R01, ex leaf petiole gall on *R. lucida*; ditto except KB02-R02; ditto except KB02-R03; ditto except KB02-R04; ditto except 34°19.408′S, 18°57.898′E, KB02-R05; ditto except 34°18.683′S, 18°56.949′E, KB02-R07; ditto except, 34°19.746′S, 18°58.848′E, KB02-R08; ditto except 34°19.046′S, 18°57.814′E, KB02-R09; ditto except 34°18.956′S, 18°57.771′E, KB02-R10; ditto except KB02-R11; ditto except: 34°18.900′S, 18°57.736′E, KB02-R12; ditto except 34°18.912′S, 18°57.554′E, KB02-R13; ditto except 34°19.422′S, 18°57.893′E, KB02-R14; Kleinmond Nature Reserve, 34°20.639′S, 19°01.994′E, S. van Noort & P. M. Huntly, 3 May 2002, June to July 2002, Strandveld, KB02-R17, ex leaf petiole gall on *R. lucida*; Harold Porter Botanical Garden, 34°21.058′S, 18°55.650′E, S. van Noort & P. M. Huntly, 5 May 2002, emerged May to June 2002, Mesic Mountain Fynbos, KB02-R23, ex leaf petiole gall on *R. lucida*; Worcester, Karoo National Botanical Gardens, 33°37′S, 19°25′E, S. van Noort & P. M. Huntly, 1 September 2002, ex leaf petiole gall on *Rhus pallens*; Cederberg, Sawadee Farm, 32°19.919′S, 18°59.238′E, S. van Noort & P. M. Huntly, 25.ix. 2003, Dry Mountain Fynbos, CE03-R02, ex gall on terminal stems of *Rhus incisa*; Silvermine, 34°07′S, 18°26′E, S. van Noort & P. M. Huntly, 17 November 2002, emerged April to June 2003, Mesic Mountain Fynbos, SM02-R01, ex leaf petiole gall on *R. lucida*; Kirstenbosch, S. van Noort & P. M. Huntly, 8 June 2002, emerged June to July 2002, Mesic Mountain Fynbos, KG02-R01, ex leaf petiole gall on *R. lucida*; Skildersgatkop, 34°07′S, 18°24.4′E, S. van Noort & P. M. Huntly, 28 April 2003, emerged May to June 2003, Strandveld, SK03-R01, ex leaf petiole gall on *R. glauca*; Travellers Rest, Sevilla, 32°05.085′S, 19°05.407′E, S. van Noort

& P. M. Huntly, 29 Devember 2002, emerged April to June 2003, Succulent Karoo, CE02-R01, ex leaf petiole gall on *R. undulata*; ditto except 32°04.659′S, 19°04.890′E, CE02-R02; Montagu, 2 km West of Die Ou Meul, 33°46.950′S, 20°06.087′E, S. van Noort & P. M. Huntly, 11 August 2002, emerged April to June 2003, Dry Mountain Fynbos, MT02-R01, ex leaf petiole and stem galls on *R. undulata*; Karoo National Park, 32°19.971′S, 22°29.518′E, S. van Noort & P. M. Huntly, 7 December 2002, emerged May to June 2003, Nama Karoo, KN02-R01, ex stem gall on *Rhus burchellii*; Citrusdal 4 km SE, 32°36.689′S, 19°02.505′E, S. van Noort & P. M. Huntly, 1 January 2003, emerged April 2003, Dry Mountain Fynbos, CE02-R02, ex leaf petiole gall on *R. undulata*; Skildersgatkop, 34°07′S, 18°24.4′E, S. van Noort & P. M. Huntly, 28 April 2003, emerged May to June 2003, Strandveld, SK03-R02, ex leaf petiole gall on *R. glauca*; Kirstenbosch, 33°59′S, 18°26′E, S. van Noort & P. M. Huntly, 14 April 2002, emerged April to June 2003, Mesic Mountain Fynbos, KTB02-R02, ex leaf petiole gall on *R. lucida*; Bainskloof, 33°33.348′S, 19°09.003′E, S. van Noort & P. M. Huntly, 21 April 2002, BK02-R01, ex leaf petiole gall on *R. pallens*; Anyskop Farm (4 km 270°W Langebaanweg), 32°58.611′S, 18°06.976′E, S. van Noort, 4 September 2002, emerged April to June 2003, Fynbos on Limestone, LW02-R01, ex leaf petiole gall on *R. glauca*; Cederberg, Sawadee Farm, 32°19.919′S, 18°59.238′E, S. van Noort & P. M. Huntly, 25 September 2003, emerged January 2004, Dry Mountain Fynbos, CE03-R01, ex leaf petiole and stem galls on *R. undulata*; The Boulders, 34°11.8′S, 18°27.3′E, S. van Noort & G.N. Stone, 24 January 2004, Strandveld, BB04-R01, ex leaf petiole gall on *R. glauca*; Clovelly, 34°07.9′S, 18°26.1′E, S. van Noort, 13 June 2004, Strandveld, ex leaf petiole gall on *R. glauca*. *Northern Cape*, Glen Lyon Farm, 3.48 km 153°SSE Nieuwoudtville, 31°23.927′S, 19°08.378′E, 7 October 2000, emerged June 2001, S. van Noort, Succulent Karoo, ex leaf petiole galls on *R. undulata*.

Description of adult

Body length, measured from the anterior margin of the head to the posterior margin of the eighth abdominal tergum: 1.6–2 mm for males, 2–2.3 mm for females. Coloration black; legs, except coxae, and antennal flagellum brown. Habitus (Figs 1O, 2A, B).

Head: In anterior view (Fig. 3A) rounded; lower face not keeled medially; with facial strigae radiating from sides of clypeus, reaching compound eyes and lower margin of antennal sockets. Upper face coriacious with some sparse punctures; vertex coriacious and more strongly punctuate, particularly between ocelli; median frontal carina and lateral frontal carinae absent. Ocellar plate not raised. Head rounded in shape; height of malar space about 0.5-fold the height of a compound eye. Clypeus more or less square. Ventral margin of clypeus almost straight, not distinctly projecting from cranial margin. Anterior tentorial pits distinct, surmounted by some arched bowed carinae. Epistomal sulcus and clypeo-pleurostomal lines indistinct. Antennal sockets situated slightly lower than mid-height of face; distance between antennal rim and compound eye approximately 1.4-fold longer than the width of antennal socket including rim. Occiput coriacious, flat, not deeply impressed around occipital foramen, without an occipital carina (Fig. 3B). Gular sulci united well before reaching hypostomata. Distance between oral and occipital foramina very long, slightly longer than oral foramen and approximately 1.5-fold as long as the height of occipital foramen.

Mouthparts (Fig. 3A, C): mandibles strong, right mandible with three teeth; left with two teeth. Maxillary cardo clearly visible. Maxillary stipes approximately 1.5-fold as long as broad, posterior surface with longitudinal carina along mesal margin. Maxillary palp five-segmented: first segment short, broader than long; second segment relatively long, gradually tapering towards base, approximately twice as long as broad; fifth segment long, twice as long as the fourth. Labial palp three-segmented: first long, gradually tapering towards base; approximately twice as long as second, third segment longer than second. Female antenna (Fig. 3D). Antenna with 13 connate antennomeres. Pedicel 0.7-fold as long as pedicel; 1.5-fold as long as broad and clearly broader than F1. Flagellum slightly broadened towards apex. Length of F1, 1.3-fold the length of F2. F3, 2.1-fold as long as broad. Ultimate flagellomere 2.3-fold as long as the penultimate. Elongate placodeal sensilla present on all flagellomeres. Male antenna (Fig. 3E). Flagellum with 12 connate flagellomeres. F1 slightly excavated in the middle and slightly expanded at apex. Length of F1, 1.3-fold the length of F2. F3, 2.5-fold as long as broad. Ultimate flagellomere twice as long as the penultimate. Elongate placodeal sensilla present on all flagellomeres excepting F1.

Mesosoma: Pronotum (Fig. 3G) medially relatively long (high), ratio of median distance between anterior and posterior margins to lateral distance between these margins 0.3, without lateral pronotal carinae. Submedian pronotal depressions oval, deep, open laterally, connected by a shallow groove medially. Pronotum medially smooth, without sculpture; lateral surface of pronotum with some longitudinal widely spaced interrupted carinae. Mesonotum (Fig. 3F). Scutum with strong transversal widely spaced and interrupted carinae. Median mesoscutal impression absent. Notauli narrow and shallow, more weakly

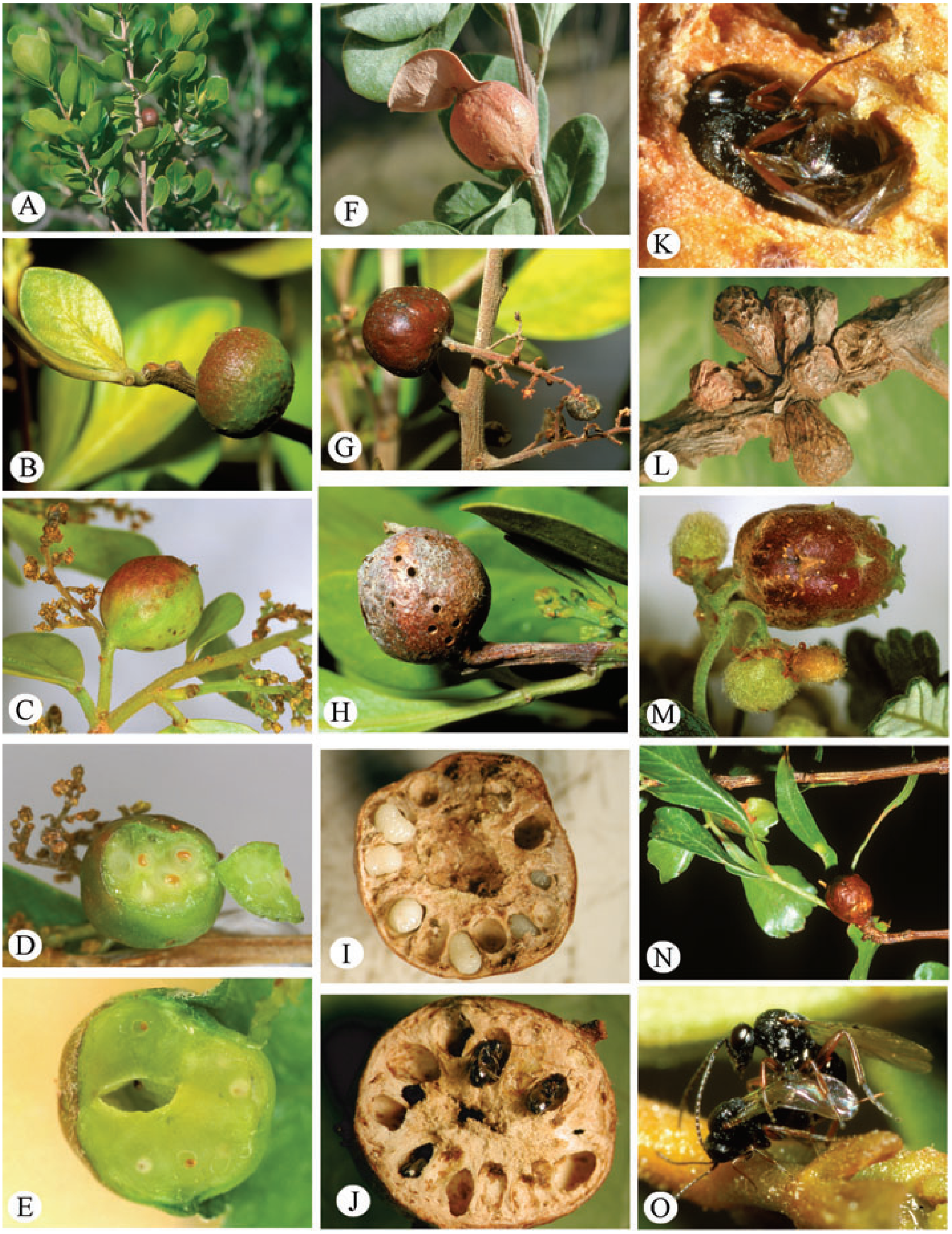

Figure 1. Galls of *Rhoophilus loewi*. A, B, leaf galls on *Rhus lucida*; C, flower gall on *Rhus lucida*; D, young gall cut open showing early instar *Rhoophilus loewi* larvae *in situ*; E, cross-section of young gall showing early instar *Rhoophilus loewi* larvae *in situ* surrounding the central *Scyrotis* locule; F, older woody leaf gall; G, older woody flower gall; H, old woody gall with *Rhoophilus* exit holes; I, cross-section of older woody leaf gall showing *Rhoophilus loewi* terminal-instar larvae *in situ*; J, cross-section of the same galls showing the *Rhoophilus loewi* adults shortly before emerging; K, *Rhoophilus loewi* adult in gall cavity shortly before emerging; L, stem galls on *Rhus undulata*; M, Flower gall on *Rhus incisa*; N, Leaf gall on *Rhus undulata*; O, *Rhoophilus loewi* adults *in copula* on *Rhus lucida*.

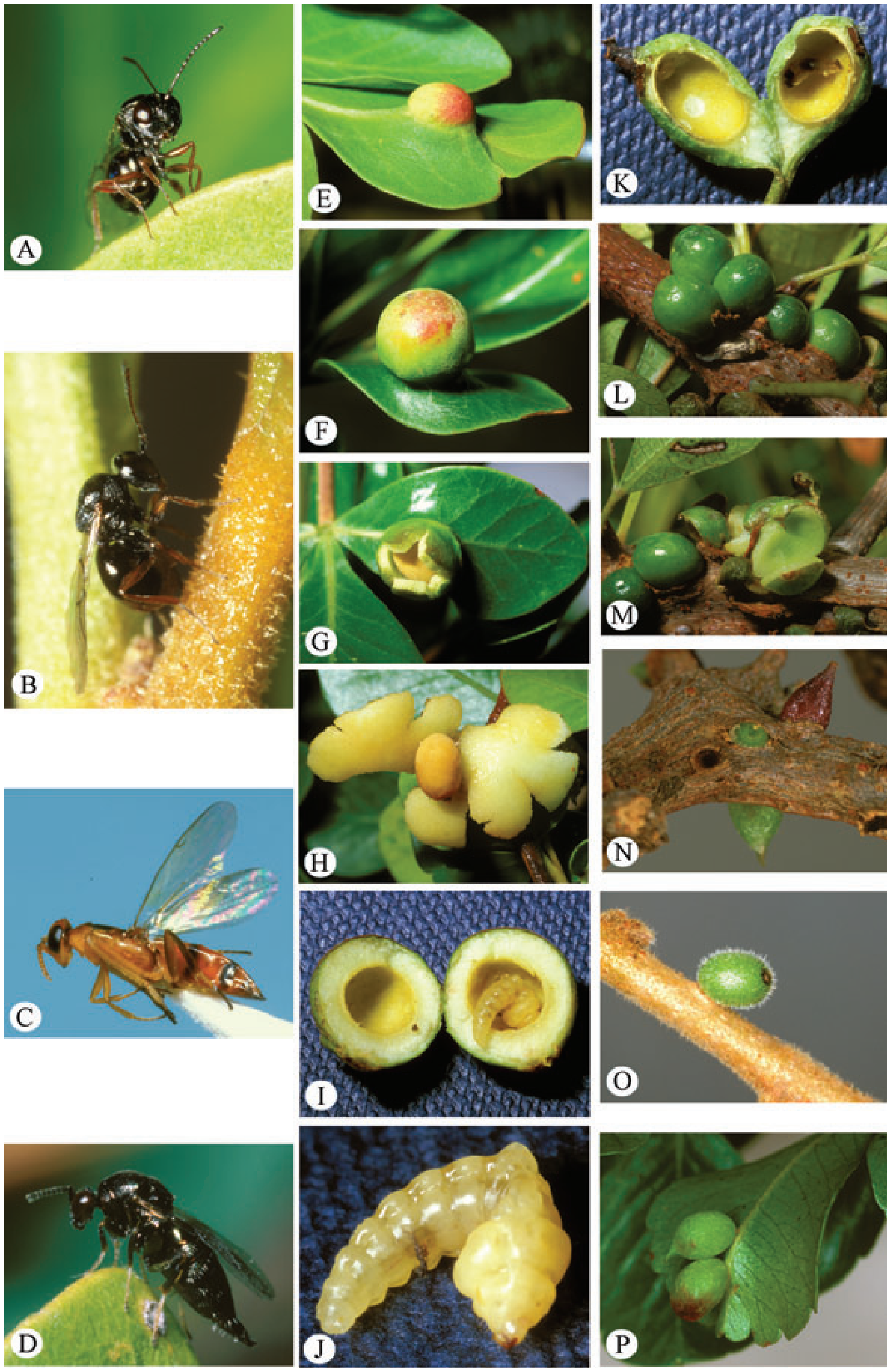

Figure 2. *Rhoophilus loewi*, chalcid parasitoids and *Scyrotis* galls. A, *Rhoophilus loewi* adult; B, *R. loewi* ovipositing; C, *Neanastatus rufatus* (Eupelmidae) parasitoid of *Scyrotis* larva; D, *Ormyrus* sp. 1, probable hyperparasitoid of *Scyrotis* larva; E, F, *Scyrotis* leaf galls on *Rhus lucida*; G, *Scyrotis* leaf gall on *R. lucida* starting to exfoliate; H, exfoliated *Scyrotis* leaf gall on *R. lucida* showing jumping bean, which will drop to ground; I, cross-section of *Scyrotis* leaf gall on *R. lucida* showing final instar *Scyrotis* larva; J, final-instar *Scyrotis* larva; K, cross-section of *Scyrotis* leaf gall on *R. lucida* showing parasitized *Scyrotis* larva on the right and chalcid ectoparasitoid larva on the left; L, stem galls on *Rhus laevigata*; M, stem galls on *Rhus laevigata* with exfoliated gall after jumping bean has dropped; N, pixie-cap stem galls on *Rhus incisa*; O, second type of stem gall on *Rhus laevigata*; P, pixie-cap leaf galls on *Rhus undulata*.

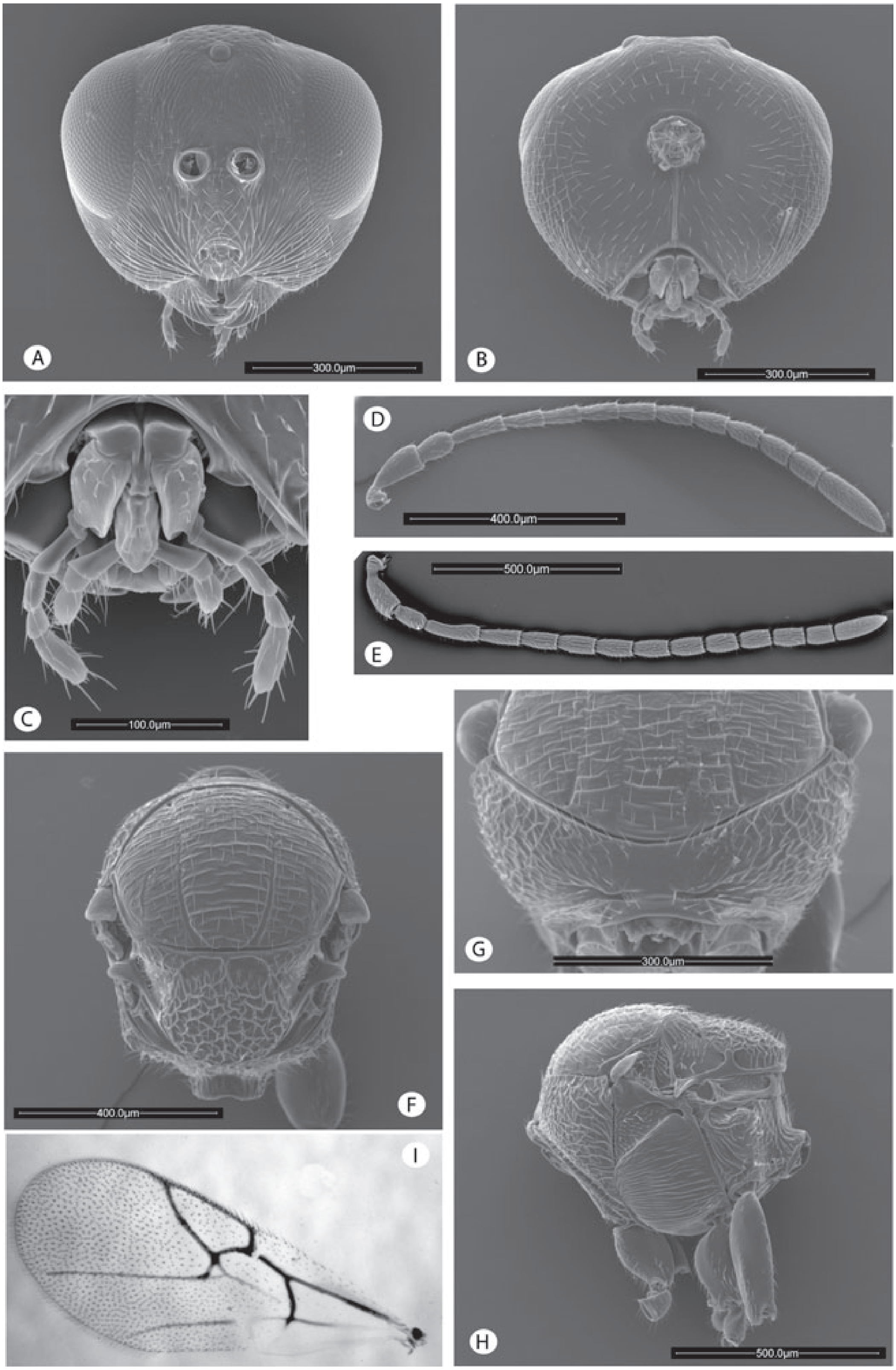

Figure 3. *Rhoophilus loewi* (scanning electron microscopy). A, head, anterior view, female; B, head, posterior view, female; C, mouth parts; D, antenna, female; E, antenna, male; F, mesosoma, dorsal view, female; G, mesosoma, anterodorsal view, female; H, mesosoma, lateral view, female; I, forewing, adult female.

impressed in anterior half of mesoscutum. Scutellar foveae rounded, smooth and shallow, posterior margin not marked. Dorsal surface of scutellum strongly rugose. Posterodorsal and posterior margin of axillula indistinct. Lateral shining strip extended dorsoposteriorly. Axillula weakly pilose. Mesopectus (mesopleuron including subpleuron and sternum) (Fig. 3H). Mesopleuron beneath mesopleural triangle longitudinally costulate. Mesopleural triangle smooth and with sparse setae; its ventral margin clearly marked with a straight sharp edge. Metanotum (Fig. 4C). Metascutellum largely glabrate; relatively long, not conspicuously constricted medially. Bar ventral to metanotal trough almost smooth. Metanotal trough weakly pilose. Metapectal–propodeal complex (Fig. 3H). Metapleural sulcus meeting anterior margin of metapectal-propodeal complex well above the mid-height of the latter. Lateral propodeal carinae subparallel, slightly flattened above and relatively broad, broader posteriorly. Lateral and median propodeal area sparsely pilose. Nucha moderately long dorsally, with strong longitudinal rugae, posterior margin slightly incised medially.

Legs: Procoxa without distinct anterolateral crest. Anterior surface of mesocoxa not strongly protruding. Metacoxa elongate. Claws simple, only with a blunt basal lobe (Fig. 4A).

Forewing (Fig. 3I): Hyaline, veins dark brown. Marginal cell closed along anterior margin R1 directed anteriorly, more or less perpendicular to anterior wing margin; Rs slightly curved. Marginal cell approximately 2.5-fold as long as broad. Bulla in R1 + Sc present. Areolet visible, closed by nebulous to tubular veins. Basal cell only with a few setae. Hair fringe along apical margin moderately long.

Female metasoma (Fig. 4B): As long as head plus mesosoma. Tergal flange of petiolar annulus relatively long. Postpetiolar metasoma slightly laterally compressed, in lateral view high, lenticular. Abdominal terga 3–7 visible. Third tergum with only two hairs anterodorsally, approximately one-half to two-thirds as long as whole metasoma. Fourth to seventh terga subequal in size, with a band of slight micropunctures laterally and medially. Ventral spine of hypopygium not projecting, united almost to apex with the lateral flaps. Hypopygium ventrally with two rows of widely separated, moderately long, hairs.

Description of the final-instar larva

Larval characters are shown in Figure 4D, E, F, G, H. Body ventrally concave, broader in the middle and slightly tapering towards anterior and posterior ends. Dimensions, approximately 2 mm length, 1.2 mm in width ($N = 6$). Integument whitish and smooth with very few short setae concentrated in the head region. Body (Fig. 4D) composed of head and 12 visible segments. First segment, in ventral view, not narrowed medially under ventral part of head; segments six to 11 of similar length but progressively narrower; last segment truncate at apex. Head (Fig. 4E) more or less rounded, broader dorsally; vertex slightly concave. Antennal areas and antennae invisible. A pair of short setae present on dorsolateral part of head and another pair visible on the antennal area. Pair of short genal setae present.

Mouthparts (Fig. 4F): Clypeus subrectangular; its ventral margin straight; pair of supraclypeal setae present. Labrum hemispheric. Two pairs of setae visible on the apical margin of labrum. Maxillae triangular, with a pair of maxillary setae. Labium with a pair of setae. Salivary opening conspicuous, in the form of a medial vertical crevice.

Mandibles (Fig. 4G, H): asymmetrical, without sculpture or hairs; the bases and the apical teeth visible beneath labrum. Right mandible (Fig. 4H) with three teeth, a larger apical acute tooth, an intermediate broad blunt tooth and a basal acute small tooth. Left mandible (Fig. 4G) with two teeth, a large apical, acute tooth and a smaller, basal tooth.

Diagnostic characters

Rhoophilus is morphologically related to the holarctic inquiline genera *Synergus*, S*aphonecrus*, and *Synophrus*, all of which typically attack oak cynipid galls. A sister group relationship between *Rhoophilus* and the oak inquiline genera *Synergus* + *Synophrus* + *Saphonecrus* (i.e. all other inquilines except *Ceroptres*) was hypothesized by Ronquist (1994) and Liljeblad & Ronquist (1998). Shared diagnostic features of this group were outlined by Ronquist (1994) and included the following. Shape of ventral clypeal margin: straight not projecting over mandibles. Extent of facial strigae: laterally reaching or almost reaching compound eye. Distance between occipital and oral foramina: longer than height of occipital foramen. Position of anterior end of metapleural sulcus: high. Position of petiolar foramen: posteriorly situated. To these adult characters, we can add one trait of the mature larva, namely the shape of apex of second tooth of the right mandible, which is strongly rounded or truncate in the larvae of all the oak inquiline genera and also in *Rhoophilus* (Nieves-Aldrey *et al*., 2005).

Diagnostic character states, both from the adult and the terminal-instar larva, showing similarities and differences of *Rhoophilus* with the oak inquiline genera are summarized in Tables 1, 2. The transverse ridges of the mesoscutum, and a mesopleuron sculptured with longitudinal ridges in *Rhoophilus* closely resemble characters in several species of the *Synergus*/*Saphonecrus* complex. However, a closer

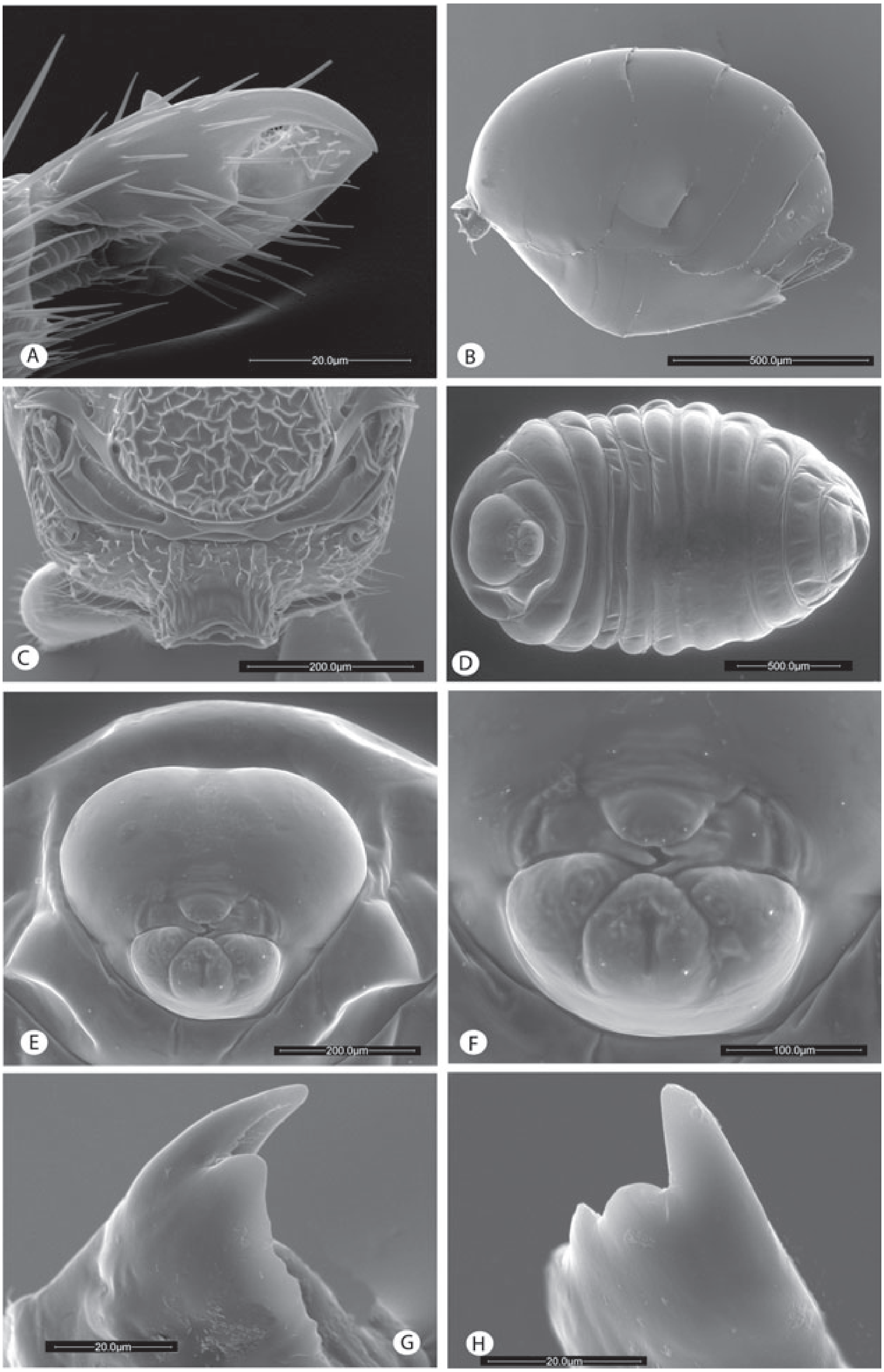

Figure 4. *Rhoophilus loewi* (scanning electron microscopy). A, tarsal claw, female; B, metasoma, lateral view, female; C, mesosoma, posterodorsal view, female; D, terminal larva, ventral view of the body; E, terminal larva, anterior view of the head; F, terminal larva, anterior view of mouth parts; G, terminal larva, anterior view of left mandible; H, terminal larva, anterior view of right mandible.

Table 1. A list of adult diagnostic morphological characters and character states in the oak associated inquiline genera and *Rhoophilus*

Diagnostic character states: adults	*Ceroptres*	*Synophrus*	*Synergus* + *Saphonecrus* complex	*Rhoophilus*
1. Shape of ventral clypeal margin and clypeus	Straight, clypeus weakly visible	Straight, clypeus clearly visible	Straight, clypeus weakly visible excepting by anterior tentorial pits	Slightly rounded, clypeus visible
2. Facial strigae on medial part of face and on clypeus	Absent	Present	Present	Absent
3. Distance between antennal socket and eye	Shorter than maximum width of antennal sockets	Shorter than maximum width of antennal sockets	Shorter than maximum width of antennal sockets	Longer than maximum width of antennal sockets
4. Shape of first segment of maxillary palpus	Subrectangular, broader than long	Triangular, longer than broad	Triangular, longer than broad	Subrectangular, broader than long
5. Shape of first segment of labial palpus	Short, abruptly tapering towards base	Short, abruptly tapering towards base	Short, abruptly tapering towards base	Long, gradually tapering towards base
6. Number of antennal segments (female)	12	13–14	13–14	13
7. Position of anterior end of metapleural sulcus	High, ratio of distance between metapleural sulcus to distance between anterior end of metapleural sulcus and anteroventral metepisternal margin < 0.65	Low, ratio of distance between metapleural sulcus to distance between anterior end of metapleural sulcus and anteroventral metepisternal margin > 0.65	High, ratio of distance between metapleural sulcus to distance between anterior end of metapleural sulcus and anteroventral metepisternal margin < 0.65	High, ratio of distance between metapleural sulcus to distance between anterior end of metapleural sulcus and anteroventral metepisternal margin < 0.65
8. Tarsal claws	With a conspicuous acute basal lobe or secondary tooth	With a conspicuous acute basal lobe or secondary tooth	With a conspicuous acute basal lobe or secondary tooth	With a blunt small basal lobe
9. Shape and size of 2tg	Very small, dorsal crescent-shaped projecting scale, smooth	Small, dorsal crescent-shaped, dorsally smooth laterally sulcate	Relatively large, ring shaped, longitudinally sulcate	Very small, dorsal crescent-shaped projecting scale, smooth
10. Size of 3tg	Small and free (not fused with 4tg)	Large, fused with 4tg into a large segment	Large, fused with 4tg into a large segment	Large, fused with 4tg into a large segment
11. Direction of R1 on radial cell	Directed anteriorly much more obliquely laterally	Directed anteriorly much more obliquely laterally	Directed anteriorly much more obliquely laterally	Directed anteriorly, more or less perpendicular to anterior wing margin

examination of the external morphology of the adult (Table 1) and the larva (Table 2) reveals several character states that enable its separation from the genera of oak inquilines. These are discussed below.

Adult morphology

1. Tarsal claws with a blunt small basal lobe (Fig. 4A). Tarsal claws have either a strong acute basal lobe or tooth in the oak inquiline genera.

Table 2. A list of terminal-instar larval diagnostic morphological characters and character states in the oak associated inquiline genera and *Rhoophilus* (data from *Ceroptres* not available)

List of character states: larvae	*Ceroptres*	*Synophrus*	*Synergus* + *Saphonecrus* complex	*Rhoophilus*
1. Shape of the salivary opening on the labium	–	With form of a medial vertical crevice	With form of a pit or hole	With form of a medial vertical crevice
2. Tuberculate sculpture surrounding salivary opening	–	Absent	Present or absent	Absent
3. Left and right mandibles	–	More or less asymmetrical	Symmetrical or asymmetrical	Strongly asymmetrical
4. Number of teeth on left mandible	–	Three	Three	Two
5. Shape of apex of second tooth of the right mandible	–	Truncate	Strongly rounded or truncate	Strongly rounded
6. Shape of apex of third tooth of right mandible	–	Acute	Blunt or rounded	Acute
7. Deep and wide gap separating the second and the third tooth, right mandible	–	Absent	Present	Absent
8. Surface of mandible	–	Sculptured at the base of the teeth with strong striations	Sculptured at the base of the teeth with strong striations	More or less smooth, without striations

2. Vein R1 directed anteriorly, more or less perpendicular to anterior wing margin (Fig. 3I). By contrast, although the marginal cell of forewing can be closed or open in the oak inquiline genera and vein R1 is always directed anteriorly, vein R1 is always directed much more obliquely laterally.

3. Distance between antennal socket and eye longer than the maximum width of antennal sockets. It is usually shorter than the maximum width in oak inquilines.

4. Mouth parts character states 4 and 5 (Table 1), modified from Ronquist (1994). However these character states are difficult to compare without dissection.

5. Tergite of second abdominal segment very small, crescent shaped and smooth. For this character, *Rhoophilus* is similar to *Ceroptres*, but the third tergite is quite different in the two genera (Table 1). The other genera of oak inquilines have a large second abdominal tergite, usually ring shaped and at least partly sulcate or ridged.

6. Lateral propodeal carinae subparallel, slightly flattened above and relatively broad, broader posteriorly. The lateral propodeal carinae are usually more sharp and narrow and not clearly broadening posteriorly in the oak inquiline genera.

Terminal instar larval morphology

The larva of *Rhoophilus* differs from the larvae of the oak inquiline genera (except *Ceroptres,* whose larva has not been studied) (Table 2) in two important diagnostic characters.

1. The presence of only two teeth on the left mandible and absence of striate sculpture at the base of the mandibular teeth. The mandible asymmetry found in *R. loewi* is relatively rare in larval cynipids, but is present in the larvae of one genus of aylacine gall inducers (*Diastrophus*) and three genera of inquilines (*Periclistus* in rose cynipid galls, and *Saphonecrus* and *Synophrus* in oak cynipid galls) (Nieves-Aldrey *et al*., 2005). These groups can all be distinguished on the basis of mandible morphology. The larvae of the Aylacini genera *Barbotinia*, *Aylax*, and *Iraella* have a right mandible with a long and narrow second tooth, rather than a broad, blunt tooth as found in *Rhoophilus*. Although the right mandibles of *Rhoophilus, Synophrus*, and *Diastrophus* are similar in form, their left mandibles differ. Whereas *R. loewi* has only two teeth, *Synophrus politus* (and all the other oak inquilines) has three teeth, with a large and broad second tooth.

2. The salivary opening on the labium in the form of a medial vertical crevice found in *Rhoophilus* is a character state also found in the oak inquiline species *S. politus* and in three genera of aylacine cynipids (*Barbotinia*, *Aylax*, and *Iraella*) inducing galls on poppies, *Papaver.* Another important character state, the tuberculate sculpture surrounding salivary opening, is found in some *Synergus* species

but is absent in *Rhoophilus* and also in *Synophrus* larvae.

Biology

Host associations

Scyrotis galls were found on nine of the 13 *Rhus* species surveyed in the present study (Table 3). As shown in Table 3, and as described below, the galls collected from different *Rhus* hosts differ in morphology and/or location on the host plant, and it is not yet clear whether the gall inducers represent one or several species of *Scyrotis*. *Rhoophilus loewi* adults were reared from all of the host plants bearing *Scyrotis* galls, except for *Rhus dentata* and *Rhus pyroides* (Table 3). The observation of a lack of *Rhoophilus* or *Scyrotis* galls on the host species that were surveyed may be an artefact of insufficient sampling. For example, *Rhus chirindensis* was only surveyed at two localities. However, some species, such as *Rhus tomentosa*,

Table 3. *Rhus* species surveyed for galls recording the presence/absence of *Scyrotis* galls and *Rhoophilus* modified galls, and morphology of *Scyrotis* galls

			Scyrotis gall morphology	
Rhus species	*Scyrotis* galls	*Rhoophilus* modified galls	Leaf galls	Stem galls
Rhus angustifolia	No	No		
Rhus burchelli	Yes	Yes	None	Round smooth galls erupting from older stem
Rhus chirindensis	No	No		
Rhus incisa	Yes	Yes	Unevenly spherical leaf petiole galls (2–4 mm diameter)	Pixie-cap shaped galls erupting from older stems, small, green turning purple
Rhus dentata	Yes	No	None	Round, very furry, brown galls erupting from older stem
Rhus glauca	Yes	Yes	Round smooth galls on leaf lamina and petiole (3–7 mm diameter)	Round smooth shiny green galls erupting from older stem
Rhus laevigata	Yes	Yes	Round smooth galls on leaf lamina (4–6 mm diameter)	Round smooth shiny green galls erupting from older stem – galls can remain inside stem. Or small sparsely hirsute oval gall on outside of terminal stems
Rhus lancea	No	No		
Rhus lucida	Yes	Yes	Pixie-cap shaped galls on leaves and petioles or oval, green, soft galls with a cherry red flush on the side exposed to the sun (4–8 mm diameter) formed on leaf lamina, leaf petiole or petiole of flower cluster	Large, round, smooth, shiny green galls erupting from older stem – galls can remain inside stem
Rhus pallens	Yes	Yes	Pixie-cap or oval shaped galls on leaves and petioles (4–5 mm diameter)	None
Rhus pyroides	Yes	No	Small oval hairy gall on leaf lamina	Small round brown furry galls erupting from older terminal stems
Rhus tomentosa	No	No		
Rhus undulata	Yes	Yes	Pixie-cap or oval shaped galls on leaves and petioles – often clustered in groups of 2–3	Galls formed inside swollen older stem – shiny green galls can erupt out of stem

were commonly encountered (in excess of 50 individual plants over more than ten localities) and galls were never observed, suggesting that this species is not used as a host by either *Scyrotis* or *Rhoophilus*.

Morphology of Scyrotis galls

Scyrotis galls can be broadly divided into two types: those induced on leaves, leaf petioles or flower cluster petioles, and those induced on older woody stems (Table 3).

1. Leaf galls. Leaf galls were found on seven *Rhus* species (Table 3; Fig. 2E, F, G, K, P). Dissection of these galls revealed a large central cavity with either a *Scyrotis* larva with an enlarged head region (Fig. 2I, J) or a more elongate ectoparasitoid wasp larva (*Ormyrus* or *Eurytoma* species) either attached to the *Scyrotis* larva or present in the cavity with the shrivelled remnants of the *Scyrotis* larva (Fig. 2K).

2. Stem galls. These galls are represented by a variety of morphologies (Table 3; Fig. 2L, M, N, O). Usually, the 'jumping beans' fall to the ground when the gall exfoliates as is the case with leaf galls, but the second type of *Scyrotis* galls occurring on the terminal stems of *R. laevigata* do not exfoliate, but gradually lose the outer thin cortex covering and instead of the 'jumping beans' dropping to the ground they persist on the thin branches.

Morphology of galls occupied by Rhoophilus

The host galls of *R. loewi* were originally described by Mayr (1881) based on material collected from *R. lucida*. The galls grow exclusively on several species of *Rhus* (Table 3). All of these galls yielded the same cynipid, *R. loewi*. On *R. lucida*, *R. loewi* oviposits into *Scyrotis* galls when they are young, and the smallest gall containing a *Rhoophilus* larva had a diameter of 2.4 mm. It has not been established how many times or where the *Rhoophilus* female oviposits into the *Scyrotis* gall, but eggs are probably laid in tissues destined to become the outer gall parenchyma. Oviposition by *Rhoophilus* causes the outer parenchyma of the *Scyrotis* gall to proliferate and expand (Fig. 1D, E). The larvae develop in discrete larval cells arranged in a ring around the gall inducing moth larva, with six to 20 inquiline cells per gall. Each *Rhoophilus* larval cell is ellipsoidal and measures approximately 2 mm long (Figure 1I, J, K). Development of the inquiline cells gradually reduces the space available to the *Scyrotis* caterpillar, and some of the dissected galls containing *Rhoophilus* larvae contained a dead *Scyrotis* larva in the compressed central space (Fig. 1E).

Scyrotis galls on *R. lucida* attacked by *Rhoophilus* are irregularly spherical, ranging in diameter from 7–11 mm when mature (Fig. 1A, B, C, D, E, F, G, H, I, J). During the early stages of *Rhoophilus* larval development the galls are relatively soft and green, often with a reddish–brown flush (Fig. 1B, C). By contrast to galls harbouring only the *Scyrotis* gall inducer, both leaf or petiole galls and stem galls containing *Rhoophilus* ultimately become extremely hard, brown and woody and persist on the host plant for a number of years after the wasps have emerged (Fig. 1F, G, H).

Scyrotis leaf galls on *R. undulata*, *R. pallens*, and *R. burchelli* attacked by *Rhoophilus* are irregularly spherical, similar in size to those on *Rhus lucida*, but generally a lighter brown and with a smoother texture (Fig. 1N). Those on *R. incisa* (Fig. 1M) and *R. glauca* are smaller (diameter 4–8 mm), with a more irregular shape than the *R. lucida* galls.

Phenology of gall formation

Scyrotis galls are evident through most of the year, having been recorded in all months with the exception of January, February and October. Recently dehisced (exfoliated) *Scyrotis* galls (Fig. 2G, H, M) were observed from May to November. On exfoliation of the gall a hard, oval case containing the final instar larva is released (Fig. 2H). These 'jumping beans' fall to the ground where through their jumping they work their way into the leaf litter.

Rhoophilus loewi females oviposit from April to August and adults emerge either the following year from January through to July from hard, brown galls or 2 years later from 2-year-old galls.

Behavioural observations

In June, adult female *Rhoophilus* were placed on cuttings of *R. lucida* without *Scyrotis* galls and were observed inserting their ovipositor into the petiole of a very young shoot of the trifoliate leaf (Fig. 2B). The probing behaviour occurred multiple times up and down the petiole.

In July, *Rhoophilus* specimens were placed on a cutting with three leaf galls of varying sizes (6–10 mm). One female investigated the largest gall, but thereafter the galls were ignored and the females again inserted their ovipositors into the petiole and main leaf veins of young leaf shoots. On one occasion, a female inserted her ovipositor into the main leaf vein (near the base) of a mature leaf with a gall (10 mm in diameter) located in the distal third of the leaf. A single female probed with her ovipositor at numerous different localities on the petiole and leaf vein, each probing act lasting *c*. 35 s. This behaviour occurred irrespective of whether *Scyrotis* galls were present or not. Eggs were not found on dissection of the oviposition sites.

Parasitoids

Percentage parasitism of *Scyrotis* larva in galls collected and dissected when fresh from *R. lucida* and

R. laevigata in the Western Cape Province is presented in Table 4. Degree of parasitism of *Rhoophilus* larva in galls collected from *R. lucida* in Kogelberg Nature Reserve (Western Cape Province) is presented in Table 5. In total, 18 species of parasitoid wasp belonging to five families in the superfamily Chalcidoidea were recorded as being associated with the *Scyrotis–Rhoophilus* interaction (Table 6). The signifi-

Table 4. Percentage parasitism of *Scyrotis* larva in galls collected and dissected while fresh from two *Rhus* species in the Western Cape Province (South Africa)

Rhus species	*N*	% unparasitized *Scyrotis* larva	% *Rhoophilus* inquiline galls	% Parasitism by *Eurytoma* or *Ormyrus*	% Empty or larva dead	Total percentage parasitism of *Scyrotis*	Locality/season (galls)
Rhus lucida	20	25	35	20	20	55	Betty's Bay/August
Rhus lucida	30	13.3	63.3	23.4	0	86.7	Betty's Bay/August
Rhus lucida	35	5.7	88.6	5.7	0	94.3	Cape Point Nursery/ September
Rhus lucida	38	2.6	97.4	0	0	97.4	Scarborough/September
Rhus lucida	11	18.2	54.5	27.3	0	81.8	Onrus/September
Rhus lucida	14	35.7	64.3	0	0	64.3	Vermont/September
Rhus lucida	21	23.8	33.3	38.2	4.7	71.4	Onrus/October
Rhus lucida	10	30	50	20	0	70	Kogel Bay/September
Rhus lucida	8	60	40	0	0	40	Gordons Bay/September
Rhus lucida	13	23	53.8	23	0	76.9	Vermont/October
Rhus lucida	219	6.8	54.8	38.4	0	93.2	Kogelberg/May
Rhus laevigata	39	30.7	0	66.7	2.6	66.7	Wingfield/August
Rhus laevigata	16	6.2	0	93.8	0	93.8	Scarborough/September

Eurytoma or *Ormyrus* larvae were observed as ectoparasitoids of *Scyrotis* larvae in dissected galls.

Table 5. Degree of parasitism of *Rhoophilus* larvae in galls collected from *Rhus lucida* in Kogelberg Nature Reserve (Western Cape Province)

Sample no	Number of *Rhoophilus* galls	Cynipidae	Ormyridae	Eulophidae	Eupelmidae		
		Rhoophilus	*Ormyrus*	*Pediobius*	*Eupelmus*	*Reikosiella*	*Mesocomys*
KB02-R01	7	29	12	10	21	2	None
KB02-R02	1	9	8	None	5	2	None
KB02-R03	11	126	9	39	15	None	None
KB02-R04	4	13	3	19	2	None	None
KB02-R05	8	25	15	30	17	None	None
KB02-R07	3	6	21	None	3	None	1
KB02-R08	4	24	5	76	21	1	None
KB02-R09	4	102	None	None	5	1	None
KB02-R10	3	26	9	4	2	None	None
KB02-R11	11	106	1	5	5	3	None
KB02-R12	2	12	5	None	5	2	None
KB02-R13	4	55	6	1	5	1	None
KB02-R14	8	31	16	28	13	4	None
KB02-R15	8	None	None	6	None	None	None
KB02-R16	1	None	None	None	None	None	1
KB02-R17	3	18	None	None	None	2	None
KB02-R23	23	124	16	115	32	2	None

Each sample comprises the galls collected from one host *Rhus lucida* shrub. Number of specimens of each taxon reared from the galls is presented.

Table 6. Chalcid parasitoid wasps (Chalcidoidea) reared from *Scyrotis* and *Rhoophilus*

Rhus species	Parasitoids of *Scyrotis*	Parasitoids of *Rhoophilus*
Rhus burchellii		*Pediobius* sp. A (Eulophidae) *Ormyrus* sp. D (*orientalis* sp.-grp) (Ormyridae)
Rhus dentata	*Eurytoma* sp. A (Eurytomidae) *Ormyrus* sp. C (*langlandi* sp.-grp) (Ormyridae)	
Rhus glauca	*Ormyrus* sp. B (*langlandi* sp.-grp) (Ormyridae)	*Pediobius* sp. A (Eulophidae) *Eupelmus* sp. B (Eupelmidae) *Reikosiella* sp. A (Eupelmidae) *Ormyrus* sp. D (*orientalis* sp.-grp) (Ormyridae)
Rhus lucida	*Pediobius* sp. B (Eulophidae) *Mesocomys* sp. B (Eupelmidae) *Eupelmus urozonus* (Eupelmidae) *Eupelmus* sp. B (Eupelmidae) *Eurytoma* sp. A (Eurytomidae) *Ormyrus* sp. A (*langlandi* sp.-grp) (Ormyridae) *Ormyrus* sp. E (*langlandi* sp.-grp) (Ormyridae)	*Pediobius* sp. A (Eulophidae) *Eupelmus urozonus* (Eupelmidae) *Reikosiella* sp. B (Eupelmidae) *Mesocomys* sp. A (Eupelmidae) *Ormyrus* sp. D (*orientalis* sp.-grp) (Ormyridae)
Rhus laevigata	*Eupelmus* sp. B (Eupelmidae) *Neanastatus rufatus* (Eupelmidae) *Eurytoma* sp. A (Eurytomidae) *Ormyrus* sp. F (*orientalis* sp.-grp) (Ormyridae)	
Rhus pyroides	*Eurytoma* sp. A (Eurytomidae)	
Rhus undulata	*Eupelmus* sp. B (Eupelmidae) *Ormyrus* sp. B (*langlandi* sp.-grp) (Ormyridae) *Pteromalus* sp. A (Pteromalidae)	*Eupelmus urozonus* (Eupelmidae) *Eupelmus* sp. B (Eupelmidae) *Uropelma* sp. A (Eupelmidae) *Ormyrus* sp. D (*orientalis* sp.-grp) (Ormyridae)

cance of these species with reference to communities associated with communities centred on cynipid gall inducers, and hence the predominant communities occupied by cynipid inquilines, is discussed below.

Distribution

Rhoophilus loewi appears to have a distribution encompassing the winter rainfall areas of the Western Cape Province and the more arid areas of western South Africa. The majority of the records are centred within the Western Cape Province with only two records from the Northern Cape Province: Niewoudtville and Modderfontein-Suid (latter specimens in NCI Pretoria) (Fig. 5). The recorded distribution is likely to be an artefact of under-sampling because the majority of survey work has been undertaken in the Western Cape Province. The distribution of a number of the recorded host-plant species for *Rhoophilus* extends beyond the documented distribution for *Rhoophilus,* indicating that *R. loewi* may enjoy a wider distribution than currently recorded. *Rhus lucida* extends up through Kwazulu-Natal into Mpumulanga and Northern Province. *Rhus undulata* extends up the west coast to southern Namibia and *R. incisa* follows suite and also extends eastwards into the Eastern Cape Province (Moffett, 1993; Von Breitenbach, 1995). We predict that the distribution gaps in the Northern Cape Province will be filled (possibly the species also will be recorded from southern Namibia) and that the distribution will extend further into Eastern Cape Province, but not further North or East within South Africa. The National Collection of Insects in Pretoria has no records from north or eastern South Africa and *Rhoophilus*-modified galls have not been observed on *Rhus* species in these areas during many years of extensive field work (G. Prinsloo, pers. com).

On the other hand, *Scyrotis* galls are found over a wider geographical distribution (Fig. 6), having also been recorded from Kwazulu-Natal, and may extend further north as well. The depicted distribution is almost certainly an artefact of insufficient sampling.

DISCUSSION

The significance of *Rhoophilus* in understanding the evolution of inquilinism in cynipids

Historically, the biology of *R. loewi* has been controversial. Despite the fact that the species had always

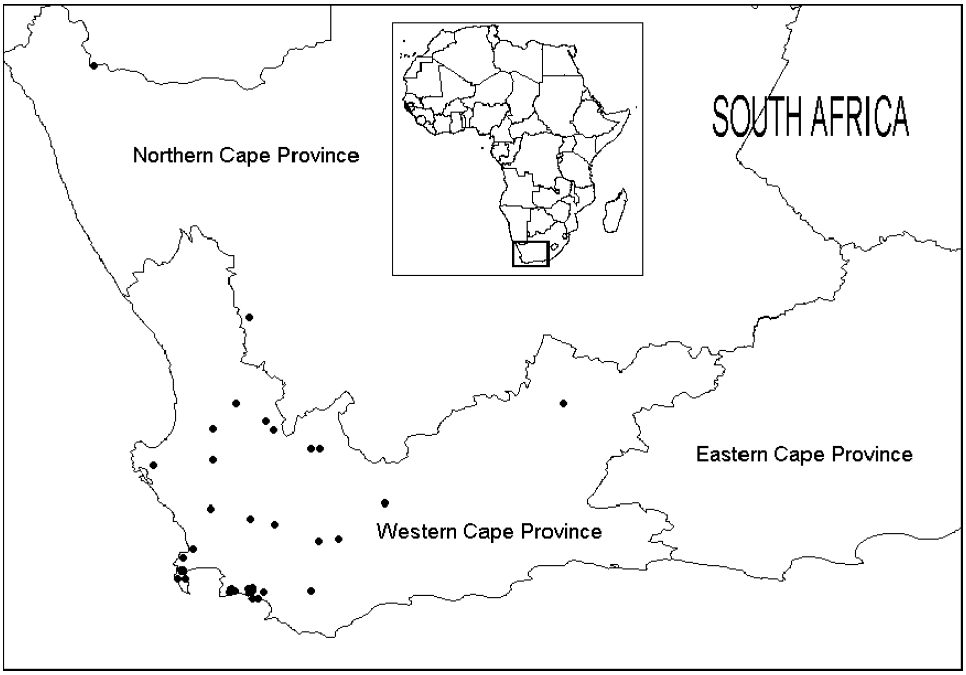

Figure 5. Distribution of *Rhoophilus loewi*.

Figure 6. Distribution of observed *Scyrotis* galls on *Rhus*.

been classified with the inquiline cynipids, its host was unknown and the species was sometimes considered as the true gall inducer wasp on *Rhus* species (Anacardiaceae) (Dalla Torre & Kieffer, 1910; Ronquist, 1999). Our repeated observation of *Rhoophilus* larval cells surrounding a central locule containing either a living or dead *Scyrotis* larva show conclusively that *R. loewi* is an inquiline in galls of *Scyrotis* species (Lepidoptera). Dissection of a range of different aged galls showed a sequential closing of the central locule, illustrating the probable cause of mortality of the *Scyrotis* larva. *Rhoophilus* is thus a 'lethal inquiline', causing the death of the gall inducer without feeding on it directly. Such an outcome is associated with attack by cynipid inquilines in cynipid galls, most noticeably by *Periclistus* inquilines in *Diplolepis* rose galls (Brooks & Shorthouse, 1997), and by *Synergus* species in galls on oak (Washburn & Cornell, 1981; Wiebes-Rijks & Shorthouse, 1992)

Rhoophilus loewi also represents the first-known case where the only known host for a cynipid wasp is not itself a cynipid. Although several cynipid inquilines have been reared from gall midges on oaks, these represent rare departures from more frequent attack of cynipid galls (Askew, 1999; Csóka, Stone & Melika, 2005).

These aspects of *Rhoophilus* biology, together with its inferred phylogenetic position, have important implications for the evolution of inquilinism in gall wasps. Ronquist (1994) and Ronquist & Liljeblad (2001) originally hypothesized that cynipid inquilines in oak galls are derived from gall-inducing cynipids close to *Diastrophus*, via an intermediate evolution of inquilinism in rose cynipid galls. This hypothesis would place the oak cynipid inquilines close to the rose cynipid inquilines, represented by species of the genus *Periclistus*. Recent phylogenetic evidence, based on combined morphological and molecular data, has challenged this hypothesis (Nylander *et al*., 2004a, b). The inquilines may in fact represent a polyphyletic or paraphyletic assemblage, in which species associated with rose cynipids are distinct from those associated with oaks. Instead, *R. loewi* is the sister group of a lineage leading to a group of three genera of inquiline cynipids (*Saphonecrus*, *Synergus*, and *Synophrus*) attacking oak galls. This pattern allows two alternative hypotheses for the evolution of this oak cynipid lineage. One is that *Rhoophilus* is the sole known survivor of a once more diverse basal lineage of inquilines attacking a taxonomic diversity of host gall inducers on plants other than oaks. For some reason, the oak cynipid inquilines represent a particularly successful descendant lineage of this group. The alternative is that *Rhoophilus* itself represents a southern African offshoot of an ancestral lineage otherwise closer in ecology and host-plant association to the extant oak cynipid inquilines. In this case, the ecology of *Rhoophilus* is of lower impact in assessing possible ancestral states in inquiline evolution. Discrimination between these two alternatives will be assisted by the discovery and phylogenetic analysis of other inquiline cynipids on non-oak hosts close to *Rhoophilus*.

Host associations of *Rhoophilus*

Unfortunately, we have had no success in rearing the adult moths from 'jumping beans' formed in galls on any of the *Rhus* species that were sampled and therefore cannot confirm the identity of the cecidosid species. *Scyrotis athleta* was recorded from galls on *R. glauca* collected on Table Mountain but, based on the wide range of *Scyrotis* gall morphology, we suspect that there are a number of *Scyrotis* species involved. Final-instar larvae were confirmed as belonging to the genus *Scyrotis* (D. R. Davis, pers. comm.)

The observed oviposition behaviour of *Rhoophilus* into the leaf petioles of cuttings of *R. lucida* in the laboratory suggests that these inquilines attack galls extremely early in their development, rather than established, morphologically differentiated galls. This is compatible with our observation of *Rhoophilus* larvae in extremely small *Scyrotis* galls. No gall development was observed, in keeping with our inference that *Rhoophilus* is an inquiline rather than a gall inducer. Dissection of probed sites yielded no eggs, and it is probable that the offered plant material contained no host galls at a suitable phenological stage for inquiline attack. Host choice by *R. loewi* requires further research.

Biogeographical significance of *Rhoophilus*

Rhoophilus loewi and the undescribed South African cynipid genus on *Scolopia mundii*, represent the only cynipid taxa with an Afrotropical distribution. Ronquist & Liljeblad (2001) hypothesized that the gall wasps (Cynipidae) arose in Europe, around the Black Sea, and that the genera *Eschatocerus* (gall inducers on *Acacia* and *Prosopis*) and *Rhoophilus* apparently spread later to South America and South Africa, respectively. However, recent phylogenetic findings contradict this hypothesis. *Eschatocerus* and *Rhoophilus* belong to older primitive lineages of cynipids and as such the biogeographical history of the basal Cynipidae is still not clear (Nylander *et al*., 2004a). The presence of *Rhoophilus* and other cynipids in southern Africa, far from other centres of cynipid diversity, suggests that other African groups may await discovery.

Comparative overview of the *Scyrotis* gall community

The vast majority of work on parasitoids of cynipid inquilines concerns the communities associated with these hosts in galls induced by other cynipids. Although these galls share cynipid inquilines, they are highly distinct in terms of host plants and biogeography. Nevertheless, a striking feature of the community reared from *Scyrotis* galls is the close parallel it shows to communities associated with cynipid gall inducers. Five of the genera recorded from *Scyrotis* galls (*Pediobius* (Eulophidae), *Pteromalus* (Pteromalidae), *Eupelmus* (Eupelmidae), *Ormyrus* (Ormyridae), and *Eurytoma* (Eurytomidae)) are known from cynipid galls (Askew, 1961, 1984; Csóka *et al*., 2005). However, only one species, *Eupelmus urozonus*, is actually common to both *Scyrotis* and cynipid galls. Although it is too early to infer the origin of parasitoid genera shared between these two groups of galls, there are known examples of parasitoids that attack both leaf-mining moths and galling cynipids, providing evidence of exchange between these moth-centred and cynipid-centred communities. For example, the eulophids *Closterocerus trifasciatus* and *Cirrospilus* species usually attack leafmining *Phyllonorycter* moth species on oaks, but also sometimes attack asexual generation 'spangle' galls induced by the oak cynipid gall wasps *Neuroterus numismalis* and *Neuroterus quercus-baccarum* (Askew & Shaw, 1974, 1979). Contrasts between the biology of species recorded in cynipid galls, and those reported here for *Scyrotis* galls shed interesting light on variation within specific parasitoid genera, and we briefly comment on four important genera.

Pediobius

In cynipid galls, *Pediobius* is so far known only as a parasitoid of the gall inducer (Askew, 1961); although inquiline cynipids are available hosts, there are no confirmed records of *Pediobius* attacking them. This provides an obvious contrast with the same genus in *Scyrotis* galls, in which *Pediobius* species are gregarious parasitoids of both gall-inducer and inquiline. Further sampling is required to determine the extent to which the two species are each restricted to one of these hosts. *Pediobius* is an endoparasitoid in both galling systems, but is not known to be gregarious in cynipid galls.

Eupelmus

In cynipid galls, *Eupelmus* species can develop as a hyperparasitoid (Askew, 1961) and as parasitoids of cynipid inquilines and gall inducers. This is perhaps the most predictable genus for sharing between cynipid and *Scyrotis* galls. The same species recorded here, *E. urozonus*, is known to act as a secondary parasitoid in the larvae of a range of Lepidoptera, Diptera and Coleoptera (Askew, 1984) on a range of plant taxa, and also attacks a broad diversity of hosts in cynipid communities (Noyes, 1998). It remains to be seen whether *Eupelmus* ever attacks *Scyrotis* itself.

Ormyrus

Members of this genus can act as hyperparasitoids (*O. pomaceus*) or parasitoids of the gall-inducer (*O. nitidulus*) in cynipid galls (Askew, 1961; Schönrogge, Stone & Crawley, 1995). We have not established whether the *Ormyrus* species are parasitizing the moth larva or whether they are hyperparasitoids of *Eurytoma* that were also reared from the *Scyrotis* galls. The latter is likely to be the case, based on other host relationships of afrotropical *Ormyrus* species, such as *Ormyrus flavipes* Boucek that was observed as a parasitoid of *Syceurytoma ficus* Boucek (Eurytomidae) (Boucek, Watsham & Wiebes, 1981), which is a parasitoid of gall-forming Epichrysomallinae (Compton & Van Noort, 1992); and Neartic *Ormyrus*, where a few species are hyperparasitoids in oak galls (Washburn & Cornell, 1979). Both of these roles are possible in *Scyrotis* galls, and further work is required to clarify which is filled by the six associated *Ormyrus* species.

Eurytoma

This genus is another whose association with *Scyrotis* galls is perhaps unsurprising. In cynipid galls *Eurytoma brunniventris* is a facultative hyperparasitoid and cannibal, and will attack any larva it encounters (Askew, 1961). It is also able to develop to maturity on gall tissue alone. Thus, although our data show the *Eurytoma* species in *Scyrotis* galls to attack the gall-inducer, future work may well show that other inhabitants are also attacked.

A final issue awaiting clarification from further work on *Scyrotis* galls is the extent to which communities associated with the gall inducer are separate from those associated with *Rhoophilus*. This is a characteristic of the communities associated with these components in complex cynipid galls (Stone *et al*., 2002). Two further features of the *Scyrotis*–*Rhoophilus* system are probably associated with attack by parasitoids and other natural enemies. First, the jumping of the *Scyrotis* pupal cases is likely to be a mechanism to bury the 'bean' in the leaf litter below the host plant to avoid predation and parasitism, as hypothesized for the 'jumping beans' of gall wasps in California (Russo, 1979). Second, the structural modification of *Scyrotis* galls when attacked by *Rhoophilus* parallels inquiline modification of galls in both oak (*Synophrus*: Pujade-Villar *et al*., 2003) and rose cynipids (*Periclistus*: Brooks & Shorthouse, 1998). This probably represents an adaptive modification of gall architecture to reduce attack by parasitoids and other enemies (Stone & Schönrogge, 2003).

Conclusion

The elucidation of the intricate and unique life history of *R. loewi* has raised new issues in research on the evolution of cynipid lineages and emphasizes the probable origin of inquilinism in cynipids from an ancestral inquilinism condition rather than an ancestral state of gall induction. Work on taxa related to *Rhoophilus* is required to determine whether this species represents an extant surviving representative of a basal transitional life history state in the evolution of a major lineage of oak cynipid inquilines, or an evolutionary experiment in association with lepidopteran gall inducers.

ACKNOWLEDGEMENTS

We thank Fredrik Ronquist and an anonymous reviewer for valuable comments on the manuscript. Fruitful discussions were held with Olle Pelmyr, Zhiwei Liu, and Don Davies. Gerhard Prinsloo provided information on collection localities and host relationships of specimens housed in the National Collection of Insects. We thank J. H. Giliomee for providing galls collected on *R. undulata* and Philippa Huntly and Margie Cochrane (Iziko SAM) for their valuable assistance in the field. Laura Tormo (technician at the MNCN Madrid) provided assistance with the standard electron microscopy pictures. The National Botanical Institute granted permission to work in the Harold Porter Botanical Gardens. Western Cape Nature Conservation kindly provided a collecting permit: no. 288/1999. This study was funded by grants received from the South African National Research Foundation (SvN) and Spanish Ministry of Science and Technology (research project REN2002-03518, to J.L.N-A). This present study is dedicated to the memory of Vin Whitehead, who passed away shortly after submission of the manuscript for publication.

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