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Cales (Hymenoptera: Chalcidoidea): morphology of an enigmatic taxon with a review of species

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Abstract. Calesinae is a small group of Chalcidoidea (Hymenoptera) that are parasitoids of whiteflies (Hemiptera: Aleyrodidae). One species, *Cales noacki* Howard, has been introduced from South America into citrus-growing regions of North America, the Mediterranean and Africa for biological control. The remaining species are found in Australia and New Zealand: a classic Gondwanan disjunction. The subfamily consists of a single genus, *Cales*, which is currently unplaced within Chalcidoidea. Its taxonomic position has historically been unstable, although most often *Cales* is associated with Aphelinidae. Here, we present a detailed morphological study of the group with an emphasis on Australian species. Although *Cales* shares many characteristics with Aphelinidae, especially Coccophaginae and *Eretmocerus*, more studies of character systems across Chalcidoidea are needed to determine which features may be synapomorphic. Consequently, we leave *Cales incertae sedis* within Chalcidoidea. We also describe a new species from New Zealand, *Cales berryi* **sp.n.**, reared from the whitefly *Asterochiton pittospori* on lemonwood, *Pittosporum eugenioides*, and we present a key and review the four known species of *Cales*.

Introduction

Although the monophyly of some chalcidoid groups is strongly supported by morphological or molecular synapomorphies, many higher-level relationships within the superfamily remain uncertain. Establishing relationships within Chalcidoidea is hindered by a lack of comprehensive morphological studies, either across character systems or across taxa. Some detailed studies are available (e.g. Darling, 1988; Gibson, 1989; Heraty *et al*., 1994, 1997; Basibuyuk & Quick, 1995; Heraty & Schauff, 1998; Krogmann & Vilhelmsen, 2006), but more information is needed to determine the utility of various morphological features for phylogenetic reconstruction. Wide diversity of form and function, resulting in uncertainty regarding sister-group relationships, has left some chalcidoid groups unplaced into higher taxonomic categories, and several families are regarded as either paraphyletic or polyphyletic (Gibson *et al*., 1999; Campbell *et al*., 2000). The genus *Cales* Howard is an economically important and easily defined group that currently defies placement into any family within Chalcidoidea.

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Taxonomic history. The taxonomic history of *Cales* and its higher classification is complex, and reflects the uncertainty various workers have encountered when trying to classify the group. *Cales noacki* was first described from specimens reared from *Orthezia* sp. (Hemiptera: Pseudococcidae) in Campinas, Brazil (Howard, 1907). Howard placed this species in the tribe Pteroptricini (now Aphelinidae: Coccophaginae), which was then included in the subfamily Aphelininae. Brèthes (1914) described *Diaspidophilus pallidus* from specimens reared from the white peach scale, *Pseudaulacaspis pentagona* (Targioni) (Hemiptera: Diaspididae), in Argentina, and placed it in the family Mymaridae. Mercet (1929) synonymized *Diaspidophilus* with *Cales* and erected the new subfamily Calesinae within Aphelinidae. Dozier (1933) placed *Cales* within Trichogrammatidae while studying whitefly parasitoids in Haiti. *Paranthemus spenceri* Girault was described from Australia and placed in Mymaridae (Girault, 1915), but *Paranthemus* was later synonymized with *Cales* by Viggiani (1981). A third species was reared from an Australian whitefly, *Orchamoplatus citri* (Takahashi) (Hemiptera: Aleyrodidae),

and described as *Cales orchamoplati* by Viggiani & Carver (1988). A fourth species, *Cales berryi* **sp.n.,** was reared from the whitefly *Asterochiton pittospori* in New Zealand, and is described herein. Another species originally placed in Calesinae by Risbec (1957), *Neocales phillipiae* Risbec, was transferred to *Chartocerus* (Signiphoridae) by Polaszek (1993).

Historical reviews of *Cales* classification are sometimes in conflict, possibly because the morphological peculiarities of the group rendered many authors reluctant to draw firm conclusions regarding their taxonomic affinities. Changes in taxonomic placement of *Cales* are reviewed by Hayat (1994), Heraty & Schauff (1998) and Gibson *et al*. (1999). Briefly, *Cales* is most often included within Aphelinidae (De Santis, 1946; Ferrière, 1965; Yasnosh, 1976; Shafee & Rizvi, 1990), although several studies have suggested that *Cales* is closer to Trichogrammatidae or Eulophidae (Viggiani & Battaglia, 1984; Polaszek, 1991; Hayat, 1994; Heraty *et al*., 1997). Most recently, Hayat (1994) excluded *Cales* from Aphelinidae, and it has since remained *incertae sedis* within Chalcidoidea. Although based on limited sampling (*C. noacki* only), molecular studies have shown *Cales* to be isolated as a unique lineage, distinct from Aphelinidae, Eulophidae or Trichogrammatidae, and potentially the sister group of Chalcidoidea, excluding Mymaridae (Campbell *et al*., 2000). A developmental study of *C. noacki* (Laudonia & Viggiani, 1986) indicates that the larval stages are distinct from other aphelinids, and are possibly unique within Chalcidoidea.

Biology and biological control. Most information about *Cales* biology is based upon observations of *C. noacki*. The first substantiated host species for *C. noacki* was the woolly whitefly, *Aleurothrixus floccosus* (Maskell) (Hemiptera: Aleyrodidae) (Dozier, 1933). It was apparently reared earlier from Pseudococcidae and Diaspididae (Howard, 1907; Brèthes, 1914), but these host records have not been substantiated through subsequent rearing. It was also reared from eggs of *Phalera bucephala* Linnaeus (Lepidoptera: Notodontidae) (Viggiani & Currado, 1978), but here may have been acting as a hyperparasitoid of another wasp (Polaszek, 1991). *Cales* are primarily endoparasitoids of the larval instars of various aleyrodids (Dozier, 1933; DeBach & Rose, 1976; Rose & Woolley, 1984). The parasitoids attack second-, third- or fourth-instar nymphs, and then emerge from the mummified host remains (Miklasiewicz & Walker, 1990).

When the woolly whitefly was discovered on California citrus in the late 1960s, *C. noacki* was introduced into Baja California and Southern California from Chile and Peru for biological control (DeBach & Rose, 1976). Since then, the continued spread of the woolly whitefly has resulted in the introduction and establishment of *C. noacki* in citrus-growing regions around the Mediterranean (European and Mediterranean Plant Protection Organization, 2002), including the Canary Islands, Madeira and the Azores (Rodríguez-Rodríguez, 1977a, b; Hernández-Suárez *et al*., 2003). *Cales noacki* was also introduced into Uganda and Kenya, where it has successfully become established and has provided substantial control of woolly whitefly populations (Legg *et al*., 2003). Additional studies of *C. noacki* in North America, following its introduction as a biological control agent, have revealed a broader host range. *Cales noacki* is known to successfully parasitize the following species: the mulberry whitefly, *Tetraleurodes mori* (Quaintance); the acacia whitefly, *Tetraleurodes acaciae* (Quaintance); and the red-banded whitefly, *Tetraleurodes perseae* Nakahara, a minor pest of avocado in California and Mexico (Rose & Woolley, 1984; Hoddle, 2006). In their survey of whitefly parasitoids in Haiti, Evans & Serra (2002) found *C. noacki* emerging from *Aleurothrixus floccosus* as well as an undescribed *Aleurothrixus* species. Viggiani & Laudonia (1984) reared *C. noacki* from the viburnum whitefly, *Aleurotuba jelineki* (Frauenf.) in Campania, Italy. *Cales noacki* was found in the Azores, Canary Islands and Madeira attacking five different whitefly species in five different genera (Hernández-Suárez *et al*., 2003). By contrast, *C. noacki* was found to be specific to *Aleurothrixus floccosus* in citrus-growing regions of the Eastern Mediterranean by Vatansever & Ulusoy (2005). The apparent high degree of polyphagy and preliminary molecular data (J.M. Heraty, unpublished data) suggest that the name '*C. noacki*' encompasses a cryptic species complex. However, the present study is concerned with the morphology and taxonomic status of *Cales* as a group, and does not attempt to address possible cryptic species within *C. noacki*, which will require extensive new collections of fresh sequenceable material from across South and Central America.

Thus far, *C. noacki* is the only *Cales* species that has been used as a biological control agent. However, the recent introduction of *O. citri* to New Zealand and subsequent damage caused by this pest to the New Zealand citrus industry has opened the possibility of using one or more Australian *Cales* for biological control (Pyle *et al*., 2005). Recent surveys for natural enemies of *O. citri* in New Zealand citrus have indicated that *Cales* is not yet present in the natural enemy complex (Jamieson *et al*., 2009).

Biogeography. Cales species exhibit a Gondwanan biogeographic pattern, with one centre of diversity in Australia/New Zealand, and another morphologically distinct lineage in the New World tropics. Within Chalcidoidea, this distribution is shared with Lycisini (Pteromalidae: Cleonyminae) (Gibson, 2003) and Rotoitidae, with the latter being an early branching taxon that appears to be sister to the rest of Chalcidoidea, excluding Mymaridae (J.M. Heraty, unpublished data).

Purpose and scope. Here, we examine the adult morphology of *Cales* in greater detail than previous studies, with greater emphasis on Australian species, describe *C. berryi* **sp.n.** from New Zealand and provide a key to the world species. *Cales* is included in an ongoing comprehensive phylogenetic study of Chalcidoidea, and therefore no phylogenetic analysis is conducted herein. The many unique features of the New World *C. noacki* provide some justification for resurrecting *Paranthemus* to refer to species from Australia and New Zealand.

However, there is little doubt that *Cales* is monophyletic, and the group contains relatively few species. Therefore, in the interest of simplicity and nomenclatural stability, we do not want to subdivide *Cales* into several genera.

Methods

Curation and imaging. Specimens for point mounts or scanning electron microscopy (SEM) were dried from ethanol using hexamethyldisilizane (HMDS) (Heraty & Hawks, 1998). Slide mounts were prepared either in Hoyers medium or Canada Balsam. Scanning electron micrographs were taken with a Phillips XL30-FEG (Phillips International B.V., The Netherlands). Line drawings of wings and genitalia were produced using a camera lucida mounted on a Leica DMRB compound microscope. Pencil drawings were subsequently scanned and electronically 'inked' using Adobe ILLUSTRATOR CS4 (Adobe Systems Incorporated, San Jose, CA). Pictures of slide-mounted wings and genitalia were made using AUTOMONTAGE™ (Syncroscopy U.S.A., Frederick, MD) with images captured by a JVC 3-CCD camera (JVC Kenwood Holdings Inc., McAllen, TX) mounted on a Zeiss Axioskop2 compound microscope (Carl Zeiss MicroImaging, LLC, Thornwood, NY).

Species key. The key should work equally well for both sexes. Males are known from all described species, but females are not known for *Cales spenceri*. Slide preparation of specimens will generally be required to differentiate among Australian and New Zealand species. *Cales noacki* is sufficiently distinct that identification from point- and card-mounted specimens is possible.

Species reviews. A synopsis of each species is provided, including a list of synonymy, remarks used for distinguishing between the four species and material examined. For *C. spenceri*, *C. orchamoplati* and the newly described species, most, if not all, of the known specimens have been examined. Known geographic distributions can be inferred from the material examined lists for these specimens, but geographic distributions for *C. spenceri* and *C. orchamoplati* are based on very few specimens, and should be interpreted cautiously. Owing to its status as a biological control agent, it was not practical to examine all known specimens of *C. noacki*. However, 104 specimens were examined, including representatives from the Caribbean, North America, North Africa and Europe.

Species description. Quantitative data were taken from slide-mounted specimens in the type series. Measurements were only recorded if the structure was reasonably flat and mostly visible within a single focal plane. Most measurements were made of the maximum length and/or width of a structure. Measurements requiring additional explanation are as follows: forewing length, distance from the distal end of humeral plate to apex of wing disc; forewing width, maximum distance across wing disc perpendicular to long axis of wing; hindwing length, distance from proximal end of humeral plate to apex of wing disc; hindwing width, maximum distance from base of hamulus to the posterior margin of wing. For an explanation of how the multiporous plate sensillum length was measured, see the inset in Fig. 4H, and for an explanation of how the ovipositor length was measured, see Fig. 8E.

Morphology and terminology. Morphological terminology is not yet standardized in the chalcidoid literature. Therefore, terms are defined and explained as they are used in the text where they may be ambiguous. Terms generally follow Gibson (1997) and Kim (2003) for general morphology, Heraty *et al*. (1997) for structures of the mesofurca and Krogmann & Vilhelmsen (2006) for some structures of the mes- and metepisternum. The present study is restricted to adult morphology. The eggs, larval instars and pupal form of *C. noacki* were described by Laudonia & Viggiani (1986).

Museums. The following institutions served as sources of material and type depositories for specimens examined for this study: AMNZ, Auckland Institute and Museum, Auckland, New Zealand; ANIC, Australian National Insect Collection, Commonwealth Scientific and Research Organization, Canberra, ACT, Australia; BMNH, The Natural History Museum, London, U.K.; CNC, Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture Canada, Ottawa, Ontario, Canada; DEZA, Dipartimento di Entomologia e Zoologia Agraria dell'Università, Portici, Italy; NZAC, Landcare Research, New Zealand Arthropod Collection, Auckland, New Zealand; QM, Queensland Museum, Brisbane, Queensland, Australia; UCRC: University of California, Riverside, Entomology Research Museum, Riverside, CA, U.S.A.; USNM: National Museum of Natural History, Washington, D.C., U.S.A.

Genus *Cales*

Cales Howard, 1907: 82–83. Type species: *Cales noacki*, by monotypy and original designation. Deposition: USNM.

Diaspidophilus Brèthes, 1914: 15–16. Type species: *Diaspidophilus pallidus*, by monotypy and original designation. Deposition: unknown. Synonymy by Gahan in Mercet, 1929: 114.

Paranthemus Girault, 1915: 165. Type species: *Paranthemus spenceri*, by monotypy and original designation. Deposition: QM. Synonymy by Hayat (1983).

Remarks. Like most chalcidoid groups, *Cales* is typically defined by a unique combination of characters that individually appear to be homoplastic within Chalcidoidea, rather than by one or more uniquely derived characters. Previous authors have referred to the sparse setation of the forewing and linear tracks of setae, even though these are not features of the Australian species, which have an almost uniform distribution of setae. Viggiani & Battaglia (1984) illustrated the

simplified male genitalia of *C. noacki*, noting the absence of a phallobase and presence of bacilliform apodemes extending into the aedeagus in addition to the aedeagal apodemes. However, the apparent lack of phallobase appears to be in error, as a characteristically expanded phallobase is present in all species examined for this study.

Morphological description

Body. Small, 0.40–0.82 mm; weakly sclerotized.

Colour. Yellowish orange or pale brown. Some specimens of *C. noacki* almost white, with pale yellow or brown markings on mesoscutellum and dorsal metasoma.

Head capsule. Face with straight transfacial sulcus (tfs) just in front of anterior ocellus (Fig. 1G). Scrobal depression shallow and short; scrobal sulcus (scs) complete and extending dorsally to delineate tfs and upper ocellar sulcus (uos) (Figs 1A, 6A). Malar sulcus (msl) present but not reaching ventral margin of eye (Figs 1A, 6A). Margins of clypeus difficult to distinguish from rest of face, but lateral limits indicated by pair of anterior tentorial pits (atp) and upper margin indicated by an arched epistomal sulcus (Figs 1A, H, 6A). Head posteriorly with transoccipital sulcus (tos) and posterior vertical occipital sulcus (pvs) extending from occipital foramen to tos (Fig. 1B); postgena inflected medially as postgenal lobe (pgl) below occipital foramen (Fig. 1B); occipital foramen separated from the mouth cavity by hypostomal bridge (hsb) (Fig. 1B, D). Posterior tentorial pit (ptp) visible on the hypostomal bridge medial to postgenal lobe (Fig. 1G: inset).

Antenna. Radicle (rad) approximately two times longer than wide in Australian species (Fig. 6B, C) and approximately four times longer than wide in *C. noacki* (Figs 4F, 5A). Scape (scp) laterally flattened and subapically expanded; pedicel (pdl) longer than wide and tapering basally (Figs 4E–G, 5A, B, D, E, F, 6B, C). Flagellum (f_{1-7}) of Australian species and female *C. noacki* four-segmented; f_1 and f_2 wider than long, and fused on the medial internal surface; f_3 longer than combined lengths of f_1 and f_2; f_3 with basiconic peg sensilla (bps; Fig. 4G); clava unsegmented and tapering apically (Figs 4E–H, 5D–F, 6B, C). Flagellum of male *C. noacki* three-segmented; f1 short and with dorsal flange (Fig. 5B); f_{2-3} four times longer than wide and tapering apically; clava unsegmented and tapering apically (Fig. 5A–C). Multiporous plate sensilla (mps) of both sexes and all species unfused along their lengths (Figs 4H, 5A–F), with male mps raised into plumose whorls along flagellum (Figs 4H, 5C, F). Clava with coeloconic sensillum (ccs) basally just proximal to base of mps (Fig. 5C). Female clava of all species with uniporous sensilla trichodea (ust) and styloconic sensilla (ss) (Fig. 4H).

Mouthparts. Labrum (lbr) projecting forward, forming a horizontal shelf, and with two short marginal setae (Fig. 1E). Mandible (man) terminating in serrate oblique tooth, ventrally with socketed tooth (mnt) (Fig. 1E, F); posterolaterally with sharp mandibular process (mnp) overlying genal margin (Fig. 1F); and with three stout setae arising from basal anterior surface (Figs 1E, F, H, 6A). Maxilla with three short stout setae (mxs; Fig. 1F). Maxillary palp (mp) one-segmented, terminating in two stout setae (Fig. 1D, E, H); labial palp (lp), reduced to single seta-like process (Fig. 1D); glossa (gl) terminating in fringe of flattened seta-like structures (Fig. 1E); other visible components of labiomaxillary complex include cardo (crd), stipes (stp), mentum (mtm) and prementum (pmn) (Fig. 1D).

Prothorax. Pronotum (no_1) short, membranous medially (not apparent on SEMs), visible dorsally as thin band closely applied to mesoscutum (Figs 2A, 6D). Propleuron (pl_1) visible ventrally as two oblique rectangular plates divided medially (Fig. 2C). Prosternum (st_1) with tuberculate intercoxal membrane pad (icmp) posterior to procoxal fossae; icmp divided into anterior and posterior bands by membranous fold (Figs 2C, D, 6E).

Mesothorax. Midlobe of the mesoscutum (mlm) of Australian and New Zealand species with pair of anterior mesoscutal setae (ams) and posterior mesoscutal setae (pms) (Figs 6D, 9A–C); mesoscutellum (sct) of these species with pair of anterior scutellar setae (ass) and posterior scutellar setae (pss) (Figs 6D, 9A–C). Mesonotal setation of *C. noacki* variable, but typically with single pair of setae on mlm, pair of minute setae medial to mesoscutellar campaniform sensilla (cs) (Fig. 2A, B) and prominent pair of pss on mesoscutellum (Figs 2A, 9D). Notaulus prominent, but not reaching transscutal articulation, and forming relatively wide separation between mlm and llm along anterior four-fifths of their lengths (Figs 3A, B, 6D). Axilla (ax) advanced; with one small seta; fused with mesoscutellum posteriorly, and not distinguishable from lateral lobe of mesoscutum (llm) by transscutal articulation (tsa) (hypothesized position of tsa represented by dotted line in Fig. 2A). Prospinasternal apodeme (psa; Fig. 3F) visible externally as a prospinasternal pit (psp) on the anterior ventral midline of the mesepisternum (es_2) (Figs 2C, D, 6E). Anterior thoracic spiracle (ats) visible within small notch in pronotal cuticle, just anterior of llm when viewed laterally (Figs 3B, E). Tegula (tgl) rounded subtriangular lobe just ventral to llm (Figs 3B–D, 6F). Prepectus (pre) mostly concealed by pronotum on intact specimens, but partially visible as small posterodorsally extending sclerite (Fig. 3B); visible laterally on dissected specimens as elongated subtriangular lobe (Figs 3D, 6G). Mesepisternum divided into upper mesepisternum (ues_2) and lower mesepisternum (les_2) by line of differentiated sculpture (Fig. 3C). Pleural sulcus (pls) extending from upper mesepimeron (uep_2), separating mesepisternum from lower mesepimeron (lep_2) (Figs 2C, 3C, 6E). Mesotrochantinal plate inflected internally (Fig. 2D). Lateral furcal arms (lf) of mesofurca anteriorly directed (Fig. 3F). Mesofurcal pit (f_2p; Figs 2C, D, 6E) present on mesepisternum anterior to mesotrochantinal plate, and separated from plate by about width of pit (Fig. 2D).

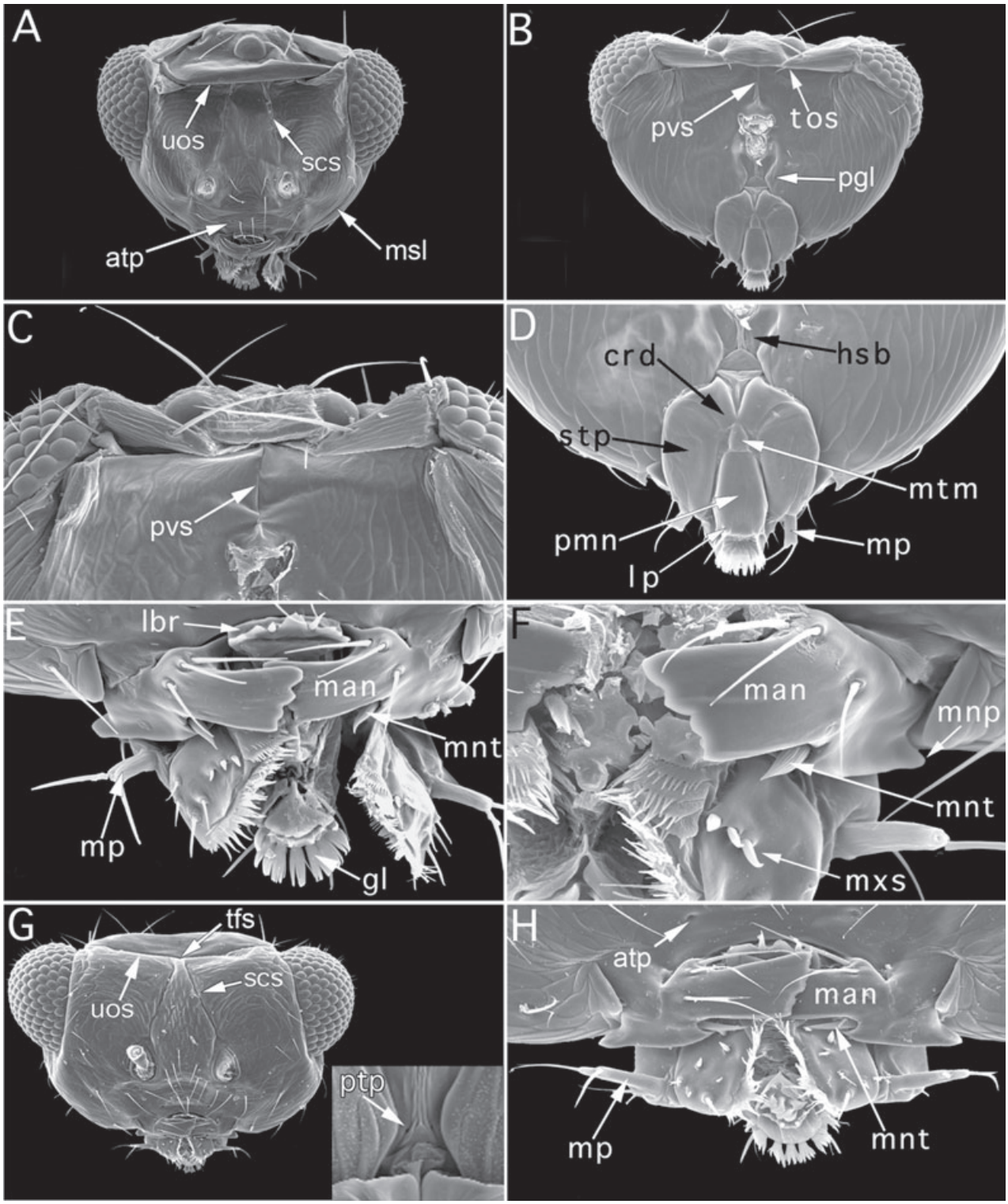

Fig. 1. A–F, *Cales noacki*. A, ♂, anterior head; B, male, posterior head; C, ♂, dorsal posterior head; D, ♂, posterior mouthparts; E, ♂, anterior mouthparts; F, ♀, mandible and maxilla detail. G–H, *Cales spenceri*, ♂. G, anterior head (inset: posterior tentorial pit); H, anterior mouthparts.

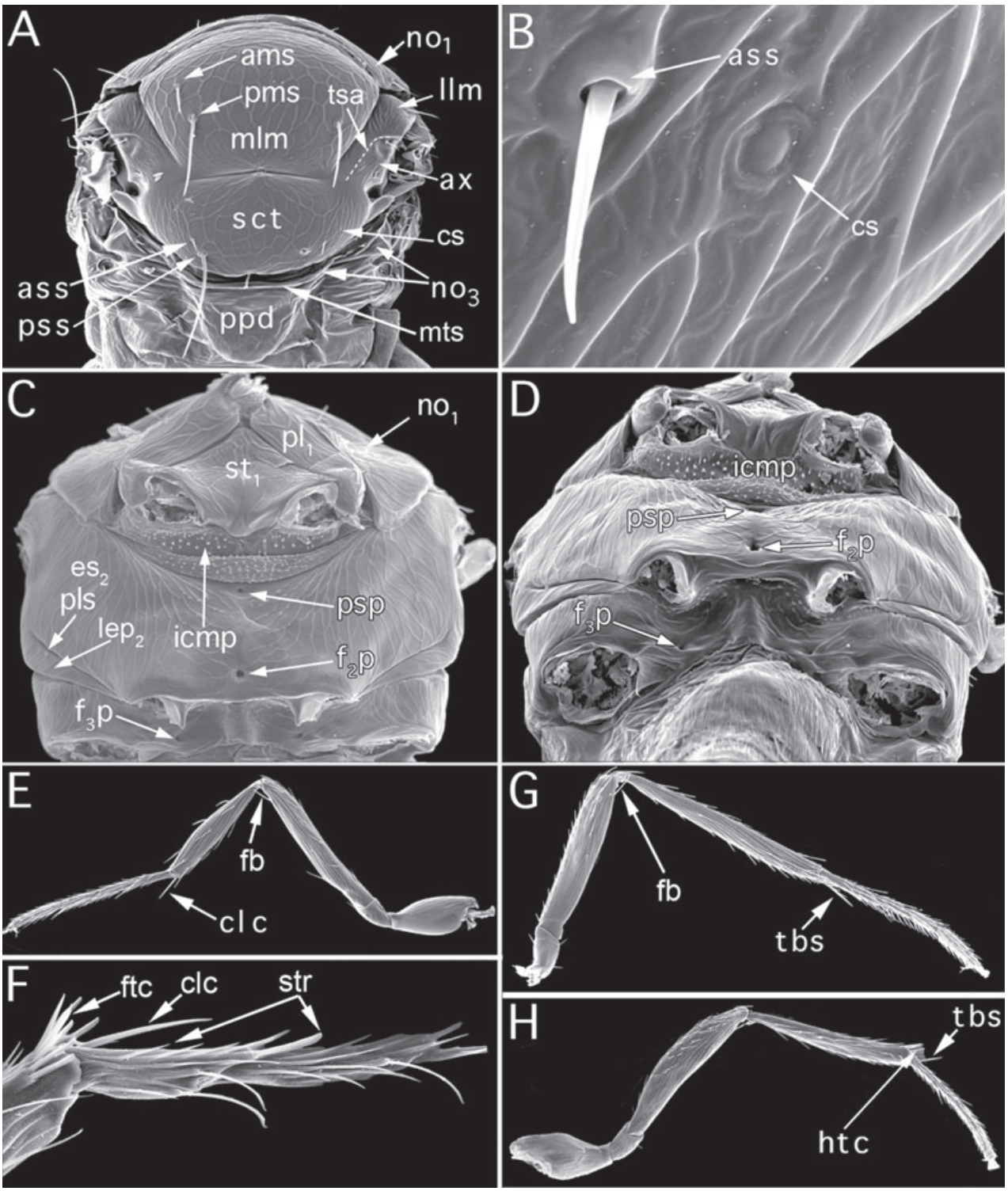

Fig. 2. *Cales noacki*. A, ♂, dorsal mesosoma; B, ♀, mesoscutellum detail; C–D, ♀, ventral mesosoma; E, ♂, foreleg; F, ♀, foretibia and basitarsal detail; G, ♀, midleg; H, ♀, hindleg.

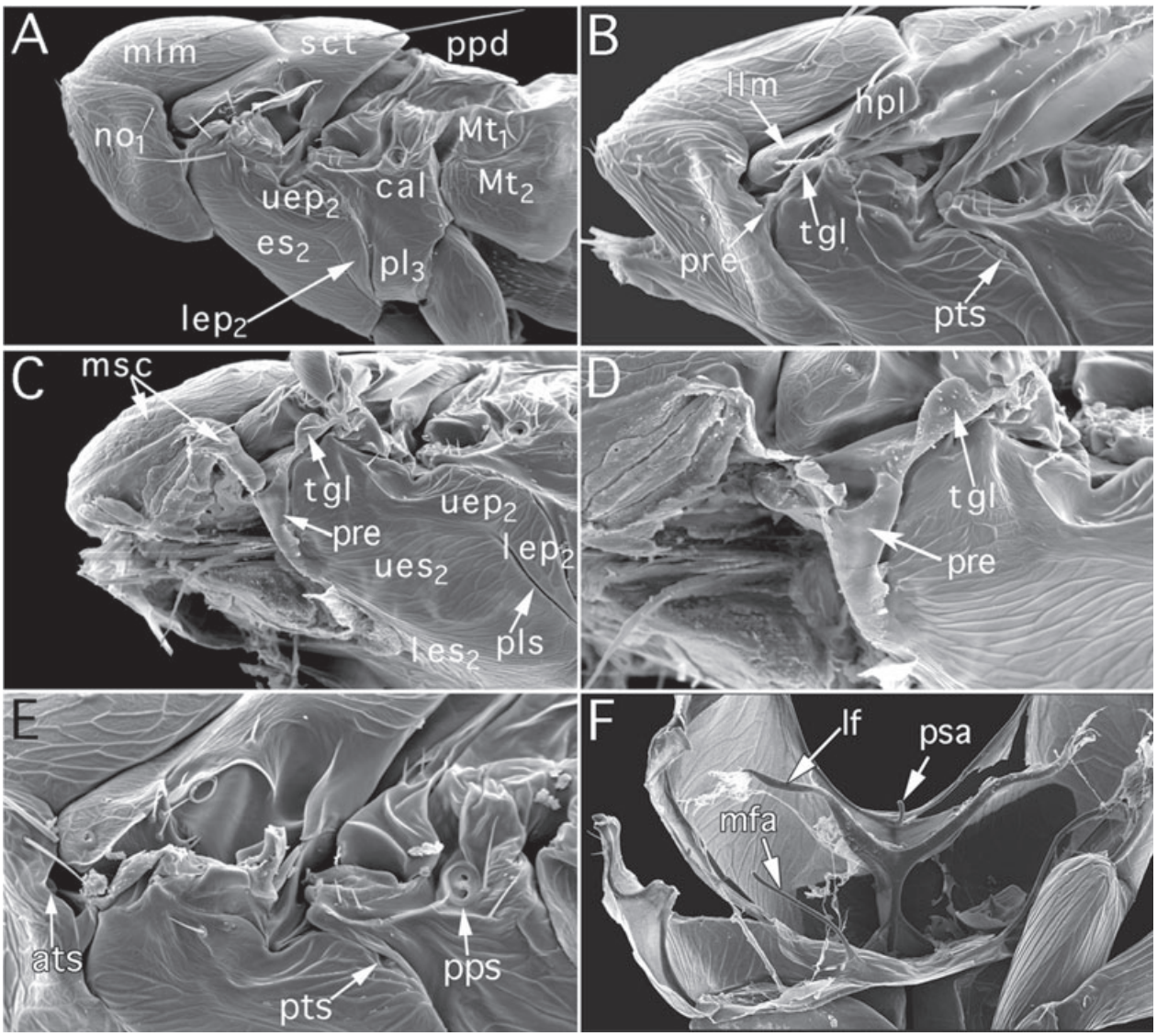

Fig. 3. A–E, *Cales noacki*. A, ♂, lateral mesosoma; B, ♂, lateral mesosoma and wing articulation; C, ♂, lateral mesosoma, pronotum removed; D, ♂, detail of lateral mesosoma, pronotum removed; E, ♀, lateral mesosoma, spiracles. F, ♀, mesofurca.

Metathorax. Metanotum (no_3) with metascutellum (mts) very short, visible dorsally as thin band between mesoscutellum and propodeum (ppd) (Figs 2A, 6D). Posterior thoracic spiracle (pts) visible on dorsal margin of upper mesepimeron (Figs 3B, E, 6F). Metapleuron (pl_3) rectangular in lateral view (Fig. 3A). Metepisternum extending anteriorly between mesocoxal fossae (Fig. 2D). Metafurcal arms (mfa; Fig. 3F) visible externally as metafurcal pits (f_3p) that are widely separated, each pit approximately aligned with medial margin of mesocoxal fossa (Figs 2C, D, 6E).

Propodeum. Propodeum (ppd) longer than metanotum and broadly joined to metasoma (Figs 2A, 6D). Propodeal spiracle (pps) surrounded by two or three stout setae; callus (cal) with single stout seta (Figs 3E, 6D).

Legs. Prominent femoral bristle (fb) present on posterior surface of distal ends of femora (Fig. 2E, G). Calcar (clc) slightly curved and unbifurcated (Fig. 2E, F). Single tibial spur (tbs) present on both mesotibia (Fig. 2G) and metatibia (Fig. 2H). Tibial combs present on foretibia (ftc; Fig. 2F) and hind tibia (htc; Fig. 2H). All tarsi four-segmented. Basal tarsomere of foretarsus with ventral row of setae terminating in larger spatulate seta, together comprising strigil (str; Fig. 2F).

Forewing. Single prominent seta present on humeral plate (hpl; Figs 7A, 8A, 10A–D). Submarginal vein with prominent companiform sensilla (cs; Fig. 7E); single submarginal vein sensillum (sms; Fig. 7E) and single prominent seta on dorsal surface present (Figs 7A, C, 8A, B, 10A–D). Basal cell

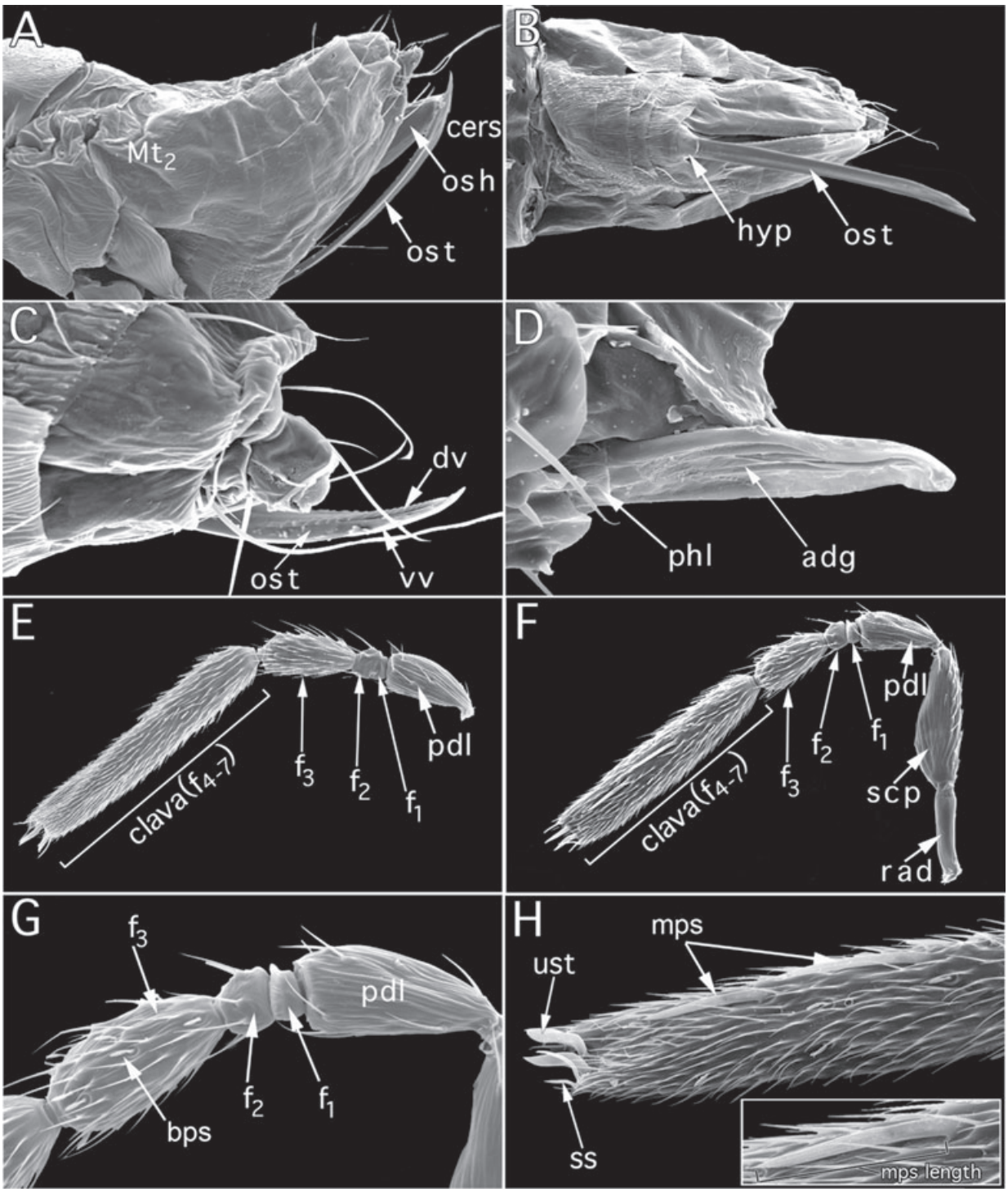

Fig. 4. *Cales noacki*. A, ♀, lateral metasoma; B, ♀, ventral metasoma; C, ♀, external genitalia; D, ♂, external genitalia; E, ♀, antenna, medial view; F, ♀, antenna, lateral view; G, ♀, pedicel and f_1–f_3 detail, lateral view; H, ♀, distal clava detail (inset: multiporous plate sensilla detail).

(bc) thickened, and with one or two rows of basal cell campaniform sensilla (bcs) posterior to submarginal vein on dorsal surface (Fig. 7A, E). Raised sensory hairs (rsh) arising from circular tubercles beneath parastigma (pst) (Fig. 7E). Marginal vein (mv) of *C. noacki* with three prominent setae (Figs 7A, 10D). Variable number of prominent setae on mv of species from Australia and New Zealand, ranging from five to seven. Socketed sensory hairs (sh) present posterior to

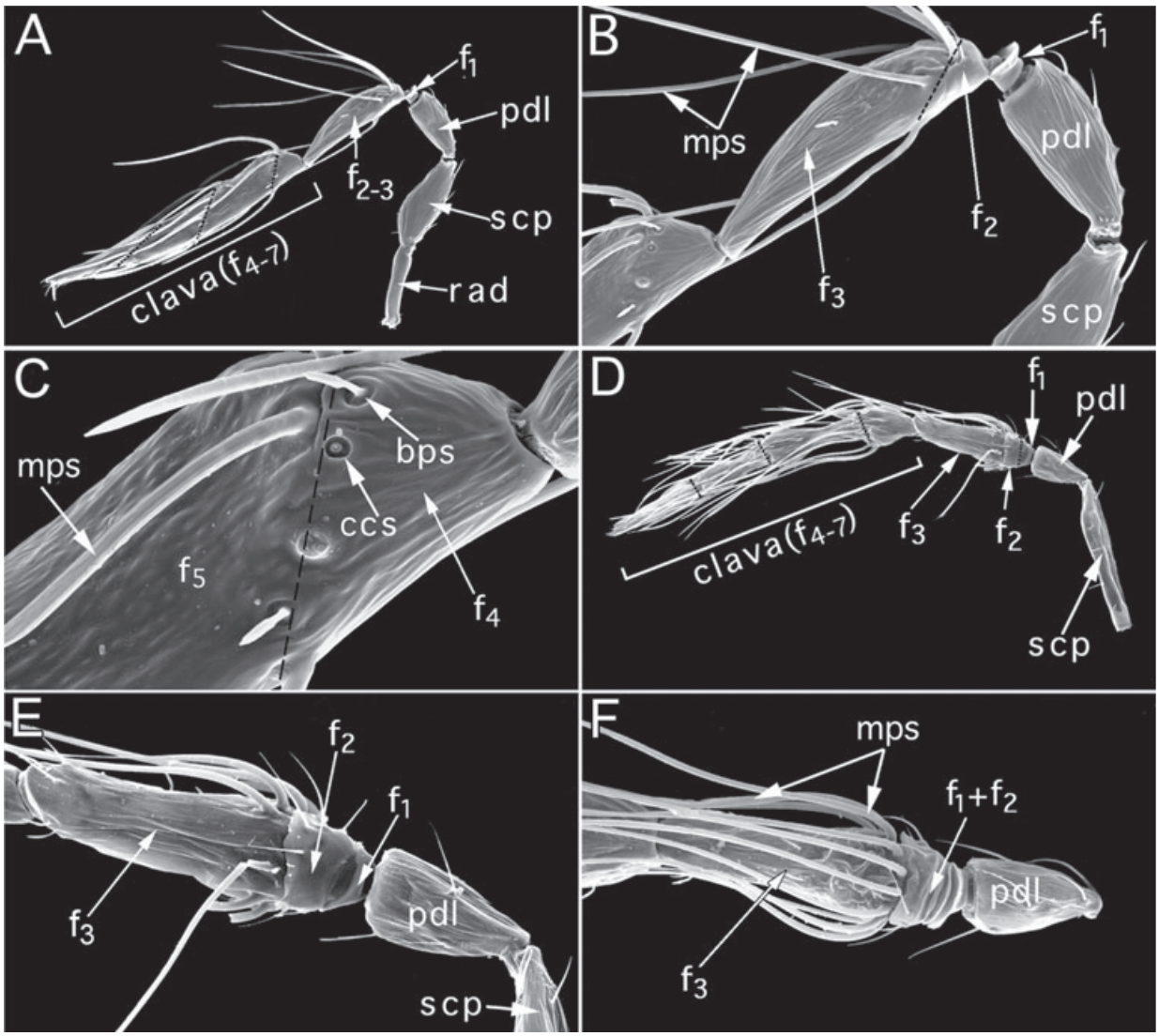

Fig. 5. A–C, *Cales noacki*. A, ♂, antenna; B, ♂, pedical and f_1–f_3 detail; C, ♂, proximate claval segment. D–F, *Cales spenceri.* D, ♂, antenna; E, ♂, medial pedicel and f_1–f_3 detail; F, ♂, lateral pedical and f_1–f_3 detail. Hypotheses of segment fusions are indicated by dashed lines.

the stigma (stg) (Fig. 7F). Four stigmal vein sensilla (svs) on uncus (unc) (Fig. 7F). Wing disc of *C. noacki* with sparse setation; most setae arranged in three well-defined rows (Figs 7A, 10D). Wing discs of Australian and New Zealand species more evenly setose, with some specimens showing a tendency toward setal tracks (Figs 7C, 10A, B). Marginal setae (ms) relatively long, 0.5–0.8× width of the forewing (Figs 7A, C, 8A, 10A–D).

Hindwing. Marginal vein strongly curved posteriorly (Figs 7B, D, 8C).

Metasoma. Metasoma broadly joined to mesosoma; mesophragma extending into metasoma. First metasomal tergite (Mt_1) dorsal to second metasomal tergite (Mt_2) when viewed laterally; Mt_1 and Mt_2 clearly delineated from each other (Fig. 3A). Cercus not advanced and bears single seta (cers; Fig. 4A; note that both right and left setae are visible, one partially obscured by the other, giving the appearance of two setae arising from a single cercus). Hypopygium (hyp) small, extending to about midpoint of metasoma (Figs 4B, 6H).

Female genitalia. Externally visible structures of female genitalia include ovipositor sheath (osh), dorsal valvifer (dv) and ventral valvifer (vv) (Fig. 4A–C). Ovipositor stylets (ost) often upturned and sabre-like when exerted (Fig. 4A, C).

Male genitalia. Genitalia of *C. spenceri* not visible on specimens examined for this study. Genitalia of *C. noacki* simplified, consisting of aedeagus (adg) and reduced phallobase (phl) (Figs 4D, 8D). Genitalia of *C. berryi* **sp.n.** and *C. orchamoplati* with laterally curving hook-like digitus (dig) on volsellus (vls)

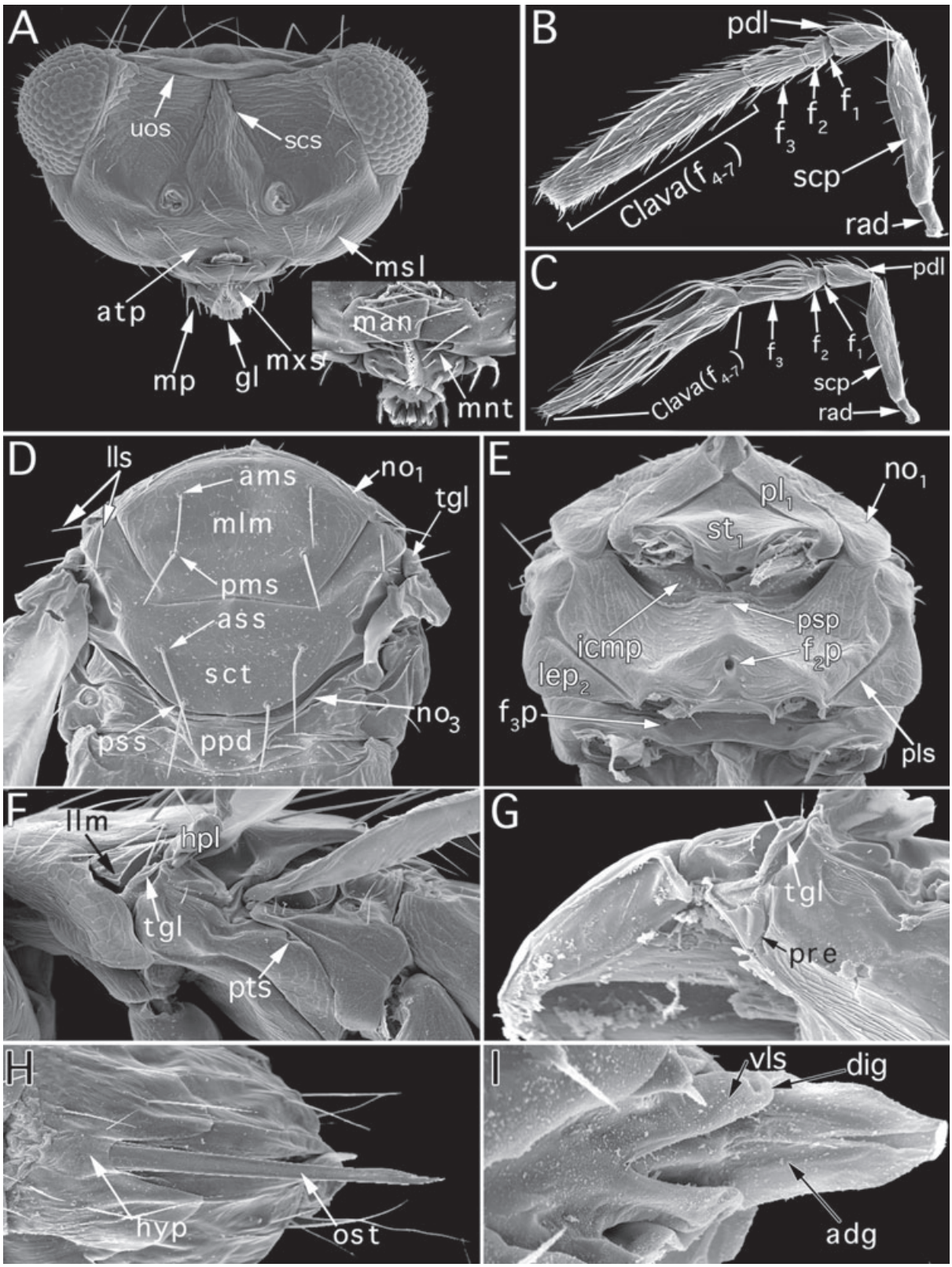

Fig. 6. *Cales berryi.* A, female, anterior head and mouthparts (inset: mouthpart detail); B, female, antenna, lateral view; C, ♂, antenna, lateral view; D, ♀, dorsal mesosoma; E, ♀, ventral mesosoma; F, ♀, lateral mesosoma; G, ♀, lateral mesosoma wing articulation; H, ♀, external genitalia; I, ♂, external genitalia.

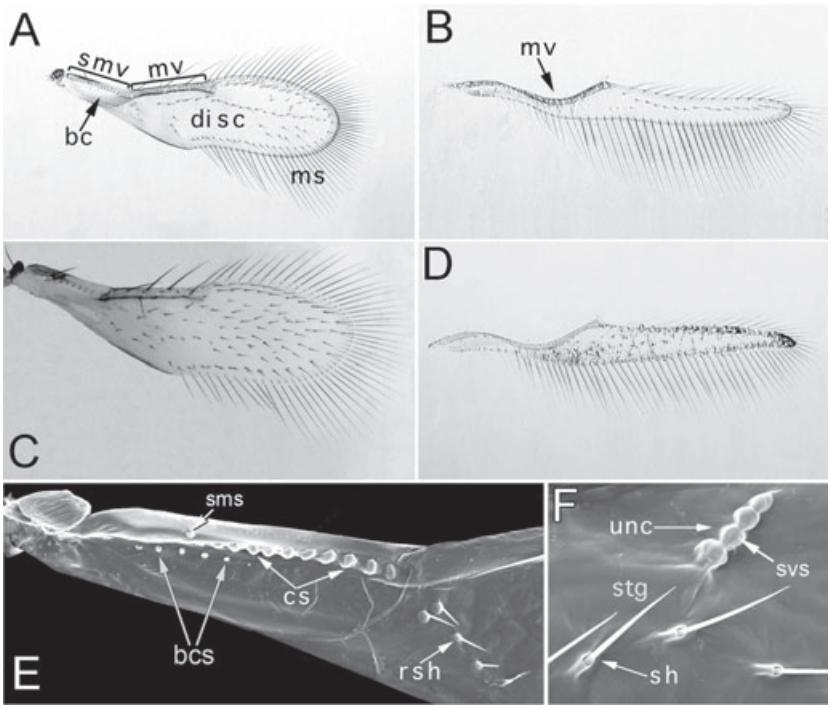

Fig. 7. A–B, *Cales noacki*. A, ♀, forewing; B, ♀, hindwing. C–D, *Cales spenceri*. C, ♂, forewing; D, ♂, hindwing. E–F, *Cales noacki*. E, ♀, forewing, detail of basal cell and marginal vein; F, ♀, forewing, detail of stigmal vein.

(Figs 6I, 8F, G). All species with expanded phallobase (subequal length and width) and paired sclerotized aedeagal rods (adr), in addition to aedeagal apodemes (aap) (Fig. 8D, F, G). Parameres (par) of all species with single stout apical seta (Fig. 8D, F, G).

Discussion

The habitus, body colour, small size and life history characteristics give a 'first impression' that *Cales* may be taxonomically associated with some members of the Aphelinidae, especially whitefly parasitioids in the genera *Encarsia* and *Eretmocerus*. Here, we present a comparative discussion to highlight the more specific morphological evidence for and against these hypotheses, as well as the evidence suggesting affinities between *Cales* and other taxa.

Antenna. The *Cales* flagellum is at most four-segmented, a condition shared with some Aphelininae and Trichogrammatidae, although the homology of segment fusion appears to be different from that found in either of these taxa, especially regarding fusion of the claval segments and overall number of potential flagellomeres. In all *Cales*, with the exception of *C. noacki* males, f_1 and f_2 are distinct laterally (Figs 4F, G, 5E, 6B, C), fused medially (Figs 4E, 5F), and f_2 is distinct both laterally and medially from f3 (Figs 4E–G, 5D–F). In *C. noacki* males, f_1 is distinct both laterally and medially from the rest of the flagellum, and f_2 is fused with f_3 (Fig. 5B, hypothesized location of fusion indicated by dashed line). This hypothesis is based on the basal location of mps in *C. spenceri* (Fig. 5F) compared with the subbasal location of the mps in male *C. noacki* (Fig. 5B). We propose that the clava of both sexes of all species is formed from a fusion of flagellomeres 4–7. The presence of four flagellomeres in the clava is based on the presence of four distinct whorls of mps in all male *Cales* (Fig. 5A, D), and the associated constrictions of the clava in male *C. spenceri* (Fig. 5D). Also, the presence of a coeloconic sensillum at the base of the clava (ccs; Fig. 5C) appears to be homologous with a similar sensillum on f_4 in Trichogrammatidae (e.g. *Ittys* and *Ceratogramma*) and other Chalcidoidea (J. George, personal communication). The segmentation of the female clava is inferred from the males, as the female has fewer rows of mps and the coeloconic sensillum is absent. The mps of most Chalcidoidea are fused along their lengths (Barlin *et al*., 1981), whereas the *Cales* mps is unfused. This condition is shared with Trichogrammatidae and *Oenrobia* (Aphelinidae: Coccophaginae).

Mouthparts. The forward-projecting labrum is similar to Rotoitidae and some Aphelinidae. The socketed ventral tooth is shared with Coccophaginae (including *Coccobius*), eriaphytine aphelinids and some Encyrtidae (Heraty & Schauff, 1998). The three short stout setae on the maxilla are apparently unique to *Cales*.

Prothorax. The tuberculate intercoxal membranous pad is also present in Aphelininae (Rosen & DeBach, 1979; Kim, 2003). The form of the icmp is variable across aphelinine taxa. In *Cales* and most Aphelininae the pad forms a continuous band posterior to the coxal fossae. A transverse membranous fold in the icmp appears to be unique to *Cales*. In *Aphytis* (Aphelinidae: Aphelininae), it is divided into left and right

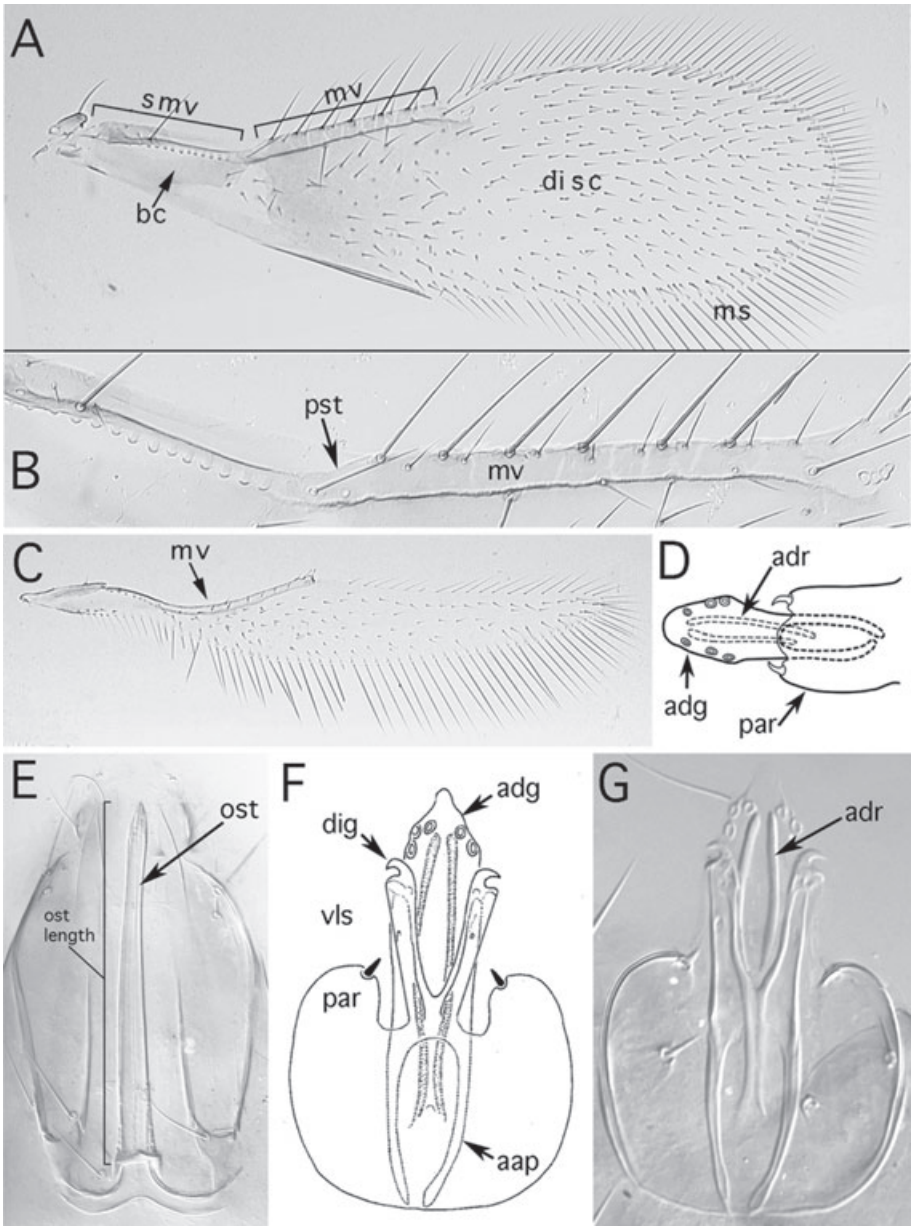

Fig. 8. A–C, *Cales berryi* **sp.n.** A, ♀, forewing; B, ♀, forewing, detail of submarginal vein and marginal vein; C, ♀, hindwing. D, *Cales noacki*. ♂, genitalia. E–G, *Cales berryi* **sp.n.** E, ♀, genitalia; F–G, ♂, genitalia.

halves, forming a separate pad posterior to each coxal fossa (Rosen & DeBach, 1979: figs 196–200).

Mesothorax. The pattern of dorsal setation of the *Cales* mesothorax is shared with *Eretmocerus.* Some clarification regarding the further reduction in mesonotal setation of *C. noacki* is necessary. Typically, this species has a single pair of posterior mesoscutal setae on the midlobe of the mesoscutum. However, smaller anterior mesoscutal setae may be present, and we observed one *C. noacki* specimen with only a single anterior mesoscutal seta on the midlobe (Fig. 2A). Mesoscutellar setation also appears to be variable for this species. Viggiani & Carver (1988) observed only a single pair of long setae on the mesoscutellum. However, Evans & Serra (2002) found a second pair of small anterior setae medial to the scutellar campaniform sensilla on specimens from Haiti. This pair of minute setae is also present on specimens from California and Italy examined for this study (Fig. 2A, B). Individuals may have a complete set of anterior scutal setae on both the midlobe of the mesoscutum and mesoscutellum, or they may lack anterior setae altogether. When anterior setae are present, they are much shorter than the posterior setae.

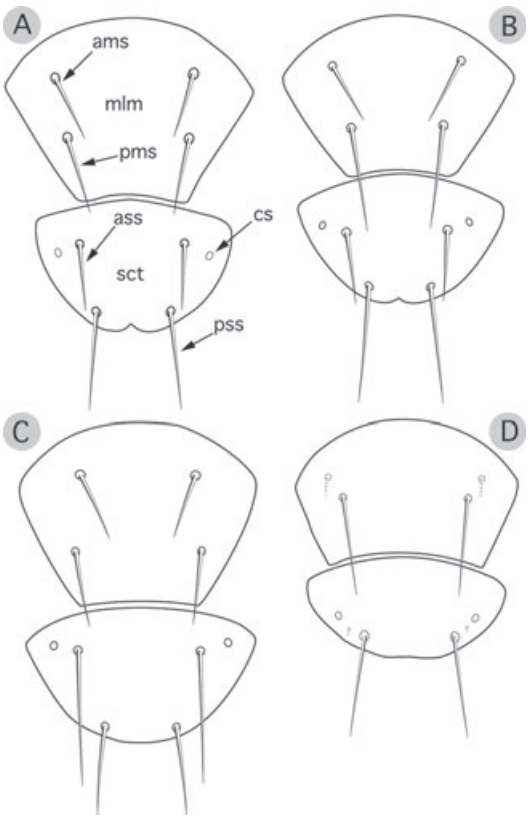

Fig. 9. A, *Cales orchamoplati*, ♂, mesoscutum. B, *Cales spenceri*, ♂, mesoscutum. C, *Cales berryi* **sp.n.**, ♂, mesoscutum. D, *Cales noacki*, ♂, mesoscutum. Minute setae on *C. noacki* mesoscutum (indicated by dashed lines) are not always present. Figures are not drawn to scale.

A pleural sulcus extends from the upper mesepimeron to the lateral edge of the mesocoxal fossa. This condition is shared with Coccophaginae and Trichogrammatidae. A pit corresponding to the prospinasternal apodeme is visible on the mesepisternum of *Cales*, a condition shared by *Cirrospilus* (Eulophidae) (Krogmann & Vilhelmsen, 2006).

The *Cales* mesofurca (Fig. 3F) was included by Heraty *et al*. (1997) in a comparative analysis across Chalcidoidea. Structure and position of the lateral furcal arms, posterior furcal-laterophragmal muscle, furcal-pleural arm muscle and metathoracic interfurcal muscle were considered most similar to *Eretmocerus*, with some similarities to Trichogrammatidae, Azotinae and Signiphoridae.

Metathorax. Gibson (1989) suggested a sister-group relationship between Aphelinidae s.l. and Signiphoridae, based on the structure of the mesocoxal articulation with the metepisternum and mesotrochantinal plate. Specifically, the mesotrochantinal plate is inflected internally with the metepisternum extending anteriorly between the mesocoxal fossae and abutting the dorsal edge mesotrochantinal plate (Gibson, 1989: character state 3). In *Cales*, the mesotrochantinal plate is inflected internally, and the metepisternum extends anteriorly between the mesocoxal fossae. However, differentiating between membranous and sclerotized tissue is very difficult in small, weakly sclerotized chalcidoids such as *Cales*, either on SEMs or slide mounts. Either the metepisternum is separated from the mesotrochantinal plate by membranous tissue (Gibson, 1989: character state 2) or the metepisternum meets the dorsal edge of the mesotrochantinal plate (G. Gibson, personal communication: character state 3a). The latter state would suggest an affinity between *Cales* and the Aphelinidae + Signiphoridae clade hypothesized by Gibson (1989), but we could not discern either state with confidence.

The posterior thoracic spiracle is visible externally in *Cales*, a character that is shared with *Chiloe* (Gibson & Huber, 2000), *Eretmocerus* and other taxa within Chalcidoidea. However, a thorough survey of this character across Chalcidoidea is needed to determine its phylogenetic implications.

Two widely separated metafurcal pits are visible on the metepisternum of *Cales*. Krogmann & Vilhelmsen (2006) found paired metafurcal pits in some Pteromalidae, Eurytomidae, Signiphoridae, Mymaridae and Agaonidae. Eulophidae and Aphelinidae possess a single medial metafurcal pit, and no metafurcal pits were observed on Trichogrammatidae.

Legs. All *Cales* have a prominent bristle on the posterior surface of the distal ends of the femora. This bristle is also present in all Aphelinidae s.l., most Eulophidae, some Pteromalidae and some Trichogrammatidae. Polaszek (1991) suggested that *Cales* might be closely related to Eulophidae based on the presence of an unbifurcated straight calcar, lack of basitarsal comb (=strigil) on the foretarsus and a reduced number of tarsal segments (from five, the presumed plesiomorphic state for Chalcidoidea, to four). All of these features are reductions that have evolved multiple times and at multiple taxonomic levels within Chalcidoidea. The structure of the calcar is similar in Trichogrammatidae, most Eulophidae, some Aphelinidae (*Euryischia* and *Eretmocerus*) and some Eucharitidae (*Pseudochalcura*) (Basibuyuk & Quicke, 1995). A reduction from five to four tarsomeres occurs in some *Encarsia*, and in all *Eretmocerus*. *Pteroptrix* spp. (Coccophaginae) also exhibit a reduction from five to four tarsomeres in all but a single Neotropical species, which has undergone a further reduction to three tarsal segments (Kim & Triapitsyn, 2003). Trichogrammatidae lack a strigil, and both Euchartidae and Eulophidae are polymorphic for this character (Basibuyuk & Quicke, 1995; Heraty, 2002). However, a row of setae terminating in larger spatulate setae present on the *Cales* foretarsus may constitute a strigil (R. Burks, personal communication).

Forewing. The second row of campaniform sensilla on the dorsal surface of the basal cell, which are posterior to the same sensilla along the submarginal vein, appear to be unique to *Cales*. Raised sensory hairs are present on the forewings of some Trichogrammatidae, although homology with the structures on *Cales* wings is uncertain. The marginal setae are relatively long, similar to many *Encarsia* species. A striking feature of the *C. noacki* forewing is the arrangement of

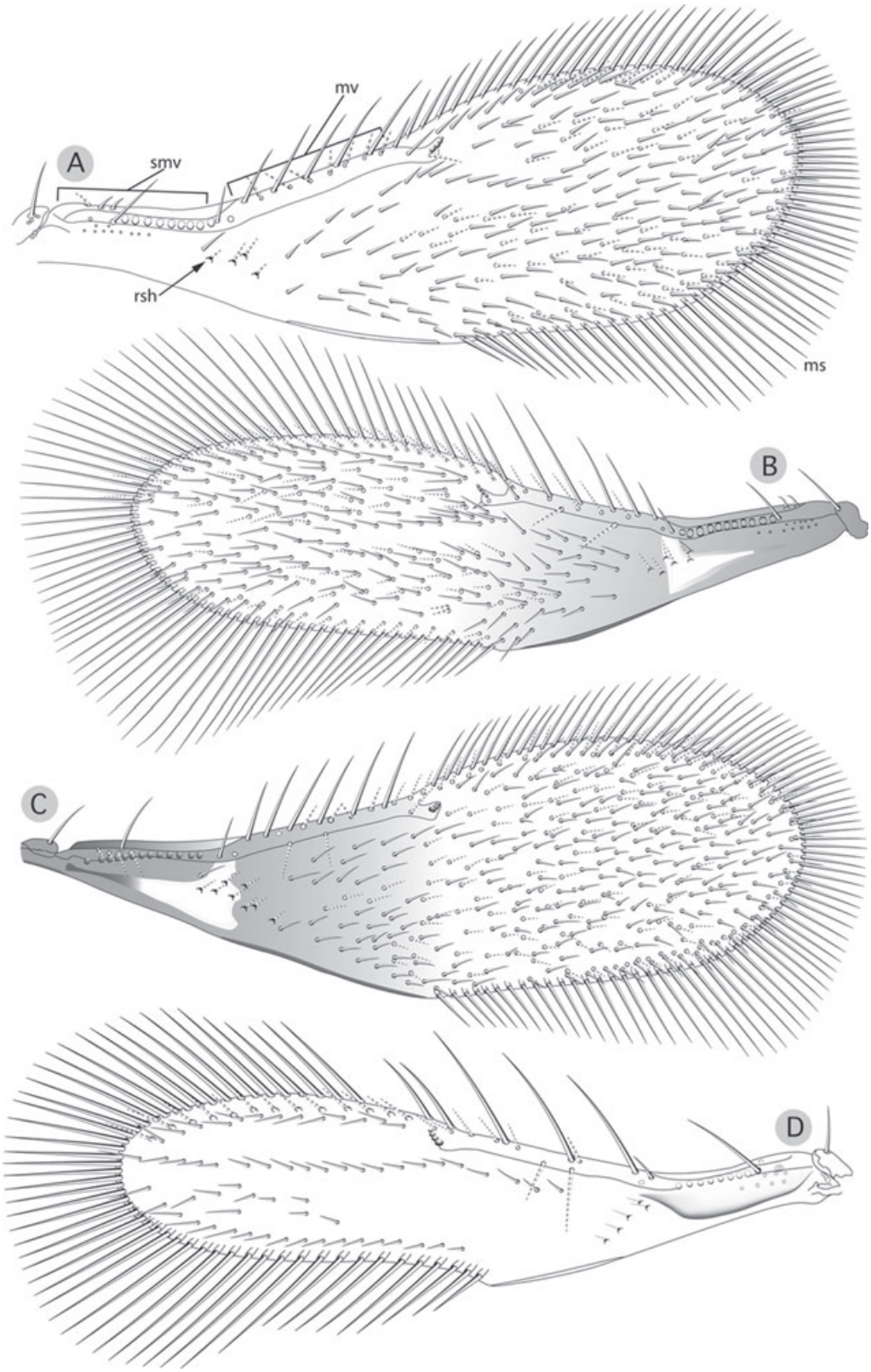

Fig. 10. A, *Cales orchamoplati*, ♂, forewing. B, *Cales spenceri*, ♂, forewing. C, *Cales berryi* **sp.n.**, ♂, forewing. D, *Cales noacki*, ♂, forewing. Dashed lines indicate setae occurring on ventral surface of wing. Figs not drawn to scale.

discal setae into distinct rows, a character typically associated with Trichogrammatidae. However, setal lines are variably present within both Trichogrammatidae and *Cales*, suggesting that the trait is homoplastic. *Ceratogramma*, an early branching genus of Trichogrammatidae (Owen *et al*., 2007), has relatively evenly setose wings, as do the Australian and New Zealand species of *Cales*. Consequently, setal tracks in *C. noacki* are likely to have been an independently derived feature, and are not evidence for a sister-group relationship with Trichogrammatidae.

Hindwing. The hindwing is similar in shape to many small Aphelinidae, except for a strongly curved marginal vein, which is similar to some Trichogrammatidae (J. George, personal communication).

Metasoma. Overall, the structure of the metasoma is typical of small, weakly sclerotized chalcidoids. The male genitalia of *C. noacki* are simplified, consisting of an aedeagus and reduced phallobase. This is contrary to Viggiani & Battaglia (1984), who report the phallobase as being completely absent. The aedeagal rods appear to be unique to *Cales*.

Key to the species of *Cales*

1. Forewing disc with setae in three distinct rows (Figs 7A, 10D). Male flagellum with three segments; radicle long, at least three times as long as wide, and subequal in length to pedicel (Figs 4F, 5A). Midlobe of mesoscutum with one pair of long prominent setae, and mesoscutellum with one pair of long prominent setae and second pair of minute setae (pss, ass; Figs 2A, 9D). Neotropics and introduced into North America, the Mediterranean and Africa ..... *C. noacki*
– Forewing disc evenly setose or at most tending toward rows, but setae not in three distinct rows (Figs 7C, 10A–C). Male flagellum with four segments; radicle short, at most two times as long as wide, and much shorter than pedicel (Fig. 6B, C). Midlobe of mesoscutum and mesoscutellum each with two pairs of long prominent setae (Fig. 9A–C). Australia or New Zealand 2

2. Forewing with longest posterior marginal seta 0.8× width of wing (Fig. 10B). Mesoscutum with posterior setae long, more than one-third length of seta extending beyond transscutal articulation when directed posteriorly (pms; Fig. 9B) Australia ..... *C. spenceri*
– Forewing with longest posterior marginal seta 0.5–0.6× width of wing (Fig. 10B, C). Mesoscutum with posterior seta short, less than one-third length of seta extending beyond transscutal articulation when directed posteriorly (Fig. 9A, C. Australia or New Zealand 3

3. Forewing with one or two rows of small campaniform sensilla on dorsal surface of basal cell, just posterior to submarginal vein (bcs; Figs 7E, 9B). Posterior margin of scutellar disc shallowly or deeply notched (Fig. 9A, B). Forewings hyaline. Australia ..... *C. orchamoplati*
– Forewing basal cell without campaniform sensilla (Figs 8A, 10C), or sensilla present only as faint vestiges in proximal area posterior to submarginal vein. Posterior margin of scutellar disc rounded or shallowly notched (Figs 6D, 9C, D). Forewing with infuscation posterior to submarginal and marginal veins (Fig. 10C). New Zealand ..... *C. berryi* **sp.n.**

Cales berryi Mottern and Heraty, sp.n.

(Figs 5C, 6E, 7C, D, F, 8C, 9C, 10C)

Diagnosis. Cales berryi **sp.n.** can be distinguished from other species in the genus by the following combination of characters. Radicle short, two times longer than wide; scape three times length of pedicel; male flagellum four-segmented. Mesoscutellum posteriorly rounded and with two pairs of prominent setae. Forewing with light infuscation on basal half, relatively uniform discal setation and with campaniform sensilla absent from dorsal surface of the basal cell in most specimens. *Cales berryi* **sp.n.** is the only species currently known from New Zealand.

Female. Body colour pale brown; vertex of head and anterior half of mesoscutum orange; posterior half of mesoscutum and mesoscutellum brown; face and legs pale, almost white. Head with fine transverse colliculate sculpture, face ventral to antennae with scattered slender setae (Fig. 6A). Malar sulcus extending half distance to eye (msl; Fig. 6A). Gena broadly rounded. Maxillary palpus one-segmented, maxilla with one stout primary seta on medial ventral edge and three secondary raised socketed setae. Antenna with radicle short, 1.5–1.9× as long as wide. Scape 4.2–5.2× as long as wide, 4.7–5.2× as long as radicle and 2.6–2.7× as long as pedicel, subapically expanded ventrally; weakly reticulate and with even scattering of semi-erect setae (Fig. 6B). Flagellum with four flagellomeres; f_1 and f_2 combined length shorter than f_3, and fused on medial surface; f_3 1.5–2.1× as long as wide, subequal in length to pedicle plus f_1 and f_2, and 0.2–0.3× as long as clava; f3 and clava with scattered mps and bps, claval setae 0.1–0.2× as long as clava; clava unsegmented (comprised of fused f_{4-7}), 4.4–5.2× as long as wide, obliquely truncate apically; mps 0.3× length of clava. Lateral lobe of mesoscutum with two setae (lls; Fig. 6D). Midlobe of mesoscutum with two pairs of setae (ams, pms; Fig. 6D) and faint reticulate sculpture. Mesoscutellum with two pairs of setae (ass, pss; Fig. 6D). Tegula narrow in lateral view, approximately five times longer than wide; subquadrate in dorsal view and with one seta (tgl; Fig. 6D, F, G). Mesepisternum weakly imbricate laterally and spiculate medially (Fig. 6E), posteriorly raised into triangular area surrounding mesofurcal pit (f_2p; Fig. 6E). Metafurcal pits close to anterior margin of metepisternum (f_3p; Fig. 6E). Foretibial calcar 0.4–0.6× length of basitarsus. Forewing with even infuscation posterior to the marginal and submarginal veins (sometimes very light and difficult to see on cleared specimens); 3.0–3.1× as long as broad; longest seta of posterior marginal fringe 0.4–0.5× width of wing; marginal vein with row of six long setae along anterior margin; discal

setation relatively uniform; stigmal vein rounded, uncus distinct, usually with four, sometimes three, campaniform sensilla (cs) (Figs 8A, 10C; see Fig. 7F for similar cs on *C. noacki* forewing). Hindwing 6.7–7.3× as long as broad, posterior marginal fringe 1.1–1.2× width of wing; discal setation uniform (Fig. 8C). Hypopygium deeply emarginate medially (hyp; Fig. 6H). Ovipositor 1.7–1.9× as long as hind basitarsus.

Male. Similar to female, except antenna with mps in transverse rows resulting from segment fusions; mps 0.5–0.6× as long as clava; clava uniformly narrowing apically, but width constricted between segment fusions (Fig. 6C). Phallobase broad and circular, parameres reduced to broad lobes with single apical stout seta (par; Fig. 8F, G), digitus elongate and stout with strong laterally directed hook (dig; Fig. 8F, G); aedeagus broadly subtriangular with between four and six prominent sensilla.

Host. Reared from *Asterochiton pittospori* Dumbleton (Aleyrodidae) on *Pittosporum eugenioides* Cunn. (Pittosporaceae).

Etymology. Named in honour of Dr Jocelyn A. Berry, who collected the type series.

Material examined. Holotype: New Zealand: ♀, slide mounted; North Island, Auckland, Mount Albert, Oakley Creek Walkway, 36°55′S, 174°47′E, 12 November 2003, J.A. Berry, ex *Asterochiton pittospori* Dumbleton on *Pittosporum eugenoides*, deposition: NZAC (UCRC_ENT 00091228). Allotype: ♂, same data as holotype (UCRC_ENT 00091219).

Additional material examined and specimen deposition may be found in Appendix S1.

***Cales noacki* Howard, 1907**
(Figs 1A–F, 2A–3E, 4A–5C, 7A, B, E, F, 8D, 9D, 10D)

Cales noacki Howard, 1907: 82–83, by monotypy and original designation. Deposition: USNM.

Diaspidophilus pallidus Brèthes, 1914: 15–16, by monotypy and original designation. Deposition: unknown. Synonymy by Gahan in Mercet, 1929: 114.

Cales pallidus Mercet, 1929: 117, new combination; synonymy with *C. noacki* by Dozier 1933: 98.

Remarks. Cales noacki is the only member of the genus known from the New World tropics, although its range has been intentionally expanded to the citrus-growing regions of North America, the Mediterranean, Africa and North Atlantic islands. It is the most distinctive species, and is easily recognized by the following combination of characters: wings hyaline, with discal setae arranged in three distinct rows in addition to scattered setae on the distal third of wing disc (Figs 7A, 10D). The radicle is about four times longer than wide compared with at most two times longer than wide in other species. The female flagellum is four-segmented and the male flagellum is three-segmented, whereas both sexes of other species have a four-segmented flagellum. Typically there is a single pair of stout setae on the midlobe of the mesoscutum and two pairs of setae on mesoscutellum, with the anterior pair of scutellar setae minute (ass; Figs 2A, B, 9D). Other *Cales* species have two prominent pairs of long setae on the midlobe of the mesoscutum and mesoscutellum.

Material examined. See Appendix S1.

***Cales orchamoplati* Viggiani and Carver, 1988**
(Figs 9A, 10A)

Cales orchamoplati Viggiani and Carver, 1988: 43–45, by original designation. Deposition: ANIC.

Remarks. Cales orchamoplati is thus far only known from Australia. It is distinguished from *C. spenceri* by its forewing setal fringe. In *C. orchamoplati*, the longest posterior marginal seta is 0.5–0.6× the width of the forewing, whereas in *C. spenceri* it is 0.8× the width of the wing. *Cales orchamoplati* is very similar to *C. berryi* **sp.n.**, but the latter species usually lacks the extra rows of campaniform sensilla in the basal cell posterior to the marginal vein of the forewing, and the wings are infuscated rather than hyaline posterior to the submarginal and marginal veins. Contrary to Viggiani & Carver (1988), the antennal scape of *C. orchamoplati* is about two times as long as the pedicel, whereas the scape of *C. spenceri* and *C.* berryi **sp.n.** is three times as long as the pedicel.

Material examined. See Appendix S1.

***Cales spenceri* (Girault, 1915)**
(Figs 1G, H, 3F, 5D–F, 7C, D, 9B, 10B)

Paranthemus spenceri Girault, 1915: 165, by monotypy and original designation. Deposition: QM. Synonymy by Hayat (1983: 78).

Cales spenceri; combination by Viggiani, 1981: 47.

Remarks. Cales spenceri is thus far only known from Australia, and only from males. It is distinguished from *C. orchamoplati* and *C. berryi* **sp.n.** by the relative length of the longest posterior seta of the forewing marginal fringe. In *C. spenceri*, the longest seta on the posterior margin of the forewing is 0.8× the width of the wing, whereas in *C. orchamoplati* and *C. berryi* **sp.n.** the ratio is 0.5–0.6×. The posterior mesoscutal setae of *C. spenceri* are relatively long, with more than one-third the length of each seta extending beyond the transscutal articulation when directed posteriorly. By contrast, the posterior mesoscutal setae of *C. orchamoplati* and *C. berryi* **sp.n.** extend about one-fourth their lengths beyond the transscutal articulation. *Cales spenceri* is often further distinguished from *C. berryi* **sp.n.** by the presence of additional rows of campaniform sensilla in the basal cell of the forewing, which are often missing in *C. berryi* **sp.n.**

Material examined. See Appendix S1.

Conclusion

Cales possesses a perplexing mix of morphological characters, evidenced by its unstable taxonomic history and its current *incertae sedis* status within Chalcidoidea. Most frequently, *Cales* are associated with the Aphelinidae. Both groups consist of small wasps that are parasitoids of sternorrhynchous Hemiptera, generally non-metallic, weakly sclerotized and have the meso- and metasoma broadly joined. However, Aphelinidae are most likely not a monophyletic group (Campbell *et al*., 2000; J.M. Heraty, unpublished data), so the question remains with which subfamily or genus could it form a sister-group relationship.

Cales shares many features with *Eretmocerus*, including a long unsegmented clava, similar setal patterns of the dorsal mesosoma, similar structure of the mesofurca, presence of the posterior thoracic spiracle reduction in tarsal segments and simple calcar. However, unlike *Cales*, *Eretmocerus* possess a broad wing disc and linea calva. Also the male genitalia of *Cales* and *Eretmocerus* are different, with *Cales* having a broad phallobase and *Eretmocerus* having an elongated phallobase. Both groups have unique male genitalia within Chalcidoidea, but they are just as different from each other as they are from other chalcidoid groups. An affinity with coccophagine aphelinids may also be hypothesized based on the presence of a ventral mandibular tooth (also found in some Encyrtidae), pleural sulcus (also found in Trichogrammatidae) and similar structure of the mesocoxal articulation, although the latter character is difficult to assess for *Cales* because of generally weak sclerotization.

Cales is an important group for biological control, and yet despite detailed morphological and biological investigations, placement of this group within Chalcidoidea is difficult. Given the apparent homoplasy of *Cales* morphology when compared with other disparate lineages of Chalcidoidea, the determination of its phylogenetic position will require morphological and molecular analyses across the entire superfamily. Therefore, *Cales* should remain unplaced for now. This study aims to contribute to this ongoing area of chalcidoid systematics by laying down a groundplan of comparative morphology, and establishing the taxonomy of one of the most enigmatic groups.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-3113.2010.00557.x

Appendix S1. Additional material examined and specimen deposition.

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References

Barlin, M.R., Vinson, S.B. & Piper, G.L. (1981) Ultrastructure of the antennal sensilla of the cockroach-egg parasitoid, *Tetrastichus hagenowii* (Hymenoptera: Eulophidae). *Journal of Morphology*, **168**, 97–108.

Basibuyuk, H.H. & Quicke, D.L.J. (1995) The morphology of the antenna cleaner in the Hymenoptera with particular reference to non-aculeate families (Insecta). *Zoologica Scripta*, **24**, 157–177.

Brèthes, J. (1914) Les ennemis de la Diaspis pentagona dans la République Argentina. *Nunquam Otiosus, Buenos Aires*, **1914**, 1–16.

Campbell, B., Heraty, J., Rasplus, J.-Y., Chan, K., Steffen-Campbell, J. & Babcock, C.S. (2000) Molecular systematics of the Chalcidoidea using 28S-D2 rDNA. *The Hymenoptera: Evolution, Biodiversity and Biological Control* (ed. by A. Austin and M. Dowton), pp. 59–73. CSIRO Publishing, Collingwood.

Darling, D.C. (1988) Comparative morphology of the labrum in Hymenoptera: the digitate labrum of Perilampidae and Eucharitidae (Chalcidoidea). *Canadian Journal of Zoology*, **66**, 2811–2835.

DeBach, P. & Rose, M. (1976) Biological control of woolly whitefly. *California Agriculture*, **30**, 4–7.

De Santis, L. (1946) Taxonomía de la familia Aphelinidae (Hymenoptera, Chalcidoidea). *Revista del Museo de La Plata (Neuva serie) Zoologia*, **5**, 1–21.

Dozier, H.L. (1933) Miscellaneous notes and descriptions of chalcidoid parasites (Hymenoptera). *Proceedings of the Entomological Society of Washington*, **35**, 85–100.

European and Mediterranean Plant Protection Organization (2002) List of biological control agents widely used in the EPPO region. *OEPP/EPPO Bulletin*, **32**, 447–461.

Evans, G.A. & Serra, C.A. (2002) Parasitoids associated with whiteflies (Homoptera: Aleyrodidae) in Hispaniola and descriptions of two new species of *Encarsia* Förster (Hymenoptera: Aphelinidae). *Journal of Hymenoptera Research*, **11**, 197–212.

Ferrière, C. (1965) *Hymenoptera Aphelinidae de l'Europe et du Bassin Méditerranéen, I.* Masson, Paris.

Gibson, G.A.P. (1989) Phylogeny and classification of Eupelmidae, with a revision of the world genera of Calosotinae and Metapelmatinae (Hymenoptera: Chalcidoidea). *Memoirs of the Entomological Society of Canada*, **149**, 1–121.

Gibson, G.A.P. (1997) Morphology and Terminology. *Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera)* (ed. by G.A.P. Gibson, J.T. Huber and J.B. Woolley), pp. 16–44. NRC Research Press, Ottawa, Illinois.

Gibson, G.A.P. (2003) Phylogenetics and Classification of Cleonyminae (Hymenoptera: Chalcidoidea: Pteromalidae). *Memoirs on Entomology International*, 16. Associated Publishers, Gainesville, Florida.

Gibson, G.A.P. & Huber, J.T. (2000) Review of the family Rotoitidae (Hymenoptera: Chalcidoidea), with description of a new genus and species from Chile. *Journal of Natural History*, **34**, 2293–2314.

Gibson, G.A.P., Heraty, J.M. & Woolley, J.B. (1999) Phylogenetics and classification of Chalcidoidea and Mymarommatoidea – a review of current concepts (Hymenoptera, Apocrita). *Zoologica Scripta*, **28**, 87–124.

Girault, A.A. (1915) Australian Hymenoptera Chalcidoidea. II. *Memoirs of the Queensland Museum*, **3**, 154–169.

Hayat, M. (1983) The genera of Aphelinidae (Hymenoptera) of the world. *Systematic Entomology*, **8**, 63–102.

Hayat, M. (1994) Notes on some genera of the Aphelinidae (Hymenoptera: Chalcidoidea), with comments on the classification of the family. *Oriental Insects*, **28**, 81–96.

Heraty, J.M. (2002) A revision of the Eucharitidae (Hymenoptera: Chalcidoidea) of the World. *Memoirs of the American Entomological Institute*, **68**, 1–359.

Heraty, J.M. & Hawks, D. (1998) Hexamethyldisilazane – A chemical alternative for drying insects. *Entomological News*, **109**, 369–374.

Heraty, J.M. & Schauff, M. (1998) Mandibular teeth in Chalcidoidea: function and phylogeny. *Journal of Natural History*, **32**, 1227–1244.

Heraty, J.M., Woolley, J.B. & Darling, D.C. (1994) Phylogenetic implications of the mesofurca and mesopostnotum in Hymenoptera. *Journal of Hymenoptera Research*, **3**, 241–277.

Heraty, J.M., Woolley, J.B. & Darling, D.C. (1997) Phylogenetic implications of the mesofurca and mesopostnotum in Chalcidoidea (Hymenoptera), with emphasis on Aphelinidae. *Systematic Entomology*, **22**, 45–65.

Hernández-Suárez, E., Carnero, A., Agular, A., Prinsloo, G., LaSalle, J. & Polaszek, A. (2003) Parasitoids of whiteflies (Hymenoptera: Aphelinidae, Eulophidae, Platygastridae; Hemiptera: Aleyrodidae) from the Macronesian archipelagos of the Canary Islands, Madeira and the Azores. *Systematics and Biodiversity*, **1**, 55–108.

Hoddle, M. (2006) Phenology, life tables, and reproductive biology of *Tetraleurodes perseae* (Hemiptera: Aleyrodidae) on California avocados. *Annals of the Entomological Society of America*, **99**, 553–559.

Howard, L.O. (1907) New genera and species of Aphelinidae, with a revised table of genera. *Technical Series, Bureau of Entomology, United States Department of Agriculture*, **12**, 69–88.

Jamieson, L.E., Chhagan, A. & Curtis, C. (2009) Seasonal phenology of Australian citrus whitefly (*Orchamoplatus citri*) in New Zealand. *New Zealand Plant Protection*, **62**, 69–75.

Kim, J.-W. (2003) *Classification and Evolution of the Aphelininae (Hymenoptera: Aphelinidae)*. PhD Dissertation, University of California, Riverside, California.

Kim, J.-W. & Triapitsyn, S.V. (2003) A new species of *Pteroptrix* (Hymenoptera: Aphelinidae) from Argentina, the first known aphelinid with three-segmented tarsi. *Entomological News*, **114**, 10–17.

Krogmann, L. & Vilhelmsen, L. (2006) Phylogenetic implications of the mesosomal skeleton in Chalcidoidea (Hymenoptera, Apocrita) – tree searches in a jungle of homoplasy. *Invertebrate Systematics*, **20**, 615–674.

Laudonia, S. & Viggiani, G. (1986) Osservazioni sugli staid preimmaginali di *Cales noacki* Howard (Hymenoptera: Aphelinidae). *Bollettino del Laboratorio di Entomologia Agraria 'Filippo Silvestri,' Portici*, **43**, 21–48.

Legg, J., Gerling, D. & Neuenschwander, P. (2003) Biological control of whiteflies in Sub-Saharan Africa. *Biological Control in IPM Systems in Africa* (ed. by P. Neuenschwander, C. Borgemeister and J. Langewald), pp. 87–100. CABI Publishing, Wallingford, Connecticut.

Mercet, R.G. (1929) Notas sobre Afelínidos (Hym. Chalc.) 2a nota. EOS. *Revista Española di Entomologia, Madrid*, **5**, 111–117.

Miklasiewicz, T.J. & Walker, G.P. (1990) Population dynamics and biological control of the woolly whitefly (Homoptera: Aleyrodidae) on citrus. *Environmental Entomology*, **19**, 1485–1490.

Owen, A.K., George, J., Pinto, J.D. & Heraty, J.M. (2007) A molecular phylogeny of the Trichogrammatidae (Hymenoptera: Chalcidoidea), with an evaluation of the utility of their male genitalia for higher level classification. *Systematic Entomology*, **32**, 227–251.

Polaszek, A. (1991) Egg parasitism in Aphelinidae (Hymenoptera: Chalcidoidea) with special reference to *Centrodora* and *Encarsia* species. *Bulletin of Entomological Research*, **81**, 97–106.

Polaszek, A. (1993) The identity of *Neocales* Risbec (Hymenoptera: Signiphoridae). *Entomologische Berichten*, **53**, 99–102.

Pyle, K., Stevens, P., Fullerton, R., Jamieson, L., Lo, P., Rogers, D. & McKenna, C. (2005) *Practical, Safe and Effective Integrated Pest Management Strategies for New Zealand Citrus.* New Zealand Citrus Growers Incorporated, Wellington.

Risbec, J. (1957) Aphelinidae de Madagascar (Hym. Chalcidoidea). *Naturaliste Malgache*, **9**, 263–272.

Rodríguez-Rodríguez, R. (1977a) Posibilidades de control biológico de la "mosca blanca" de los agrios, *Aleurothrixus floccosus* (Mask.) por el parásito introducido *Cales noacki* (How.). *Xoba*, **1**, 45–48.

Rodríguez-Rodríguez, R. (1977b) Posibilidades de control biológico de la "mosca blanca" de los agrios, *Aleurothrixus floccosus* (Mask.) por el parásito introducido *Cales noacki* (How.) (continuación). *Xoba*, **1**, 108–113.

Rose, M. & Woolley, J.B. (1984) Previously imported parasite may control invading whitefly. *California Agriculture*, **38**, 24–25.

Rosen, D. & DeBach, P. (1979) *Species of Aphytis of the World (Hymenoptera: Aphelinidae)*, *Series Entomologica, Vol. 17*. Dr. W. Junk BV Publishers, The Hague, Boston, Massachusetts, London.

Shafee, S.A. & Rizvi, S. (1990) Classification and phylogeny of the family Aphelinidae (Hymenoptera: Chalcidoidea). *Indian Journal of Systematic Entomology*, **7**, 103–115.

Vatansever, G. & Ulusoy, M.R. (2005) Parazitoit *Cales noacki* Howard (Hymenoptera: Aphelinidae) 'Nin Konukçulari ve doğadaki yillik döl sayisi'. *BAÜ Fen Bilimleri Enstitüsü Dergisi*, **7**, 12–16.

Viggiani, G. (1981) Note sui generi *Paranthemus* Girault e *Debachiella* Gordh et Rosen (Hym. Aphelinidae). *Bollettino della Societa Entomologia Italiana*, **113**, 47–49.

Viggiani, G. & Battaglia, D. (1984) Male genitalia in the Aphelinidae (Hym. Chalcidoidea). *Bollettino del Laboratorio di Entomologia Agraria Filippo Silvestri*, **41**, 149–171.

Viggiani, G. & Carver, M. (1988) *Cales orchamoplati* sp. n. (Hymenoptera: Aphelinidae) from Australia. *Journal of the Australian Entomological Society*, **27**, 43–45.

Viggiani, G. & Currado, L. (1978) Sul parassitismo di *Cales noacki* How. (Hym. Aphelinidae) in uova di *Phalera bucephala* (Lep. Notodontidae). *Atti XI Congresso Nazionale Italiano di Entomologia Portici-Sorrento*, 10–15 maggio 1976, pp. 317–319.

Viggiani, G. & Laudonia, S. (1984) *Aleurotuba jelineki* (Frauenf.) (Homoptera: Aleyrodidae), nuovo ospite di *Cales noacki* Howard (Hymenoptera: Aphelinidae). *Bollettino del Laboratorio di Entomologia Agraria Filippo Silvestri*, **41**, 139–142.

Yasnosh, V.A. (1976) Classification of the parasitic Hymenoptera of the family Aphelinidae (Chalcidoidea). *Entomological Review*, **55**, 114–120.

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