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Revision and phylogenetics of the genus *Paraulax* Kieffer (Hymenoptera, Cynipidae) with biological notes and description of a new tribe, a new genus, and five new species

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Abstract

The gall wasp genus *Paraulax* (Hymenoptera, Cynipidae) associated with southern beeches (*Nothofagus* (Nothofagaceae)) from South America is revised. The genus *Paraulax* and its type species, *P. perplexa*, are redescribed and a neotype is designated. Two additional species of *Paraulax* are described as new: *P. queulensis* and *P. ronquisti*. After having been first tentatively placed in the Cynipini and later transferred to the Pediaspidini, this genus is here placed in the newly erected tribe Paraulacini, together with the herein described genus *Cecinothofagus* and the three species that are described as new: *C. gallaecoihue*, *C. gallaelenga* and *C. ibarrai*.

The biology of the members of this new tribe is discussed. Contrary to a prior hypothesis that postulated *Paraulax* (sensu lato) to be true gall-inducers, as most cynipids, evidence here shows that the three species of the new genus *Cecinothofagus* are instead parasitoids or lethal inquilines inhabiting galls induced by species of *Aditrochus* (Pteromalidae) on *Nothofagus*. The biology of the *Paraulax* species is unknown but since they too are associated with *Nothofagus* forests their biology is likely associated with the pteromalid gall community. We describe host plant associations as well as the morphology and phenology of the host gall.

A phylogenetic reconstruction of the Paraulacini and selected Cynipidae taxa, based on 28S and COI, is performed. Both markers indicate the Paraulacini to be monophyletic and support a sister group relationship with the Pediaspidini. Results from 28S are congruent with both the morphological evidence and the proposed classification.

Key words: Cynipidae, evolution, gall wasp, inquiline, life history, South America, *Paraulax*, *Cecinothofagus*, *Aditrochus*, *Nothofagus*

Introduction

The Gall wasps (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. In this second case, the inquilines usually inhabit the gall of another cynipid, a relation that has been called agastoparasitism (Ronquist 1994). Gall inducing cynipids are separated into five tribes, each associated with a different set of plant hosts – the Cynipini gall plants of the family Fagaceae, the Pediaspidini, according more recent classsification (Liljeblad *et al.* 2008), gall southern beeches (*Nothofagus*) and maples (*Acer*), the Diplolepidini gall plants of the genus *Rosa* (Rosaceae), the Eschatocerini gall *Acacia* and *Prosopis* (Fabaceae), while the Aylacini gall a range of herbaceous plants (Ronquist 1999; Nieves-Aldrey 2001; Liu & Ronquist 2006). The inquiline gall wasps are currently classified as members of a single tribe, the Synergini, although molecular evidence suggests that the group is not monophyletic and group in at least two separate clades, one associated to galls on Fagaceae and Anacardiaceae, and other in galls on Rosaceae (Nylander *et al.* 2004; Van Noort *et al*. 2007). The largest cynipid radiation on a specific host plant group is represented by the oak gall wasps (Cynipini) with about 1000 described species all in the Northern Hemisphere. In this association in particular, like cynipids in general, they appear to have mantained a high degree of host plant specificity (Ronquist & Liljeblad 2001; Liljeblad *et al*. 2008; Stone *et al*. 2002, 2009).

The Cynipidae are predominately a Northern Hemisphere group, and most of the approximately 1300 described species are Holarctic (Nieves-Aldrey 2001; Csoka *et al.* 2005; Liu & Ronquist 2006; Liljeblad *et al.* 2008). The exceptions are three genera: *Paraulax* Kieffer and *Eschatocerus* Mayr that are native of temperate South America (Díaz 1981; Liu & Ronquist 2006), and the South Africa endemic *Rhoophilus* Mayr (van Noort *et al*. 2007). Another cynipid of uncertain taxonomic status, linked to galls on *Scolopia mundii* (Eckl. & Zeyh.) Warb. (Flacourtiaceae) is known from eastern South Africa, but remains undescribed (Liljeblad *et al.* 2008; Liljeblad, Nieves-Aldrey & Melika *in prep.*).

Paraulax is a poorly known and interesting genus that has rarely been collected, and thus is virtually absent from entomological collections. Furthermore, the location of the types of *P. perplexa*, the only described species until now, is unknown and presumed to be lost (Weld 1952). There is no host record for *P. perplexa* and references to the biology of this species have been indirect or uncertain.

The taxonomical affinities of *Paraulax* have always been problematic. In the past, it has been tentatively placed in the Aylacini (Dalla Torre & Kieffer 1910; Weld 1952) and the Cynipini (Ronquist 1999). More recently it was transferred to the Pediaspidini, albeit based on the results from a study of the morphology of a single undescribed species (Liljeblad *et al*. 2008).

Morphologically *Paraulax* is a distinctive taxon. The general habitus is unique, in some ways resembling basal figitids with a mesopleural impression, a distinct pronotal plate, a distinctive female antennal club, and a modified male second antennal flagellomere, deviating from all other Cynipidae (the modified antennal flagellomere is always the first in cynipid males). Other *Paraulax* characters, however, are typical of the gall wasps like that of the wing venation. The Rs + M is oriented towards the middle of the basal vein and not to the junction of the basal with the M + Cu as is the case with figitids. We need to mention, however, that the validity of this problematic character have been questioned recently (Paretas-Martínez *et al*. 2006).

Paraulax perplexa, the only species formally described until now, was originally collected in *Nothofagus* forests of Central Chile (Kieffer 1904). Although its taxonomic and phylogenetic placement with the Cynipidae suggests that *Paraulax* is a gall inducer, this biological role has never been confirmed, and the host plant has remained unknown. *Paraulax* is intriguing because it is the sole native cynipid associated with *Nothofagus* forests in South America; the only other cynipids recorded from South America are the previously mentioned species belonging to *Eschatocerus*. Apart from being gall inducers of *Prosopis* and *Acacia* (Fabaceae) little is known about the biology of the latter. De Santis *et al*. (1993) recorded indeterminate species identified as *Paraulax* from galls on several species of *Nothofagus* from Argentina, from which they also reared and described some species of *Aditrochus* Rübsaamen (Pteromalidae). Most subsequent authors (Ronquist 1999; Ronquist & Nieves-Aldrey 2001; Csoka *et al*. 2005; Liu & Ronquist, 2006) assumed that *Paraulax* was the gall inducer of the *Nothofagus* galls but this has never actually been demonstrated. The specific biology of the various cynipoids, chalcidoids and other insect inhabitants of *Nothofagus* galls has not been investigated by detailed dissections alongside controlled rearings. However, among reared insects there are potentially three candidates: the pteromalid *Aditrochus*, the cynipid *Paraulax* and coleopteran species of the family Apionidae (Kissinger 2005). The galls studied and figured by De Santis *et al*. (1993), presumably induced by Hymenoptera, are of particular interest, hosting some taxa of Chalcidoidea and Cynipoidea that are potentially crucial to the understanding of their early evolution.

The genus *Nothofagus*, of the family Nothofagaceae, includes evergreen and deciduous trees known as southern beeches. This trans-Antarctic element is made up of thirty five described species distributed among New Zeeland, Australia, New Guinea, New Caledonia and cold temperate South America. Ten species are known from Chile and Argentina. The most common and widespread of these species are *N. obliqua* (Mirb.) Oerst (roble), *N. dombeyi* (Mirb.) Blume (coihue), *N. pumilio* (Poepp & Endl.) Krasser (lenga) and *N. antarctica* (G. Forster) Oerst. (ñirre) (Hoffmann 1978).

In the present study we re-describe *Paraulax* and the type species *Paraulax perplexa*. We also describe two new species of *Paraulax* as well as the new genus *Cecinothofagus*, closely allied to *Paraulax*, including three new species of its own. Both genera are included in a new tribe, Paraulacini **new tribe**, herein described. The new genus is associated with galls of *Aditrochus* on *Nothofagus.* We provide evidence that the species of *Cecinothofagus* develop as parasitoids or perhaps lethal inquilines within galls induced by species of *Aditrochus*. Molecular results from Nylander *et al*. (2004) emphasize the importance of elucidating the phylogenetic relationship and biology of the genus *Paraulax* in order to understand the evolutionary history of the Cynipidae and their host plant associations. We performed a phylogenetic analysis of molecular data (28S and COI markers) from the Paraulacini, including one species of *Paraulax* and three of *Cecinothofagus*, in order to assess the relationships of this group to the basal lineages of the Cynipidae+Figitidae. We discuss the evolutionary implications of unravelling the phylogeny and life history of these intriguing cynipids.

Material and methods

Study material. Material examined from collections

Part of the studied material was borrowed from the following institutions:

American Entomological Institute, Gainesville, FL, U.S.A. (AEIG) (D. Wahl); Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A. (MCZC); University of California, Riverside, Riverside, CA, U.S.A. (UCRC) (D. Yanega); Museum für Naturkunde der Humboldtuniversität, Berlin, Germany (ZMHB) (F. Koch); Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (CNC) (J. Read).

Field work. Samplings were made and material was collected by the first author, mainly during two collecting surveys in January–February 2005 and November–December 2006 in Chile. Seven *Nothofagus* species (*N. obliqua* (Mirb.) Oerst., *N. pumilio* (Poepp & Endl.) Krasser, *N. dombeyi* (Mirb.) Blume, *N. antarctica* (G. Forster) Oerst., *N. glauca* (Phil.) Krasser, *N. alessandri* Espinosa and *N. betuloides* (Mirb.) Oerst.) were sampled in national parks and reserves of the VII (Maule), IX (Araucanía), X (Los Lagos) and XII (Magallanes) regions of Chile. Additionally some material was collected by H. Ibarra and S. Rizzutto in Chile and Argentina, respectively, and submitted to the first author for study. The trees were visually surveyed for galls. Galls were then hand-collected and taken back to the laboratory where ranges of different sized galls were dissected. Wasps were mainly obtained by dissection of freshly collected galls. Dissected pupae were stored in gelatine capsules until metamorphosis. Some adults were reared from galls kept in rearing cages with netting lids. Additional specimens of *Paraulax*, separate from the material used for dissections or rearings, were collected from seven Malaise traps. These operated at la Reserva Nacional Los Queules (Chile, Maule, VII Region), for an entire year. The insects were caught direcly into 70% ethanol, and cynipids were successively sorted out from these samples. The geographical distribution of the collecting sites of the studied material is represented in the figure 15.

TABLE 1. Listing of Paraulacini included in the phylogenetic analysis, with their respective collecting data and GenBank accesion numbers for sequenced genes. For data about other Cynipoidea in the present paper we refer to Nylander *et al.* (2004).

Taxon	Collecting site	Collecting method	Date	Collector	COI	28S
Paraulax perplexa	Los Queules	Malaise trap	ix-x.2006	J. L. Nieves-Aldrey & A. Grez	FJ998299	FJ998295
Cecinothofagus gallaecoihue	Puerto Varas to Ensenada	Ex gall *Nothofagus. dombeyi*	2.xii.2006	J. L. Nieves-Aldrey	FJ998296	FJ998292
Cecinothofagus gallaelenga	Reserva Forestal Magallanes	Ex gall *Nothofagus pumilio*	9.xii.2006	J. L. Nieves-Aldrey	FJ998297	FJ998293
Cecinothofagus ibarrai	Ensenada to Ralún	Ex gall *Nothofagus dombeyi*	2.xii.2006	J. L. Nieves-Aldrey	FJ998298	FJ998294

Specimen preparation. For observation under a scanning electron microscope (SEM), adult cynipids were dissected in 70% ethanol, air dried, mounted on a stub and coated with gold, and micrographs were taken with a FEI QUANTA 200 (high vacuum technique) for several standardized views. Forewings were mounted in Euparal on slides, and later examined under a Wild MZ8 stereo microscope. Representatives of some species with poor representation in the samples were not dissected but instead directly observed using SEM at low vacuum, without coating. Images of adult habitus and gall dissections were taken with a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereo microscope. Measurements were made with a calibrated micrometer scale attached to an ocular of the light microscope. Terminology of morphological structures and abbreviations follow Ronquist and Nordlander (1989), Ronquist (1995), Liljeblad *et al.* (2008) and Nieves-Aldrey (2001). Type specimens of the newly described species are deposited in the Museo Chileno de Historia Natural (Santiago, Chile), Museo Nacional de Ciencias Naturales (Madrid, Spain), Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Canada) and Museum für Naturkunde der Humboldtuniversität (Berlin, Germany).

Molecular methods. Selection of taxa for study

Ingroup. We assembled DNA data for a total of four species of Paraulacini, three representing the new genus *Cecinothofagus* and *Paraulax perplexa*. Unfortunately we were not able to include representatives of *P. queulensis* and *P. ronquisti*, here described as new, in the analysis because of the paucity of specimens available for DNA extraction. However, morphologically, these species are closely related to *Paraulax perplexa*.

Outgroups. We used the molecular analysis of Nylander (2004) for selection of taxa representative of the main cynipid lineages and basal figitids (*Parnips*, *Plectocynips*, *Melanips*), as outgroups. Sequences are available in GenBank.

For the ingroup taxa we sequenced parts of two genes: the mitochondrial gene cytochrome oxidase *c* subunit I (COI, 1,078 bp), and the nuclear ribosomal gene 28S (1,199 bp). GenBank accession numbers for the analyzed species of Paraulacini are given in Table I. For details about DNA amplification protocols and primers we refer to Rokas *et al*. (2002).

The protein-coding gene (COI) was easily aligned by eye. The ribosomal (28S) sequences differed in length and some of the more variable regions were difficult to align manually. We adopted an alignment-sensitivity and character exclusion approach to this problem. The program ClustalW version 1.81 (Thompson *et al*. 1994) was used with a range of alignment parameter combinations: gap opening penalty set to 10, 15, and 20, each combined with a gap extension penalty set to 1, 3, 5, and 7. Bootstrap analyses (Felsenstein 1985) were run on the data remaining after each character deletion (combined with the COI data sets) using approximate parsimony searches in PAUP* (Swofford 2002) and the resulting trees were visually examined for congruence.

Phylogenetic analysis. The estimation of the evolutionary model was made under Akaike criterium (AIC) using MODELTEST v. 3.7 (Posada & Crandall 1998).

We performed a Bayesian analysis with MrBayes 3.1 (Ronquist & Huelsenbeck 2003) using Metropolis-coupled Markov chain Monte Carlo methods. Two parallel runs, each with four heated chains (heating temperature set to 0.04) where run for 10 million generations and sampled every 100 generations. MrBayes will by default discard the first 25 % samples from the cold chain (`relburnin=yes` and `burninfrac=0.25`). The COI and 28S genes where analyzed both individually and combined, assuming the GTR+I+G model of nucleotide substitution (Tavaré 1986, Yang 1994, Gu *et al*. 1995). In the combined analysis, the genes where allowed to have their own, unlinked, parameter values (Nylander *et al*. 2004). The default prior settings where used for trees and model parameters. The tree was rooted with the simultaneous inclusion of the five outgroup taxa.

Results

Paraulacini Nieves-Aldrey & Liljeblad new tribe

Type genus *Paraulax* Kieffer, 1904.

Diagnosis. Differs from all other cynipids by the presence of the following autapomorphies: modified flagellomere of male antenna always F2, F3 or both (never F1 as in other Cynipidae) (Figs. 2E, 4G, 4I & 5A); presence of a structure of 4–5 rows of sharp, closely spaced and deep costulae on swelling of basal one-third of profemur (Figs. 3B & 3C); presence of 5-9 vertical carinae in the ventral region of the gena (Fig. 4B). The tribe can also be distinguished by a combination of the following characters: female antenna with 10 flagellomeres, F10 clavate (Figs. 2C & 2D); ventral part of clypeus not or only slightly projecting over mandibles; dorsolateral margin of pronotal plate projecting laterally (Figs. 2H & 2I); genal occipital carina present; scutellar foveae almost absent (Figs. 6D & 9A) or, if present, always shallow or indistinct (Figs. 2I & 4C), while the area posterior to the transscutal fissure always is concave; round, distinctly margined posteromedian scutellar impression absent; mesopleural impression present (Figs. 2G, 4B & 5C).

Description. Predominantly black, sometimes brown to red-brown, with weakly shining or dull sculpture. Relatively small (1.7–2.9 mm). Female antenna with 10 flagellomeres, male with 13. Face usually with a distinct median vertical carina and facial strigae radiating from clypeus laterally (Figs. 6A & 8A). Pronotal plate conspicuous with dorsolateral margins projected laterally. Notauli complete. Scutellar foveae faint or indistinct. Mesopleural impression present, more or less extended. Claws bifid, with a relatively long basal lobe or tooth (Figs. 3D & 4D), or, if simple, sometimes with an acute tiny lobe (Fig. 9D). Forewing with radial cell closed along anterior margin; R1 tubular albeit slightly depigmented along radial cell (Figs. 3E & 4H); vein Rs+M and M, directed towards lower half of median vein (Figs. 3E, 4K, 7F & 8H). Female metasoma laterally compressed. Abdominal petiole smooth dorsally, ventrally with deep longitudinal grooves. T2 smooth and shining, covering about 2/3 of metasoma. Projecting part of hypopygial spine relatively short, 3–4 times longer than wide (Fig. 3G).

Diversity and distribution. Includes two genera occurring in the South of the Neotropical Region, in temperate *Nothofagus* forests of Argentina and Chile, one of them associated with galls of *Aditrochus* (Pteromalidae) on *Nothofagus*.

Remarks. A recent morphological phylogenetic study found *Paraulax* to be closely related to the Pediaspidini (Liljeblad *et al*. 2008). We justify the erection of a new tribe as follows: with several members, including a new genus, the new tribe itself is strongly supported by the molecular data of the present analysis (100% bootstrap) whereas the grouping with *Pediaspis* is only recovered with a 75% of bootstrap support; the new group is morphologically distinct and supported by several synapomorphies; the erection of a new tribe for the cynipids associated with Nothofagaceae is congruent with the traditional tribal classification of the Cynipidae, which to a large degree is based on biological associations such as higher level systematics of the host plants.

The tribe Paraulacini, as here defined, share with the Pediaspidini, among other character states, a relatively long pronotum medially, the pronotal plate being extended dorsally, a mostly smooth mesopleuron, usually with a visible mesopleural impression, and the scutellar foveae faint or absent. The two tribes can, however, be readily distinguished as follows:

1. Female antenna with 12 or more flagellomeres (Fig. 1A); last flagellomere not wider than the penultimate; male antenna with modified F1 (Fig. 1B). Ventral area of gena without vertical carinae. Ventral part of clypeus broadly projecting over mandibles (Fig. 1C); genal carina absent. Dorsolateral margin of pronotal plate not projecting laterally (Fig. 1D). Scutellar foveae absent (Fig. 1E); area behind transscutal fissure flat or convex. A round, distinctly margined posteromedian scutellar impression present (Fig. 1E). Mesopleural impression absent or faint (Fig. 1F). Profemur not modified. Includes one Palaearctic genus inducing galls on *Acer* and another genus from the Himalayan region with biology unknown .... *Pediaspidini*

\- Female antenna with 10 flagellomeres (Fig. 2C); last flagellomere wider than the penultimate; male antenna with either F2, F3 or both modified (Figs. 2F & 4G). Ventral area of gena with 5–9 vertical carinae (Fig. 4B); genal carina present. Ventral part of clypeus at most slightly projecting over mandibles (Fig. 2A). Dorsolateral margin of pronotal plate strongly projecting laterally (Figs. 2H & 2I). Scutellar foveae absent or present, always shallow or indistinct, while the area posterior to the transscutal fissure always is concave (Figs. 2G & 2I). Round, distinctly margined posteromedian scutellar impression absent (Fig. 2I). Mesopleural impression present (Figs. 2G & 7A). Profemur ventrally with a swelling composed of 4–5 rows of sharp, closely spaced, deep costulae (Figs. 3B & 3C). Includes two neotropical genera associated with galls of *Aditrochus* (Pteromalidae) on *Nothofagus* .... *Paraulacini*

Key to the genera of Paraulacini

1. Face without a distinct median vertical carina (Fig. 2A); facial strigae radiating from clypeus laterally present also medially, reaching ventral margin of antennal sockets. F2 and F3 of the male antenna modified (Figs. 2E, 2F, 4G & 5A). Dorsolateral margin of pronotal plate strongly projecting laterally (Figs. 2H & 2I). Scutellar foveae sometimes indicated, albeit shallow (Figs. 2I & 4C). Sculpture present dorsal to mesopleural impression (Figs. 2G & 4B). Claws with an acute basal lobe or tooth; lobe 1/3 to ¼ length of apical tooth (Figs. 3D & 4D). .... *Paraulax*
- Face with a distinct median vertical carina (Figs. 6A & 8A); facial strigae radiating from clypeus present laterally but not medially, laterally only reaching ventral margin of compound eye. Only segment F2 of male antenna modified (Figs. 4I, 6F & 8D). Dorsolateral margin of pronotal plate only projecting somewhat laterally. Scutellar foveae absent or indistinct (Figs. 4J, 6D & 9A). Sculpture dorsal to mesopleural impression usually absent or weak (Figs. 7A & 9B). Claws simple, sometimes with a blunt, short basal lobe, or with an acute, tiny lobe measuring less than 1/6 of length apical tooth (Fig. 9D). .... *Cecinothofagus* **gen. n.**

Genera of Paraulacini

Paraulax Kieffer, 1904

Paraulax Kieffer, 1904: 59. Type species: *Paraulax perplexa* Kieffer, 1904: 60, by original designation.
Note. As was pointed out by Rohwer & Fagan (1919), the description of *Paraulax* was duplicated in Kieffer, 1904b: 43, being impossible to determine which has priority. However Neave (1940): 605, gave the first reference above as valid that is here accepted.

Diagnosis. Similar to *Cecinothofagus* in general appearance, but separated by the following character states: face without a distinct median vertical carina (Fig. 2A); facial strigae radiating from clypeus laterally present also medially, reaching ventral margin of antennal socket (Fig. 2A). Ventral part of clypeus slightly projecting over mandibles (Fig. 2A). Last flagellomere of the female antenna 3 times longer than wide (Fig. 2D); more than 2.5 times as long as penultimate. F2 and F3 of male antenna modified (Fig. 2E). Dorsolateral margin of pronotal plate strongly projecting laterally (Fig. 2H). Notauli straight, strongly converging and close posteriorly, almost as wide as anteriorly (Fig. 2I). Separation of notauli at the meeting of the transcutal fissure relatively short 0.2–0.3 times compared to separation at anterior margin of mesoscutum. Scutellar foveae sometimes indicated, albeit shallow (Fig. 2I). Sculpture present dorsal to mesopleural impression (Fig. 2G). Claws with an acute basal lobe or tooth; about 1/3 to ¼ length of apical tooth (Fig. 3D). Projecting part of hypopygial spine relatively long, 4 times longer than wide (Fig. 3G).

Redescription. Head. Some scattered setae along face, gena and occiput dorsally. Gena not expanded behind compound eye. Vertical median carina absent; strong facial strigae radiating from clypeus, laterally reaching ventral margin of eye, medially almost reaching torulus; Frons and vertex with coriaceous sculpture. Clypeus indistinct, ventral margin slightly projecting over mandibles. Subocular impression present though not well marked (Fig. 1A). gena with 5–7 regular vertical carinae present ventrolaterally (Fig. 4B). Anterior tentorial pits visible; epistomal sulcus and clypeo-pleurostomal lines indistinct. Occiput without dorsal occipital carina (Fig. 2B); some strong longitudinal rugae present on lateral margin of head, but without a distinct genal carina. Hypostomal sulci meeting slightly before hypostoma.

Antenna. Female with 10 flagellomeres; flagellum widening towards apex (Fig. 2C); Placodeal sensilla visible on F7–F10 (Fig. 2D). Apical flagellomere spindle-shaped, not apically truncate. Male with 13 flagellomeres. Flagellum not widening towards apex. F1 cylindrical, F2 and F3 excavated and curved in basal third (Fig. 2F). Placodeal sensilla present on all flagellomeres except F1.

Pronotum. Pronotal plate distinct, dorsal part distinctly set off, with anterolateral margins marked and moderately projecting laterally. Admedian pronotal depressions widely separated (Fig. 2H). Lateral surface of pronotum coriaceous, some strong, short rugae running from the lateral margin of pronotal plate (Fig. 2G).

Mesoscutum with weak coriaceous sculpture, more marked on lateral lobes. Mesoscutal pubescence comprised of some sparse setae. Median mesoscutal impression absent. Notauli complete, straight and narrow, converging posteriorly (Figs. 2I & 4C). Anteroadmedian signa visible. Mesoscutum and mesoscutellum separated by a narrow transscutal fissure. Scutellar foveae indistinct, visible only as a shallow depression with some rugae (Figs. 2I & 4C). Scutellum, in dorsal view with strong rugae. Posterodorsal and posterior margins of axillula distinct. Mesopleuron ventrally of mesopleural triangle with a marked longitudinal mesopleural impression, more or less complete, ending at margin of mesopleural triangle (Fig. 2G). Above furrow with some irregular longitudinal striae and coriaceous sculpture (Figs. 2G & 4B). Mesopleuron smooth below mesopleural impression. Metascutellum distinctly constricted medially.

Metapectal-propodeal complex. Metapleural sulcus meeting posterior margin of mesopectus at about mid height of metapectal-propodeal complex (Fig. 2G). Lateral propodeal carinae narrow, parallel (Fig. 3A). Lateral and median propodeal areas smooth, pubescent. Nucha dorsally with some irregular longitudinal rugae.

Legs. Profemur with a ventral swelling in basal third, with 4–5 rows of sharp closely spaced, deep costulae (Figs. 3B & 3C). Metatarsal claws with a basal acute lobe or tooth (Figs. 3D & 4D).

Forewing. Radial cell closed along anterior margin; R1 slightly depigmented along radial cell (Figs. 3E & 4H); areolet absent; vein Rs+M and M almost invisible, directed towards lower half of median vein. Fringe of long setae along apical margin of wing.

Female metasoma laterally compressed (Fig. 2F). Abdominal petiole smooth dorsally, ventrally with deep longitudinal grooves, about as long as high. T2 smooth and shining, covering about 2/3 of metasoma; anteromedian area of T2 with only 4–5 long setae (Figs. 2F & 4A). Projecting part of hypopygial spine 4 times as long as high; apical pubescence projecting beyond apex, subapical setae longer than apical ones, forming a small tuft (Figs. 3G & 4E).

Included species

Paraulax perplexa Kieffer, 1904. Types lost. A neotype here designated.

P. queulensis sp. n.

P. ronquisti sp. n.

Distribution. Chile, as far as we know, and as here defined, the species of *Paraulax* occur in the VI to X regions of Chile, in *Nothofagus* forest habitats, mainly *N. obliqua*, roughly extending from Santiago to Villarrica (Fig. 15).

Biology. Unknown. Adults were captured in *Nothofagus* forests, probably associated with galls induced by species of *Aditrochus* (Pteromalidae) on *Nothofagus obliqua*.

Remarks. Closely related to *Cecinothofagus*, the sister genus within the Paraulacini. Although many characters are shared with *Cecinothofagus*, the two genera are readily separated as detailed in the diagnosis and the key for identification.

Key to species of *Paraulax*

1. Sculpture of mesoscutum weakly coriaceous, without transverse striae (Fig. 2I). Mesopleural impression relatively short, not reaching ventral margin of mesopleural triangle (Fig. 2G). Short, longitudinal costulae running from lateral margin of pronotal plate to lateral surface of pronotum (Fig. 2G). F2 of male antenna strongly expanded at apex (Fig. 2F). Radial cell less than 3.5 times longer than wide (Fig. 3E) 2

\- Sculpture of mesoscutum coriaceous with weak transverse striae (Fig. 4C). Mesopleural impression long, complete, reaching ventral margin of mesopleural triangle (Fig. 4B). Long, well marked longitudinal costulae running from lateral margin of pronotal plate to lateral surface of pronotum (Fig. 4B). F2 of male antenna not strongly expanded at apex (Fig. 4G). Radial cell long, more than 4 times longer than wide (Fig. 4H) .... *P. queulensis*

2. Body not overly elongate; about 3 times as long as high in lateral view (Fig. 10A). F2 of male antenna strongly broadened and distally truncate (Fig. 2F); F3 inflated in distal third (Fig. 2F). Notauli complete (Fig. 2I). Mesopleuron with weak sculpture dorsal to mesopleural impression (Fig. 2G). Body black .... *Paraulax perplexa*

\- Body clearly elongate, about 4 times as long as high in lateral view (Fig. 10E). F2 and F3 of male antenna expanded in distal 2/3 (Fig. 5A); F2 not truncate at apex. Notauli anteriorly faint (Fig. 5B). Mesopleuron smooth and shining at faint mesopleural impression (Fig. 5C). Body red-brown .... *P. ronquisti*

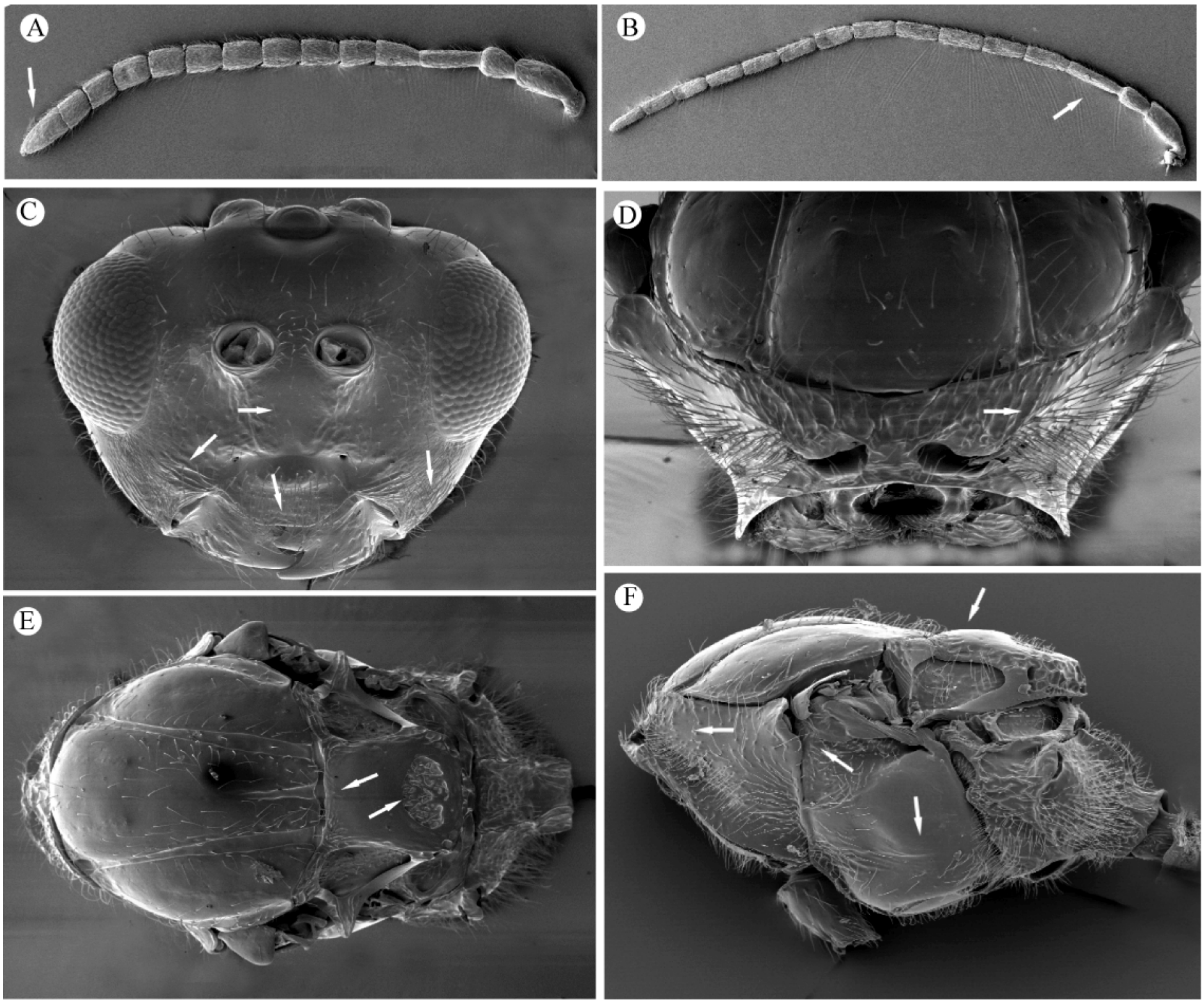

FIGURE 1. *Pediaspis aceris*: (A) Female antenna. (B) Male antenna. (C) Head anterior view. (D) Pronotum anterior view. (E) Mesosoma dorsal view. (F) Mesosoma lateral view.

Paraulax perplexa Kieffer, 1904
(Figs. 2, 3 & 10A–B)

Paraulax perplexa Kieffer, 1904
P. perplexus Kieffer in: *Bull. Soc. Metz,* ser 2 v.11 p. 60 (female and male). Bisexual.

Type material. Neotype ♀ here designated: CHILE, El Maule, VII Región, Cauquenes, Reserva Nacional Los Queules, 35º59´10´´S, 72º42´30´´O, 420 m; caught with a Malaise trap operating in a fragment of native forest, 27.ix/25.x.2006. J.L. Nieves-Aldrey & A. Grez leg. Deposited in Museo Chileno de Historia Natural, Santiago de Chile, card mounted. Other material from type series: 4♂ same data as Neotype, except 2♂ collected on 22.viii/22.ix. 1♂ in MCHN, remaining exemplars in Museo Nacional Ciencias Naturales, Madrid (Spain). Additional material (1♂, 1♀ from the type series were dissected for SEM observation); one additional female preserved in ethanol (extracted DNA). Non-type material: 1♀, Chile, Ñuble, Ese Recinto. 1330 m, 29/XII/1982, Newton & Thayer leg (AEI).

Diagnosis. *P. perplexa* differs from *P. queulensis* and *P. ronquisti* by a not elongate body (Figs. 10A), in the female only 3 times longer than high. The males of this species are readily distinguished of the other species of Paraulax by the strongly broadened and distally truncate second flagellomere (Fig. 2F).

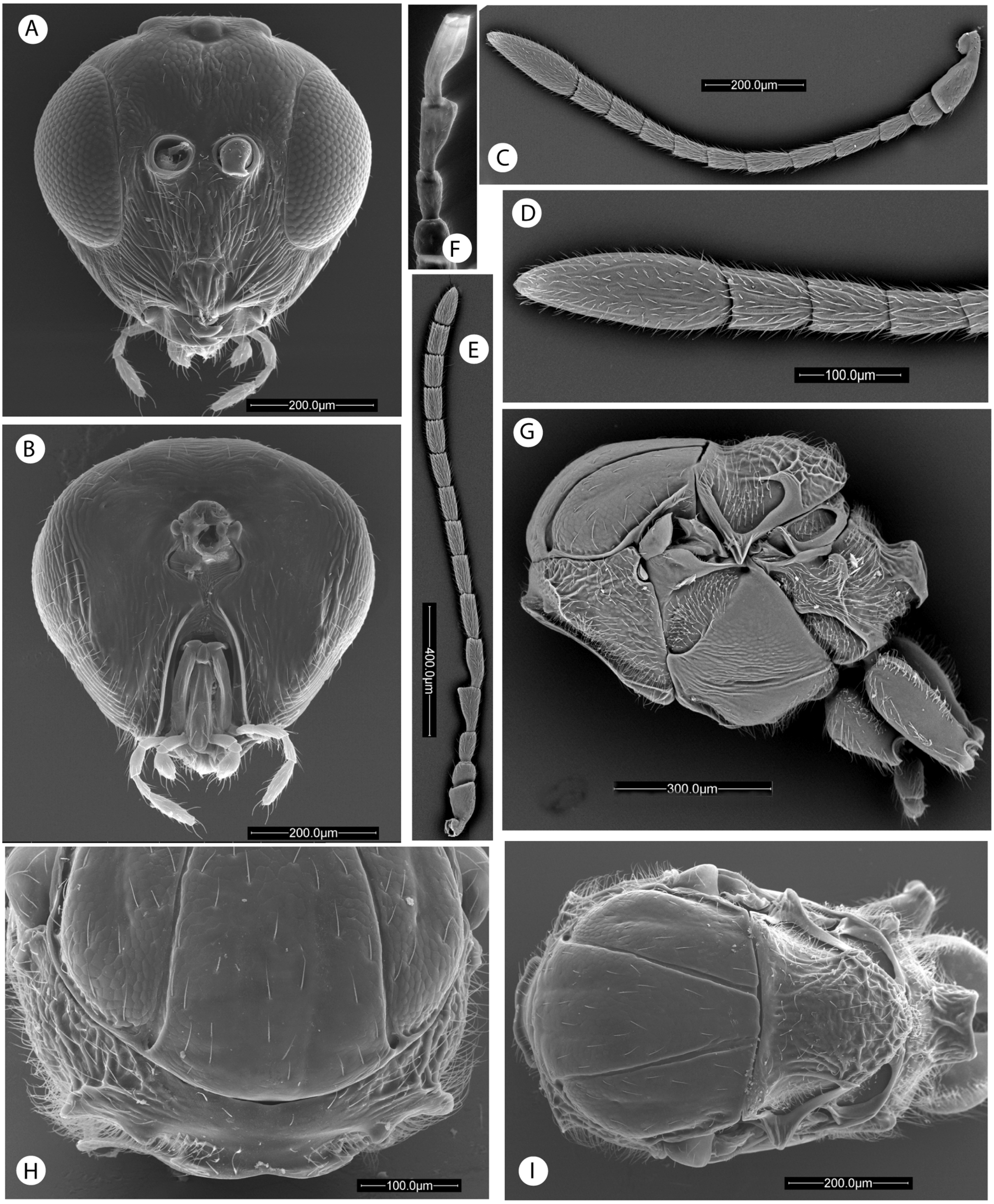

FIGURE 2. *Paraulax perplexa:* (A) Head anterior view. (B) Head posterior view. (C) Female antenna. (D) Detail of last flagellomeres. (E). Male antenna. (F) Detail of basal flagellomeres. (G) Mesosoma lateral view. (H) Pronotum anterior view. (I) Mesosoma dorsal view.

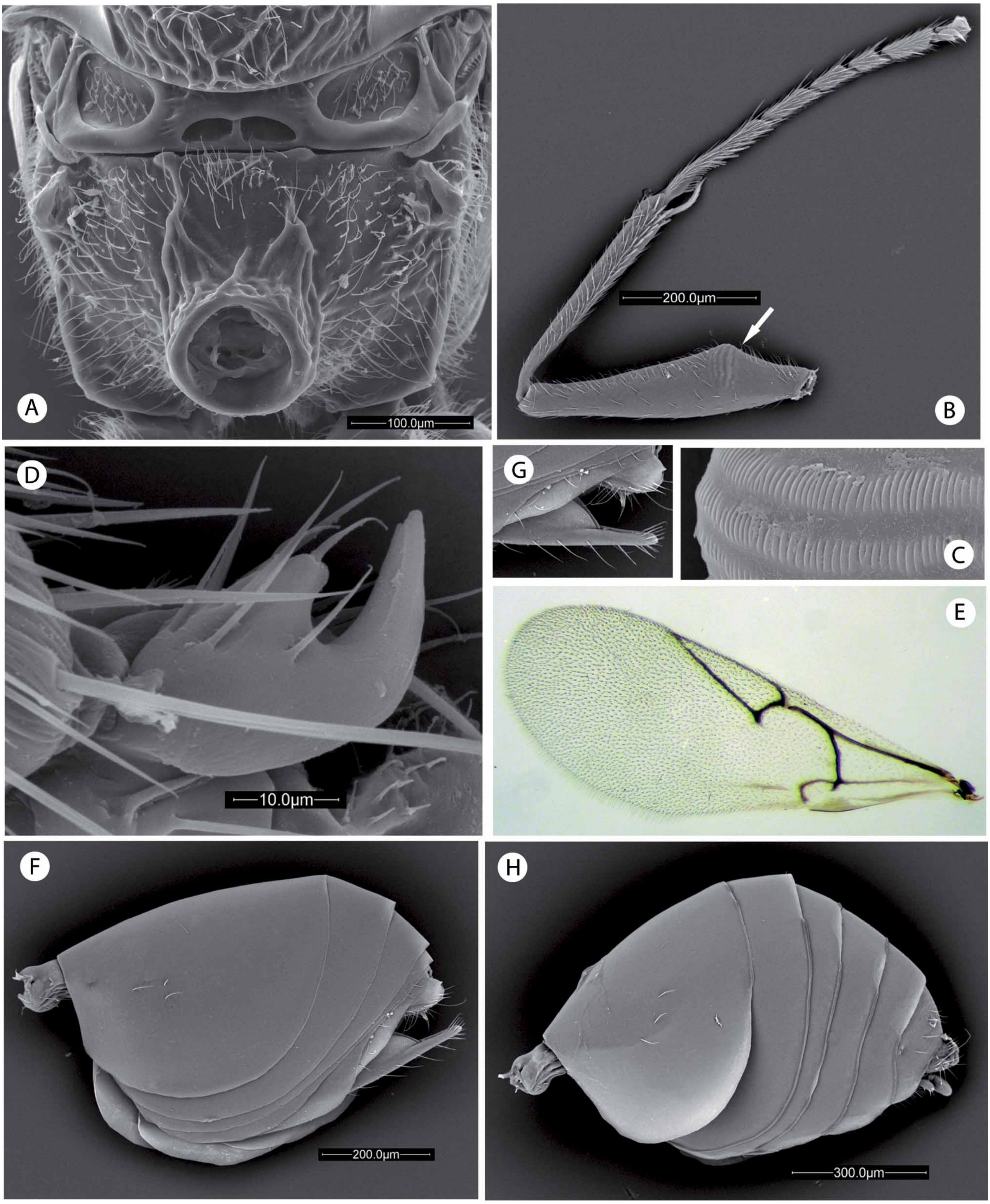

FIGURE 3. *Paraulax perplexa:* (A) Propodeum. (B) Fore leg, arrow pointing to swelling of profemur (C) Magnification of the structure of rows of sharp, closely spaced, deep costulae. (D) Metatarsal claw. (E) Forewing. (F) Female metasoma and (G) Detail of ventral spine of hypopygium. (H) Male metasoma.

Redescription. Body length (measured from anterior margin of head to posterior margin of metasoma) 1.8 mm (range 1.7–2.0; N = 2) for females; 1.6 mm (range 1.5–1.8; N = 4) for males. Coloration: female body entirely black; antennal flagellum, tarsi, pro and mesotibia and apex of femora dark brown. Forewing hyaline, veins brown. Male similar in coloration to female, but antenna and fore legs slightly paler.

Female. Head. In dorsal view 2.1 times as wide as long. Gena not expanded behind compound eye. POL 1.6 times as long as OOL, posterior ocellus separated from inner orbit of eye by about 2 times its diameter. In anterior view (Fig. 2A) head more or less rounded, 1.1 times as wide as high. Face with some sparse setae, more abundant in lower face; facial strigae present, radiating from clypeus, strong, laterally reaching ventral margin of eye and medially almost reaching ventral margin of torulus; vertical median carina absent (Fig. 2A). Frons and vertex with coriaceous sculpture; ocellar plate slightly raised; malar space 0.38 times height of compound eye. Clypeus indistinct, more or less rectangular; ventral margin slightly projecting over mandibles. Subocular impression present though not well marked. Ventrolaterally on gena 5–7 regular vertical carinae present. Anterior tentorial pits visible; epistomal sulcus and clypeo-pleurostomal lines indistinct. Torulus situated at mid-height of compound eye; transfacial line 0.9 times height of eye; distance between antennal rim and compound eye 0.5 times width of antennal socket including rim. Occiput dorsally pubescent with coriaceous-alutaceous sculpture, without dorsal occipital carina; some strong longitudinal rugae on lateral margins of head, but without distinct genal occipital carina (Fig. 2B). Posterior tentorial pits narrow, arched. Hypostomal sulci meeting slightly before hypostoma (Fig. 2B). Distance between occipital and oral foramina as long as height of occipital foramen.

Mouthparts (Fig. 2B). Mandibles exposed; right mandible with three teeth; left with two teeth. Cardo of maxilla visible, maxillary stipes 5.8 times longer than wide. Maxillary palp with five segments; last segment 3.3 times longer than wide. Labial palp with three segments.

Antenna (Fig. 2C). 0.7 times length of body, with 12 segments; flagellum widening towards apex; antennal segments with coriaceous sculpture and setae no longer than width of a segment. Placodeal sensilla visible only on F7–F10 (Fig. 2D). Relative lengths of antennal segments: 25:12:15:20:20:20:17:15:15:16:17:45; pedicel 0.9 times its width; 0.8 times length of F1; F1 1.9 times longer than wide. Ultimate flagellomere spindle-shaped, 3 times longer than wide, 1.2 times wider than penultimate, not truncate at apex.

Mesosoma. Pronotum, anterior view, almost glabrous medially, strongly pubescent laterally (Fig. 2H). Ratio of median to lateral length of pronotum 0.3. Pronotal plate distinct, 5.5 wider than long; dorsal part distinctly set off, anterolateral margin marked and somewhat projecting laterad; some strong longitudinal rugae visible in anterior and lateral view between margin of pronotal plate and surface of pronotum laterally. Admedian pronotal depressions separated by more than median length of pronotum. Posterior pronotal plate more or less rectangular, bare and smooth, ventral and lateral margins marked. Lateral surface of pronotum coriaceous, some strong, short rugae running from the lateral margin of pronotal plate (Fig. 2G).

Mesonotum. Mesoscutum (Fig. 2I) 1.2 times wider than long; with weak coriaceous sculpture, more distinct at lateral lobe, with few setae. Median mesoscutal impression absent. Notauli percurrent, straight and narrow, converging posteriorly. Separation of notauli posteriorly at transscutal fissure relatively narrow, 0.3 times width of separation at anterior margin of mesoscutum. Anteroadmedian signa visible. Mesoscutum and scutellum separated by narrow transscutal fissure. Scutellar foveae indistinct, visible only as shallow depression with some rugae (Fig. 2I). Scutellum, in dorsal view with strong rugae also present medially; in lateral view convex, with prominent rugose sculpture. Posterodorsal and posterior margins of axillula distinct. Mesopleuron (Fig. 2G) ventral to mesopleural triangle with a prominent longitudinal mesopleural impression, more or less complete, ending at margin of mesopleural triangle. Some irregular longitudinal striae and coriaceous sculpture dorsal to furrow. Mesopleuron smooth ventral to mesopleural impression. Mesopleural triangle distinctly impressed and densely pubescent; dorsal margin diffuse anteriorly, not meeting area near prepectus but meeting posterolateral margin of pronotum well below prepectus.

Metanotum (Fig. 3A). Metascutellum with distinct median constriction. Ventrally divided in two parts by a median vertical bar. Median width wider than metanotal trough. Metanotal trough smooth, pubescent.

Metapectal-propodeal complex. Metapleural sulcus (Fig. 2G) meeting posterior margin of mesopectus at about mid height of metapectal-propodeal complex. Lateral propodeal carinae narrow, parallel, subdivided into irregular carinae near nucha (Fig. 3A). Lateral and median propodeal areas smooth, pubescent. Nucha dorsally with some irregular longitudinal rugae.

Legs. Profemur with ventral swelling in basal third, wearing 4–5 rows of sharp closely spaced, deep costulae (Figs. 3B & 3C). Protarsi 1.2 times longer than protibia. Metatarsal claw with a acute basal lobe or tooth, about ¼ of length of apical tooth (Fig. 3D).

Forewing (Fig. 3E). 1.2 times longer than body. Radial cell closed along anterior margin, 3.7 times longer than wide; R1 slightly depigmented along margin of radial cell; radius (Rs) straight, reaching anterior margin of wing. Areolet absent; vein Rs+M and M almost invisible, directed towards lower half of median vein. Fringe of long setae along apical margin of wing.

Metasoma. Metasoma (Fig. 3F) shorter than head plus mesosoma; in lateral view 1.4 times longer than high; laterally compressed. Abdominal petiole smooth dorsally, ventrally with deep longitudinal grooves; about as long as high. T2 smooth and shining, covering about 2/3 of metasoma; anteromedian area of T2 with only 4–5 long setae. Projecting part of hypopygial spine 4 times longer than high; apical pubescence of hypopigial spine projecting beyond apex of spine, subapical setae longer than apical hairs, together forming a small tuft.

Male. Similar to female except as described below (size and coloration already discussed). Head as wide as high. Antenna (Fig. 2E) with 13 flagellomeres. Flagellum not widening towards apex. F2 abruptly expanded from base towards apex, apex 2.5 times wider than base. F3 slightly curved at basal third, slightly wider towards apex (Fig. 2F); F4 and following flagellomeres cylindrical, not modified. Relative length of antennomeres: 15:10:13:20:21:20:17:15:14:15:14:14:14:13:17. Placodeal sensilla present on all flagellomeres, except F1, arranged in row of 4–5 sensilla on each flagellomere. Metasoma (Fig. 3H); T2 covering ¼ of length of metasoma. Anteromedian area of T2 with group of only 3 setae.

Distribution. Chile, Concepción and Los Queules (IX and X Regiones) (Fig. 15).

Biology. Unknown. One potential host is *Nothofagus* galls induced by species of *Espinosa* Gahan, and maybe also *Aditrochus*, both ormocerine chalcids (Pteromalidae: Ormocerinae). In the collecting area of Los Queules we sampled two potential *Espinosa* host galls, both on *Nothofagus obliqua*; *Espinosa nothofagi* Gahan (Fig. 12G) and *Espinosa* sp. (Fig. 12H), identified according to De Santis *et al*. (1993). Collection data indicate a flight period in late winter and early spring (from August to October).

Remarks. Weld (1952) stated that Kieffer´s types of *perplexa* were specimens captured near Concepción, Chile, Pablo Herbst leg., with unknown habitat. The material was sent to Kieffer in different years from different localities. Hence, Kieffer inferred that the species must be abundant. The location of the types is unknown.

A neotype is here designated with the purpose of clarifying the taxonomic position of this taxon.

We further justify this nomenclatural act by the close resemblance of this species with the original, albeit somewhat short, description. Of special importance in the original description is the mention of the following diagnostic characters: “face irrégulierement ridée” but without mention of a median vertical carina; 12 antennal segments as long as the three preceding segments; 4 antennal segments of the male apically truncate; the “mesopleures finement striées”; the toothed tarsal claws. All these characters fit with the characters presented for the neotype, and does not apply to the species reared from *Aditrochus* galls that in this paper have been included in the new genus *Cecinothofagus*.

Also, the collecting locality of the neotype material is near the original locality, and the two localities (Concepción and los Queules) share the same vegetation type described as Bosque Maulino, with *Nothofagus obliqua* forest as the predominant habitat.

The neotype is deposited in the Museo Chileno de Historia Natural (Santiago de Chile).

Paraulax queulensis **Nieves-Aldrey & Liljeblad sp. nov.**
(Figs. 4A–H & 10C–D)

Type material. Holotype ♀ (in Museo Chileno de Historia Natural, Santiago de Chile, card mounted), CHILE, El Maule, VII Región, Cauquenes, Reserva Nacional Los Queules, 35º59´10´´S, 72º42´30´´O, 420 m;

caught with a Malaise trap operating in a fragment of native forest, 21.ix/23.x.2005. J.L. Nieves-Aldrey & A. Grez leg. Paratypes: 1♂ same data as holotype, except collected 22/08-27/09-2006. In MNCN; 1♂, Chile, Talca, Altos de Vilches. 18-25/X/1964, C. C. Porter leg. (MCZC). 1♀, Chile, Villarrica, Flor del Lago Ranch, canopy fogging of *Nothofagus obliqua*, 12/XII/2001, Arias et al. leg. (UCRC).

Etymology. Named after the locality where it was collected, Reserva Nacional Los Queules.

Diagnosis. Closely allied to *P. perplexa* being similar in color, habitus and a majority of morphological characters. Differs by a more elongate body (Figs. 4A & 10C), in the female 4 times longer than high; mesosoma 1.6 longer than high and metasoma 1.9 longer than high. Mesosoma also more dorsoventrally depressed (Fig. 4A). Pronotum laterally 1.5 longer than high (only 1.1 in *P. perplexa*). Longitudinal costulae running from lateral margin of pronotal plate to lateral surface of pronotum conspicuous and longer in *P. queulensis* (Fig. 4B). Sculpture of mesoscutum coriaceous, striate (Fig. 4C). Scutellar foveae more or less discernible even if shallow (Fig. 4C). Mesopleural horizontal impression in lower part of mesopleuron meeting anterior margin of mesopleuron at a point further from meeting of anterior mesopleural margin and posterior pronotal margin (Fig. 4B). Radial cell relatively long; 4.5 times longer than wide (Fig. 4H). Antenna also differing; pedicel of female antenna 1.4 times longer than wide, as long as F1; F2 of male antenna not abruptly expanded towards apex, only excavated at base with F3 similar to F2 (Fig. 4G) (these two segments not at all like in males of *P. perplexa*).

Description. Body length 2.1 mm (N = 1) for females; 2.5 mm (N = 1) for males. Color of body, coxae and first two antennomeres in both sexes black; antennal flagellum, tarsi, pro and mesotibia and apex of femora dark brown. Forewing hyaline, veins brown.

Female. Head, in dorsal view 1.9 times wider than long. Gena slightly expanded behind compound eye. POL 1.7 times longer than OOL, posterior ocellus separated from inner orbit of eye by about 2 times its diameter. Head in anterior view more or less oval. Face with sparse setation, denser in lower face; strong facial strigae radiating from clypeus, laterally reaching ventral margin of eye and centrally almost reaching ventral margin of toruli; vertical median carina absent. Upper face (frons) and vertex with shining coriaceous sculpture. Clypeus indistinct, more or less rectangular; ventral margin slightly projecting over mandibles. Subocular impression present though not well marked. About 10 regular vertical carinae present ventrolaterally in depression on gena (Fig. 4B). Occiput dorsally pubescent with coriaceous-alutaceous sculpture.

Antenna (Fig. 4F) 0.6 times length of body, with 12 antennomeres; flagellum slightly widened towards apex; antennal segments with coriaceous sculpture and setae not longer than width of a segment. Placodeal sensilla visible only on flagellar segments F7–F10. Ratio of antennal segment lengths: 15:10:9:15:16:16:14:12:12:13:12:31; pedicel 1.4 times longer than wide; as long as F1; F1 2.2 times longer than wide. Apical flagellomere spindle-shaped, 3 times longer than wide, 1.4 times wider than penultimate, not truncate at apex.

Mesosoma. Pronotum, anterior view, almost glabrous in median area, strongly pubescent laterally. Pronotal plate distinct, dorsal part distinctly set off, anterolateral margins prominent and moderately projecting laterally. Pronotum in lateral view 1.5 times longer than high. Lateral surface of pronotum coriaceous, with a few strong, long rugae running horizontally from lateral margin of pronotal plate to posterior margin of pronotum (Fig. 4B).

Mesonotum. Mesoscutum as wide as long; sculpture coriaceous-striate, more prominent on lateral lobe (Fig. 4C). Median mesoscutal impression indicated only close to transscutal fissure. Notauli percurrent, straight and narrow, converging posteriorly.Separation of notauli posteriorly at transscutal fissure 1/3 of separation at anterior margin of mesoscutum. Anteroadmedian signa just visible. Scutellar foveae discernible (Fig. 4C), shallow, with some rugae, confluent, indistinctly separated. Scutellum in dorsal view with strong transverse rugae, more irregular in posterior 1/5 of scutellum. Mesopleuron (Fig. 4B) with a marked longitudinal impression, complete from anterior to posterior margins of mesopleuron. Some irregular longitudinal striae and area of coriaceous sculpture present above mesopleural impression. Smooth area

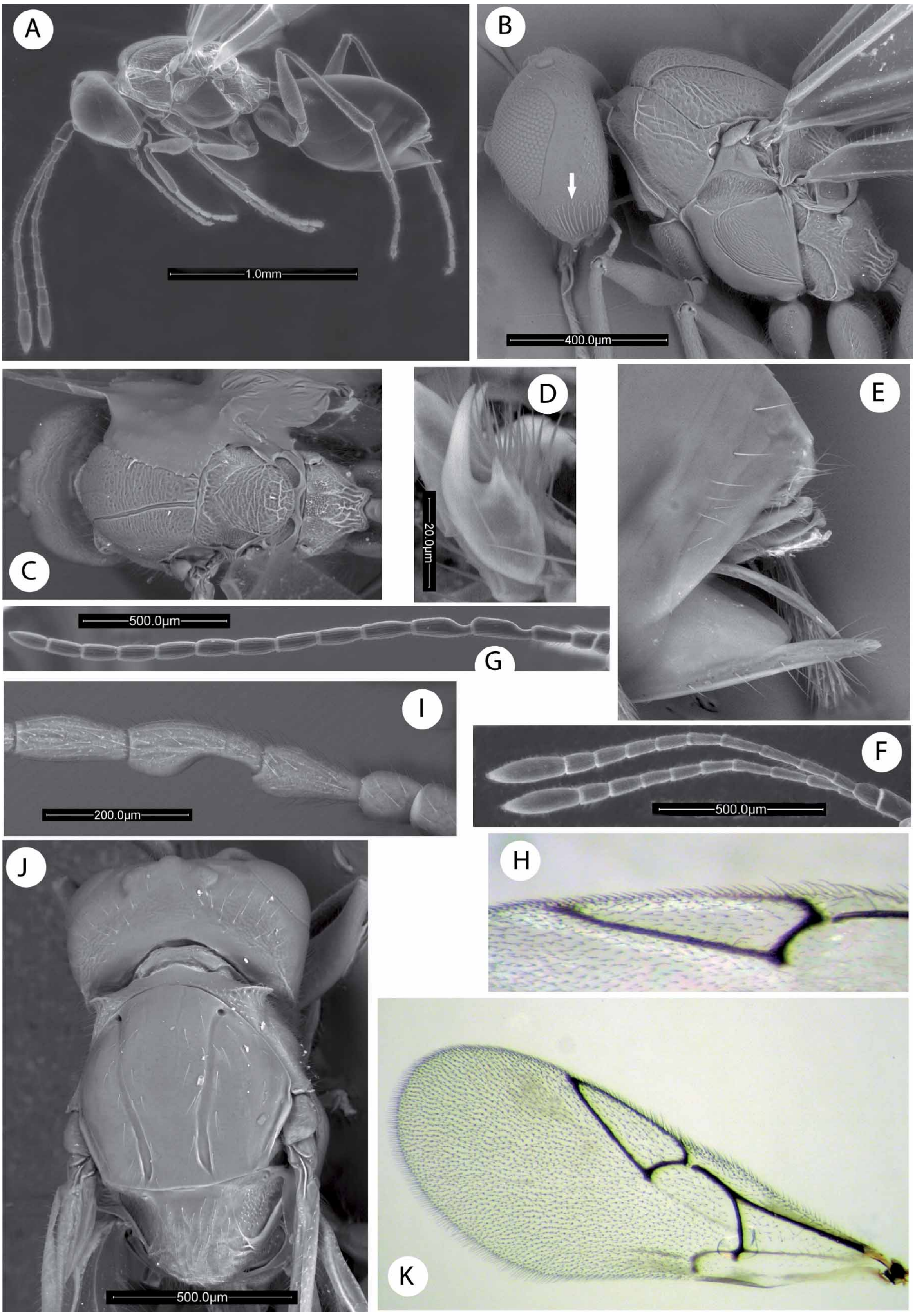

FIGURE 4. *Paraulax queulensis* **n. sp.** and *Cecinothofagus ibarrai* **n. sp.**: (A–H) *P. queulensis*: (A) Habitus lateral view. (B) Head and mesosoma lateral view. (C) Mesosoma dorsal view. (D) Metatarsal claw. (E) Ventral spine of hypopygium. (F) Female antennae. (G) Male antenna. (H) Forewing. (I–K) *Cecinothofagus ibarrai*. (I) Male antenna. (J) Mesosoma dorsal view. (K) Forewing.

ventral to mesopleural impression. Mesopleural triangle rhomboidal, distinctly impressed and densely pubescent; its dorsal margin diffuse at anterior end, not meeting area near prepectus but meeting posterolateral margin of pronotum well below prepectus.

Metanotum (Fig. 4C). Metascutellum distinctly constricted in median area. Area posterior to median constriction of metascutellum not divided by a median vertical bar. Metascutellum as wide as a metanotal trough at center. Metanotal trough smooth, pubescent.

Lateral propodeal carinae narrow, parallel, subdivided into irregular carinae near nucha. Lateral and median propodeal areas smooth, pubescent. Nucha dorsally with strong, irregular longitudinal rugae.

Legs. Profemur with ventral swelling in basal third, with 4–5 rows of sharp, closely spaced, deep costulae. Metatarsal claws with basal acute lobe or tooth, about one fifth of length of apical tooth (Fig. 4D).

Forewing (Fig. 4H), slightly longer than body. Radial cell closed along anterior margin, 4.4 times longer than wide; R1 slightly depigmented along posterior one half of radial cell; radius (Rs) straight, reaching anterior margin of wing. Areolet absent; vein Rs+M and M invisible. Fringe of long setae along apical margin of wing.

Metasoma. Metasoma (Fig. 4A) slightly shorter than head plus mesosoma; in lateral view 1.7 times longer than high; laterally compressed. Abdominal petiole dorsally smooth, ventrally with deep longitudinal grooves; about as long as high. T2 smooth and shining, covering about half of metasoma; anteromedian area of T2 with only 4–5 long setae. Projecting part of hypopygial spine 4 times longer than high; apical pubescence of hypopigial spine projecting beyond apex, subapical setae longer than apical ones, forming a small tuft (Fig. 4E).

Male. Similar to female except for the following: Antenna (Fig. 4G) with 15 antennomeres. Flagellum not widened towards apex. F1 cylindrical, 1.6 longer than pedicel; F2 and F3 excavated and curved in basal third; not expanded towards apex; outer apical margin of flagellum straight; about 2.5 times longer than pedicel. Relative length of antennomeres: 15:10:16:24:24:20:18:17:16:15:16:15:14:13:15. Placodeal sensillae present on all flagellomeres except F1, arranged in a row of 4–5 sensillae on each flagellomere.

Distribution. Chile, From Talca, in the north, to Villarrica (Fig. 15). As *P. perplexa*, it seems to be associated with *Nothofagus obliqua* forests.

Biology. Unknown. Likely associated with galls induced by *Espinosa* on *N. obliqua*.

Flight period is late winter and early spring like *P. perplexa* (viii, ix and x).

Paraulax ronquisti **Nieves-Aldrey & Liljeblad sp. nov.**

(Figs. 5 & 10E)

Type material. Holotype ♂ (in Museum, Berlin, pin mounted, Green label: CHILE, Mittel Chile, Contulmo, 20.10.1903, Schöneman S, leg. White label: Från låda 35. *Paraulax sp* ♂ det Ronquist 91.

Etymology. Named in honour of our friend Fredrik Ronquist, one of the most prominent scientists working with Cynipoidea.

Diagnosis. This new species differs from *P. perplexa* and *P. queulensis* by the red-brown color (Fig. 10E), shape of the antennal male flagellomeres F3 and F4 (Fig. 5A), the faint notauli and the predominantly smooth and shining mesopleuron. It has a similar elongate body like *P. queulensis*, but the coloration, antennal configuration and body sculpture differ as outlined above.

Description. Body length 2.2 mm (N = 1). Coloration of body and legs red-brown, tarsi and antenna paler, yellowish. Forewing hyaline, veins light, yellowish.

Male. Head, in dorsal view 1.9 times wider than long. Gena slightly expanded behind compound eye. POL 2 times longer than OOL, posterior ocellus separated from inner orbit of eye by about 1.5 times its diameter. Head in anterior view more or less oval. Face with white setae, much denser in lower face; strong facial strigae radiating from clypeus,, laterally reaching ventral margin of eye and almost reaching ventral margin of toruli in median area; vertical median carina absent. Upper face (frons) and vertex with shining, almost smooth sculpture. Clypeus indistinct, more or less rectangular; ventral margin slightly projecting over mandibles. Subocular impression not visible. About 10 regular vertical carinae present ventrolaterally in depression on gena.

Antenna 0.6 times length of body, with 15 antennomeres. Flagellum not widening towards apex. F1 cylindrical, not excavated basally, slightly broadened towards apex, 1.4 times longer than pedicel; F2 and F3 excavated, slightly curved in basal third and inflated at apex, outer apical margin curved (Fig. 5A); less than 2 times length of pedicel. Relative length of antennomeres: 22:13:14:19:20:21:20:17:18:19:16:15:15:15:20. Placodeal sensillae present on F5–F13.

Mesosoma. Pronotum with distinct pronotal plate; dorsal part distinctly set off, anterolateral margin marked and moderately projecting laterally. Pronotum in lateral view 1.7 times longer than high. Lateral surface of pronotum pubescent, almost entirely smooth and shining, only a few short, horizontal rugae running from lateral margin of pronotal plate to posterior margin of pronotum.

Mesonotum. Mesoscutum in dorsal view (Fig. 5B) 1.1 times longer than wide; coriaceous-imbricate sculpture. Median mesoscutal impression invisible. Notauli inconspicuous. Anteroadmedian signa visible. Scutellar foveae shallow, confluent, forming a transverse depression. Scutellum in dorsal view with coriaceous rugose sculpture. Mesopleuron (Fig. 5C) with a longitudinal mesopleural impression running on posterior half of mesopleuron. Area surrounding mesopleural impression almost entirely smooth and shining. Mesopleural triangle not distinctly impressed basally, pubescent; dorsal margin meeting area near prepectus. Metanotum. Metascutellum distinctly constricted medially. Not divided into two parts by median vertical bar below median constriction. Lateral and median propodeal areas smooth, pubescent. Nucha with strong, irregular, longitudinal rugae dorsally.

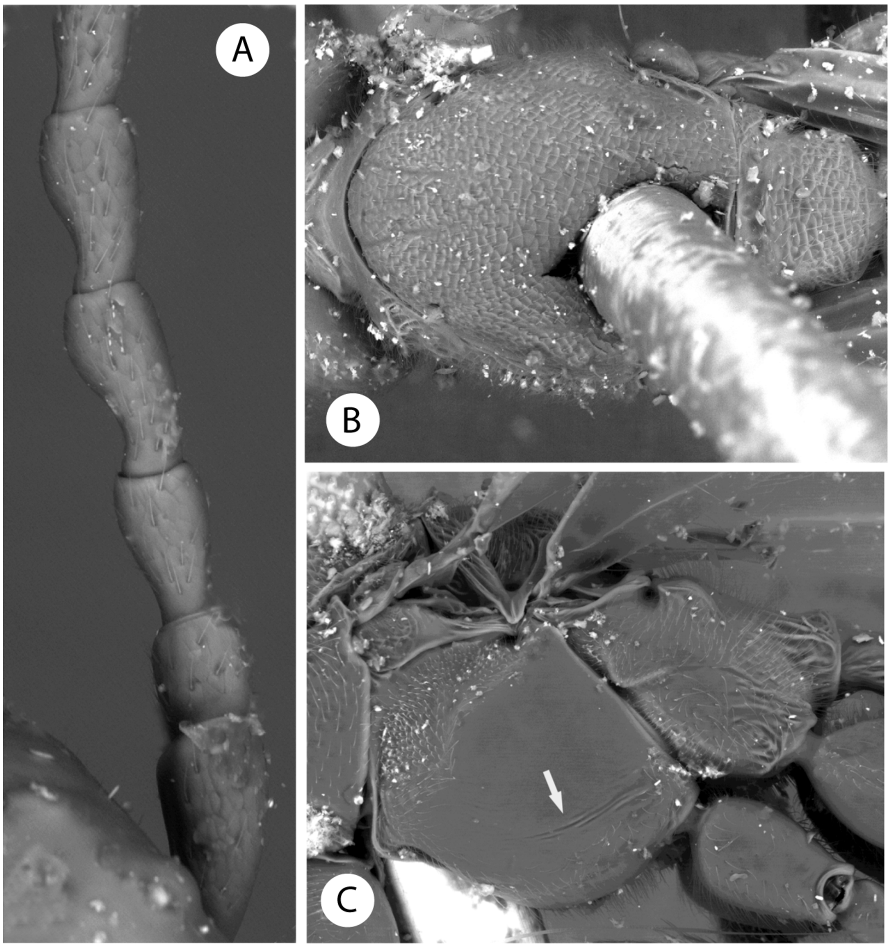

FIGURE 5. *Paraulax ronquisti:* (A) Male antenna. (B) Mesosoma dorsal view. (C) Mesopleuron.

Forewing slightly longer than body. Radial cell 3 times longer than wide, closed along anterior margin but R1 slightly depigmented along margin of radial cell; radius (Rs) straight, reaching anterior margin of wing. Areolet absent; vein Rs+M and M invisible. Fringe of long setae along apical margin of wing.

Metasoma. Metasoma as long as mesosoma. Abdominal petiole 1.5 times longer than high. T2 smooth and shining.

Female. Unknown.

Distribution. Recorded only in Contulmo, between Concepción and Valdivia, central Chile (Fig. 15).

Biology.: Unknown.

Cecinothofagus Nieves-Aldrey & Liljeblad, gen. n.

Type species: *Cecinothofagus gallaelenga* Nieves-Aldrey & Liljeblad, new species, by present designation

Etymology. An abbreviation alluding to the particle *Ceci*- (meaning cecidium or gall) and the name of the host plant genus *Nothofagus* (the southern beeches).

Diagnosis. Differs from *Paraulax* by the following:

Distinct median vertical carina extending from ventral margin of clypeus to nearly reaching ventral margin of antennal sockets (Figs. 6A & 8A). Facial strigae radiating from lateral clypeus, laterally only reaching ventral margin of compound eye. Ventral part of clypeus straight, not projecting over mandibles (Fig. 6A). Lateral, sharp occipital carina present. Last antennal flagellomere 1.5 to 1.7 times longer than wide (Fig. 6E). F3 of male antenna not modified (Fig. 6F).

Longitudinal costulae running from lateral margin of pronotal plate to lateral surface of pronotum: absent or very short (Fig. 7A). Notauli sinuate, relatively wider posteriorly, not strongly converging (Fig. 6D); distance between notauli at transcutal fissure >0.5 times separation at anterior margin of mesoscutum. Scutellar foveae absent (Fig. 6D); scutellum with rugulose-rugose sculpture present marginally but more or less erased in median area. Area above mesopleural impression smooth or weakly coriaceous, usually without longitudinal striae (Figs. 7A & 9B). Metascutellum narrower than a metanotal trough in middle. Claws simple, sometimes with a blunt, short basal lobe or with an acute, small lobe measuring less than 1/6 times length of apical tooth (Fig. 9D). 3tg of medium size, 0.3–0.5 times length of metasoma. Lateral pubescence on T2 dense. Length of projecting part of hypopygial spine (beyond attachment of lateral flap) <3 times height.

Description. Head. Slightly pubescent; some long, scattered setae on upper frons, vertex and face; some setae also dorsally on occiput, along oral fossa and gena. Gena not expanded behind compound eye. A vertical median carina present (Figs. 6A & 8A); facial strigae radiating from clypeus extending laterally, reaching ventral margin of eye; almost absent in median area. Upper face (frons) and vertex usually shining, with delicate, coriaceous sculpture. Clypeus indistinct, ventral margin straight, not projecting over mandibles (Fig.8A). Subocular impression present, not well marked. 5–7 regular vertical carinae present ventrolaterally on gena (Fig. 6H). Anterior tentorial pits visible; epistomal sulcus and clypeo-pleurostomal lines indistinct. Occiput without dorsal occipital carina; genal carina present (Fig. 6B). Hypostomal sulci meeting slightly before hypostoma.

Antenna. Female: 12 segments (Fig. 6E); flagellum broadening towards apex; with relatively long, erect setae and placodeal sensilla visible only on flagellar segments F7–F10. Ultimate flagellomere broader than penultimate; more or less spindled-shaped, with a rounded end. Male: 15 segments (Fig. 6F). Flagellum not broadening towards apex. F1 cylindrical, F2, and usually also F3, excavated and curved in basal third (Figs. 6G & 8D) sometimes apically expanding (Fig. 4I). Placodeal sensillae present on all flagellomeres.

Pronotum. Pronotal plate distinct (Fig. 6C, 8G), usually without sculpture; dorsal part distinctly set off, anterolateral margin marked and moderately projecting laterad. Admedian pronotal depressions widely separated. Lateral surface of pronotum coriaceous, withouth longitudinal rugae (Figs. 7A & 8B).

Mesoscutum almost entirely smooth and shining or with delicate or weak coriaceous sculpture, more marked on lateral lobe (Fig. 8A). Some long setae scattered along notauli. Median mesoscutal impression absent (Fig. 6D). Notauli percurrent, well separated posteriorly; sometimes ending before transscutal fissure. Anteroadmedian signa visible. Transscutal fissure narrow. Scutellar foveae indistinct, visible only as shallow, usually smooth depression (Fig. 6D). Scutellum in dorsal view with weak rugae. Posterodorsal and posterior margins of axillula distinct. Mesopleuron beneath mesopleural triangle with marked, longitudinal mesopleural impression, usually incomplete, not reaching margin of mesopleural triangle (Fig. 7A). Area surrounding mesopleural impression almost entirely smooth, withouth visible sculpture. Metascutellum distinctly constricted medially.

Metapectal-propodeal complex. Metapleural sulcus (Fig. 7A) meeting posterior margin of mesopectus at about mid height of metapectal-propodeal complex. Lateral propodeal carinae narrow, parallel. Lateral and median propodeal areas smooth, pubescent (Fig. 7B). Nucha dorsally with some irregular longitudinal rugae.

Legs. Profemur with ventral swelling in basal third, with 4–5 rows of sharp, closely spaced, deep costulae (Fig. 7C). Metatarsal claw simple; sometimes with blunt, short basal lobe or with acute, small lobe less than 1/6 of length of apical tooth (Fig. 9D).

Forewing. Radial cell closed along anterior margin (Figs. 7F & 8H); R1 not or only slightly depigmented along radial cell; areolet absent; vein Rs+M and M weak but visible, directed towards lower half of median vein. Fringe of long setae along apical margin of wing.

Female metasoma laterally compressed (Fig. 7D). Abdominal petiole dorsally smooth, ventrally with deep, longitudinal grooves, about as long as high. T2 smooth and shining, covering about 2/3 of metasoma; anteromedian area of T2 with group of long setae. Projecting part of hypopygial spine about 2–3 times longer than high; apical pubescence of hypopigial spine projecting beyond apex, subapical setae longer than apical ones, together forming a small tuft (Figs. 7D & 9E).

Included species

C. gallaecoihue sp. n.
C. gallaelenga sp. n.
C. ibarrai sp. n.

Distribution. Chile and Argentina, following the distribution of the host plants: *Nothofagus dombeyi* and *N. pumilio*. These species of southern beech are more common around Concepcion down to the southernmost regions of Chile, below parallel 35 (Fig. 15).

Biology. All three species of *Cecinothofagus* inhabit galls induced by *Aditrochus* species (Chalcidoidea: Pteromalidae) on *Nothofagus*. Cynipids reared from these galls have generally been cited as the likely gall inducers (Ronquist 1999; Csoka *et al*. 2005). Our field observations, however, including dissections of fresh galls, are conclusive in showing that these species of *Cecinothofagus* were not the gall inducers but rather lethal inquilines or parasitoids of the *Aditrochus* larvae.

Aditrochus species belong to the pteromalid subfamily Ormocerinae (tribal subdivision no longer in use) which are traditionally treated as basal pteromalids. The body is mostly non-metallic and have an antenna with 13 fully developed segments and only one anellus. Its habitus in some aspects is more cynipoid-like than chalcidoid-like. As far as is currently known, most ormocerini genera include species which are believed to develop inside galls as parasites of other gall makers. It is not clear whether these really are parasitoids of the true gall-inducer or rather the gall-inducer themselves, or maybe inquilines. At least in one ormocerine species, however, the gall inducing behaviour has been demonstrated (Shorthouse *et al*. 1986). This is *Hemadas nubilipennis* (Ashmead) which induces galls on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*).When dissecting young galls on *Nothofagus* we always found the *Aditrochus* larvae or pupae in the central cell of the gall. In older galls, however, we also found larvae or pupae belonging to *Cecinothofagus* or *Plectocynips* (Figitidae). Despite this, there is a single observation by Pujade-Villar &

Hanson (2006) reporting a *Paraulax* emerging from peripherical cells in a gall induced by *Aditrochus*, thus suggesting *Paraulax* to be an inquiline. This behavior, however, was never observed by us in any of the several dozens of galls dissected. On the contrary, of all our examined cases we never found any walls separating secondary cells as is the case for some lethal inquiline species of the tribe Synergini (Cynipidae). It seems more likely that the species of *Cecinothofagus* is a parasitoid or a solitary lethal inquiline. The adult *Cecinothofagus* did always emerge from the solitary central host cell.

Remarks. The new genus *Cecinothofagus* is morphologically well defined and easily can be distinguished from the species of *Paraulax*. Molecular data on the monophyly of this genus is contradictory however. While the 28S marker is clearly in support of a monophyletic *Cecinothofagus*, the combined analysis (28S and COI) fails to come up with this grouping, instead presenting it as paraphyletic (Fig. 14). It should be emphasized, however, that only one of the three *Paraulax* species was included in the molecular analysis and no nuclear markers could be included, suggesting that the current results should be interpreted with caution.

Key for the identification of species of *Cecinothofagus*

1. Pedicel distinctly shorter than F1 (Fig. 8B); F1 more than two times longer than wide. male F2 slightly or strongly expanded distally (Figs. 8D & 4I). Mesopleuron smooth above mesopleural impression, without visible sculpture (Fig. 9B). Mesoscutal pubescence relatively long, distributed along notauli, scarce or absent anteriorly on median lobe of mesoscutum (Fig. 9A). Mesopleural impression short, incomplete, reduced anteriorly and posteriorly (Fig. 9B). Notauli reaching or almost reaching transscutal fissure. Body shiny black; coxae black 2
- Pedicel as long as or slightly longer than F1 (Fig. 6E). F1 less than two times longer than wide. F2 of male antenna only slightly expanded distally (Fig. 6G). Mesopleuron with weak coriaceous sculpture and some horizontal rugae above mesopleural impression (Fig. 7A). Mesoscutal pubescence more evenly distributed and denser, especially anteriorly on median lobe of mesoscutum (Fig. 6D). Mesopleural impression relatively long, almost reaching ventral margin of mesopleural triangle (Fig. 7A). Notauli not reaching transcutal fissure (Fig 6D). Body dull, black or brownish; coxae brown or reddish brown .... *C. gallaecoihue*

2. Male F1 not broadened distally; F2 only slightly excavated basally and almost not expanded at all apically (Fig. 8D). Female F10 2 times longer than wide (Fig. 8B). Notauli reaching transscutal fissure (Fig. 9A). Vein R1 well pigmented along margin of radial cell; Rs+m and M visible (Fig. 8H). In leaf galls on *Nothofagus pumilio* (Figs. 12E & 12F) .... *C. gallaelenga*
- Male F1 broadened toward apex; F2 excavated basally and strongly expanded towards apex (Fig. 4I). Female F10 about 2.5 times longer than wide. Notauli interrupted close to transscutal fissure (Fig. 4J). Vein R1 less marked along margin of radial cell, vein M invisible (Fig. 4K). In bud galls on *Nothofagus dombeyi* (Fig. 12C) ... *C. ibarrai*

Cecinothofagus gallaecoihue **Nieves-Aldrey & Liljeblad sp. nov.**

(Figs. 6, 7, 11A & 11B)

Type material. Holotype ♀ (in Museo Chileno de Historia Natural, Santiago de Chile, card mounted, CHILE, Osorno, 40º 31´26.09´´S 73º06´08.61´´O, 70 m; ex gall on *Nothofagus dombeyi* (Mirb.) Blume “coihue” (Nothofagaceae), gall collected 30.xii.1993. insect emerged i.94, H. Ibarra leg. Paratypes: 3♂, 1♀ same data as holotype. (males emerged xi, 1993). One paratype ♂ in MCHN, the remaining paratypes in Museo Nacional Ciencias Naturales, Madrid (Spain). Non-type material: 1 ♂, Chile, Lago Frio, Coyhaique, 21–22.i.1961. L. Oena leg (AEIG); 1♀, Chile, Cautin, 10 km S. Pucon, Parque Nacional Volcán Villarrica, 15.xii.1984. S. & J. Peck leg (CNC); 1 male, Chile, Ñuble pro. Las Trancas, 19.5 km ESE Recinto, 1250 m., 10.xii.1982. Trap in *Nothofagus forest*. A. Newton, M. Thayer leg. (CNC); 1♀, Chile, Ñuble, Los Trancos, 16-19.i.1972, 1300m. I. Pena leg. (CNC); 1♀, Chile, P:N. Nahuelbuta, 1168m, 8.ii.2005, reared from galls *Nothofagus sp*. UCR AToL (UCRC). Other material: 1♂, 1♀ of the type series were dissected for SEM observation. Puerto Varas-Ensenada, ex gall *Aditrochus coihuensis* on *Nothofagus dombeyi*; collected 2.xii.2006, J.L. Nieves-Aldrey leg. 1 ♂ in ethanol (same data type material).

Etymology. Named after its biology, a species inhabiting a gall on “coihue”, the common name of its host plant *Nothofagus dombeyi*.

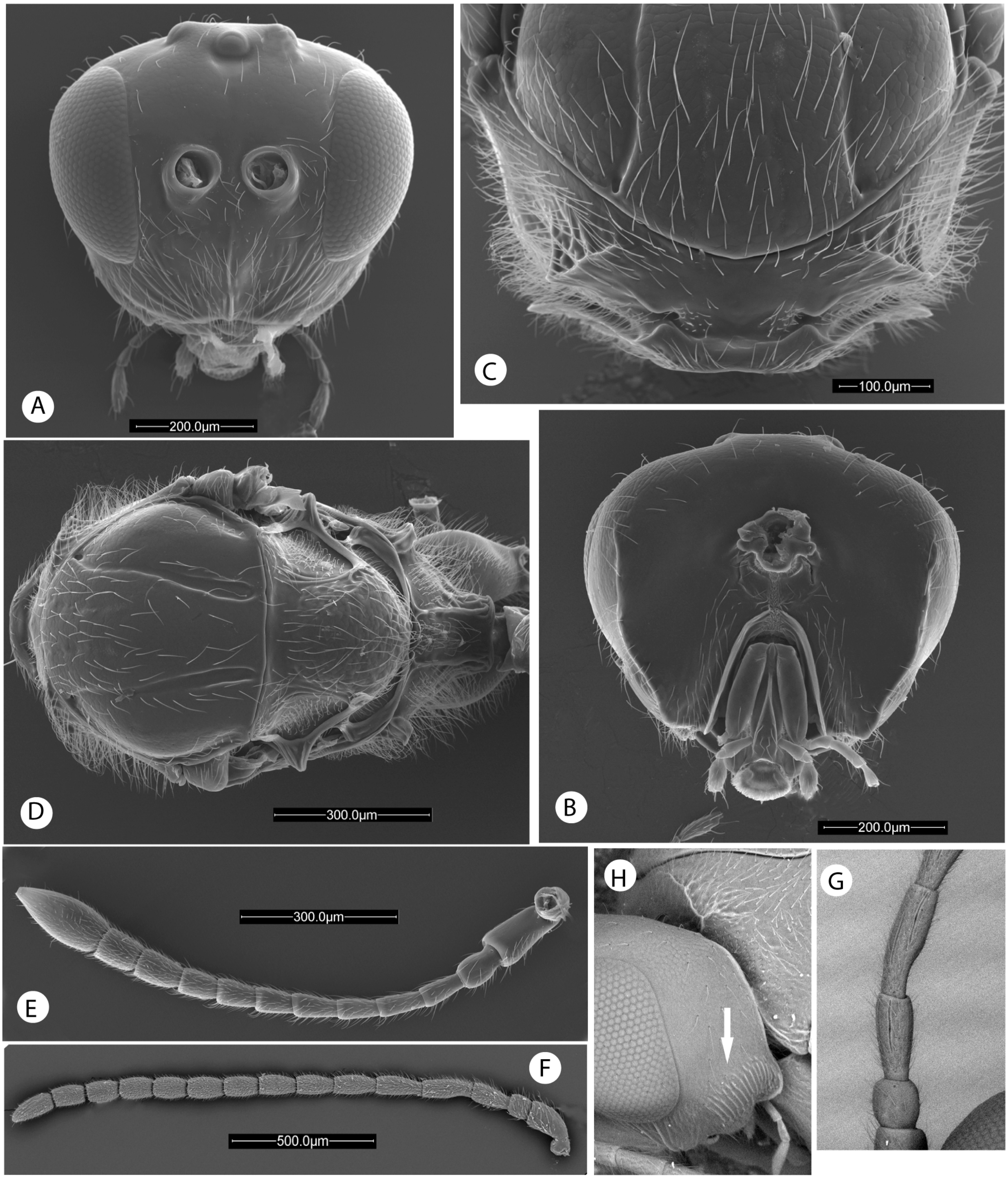

FIGURE 6. *Cecinothofagus gallaecoihue* **n. sp.**: (A) Head anterior view. (B) Head posterior view. (C) Pronotum anterior view. (D) Mesosoma dorsal view. (E) Female antenna. (F) Male antenna and (G) detail of basal flagellomeres. (H) Head lateral view showing vertical carinae on gena.

Diagnosis. A species closely allied with *Cecinothofagus gallaelenga*, from which it differs by the predominantly red-brown color, the denser and more regularly distributed mesoscutal pubescence, conspicuous anteriorly on the median lobe of the mesoscutum, mesopleural impression relatively long, almost reaching the ventral margin of the mesopleural triangle and the notauli not reaching the transcutal fissure. In addition, these two species are well differentiated by their biology: *C. gallaecoihue* attacks only bud galls of *Aditrochus coihuensis* on *Nothofagus dombeyi*.

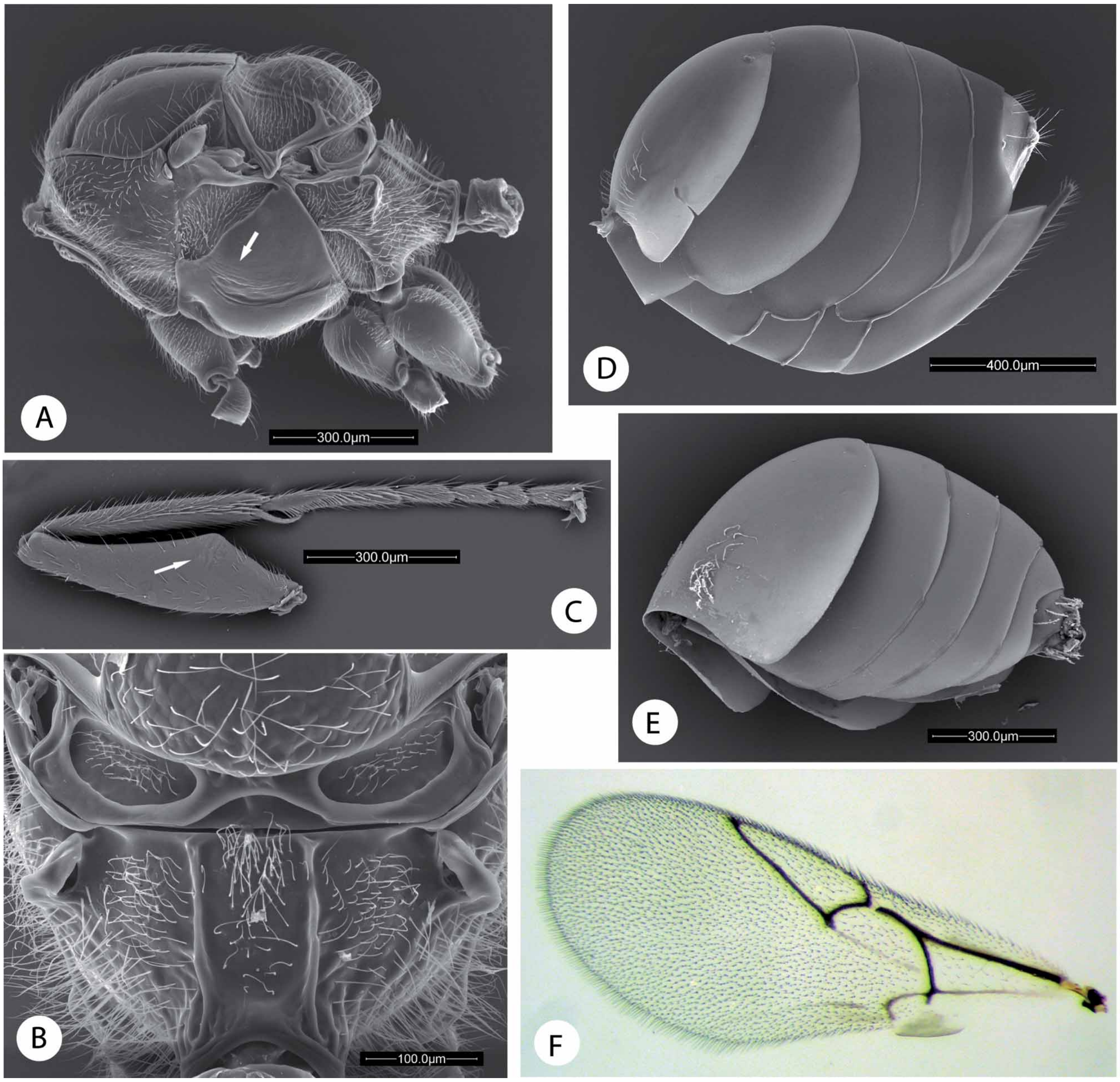

FIGURE 7. *Cecinothofagus gallaecoihue* **n. sp.**: (A) Mesosoma lateral view. (B) Propodeum. (C) Foreleg. (D) Female metasoma lateral view. (E) Male metasoma. (F) Forewing.

Description. Body length 2.7 mm (N = 2) for females; 2.3 mm (range 2.2–2.3; N = 3) for males. Coloration of females, head and metosoma black, except lower face and apex of mandibles reddish; metasoma blackish or dark brown; antennal flagellum yellowish brown, legs dark brown or reddish brown, with apex of femora, tibiae and tarsi mostly dark yellowish. Forewing hyaline, veins light brown. Male similar in coloration to female, but varying from a much lighter coloration in one specimen to other predominantly black individuals.

Female. Head in dorsal view 2 times wider than long. Gena not expanded behind compound eye; in dorsal view almost as long as length of compound eye. POL 2 times longer than OOL, posterior ocellus separated from inner orbit of eye by about 2 times its diameter. Head in anterior view (Fig. 6A) more or less trapezoid, 1.2 times wider than high, lateral margin of gena not forming a continuous arch with outer margin of compound eye. Face with a few long setae, denser in lower face and almost lacking in median area on frons; facial strigae radiating from clypeus absent in median area; laterally well marked, reaching close o ventral margin of compound eye; strong vertical median carina present, running from ventral margin of clypeus almost reaching ventral margin of toruli (Fig. 6A). Upper face (frons) almost entirely smooth and shining; vertex with delicate, almost obsolete, coriaceous sculpture. Ocellar plate slightly raised; malar space about 0.2 times height of compound eye. Clypeus indistinct, ventral margin straight, not incised. Subocular impression present but not well marked. 5–7 regular vertical carinae present ventrolaterally on gena (Fig. 6H). Anterior tentorial pits conspicuous; epistomal sulcus and clypeo-pleurostomal lines indistinct. Antennal socket (torulus) situated a little below mid-height of compound eye; distance between antennal rim and compound eye 0.5 times length width of antennal socket including rim. Occiput dorsally pubescent with coriaceous sculpture, without dorsal occipital carina, but a sharp well marked genal occipital carina present (Fig. 6B). Posterior tentorial pits narrow, slit-like. Hypostomal sulci meeting at hypostoma. Distance between occipital and oral foramina 0.6 times height of occipital foramen.

Mouthparts (Fig. 6B). Mandibles strong, exposed; right mandible with three teeth; left with two teeth. Cardo of maxilla visible, maxillary stipes about 2.3 times longer than wide. Maxillary palp five-segmented. Labial palp three-segmented. Lateral margin of oral fosa with a band of 3–4 rows of white setae.

Antenna (Fig. 6E) Half as long as body, with 12 antennomeres; flagellum broadened towards apex; last flagellomere distinctly wider than penultimate; truncate at apex. Antennomeres with sparse setation, shorter than width of a basal flagellar segment. Placodeal sensilla indistinct, visible only on flagellar segments F7–F10. Relative length of antennal segments: 26:18:17:19:17:18:15:16:15:19:17:40; pedicel 1.4 times longer than wide; F1 1.8 times longer than wide. Ultimate flagellomere 2.1 times longer than wide, 1.3 times wider than penultimate and 2.3 times longer than F9, ending in a semicircular, truncate apex.

Mesosoma. Pronotum in anterior view almost glabrous medially but strongly pubescent laterally (Fig. 6C). Ratio of length of pronotum medially/length laterally 0.4. Pronotal plate distinct; dorsal part distinctly set off, anterolateral margin marked and moderately projecting laterad; no longitudinal rugae visible in lateral view along lateral margin of pronotal plate to lateral surface of pronotum, but some visible in anterior view. Admedian pronotal depressions oval/transverse, open laterally, separated by as much as median length of pronotum. Posterior pronotal plate more or less rectangular, smooth and with long setae, ventral and lateral margins marked. Lateral surface of pronotum smooth; with sparse, white pubescence.

Mesonotum. Mesoscutum (Fig. 6D) 1.2 times wider than long; shining, without marked sculpture, at most some superficial, delicately coriaceous sculpture present. Long setae running along margins of notauli and on anteriomedian and median area of mesoscutum. Median mesoscutal impression absent. Notauli percurrent, sinuate, not strongly converging posteriorly, not reaching transscutal fissure (Fig. 6D). Posterior separation of notauli at transscutal fissure relatively wide, >0.5 wider than separation at anterior margin of mesoscutum. Anteroadmedian signa visible. Mesoscutum and scutellum separated by a narrow transscutal fissure. Scutellar foveae indistinct, visible only as shallow, smooth and glabrous depression (Fig. 6D). Scutellum in dorsal view, more or less pentagonal; in lateral view strongly convex. Dorsal surface of scutellum coriaceous with some rugae more marked on lateral and posterior areas while almost absent in median area. Posterodorsal and posterior margins of axillula distinct. Mesopleuron (Fig. 7A) beneath mesopleural triangle smooth and glabrous. Mesopleural triangle distinctly impressed and densely pubescent; dorsal margin diffuse at anterior end, not reaching area near prepectus but reaching posterolateral margin of pronotum well below prepectus. Horizontal furrow in lower part of mesopleuron present, relatively wide and complete, almost reaching ventral margin of mesopleural triangle. Small band of almost obsolete longitudinal sculpture visible above horizontal furrow.

Metanotum (Fig. 7B). Metascutellum distinctly constricted medially. Area posterior to median constriction of metascutellum not divided by a median vertical bar. Metascutellum medially narrower than metanotal trough. Metanotal trough smooth, pubescent.

Metapectal-propodeal complex. Metapleural sulcus (Fig. 7A) meeting posterior margin of mesopectus at about mid height of metapectal-propodeal complex. Lateral propodeal carinae narrow, parallel (Fig. 7B).

Width of median propodeal area 0.7 times its length. Lateral and median propodeal areas smooth, pubescent. Nucha dorsally with some irregular rugae.

Legs. Profemur with a process of 4–5 rows of sharp, closely spaced, deep costulae visible as swelling on basal third of profemur (Fig. 7C). Tarsal claw with moderately bent apex; its base produced into a secondary small, blunt lobe, not distinctly developed as a secondary tooth.

Forewing (Fig. 7F). As long as body. Radial cell closed along anterior margin, about 3 times longer than wide; R1 slightly despigmented along radial cell; radius (Rs) straight, reaching anterior margin of wing. Areolet indistinct; vein Rs+M weakly visible, directed towards lower half of medial vein; M invisible. Fringe of long setae along apical margin of wing.

Metasoma. Metasoma (Fig. 7D) shorter than head plus mesosoma; in lateral view 1.4 times longer than high; laterally compressed. Abdominal petiole dorsally smooth, ventrally with deep longitudinal grooves. T1 crescent-shaped; not keeled dorsally. T2 covering about 1/3 of metasoma; anteromedian area of T2 with small patch of setae, without micropunctures. Projecting part of hypopygial spine 2.7 longer than high; apical pubescence of hypopigial spine projecting beyond apex, subapical setae longer than apical hairs, forming a small tuft.

Male. Similar to female except as described below (size and colouration already discussed). Male antenna (Fig. 6F) with 15 antennomeres. Flagellum not distinctly expanded towards apex. F2 slightly curved and slightly expanded towards apex in basal 2/3 (Fig. 6G); F3 not modified. Relative length of antennomeres: 15:8:15:20:18:17:15:15:14:14:13:13:12:12:18. Placodeal sensillae present on all flagellomeres. Metasoma (Fig. 7E) smaller than that of female; 1.5 times longer than high; T2 covering ¼ of metasoma. Anteromedian area of T2 with a group of not so dense setae.

Distribution. Chile and Argentina, following the distribution of the *Nothofagus dombeyi* (coihue or coigüe). The coihue is one of the most common South American *Nothofagus* species, being widely distributed over southern central Chile and southern Andes of Patagonia and Tierra del Fuego (Hoffmann 1978).

Biology. An inquiline or parasitoid in galls induced by *Aditrochus coihuensis* Ovruski (Chalcidoidea, Pteromalidae) on buds of twigs of *Nothofagus dombeyi*. (Nothofagaceae) (Figs. 12A–C).

Cecinothofagus gallaelenga Nieves-Aldrey & Liljeblad sp. nov.

(Figs. 8, 9, & 11G)

Type material. Holotype ♀ (in Museo Chileno de Historia Natural, Santiago de Chile, card mounted). CHILE, Punta Arenas, Reserva Forestal Magallanes, 53º 08' 46 53" S, 71º 00' 12 68" W, 350 m; ex gall on leafs of *Nothofagus pumilio* (Poepp & Endl.) Krasser "lenga" (Nothofagaceae), gall collected 9.xii.2006. insect emerged xii.06, J.L. Nieves leg. Paratypes: 1♂, 3♀ same data as holotype. One paratype in MCHN, the remaining paratypes in Museo Nacional Ciencias Naturales, Madrid (Spain), excepting one female in Pest Diagnostic Laboratory, Tanakajd, Hungary (G. Melika). Non-type material: 1 ♀, Argentina, Tierra del Fuego, Ea. San Justo (1–15.ii.1998, *Nothofagus forest*. C.R. Spagarino leg. (CNC).

Additionally, 1♂, 1♀ of the type series were dissected for SEM observation; several pupae and adults in ethanol (same data as type material). Galls of *Aditrochus fagicolus* Rübsaamen on *Nothofagus pumilio* containing larvae or pupae of *C. gallaelenga* were collected also at other Chilean localities as follows: Parque Nacional Conguillio, Laguna Captrén (30-i-05); Volcán Osorno (1200m) (2-xii-2006); Puerto Natales-Parque Nacional Torres del Payne (8-xii-2006). All material J.L. Nieves leg.

Etymology. Named after its biology, a species inhabiting a gall on "lenga", the common name of its host plant *Nothofagus pumilio*.

Diagnosis. This new species is closely allied with *Paraulax gallecoihue*, but differs by the predominantly black color; pedicel distinctly shorter than F1, mesopleuron smooth above mesopleural impression, mesoscutal pubescence scarce or absent anteriorly on median lobe of mesoscutum and by the short, incomplete mesopleural impression. Besides morphology, they are also well differentiated by their biology. *P.*

gallaelenga is associated with *N. pumilio* inhabiting leaf galls of *Aditrochus fagicolus*, while *P. gallaecohiue* attacks bud galls of *Aditrochus coihuensis* on *Nothofagus dombeyi*.

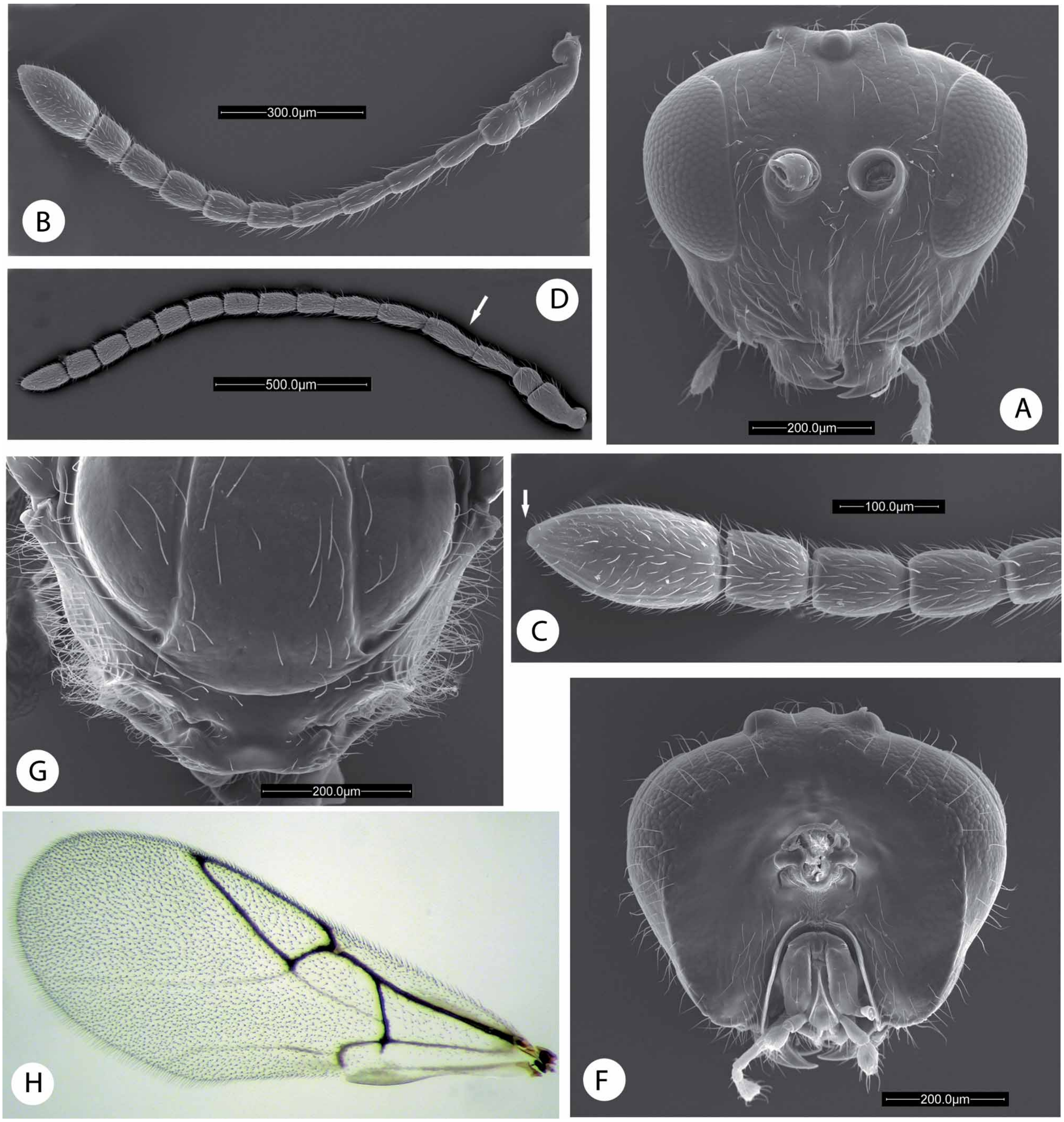

FIGURE 8. *Cecinothofagus gallaelenga* **n. sp.**: (A) Head anterior view. (B) Female antenna and (C) detail of apical flagellomeres. (D) Male antenna. (F) Head posterior view. (G) Pronotum anterior view. (H) Forewing.

Description. Body length (measured from anterior margin of head to posterior margin of metasoma) 2.5 mm (range 2.5–2.58; N = 4) for females; 2.7 mm (N = 1) for males. Coloration of females shining black, except flagellum, almost entire protibia, base and apex of femora and tarsi, which are dark brown. Forewing hyaline, veins dark brown. Male with coloration similar to female, but metasoma paler.

Female. Head in dorsal view 2.1 times wider than long. Gena not expanded behind compound eye. POL 1.6 times longer than OOL, posterior ocellus separated from inner orbit of eye by about 2 times its diameter. Head in anterior view (Fig. 8A) more or less trapezoid, 1.2 times wider than high, with slightly concave lateral margin of gena in the middle. Face with sparse, long setation, denser in lower face and almost lacking medially on frons; facial strigae radiating from clypeus absent medially; laterally well marked, reaching close to ventral margin of compound eye; strong, vertical median carina present, running from ventral margin of clypeus almost reaching ventral margin of toruli. Frons delicately coriaceous, almost entirely smooth and shining medially; vertex shining delicately coriaceous. Ocellar plate slightly raised (Fig. 8A); malar space 0.47 times height of compound eye. Clypeus indistinct, ventral margin straight, not incised. Subocular impression present, not well marked. 5–7 regular, vertical carinae present ventrolaterally on gena. Anterior tentorial pit conspicuous; epistomal sulcus and clypeo-pleurostomal lines indistinct. Toruli situated slightly below mid-height of compound eye; distance between antennal rim and compound eye 0.48 times width of antennal socket including rim. Occiput dorsally pubescent with coriaceous sculpture, without dorsal occipital carina, but sharp, well marked genal occipital carina present (Fig. 8F). Posterior tentorial pits narrow, slit-like. Hypostomal sulci meeting at hypostoma. Distance between occipital and oral foramina 0.4 times height of occipital foramen.

Mouthparts (Fig. 8F). Mandibles strong, exposed; right mandible with three teeth; left with two teeth. Cardo of maxilla visible, maxillary stipes about 2.3 times longer than wide. Maxillary palp five-segmented. Labial palp three-segmented.

Antenna (Fig. 8B) half as long as body, with 12 antennomeres; flagellum broadened towards apex; with distinct clava. Pedicel and F1–F5 with sparse, long setation, longer than width of flagellum basally. Placodeal sensilla indistinct, visible only on F7–F10. Relative lengths of antennal segments: 30:18:21:23:22:21:19:19:19:19:18:40; pedicel 1.2 times longer than wide; F1 2.1 times longer. Ultimate flagellomere 1.9 times longer than wide, 2.2 times as long as F9, ending in a semicircular, truncate apex.

Mesosoma. Pronotum in anterior view, almost entirely glabrous medially, strongly pubescent laterally. Ratio of length of pronotum medially/laterally = 0.3. Pronotal plate distinct; dorsal part distinctly set off, with anterolateral margins marked and moderately projecting laterad (Fig. 8G); longitudinal rugae from lateral margin of pronotal plate to lateral surface of pronotum not visible in lateral view but some visible in anterior view. Admedian pronotal depressions oval/ovalltransverse, open laterally, separated by as much as median length of pronotum. Posterior pronotal plate more or less rectangular, bare and smooth, ventral and lateral margins marked. Lateral surface of pronotum smooth; with sparse, white pubescence.

Mesonotum. Mesoscutum 1.1 times wider than long; predominantly without visible sculpture, at most some superficial, delicately coriaceous sculpture present. Mesoscutal pubescence composed of a few long setae concentrated along margins of notauli (9A). Median mesoscutal impression absent. Notauli percurrent, sinuate, not strongly converging posteriorly, almost reaching transscutal fissure (Fig. 9A). Posterior separation of notauli at transscutal fissure relatively wide, >0.5 times separation at anterior margin of mesoscutum. Anteroadmedian signa indistinct. Mesoscutum and scutellum separated by a narrow transscutal fissure. Scutellar foveae indistinct, visible only as a shallow, smooth and glabrous depression. Scutellum, in dorsal view more or less pentagonal in shape; in lateral view strongly convex. Dorsal surface of scutellum coriaceous with some rugae, more marked in lateral areas, almost absent medially (9A). Posterodorsal and posterior margins of axillula distinct. Mesopleuron (Fig. 9B) beneath mesopleural triangle smooth and glabrous. Mesopleural triangle distinctly impressed and densely pubescent; dorsal margin anteriorly diffuse, not meeting area near prepectus, meeting posterolateral margin of pronotum well below prepectus. Horizontal furrow in lower part of mesopleuron present, relatively wide and incomplete, reduced anteriorly and posteriorly, not reaching ventral margin of mesopleural triangle.

Metanotum. Metascutellum distinctly constricted medially. Area posterior to median constriction of metascutellum not divided by a median vertical bar. Metascutellum narrower in median part than metanotal trough. Metanotal trough smooth, pubescent.

Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid height of metapectal-propodeal complex. Lateral propodeal carinae narrow, parallel (Fig. 9C). Lateral and median propodeal areas smooth, pubescent. Nucha dorsally with some irregular rugae.

Legs. Profemur with process of 4–5 rows of sharp, closely spaced, deep costulae visible as swelling on basal third of profemur. Tarsal claw with moderately bent apex; base produced into a secondary small, acute tooth, measuring less than 1/6 of length of apical tooth (Fig. 9D).

Forewing (Fig. 8H). Slightly longer than body. Radial cell closed along anterior margin, about 3 times longer than wide; R1 pigmented along radial cell; radius (Rs) straight, reaching anterior margin of wing. Areolet indistinct; vein Rs+M weakly pigmented, but visible, directed towards lower half of median vein. Fringe of long setae along apical margin of wing.

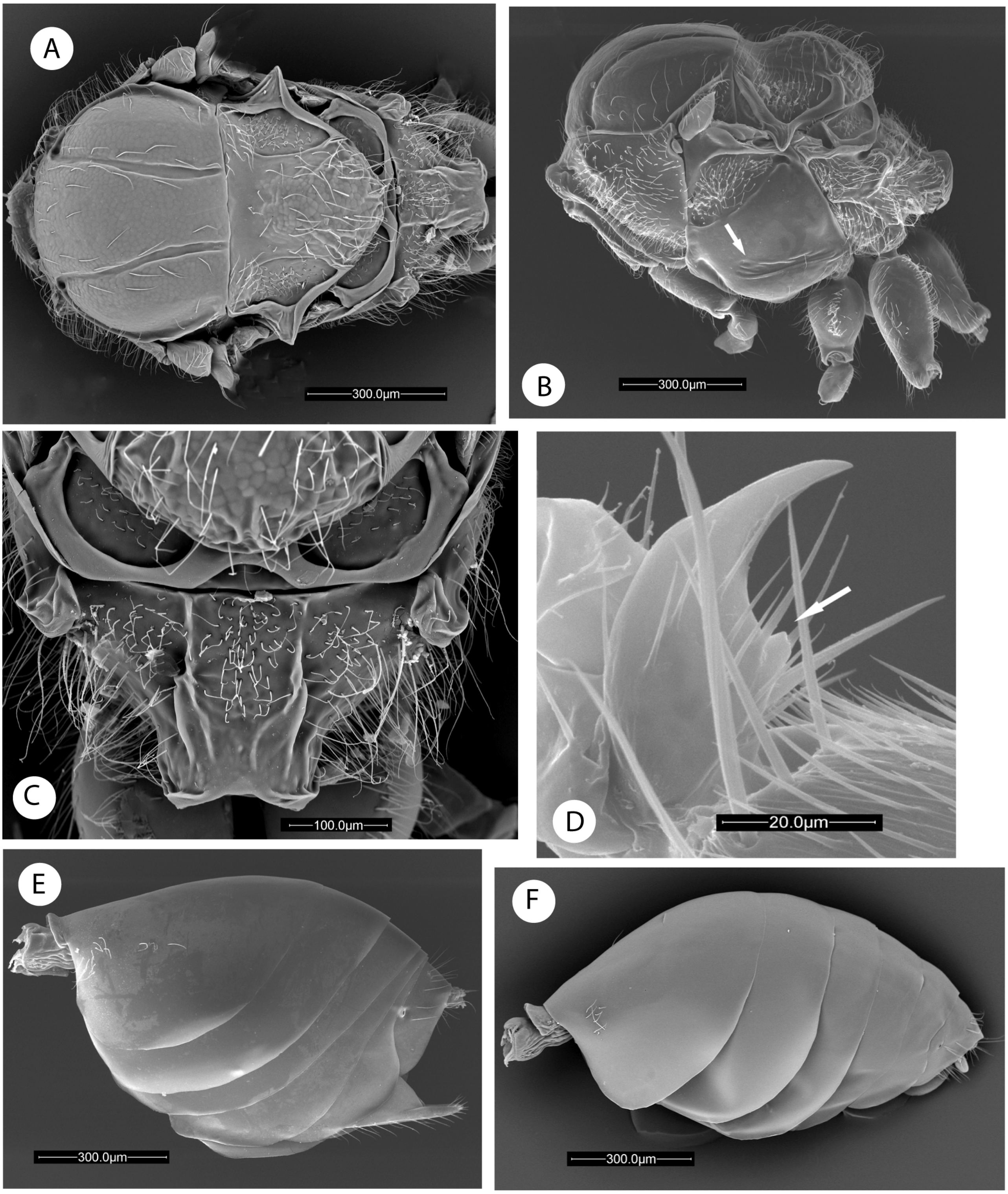

FIGURE 9. *Cecinothofagus gallaelenga* **n. sp.**: (A) Mesosoma dorsal view. (B) Mesosoma lateral view. (C) Propodeum (D) Metatarsal claw. (E) Female metasoma lateral view. (F) Male metasoma.

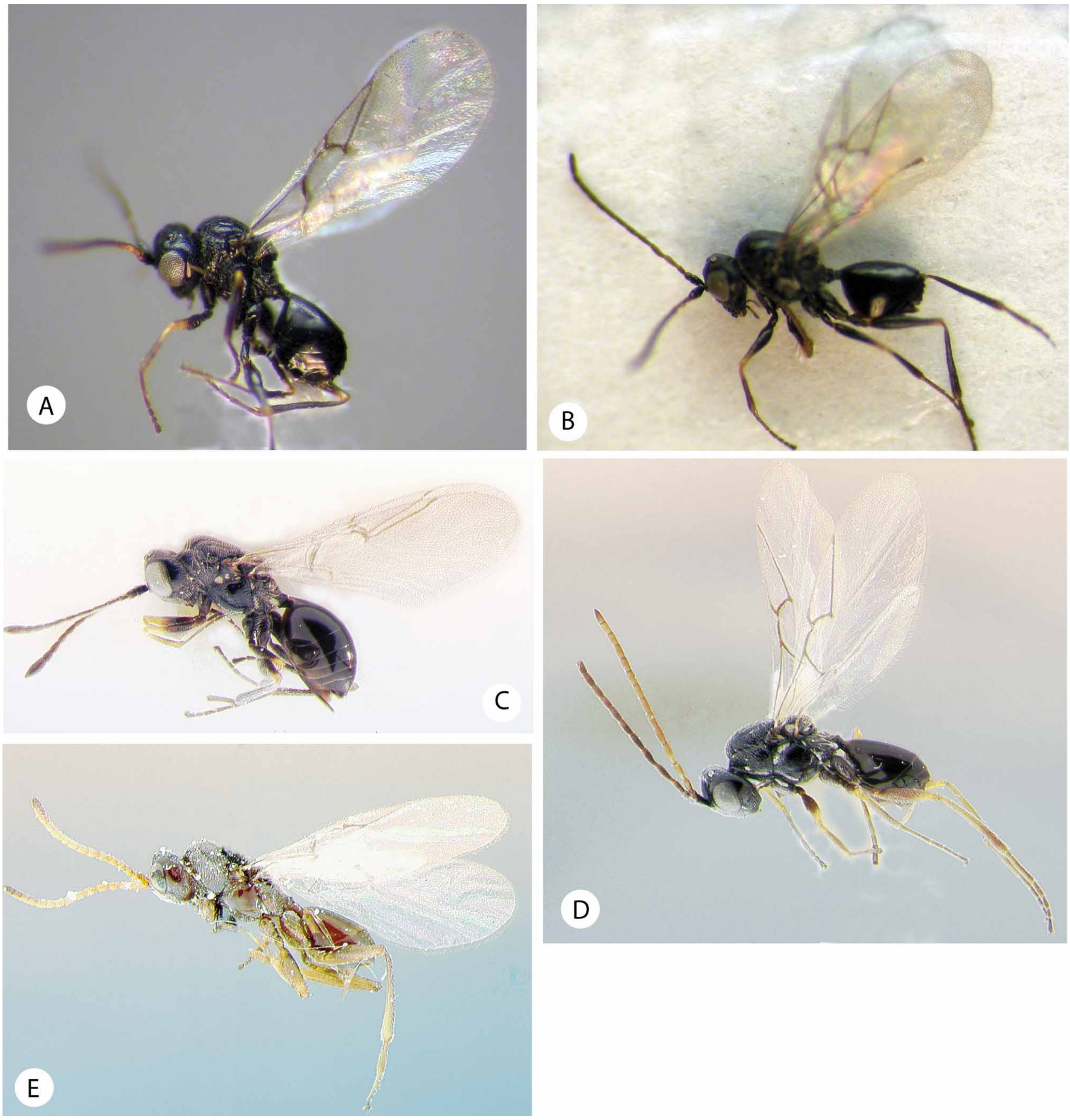

FIGURE 10. Habitus of species of *Paraulax*: (A) *P. perplexa*, female. (B) *P. perplexa*, male. (C) *P. queulensis*, female. (D) *P. queulensis*, male. (E) *P. ronquisti*, male.

Metasoma. Metasoma (Fig. 9E) shorter than head plus mesosoma; in lateral view 1.4 times longer than high; laterally compressed. Abdominal petiole dorsally smooth, ventrally with deep longitudinal grooves. T1 crescent-shaped; not dorsally keeled. T2 covering about half of metasoma; anteromedian area of T2 with group of 10–12 setae, not enough to form a conspicuous setal patch; smooth and shining, without micropuncture. Projecting part of hypopygial spine 2.6 longer than high; apical pubescence of hypopygial spine projecting beyond apex, subapical setae longer than apical ones, together forming a small tuft.

Male. Similar to female except as follows (size and colouration already discussed). Antenna (Fig. 8D) 15-segmented. Flagellum not distinctly expanded towards apex. F2 slightly curved and slightly expanding from base to apex. Relative length of antennomeres: 17:10:18:22:20:18:15:15:14:14:13:13:13:13:19. Placodeal sensillae present on all flagellomeres. Metasoma (Fig. 9F) smaller than that of female; 1.8 times longer han high; T2 covering ¼ 'length of metasoma. Anteromedian area of T2 with group of only 6–7 setae.

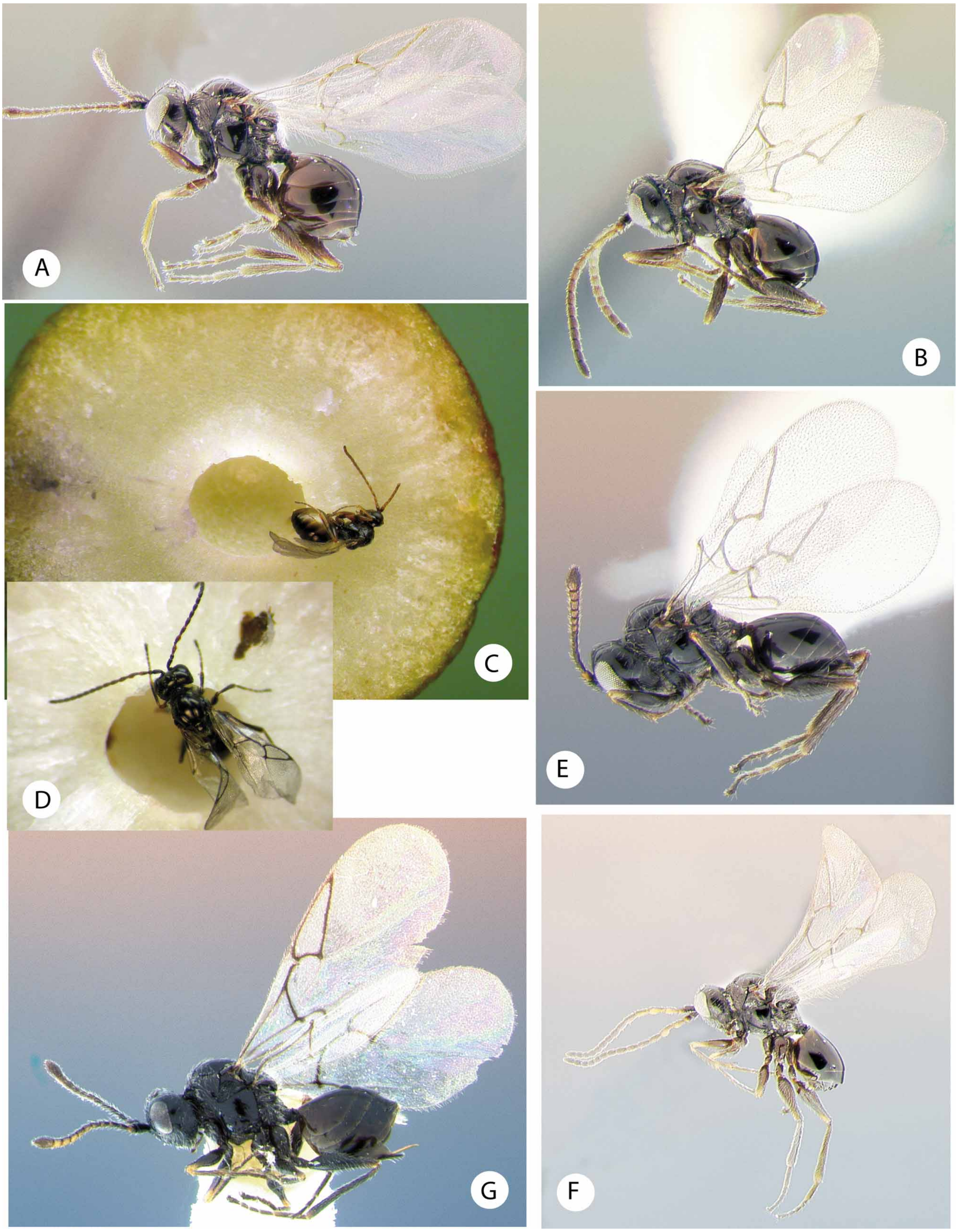

FIGURE 11. Habitus of species of *Cecinothofagus:* (A) *C. gallaecoihue*, female. (B) *C. gallaecoihue*, male. (C) *C. gallaecoihue* from a gall. (D) *C. ibarrai*, male emerging from a gall. (E) *C. ibarrai*, female. (F) *C. ibarrai*, male. (G) *C. gallaelenga*, female.

FIGURE 12. Host galls of *Cecinothofagus*, induced by species of *Aditrochus* and *Espinosa* (Chalcidoidea, Pteromalidae) on species of *Nothofagus*: (A) Gall of *Aditrochus coihuensis* on *Nothofagus dombeyi*. (B) Section of gall. (C) A group of galls not showing the apical point. (D) Gall of an unidentified *Aditrochus* species on *Nothofagus dombeyi*. (E) Galls of *Aditrochus fagicolus* on *Nothofagus pumilio*. (F) Section of gall. (G) Gall of *Espinosa nothofagi* on *Nothofagus obliqua*. (H) Gall of an unidentified *Espinosa* species on *Nothofagus obliqua*.

Distribution. The distribution of this species is linked to the habitat of its host gall, the *Nothofagus pumilio* (lenga) forests of Chile and Argentina. The "lenga" is distributed mainly throughout the southern Andes from aproximately 35º parallel in Chile (where it is confined to higher elevations) to the southernmost parts of Patagonia and Tierra del Fuego (where it occurs also at sea level) (Fig. 15) (Hoffmann 1978).

Biology. A lethal inquiline or parasitoid in leaf galls of *Aditrochus fagicolus* Rübsaamen (Chalcidoidea, Pteromalidae) on *Nothofagus pumilio* (Poepp et Endl.) Krasser. (Nothofagaceae) (Figs. 12E & 12F). *Nothofagus pumilio*, commonly named "lenga", is the most important forest component of South Patagonia. Galls develop in the leaf blade , attached to the midrib. The gall is a globular swelling protruding from both sides of the leaf. It is green or reddish, with a surface of fine hairs. A section through a gall (Fig. 12F) shows that i is unilocular (a single, central larval cell), structurally similar to the bud galls on *N. dombeyi*.

Cecinothofagus ibarrai Nieves-Aldrey & Liljeblad sp. nov.

(Figs. 4I–K & 11E–F)

Type material. Holotype ♀ (in Museo Chileno de Historia Natural, Santiago de Chile, card mounted) CHILE, Puerto Varas-Ensenada, 41º 12´52.55´´S 72º41´30.37´´O, 102 m; ex gall *Aditrochus coihuensis* on *Nothofagus dombeyi* (Mirb.) Blume "coigüe" (Nothofagaceae), gall collected 2/xii/2006. insect emerged xii/2006, J.L. Nieves-Aldrey leg. Paratypes: 1♂, 1♀ same data as holotype; 1♀ same data, except gall collected at Ensenada-Ralún. Additional material: one male preserved in ethanol, same data as holotype. One paratype ♂ in MCHN, the remaining paratypes in Museo Nacional Ciencias Naturales, Madrid (Spain). Non-type material: 1♀, Chile, PN Nahuelbuta, 961 m., 12.xii.2001, canopy fogging *Nothofagus dombeyi*. Arias et al. leg. (UCRC); 1♂ Chile, Malleco, 1500 m 110 km W Curacautin, 12.xii.1984. *Nothofagus-Araucaria* forest. S & J Peck leg. (CNC). 1♂ ARGENTINA, Esquel-Chobut ex gall on *Nothofagus dombeyi*, 03.xii.00. S. Rizzuto leg. (MNCN). This specimen agrees with the diagnostic antennal characters of *P. ibarrai* but resembles *P. gallaecoihue* in coloration and notauli characteristics.

Etymology. Named after Hector Ibarra, Chilean colleague, who helps us study galls on *Nothofagus* in Chile.

Diagnosis. Closely allied to *P. gallaecoihue*. Differs by body almost completely shining black (Fig 11E); legs and antenna blackish or dark brown. The main morphological difference refers to the antennal conformation. While in *P. ibarrae* F2 of the male antenna is conspicuously expanded distally (Fig. 4I), it is only slightly modified in *P. gallaecoihue*. Females are readily differentiated by the relative lengths of, antennomeres A2–A4.

Description. Body length 2.55 mm (range 2.5–2.6; N = 2) for females; 2.8 mm (range 2.7–2.9; N = 2) for males. Coloration of female, body shining black; antenna dark brown; legs black except apex of femora, tibia and tarsi brown. Forewing hyaline, veins dark brown. Male similar in coloration to female, but metasoma and flagellum not as dark.

Female. Head, in dorsal view (Fig. 4J) 1.8 times wider than long. Gena not expanded behind compound eye; in dorsal view almost as long as compound eye. POL 1.8 times longer than OOL, posterior ocellus separated from inner orbit of eye by about 1.8 times its diameter. In anterior view, head more or less subquadrate or slightly trapezoid, 1.1 times wider than high, lateral margin of gena not forming a continuous arch with outer margin of compound eye. Face with sparse, long setation, denser in lower face, almost lacking in median area of frons; facial strigae radiating from clypeus medially absent; laterally well marked, reaching close to ventral margin of compound eye; strong vertical median carina present, running from ventral margin of clypeus almost reaching ventral margin of toruli. Upper face (frons) and vertex almost entirely smooth and glabrous. Ocellar plate slightly raised; malar space about 0.6 times height of compound eye. Clypeus indistinct, ventral margin straight, not incised. Subocular impression indistinct, visible as a shallow furrow. 6–8 regular, vertical carinae present ventrolaterally in a depression on the gena. Anterior tentorial pits conspicuous; epistomal sulcus and clypeo-pleurostomal lines indistinct. Antennal socket (torulus) situated at about mid height of compound eye; distance between antennal rim and compound eye 0.5 times width of antennal socket including rim. Occiput with coriaceous sculpture, dorsally pubescent, without dorsal occipital carina, sharp, well marked genal occipital carina present. Posterior tentorial pits narrow, slit-like. Hypostomal sulci meeting at hypostoma. Distance between occipital and oral foramina 0.7 times height of occipital foramen.

Mouthparts. Mandibles strong, exposed; right mandible with three teeth; left with two teeth. Cardo of maxilla visible, maxillary stipes about 2.3 times longer than wide. Maxillary palp five-segmented. Labial palp three-segmented. Lateral margins of oral fossa with a band of 3–4 rows of white setae.

Antenna 0.5 times length of body, 12-segmented; flagellum slightly broadened towards apex; last flagellomere distinctly wider than penultimate; slightly truncate at apex, ending in a semicircular point. Antennomeres with sparse setation, about as long as width of flagellum basally. Placodeal sensilla indistinct, visible only on F7–F10. Relative length of antennomeres: 30:13:18:22:18:19:15:14:14:16:15:42; pedicel 1.2 times longer than wide; F1 0.8 times length of F2. Ultimate flagellomere 2.4 times longer than wide, 1.3 times wider han penultimate and 2.8 times longer than F9, ending in a semicircular, truncate apex.

Mesosoma. Pronotum in anterior view, almost glabrous medially, strongly pubescent laterally. Ratio of length of pronotum medially/length laterally = 0.4. Pronotal plate distinct; dorsal part distinctly set off, anterolateral margins marked and moderately projecting laterad (Fig. 4J). Admedian pronotal depressions oval/transverse, open laterally, separated by as much as median length of pronotum. Lateral surface of pronotum smooth; sparsely pubescent by long, white setae. A few short, horizontal rugae running from lateral margin of pronotal plate.

Mesonotum. Mesoscutum (Fig. 4J) 1.2 times wider than long; shining, without visible median sculpture, at most some superficial, delicately coriaceous sculpture present laterally. Pubescence in the form of long setae present only along margins of notauli. Median mesoscutal impression absent. Notauli complete, sinuate, not strongly converging posteriorly, not reaching the transscutal fissure, wider in posterior half. Separation of notauli at transscutal fissure relatively wide, 0.5 times separation at anterior margin of mesoscutum. Anteroadmedian signa weakly visible. Mesoscutum and scutellum separated by a narrow transscutal fissure. Scutellar foveae indistinct, visible only as a shallow, smooth and glabrous depression. Scutellum, in dorsal view more or less pentagonal in shape; in lateral view strongly convex. Dorsal surface of scutellum coriaceous with some rugae, more marked on lateral and posterior areas and almost absent medially. Posterodorsal and posterior margins of axillula distinct. Mesopleuron beneath mesopleural triangle smooth and glabrous excep for horizontal furrow or mesopleural impression in lower part; mesopleural impression relatively wide but incomplete, not reaching ventral margin of mesopleural triangle. Mesopleural triangle distinctly impressed and densely pubescent; dorsal margin diffuse anteriorly, not meeting area near prepectus, instead meeting posterolateral margin of pronotum well below prepectus.

Metanotum. Metascutellum distinctly constricted medially. Area posterior to median constriction of metascutellum not divided by a median vertical bar. Median metascutellum narrower than metanotal trough. Metanotal trough smooth, pubescent.

Metapectal-propodeal complex. Metapleural sulcus reaching posterior margin of mesopectus at about mid height of metapectal-propodeal complex. Lateral propodeal carinae narrow, parallel. Width of median propodeal area 0.8 times length. Lateral and median propodeal areas smooth, pubescent. Nucha dorsally with some irregular rugae.

Legs. Profemur with process of 4–5 rows of sharp, closely spaced, deep costulae visible as swelling in basal third of profemur. Tarsal claw with basal, small lobe, not distinctly developed into secondary tooth.

Forewing (Fig. 4K). As long as body. Radial cell closed along anterior margin, about 3 times longer than wide; radius (Rs) straight, reaching anterior margin of wing. Areolet indistinct; vein Rs+M weakly visible, directed towards lower half of median vein; M weakly indicated anteriorly. Fringe of long setae along apical margin of wing.

Metasoma. Metasoma shorter than head plus mesosoma; in lateral view 1.7 times longer than high; laterally compressed. Abdominal petiole dorsally smooth, ventrally with deep longitudinal grooves. T1 flapshaped; laterally 2 times higher than long, with some longitudinal rugae. T2 covering about half of metasoma; anteromedian area of T2 with group of a few long setae. Projecting part of hypopygial spine 3.4 times longer than high; apical pubescence of hypopigial spine projecting beyond apex, subapical setae longer than apical ones, together forming a small tuft.

Male. Similar to female except as follows. Male antenna (Fig. 4I) with 15 segments. Flagellum not distinctly expanded towards apex. F1 slightly broadening from base to apex; F2 curved basally, strongly expanded in apical third; F3 not modified. Relative length of antennomeres: 19:9:19:24:20:18:16:15:13:15:13:14:12:13:20. Placodeal sensillae present on all flagellomeres. Metasoma smaller than that of female; 1.5 times longer than high; T2 0.4 times length of metasoma. Anteromedian area of T2 with group of 3–4 setae.

Distribution. Recorded from *Nothofagus dombeyi* forests in Argentina and Chile (Fig. 15). Since two cynipid species share the same host gall and plant, the potential distribution is similar to that of the related species *C. gallaecoihue*.

Biology. As with *C. gallaecoihue*, this species is an inquiline or parasitoid in bud galls induced by *Aditrochus coihuensis* (Chalcidoidea, Pteromalidae) on *Nothofagus dombeyi* (Mirb.) Blume (Nothofagaceae). *N. dombeyi*, commonly named “coihue”, is an evergreen tree native of Southern Argentina and Chile. The host gall induced by *Aditrochus coihuensis* is a large spherical bud gall (Fig. 12C), sometimes with an apical point (Fig. 12A). The surface is covered by small, blister-like, brown protuberances (lenticeles). The gall is locally common. It is variable in size, measuring between 4–20 mm with an average for the larger galls of 10–12 mm. A sectioned gall (Fig. 12B) shows the central larval chamber, the sclerenchyma wall of the larval cell and the outer layers of parenchyma and sclerenchyma. This is similar to the structurally complex oak galls induced by some species in the genera *Cynips* and *Andricus*.

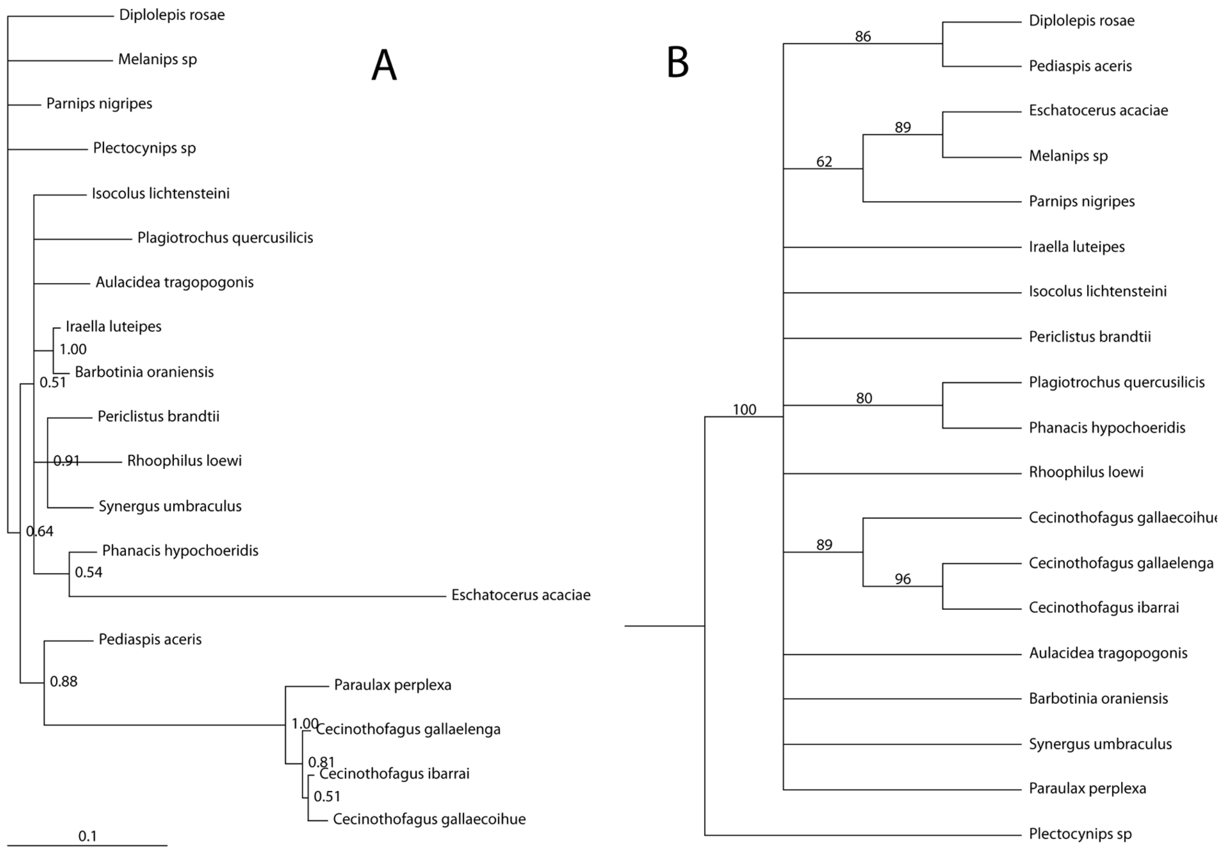

FIGURE 13. The 50% Majority-rule consensus trees from the Bayesian analysis of the 28S, phylogram (A) and the COI, cladogram (B) gene fragments. Numbers on branches indicate posterior clade probabilities (only values between 0.50 and 1.00 are given).

Phylogenetic analysis

The results of the molecular analysis found *Paraulax* deeply nested within the Cynipidae, confirming the classification of the Paraulacini as a cynipid rather than a figitid. Furthermore, the placement of the two basal figitid taxa: *Plectocynips* (Plectocynipinae) and *Parnips* (Parnipinae) is mostly congruent with the results of Buffington *et al*. (2007). Besides a strongly supported core Cynipidae, the basal relationships of key taxa such as the cynipids *Diplolepis*, *Eschatocerus*, *Pediaspis* and figitids like *Parnips* and *Melanips*, are much more ambiguous or weakly supported.

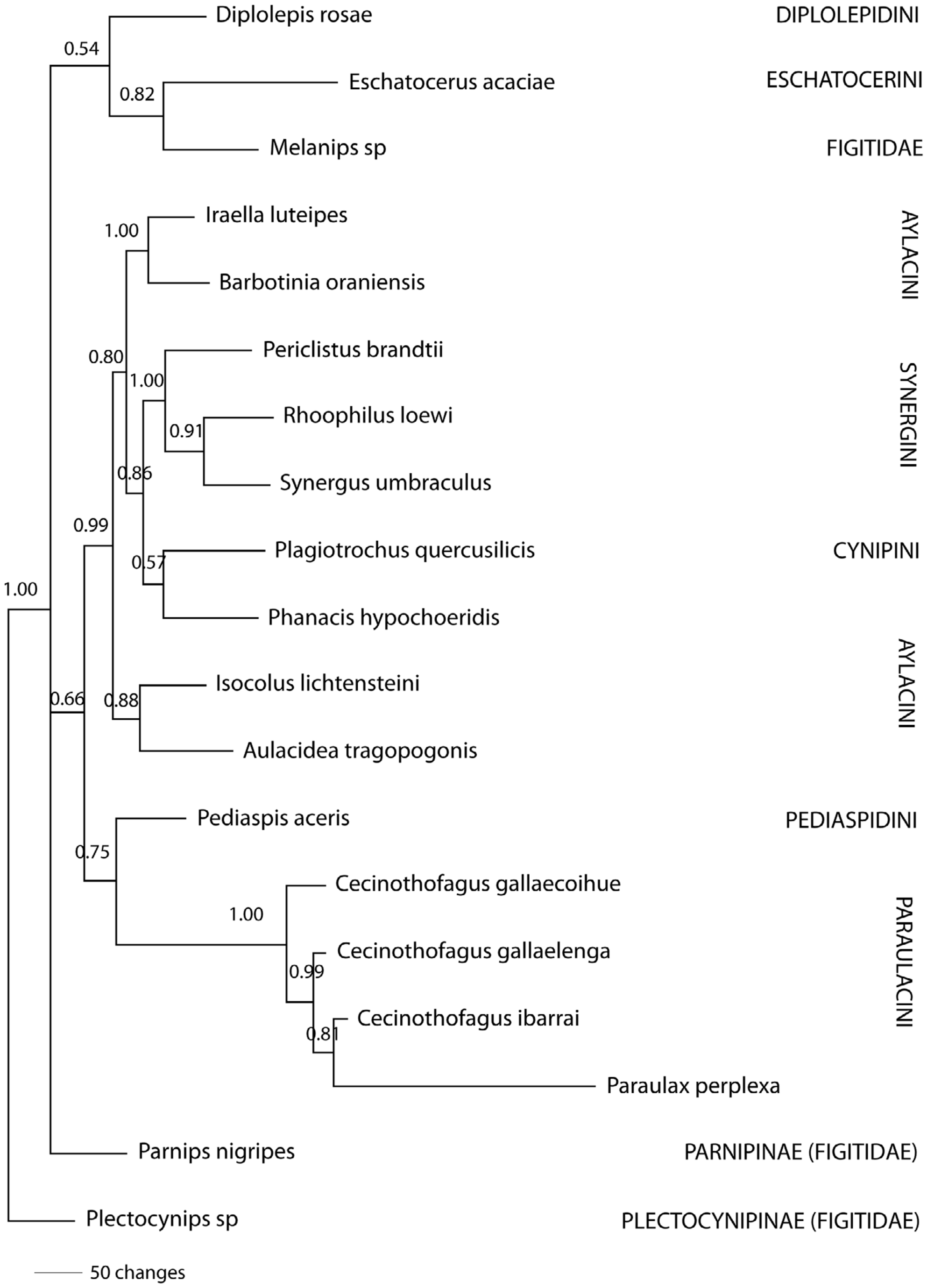

FIGURE 14. The 50% Majority-rule consensus tree from the Bayesian analysis of the two genes (28S, COI) combined. Numbers on branches indicate posterior clade probabilities (only values between 0.50 and 1.00 are given). Current suprageneric classification is given to the right.

FIGURE 15. Map of collection localities of species of Paraulacini in Chile and Argentina: *Paraulax perplexa* (1), *P. queulensis* (2), *P. ronquisti* (3), *Cecinothofagus gallaecoihue* (4), *C. gallaelenga* (5), *C. ibarrai* (6)

The phylogenetic signal is clearly indicating the distinctiveness of *Paraulax perplexa* from the species included in *Cecinothofagus*. While both the 28S and the COI marker recovered a monophyletic *Cecinothofagus*, the combined Bayesian analysis (Fig. 14) suggests the new genus to be paraphyletic with respect to *Paraulax perplexa*.

The molecular results based on the ribosomal 28S marker confirms the results of the morphological phylogeny of Liljeblad *et al*. (2008) placing *Paraulax* as the sister group to Pediaspidini. The Bayesian analysis recovered a tree (Fig. 13A) with the Paraulacini grouped with the Pediaspidini (with a posterior probability of 0.88). The Bayesian analysis with the COI marker, however, found a clade with the *Cecinothofagus* species only but failed to recover both a monophyletic Paraulacini as well as them being the sister group of *Pediaspis* (Fig. 13B). The combined Bayesian analysis of the 28S + COI (Fig. 14) is similar to the 28S analysis, recovering a monophyletic clade grouping *Paraulax* + *Cecinothofagus*, and them being the sister group of *Pediaspis aceris* (0.75 posterior probability). It should be however noted the long branch of the Paraulacini clade (Fig. 13A) indicating the distinctiveness of this clade, but also making questionable its grouping with *Pediaspis*, because the relatively low posterior probability support and the possibility of long-branch attraction effect (Bersten 2005).

Discussion

Classification. Keeping in line with the traditional way of classifying cynipids, we prefer to put *Paraulax* and *Cecinothofagus* in the new tribe Paraulacini in spite of their affinity with the Pediaspidini. We justify this by both their distinct geographical distribution and their unique host plant choice. The only other native South American cynipids are three species in the genus *Eschatocerus* Mayr which, however, are found in Argentina and Uruguay as opposed to Chile (Díaz 1981).

Biology. Despite the fact that *Paraulax perplexa* has long been tentatively classified with the Cynipini, the cynipids inducing galls on Fagaceae (Ronquist 1999), and later with the Pediaspidini (Liljeblad 2002, Csoka *et al*. 2005, Liljeblad *et al*. 2008), its real biology was unknown though the species were considered either the true or the potential gall inducers on *Nothofagus* (Dalla Torre & Kieffer 1910; De Santis *et al*. 1993; Ronquist 1999; Csoka *et al.* 2005). Our repeated observation of *Cecinothofagus* species, after dissections and rearings from *Nothofagus* galls, show conclusively that the host galls are occupied very early by larvae of *Aditrochus* (Pteromalidae), these species should therefore be considered the legitimate gall-inducers of these *Nothofagus* galls. There is no reason to doubt this, since other lineages of the supposedly basal pteromalid subfamily Ormocerinae have proved in several cases (*Hemadas nubilipennis* (Ashmead), which is an inducer of a gall on *Vaccinium angustifolium* Ait. (Ericaceae)*; Trichilogaster* Mayr, a gall inducer on *Acacia*, and others) to be true gall inducers and not parasitoids as most of Pteromalidae (LaSalle 2005). An additional observation that supports this conclusion, beside the cynipid-like habitus of *Aditrochus*, is that they have a uniquely pedunculate egg, very different from the eggs of parasitoid pteromalids but strikingly similar to the eggs of most cynipids (Nieves-Aldrey & Vårdal *unpublished*).

If *Cecinothofagus* species are not the inducers of the galls from which they are reared, what is their real biology? There are two hypotheses: they could be inquilines (whether lethal or not) or parasitoids, the latter case involving or not secondary phytophagy, as in the behaviour exhibited by many chalcid larvae (Lego & Shorthouse 2006; Gómez *et al. in press*). These two hypotheses are discussed below.

Inquiline hypothesis. We found very little support for this hypothesis. With regard to non lethal inquilines, the only inhabitant found clearly displaying this behaviour was the weevil *Noterapion meorrhynchum* (Philippi & Philippi) (Coleoptera, Apionidae, Apioninae, Noterapionini) with the larva feeding off peripheral tissue of the gall without killing the host larva. We never observed peripheral cells occupied by larvae or pupae of *Cecinothofagus*. Regarding lethal inquilines, it is common that cynipid lethal inquilines induce secondary cells in the host cynipid central cell, sometimes separated by tiny, translucent walls (Nieves-Aldrey 2001). This behaviour, however, was never observed in association with *Cecinothofagus* pupae or adults, who were always observed occupying an undivided single, central cell.

Interestingly, within one gall of *Aditrochus fagicolus* we found a single cynipid larva which could, with some reservation, be taken as belonging to *Cecinothofagus gallaelenga*. The mandible of this larva had the two strong teeth typical of cynipid larvae (Nieves-Aldrey *et al*. 2005). This unique observation lends some support for the lethal inquiline hypothesis but needs to be repeated with the identity of the cynipid-like larva confirmed.

Parasitoid hypothesis. If *Cecinothofagus* larvae are parasitoids, they are most likely endoparasitic like most other entomophagous cynipoids. This is compatible with the fact that we never found *Cecinothofagus* larvae feeding externally on *Aditrochus* larvae. On the contrary, we sometimes observed *Aditrochus* larvae parasitised by internally feeding larvae, though we unfortunately failed to check if this internal parasitism was caused by larvae of *Cecinothofagus*. With regard to the secondary phytophagy exhibited by many parasitoids, particularly eurytomids (Chalcidoidea, Eurytomidae) (Lego & Shorthouse 2006; Gómez *et al*. in press), this was something we never observed in any of the dissected *Aditrochus* galls. This behaviour can be traced by the modification of the host cells these larve do after killing their host, feeding on the cell walls. In conclusion, with the data available, the more likely hypothesis of the biology of *Cecinothofagus* seems to be that they are internal parasitoids, non-secondary phytophagous parasitoids, of *Aditrochus* larvae, though a case could also be made for them being lethal inquilines.

If the parasitic behavior of the Paraulacini is confirmed, it would represent the first case of a non-phytophagous cynipid. If they, instead, are found to be phytophagous inquilines, it would be just as important for our understanding of the evolution of inquilinism within the Cynipidae.

The fact that these galls on *Nothofagus* are morphologically complex, similar to those exhibited by many derived species of Cynipini on *Quercus*—even if not induced by *Paraulax*, which turns out to be either lethal inquilines or parasitoids—still makes the biology of the Paraulacini highly unusual among the Cynipidae, and thus of considerable interest.

Further evolutionary implications. The observations on the biology of *Cecinothofagus* in this paper implies that both the biology of the Cynipidae and the evolution of the gall wasp–host plant association are more complex than has previously been hypothesized. After these, and other recent findings, the family includes not only gall makers and inquilines of other cynipids (agastoparasites sensu Ronquist (1994), but also inquilines of lepidoptera larvae, as was demonstrated with *Rhoopilus* (Van Noort *et al*. 2007), and now inquilines or parasitoids of chalcids. It is surely no mere coincidence that this, the biology of the Paraulacini, is so similar to that of some basal figitid lineages (Plectocynipinae and Thrasorinae being parasitoids of gall inducing chalcids: Ronquist & Nieves-Aldrey 2001; Buffington *et al*. 2007; Buffington 2008). The coincidence is even more striking when you consider that the Paraulacini (at least as examplified by *Cecinothofagus*) have the exact same habitat (*Nothofagus* galls), and likely biology, as *Plectocynips*. This basal genus of figitids was recently transferred from Thrasorinae to its own subfamily Plectocynipinae (Ros-Farré & Pujade-Villar 2007). Interestingly enough, the other basal lineages of the Figitidae, the Parnipinae, Thrasorinae and Euceroptrinae, also include species whose biology could be said to lie somewhere between entomophagy and phytophagy (Ronquist & Nieves-Aldrey 2001; Buffington 2008; Buffington & Liljeblad 2008).

Ronquist (1994) and Ronquist and Liljeblad (2001) originally hypothesized that cynipid inquilines in oak galls are derived from cynipids inducing galls on herbs belonging to Papaveraceae or Asteraceae. Our results, together with those of previous molecular analyses (Nylander 2004; Nylander *et al. in prep*.), contradict this scenario and propose as more basal cynipid groups those associated wih plants of the families Rosaceae, Sapindaceae, Nothofagaceae and Fabaceae rather than herbs or the Fagaceae. Specifically, our results place the Paraulacini among the most basal Cynipidae and indicate that gall induction could have started with parasitoid, or partially phytophagous, cynipoids associated with primitive pteromalids inducing galls on *Nothofagus*.

Biogeography and the origin of the microcynipoids. The species of Paraulacini and Eschatocerini represent the only cynipid taxa with a temperate Neotropical distribution. Ronquist and 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* arose by dispersal events to South America and South Africa respectively. However, recent phylogenetic findings contradict this hypothesis. *Eschatocerus*, *Paraulax* and *Rhoophilus* seem to belong to older, more basal cynipid lineages, and as such the early biogeographical history of the Cynipidae is still not clear (Nylander *et al.* 2004). If anything, it strangely indicates a common Gondwanan origin since that would also explain the distribution of the genus

Himalocynips (in Pediaspidini and hence closely related to Paraulacini) as a Gondwanian relict on the Indian continent. This suggests chances of finding microcynipoids associated with galls induced by chalcids also in the Australasian region. As it turns out, there are such records from Australia, with members of the above mentioned figitid subfamily Thrasorinae being reported from chalcid galls on *Eucalyptus* and possibly also *Acacia* (Buffington, 2008). This scenario implies that the microcynipoids are older than the fossil record tells us (confer e.g. Ronquist 1999), but all in all it just puts further emphasis on the need for an exhaustive phylogenetic analysis including both the Cynipidae and Figitidae. With its seemingly plesiomorphic set of morphological attributes, the undescribed South African cynipid from galls on *Scolopia mundii* (Liljeblad *et al.* in prep.) could very well prove to be key in such an undertaking.

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