



A new subfamily of Figitidae (Hymenoptera, Cynipoidea)

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Larvae of the parasitic wasp family Figitidae develop as internal parasitoids of other endopterygote insect larvae. The hosts are typically dipteran larvae living in other microhabitats but the earliest figitids probably attacked gall-inhabiting hymenopteran larvae. Here, we formally describe a new genus (*Parnips*) and subfamily (Parnipinae) for a species that is likely to be a surviving representative of these early gall-associated figitids. The species, *P. nigripes*, has been reared repeatedly from galls inside the seed capsules of annual poppies (*Papaver dubium* and *P. rhoeas*) in the Mediterranean region together with the gall inducer *Barbotinia oraniensis* belonging to the Cynipidae, the sister group of Figitidae. *Parnips nigripes* is strikingly cynipid-like and was first assumed to be a cynipid gall inducer of the genus *Aulacidea*. Phylogenetic analyses have since indicated that the similarity with the Cynipidae is symplesiomorphic and that *P. nigripes* belongs to the Figitidae, where it forms the sister group of all other extant figitids. Recently, it has also been shown that *P. nigripes* is a parasitoid of the gall-inducing *Barbotinia oraniensis*, consistent with its proposed phylogenetic position. *Parnips nigripes* shares several unusual morphological traits with its host. We speculate that many of these similarities are homologous even though the lineages separated at least 83 million years ago.

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ADDITIONAL KEY WORDS: systematics – phylogeny – evolution – origin – gall – Cynipidae – *Papaver* – Mediterranean.

INTRODUCTION

Members of the parasitic wasp family Figitidae (*sensu lato*) are early internal–late external parasitoids of endopterygote insect larvae. The egg is deposited inside a young host larva, which continues to develop normally despite the presence of the parasite inside. After some period of feeding internally, the parasite larva eventually emerges from the moribund host, before the latter pupates, and spends the last one or two instars feeding externally on the host remains (Ronquist, 1999 and references cited therein). Because growth of the host larva is not halted by the parasite attack, figitids are classified as koinobiont parasitoids (Askew & Shaw, 1986).

The hosts of figitids are typically larvae of Diptera: Cyclorrhapha developing in living plants (as fruit feed-

ers, leaf miners or stem borers), in fungi, or in decomposing organic matter, such as rotting fruit, carrion and dung. Another substantial group of figitids, including several subfamilies, are associated with predators or parasitoids in the aphid and psyllid communities. The attacked hosts include aphid-feeding larvae of Chamaemyiidae (Diptera: Cyclorrhapha), aphid and psyllid parasitoids in the Braconidae and Encyrtidae (Hymenoptera: Apocrita), and aphid-feeding larvae of Chrysopidae and Hemerobiidae (Neuroptera) (Ronquist 1995a, 1999).

A small group of figitids, referred to as the *figitoid inquilines* (Ronquist, 1994), are unusual in being associated with hymenopteran galls. The group includes the described genera *Euceroptres*, *Thrasorus*, *Myrtopsen*, *Plectocynips* and *Pegacynips* (Table 1). Until recently, the life history of the figitoid inquilines was unknown. Because several of the genera are strikingly similar to the gall-inducing Cynipidae, the sister group of the Figitidae (Ronquist, 1995a, 1999), they were

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Table 1. Summary of the known distribution and biology of the gall-associated figitids (data from Ronquist, 1994 and references cited therein, unless stated otherwise). *Parnips* is a parasitoid of *Barbotinia*; the other species are likely to be parasitoids of the host gall inducer or another hymenopteran inhabitant in the galls from which they have been reared

Taxon	Host gall inducer	Host gall	Host plant	Distribution
Parnipinae				
<i>Parnips</i>	<i>Barbotinia</i> (Cynipidae: Aylacini)	Single-chambered gall in seed capsule	<i>Papaver</i> (Papaveraceae)	Mediterranean
Thrasorinae				
<i>Euceroptres</i>	<i>Andricus</i> , <i>Callirhytis</i> , <i>Disholcaspis</i> (Cynipidae: Cynipini)	Single- or multi-chambered galls on stem or leaf petiole	<i>Quercus</i> (Fagaceae)	North America ¹
<i>Thrasorus</i>	Ormocerinae (Chalcidoidea: Pteromalidae)	Multi-chambered stem galls	<i>Eucalyptus</i> (Myrtaceae) <i>Acacia</i> (Fabaceae)	Australia
<i>Myrtopsen</i>	<i>Tanaostigmodes</i> (Chalcidoidea: Tanaostigmatidae)	Multi-chambered stem or bud galls	<i>Mimosa</i> (Fabaceae) <i>Eugenia</i> , <i>Blepharocalyx</i> (Myrtaceae)	S. North America South America
<i>Plectocynips</i>	? <i>Paraulax</i> (Cynipidae) ²	?	<i>Nothofagus dombeyi</i> (Fagaceae)	S. South America
<i>Pegacynips</i>	? <i>Paraulax</i> (Cynipidae) ³	?	? <i>Nothofagus</i> (Fagaceae)	S. South America

¹ *Ceroptres japonicus* Ashmead, 1904, described from Japan, was placed by Weld (1926, 1952) in *Euceroptres*. However, examination of the type specimen in the USNM shows that this species belongs to *Phaenoglyphis* (Figitidae: Charipinae) and not to *Euceroptres* (Ronquist, unpublished data).

² The type material from southern Argentina was obtained from galls on *Nothofagus dombeyi* (Diaz, 1976); these galls were not described. However, several *Nothofagus* galls, often in buds or on leaves, occur in southern South America. Rearings from these galls have produced a variety of chalcidoids as well as members of the genus *Paraulax* (De Santis, Fidalgo & Ovruski, 1993). *Paraulax* belongs to the woody rosid gallers in the Cynipidae and is apparently closely related to the oak gall wasps (Cynipini) (Ronquist, unpublished data). Presumably, *Paraulax* is the agent causing the *Nothofagus* galls.

³ This genus, which is closely related to *Plectocynips*, is often collected in *Nothofagus* forests in southern South America together with *Paraulax*.

long assumed to be gall inducers or phytophagous inquiline (gall inhabitants) belonging to the Cynipidae. This is particularly true for the genera *Euceroptres* and *Myrtopsen* and to some extent for *Thrasorus* (Weld, 1952; Riek, 1971; Diaz, 1980). However, it has been clear for some time that most of the cynipid similarities are symplesiomorphies and that several putative synapomorphies group the figitoid inquilines with figitids rather than with cynipids (Ronquist, 1994, 1995a, 1999).

The most cynipid-like figitoid inquiline was discovered in Algeria in the early 1960s by Barbotin (1964). He reared two new cynipoid species in considerable numbers from galls inside the seed capsules of annual poppies (*Papaver rhoeas* and *P. dubium*). Although there was no direct evidence, Barbotin assumed that both species were gall inducers belonging to the Cynipidae, since they emerged at the same time from identical galls and were both cynipid-like. Similar species pairs causing identical galls on the same host plant are known among other herb-galling Cynipidae (e.g. Nieves-Aldrey, 1995). Barbotin (1964) described one species as *Aulacidea nigripes* and the other as

Aylax oraniensis. Both species have since been found to occur in Spain (Nieves-Aldrey, 1985) and may well be widely distributed in the Mediterranean region.

Because of its distinctness from other species of *Aylax*, Nieves-Aldrey (1994) later proposed a monotypic genus, named *Barbotinia*, for *A. oraniensis*. Dissection of numerous mature galls confirms that *B. oraniensis* is a true gall inducer (Ronquist, unpubl. data) and phylogenetic analysis based on skeletal morphology places it in a basal position inside the gall-inducing Cynipidae (Liljeblad & Ronquist, 1998) (Fig. 1).

The case is different for *A. nigripes*. Although this species is cynipid-like, it also shares some unusual features with core figitids, such as the genus *Melanips*, causing Nieves-Aldrey (1994) to exclude it from the Cynipidae and Ronquist (1994) to include it among the figitoid inquilines. Subsequent phylogenetic analyses based on morphological characters (Fig. 1) indicate that: (1) *A. nigripes* falls outside of the gall-inducing Cynipidae, like other figitoid inquilines (Ronquist, 1995a; Liljeblad & Ronquist, 1998); (2) the figitoid inquilines, excluding *A. nigripes*, form a single lineage, the Thrasorinae (Ronquist, 1999); and (3) *A. nigripes*

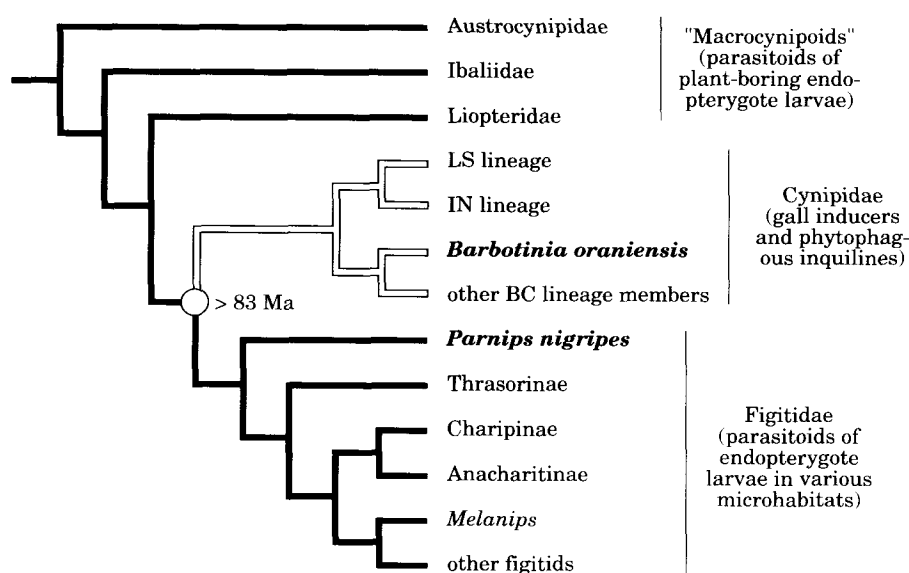


Figure 1. Phylogenetic position of *Parnips nigripes* and its host, *Barbotinia oraniensis*, among the extant Cynipoidea (data from Ronquist, 1995a, 1999; Liljeblad & Ronquist 1998). The most recent common ancestor of the Figitidae and Cynipidae, which is also the most recent common ancestor of *Parnips* and *Barbotinia*, lived at least 83 million years ago, as evidenced by the oldest known fossil figitids. (□) Phytophagous forms, (—) insect-parasitic forms. LS = *Liposthenes*–*Synergus* lineage, IN = *Isocolus*–*Neaylax* lineage, BC = *Barbotinia*–*Cynips* lineage.

forms the sister group of the remaining Figitidae, including the Thrasorinae (Ronquist, 1999). Recently, it has also been shown that *A. nigripes* is not a gall inducer or phytophagous inquiline but a koinobiont parasitoid of *Barbotinia oraniensis*, consistent with its proposed phylogenetic position (Ronquist & Nieves-Aldrey, unpubl. data).

These findings necessitate the erection of a new genus and subfamily for *A. nigripes*. Here, we formally describe these new taxa as *Parnips* and Parnipinae, respectively. Furthermore, we discuss the detailed morphological and biological similarities between *P. nigripes* and its host, *B. oraniensis*, and argue that many of these traits were inherited from the most recent common ancestor of the Figitidae and Cynipidae, which lived at least 83 million years ago (Mya) (Upper Cretaceous).

MATERIAL AND METHODS

Material. The examined material of *P. nigripes* is listed below. Comparisons with other cynipoids are based on published information (Nieves-Aldrey, 1994; Ronquist, 1995a; Liljeblad & Ronquist, 1998; Ronquist, 1999).

Methods. Specimens used for illustrations were killed and stored in 70% ethanol. Specimens for SEM were dissected into body parts and cleaned overnight in a 1:1 mixture of concentrated ammonia and water. The dissected parts were then washed in water, taken

through a series of ethanol solutions of increasing concentration, from 30% to absolute, and then air dried and gold coated before examination. Ovipositor and phallus were dissected out and treated in 10% KOH overnight at room temperature. They were then washed with water and transferred to glycerol before being examined with brightfield and Nomarski interference contrast techniques.

Terminology. Structural terminology and abbreviations follow Ronquist & Nordlander (1989) and Ronquist (1995b).

TAXONOMY

PARNIPINAE RONQUIST & NIEVES-ALDREY, SUBFAM. NOV.

Based on *Parnips* new genus (Fig. 2).

Diagnosis. Differs from all other figitids by the combination of a dull mesoscutum and the lack of a horizontal mesopleural furrow (Fig. 4A,B). Differs from cynipids by having a prominent lateral pronotal carina (lpc, Fig. 4A) (present only in *Synergus* among cynipids), a closed marginal cell (Fig. 6) (usually open in cynipids), Rs + M issuing from the posterior end of the basal vein (Fig. 6), and a basal flexion point in the ninth tergum of the female (flp, Fig. 8). The new

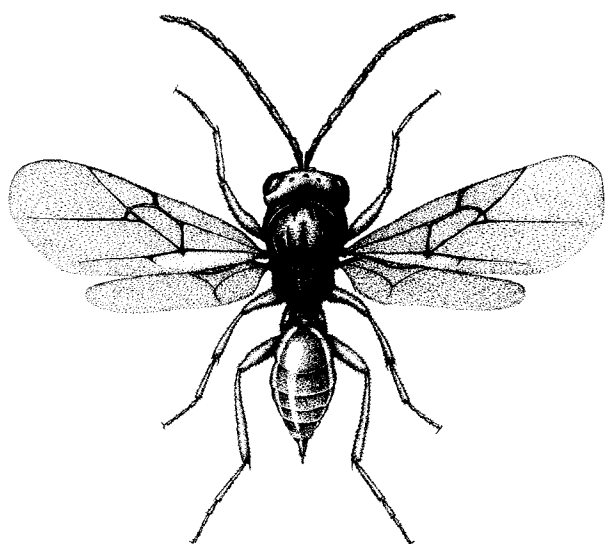


Figure 2. Habitus of *Parnips nigripes*.

subfamily also differs in a number of additional respects from cynipids, figitids and other cynipoids (Ronquist, 1995a, 1999; Liljeblad & Ronquist, 1998). Possible autapomorphies (see also discussion below) of the Parnipinae include the pronotal depressions being united medially with a shallow transverse furrow (Fig. 5A), the procoxa having a distinct anterolateral crest, and the median mesoscutal impression and notauli being indistinct anteriorly (Fig. 4B) (Ronquist 1995a, 1999; Liljeblad & Ronquist, 1998). However, none of these characters is uniquely derived within the Figitidae + Cynipidae.

Description. Female antenna connate, not moniliform. Lower face without median frontal carina (Fig. 3A). Head not distinctly depressed posteriorly (Fig. 3B). Occipital carina missing. Anterior flange of pronotum short (Fig. 4A). Lateral pronotal carina (lpc, Fig. 4A) prominent. Dorsal pronotal area (dpa, Fig. 4B) short, pronotal crest missing. Mesoscutum with dull sculpture, without prominent transverse costae. Mesopleural triangle distinctly impressed (Fig. 4A). Posterior subalar pit present. Mesopleuron without horizontal furrow or carinae. Bulla in R1 + Sc present (Fig. 6). Submedian pits on articular bulb of petiole deep and distinct (Fig. 7). Abdominal terga 3–8 free. Third abdominal tergum of female longer than the fourth along the dorsal curvature of the metasoma; posterior margin oblique in lateral view (Fig. 7A). Ovipositor coiled spirally almost 360°, not elbowed (Fig. 8). Ninth tergum of female with a distinct flexion point above the base of the third valvula. Dorsal process anterior to the flexion point absent. Basal part of terebra twisted 180° so that the first valvulae are in

dorsal position at the apex. First valvula narrowing gradually, not broadened apically.

Diversity and distribution. Includes a single genus and species occurring in the Mediterranean region.

PARNIPS RONQUIST & NIEVES-ALDREY, GEN. NOV.

Type species. *Aulacidea nigripes* Barbotin, 1964.

Etymology. An abbreviation alluding to the particle *par-* (meaning close to) and the figitid genus *Melanips* (from Greek, meaning dark woodworm) (Masculine gender).

Diagnosis. Most similar to the figitid genera *Melanips* (Figitinae), *Euceroptres* (Thrasorinae), and *Hemicrisis* (Charipinae). However, *Parnips* differs from all of these genera in lacking a horizontal mesopleural furrow/carina and in having the first male flagellomere unmodified, the mesopleuron almost entirely dull, the third abdominal tergum of the female smaller, and the female metasoma higher. *Parnips* differs further from *Melanips* and *Hemicrisis* in lacking a dense hair patch on the third abdominal tergum. *Parnips* can also be distinguished from *Hemicrisis* by the larger size and the sculptured scutellum, which is not smooth and evenly rounded. Additional features distinguishing *Parnips* from *Euceroptres* include *Parnips* having a considerably narrower and more elongate metacoxa.

Description. See the description of the only included species below.

PARNIPS NIGRIPES (BARBOTIN, 1964) COMB. NOV.

Syntypes. 25♂, 35♀. ALGERIA, Oran. Reared from *B. oraniensis* galls on *Papaver rhoeas* and *P. dubium*, emerged mid February to early April 1961, 1962 or 1963. Originally in the private collection of F. Barbotin, now most syntypes are in the collection of the University of Barcelona. Examined material: 23♂, 34♀ (Universitat de Barcelona); 1♂, 1♀ (USNM, Washington, DC).

Additional material studied. 2♂, 4♀. SPAIN, Madrid, Aldea del Fresno, 27 May 1987. Reared from *B. oraniensis* galls on *Papaver* sp., emerged April 1988. 2♂, 1♀. Same locality, galls collected 6 June 1988, wasps emerged April 1989. 1♀. Madrid, Arganda, 25 June 1986. Reared from *B. oraniensis* galls on *Papaver* sp., emerged April 1987. 2♀. Madrid, Arganda, 5 May 1991. Caught in flight. 1♂, 1♀. Guadalajara, Pozo de Guadalajara. Reared from *B. oraniensis* galls on *Papaver* sp., 6 October, 1983, emerged April 1984. 1♂. Madrid, Rivas Vaciamadrid. Reared from *B. oraniensis* galls on *Papaver* sp., 26 June 1985, emerged March 1986. 1♂. Same locality, galls collected 6 July 1988,

emerged April 1989. Deposited in the Museo Nacional de Ciencias Naturales, Madrid. 1♀. Madrid, Aldea del Fresno, 6 July 1988. Reared from *B. oraniensis* galls on *Papaver* sp., emerged April 1989. 1♂. Madrid, Rivas Vaciamadrid, 27 May 1987. Reared from *B. oraniensis* galls on *Papaver* sp., emerged April 1988. 3♀ 1♂. Madrid, Aldea del Fresno and San Martin de Valdeiglesias, 29 September, 1997. Reared from *B. oraniensis* galls on *Papaver rhoeas*, emerged April to May, 1998. 5♀ 4♂. Madrid, Aldea del Fresno, October 1998. Reared from *B. oraniensis* galls on *Papaver rhoeas*, emerged May 1999. Deposited in the Zoological Museum, Uppsala University, Uppsala.

Description

Body length. Measured from the anterior margin of the head to the posterior margin of the eighth abdominal tergum: 2.5 ± 0.5 mm (range 1.6–2.8; $N = 11$) for males, 3.0 ± 0.5 mm (range 2.4–3.7; $N = 18$) for females.

Head, anterior view (Fig. 3A). Lower face not keeled medially; facial strigae radiating from clypeus, stopping near compound eyes and reaching lower margin of antennal sockets. Upper face and vertex coriarius; median frontal carina and lateral frontal carinae absent. Ocellar plate not raised. Head strongly narrowing ventrally; lateral margin of gena straight, height of malar space about 0.65 times the height of a compound eye. Clypeus slightly trapezoid. Ventral margin of clypeus almost straight, not distinctly projecting from cranial margin. Anterior tentorial pits small, sometimes obscured. Epistomal sulcus and clypeo-pleurostomal lines weakly marked. Antennal sockets situated at mid-height of compound eye; distance between antennal rim and compound eye slightly longer than width of antennal socket including rim.

Head, posterior view (Fig. 3B). Occiput coriarius, flat, not deeply impressed around occipital foramen. Occipital carina lacking completely, head curving smoothly from lateral to posterior surface. Gular sulci free, well separated at hypostomata. Oral foramen long, more than three times as long as occipital foramen; distance between oral and occipital foramina short, shorter than the height of the occipital foramen.

Mouthparts. Mandibles large, right mandible with three teeth; left with two teeth. Maxillary stipes narrow and elongate, about four times as long as broad, posterior surface with longitudinal carina along mesal margin. Maxillary palp five-segmented: first segment short, longer than broad; second to fourth segment relatively long, 2.5–4 times as long as broad; fifth segment long, longer than fourth. Labial palp three-segmented: first and second segment subequal in length, third segment longer than second.

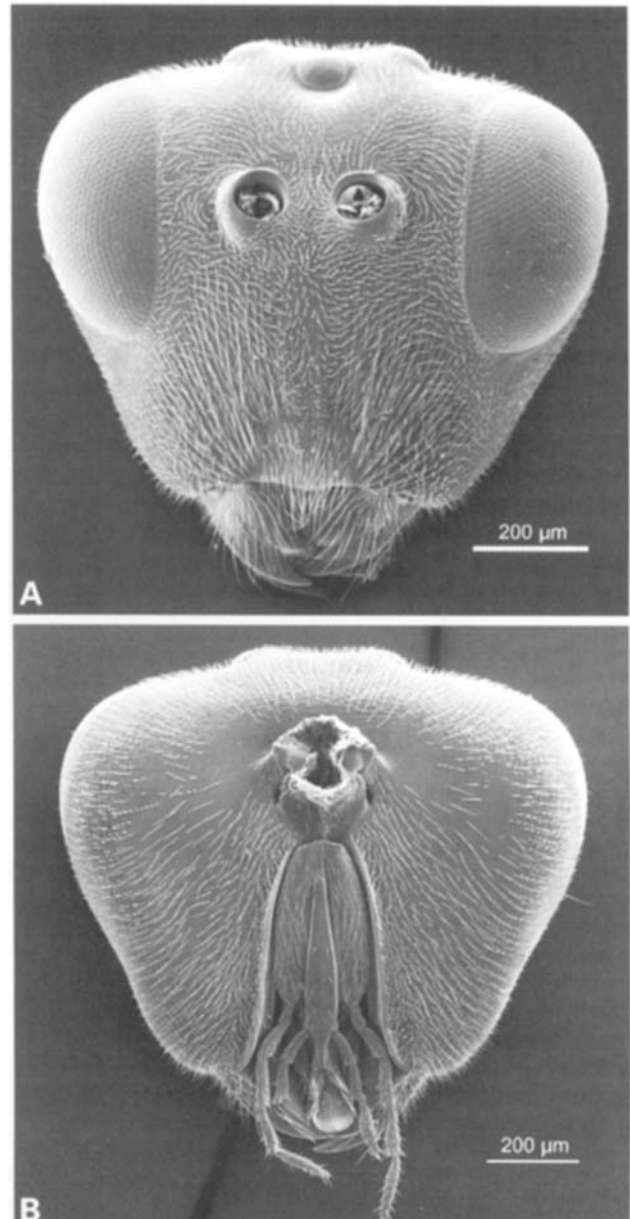


Figure 3. Head of *Parnips nigripes*, female (SEM). A, anterior view. B, posterior view.

Female antenna. Flagellum with 11 connate articles. Length of F1 1.1 times length of F2. F3 2.3 times as long as broad. Ultimate flagellomere 1.8 times as long as the penultimate. Elongate placodeal sensilla present on all flagellomeres.

Male antenna. Flagellum with 12 connate articles. F1 cylindrical in shape, neither excavated nor expanded, without a longitudinal ridge. Length of F1 1.0 times the length of F2. F3 2.3 times as long as broad. Ultimate flagellomere 1.4 times as long as the penultimate.

Elongate placodeal sensilla present on all flagellomeres.

Pronotum (Figs 4A,B, 5A). Pronotum medially long (high), ratio of median distance between anterior and posterior margins to lateral distance between these margins 0.5. Lateral pronotal carinae (lpc, Fig. 4A) widely separated medially, prominent, meeting posteroventral pronotal margin. Submedian pronotal depressions oval, small and shallow, open laterally, connected by a shallow groove medially. Posterior pronotal plate not differentiated, except that the lateroventral corners are marked by the pronotal surface beneath them being depressed. Pronotum in profile distinctly angled dorsally a short distance in front of the posterior margin, a tiny rim-like dorsal pronotal area (dpa, Fig. 4B) present behind this angle. Lateral surface of pronotum coriarius with some irregular, horizontal costulae posteriorly in lower half.

Mesonotum (Fig. 4A,B). Scutum coriarius-colliculate, posteriorly rugulose to transversely weakly costulate, dull. Median mesoscutal impression weakly impressed in posterior one third of mesoscutum, ending in a more distinctly impressed pit. Notauli narrow and shallow, faint in anterior half of mesoscutum, distinct in posterior half. Scutellar foveae shallow, posterior margin not marked. Dorsal surface of scutellum rugose. Posterodorsal and posterior margin of axillula indistinct. Lateral shining strip not extended dorso-posteriorly.

Mesopectus (*mesopleuron including subpleuron and sternum*) (Fig. 4A). Mesopleuron dull except for a minute shining patch at the posteroventral corner of the speculum. Mesopleuron beneath mesopleural triangle coriarius-colliculate, partly weakly rugulose, speculum also weakly longitudinally costulate. Middle part of mesopleuron without horizontal furrow or carinae. Mesopleural triangle distinctly impressed, ventral margin clearly marked except medially.

Metanotum (Figs 4A, 5B). Metascutellum largely glabrate; long, not conspicuously constricted medially. Bar ventral to metanotal trough almost smooth. Metanotal trough moderately wide.

Metapectal-propodeal complex (Figs 4A, 5B). Metapectal sulcus meeting anterior margin of metapectal-propodeal complex slightly above the mid-height of the latter. Metepimeron semicircular, small. Lateral propodeal carinae subparallel, narrow, not flattened above. Lateral and median propodeal area sparsely rugose to almost smooth. Nucha moderately long dorsally, almost smooth, posterior margin distinctly incised medially.

Legs. Procoxa with distinct anterolateral crest. Anterior surface of mesocoxa strongly protruding, its peak close to base of coxa. Metacoxa elongate. Longitudinal carina on posterior surface of metatibia minute, barely more than a fold in the cuticle, present medially to subdistally. Claws without a basal lobe or tooth.

Forewing (Fig. 6). Slightly infusate. Marginal cell closed along anterior margin. Rs+M arising from the junction between the basal vein and M+Cu, i.e. the basal vein consists only of Rs. Bulla in R_1 +Sc present. Areolet moderately large, closed by nebulous to tubular veins. Hair fringe along apical margin short.

Female metasoma (Fig. 7A). Tergal flange of petiolar annulus relatively long, glabrous, with a few short longitudinal carinae indicated basally. Distinct ventral flange missing but the ventral margin of the petiole is distinctly recurved posteriorly, forming an anterior prominence in front of the third abdominal sternum. Postpetiolar metasoma slightly laterally compressed, in lateral view high, lenticular. Euventral margin of metasoma distinctly angled between the hypopygium and the anterior sterna: euventral margin of anterior sterna almost vertical, euventral margin of hypopygium obliquely horizontal. Abdominal terga 3–8 free, not fused. Third tergum with a few hairs anterodorsal to the spiracular remnant, otherwise nude, about twice as long as fourth tergum along dorsal curvature of metasoma. Posterior margin of third tergum in lateral view strongly slanted. Fourth to seventh terga subequal in size, distinctly and densely micropunctate, nude. Eighth tergum micropunctate and with additional, coarser hair punctures. Ventral spine of hypopygium not projecting, united almost to apex with the lateral flaps. Hypopygium ventrally with a relatively broad band of short pubescence.

Ovipositor. Basal part of ovipositor curved spirally almost 360°, with a distinct flexion point in the ninth tergum at the base of the third valvula (b3v, Fig. 8). The flexion point consists of a triangular, membranous piece of the ninth tergum (flp, Fig. 8) flanked by more heavily sclerotized parts anteriorly and posteriorly. The anterior part of the ovipositor can be folded downwards and outwards at the flexion point, increasing the action radius of the terebra. Terebra rotated 180° basally (tw, Fig. 8), such that the first valvulae become dorsal rather than ventral in the composite terebra. In the two examined specimens, the rotation of the terebra is clock-wise if seen from the proximal end. Third valvula distinctly projecting beyond apex of ninth tergum. Third valvula with a clear area (cla, Fig. 8) in the middle, apically densely covered with short hairs on the lateral surface. Cercus (ce, Fig. 8) rigidly attached to ninth tergum, discernible as a partly projecting, pubescent lobe.

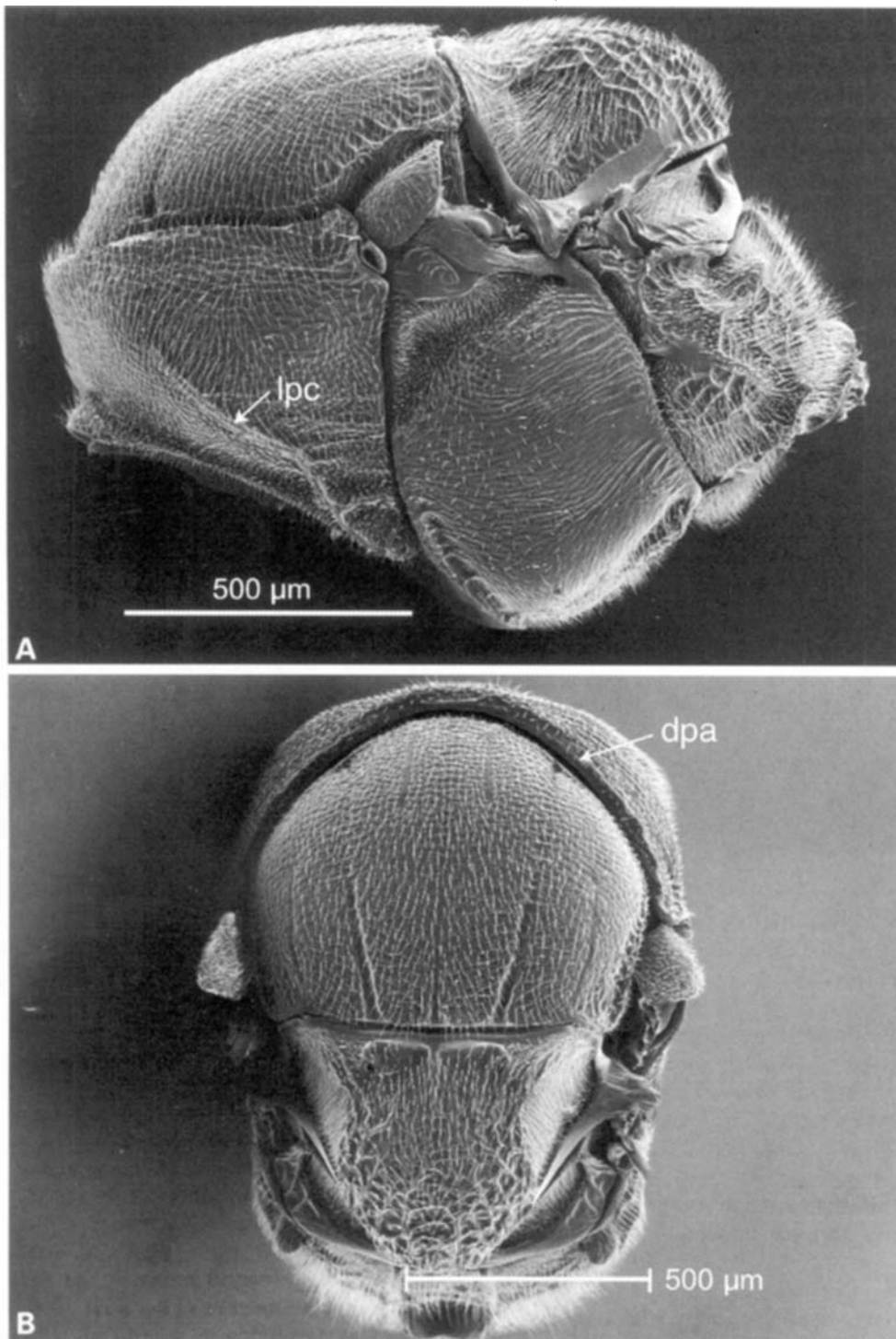


Figure 4. Mesosoma of *Parnips nigripes*, female (SEM). A, lateral view. B, dorsal view. Abbreviations: lpc – lateral pronotal carina; dpa – dorsal pronotal area.

Male metasoma (Fig. 7B). Similar to female metasoma except for the following features: Tergal flange of petiole much larger, almost covering the dorsal aspect of the petiole completely. Postpetiolar metasoma smaller

and more elongate. Euventral margin slightly curved ventrally anteriorly, horizontal or oblique posteriorly, not angled. Third tergum slightly more than twice the length of the fourth along the dorsal curvature of the

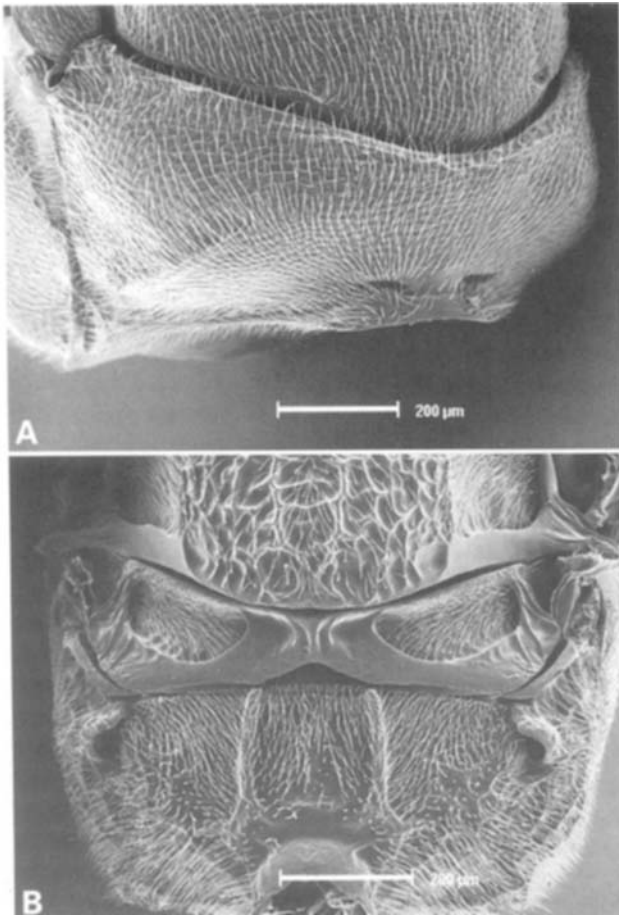


Figure 5. Mesosoma of *Parnips nigripes*, female (SEM). A, oblique anterolateral view showing the pronotum. B, posterodorsal view.

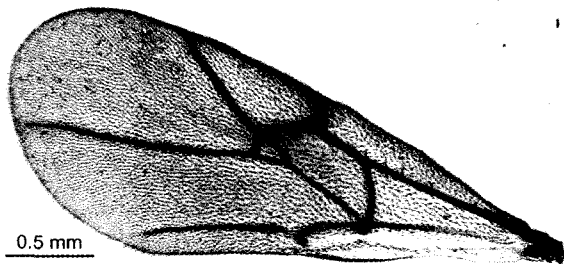


Figure 6. Left forewing of *Parnips nigripes*, female.

metasoma. Eighth sternum with short, dense pubescence ventrally. Cercus present as a distinct, separate oval sclerite surrounded by a largely membranous ninth tergum.

Phallus. Proximal margin of phallus not distinctly incised, almost straight. Basal ring large (Fig. 9A). Paramere only slightly extending beyond digitus (Fig.

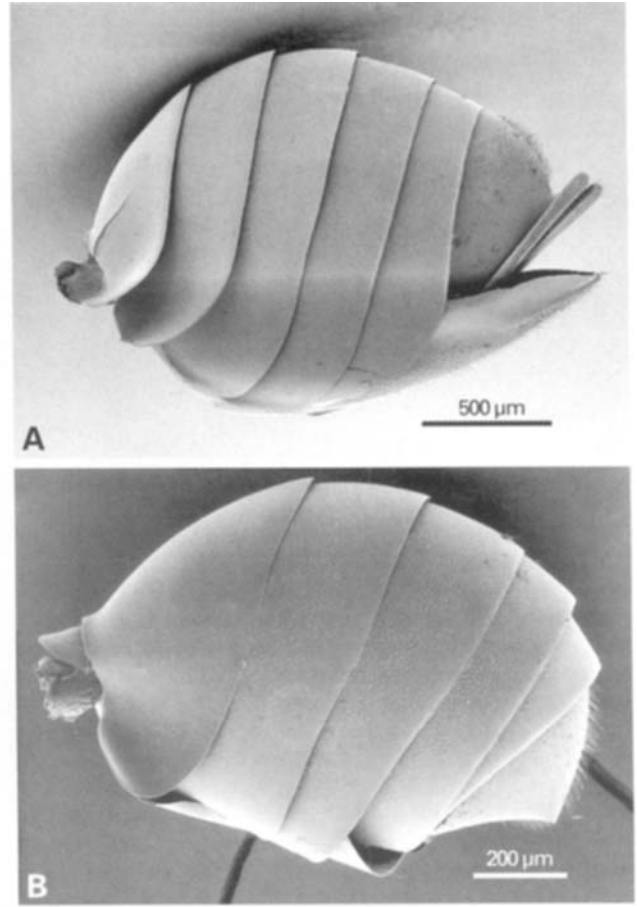


Figure 7. Metasoma of *Parnips nigripes*, lateral view (SEM). A, female. B, male.

9B). Aedeagus not distinctly expanded subapically, apically truncate (Fig. 9A).

Coloration. Black; tarsi, tibia and apex of femora yellowish to reddish brown.

Biology. The species is a koinobiont parasitoid of *Barbotinia oraniensis*, a cynipid inducing spherical galls inside the seed capsules of annual species of poppies (*Papaver rhoeas* and *P. dubium*) (Ronquist & Nieves-Aldrey, unpubl. data). Good field data on the activity period of the adults is missing. In gall rearings, *Parnips nigripes* emerges in February to May, simultaneously with *Barbotinia oraniensis* (Barbotin, 1964; Ronquist & Nieves-Aldrey, unpubl. data). The adults live for a few weeks in the laboratory when provided free access to water and a diluted honey solution. The early emergence and short life span of the adults suggest that oviposition is into eggs or young larvae of the host, which is typical for insect-parasitic cynipoids. Around Madrid, the *P. nigripes* larva is fully-grown in late September, when it can be found in the gall together with the skin and mandibles of the last instar host

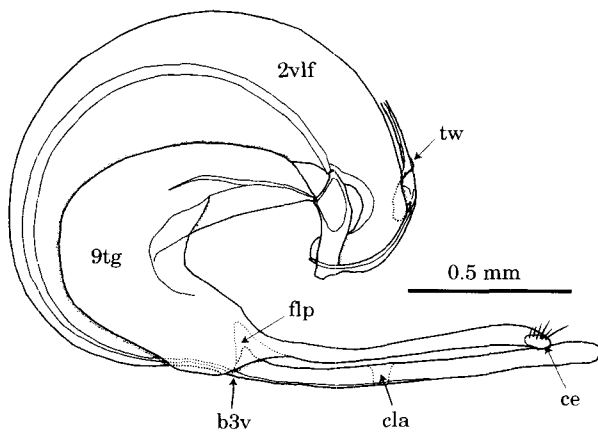


Figure 8. Ovipositor of *Parnips nigripes*, lateral view from the left side. Drawing from a slide mount of an ovipositor cleared in KOH. Abbreviations: b3v – base of third valvula; ce – cercus; cla – clear (but not weak) area in the third valvula; flp – flexion point in the ninth tergum, consisting of a weak and flexible, triangular area surrounded by more heavily sclerotized regions; tw – basal twist in terebra; 2vlf – second valvifer; 9tg – ninth abdominal tergum.

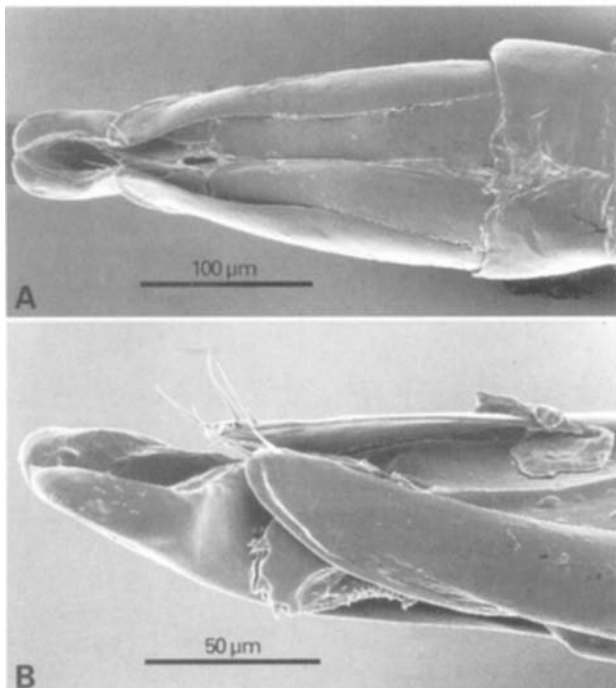


Figure 9. Phallus of *Parnips nigripes* (SEM). A, ventral view. B, ventrolateral view of apex.

larva. The galls containing *P. nigripes* are virtually indistinguishable from those containing *B. oraniensis* and the two species are of similar size, the male being smaller in both. Since oviposition evidently occurs early in the life cycle of the host, and the latter succeeds

in completing its development to the last instar, *P. nigripes* is clearly a koinobiont parasitoid. Presumably, it is an early internal–late external parasitoid like all parasitic cynipoids studied in detail thus far (Ronquist, 1999 and references cited therein).

Distribution. *Parnips nigripes* has only been recorded from Algeria (the provinces of Oran, Mascara and Saida) and the centre of Spain (Barbotin, 1964; Nieves-Aldrey, 1985). However, galls of its host (*Barbotinia oraniensis*) have also been found in southern Spain (Nieves-Aldrey, unpubl. data) and Italy (Nieves-Aldrey, 1994) as well as in France and Romania (F. Barbotin, pers. comm.). Thus, *P. nigripes* may well be widely distributed in southern Europe and around the Mediterranean Sea.

DISCUSSION

Although *Parnips nigripes* is superficially cynipid-like, detailed analysis of the morphological evidence clearly shows that it is a figitid. For instance, *P. nigripes* shares the two principal figitid synapomorphies, both uniquely derived within the Cynipoidea and universally present in the Figitidae (Ronquist, 1994, 1995a, 1999): (1) a point of weakness or flexibility in the ovipositor (flp, Fig. 8) and (2) a posteriorly displaced Rs + M vein (Fig. 6). Many additional morphological characters suggest figitid rather than cynipid affinities of *P. nigripes* (Ronquist, 1994, 1995a, 1999; Liljebld & Ronquist, 1998). For instance, cynipids primitively have a medially constricted metascutellum, an open marginal cell and the lateral pronotal carina absent whereas *P. nigripes* has a square metascutellum, a closed marginal cell, and a prominent lateral pronotal carina, like most figitids.

The basal position of the Parnipinae in the Figitidae is primarily supported by the presence of the transverse mesopleural furrow/carina in figitids excluding *Parnips* (the furrow/carina is only secondarily lost in advanced charipines, in emarginines, and a few additional, clearly subordinate figitid taxa). It is also supported by congruence with the distribution of other characters in the Figitidae, including ovipositor features (Ronquist, 1999). For instance, *Parnips* and thra-sorines are unique among figitids in having a spirally coiled ovipositor, which is primitive for cynipoids, rather than the typical derived, elbowed figitid ovipositor (Fergusson, 1988; Ronquist, 1995a, 1999). The overall resemblance between *Parnips nigripes* and cynipids suggests that additional unique figitid pleiomorphies may eventually be found in the former.

The phylogenetic position of *P. nigripes* is such that, considering the current classification of the Cynipoidea, there are primarily two alternatives for its

higher classification: either it is recognised as a subfamily of the Figitidae or it is treated as a separate family. The Figitidae have been variously circumscribed in the past but there are several advantages of using the name in a broad sense for the entire sister group of the Cynipidae (Ronquist, 1999). Therefore, and to keep the number of cynipoid families to a minimum, we prefer not to give *Parnips* separate family status.

It is difficult to identify convincing autapomorphies for *P. nigripes* because the species appears to have retained most of its morphological characters from the figitid ground plan. The analysis of higher cynipid relationships by Liljeblad and Ronquist (1998), which included *P. nigripes* and *Euceroptres montanus* as figitid exemplars, identified ten putative autapomorphies of *P. nigripes*: (1) clypeus with ventral margin straight, not projecting; (2) F1 long; (3) male flagellum with 12 articles; (4) submedian pronotal depressions united medially; (5) horizontal ridges present postero-ventrally on the lateral surface of the pronotum; (6) notauli present only posteriorly; (7) median mesoscutal impression reduced to a posterior pit; (8) metanotal trough broad; (9) anterolateral crest present on procoxa; and (10) third valvulae projecting beyond the ninth tergum. To this list, one might add the lack of a modified flagellomere in the male antenna (Ronquist, 1999) and the long and narrow labiomaxillary complex (Fig. 3B). Of these 12 characters, the three antennal ones are too homoplastic in the Cynipoidea to allow reliable conclusions regarding the direction of character evolution. Furthermore, the metanotal trough is only slightly wider in *P. nigripes* than in *Euceroptres* and additional sampling of figitids would be needed to confirm the apomorphic nature of the *P. nigripes* state.

Thus, eight putative autapomorphies remain. In four of these, however, *P. nigripes* is remarkably similar to its host, *B. oraniensis*, in the Cynipidae. This is true for the straight ventral margin of the clypeus (compare Fig. 10A with Fig. 3A), the long labiomaxillary complex (Figs 10B and 3B), the horizontal ridges on the lateral surface of the pronotum, and the long third valvulae. The alternative hypothesis of shared primitive presence cannot be safely ruled out for any of these characters. For instance, the straight clypeal margin occurs in many cynipids as well as in Austrocynipidae, the sister group of all other cynipoids (Fig. 1) (Riek, 1971). When the Austrocynipidae, not considered by Liljeblad & Ronquist (1998), are introduced into the analysis, Fitch parsimony can no longer distinguish between reconstructions implying shared presence and independent derivation. The horizontal ridges on the lateral surface of the pronotum and the long third valvulae are relatively homoplastic characters in the Cynipidae (Liljeblad & Ronquist, 1998) and, again, the hypothesis of shared plesiomorphy cannot be safely

dismissed. As far as we are aware, the long and narrow labiomaxillary complex is unique to *Parnips* and *Barbotinia* among cynipoids (Figs 3B, 10B). If current phylogenetic hypotheses are correct, Fitch parsimony favours independent derivation in *Parnips* and *Barbotinia* (two gains) over shared presence (one gain and three losses). However, because of the detailed similarity between *Parnips* and *Barbotinia*, one could possibly argue that three independent losses are more likely than one convergent gain, and thus that the latter hypothesis is more plausible. Again, shared presence remains a viable alternative.

Hence, four putative autapomorphies of *P. nigripes* may be identified: (1) the united submedian pronotal depressions; (2) the superficial notauli; (3) the short median mesoscutal impression; and (4) the presence of an anterolateral procoxal crest. None of these states are unique to *P. nigripes* among figitids and cynipids. Perhaps the strongest case for autapomorphic status can be made for the last character, which only has three isolated occurrences in other cynipoids recorded thus far: in *Ibalia* (Ibaliidae), *Liposthenes* (Cynipidae) and *Synergus* (Cynipidae) (Ronquist & Nordlander, 1989; Ronquist, 1994, 1995a; Liljeblad & Ronquist, 1998).

Parnips nigripes is remarkably similar to its host, *Barbotinia oraniensis*, not only in the characters listed above but also in general morphology, coloration and habitus, despite these genera belonging on each side of the fundamental phylogenetic divider between the insect-parasitic figitids and the phytophagous cynipids (Fig. 1). The similarities are so extensive that the species are easily mistaken if not examined in detail. For instance, in the syntype series of *Aulacidea nigripes*, there is a pin with four specimens, only one of which belongs to *Parnips*; the other specimens belong to *Barbotinia*. Given the basal phylogenetic position of these two genera in their respective families, and the large proportion of figitid + cynipid plesiomorphies in the skeletal characters analysed thus far, it seems likely that much of the general resemblance between them is due to shared inheritance from the most recent common ancestor of figitids and cynipids. There appears to be no reason for the parasitoid to mimic the appearance of its host but some similarities may, of course, be caused by environmentally induced convergence.

The oldest known fossil figitids, two amber specimens from the Santonian (Upper Cretaceous, 83–87 Mya) placed in the subfamily Palaeocynipinae (Kovalev, 1994; Ronquist, 1999), mix characters of *P. nigripes* and charipine figitids. Their small size (0.7–0.8 mm), the modified male flagellum, the weakly sculptured scutum and scutellum, and the sparse pubescence suggest charipine affinities. Otherwise they are more similar to *P. nigripes*, for instance in the lack

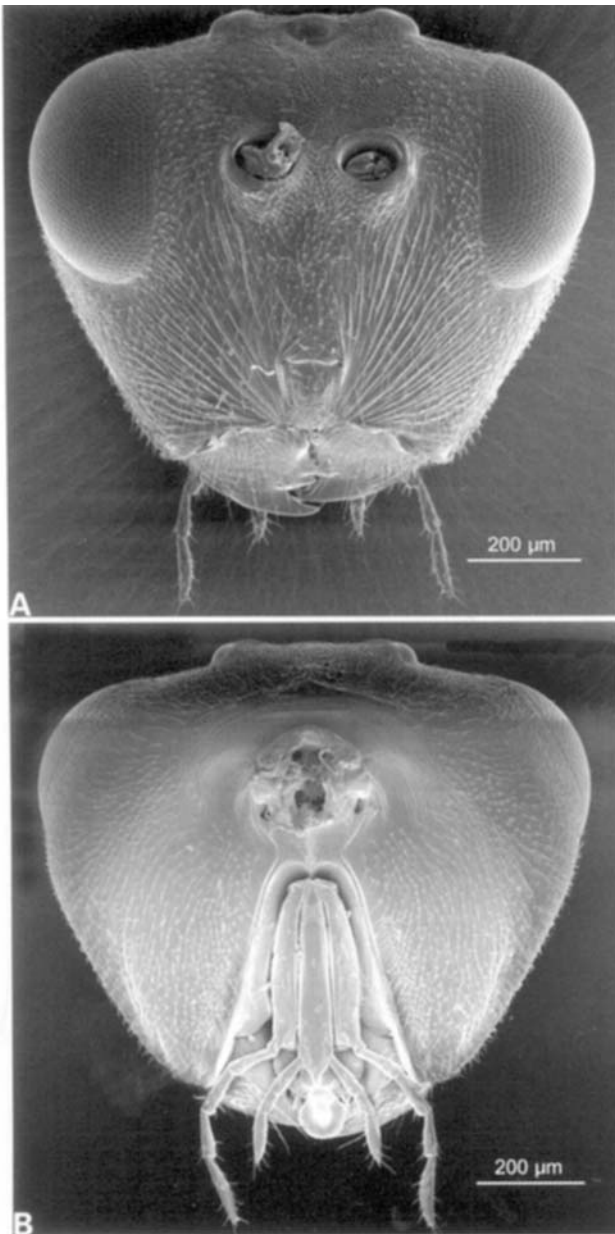


Figure 10. Head of *Barbotinia oraniensis*, the host of *Parnips nigripes*, female (SEM). A, anterior view. B, posterior view. Notice the striking similarity between *Barbotinia* and *Parnips* in unusual cynipoid features such as the straight clypeal margin and the extremely elongate labio-maxillary complex.

of a mesopleural carina/ledge, the absence of a dense hair patch on the third tergum, and the well developed areolet. Both *P. nigripes* and its host, *B. oraniensis*, are similar to even older cynipoid fossils in the family Gerocynipidae from the Cenomanian (Upper Cretaceous, 90–97 Mya) in having a large and lenticular metasoma and long third valvulae. The phylogenetic position of gerocynipids has not been analysed formally

yet but Ronquist (1999) suggested that they might belong to the stem group of extant microcynipoids (Figitidae + Cynipidae).

Parnips nigripes may well be a 'living fossil' not only with respect to its morphology but also with respect to its biology and distribution. Parsimony mapping of biological traits on current phylogenetic estimates indicates that the last figitid + cynipid ancestor was a koinobiont parasitoid of a gall-inducing or gall-inhabiting hymenopteran larva developing inside the seed capsules of *Papaver* (Ronquist, 1999, unpubl. data). All of these traits are shared by *P. nigripes*. Of course, the host of the figitid + cynipid ancestor could not have been a cynipid like *Barbotinia oraniensis*, since gall-inducing cynipids did not exist at that time. Instead, the ancestor must have attacked some other gall-inhabiting hymenopteran, perhaps a chalcidoid. Furthermore, the genus *Papaver* may not have existed 83 Mya even though the Papaveraceae appear to be older than most angiosperm families, since it belongs to a depauperate basal branch in the eudicot part of the angiosperm phylogeny (APG, 1999), and putative macrofossil poppies are known from the Cretaceous of North America (Smith, 1996). In any case, gall-inducing and gall-parasitic cynipoids are phylogenetically conservative in their host-plant associations, so it seems likely that the microcynipoid ancestor was associated with some ancestral member or close relative of the Papaveraceae.

Cynipids probably attack more plants in the Papaveraceae than is currently known. For instance, recent studies of papaveraceous plants have revealed one undescribed cynipid gall on *Fumaria* in the Mediterranean (Nieves-Aldrey, unpubl. data; Ronquist, unpubl. data) and another one on *Corydalis* in Tibet (Ronquist, unpubl. data). Further studies will have to show whether these galls occupy basal positions in the cynipid phylogeny, and whether they are associated with figitid parasitoids.

If the scenario described above is correct, then the gall-inducing cynipids, perhaps the most advanced of all gall-inducing insects, evolved from parasitoids of gall-inhabiting, perhaps gall-inducing, hymenopteran larvae. Because *Parnips nigripes* appears to have retained many ancestral features of the parasitic ancestors of gall wasps, and its host, *Barbotinia oraniensis*, seems to be similar to the first gall inducers, these species provide an excellent model system for studies of the origin of the ability to induce galls in cynipids.

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REFERENCES

- Angiosperm Phylogeny Group. 1999.** An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* **85**: 531–553.
- Askew RR, Shaw MR. 1986.** Parasitoid communities: their size, structure and development. In: Waage J, Greathead D, eds. *Insect parasitoids*. London: Academic Press, 225–264.
- Barbotin F. 1964.** Sur une nouvelle galle et deux nouveaux cynipides en provenance d'Algérie. *Marcellia* **31**: 151–157.
- Díaz NB. 1980.** Cynipoideos galígenos e inquilinos de la República Argentina. *Revista de la Sociedad Entomológica de Argentina* **39**: 221–226.
- De Santis L, Fidalgo P, Ovruski S. 1993.** Himenópteros parasitoides de los géneros *Aditrochus* Ruebsaamen y *Espinosa* Gahan (Insecta, Hymenoptera, Pteromalidae) asociados a agallas en *Nothofagus* (Fagaceae) del sur de Argentina y Chile. *Acta entomologica Chilena* **18**: 133–146.
- Fergusson NDM. 1988.** A comparative study of the structures of phylogenetic importance of female genitalia of the Cynipoidea (Hymenoptera). *Systematic Entomology* **13**: 13–30.
- Kovalev OV. 1994.** [Palaeontological history, phylogeny and the system of brachycleistogastromorphs and cynipomorphs (Hymenoptera, Brachycleistogastromorpha infraorder n., Cynipomorpha, infraorder n.) with description of new fossil and recent families, subfamilies and genera]. *Entomologicheskoe Obozrenie* **73**: 385–426. [In Russian].
- Liljeblad J, Ronquist F. 1998.** A phylogenetic analysis of higher-level gall wasp relationships (Hymenoptera: Cynipidae). *Systematic Entomology* **23**: 29–252.
- Nieves-Aldrey JL. 1985.** Nuevos Aylaxini (Hym., Cynipidae) para la Península Ibérica con descripción de una nueva especie de Aylax Htg. *Boletim da Sociedade Portuguesa de Entomologia Suppl. 1* (Actas do III Congreso Ibérico de Entomologia. Lisboa): 117–128.
- Nieves-Aldrey JL. 1994.** Revision of West-European Genera of the Tribe Aylaxini Ashmead (Hymenoptera, Cynipidae). *Journal of Hymenoptera Research* **3**: 175–206.
- Nieves-Aldrey JL. 1995.** Two new species of Aylaxini (Hymenoptera: Cynipidae) from France, associated with *Silybum* and a new gall from *Scorzonera* (Asteraceae). *Annales de la Société Entomologique de France* **31**: 369–375.
- Riek EF. 1971.** A new subfamily of cynipoid wasps (Hymenoptera: Cynipoidea) from Australia. In: *Entomological essays to commemorate the retirement of Professor K. Yasumatsu*. Tokyo: Hokuryukan, 107–112.
- Ronquist F. 1994.** Evolution of parasitism among closely related species: phylogenetic relationships and the origin of inquilinism in gall wasps (Hymenoptera, Cynipidae). *Evolution* **48**: 241–266.
- Ronquist F. 1995a.** Phylogeny and early evolution of the Cynipoidea (Hymenoptera). *Systematic Entomology* **20**: 309–335.
- Ronquist F. 1995b.** Phylogeny and classification of the Liopteridae, an archaic group of cynipoid wasps (Hymenoptera). *Entomologica Scandinavica Supplement* **46**: 1–74.
- Ronquist F. 1999.** Phylogeny, classification and evolution of the Cynipoidea. *Zoologica Scripta* **28**: 139–164.
- Ronquist F, Nordlander G. 1989.** Skeletal morphology of an archaic cynipoid, *Ibalia rufipes* (Hymenoptera: Ibalidae). *Entomologica Scandinavica Supplement* **33**: 1–60.
- Smith UR. 1996.** Strange fruit of the Cretaceous poppy. In: Repetski J, ed. *Sixth North American paleontological convention; abstracts of papers*. Knoxville: The Paleontological Society, 365.
- Weld LH. 1926.** Field notes on gall-inhabiting cynipid wasps with descriptions of new species. *Proceedings of the US National Museum* **68**: 1–131.
- Weld LH. 1952.** *Cynipoidea (Hym.) 1905–1950*. Ann Arbor: Privately printed.