Revision of the Australian species of *Pleistodontes* (Hymenoptera: Agaonidae) fig-pollinating wasps and their host-plant associations

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The Australian species of *Pleistodontes*, fig-pollinating wasps, are revised. In Australia, 14 species of *Ficus* belonging to the *Urostigma* sect. *Malvanthera* are known. From these *Ficus*, 17 species of *Pleistodontes* are recorded, of which seven are described as new. All type material has been examined and four new specific synonymies are proposed. One species, *P. regalis* Grandi, is resurrected from synonymy, while another, *P. nitens* (Girault) is redescribed. A key to females of Australian *Pleistodontes* is provided. All species are defined by means of full morphological descriptions, diagnosis, SEM photographs and drawings. Lectotypes are designated for nine species. The known distribution of each species is also given. Host plant (*Ficus*) associations are re-assessed in the light of this work and the recent revision of Australian *Ficus* sect. *Malvanthera*. In most cases there is a one-to-one relationship between *Ficus* and *Pleistodontes* species; however, three notable exceptions are discussed. Finally, our morphological study suggests strongly that the genus *Pleistodontes* includes some species that pollinate fig flowers actively and others that effect only passive pollination. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, **136**, 637–683.

ADDITIONAL KEYWORDS: Chalcidoidea – Agaoninae – Moraceae – *Ficus – Malvanthera* – mutualism – coevolution – pollination.

INTRODUCTION

Ficus (Urticales: Moraceae) is one of the largest genera of terrestrial plants, with over 750 described species (Berg, 1989) and the majority of these (some 500 species) are found in Australasia. Each fig (*Ficus*) species is generally pollinated by its own unique (but see Rasplus, 1996 for exceptions) pollinator wasp species (Hymenoptera: Agaonidae), whose larvae also feed and develop within the syconia (fig fruits) of the host plant. Figs also play host to a number of nonpollinat-

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ing wasps from diverse taxonomic lineages (Rasplus *et al.*, 1998). The intimate fig-pollinator wasp association is an obligate mutualism and has been the subject of many behavioural, ecological, and coevolutionary studies. However, despite the status of this mutualism as a model system for testing evolutionary and ecological hypotheses, fig wasp communities are poorly known taxonomically, and even the pollinators of many figs remain undescribed.

In Australia, 41 fig species have so far been recorded (D.J. Dixon, unpubl. data), of which *Ficus* species in the *Urostigma* sect. *Malvanthera* Corner represent the most speciose and conspicuous endemic radiation. The section *Malvanthera* ser. *Malvanthereae* Corner comprises 21 species, 14 of which are endemic to Australia (Table 1) (Dixon, 1999, 2001a,b,c; Dixon,

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Ficus	Pleistodontes
F. atricha D.J. Dixon, 2001a	Pollinator wasp not collected
F. cerasicarpa D.J. Dixon, 2001a	P. macrocainus sp.nov.
F. brachypoda (Miq.) Miq., 1867	-
F. brachypoda (Miq.) Miq., 1867	P. athysanus sp.nov.
F. crassipes F.M. Bailey, 1889	P. nitens (Girault)
· ·	P. addicotti Wiebes
F. destruens F. Muell. ex C.T. White, 1933	P. rigisamos Wiebes
F. lilliputiana D.J. Dixon, 2001b	P. proximus Wiebes
F. macrophylla Desf. ex Pers., 1847	P. froggatti Mayr
F. obliqua G. Forster, 1847	P. greenwoodi Grandi
* ·	P. xanthocephalus sp.nov.
F. platypoda (Miq.) A. Cunn. ex Miq., 1847	P. cuneatus Wiebes
F. pleurocarpa F. Muell., 1874	P. regalis Grandi
	P. deuterus sp. nov.
F. rubiginosa Desf. ex Vent., 1805	P. imperialis Saunders
F. subpuberula Corner, 1959	P. astrabocheilus sp.nov.
F. triradiata Corner, 1960	P. schizodontus sp.nov.
F. watkinsiana F.M. Bailey, 1891	P. nigriventris (Girault)
Ficus sp. unknown host	P. achorus sp.nov.

Table 1. Australian malvantheran fig species and their associated *Pleistodontes*

Jackes & Bielig, 2001). Malvantheran figs are pollinated by different species of agaonid wasps, all belonging to the genus *Pleistodontes* Saunders. The wasps collected by one of us (D.J. Dixon) while revising the Urostigma sect. Malvanthera, as well as other recent collecting trips in Queensland, have provided many new Pleistodontes samples. Consequently, we decided to revise the Australian species of *Pleistodontes* and, for this purpose, examined all the accessible type material. This study is timely because we now have access to large numbers of specimens with authenticated host plant records, as well as a revised taxonomy of the associated host plants. This allows us to conduct the first detailed assessment of *Ficus*-pollinator species associations using data from a genus of wasps (*Pleistodontes*) and section of figs (*Malvanthera*), both of which have been the subject of recent revision.

The *Malvanthera–Pleistodontes* co-radiation is also of great interest in the light of a recent comparative study of variation in the morphology and behaviour of fig-pollinating wasps. Kjellberg *et al.* (2001) found that there have been several changes between passive and active pollination (or vice versa) in fig-pollinating wasps, and that the mode of wasp pollination behaviour is highly correlated with the anther : ovule ratio observed in the host figs. Active pollinators use coxal corbiculae to move pollen to and from their mesosternal pollen pockets while passive pollinators lack this behaviour. Most genera of fig wasps appear to have either active or passive pollination behaviour but Kjellberg *et al.* (2001) identified *Pleistodontes* as an interesting case where behaviour was likely to vary between species if, as believed, anther : ovule ratios and the presence or absence of coxal combs are good indicators of pollination behaviour. In describing the *Pleistodontes* species, we consider variation in the two key morphological features – mesosternal pollen pockets and coxal corbiculae – associated with active pollination behaviour (Table 2).

In this paper, we clarify confused nomenclature and synonymy surrounding the genus *Pleistodontes* (Appendix), describing new species and elucidating host relationships. The latter is critical in understanding the ecologically important mutualism that exists between fig trees and fig wasps. The data presented here are a foundation for testing hypotheses of coevolution and cospeciation within the mutualism and have a far wider impact than the specialist taxonomic field.

TAXONOMIC HISTORY OF PLEISTODONTES

Saunders (1882), in a preliminary note, made available the name of *Pleistodontes imperialis* and then, in 1883, described, illustrated and named the genus *Pleistodontes* in allusion to the multiserrate mandibular appendages of the female (Saunders, 1883). *'Pleistodontes imperialis* (Saunders)' was redescribed by Froggatt (1901) who, in fact, misidentified the species and described the pollinator of *Ficus macrophylla*

Table 2. Summary of the presence or absence of pollenpockets and coxal corbicula in Australian *Pleistodontes*species

Pleistodontes	Pollen pockets	Coxal corbicula
P. froggatti Mayr	large	absent
P. deuterus sp. nov.	absent	absent
P. regalis Grandi	small	absent
P. nitens (Girault)	small	absent
<i>P. achorus</i> sp. nov.	small	absent
P. nigriventris (Girault)	small	absent
P. addicotti Wiebes	small	absent
P. schizodontus sp. nov.	small	absent
P. rigisamos Wiebes	small	absent
P. cuneatus Wiebes	large	present
P. proximus Wiebes	large	present
P. athysanus sp. nov.	large	present
P. astrabocheilus sp. nov.	large	present
P. imperialis Saunders	large	present
P. macrocainus sp. nov.	large	present
P. xanthocephalus sp. nov.	large	present
P. greenwoodi Grandi	large	present

Desf. ex Pers., which was not named at that time. Mayr (1906) recognized Froggatt's error and described *Pleistodontes froggatti* Mayr. From 1915 to 1939, Girault named seven new Australian species, which presently belong to the genus *Pleistodontes*. However, at the beginning of our study, only two of Girault's species were still considered valid. The first was *Pleistodontes nitens* (Girault, 1915b), the supposed pollinator of *Ficus pleurocarpa* F. Muell., following the synonymy of *Pleistodontes regalis* Grandi, 1952 by Boucek (1988: 192), while the second was *Pleistodontes nigriventris* (Girault, 1915a), which is the pollinator of *Ficus watkinsiana* F.M. Bailey.

One of the other species, *Pleistodontes semiruficeps* Girault, 1929, a species reared from F. macrophylla f. columnaris (C. Moore) D.J. Dixon in Lord Howe Island (Corner, 1963) was formally synonymized with P. froggatti by Boucek (1988: 191). Another four names remain unrecognized and/or have never been formally synonymized. Pleistodontes nigris Girault, 1925 (from F. macrophylla) and Pleistodontes nigricaput Girault, 1927 (from F. rubiginosa Desf. ex Vent.) are considered to be, respectively, the same as P. froggatti (Wiebes, 1977a: 140) and P. imperialis but were never formally synonymized. Pleistodontes liszti Girault, 1932, a species still unrecognized, and Pleistodontes medionigra (Girault, 1933), transferred by Hill (1967a: 92) to Pleistodontes, are both considered to be the same as P. imperialis (Boucek, 1988) but are not formally synonymized. Finally, Girault (1939) was of the opinion that P. froggatti of Grandi (1916a) was different from Mayr's species, and used a replacement name, *Pleist-odontes mayri* Girault, 1939 for Grandi's taxon. However, Grandi (1928b), in revising the species described by Mayr, confirmed his original interpretation of *P. froggatti*. Consequently, *P. mayri* Girault is considered an unnecessary replacement name; it was recognized as 'quite redundant' by Wiebes (1963) and as a synonym of *P. froggatti* by Boucek (1988).

Grandi (1916b) redescribed P. froggatti Mayr and later P. imperialis, as well as describing Pleistodontes greenwoodi (Grandi, 1928a). Subsequently, he described Pleistodontes regalis Grandi, 1952 from Ficus pleurocarpa. Wiebes added seven new species from Papua New Guinea and adjacent islands, mostly collected from syconia by Corner or caught at light traps (Wiebes, 1963, 1968, 1977a). Boucek (1988), in his monumental work on the Australasian Chalcidoidea, made only two changes in Pleistodontes, synonymizing P. regalis with P. nitens and P. semiruficeps with P. froggatti. In the 1990s, Wiebes described four new species from Australia: Pleistodontes cuneatus Wiebes, Pleistodontes proximus Wiebes, Pleistodontes addicotti Wiebes and Pleistodontes rigisamos Wiebes. He also reallocated Blastophaga clavigera Mayr, 1885 to Pleistodontes (Wiebes, 1994a: 132). This species, collected in the botanical garden of Bogor (Java) in the 1800s has not been found since. It long remained unrecognized until Grandi (1928b) redescribed the species and placed it in the 'junk' genus Blastophaga. Consequently, at the beginning of this study, the genus *Pleistodontes* comprised 18 Australasian species.

MATERIAL AND METHODS

Thousands of specimens were examined from different museums and collections (see list). Most of the specimens studied by the late J.T. Wiebes were re-examined in RMNH and ANIC. Type-lots designated by Wiebes were removed from alcohol using critical point drying (CPD) (Gordh & Hall, 1979) and remounted on rectangular card following Noyes (1982).

Fresh material was reared from maturing fig syconia collected a few hours prior to the escape of the insects. Figs were opened and placed in muslin-topped emergence boxes. Emerging female wasps (winged) were removed, using a pooter, and killed in a dish containing 70% ethanol (Quicke, Belshaw & Lopez-Vaamonde, 1999). Syconia were then sliced open and examined under a binocular microscope in order to collect the non-emerging wingless male wasps. Wasps were later dried using CPD and mounted on rectangular cards. Antennae were mounted in balsam on small translucant plastic cards (7 × 13 mm), which are pinned under the specimens. Line drawings of the antennae were made directly from slide-mounted material, using a drawing tube attachment on a compound microscope. Insects were prepared for scanning electron microscopy following Gibson (1984) and Noyes (1990).

Morphological terminology follows Boucek (1988) and Van Noort (1993). All measurements were taken from dry-mounted specimens. Length of specimen does not include the length of ovipositor sheaths. Abbreviations used in the text include: POD, Post-Ocellar Distance = distance between hind ocelli; OOD, Ocellus–Ocular Distance = distance between lateral ocellus and eye; MPS, Multiporous Plate Sensilla. Measurements are given as the number of micrometer graduations and were always taken at the same magnification, such that 26 graduations = 0.1 mm. The figures are grouped at the end of the paper.

The following abbreviations are used for institutions and collections housing *Pleistodontes* specimens: ANIC, Australian National Insect Collection, CSIRO, Canberra. Australia; BMNH, The Natural History Museum, London, UK; BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA; CCLV, Collection of Carlos Lopez-Vaamonde, London, UK; CJYR, Collection of Jean-Yves Rasplus, Montpellier, France: CNCI. Canadian National Collection of Insects, Ottawa, Canada; IEGG, Universita di Bologna, Dipartimento Scienze e Tecnologie Agroambientali, ex Istituto di Entomologia 'Guido Grandi', Italy; NHMV, Natuurhistorisches Museum, Vienna, Austria; QMBA, The Queensland Museum, Brisbane, Australia; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, Holland; SAMA, South Australian Museum, Adelaide, Australia; SAMC, South African Museum, Cape Town, South Africa; ZMUC, Zoological Museum Copenhagen, Denmark.

SYSTEMATICS

GENUS PLEISTODONTES SAUNDERS, 1882

- *Pleistodontes* Saunders, 1882: 164 and 1883: 8–10. Type species: *Pleistodontes imperialis* Saunders by monotypy.
- *Plistodontes* Schulz, 1906: 148. Unnecessary emendation.
- Neoceratosolens Girault, 1915b: 312. Type species Neoceratosolens nitens Girault by original designation. Synonymy by Hill (1967b: 92).
- Proceratosolens Girault, 1933: 3. Type species Proceratosolens medionigra Girault: by monotypy. Synonymy by Hill (1967b: 92).

Diagnosis

The genus *Pleistodontes* is rather difficult to define despite a relatively homogeneous morphology. The female head is elongate, mostly longer than wide (but in some species as long as wide, e.g. Pleistodontes mandibularis Wiebes from Papua New Guinea), bearing three ocelli on the vertex. The head is fully chitinized without a membranous area above the toruli; at most, P. greenwoodi and Pleistodontes xanthocephalus sp. nov. exhibit a V-shaped membranous line on the median line of the head. Eyes usually shorter than the genae but as long as the genae in some species. Mandibular appendage elongate, usually bearing more than 20 transverse laminae, rarely less (11-13 in P. rigisamos), sometimes bearing transverse rows of small teeth (e.g. P. regalis, P. nitens, P. froggatti). Antennal scape usually elongate (at least 2-3 × as long as broad), sometimes shorter, mostly bearing a dorsal lamina which can be curved outwards and downwards. Pedicel rather short without dorsal spines. Third antennal segment elongates into a triangular process, always undivided and frequently elongate. Some species have no triangular expansion on the third antennal segment (First funicular segment, F1). Antenna bear one or two rows of sensilla linearia. Mesosoma bears pollen pockets, sometimes reduced, or absent (all Papuan species and one Australian species). Venation is always complete. The fore tibia usually bears 2-3 spines in the dorso-apical comb, rarely only one, and four in one Papuan species (Pleistodontes immaturus Wiebes). Apical spiracles small, rarely surrounded by large concave peritremata (P. nitens). Ovipositor sheaths about as long as or shorter than metasoma (all Australian species), but can be up to twice the length of the metasoma in some Papuan species.

In most species, the antenna has three transverse or (sub)quadrate segments between the pedicel and the two-segmented club. One Papuan species (*Pleistodontes blandus* Wiebes) has two segments. All male tarsi are pentamerous. Usually, the mesoscutum is separated from the mesonotum. It is fused in one Papuan species (*P. blandus*). The metanotum is fused to the propodeum, at least partly. In one species (*P. froggatti*) the metanotum is separated from the propodeum.

Diversity

Pleistodontes contains 25 valid species (17 in Australia), including the seven species described as new in this paper. However, there are almost certainly further species to be described, especially from Papua New Guinea. In our opinion *Pleistodontes claviger* (Mayr, 1885), collected in the botanical garden of Bogor (Java) from syconia of *Ficus elastica* Roxb. ex Hornem., does not belong to *Pleistodontes*. While *F. elastica* is a species closely related to the *Urostigma* sect. *Malvanthera*, both from a morphological (K. Berg and D.J. Dixon, pers. comm.) and a molecular point of view (E. Jousselin, pers. comm.), its supposed pollinator is clearly not in the genus *Pleistodontes*. In the absence of type material, several morphological features, described by Mayr (1885) and Grandi (1928b), enable us to exclude *P. claviger* from *Pleistodontes*:

- (i) The third antennal segment is subdivided into two parts (see Grandi, 1928b: fig. VIII-1, p. 127) but is entire in all *Pleistodontes* species.
- (ii) The roundish shape of the pedicel and the massive shape of the scape are unknown features in *Pleistodontes*.
- (iii) The mandibular appendage is very short, bearing 7-8 transverse lamellae (see Grandi, 1928b: fig. VIII-2, p. 127), unlike any known *Pleistodontes* species. *P. rigisamos*, the species with the shortest appendage, bears 11-13 lamellae, but all other species have between 15 and 80 lamellae (an average of about 30).
- (iv) The mandible has one distinct apical tooth and bears about six ventral ridges, a combination not exhibited by other species of *Pleistodontes*.
- (v) All known species of *Pleistodontes*, except *P. claviger*, bear *sensilla linearia* (non elongate multiporous plate *sensilla*).

In fact, only two morphological characters are at all consistent with a classification into *Pleistodontes*: (1) the pentamerous tarsi of the males, although several *Waterstoniella* males also have pentamerous tarsi; (2) the complete fusion of the mesonotum, metanotum and propodeum of the males (Grandi, 1928b: fig. IX-3, p. 129), which is an aberrant feature in *Pleistodontes*, shown only by *P. blandus*.

Clearly, further collections of *B. claviger* are needed to confirm its taxonomic position and host association. The host plant, *F. elastica*, is a widespread species, introduced by humans as an ornamental throughout the tropics and may have been colonized successfully by a different pollinator species in Java, as has been reported for *Ficus lutea* Vahl in Africa (Compton, 1990).

Biology

Where the host *Ficus* of a *Pleistodontes* species is known, it always belongs to the *Urostigma* sect. *Malvanthera*. All species develop in the syconia and pollinate, either actively or passively, their host plant. Most of the pollinator species are species-specific with their host fig; however, there are a few exceptions to this one-to-one rule (see Discussion). Nothing is known of the immature stages of *Pleistodontes*.

Distribution

The genus is restricted to Australia, New Guinea and adjacent islands. *Ficus obliqua* G. Forst., and probably its pollinator, has a slightly wider natural distribu-

tion, reaching New Caledonia. Furthermore, *Ficus* macrophylla and *Ficus* rubiginosa Desf. ex Vent. and their pollinators have been introduced to several different countries (Israel, New Zealand and USA).

Comments

Following Rasplus et al. (1998) we consider the family Agaonidae to comprise solely the pollinating wasps of Ficus. All the nonpollinating fig wasps belong to other Chalcidoid families. Supposedly, females of subfamily Agaoninae have mandibular appendages with many transverse combs of teeth, whereas the females of subfamily Blastophaginae have only a few transverse lamellae. However, this is problematic with Pleistodontes, since both forms of appendage are found in the genus (in contrast to other Australasian genera of Agaonidae, which can all be placed in Blastophaginae). For this reason, Boucek (1988) questioned the validity of Pleistodontes; however, it now seems more likely that the current subfamilial classification is wrong since molecular studies strongly support the monophyly of *Pleistodontes* (Lopez-Vaamonde *et al.*, 2001) but contradict the integrity of the two subfamilies (Machado et al., 2001). Clearly, Agaonidae needs a thorough phylogenetic analysis to better determine the intrafamilial classification.

DESCRIPTIONS OF THE SPECIES

Pleistodontes froggatti Mayr, 1906 (Figs 1, 2, 5, 11, 27, 29)

- *Pleistodontes froggatti* Mayr, 1906: 157–160. (Holotype, female, NHMV, examined.)
- Pleistodontes semirucifeps Girault, 1929: 318. (Holotype, female, SAMA, examined.) Synonymy by Boucek (1988: 191). Synonymy confirmed.
- *Pleistodontes listzi* Girault, 1932: 2 (Lectotype female, here designated, QMBA, examined). **Syn. nov**.
- *Pleistodontes mayri* Girault, 1939: 325 (No type material associated with this name).

Other citations

Pleistodontes froggatti – Grandi, 1916b: 150–159 (redescription female and male); Pemberton, 1921: 297–319 (biological notes); Muir, 1922: 12 (introduction into Hawaii); Swezey, 1923: 304; Timberlake, 1924: 419 (Honolulu and Waimea); Swezey, 1925: 372 (introduction into Hawaii); Timberlake, 1927: 552; Girault, 1927: 338, Cairns (female taken at light); Grandi, 1928b: 200 (type specimen examined); Lyon, 1929: 83–97; Pemberton, 1934: 379; Sakimura & Linsford, 1940: 454; Wiebes, 1963: 307; Corner, 1965: 25; Wiebes, 1966: 21; Wiebes, 1977b: 213–214; Wiebes,

KEY TO AUSTRALIAN SPECIES OF *PLEISTODONTES* (FEMALES)

Males are very difficult, sometimes impossible, to identify to species level. Furthermore, since they are wingless and generally do not leave the syconia, they are rarely collected except by dissection of ripe fig syconia. Consequently, we provide here a key that permits identification of only females of all Australian *Pleistodontes* species. Some *Ficus* species are host to two *Pleistodontes* species. In such cases, we also highlight, in the species descriptions section, key characters to distinguish females and males of the two species. However, this is not always possible for the males.

-	
1	Inree apical teeth of the mandible are directed backwards (Figs 2, 8). First segment of the fore tarsi
	long, clearly longer than the second plus the third, bearing conspicuous spurs (Figs 27, 28). Third
	antennal segment with a very short spine never reaching the fourth antennal segment (Figs 11–13).
	Anterior part of the genae bearing laterally dense punctuation (Figs 5–7). Mandibular appendage
	bearing rows of small teeth (Figs 2, 8)
_	Teeth of mandible always facing inward (endodont) (Figs 19, 21, 43, 44, 88, 89). First segment of
	the fore tarsi short, about as long the following segments, without conspicuous spurs (Figs 26, 90, 91)
	Third antennal segment with a long spine reaching at least the base of the fourth antennal segment
	Conservation ready with sparse number of Firs 16, 18, 39, 40) Mandibular appendages mostly
	beging worth largely with sparse punctures (159 50) (all D minuture and D meloning worth any of
	bearing ventral lamenae (Figs 19, 22, 44, 45, 52–56) (only F. nuens and F. achorus with rows of
	small teeth, Fig. 21)
2(1)	Meso and metasoma dorsally with very short sparse setae so appearing nearly glabrous. Interior part
	of the fore coxae glabrous without any pilosity or corbiculae. Pollen pockets present and conspicuous
	(Fig. 29). Fifth antennal segment about $4 \times as$ long as wide (Fig. 11). Side of the pronotum shiny.
	Host plant F. macrophyllaP. froggatti Mayr
_	Meso- and metasoma dorsally covered with long conspicuous setae. Interior part of the fore coxae
	hearing dense nilosity Pollen pockets absent or strongly reduced (Figs 30, 31) Fifth antennal segment
	$z_{\rm rest}$ $z_{$
	at most 2/4 as the gas whete (Figs 12, 15), but of the prohotum with very shallow sculpture so
0(0)	appearing matt. Host plant F. plearocarpa
3(2)	Head $2.0-2.2 \times \text{as long as while across the compound eyes (Fig. 3). Gena 2.7-3.1 \times \text{as long as the}$
	(length of the) eye. The mandibular appendages bear about 38 rows of small teeth. Pronotum dorsally,
	entirely smooth. Shape of the internal projection of the scape roundish (Fig. 12). Second funicular
	segment about $1.5 \times as$ long as wide (Fig. 12). Pollen pockets absent (Fig. 31). Host plant
	<i>F. pleurocarpaP. deuterus</i> sp. nov.
_	Head $2.5-2.6 \times$ as long as wide across the compound eyes (Fig. 4). Gena $3.8-4.2 \times$ as long as the
	compound eve. The mandibular appendages bear about 70 rows of small teeth (Fig. 8). Anterior
	guarter of the pronotum with a rectangular area of fine striction (sometimes hidden when the
	hand is turned up) (Fig. 14). Shape of the internal projection of the scape subtriangular (Fig. 13)
	Second functually assessed to be little mean than 2 year long as wide (Fig. 12).
	Second function segment about (or a fittle more than) $2 \times a_{\rm S}$ foring as while (Fig. 13), Fohen pockets
	present but strongly reduced (Fig. 30) so dimcuit to see under microscope. Host plant
	F. pleurocarpa
4(1)	Posterior margin of gastral tergites incised three times (in the middle and laterally) (Fig. 15).
	Propodeal spiracle subcircular. Large species (3 mm or more) at least partly
	yellowish
_	Posterior margin of gastral tergites only incised medially. Propodeal spiracle elongate. Smaller
	species (at most 2.5 mm) mostly black except for lower face and coxae
5(4)	Mandibular appendage bearing rows of small teeth (Figs 20, 21)
_	Mandibular annendage hearing about 25 lamellae (Figs 19, 22) 7
6(5)	Mandibular appendage bearing about 80 rows of small teeth Mandible with 5 teeth (Fig. 21) Seventh
0(0)	initial appendage bearing about 90 for the 6th or the 5th (Fig. 27). Destination with θ team $1/2$, because
	antenna segment shorter than enter the oth of the oth (T_{ij}, J_{ij}) , its unarguar ven more than 2 \times as
	long as the marginal. Metasomal pertremata very large. Host plant <i>P. crassipesP. nitens</i> (Grauit)
_	Mandibular appendage bearing about 40 rows of small teeth. Mandible with 4
	teeth. Seventh antennal segment longer than the 6th and about the same
	length as the 5th (Fig. 38). Postmarginal vein at most $1.5 imes$ as long as the marginal. Metasomal
	peritremata not so enlarged. Host plant unknown
7(5)	Gena more than $2.5 \times as$ long as the eye (Fig. 18). Mandibular appendage, in lateral view of the
	head, reaching the anterior margin of the eye (Fig. 22). Ovipositor sheaths about as long as metasoma.
	Hypopygial spine projects beyond the tip of metasoma (base of the exserted part of the ovipositor).
	Dorsal part of the mesosoma with extended vellow coloration. Host plant
	F watkinsiana P nigrivontrie (Circuit)

Gena about $2 \times as$ long as the eye (Fig. 16). Mandibular appendage reaching the middle of the eye (Fig. 19). Ovipositor sheaths clearly shorter than metasoma. Hypopygial spine not reaching the tip of

F. crassipes......P. addicotti Wiebes

the metasoma. Dorsal part of the mesosoma entirely brown. Host plant

8(4)	Mandibular appendages bearing transverse lamellae subdivided longitudinally by a smooth median area (so appearing as two rows of small teeth) (Fig. 44). Posterior margin of the gastral tergites crenate (Fig. 48). Hypopygial spine blunt and short. Third antennal segments trapezoidal with a short spine (Fig. 10). Metasoma and mesosterna (Fig. 46) with long pilosity. Host plant
	F. triradiata
-	Mandibular appendages bearing non subdivided lamellae (Figs 45, 52,53–56). Posterior margin of the
	gastral tergites entire. Hypopygium acute. Third antennal segments mostly with an acute spine
	(Figs 63–70). Metasoma and mesosterna with short pilosity
9(8)	The median line of the head (under the ocelli) without a white V-shaped membranous area, so the
	head appears entirely chitinized (Figs 41, 50, 57–60, 62). Mandibles with the first two teeth not
	separated by a ridge (a mandibular lamella not ending in a tooth and not reaching the interior margin
	of the mandible) between the first and second teeth (Fig. 88)10
-	The head bears, within the scrobe under the median ocellus, a white V-shaped membranous line
	(Figs 83, 85). The first two teeth of the mandible well apart and separated by a ridge which stops
	before reaching the interior margin of the mandible (Fig. 89)16
10(9)	Scape with an antero-dorsal expansion covering the very small pedicel (Fig. 9). Mandibular
	appendage short, about as long as the mandible, and bearing 11–13 lamellae (Fig. 45). Ovipositor
	sheaths short, about as long as fore femur, and about half the length of metasoma. Host plant
	F. destruensP. rigisamos Wiebes
-	Scape not expanded over the pedicel. Mandibular appendage clearly longer than the mandible
	and bearing more than 15 lamellae (Figs 51–56). Ovipositor sheaths always longer than fore
	femur
11(10)	Mandibular appendages large (about $3.5 imes$ as long as wide), expanded laterally and visible in lateral
	view along the genae (Figs 51, 52). Clypeal margin with a long median expansion bearing two carinae
	(Fig. 49). Head about $2 \times as$ long as large (Fig. 50). Scape elongate, $2.8 \times as$ long as wide (Fig. 68).
	Host plant F. platypoda P. cuneatus Wiebes
_	Mandibular appendages slim (about $5 \times as$ long as wide) (Figs 53–56). Clypeal margin without
	median expansion or the median expansion no longer than the lateral lobes (Figs 72–76). Head
	shorter, at most $1.8 \times$ as long as wide (Figs 57–60, 62). Scape broad, at most $2 \times$ as long as
	wide
12(11)	Clypeal margin without median lobe (tooth) (NB: careful observation is needed for this couplet)
	(Figs 74–76)
_	Clypeal margin with a small median lobe (tooth) (Figs 72, 73)15
13(12)	Fringe present on the anterior wing margin, pilosity clearly visible on the disc. Head short, at most $1.35 \times $ as long as wide (Figs 62, 94). Genae at most $1.7 \times $ as long as the eye (Figs 62, 94). Host plant
	r. unipution
_	1.45 v to 1.6 v og long og wide (Figs 50, 60, 04). Conce more then 1.8 v og long og the eve
	(Figs 50, 60, 04)
14(19)	(Figs 55, 60, 94)
14(13)	Genae with strated scupture (Fig. 01). Gena $1.0-2 \times \text{as folig}$ as the eye (Figs 00, 94). Anterior part
	<i>E brachwarda</i>
	Conce greath or with grantly contrared numerity of Conce 2.2.2.4 × or long on the over (Fig. 50)
	Pronotium subrectangular in dorsal view its antarior corpor ovnanded laterally. Lower part of the
	head vallow. Host plant <i>F</i> subpuberula
15(19)	Fringe of the fore wing always present nilosity conspicuous. Cone more than twice as long as the
10(12)	eve (Fig. 57) Mandibular annendages bearing more than 22 lamellae (Fig. 52). Coelli surrounded by
	smooth cuticle Lateral part of the proportium smooth Host plant F rubiginosa P imporialia Soundars
_	Fringe of the fore wing nearly absent nilosity obsolete Gone about $1.6-1.8 \times 32$ long as the ave
_	(Fig. 58) Mandihular annendages with about $18-90$ lamellae (Fig. 54). Ocalli surrounded by
	strictions especially on the OOD line, but thorough examination is needed (Fig. 77). Lateral part
	of the property in its antorior part with vertical strictions. Hest plants F consciences and
	<i>F brachypoda</i>
	r. or achypout
	Continuea

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1977a: 139; Boucek, 1988: 191; McKey, 1989: 665; Wiebes, 1990: 224; Wiebes, 1991: 141 (several localities from Queensland, Western Australia and New South Wales); Wiebes, 1994b: 26–27.

Pleistodontes imperialis – Froggatt, 1901: 447–451 (biology of *P. froggatti* misidentified as *P. imperialis*).

Pleistodontes semiruficeps – Wiebes, 1963: 96; Wiebes, 1977a: 141; Dahms, 1986: 521 (description of the type specimen); Boucek, 1988: 191 (synonymy with *P. froggatti*).

Pleistodontes listzi – Wiebes, 1977a: 139; Dahms, 1984: 758–759 (catalogue of Girault's types); Boucek, 1988: 192.

Pleistodontes mayri – Wiebes, 1963: 307 (considered redundant); Wiebes, 1977a: 139; Dahms, 1984: 802 (catalogue of Girault's types); Boucek, 1988: 191 (unnecessary replacement name).

Description

Female: 3.0–3.4 mm. Proximal third of the head (frons and upper face), mesosoma and metasoma black. Distal part of the head reddish-brown. Legs, antennae and ventral part of the metasoma brownish.

Head elongate, dorsally $2.75 \times$ as long as wide (sometimes shorter) across compound eyes; eye $1.4 \times$ as long as wide; gena about $4.5 \times$ as long as the eye (Fig. 1; figures grouped at end of paper); area between ocelli fairly concave without sculpture; antennal scape folded; third antennal segment with a short external prominence (spine) that only reaches the proximal part of fourth segment, which is about $2 \times$ as long as wide (Fig. 11); clypeal margin as in Figure 5; mandible with 3 teeth directed backward and 4–5 ventral ridges not clearly delimited on inner side; mandibular appendage $6.6 \times$ as long as wide, bearing 42–45 rows of teeth (Fig. 2).

Mesosoma: with mesosternal pollen pockets (Fig. 29); no setae on the surface of the pronotum, mesoscutum and scutellum; propodeal spiracula elongate and thin (appearing nearly closed; fore coxa without corbicula (coxal comb of setae), but with only few setae not arranged in a comb; fore femora very shallowly striated (Fig. 27); fore tibia with two well-separated teeth on the dorsal side and one on the ventral; fore basitarsus bearing about 20 conical spines (Fig. 27); hind tibia with two teeth, one short

monocuspidate and one tricuspidate (the third cuspid difficult to see) a little shorter than the first one; fore wing clearly setose; stigmal vein as long as marginal.

Metasoma: hypopygium glabrous; hypopygial spine sharp bearing few setae at the extremity; spiracula of the eighth urotergite large and pear shaped; posterior edge of tergites smooth and medially incised on the two first tergites; tergites smooth and glabrous except the fifth one, which bears few scattered setae; ovipositor sheaths about as long as or a little shorter than metasoma.

Measurements. Head: l = 148, w = 53; compound eye: l = 25, w = 18; length of gena = 113; POD = 20; OOD = 9; antennal scape: l = 61, w = 16; fore wing: M = 23, S = 23, PM = 50.

Male: 1.5 mm. Body yellow, head orange, mandibles and anterior ventral part of compound eye dark testaceous; dense long setae on the dorsal anterior part of the eye; head nearly as long as wide (1.1 ×); temple 2.8 × as long as eye; gena short; head 4.3 × as long as antennal groove; septum long; antennal scrobe 1.3 × as long as septum. Pronotum 1.5 × as long as wide with posterior part wider than anterior; mesoscutum 1.6 × as wide as long.

Measurements. Head: l = 60, w = 52; eye: l = 13; temple: l = 36; gena: l = 5; antennal groove: l = 19; septum: l = 14; pronotum: l = 73, w = 49; mesoscutum: l = 30, w = 49; propodeum spiracle: anterior = 21, posterior = 15, interspace = 31.

Material examined

Type material. P. semiruficeps. Syntypes 8 females, the specimen glued at the base of the triangular card is designated 'ty', probably Girault's hand, labelled 'reared from Banyan Figs' 'Lord Howe I., A.M. Lea' 'Type' 'Pleistodontes semiruficeps Gir., TYPE' 'Pleist-odontes partiruficeps Gir., Types'.

P. listzi. As author did not designate one specimen as a holotype the card mounted female – card 1: Dahms (1984: 758) – is here designated as lectotype in accordance with the Rules of Zoological Nomenclature. The specimen is labelled: 'B4.12 h, Gatton, Coll. 21.12.31' 'Pleistodontes listzi Girault, Type' 'Pleistodontes froggatti Mayr. E.F. Riek det. 1959'. Parts of this specimen (1 fore wing, 2 antennae and 1 hind wing) are slide mounted. Slide 1: Dahms (1984: 758). From the label pinned on the lectotype specimen, E.F. Riek recognized the synonymy of *P. listzi* in 1958, which we now confirm and formalize.

Additional material

AUSTRALIA, NEW SOUTH WALES: 10 females 10 males, Sydney, 16.i.1921, ex F. macrophylla (C.E. Pemberton) (RMNH 687, + 2 females mounted on card RMNH 688); 16 females 23 males, Sydney, Botanical Garden 1989, ex F. macrophylla (K. Cohen) (RMNH 5036); 12 females 2 males, Sydney, 1.ii.1995, ex F. macrophylla (J.M. Cook); 11 females, Sydney, 5.i.1997, ex F. macrophylla (J.M. Cook); 2 females, Sydney, xi.1993, ex F. macrophylla (K. Davies); 5 females 2 males, Sydney, viii.1952 & 7.ix.1953, ex F. macrophylla (E.F. Riek); 1 female, Noraville, 31.viii.1976, ex F. macrophylla (B.J. Wallace); 1 female, Euroka via Kempsey, 1–2.iii.1979 (C. Brennan); 1 female, Buckett's Road, Gloucester, 7.iii.1979 (A. Postle); 1 female, Dorrigo N.P., 30°22'S-152°45'E, 2-15.x.1984. Pantraps (I. Naumann & J. Cardale): 1 female, Point Lookout, New England N.P., 30°29'S-152°25'E, 12.ii.1984 (I. Naumann); 1 female, Minnamurra Falls, 31.i.1962 (D.H. Colless); 1 female, Lord Howe Island (A. M. Lea) (Pleistodontes seminigriceps Grlt); females and males, upper Kinchela rd, NE of Gladstone and Kempsey, 7.i.1987, ex F. macrophylla (J.F. Addicott) (RMNH 5089); females and males, Wingham Brush, 6.xi.1989, ex F. macrophylla (J. Meyer & J.T. Wiebes) (RMNH 5002). QUEENSLAND: 5 females, Brisbane, ix.1978, ex F. macrophylla (J. Galil) (RMNH 3694); 5 females 5 males, Brisbane, 6.ii.1995, ex F. macrophylla (J.M. Cook); 1 female 4 males, Brisbane, 14.viii.1952 (E.F. Riek; females and males, Grafton, 25.i.1999, ex F. macrophylla (S. Meusnier & J.Y. Rasplus); females and males, Ballina, 25.i.1999, ex F. macrophylla (S. Meusnier & J.Y. Rasplus); 1 female, Brisbane, 22.v.1946 (Rosser); 3 females, Tambourine Mountains. 19-26.iv.1935 & 1-9.v.1935, B. M. 1935-240 (R.E. Turner); 9 females, Brisbane, xi.1976 (Z. Boucek); 3 females, Brisbane, 16.xii.1976 & i.1977 (Z. Boucek); 1 female 1 male, Mount Glorious near Brisbane, 3.iii.1994 (L. Masner); females and males, Cleveland, 23.i.1999, ex F. macrophylla (S. Meusnier & J.Y. Rasplus); 4 females 2 males, Lamington National Park, 25.xii.1971, ex F. macrophylla (S.R. Monteith); 1 female, Little Yabba Creek, Via Kenilworth, 8.ix.1979, in rainforest (I.D. Naumann); 2 females, Bunya Mountains, 26.iii.1957 (E.F. Riek); 1 female, Horse Gully, foot of Bunya Mountains, 26°42'S-150°31'E, 7.x.1984 (I. Naumann & J. Cardale); 2 females, nr Westcott Plain, Bunya Mountains N.P., 5-7.x.1984 (I. Naumann & J. Cardale); 1 female, nr Paradise Falls, Bunya Mountains N.P., 26°52S-151°35E, 6.x.1984 (I. Naumann & J.

Cardale); 1 female, Cunningham's Gap, 1–2.vi.1966, 2484 feet (Z. Liepa); 1 female, Russell Park near Mt Mowbullan, 7.x.1984 (I. Naumann & J. Cardale). SOUTH AUSTRALIA: Adelaide, 5.v.1978 (A.D. Austin); 3 females, Adelaide, S. A. Waite Arboretum, x.1993, ex *F. macrophylla* (K. Davies). VICTORIA: 5 females 8 males, Melbourne, xii.1995, ex *F. macrophylla* (J.M. Cook). WESTERN AUSTRALIA: females and males, Perth, 22.x.1989, ex *F. macrophylla* (J. Meyer & J.T. Wiebes) (RMNH 4999). USA, HAWAII: 6 females 6 males, Honolulu Oahu, 2.ix.1923, ex *F. macrophylla*, B.M. 1942– 950 (R.C.L. Perkins); females and males, Honolulu, nr Bishop Museum, 14.x.1964 ex *F. macrophylla* (J.T. Wiebes) (RMNH 1652) (Material in ANIC, BMNH, CCLV, CJYR, QMBA, RMNH).

Biology

Pleistodontes froggatti is the pollinator of *F. macrophylla* Desf. ex Pers. *s.l.* This species is sometimes collected at light, suggesting nocturnal flight.

Geographical distribution

Ficus macrophylla is a free standing tree or hemiepiphyte, which occurs naturally in south-east Queensland, north-east New South Wales and on Lord Howe Island. Within Australia its distribution has been extended considerably by its frequent use as an ornamental and shade tree. It has been introduced into Hawaii (Swezey, 1925) and New Zealand (Gardner & Early, 1996). The pollinator has been found over most of the host distribution range. It is also known from New Zealand (see Early, 2000: 28).

Comments

Froggatt (1901) described the biology of *P. froggatti* but misidentified it as *P. imperialis*. Mayr (1906) studied Froggatt's material, discovered the misidentification, and described the specimens as a new species.

Figs of *F. macrophylla* exhibit a high anther-toovule ratio (0.53), suggesting a passive mode of pollination (Kjellberg *et al.*, 2001). Accordingly *P. froggatti* lacks coxal combs (corbiculae), but it still has mesothoracic pollen pockets. This may represent an ongoing transition between modes of pollination and would benefit from further investigation.

PLEISTODONTES DEUTERUS SP. NOV. (FIGS 3, 6, 12, 28, 31, 92)

Description

Female: 3–3.5 mm. Whole body including legs black, tarsi and antennae brown; occasional dwarf individuals are also observed.

Head parallel sided dorsally $2.1 \times$ as long as wide across compound eyes (Fig. 3); eye $1.6 \times$ as long as wide; gena about $2.76 \times$ as long as eye (Fig. 3); area between ocelli concave, forming a T-shaped area with finely rugose sculpture; antennal scape folded and with a rugose sculpture; third antennal segment with a short triangular prominent spine not reaching the distal part of the fourth segment which is about as long as wide (Fig. 12); fifth and following antennal segments with one row of sensilla (Fig. 12); clypeal margin as on Figure 6; mandible with 5–6 ventral ridges, the first extended into a tridentate tooth; apical tooth faces forward so when the mandibles are closed their tips are directed anteriorly; mandibular appendage composed of 37–39 rows of denticles.

Mesosoma: without mesosternal pollen pockets (Fig. 31); mesopleura with a subtriangular area finely carinated and without any pollen pocket apertures (Fig. 31), this area can be filled with pollen; propodeal spiracula very elongate; pronotum, mesoscutum, scutellum, and propodeum with long conspicuous yellowish setae; a patch of long setae on axilla; interior side of fore coxae with a patch of strong setae not arranged in a comb; fore tibia strongly striated (Fig. 28) bearing three teeth, two dorsal and one ventral; fore basitarsus with about 30 conical spines and dense long setae (Fig. 28); hind tibia with two teeth, one elongate monocuspidate, curved at the extremity, the other tricuspidate; fore wing pilose.

Metasoma: hypopygium large with a small, glabrous, median tooth; hypopygial spine very short and blunt; spiracula of the eighth urotergite circular in shape; posterior margin of tergites denticulate; pilosity on the gastral tergite well developed reaching the posterior margin of the tergite; tergite incised in the middle; ovipositor about as long as the metasoma.

Measurements. Head: l = 130, w = 62; compound eye: l = 30, w = 18; length of gena = 83; POD = 20; OOD = 14; antennal scape: l = 55, w = 19; fore wing: M = 21, S = 20, PM = 54.

Within the syconia of *F. pleurocarpa*, the overall appearance of *P. deuterus* females is very dark (black) with gracile, elongate bodies, while *P. regalis* females have lighter (browner) bodies (especially face) and a more robust shape. The number of rows of denticles/ lamellae on the mandibular appendages provides a good character to separate the species.

Male: 1.9–2.2 mm. As with females there are some dwarf males which have not been taken into account in the description. Head and mesosoma dark testaceous, very shiny; medium part of pronotum, mesoscutum, propodeum + scutellum darker; fore and hind femora darker; metasoma yellowish; sparse long setae on the ventral anterior part of the eye.

Head nearly as long as wide $(1.2 \times)$; eye small; temple $4.3 \times$ as long as eye; short gena with small pointed

carina around the ventral anterior part of the eye; head $5.1 \times as$ long as antennal scrobe; antennal scrobe $3.4 \times as$ long as septum; pronotum $1.3 \times as$ long as wide with posterior part wider than anterior; mesoscutum $2.7 \times as$ wide as long.

Measurements. Head: l = 71, w = 61; eye: l = 9; temple: l = 39; gena: l = 5; antennal groove: l = 14; septum: l = 6; pronotum: l = 95, w = 72; mesoscutum: l = 28, w = 77; propodeum spiracle: anterior = 35, posterior = 23, interspace = 58.

Within the syconia of *F. pleurocarpa*, males of *P. deuterus* can easily be recognized from males of *P. regalis* by the presence of a medio-longitudinal incision on the anterior margin of the first metasomal tergite (Fig. 92). Furthermore, males of *P. deuterus* bear an engraved oblique line between the metanotum and the propodeum while both segments are completely fused without any visible line or sulcus in *P. regalis* (Fig. 93). However this line is not visible on the smaller specimens.

Material examined

Type material. Holotype female deposited in QMBA. AUSTRALIA, QUEENSLAND: Topaz, ex F. pleurocarpa, 14.i.1999 (J.Y. Rasplus & S. Meusnier). Paratypes: 50 females, 51 males, same data as holotype; 20 females and males, Millaa Millaa, 24.i.2001, ex F. pleurocarpa (J. Cook); 20 females and males, Butchers Creek, 24.i.2001, ex F. pleurocarpa (J. Cook); 1 female, Mt Sorrow, 3 km W Cape Tribulation, 16°05′S-145°27′E, 14.vi.1996, 300-500 m, rainforest (C.J. Burwell); 1 female 2 males, Cape Tribulation, Mt Sorrow, 16°05′S-145°27′E, 25.ii.1993, ex F. pleurocarpa (G. Weiblen) (no. GW208.1); 2 females, Hugh Nelson Range, 21 km S. Atherton, 9.i-10.ii.1984 & 13.iii-1.iv.1984, flight intercept trap & malaise trap (Storey & Brown). (QMBA, BMNH, ANIC, SAMC, CCLV, CJYR, CCNI).

Biology

Pleistodontes deuterus is associated with *F. pleurocarpa* F. Muell., which is also the host of *P. regalis*. This constitutes one of the few instances where two species of pollinator have been recorded from the same *Ficus* species.

Geographical distribution

Ficus pleurocarpa is a hemi-epiphytic fig, found only in the rainforests of north Queensland (Corner, 1965), occurring on the Atherton Tablelands (e.g. Malanda, Millaa Millaa, Mt Bartle Frere, Topaz) and in the Daintree region (Mt Sorrow). The pollinator, *P. deuterus*, has only been found in six localities within the host range in Queensland.

Etymology

The latinized species name is derived from Greek *deuteros* (= the second), in reference to the fact that *F. pleurocarpa* was already known to be pollinated by *P. regalis*.

Pleistodontes regalis Grandi, 1952 stat. rev. (Figs 4, 7, 8, 13, 14, 30, 93)

Pleistodontes regalis Grandi, 1952: 61–67. (Lectotype female, here designated, IEGG, examined).

Other citations

Wiebes, 1966: 26; Ramirez, 1974: 775; Boucek, 1988: 192 (synonymy under *P. nitens*); Wiebes, 1990: 225; Ramirez, 1991: 88; Wiebes, 1991: 141–142; Wiebes, 1994b: 27 (the last citations of Wiebes were done under the name *P. nitens* but refer to *P. regalis*).

Description

Female: 3.0–3.4 mm (excluding occasional dwarfs); proximal third of the head (frons and upper face), mesosoma and metasoma dorsally black; distal two thirds of the head reddish-brown; legs, antennae and ventral part of the metasoma yellowish.

Head elongate, dorsally $2.7 \times as$ long as wide across compound eye (Fig. 4); eye $1.5 \times as$ long as wide; gena $3.7-4.4 \times as$ long as eye (Fig. 4); area between ocelli concave with shallow punctuated sculpture; antennal scape folded; third antennal segment with a very short external prominence (spine), this hardly reaches the proximal part of the fourth segment, which is about $1.5 \times as$ long as wide (Fig. 13); clypeal margin as in Figure 7; mandible with 3 teeth directed backwards and about 4 ventral ridges that are not clearly delimited on the inner side (Fig. 8); mandibular appendage $5.3 \times as$ long as wide bearing about 75 rows of teeth (Fig. 8).

Mesosoma: bearing very small mesosternal pollen pockets (difficult to see under microscope), very probably non-functional (Fig. 30); conspicuous, yellow setae present on the surface of the pronotum, mesoscutum, scutellum and propodeum; pronotum with a subrectangular area of fine striation on its anterior quarter (Fig. 14); propodeal spiracula elongate, but clearly open (not as thin as in P. froggatti; interior side of the fore coxa bearing numerous setae, not arranged in a comb; fore femur distinctly and longitudinally striated; fore basitarsus bearing about 40 conical spines; fore tibia with two close teeth on the dorsal side and one on the ventral side; hind tibia with two teeth, one long bicuspidate and one tricuspidate clearly shorter than the first one; fore wing setose; stigmal vein shorter than marginal vein.

Metasoma: hypopygium glabrous; hypopygial spine blunt bearing few setae at the extremity; spiracula of the eighth urotergite large and pear shaped; posterior edge of tergites smooth and medially incised on the two first tergites; all tergites bear relatively long setae; ovipositor sheaths about as long as or a little shorter than metasoma.

Measurements. Head: l = 143, w = 52; compound eye: l = 24, w = 15; length of gena = 103; POD = 22; OOD = 10; antennal scape: l = 77, w = 16; fore wing: M = 25, S = 20, PM = 59.

Male: 1.5 mm. Head and body yellowish brown, mandibles and anterior ventral part of compound eye dark testaceous; dense long setae on the dorsal anterior part of the eye.

Head as long as wide; temple $3.3 \times as$ long as eye; gena short; head $2.4 \times as$ long as antennal scrobe; septum long; antennal scrobe $1.3 \times as$ long as septum. Pronotum $1.5 \times as$ long as wide with posterior part wider than anterior; mesoscutum about $2 \times as$ wide as long.

Measurements. Head: l = 50, w = 50; eye: l = 10; temple: l = 33; gena: l = 4; antennal groove: l = 21; septum: l = 16; pronotum: l = 61, w = 42; mesoscutum: l = 21, w = 44; propodeum spiracle: anterior = 22, posterior = 20, interspace = 27.

Material examined

Type material. Six slides were found in the IEGG collection in Bologna, thanks to the help of M.L. Dindo. Four contain pieces of females, two others dissected males. Most of the females were dissected on separate slides and their respective parts mixed, so that we were unable to recognize a complete female. However, all these specimens are conspecific. Consequently, we propose that the complete metasoma, complete head, mostly complete mesosoma and anterior leg present on one slide belong to the same individual and designate this individual female as lectotype, so that nomenclature will be stabilized. The slide (like the five others) is labelled '*Pleistodontes regalis* female Grnd Atherton and Australia xi.1949 *Ficus pleurocarpa*'.

Additional material

AUSTRALIA, QUEENSLAND: 3 females 1 male, Topaz, 14.i.1999, *Ficus pleurocarpa* (J.Y. Rasplus & S. Meusnier); 3 females, Bellenden Ker Range, Cableway Base Station, 100 m, at mercury vapour light in rainforest, 17–24.xi.1981 (Earthwatch. Qld Museum); Mt Lewis road, 16 km from highway, 18.xii.1989, 950 m, Pyrethrum/trees & logs (Monteith & Thompson); 1 female, Mt Sorrow, 3 km W Cape Tribulation, 16°05'S– 145°27'E, 14.vi.1996, 300–500 m, rainforest (C.J. Burwell); 2 females, Mt Sorrow, 2.i.1999, ex *F. pleurocarpa*

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(C.L. Vaamonde); 1 female 4 males, Malanda, jungle, 15.vi.1966 (D. Nicholson) (RMNH 1018); 1 female 2 males, Cape Tribulation, Mt Sorrow, $16^{\circ}05'S-145^{\circ}27'E$, 25.i.1993, ex *F. pleurocarpa* (G. Weiblen); 4 females 1 male, road to Bartle Frere, walking track to summit, $17^{\circ}22'S-145^{\circ}44'E$, 21.xi.1996, rainforest, ex *F. pleurocarpa* (D.J. Dixon) (PhD 339). 19 females 22 males, 13.1 km Malanda Road on Topaz Road and Bonjee Road, ex *F. pleurocarpa* (J.F. Addicott); 1 female, Mt Edith Forest Road, 1 mile off Danbulla Road, 5.v. 1967 (D.H. Colless); females and males, Millaa Millaa, 24.i.2001 and 9.ii.2001, ex *F. pleurocarpa* (J. Cook). (QMBA, CJYR, CCLV, RMNH, ANIC).

Biology

The species is associated with *F. pleurocarpa*, in syconia of which it sometimes occurs with *P. deuterus*. It has also been collected at night with mercury vapour light. See *P. deuterus* description for discussion of main distinguishing characters for males and females of the two co-pollinators of *F. pleurocarpa*.

Distribution

Both *P. regalis* and its host, *F. pleurocarpa*, are restricted to north Queensland, occurring on the Atherton Tablelands (e.g. Malanda, Millaa Millaa, Mt Bartle Frere, Topaz) and in the Daintree region (Mt. Sorrow).

Comments

Pleistodontes regalis has been regarded as identical to *P. nitens* and synonymized by Boucek (1988: 192), probably on the basis of the number of 'cross-combs on the mandibular appendage'. However, *P. regalis* and *P. nitens* are clearly two different species (see key). Consequently, the status of *P. regalis* is now restored. Wiebes, who probably never examined the type of *P. nitens*, followed Boucek's interpretation (Wiebes, 1990, 1991, 1994b). We have examined specimens identified as *P. nitens* by Wiebes, and found that they all belong to *P. regalis*. Furthermore, his description of *P. nitens* (Wiebes, 1994b: 27) fits well with the specimens collected on the Atherton Tablelands in syconia of *F. pleurocarpa*.

PLEISTODONTES NITENS (GIRAULT, 1915) (FIGS 15, 17, 20, 21, 25, 34, 37)

Neoceratosolens nitens Girault, 1915b: 313. Holotype, female, QMBA, examined.

Other citations

Pleistodontes nitens – Hill, 1967a: 92 (following Riek's information, synonymized Neoceratosolens with

Pleistodontes and consequently transferred by implication *N. nitens* to *Pleistodontes*); Wiebes, 1977a: 141; Dahms, 1986: 349 (catalogue of Girault's types); Boucek, 1988: 192 (synonymy of *P. regalis*, see comments under this last species); Wiebes, 1990: 225; Wiebes, 1991: 141–142; Wiebes, 1994b: 27 (these last three citations were in fact *P. regalis*, see comments under *P. regalis*).

Description

Female: 2.7–3.0 mm. Face and frons, dorsal part of the mesosoma and metasoma dark brown; lateral side of the pronotum, pleurae and ventral part of the mesosoma, legs, ventral part of the metasoma yellow.

Head elongate, dorsally about $2 \times$ as long as wide across compound eyes (Fig. 17); eye $1.5 \times$ as long as wide; gena $2.6 \times$ as long as eye (Fig. 17); ocelli, small, disposed in a groove; area between ocelli without sculpture; OOD about $2.3 \times$ the diameter of the posterior ocellus; antennal scape about $2.3 \times$ as long as wide: third antennal segment bearing a large, wide, and prominent triangular spine, reaching the distal part of the 5th segment (Fig. 37). The 7th funicular segment (clava 1) is shorter than the 6th and also shorter than the 5th (respectively 13:17:19) (Fig. 37); clypeal margin with a strong median carina, bearing few setae, surrounded by moderate lobes (Fig. 25); mandible with 5 teeth and 8-9 ventral ridges (Fig. 21); mandibular appendage $4.5 \times as$ long as wide bearing about 80 rows of small teeth (Fig. 20).

Mesosoma: with small mesosternal pollen pockets (Fig. 34); no setae on the surface of the pronotum, mesoscutum and scutellum; propodeal spiracula rather large and rounded, lateral sides of the propodeum bearing few scattered setae; interior side of fore coxa bearing numerous fine setae, not arranged in a comb; fore tibia with two teeth on the dorsal side and one on the ventral; hind tibia with two teeth, one bifid and one bicuspidate, wings pilose; marginal vein about $1.5 \times$ as long as stigmal, postmarginal $1.3 \times$ as long as marginal and about $2.0 \times$ as long as stigmal.

Metasoma: hypopygium with few setae; hypopygial spine long and acute; spiracula of the eighth urotergite very large and subspherical in shape; posterior margin of tergites smooth, incised medially and submedially (Fig. 15); first to third tergite bare; fourth and fifth bearing setae which do not reach the posterior margin of the tergite; ovipositor sheaths short, about two thirds as long as metasoma.

Measurements. Head: l = 151, w = 76; compound eye: l = 35, w = 23; length of gena = 92; POD = 32; OOD = 13; antennal scape: l = 45, w = 20; fore wing: M = 28, S = 18, PM = 37. *Mala* Unknown

Material examined

Type material. Holotype, female labelled 'Holotype Hy. 3364 E.C.D. 1985' 'Neoceratosolens nitens Girault, Types female', 'Pleistodontes nitens (Grlt.) E.F. Riek det.' According to Girault (1915b), the specimen was from Queensland: Babinda, 14.ii.1914 (A.P. Dodd). According to Dahms (1986), the 'Types' on the label is an error since there is no indication of any extra specimens.

Additional material

QUEENSLAND: 8 females, Topaz, 14.i.1999, ex *F. crassipes* (J.Y. Rasplus & S. Meusnier); 1 female, Mt Bartle Frere West side, 700 m, 30.vii.1982, leaf and log litter, rainforest, SBP95 (S. & J. Peck); 3 females, Upper Cooper Creek, Daintree, 5.ii.1999, ex. *F. crassipes* (C. Lopez-Vaamonde) (material in CCLV, CJYR, QMBA).

Biology

This species was found emerging from syconia of *F. crassipes* in the company of *P. addicotti*, making it one of the few confirmed cases of a *Ficus* species pollinated by two sympatric pollinators.

Distribution

F. crassipes is a hemi-epiphytic fig, which is restricted to the rainforests of the Atherton Tablelands and Daintree. The pollinator, *P. nitens*, is only known from three localities in the Tablelands.

Comments

Up to now *P. nitens* has been misinterpreted (Boucek, 1988; Wiebes, 1990, 1991, 1994b) – see comments under *P. regalis*. Our examination of the type material and recent collections of this species enabled us to correct this mistake.

Pleistodontes achorus sp. nov. (FIGS 38, 39)

Description

Female: 3.5 mm. Head, mesosoma and metasoma dorsally dark brown. The lateral side of the pronotum, pleurae and ventral parts of the mesosoma, legs, and metasoma light brownish.

Head elongate, dorsally a little over twice as long as the width across the compound eyes (Fig. 39). The eye is $1.6 \times as$ long as wide and the gena is $2.9 \times as$ long as the eye (Fig. 39). Ocelli small, disposed in a groove. Area between ocelli without sculpture. OOD about $2.6 \times$ the diameter of the posterior ocellus. The antennal scape is $2.4 \times as$ long as wide. The third antennal segment bears a large and wide triangular prominence reaching the first third of the 5th segment (Fig. 38). The 7th funicular segment (clava 1) is longer than the 6th and about the same length as the 5th (respectively 15 : 12 : 15) (Fig. 38). The clypeal margin shows a strong median carina bearing few setae surrounded by lobes (Fig. 39). The mandible has 4 teeth and 8 ventral ridges. The mandibular appendage is $4.5 \times$ as long as wide and bears about 40 rows of small teeth. Marginal vein about $1.2 \times$ as long as the stigmal, postmarginal $2.2 \times$ as long as marginal and about $2.6 \times$ as long as stigmal.

Mesosoma: the mesopleura bears small mesosternal pollen pockets, about the same size and shape as those of *P. nitens.* No setae on the surface of the pronotum, mesoscutum and scutellum. Propodeal spiracula rather large and rounded, lateral sides of the propodeum bear few scattered setae. The interior side of the fore coxa bears numerous fine setae, not arranged in a comb. The fore tibia has two teeth on the dorsal side and one on the ventral. The hind tibia has two teeth, one bifid and one bicuspidate. Wings pilose.

Metasoma: the hypopygium bears few setae. The hypopygial spine is long and acute. The spiracula of the eighth urotergite are large but smaller than in *P. nitens.* Posterior edge of tergites smooth, incised medially and submedially (as in Fig. 15). The first to third tergites are bare. The fourth and fifth bear setae which do not reach the posterior margin of the tergite. Ovipositor sheaths are short, about two thirds as long as the metasoma.

Measurements. Head: l = 153, w = 71; compound eye: l = 33, w = 21; length of gena = 96; POD = 22; OOD = 8; antennal scape: l = 60, w = 25; fore wing: M = 30, S = 25, PM = 65.

Male. Unknown.

Comments

Pleistodontes achorus is very close to *P. nitens* but exhibits several differences. The most striking one is the number of rows of small teeth on the mandibular appendage (about 40 rows instead of *c*. 80 in the holotype of *P. nitens*).

Material examined

Type material. Holotype, female (deposited in QMBA). AUSTRALIA, QUEENSLAND: Stony Creek 2.5 km NE of Mt Sturgeon, 16°25'S-145°13'E, 1200 m, 15– 21.x.1990, Pitfalls (Monteith, Janetzki, Cook & Roberts).

Biology

The biology of *P. achorus* is unknown. It may be associated with an already known *Ficus*. Based on the size of wasp and its type locality, *F. crassipes*, *F. watkinsiana*, *F. triaradiata* and *F. pleurocarpa* are the most likely host plants.

Distribution

P. achorus is only known from the type locality.

Etymology

The latinized species name is derived from Greek *achoros* (= homeless), in reference to the unknown host *Ficus* of this species.

PLEISTODONTES NIGRIVENTRIS (GIRAULT, 1915) (FIGS 18, 22, 23, 32, 35)

- Agaon nigriventre Girault, 1915a: 44–45. Holotype, female, QMBA, examined.
- *Pleistodontes nigriventris* Girault, 1915b: 311. Both names based on the same holotype were synonymized by Riek in Wiebes (1961: 237).

Other citations

Pleistodontes nigriventris (Girault) – Girault, 1917: 36 (transfer to *Pleistodontes*); Grandi, 1955: 228; Wiebes, 1977a: 140–141; Dahms, 1986: 345 (catalogue of Girault's types); Boucek, 1988: 192 (fig host *F. watkinsiana*); Wiebes, 1990: 220–222; Wiebes, 1991: 144 (several localities in eastern Queensland and New South Wales), Wiebes, 1994b: 28.

Description

Female: 1.7–2.1 mm. Body yellow except for vertex, a spot under the eye, funicule, pronotum in the middle, scutellum posteriorly, and tergites dorsally (except the anterior half of the first one), which are black.

Head elongate, about $2 \times as$ long as wide across compound eyes (Fig. 18); eye $1.6 \times as$ long as wide; gena $2.6 \times as$ long as eye; area between ocelli strongly convex without sculpture; OOD about $4 \times$ the diameter of the posterior ocellus; antennal scape fairly folded and about $1.9 \times as$ long as wide (Fig. 35); third antennal segment with a small and short triangular prominence (spine), reaching at most to the distal part of the fourth segment (Fig. 35); clypeal margin with a median tooth surrounded by moderate lobes (Fig. 23); mandible bearing 5 teeth and 9–10 ventral ridges; mandibular appendage long, $5.5 \times as$ long as wide, and bearing 24-25 lamellae (Fig. 22).

Mesosoma: with small mesosternal pollen pockets (Fig. 32); no setae on the surface of the pronotum, mesoscutum and scutellum; propodeal spiracula large and ovoid; interior side of the fore coxa with numerous

fine setae, not arranged in a comb; fore tibia with two long teeth on the dorsal side and one on the ventral; hind tibia with two teeth, one simple (axial) and one tricuspidate (antiaxial); fore wing clearly setose; the fringe apparent; stigmal vein as long as marginal; postmarginal about $1.7 \times$ as long as stigmal and $1.8 \times$ as long as marginal.

Metasoma: hypopygium glabrous; hypopygial spine long and sharp; spiracula of the eighth urotergite large and subcircular in shape; posterior margin of tergites smooth and not incised; tergites smooth with at least one row of short setae, which does not reach the posterior margin of the tergite; ovipositor sheaths short, about half as long as metasoma.

Measurements. Head: l = 117, w = 64; compound eye: l = 30, w = 18; length of gena = 77; POD = 20; OOD = 12; antennal scape: l = 50, w = 26; fore wing: M = 25, S = 26, PM = 44.

Male: 1.5–1.6 mm. Body yellow. Head, pronotum, and fore leg darker; dense short setae on the frons; sparse short setae on gena.

Head about as long as wide $(1.1 \times)$; temple $2.6 \times$ as long as the eye; short gena carinated; head $3.6 \times$ as long as antennal scrobe; antennal scrobe $3 \times$ as long as septum; pronotum $1.2 \times$ as long as wide; posterior part wider than anterior part; mesoscutum $1.3 \times$ as wide as long.

Measurements. Head: l = 54, w = 58; eye: l = 14; temple: l = 37; gena: l = 6; antennal groove: l = 15; septum: l = 5; pronotum: l = 80, w = 67; mesoscutum: l = 35, w = 47; propodeum spiracle: anterior = 30, posterior = 19, interspace = 39.

Material examined

Type material. Holotype, female. AUSTRALIA. On a card labelled 'Mt Tambourine, Q: A.M. Lea' 'Agaon nigriventre Gir., Type' '*Pleistodontes nigriventris* (Grlt). E.F. Riek. Det. 1959' 'Holotype, Hy 3360, E.C.D. 1985'.

Additional material

AUSTRALIA, QUEENSLAND, 1 female, Atherton, 20.v.1927, ex F. watkinsiana (J.L. Ardent); 1 female, 17°14'S-145°25'E, 3 km West of Bones Knob, 10.xii.1995-9.ii.1996, intercept trap, 1100 m (G. Monteith, Cook, Thompson); 1 female, Lamington N.P., 25.xii.1971, ex F. watkinsiana (S.R. Monteith); 5 females. Atherton Tablelands, Lake Eacham: 9.xii.1996, ex F. watkinsiana (J.M. Cook); 1 female, Mt Glorious, 28.ii.1984, sweeping in rainforest (I.D. Galloway); 2 females, Coolola National Park, 7.iii.1984, beside walking track in rainforest (I.D. Galloway); 188 females, Kairi Garden, 17.i.2001 (J. Cook); 1 female, Kuranda, 7.xii.1992 (Z. Boucek); 1 female, Mount Glorious near Brisbane, 3.iii.1984 (L. Masner); 1 female, near Wilson's Peak, 9.i.1977 (Z. Boucek); 4 females, Tambourine Mountains, 1-9.v.1935 (R.E. Turner); 37 females 17 males, Iluka Floral Reserve, 8.i.1987, ex F. watkinsiana (J.F. Addicott) (RMNH 5090); 253 females 305 males, Junction A1, Herberton Road, W. of Atherton, 21.ii.1987, ex F. watkinsiana (J.F. Addicott) (RMNH 5102); 355 females 160 males, 4.6 km E. of Ravenshoe on Millaa Millaa Road, 21.ii.1987, ex F. watkinsiana (J.F. Addicott) (RMNH 5110). NEW SOUTH WALES, 22 females 2 males, Sydney, ix.1978, ex F. watkinsiana (J. Galil) (RMNH 3699); 36 females 12 males, Sydney, 3.i.1997, ex F. watkinsiana (J.M. Cook); 18 females 3 males, Ballina, 25.i.1999, ex F. watkinsiana (J.Y. Rasplus & S. Meusnier); 1 female, Bruxner Park via Coffs Harbour, 12.xi.1980, Pyrethrum, rainforest (G. Monteith); 1 female, Dorrigo N.P., 30°22'S-152°45'E, 13.ii.1984, Pantraps (I. D. Naumann); 1 female, Beaury State Forest, 28°29'S-152°23'E, 700 m, 15-17.ii.1983, ANIC 780 (T. Weir & A. Calder); 1 female Brindle Creek, Border Ras. N.P., 14.ii.1984 (I.D. Naumann); Tooloom Plateau, 14 km, W. Urbenville, 14.ii.1984 (I.D. Naumann), 1 female, Warrell Creek, North Coast, 1.x.1962 (D.H. Colless); 1 female, Bruxner Park, Coff's Harbour, 1.x.1962 (D.H. Colless); 3 females, Sheepstation Creek, 16 km N.E. of Wiangaree, 600 m, 13.vi-24.viii.1982, flight intercept trap in rainforest (S. & J. Peck); 1 female, Richmond Range, 28°48'S-152°59'E, 600 m, 13-14.ii.1983 (T. Weir & A. Calder).

Biology

Pleistodontes nigriventris is the pollinator of *F. watkinsiana*.

Geographical distribution

Pleistodontes nigriventris occurs throughout the range of *F. watkinsiana*, a rainforest hemi-epiphytic fig which occurs in two distinct populations, one in Queensland between Cairns and Townsville, the other in south-east Queensland and north-east New South Wales.

Comments

The female was redescribed from material collected in Sydney (Wiebes, 1990), where the host plant is introduced.

PLEISTODONTES ADDICOTTI WIEBES, 1991 (FIGS 16, 19, 24, 26, 33, 36)

Pleistodontes addicotti Wiebes, 1991: 142–144. Lectotype female, here designated, RMNH, examined. Other citations Wiebes, 1994b: 27–28.

Description

Female: 3.2–3.6 mm. Face and frons, dorsal part of the mesosoma and metasoma black; gena and lower face, scape pedicel and the third and fourth antennal segments, lateral side of the pronotum, pleura and ventral part of the mesosoma, legs, ventral part of the metasoma reddish-yellow.

Head elongate, dorsally about $2 \times$ as long as wide across the compound eyes (Fig. 16); eye $1.5 \times$ as long as wide; gena $2.1 \times$ as long as the eye (Fig. 16); ocelli in a groove; area between ocelli without sculpture; OOD about $2 \times$ the diameter of the posterior ocellus; antennal scape folded and about $2.1 \times$ as long as wide; third antennal segment with a large and wide triangular prominence (spine) reaching the middle of the fifth segment (Fig. 36); clypeal margin with a strong median carina, bearing few setae, surrounded by small lobes (Fig. 24); mandible with 5 teeth and 12–14 ventral ridges (Fig. 19); mandibular appendage $3.4 \times$ as long as wide bearing 25-26 lamellae (Fig. 19).

Mesosoma: with small and nearly closed pollen pockets (Fig. 33); no setae on the surface of the pronotum, mesoscutum and scutellum; propodeal spiracula large and rounded; interior side of the fore coxa with numerous fine and long setae, not arranged in a comb; fore tibia with two teeth on the dorsal side and one on the ventral (Fig. 26); hind tibia with two teeth, one bifid and one tricuspidate; fore wing clearly setose, fringe apparent; stigmal vein slightly shorter than marginal; postmarginal 1.7 × as long as marginal and nearly 2 × as long as stigmal.

Metasoma: hypopygium glabrous; hypopygial spine short and blunt, clearly shorter than the surrounding lobes; spiracula of the eighth urotergite large and ovoid; posterior margin of tergites smooth and medially and submedially incised; tergites smooth, the fourth and the fifth bearing setae which do not reach the posterior margin of the tergite. Ovipositor sheaths short, about a quarter as long as the metasoma.

Measurements. Head: l = 152, w = 77; compound eye: l = 38, w = 25; length of gena = 80; POD = 27; OOD = 11; antennal scape: l = 63, w = 30; fore wing: M = 34, S = 30, PM = 59.

Male: 2–2.2 mm. Head pronotum and fore leg dark orange; proximal part of pronotum, distal half of mesoscutum, propodeum + scutellum, mid, hind leg, and mesosoma yellow; dorsal, proximal half of head, gena and dorsal, distal half of mesoscutum brown; dense short setae on the dorsal anterior part of the eye extending towards the frons.

Head nearly as long as wide $(1.1 \times)$; temple $2.7 \times$ as long as the eye; short gena carinated; head $1.75 \times$ as

long as the antennal scrobe; septum long; antennal scrobe $1.6 \times as$ long as the septum; pronotum $1.2 \times as$ long as wide; posterior part wider than anterior part; mesoscutum $1.3 \times as$ wide as long.

Measurements. Head: l = 70, w = 78; eye: l = 15; temple: l = 40; gena: l = 6; antennal groove: l = 40; septum: l = 25; pronotum: l = 103, w = 87; mesoscutum: l = 60, w = 81; propodeum spiracle: anterior = 41, posterior = 29, interspace = 57.

Material examined

Type material. In the description of *P. addicotti*, no holotype was designated by Wiebes. We have remounted on card all the available material (vials 5103 & 5104). These vials were labelled '*Pleistodontes addicotti* Wiebes type-lot' 'Australia Queensland 16.4 km NE of Ravenshoe on A1 2.ii.1987 Ficus crassipes J.F. Addicott'. One female is designated as lectotype to stabilize the nomenclature. All the other specimens are labelled paralectotypes. One vial (RMNH 5080) that was sent to the ANIC collection cannot be located; this vial apparently contains paralectotypes.

Additional material

AUSTRALIA, QUEENSLAND: females and males, 6.3 km along Malanda road (J.F. Addicott); 2 females 1 male 7.7 km East of Herberton Road on A1 Highway (J.F. Addicott); 20 females 20 males Topaz, Trevaleigh Farm, 14.i.1999, *F. crassipes* (J.Y. Rasplus & S. Meusnier); females and males, Yungaburra, 24.i.2001, ex *F. crassipes* (J. Cook); 1 female, Mt Sorrow, 3 km W Cape Tribulation, 16°05′S–145°27′E, 14.vi.1996, 300– 500 m (C.J. Burwell); 1 female, 3 miles SSW of Millaa Millaa, 29.viii.1989, oil bath trap (R.J. Elde)r; 1 female, Mount Mee, 9.i.1971 (S.R. Monteith).

Biology

Pleistodontes addicotti is found in the syconia of *Ficus crassipes* F.M. Bailey. *P. nitens* has also been recorded from the same host fig species. Females of the two species are easily distinguished since *P. nitens* has about 80 rows of denticles on the mandibular appendages whereas *P. addicotti* has 25–26 rows of lamellae. The males of *P. nitens* have not been described.

Geographical distribution

P. addicotti occurs throughout the range of its host, *Ficus crassipes*, a hemi-epiphytic fig, which occurs only in the rainforests of the Atherthon Tablelands and Daintree regions in north Queensland.

PLEISTODONTES SCHIZODONTUS SP. NOV. (FIGS 10, 40, 42, 44, 46, 48)

Description

Female: 1.7–2.2 mm. Head, mesosoma and tergites of the metasoma black; antennae, fore coxae, legs and underside of the metasoma yellowish; fore femora darkened.

Head $1.2-1.3 \times as$ long as wide across the compound eyes (Fig. 40); eye $1.2 \times$ as long as wide; gena $1.8 \times$ as long as the eye (Fig. 40); area between ocelli concave with very fine sculpture; POD $2 \times$ OOD; antennal scape elongate, not folded, and only enlarged in the distal two thirds (Fig. 10); third antennal segment subtrapezoidal bears a short prominence (spine) which reaches the distal extremity of the fourth segment (Fig. 10); antennal segments with one row of long sensilla; clypeal margin with a short median prominence hardly visible and surrounded by very small lobes (Fig. 42); mandible with 8 ventral ridges, the first mandibular tooth is long and is the only one visible (Fig. 44); mandibular appendage $4.1 \times as$ long as wide bearing 20-24 ventral lamellae which are interrupted in the middle by a longitudinal smooth line so the lamellae appear as two teeth on each side of the mandibular appendage (Fig. 44).

Mesosoma: with small mesosternal pollen pockets (Fig. 46); ventral part of the mesosoma with long pilosity; propodeal spiracle elongate oblong; interior side of fore coxa with numerous fine and long setae, partly aligned but not really arranged in a comb; fore tibia with two dorsal and one ventral tooth; hind tibia with two teeth, one elongate monocuspidate, curved at the extremity, the other tricuspidate; fore wing pilose; marginal vein 1.4 × as long as stigmal, postmarginal 2.3 × as long as stigmal.

Metasoma: hypopygium large and glabrous, with a small median tooth; hypopygial spine very short; spiracula of the eighth urotergite circular in shape; posterior margin of tergites denticulate (Fig. 48); tergites with scaly sculpture, which is more accentuated around the spiracula of the eighth urotergite; pilosity on the gastral tergite well developed reaching the posterior margin of the tergite (Fig. 48); posterior margin of the tergite (Fig. 48); posterior margin of the tergite incised in the middle (Fig. 48); ovipositor sheaths about as long as the metasoma.

Measurements. Head: l = 70, w = 52, compound eye: l = 21, w = 18; length of gena = 37; POD = 16; OOD = 8; antennal scape: l = 26, w = 10; fore wing: M = 21; S = 15; PM = 35.

Male: 1–1.2 mm. Head yellow, brown testaceous near the eyes; mesosoma dark yellow; metasoma light yellow; long sparse setae on the malar space; strong carina around the distal part of compound eyes.

Head lentiform, expanded laterally (viewed dorsally) and $1.2-1.3 \times$ as wide as long; eye $1.5-1.7 \times$ as

long as the temple; short gena strongly carinated; head $2.5 \times$ as long as the antennal scrobe; antennal groove $3.4 \times$ as the septum; pronotum slightly wider than long (1.04; posterior part wider than anterior part; mesoscutum $1.5 \times$ as wide as long; propodeum + scutellum $1.2 \times$ as wide as long.

Measurements. Head: l = 43, w = 51; eye: l = 10; temple: l = 15-17; gena: l = 4; antennal groove: l = 17; septum: l = 5; pronotum: l = 50, w = 52; mesoscutum: l = 27, w = 42; propodeum + scutellum: l = 35, w = 43; propodeum spiracle: anterior = 19, posterior = 11, interspace = 25.

Material examined

Type material. Holotype female (deposited in QMBA): AUSTRALIA, QUEENSLAND: Atherton Tablelands, Mount Windsor; 9.xii.1996 (D. J. Dixon) (PhD 354); ex Ficus triradiata. Paratypes: 57 females 44 males, same data as holotype; 2 females, Windsor and NW, open sclerophyll forest, 16°13'S-145°59'E, 23-24.xi.1997, 1100 m (C.J. Burwell); 1 female, Windsor and via Mt Carbine, 26.xii.1983-24.i.1984, malaise trap; 1 female, N. Queensland, 2 km SE Mt Spurgeon via Mt Carbine, 20.xii.1988, 1100 m, Pyrethrum/trees & logs (Monteith & Thompson). (BMNH, ANIC, RMNH, SAMC, CCLV, CJYR).

Biology

Pleistodontes schizodontus is associated with *Ficus triradiata* Corner, a rainforest hemi-epiphyte.

Geographical distribution

Pleistodontes schizodontus is only known from the vicinity of Mount Windsor (NE Queensland). Its host is endemic to a small montane area of north-eastern Queensland: Mount Lewis, Mount Windsor, and the Daintree (Chew, 1989).

Etymology

The latinized species name is derived from Greek *schizo* (= cut) and *odontes* (= teeth), in reference to the shape of the lamellae of the mandibular appendages (Fig. 44).

PLEISTODONTES RIGISAMOS WIEBES, 1991 (FIGS 9, 41, 43, 45, 47)

Pleistodontes rigisamos Wiebes, 1991: 145–147. Lectotype female, here designated, ANIC, examined.

Other citations Wiebes, 1994b: 29.

Description

Female. 1.1–2.1 mm. Vertex (mid-way above a line crossing the eyes), funicule, pronotum partly, mesoscutum, scutellum laterally, mesepemiron and mesopleura partly, propodeum and tergites dorsally black; the lower part of the head, scape, pronotum laterally, median part of the scutellum, legs, ventral part of the mesosoma and the metasoma reddish-yellow.

Head fairly elongate, dorsally about $1.2 \times as$ long as wide across the compound eyes (Fig. 41); eye $1.5 \times as$ long as wide; gena $1.4 \times as$ long as the eye (Fig. 41); area between ocelli convex without sculpture; OOD about $3 \times$ the diameter of the posterior ocellus; antennal scape not folded and about $2.6 \times as$ long as wide, bearing a flat expansion over the pedicel (Fig. 9); third antennal segment with a small and short triangular prominence (spine), reaching at most the base of the fifth segment (Fig. 9); clypeal margin with a relatively long median tooth surrounded by small lobes (Fig. 43); mandible with 3-4 teeth and 10 ventral ridges (Fig. 45); mandibular appendage short, about as long as the mandible and $2 \times as$ long as wide bearing 11-12 lamellae (Fig. 43).

Mesosoma: with very small pollen pockets, nearly abortive (Fig. 47); pronotum and scutellum bear few short setae; propodeal spiracula relatively small and elongate; interior side of the fore coxa with numerous short setae, not arranged in a comb; fore tibia with two teeth on the dorsal side and one on the ventral; hind tibia with two teeth, one bifid (axial) and one tricuspidate (antiaxial; fore wing clearly setose; the fringe apparent; stigmal vein as long as marginal; postmarginal short, only slightly as long as stigmal.

Metasoma: hypopygium glabrous; hypopygial spine short and sharp; spiracula of the eighth urotergite small and subcircular in shape; posterior margin of tergites smooth, medially and submedially incised; tergites smooth, without pilosity excepted some scattered very short setae on the fifth tergite; ovipositor sheaths about as long as the metasoma.

Measurements. Head: l = 76, w = 65, compound eye: l = 25, w = 17; length of gena = 35; POD = 26; OOD = 13; antennal scape: l = 40, w = 15; fore wing: M = 13, S = 15, PM = 22.

Male: 0.7–1.2 mm. Body orange. Frons has long dense setae.

Head slightly wider than long $(1.1 \times)$; temple $3.5 \times$ as long as the eye; short gena carinated; head is $2.6 \times$ as long as the antennal scrobe; antennal groove $2.3 \times$ as long as the septum; pronotum nearly as long as wide; mesoscutum $3 \times$ as wide as long.

Measurements. Head: l = 45, w = 52; eye: l = 6; temple: l = 21; gena: l = 4; antennal groove: l = 25; septum: l = 11; pronotum: l = 39, w = 35; mesoscutum: l = 10 w = 30; propodeum spiracle: anterior = 14, posterior = 6, interspace = 20.

Material examined

Type material. In the description of *P. rigisamos*, no holotype was designated by Wiebes. We have remounted on card all the 'type lot' material (vials 5073 in ANIC). These vials were labelled '*Pleistodontes rigisamos* Wiebes type-lot' 'Australia Theresa Creek Road at t.o. to Millaa Millaa Falls, 19.ix.1986 (J.F. Addicott)'. One female is designated as lectotype; all other specimens are labelled paralectotypes.

Additional material

AUSTRALIA, QUEENSLAND: 28 females 15 males, Atherton Road, 14.i.1999, ex Ficus destruens (J.Y. Rasplus & S. Meusnier); 5 females, Gordonvale Highway, 7.i.1999, ex F. destruens (J.M. Cook) (no. 996); 3 females 11 males, 41.6 km along Danbulla forest road from Lake Tinaroo Dam end, 17°13'S-145°39'E, ex F. destruens (D.J. Dixon) (PhD 329); 5 females 10 males, Theresa Creek Road, Millaa Millaa, 17°30'S-145°36'E, ex F. destruens (D.J. Dixon) (PhD 331); females and males. 1.9 km S of Millaa Millaa on Ravenshoe road, 22.ii.1987 (J.F. Addicott); 1 female, Mt Halifax summit, 19°07'S-146°23'E, 21.iii-10.v.1991, 1050 m, Heath, pitfalls & intercepts (D. Cook); 2 females, Hugh Nelson Range, 21 km S. Atherton, 13.iii-1.iv.1984, malaise trap; 2 females, W base of Mt Hartley, 11.v.1996, rainforest (C.J. Burwell); 1 female, Gap Greek, 5 km ESE Mt Finnigan, 15°50'S-145°20'E, 13-16.v.1981 (I.D. Naumann); 1 female, 14 km W by N of Hope Vale Mission, 15°16'S-144°59'E, 7-10.v.1981 (I.D. Naumann); 1 female, Stone Creek via Garradunga, 5.vi.1996, rainforest (C.J. Burwell); 1 female, 16 km up Davies Creek Road via Mareeba, 18.ii–3.iii.1983, intercept site 9 (Storey & Titmarsh); 1 female, Mt Sorrow, 3 km W Cape Tribulation, 16°05'S-145°27'E, 14.v.1996, 300-500 m, rainforest (C.J. Burwell); 2 females, Bellenden Ker summit, 17°16'S-145°52'E, 28.viii-8.x.1991, 1560 m, flight intercept trap (Monteith & Janetzki); 2 females, Massey Range, 6 km NW of Bellenden Ker, 1150 m, 17°14'S-145°48'E, 11.x.1990, Pyrethrum (Monteith & Janetzki); 2 females, 26 km up Tinaroo Creek road via Mareeba, 28.i-16.ii.1983 & 16.ii-17.iii.1983, flight intercept (Storey & Brown; 1 female, Josephine Falls, Mt Bartle Frere, 17°27'S-145°52'E, 10.vii.1984, yellow pan traps rainforest (B. Halliday).

Biology

Pleistodontes rigisamos pollinates *Ficus destruens* F. Muell. ex C.T. White. From the relatively small size of the pollen pockets and lack of corbiculae, we suspect that *P. rigisamos* is a passive pollinator.

Geographical distribution

Both *P. rigisamos* and its hemi-epiphytic host, *Ficus* destruens, occur in the rainforests of north-eastern Queensland (Corner, 1965).

PLEISTODONTES CUNEATUS WIEBES, 1990 (FIGS 49–52, 68, 78)

Wiebes, 1990: 224, figs 2, 3, 7. Lectotype female, here designated; RMNH, examined.

Other citations

Wiebes, 1991: 141 (new material from Australia); Wiebes, 1994b: 29–30.

Description

Female: 1.6–2 mm. Head, mesosoma and metasoma black; anterior part of the head brown; antennae and legs yellow, the fore coxa lighter, hind coxa and femora darkened.

Head about $1.5-1.7 \times$ as long as wide across the compound eyes; eye about $1.4 \times$ as long as wide; gena nearly twice as long as the compound eve (1.8)(Fig. 50); area between ocelli concave with finely engraved striation; POD $5 \times$ as long as OOD; diameter of the lateral ocelli equal to OOD; antennal scape folded and $2.8 \times as$ long as wide; antennal spine short, blunt and does not reach the base of the fifth segment (Fig. 68); fifth segment is $1.5-1.6 \times$ as long as wide (Fig. 68); last three antennal segments form a distinct subquadrate club; clypeal margin with a distinct median prominence (Fig. 49); mandible with 6-7 ventral ridges, three of which are extended into teeth (Fig. 52); first tooth folded over the second (Fig. 52; mandibular appendage visible in lateral view of the head (Fig. 51), about $3-4 \times$ as long as wide, bearing 17-19 ventral lamellae with some vestiges at the antiaxial side (Fig. 52).

Mesosoma: with pollen pockets (Fig. 78), no markings, setae or elevations on the shiny surface of mesoscutum and scutellum; propodeal spiracula reniform; fore coxa with a corbicula (Fig. 78); hind tibia with two teeth, one axial simple and curved, and one antiaxial bicuspidate; fore wing with a well developed pilosity; postmarginal vein slightly as long as stigmal.

Metasoma: hypopygium glabrous; hypopygial spine very long, exceeding the last urotergite and sharp; spiracula of the eighth urotergite rounded; posterior edge of tergites smooth not subdivided; ovipositor sheaths as long as metasoma.

Measurements. Head: l = 65, w = 43; compound eye: l = 24, w = 17; length of the gena = 45; POD = 15; OOD = 3; antennal scape: l = 28, w = 10; fore wing: M = 15, S = 19, PM = 21. *Male:* 1.1 mm. Head dark testaceous; mesosoma and metasoma whitish; dense short setae on the dorso anterior part of the eye.

Head quadrate, roughly as long as wide; temple $2 \times$ as long as the eye; gena short with a small carina around the ventral anterior part of the eye; head $2.5 \times$ as long as the antennal scrobe; antennal groove $3.4 \times$ as long as the septum; pronotum $1.2-1.3 \times$ as long as wide; posterior part wider than anterior; mesoscutum $1.4 \times$ as wide as long; propodeum + scutellum $1.2 \times$ as wide as long.

Measurements. Head: l = 42, w = 41; eye: l = 13; temple: l = 26; gena: l = 4; antennal groove: l = 12; septum: l = 2; pronotum: l = 42, w = 35; mesoscutum: l = 22, w = 31; propodeum spiracle: anterior = 17; posterior = 11; interspace = 25.

Material examined

Type material. All individuals from the vial (RMNH 4985) have been remounted on rectangular card. The vial is labelled '*P. cuneatus* Wiebes Type-lot' 'Australia Western Australia Kimberley Hidden Valley near Kununurra 4.xi.1982 *F. leucotricha* C. Glover n°121'. To definitively stabilize the nomeclature, one female is designated as lectotype and all other specimens labelled paralectotypes.

Additional material

AUSTRALIA, NORTHERN TERRITORY: 17 females 4 males, L. Nourlangie Rock, Kakadu N.P., 16.ii.1987 (J.F. Addicott). WESTERN AUSTRALIA: 1 male, Kununurra, 15°39'57"S–138°39'51"E, 10.xi.1997, ex *F. platypoda* (D.J. Dixon & I. Champion) (PhD 441); 4 females, Kununurra, 15°49'55"S–128°51'23"E, 23.xi.1997, ex *Ficus platypoda* (D.J. Dixon & I. Champion) (PhD 455); females and males, Kununurra, Students K. distr. High School, ix.1982, ex *F. leucotricha* (K.F. Kenneally) (RMNH 4660); 20 females 10 males, E. Kimberley, 24 km E of Bungle Bungle Outcamp, 12.vii.1984, ex *F. leucotricha* (K.F. Kenneally) (RMNH 4989).

Biology

Pleistodontes cuneatus Wiebes is the pollinator of *Ficus platypoda* (Miq.) ex A. Cunn. Wiebes (1990, 1991) cited *Ficus leucotricha* (Miq.) Miq. as the host fig of *P. cuneatus*. However, Dixon (2001c) considers *F. leucotricha* to be a synonym of *F. platypoda*.

Geographical distribution

Both *Ficus platypoda* and its pollinator, *P. cuneatus*, have been recorded from rocky outcrops in north-western Australia and the Northern Territory.

Pleistodontes proximus Wiebes, 1990 (Figs 55, 62, 64, 71, 76, 94)

Wiebes, 1990: 223–224, figs 10, 11. Lectotype female, here designated, RMNH, examined.

Other citations

Description

Female: 1.4–1.5 mm. Head, metasoma and mesosoma black; antennae, legs and mandibles yellow; hind and mid femora darkened.

Head $1.27-1.32 \times$ as long as wide across the compound eyes (Fig. 94); eye $1.2 \times as$ long as wide; gena is about $1.6-1.7 \times$ as long as the eye (Fig. 94); area between ocelli concave, smooth without any markings; POD about $4 \times$ as long as OOD; diameter of ocelli slightly smaller than OOD (3:4); antennal scape twice as long as wide (Fig. 64); antennal spine of the third antennal segment sharp and reaches the middle of the fifth segment; the last three segments of the funicle form a distinct club (Fig. 64); clypeal margin straight, without median lobe (Fig. 76), lateral lobes acute (Fig. 76); mandible with 9 ventral ridges, three of which extended into a tooth (Fig. 55); mandibular appendage more than $5 \times as$ long as wide bearing 18-19 ventral lamellae (Fig. 55); gena with a distinct area of striations (Fig. 71).

Mesosoma: with distinct mesosternal pollen pockets; propodeal spiracle reniform; fore coxa with a corbicula; hind tibia with two teeth, one axial simple, the other antiaxial bicuspidate; fore wing densely pilose; stigmal vein $1.2 \times$ as long as the marginal; postmarginal vein $1.2 \times$ as long as the stigmal and $1.5 \times$ as long as the marginal vein.

Metasoma: hypopygium glabrous; hypopygial spine long and sharp; spiracula of the eighth urotergite rounded; posterior margin of tergites smooth not subdivided; ovipositor sheaths as long as metasoma.

Measurements. Head: l = 54, w = 42; compound eye: l = 20, w = 17; length of gena = 33; POD = 16–17; OOD = 3–4; antennal scape: l = 23, w = 11; fore wing: M = 13, S = 15, PM = 20).

Male: 0.9 mm. Body whitish; head, testaceous; gena, mandibles and around eye darker; long sparse setae along the genae

Head slightly as long as wide $(1.1 \times)$; temple $1.7 \times$ as long as the eye; gena short carinated; head $2.6 \times$ as long as the antennal scrobe; antennal scrobe $1.6 \times$ as long as the septum; pronotum nearly as long as wide; mesoscutum $1.6 \times$ as wide as long.

Measurements. Head: l = 41, w = 40; eye: l = 14; temple: l = 24; gena: l = 2; antennal groove: l = 16; septum:

Wiebes, 1991: 151 (This citation is a misidentification and corresponds in fact to *P. athysanus* sp. nov.); Wiebes, 1994b: 31.

l = 10; pronotum: l = 25, w = 37; mesoscutum: l = 21, w = 34; propodeum spiracle: anterior = 9, posterior = 12, interspace = 25.

Material examined

Type material. We found four vials in the RMNH collection (RMNH 4575), all labelled '*Pleistodontes proximus* Wiebes type-lot' 'Western Australia Kimberley Hidden Valley 3.3 km E. Kununurra 9.viii.1981 *F. platypoda* K.J. Kenneally 7690'. This material, consisting of 2 males and 2 females, has been remounted on card, because no holotype was designated. One female is here designated as lectotype.

Additional material

WESTERN AUSTRALIA: 20 females, 12 males Lake Argyle, 16°05′48″S–128°45′17″E, 31.xi.1997, ex *F. lilliputiana* (D.J. Dixon & I. Champion) (PhD 449 & 450).

Biology

The species is associated with *Ficus lilliputiana* D.J. Dixon, a newly described species (Dixon, 2001a). The fig specimen collected by K.J. Kenneally belongs to this species (Dixon, 2001b) and not to *F. platypoda* as cited by Wiebes (1990: 223).

Geographical distribution

Ficus lilliputiana is a lithophytic fig having a restricted distribution around Kununurra area of the Kimberley region (Dixon, 2001a). Its pollinator *P. proximus* mirrors the host's distribution.

PLEISTODONTES ATHYSANUS SP. NOV. (FIGS 60, 61, 70, 75, 94)

Description

Female: 1.4–1.6 mm. Head, metasoma and mesosoma black; antennae, legs and mandibles yellow; hind and mid femora sometimes darkened.

Head 1.4–1.5 × as long as wide across the compound eyes (Fig. 94); eye $1.3 \times$ as long as wide; gena about $1.8-2 \times$ as long as the eye (Fig. 94); area between ocelli concave, smooth without any markings; POD is about $4 \times$ as long as OOD; diameter of ocelli slightly smaller than OOD (3 : 4); antennal scape twice as long as wide (Fig. 70); antennal spine sharp reaching the middle of the fifth segment; last three segments form a distinct club (Fig. 70); clypeal margin straight, without median lobe (Fig. 75), lateral lobes rounded (Fig. 75); mandible with 8–9 ventral ridges, three of which are extended into a tooth (Fig. 61); mandibular appendage more than $5 \times$ as long as wide bearing 18 ventral lamellae (Fig. 61); gena with a distinct area of striations (Fig. 61).

Mesosoma: with distinct mesosternal pollen pockets; propodeal spiracle reniform; fore coxa with a corbicula; hind tibia with two teeth, one axial simple, the other antiaxial bicuspidate; fore wing glabrous, without fringe; stigmal vein as long as the marginal; postmarginal $1.3 \times as$ long as the stigmal and $1.3 \times as$ long as the marginal vein.

Metasoma: hypopygium glabrous; hypopygial spine long and sharp; spiracula of the eighth urotergite rounded; posterior edge of tergites smooth, not subdivided; ovipositor sheaths as long as metasoma.

Measurements. Head: l = 60, w = 40; compound eye: l = 19, w = 14; length of gena = 35; POD = 14; OOD = 4; antennal scape: l = 20, w = 11; fore wing: M = 14, S = 13, PM = 18.

Male: 0.8–1.0 mm. Body whitish; head testaceous; genae, mandibles and area around eye brownish.

Head $1.2 \times$ as long as wide; temple $1.8 \times$ as long as the eye; gena short and carinated; head $2.9 \times$ as long as the antennal scrobe; antennal scrobe $1.6 \times$ as long as the septum; pronotum $1.2 \times$ as long as wide; mesoscutum $1.2 \times$ as wide as long.

Measurements. Head: l = 47, w = 40; eye: l = 14; temple: l = 25; gena: l = 3; antennal groove: l = 16; septum (l = 10; pronotum: l = 30, w = 37; mesoscutum: l = 25, w = 30; propodeum spiracle: anterior = 8, posterior = 10, interspace = 24.

Material examined

Type material. Holotype, female (deposited in QMBA): AUSTRALIA, NORTHERN TERRITORY: Darwin River, 12°49'32"S-130°57'55"E, 30.x.1997, ex F. brachypoda (D.J. Dixon & I. Champion) (PhD 470) (deposited in QMBA): Paratypes: AUSTRALIA, NORTHERN TERRI-TORY: 15 females 1 male, Darwin River, 12°49'32"S-130°57′55″E, 30.x.1997, ex F. brachypoda (D.J. Dixon & I. Champion) (PhD 470), 6 females 2 males, 27 km N. Pine Creek on Stuart Highway, 15.ii.1987 (J.F. Addicott). WESTERN AUSTRALIA: 1 female, 4 km S by W Mining Camp, Mitchell Plateau, 14°52'S-125°50'E, 13.v.1983, at light (J. Cardale); 1 female, 10 km NW by Mining Camp, Mitchell Plateau, Ν 14°45′S– 125°470'E, 11.v.1983, at light (J. Cardale); 1 female, Surveyors Pool, $14^{\circ}40'$ S- $125^{\circ}44'$ E, 15.v.1983 (I.D. Naumann & J. Cardale). (BMNH, ANIC, RMNH, SAMC, CCLV, CJYR).

Comments

Specimens identified as *P. proximus* by Wiebes (1991) and collected by J.F. Addicott in Northern Territory (25 km S. Katherine on Stuart Highway and N. Pine

Creek on Stuart Highway), belong in fact to *P. athysanus* sp. nov. and are considered as paratypes.

Biology

This species occurs in syconia of *Ficus brachypoda* (Miq.) Miq. Two specimens were collected among tens of *P. macrocainus* in Queensland: Mount Isa, Mines Weather Station, $20^{\circ}44'19''S-139^{\circ}29'02''E$, 12.x.1997, ex *F. cerasicarpa* (D.J. Dixon & I. Champion) (PhD 405). This host record needs confirmation.

Geographical distribution

Both *P. athysanus* and its host, *Ficus brachypoda*, a lithophytic fig, are widely distributed across the Northern Territory, northern South Australia and the northern parts of Western Australia.

Etymology

The latinized species name is derived from the Greek a (= without) and *thysanos* (= fringe) in reference to the absence of a fringe on the anterior wing.

PLEISTODONTES ASTRABOCHEILUS SP. NOV. (FIGS 56, 59, 63, 74, 79)

Description

Female: 1.9–2.1 mm. Head, mesosoma and metasoma black; antennae, legs, mandibles, genae and lower face yellow; hind femora partly black.

Head dorsally $1.5-1.6 \times as$ long as wide across the compound eyes (Fig. 59); eye $1.3 \times as$ long as wide; gena about $1.9 \times as$ long as the eye (Fig. 59); area between ocelli concave with finely engraved striation; POD less than $3 \times as$ long as OOD; diameter of ocelli smaller than OOD (4 : 6); antennal scape folded with flat dorsal expansion, $1.6 \times as$ long as wide; antennal spine is sharp reaching the middle of the fifth segment (Fig. 63); fifth segment $1.4 \times as$ long as wide; last three funicular segments form a distinct club (Fig. 63); clypeal margin without median lobe, only showing two well marked lobes (Fig. 74); mandible with 10 ventral ridges, four of which extended into a tooth (Fig. 56); mandibular appendage about $6 \times as$ long as wide, bearing 24-25 ventral lamellae (Fig. 56).

Mesosoma: with distinct mesosternal pollen pockets (Fig. 79); no markings, setae or elevations on the shiny surface of mesoscutum and scutellum; propodeal spiracle linear shaped; fore coxa with a corbicula (Fig. 79); hind tibia with two spurs, one long axial bicuspidate and a short antiaxial tricuspidate spur; fore wing with distinct pilosity though short; marginal fringe absent; stigmal vein $1.3 \times$ as long as the mar-

ginal; postmarginal vein $1.2 \times$ as long as the stigmal and $1.6 \times$ as long as the marginal vein.

Metasoma: hypopygium glabrous; hypopygial spine very long and sharp, length exceeding the last urotergite; spiraculae of the eighth urotergite rounded; posterior margin of tergites smooth not subdivided; ovipositor sheaths clearly shorter than metasoma (0.7).

Measurements. Head: l = 83, w = 52; compound eye: l = 24, w = 18; length of the gena = 45; POD = 17; OOD = 6; antennal scape: l = 28, w = 17; fore wing: M = 14, S = 18, PM = 22.

Male: 1.1–1.2 mm. Head dark yellow, with brown testaceous coloration on the malar space (gena) and dorsal part of the compound eye and extending towards the posterior part of the head; mesosoma and metasoma whitish yellow; fore and hind tibia dark yellow; dense short setae on the dorsal part of the eye and long sparse setae on the malar space.

Head slightly longer than wide $(1.2 \times)$; eye $2.2 \times$ as long as the temple; gena short; head $3.9 \times$ as long as the antennal scrobe; antennal acrobe $1.4 \times$ as long as the septum; pronotum slightly longer than wide (1.1; posterior part slightly wider than anterior part; mesoscutum $1.6 \times$ as wide as long; propodeum + scutellum $1.5 \times$ as wide as long.

Measurements. Head: l = 51, w = 45; eye: l = 15; temple: l = 33; gena: l = 4; antennal groove: l = 13; septum: l = 9; pronotum: l = 41, w = 37; mesoscutum: l = 27, w = 43; propodeum + scutellum: l = 33, w = 48; propodeum spiracle: anterior = 20, posterior = 12, interspace = 33.

Material examined

Type material. Holotype female (deposited in QMBA): AUSTRALIA, NORTHERN TERRITORY: Kununurra, Twin pools, 15°39′57″S-28°39′51″E, 20.xi.1997, ex F. subpuberula (D.J. Dixon & I. Champion) (PhD 442). Paratypes: NORTHERN TERRITORY: 6 females 9 males, same data as holotype; 24 females 5 males, Edith Falls, ex F. subpuberula (D.J. Dixon & I. Champion) (PhD 419); 5 females 2 males, Edith Falls, 16.xi.1997, ex F. subpuberula (D.J. Dixon & I. Champion) (PhD 418). NORTHERN TERRITORY: 2 females 2 males, N of Cahills Xing, East Alligator river, 7-8.vi.1973, ex. F. subpuberula (J.C. Cardale). WESTERN AUSTRALIA: 2 females, Drysdale River, 14°39'S-126°57'E, 18-21.viii.1975, Drysdale Survey 1975, site C5 (I.F.B. Common & M.S. Upton). (BMNH ANIC, RMNH, SAMC, CCLV, CJYR).

Biology

Pleistodontes astrabocheilus sp. nov. is the pollinator of *Ficus subpuberula* Corner.

Geographical distribution

Pleistodontes astrabocheilus is known only from two localities, one in western Australia, the other in the Northern Territory. Its host is lithophytic, growing on rocky outcrops. The fig is known to occur in northern Australia from Western Queensland to the Kimberley area of Western Australia.

Etymology

The latinized species name is derived from the Greek terms *astrabes* (= straight) and *cheilos* (= lip), and refers to the straight clypeal margin.

PLEISTODONTES IMPERIALIS SAUNDERS, 1883 (FIGS 53, 57, 65, 72)

- *Pleistodontes imperialis* Saunders, 1882: 10. (Lectotype female, here designated, BMNH, examined).
- Pleistodontes nigricaput Girault, 1927: 337. (Lectotype female, here designated, QMBA, examined). Syn. nov.
- *Pleistodontes nigris* Girault, 1925: 2. (Lectotype female, here designated, QMBA, examined). **Syn. nov**.

Other citations

Pleistodontes imperialis Saunders – Mayr, 1906: 159– 160; Gahan & Fagan, 1923: 116; Swezey, 1923: 304 (introduction into Hawaii); Timberlake, 1927: 552; Grandi, 1928b: 200-203 (redescription); Pemberton, 1934: 379; Sakimura & Linsford, 1940: 454; Ramirez, 1978: 288, 292 (drawing of the coxal corbiculae); Wiebes, 1963: 307-309 (redescription of the male); Wiebes, 1966: 24, 29; Condit, 1969: 123; Valentine & Walker, 1983: 397-398; Gardner, 1983: 2 (introduction into New Zealand); Corner, 1985: 190; Ramirez & Montero, 1988: 442 (possible presence in California); Boucek, 1988: 192; McKey, 1989: 665; Wiebes, 1990: 222-223; Wiebes, 1991: 147-149 (numerous localities from Australia); Boucek, 1993: 205 (misidentification under P. greenwoodi); Wiebes, 1994b: 30–31; Gardner & Early, 1996: 103-110; Boucek in Gibson, Huber & Woolley, 1997: 121 (erroneous citation from USA under the name *P. greenwoodi*).

Pleistodontes nigricaput Girault – Wiebes, 1977a: 140; Dahms, 1986: 332–333 (catalogue of Girault's types); Boucek, 1988: 192.

Pleistodontes nigris Girault – Wiebes, 1977a: 140; Dahms, 1986: 341 (catalogue of Girault's types); Boucek, 1988: 192.

Description

Female: 1.8–1.9 mm. The colour varies from entirely dark testaceous (Sydney), to dorsally testaceous

with legs, mandibles, lower face and gena yellow (Mareeba), to nearly completely yellow (some specimens from Townsville).

Head about 1.6–1.8 × as long as wide across the compound eyes (Fig. 53); eye 1.3–1.4 × as long as wide; gena 2.1–2.5 × as long as the compound eye (Fig. 53); area between ocelli with markings; POD is 2.4–3 × as long as OOD; diameter of lateral ocelli half as long as OOD (3 : 6); antennal scape 1.6–1.7 × as long as wide; antennal spine sharp and reaches the base of the fifth segment (Fig. 65); last three segments of the funicle forming a distinct club; clypeal margin with a spiniform median lobe longer than the lateral lobes (Fig. 72); mandible with 9–10 ventral ridges, five of which are extended into a tooth (Fig. 53); first tooth has a middle prominence; mandibular appendage is about 5 × as long as wide bearing 25–29 ventral lamel-lae (Fig. 53).

Mesosoma: with distinct mesosternal pollen pockets; no markings, setae or elevations on the surface of mesoscutum and scutellum; propodeal spiracle reniform; fore coxa with a corbicula; bifid spur on the fore tibia; hind tibia with two bicuspid spurs, one long axial and one short antiaxial; fore wing densely pilose; marginal fringe long and clearly visible; stigmal vein $1.5 \times$ as long as the marginal; postmarginal vein $1.6 \times$ as long as stigmal and $2.3 \times$ as long as the marginal.

Metasoma: hypopygium glabrous; hypopygial spine curved upwards, reaching the base of the ovipositor sheaths; spiracula of the eighth urotergite rounded; posterior margin of tergites smooth not subdivided; ovipositor sheaths slightly shorter than metasoma.

Measurements. Head: l = 76, w = 45; compound eye: l = 20, w = 14; length of gena = 50; POD = 18; OOD = 6; antennal scape: l = 16, w = 13; fore wing: M = 12, S = 18, PM = 28.

Male: 1.2–1.4 mm. Body whitish yellow; head testaceous, with two darker bands around the eye extending towards the temple; long sparse setae on the frons, genae and mandibles.

Head $1.3 \times as$ long as wide; eye dorsally and ventrally carinated; temple $2.4 \times as$ long as the eye; gena short and carinated; head $4.3 \times as$ long as the antennal scrobe; antennal scrobe $1.7 \times as$ long as the septum; pronotum as long as wide; mesoscutum $1.4 \times as$ wide as long.

Measurements. Head: l = 52, w = 41; eye: l = 11; temple: l = 26; gena: l = 6; antennal groove: l = 12; septum: l = 7; pronotum: l = 41, w = 40; mesoscutum: l = 31, w = 45; propodeum spiracle: anterior = 15, posterior = 11, interspace = 30.

Material examined

Type material. Pleistodontes imperialis. In the BMNH collection, we have found 11 females and seven males

mounted on card and labelled 'Ex. Coll. S. Saunders 84-31, P. imperialis from F. macrophylla NSW'. One female is labelled Lectotype but as far as we know no designation of lectotype has been published. To stabilize the nomenclature and because no holotype was designated by Saunders, this female is here designated as the *P. imperialis* lectotype. It is a specimen in good condition, although the eyes have collapsed, and labelled as follows: 'Ficus australis Willd. NSW., Ex. coll. S. Saunders 84-31, Lectotype (round blue label), P. imperialis Saunders'. Saunders' type material also contains three females emerging from three florets mounted on three different cards with the following labels: 'N.S.W. F. australis June, Ex. Coll. S. Saunders 84-31, P. imperialis'; 19 slides made by Saunders and identified as P. imperialis, 4 slides unidentified. Finally there is one card with a fig of *F. rubiginosa* split open showing florets with exit holes and two labels: 'F. australis, ex. coll. S. Saunders 84-31'. This old material is in fairly good condition. We are sure that Saunders used all this material to describe P. imperialis. The drawings illustrating the description and the description itself were probably based on many slides rather than one particular slide .

Pleistodontes nigricaput. Among the syntypes examined (QMBA), one female (fourth female from the left) glued with 6 other females and labelled 'Sydney' 'ex Jackson Fig, Coates' 'Syntypes T.9326' is here designated as lectotype, to stabilize the nomenclature.

Pleistodontes nigris. We examined the slide containing the female syntypes (QMBA). The slide contains 5 females (one in two pieces) and not 4 as stipulated by Dahms (1986: 341). The central specimen is here designated as lectotype, to stabilize the nomenclature. The slide, containing also parts of Ormyrus silvae Gir., is labelled 'Ormyrus silvae Girault, female type, P. nigris. Type. Bred from Moreton Bay Figs, Brisbane, March 1914, H. Hacker' 'Syntypes, T.9329, E.C.D. 1985'. Another slide, which is not considered to belong to the type lot is labelled 'Pleistodontes nigris Gir. female, Gatton, 13 October 1931, B. Blumberg'.

Additional material

AUSTRALIA, AUSTRALIAN CAPITAL TERRITORY: 1 female, Black Mountain, 28–29.iii.1968, light trap. NEW SOUTH WALES: 17 females 7 males, Sydney, 1.i.1995, ex *F. rubiginosa* (J. Cook) (in CCLV); 17 females 10 males, Sydney, 1.i.1997, ex *F. rubiginosa* (J.M. Cook) (in CCLV); 2 females, Sydney, Coll. B.M. 1942–95, ex *F. rubiginosa* (R.C.L. Perkins); 1 female, Sydney, Macmaster Laboratory, 31.x.1978 (A. Postle); 2 females 2 males, Sydney, 3.vii.1959 (E.F. Riek); 1 female, Nimmitabel, 8.iii.1963 (D.H. Colless); females and males, Sydney, Botanical Garden, ix.1978, ex *F. rubiginosa* (J. Galil) (RMNH 3695); females and males, Sydney, Botanical Garden, 28.x.1989, ex F. rubiginosa (J. Meyer & J.T. Wiebes) (RMNH 5003); females and males, Sydney, Botanical Garden 1989, ex F. rubiginosa (K. Cohen) (RMNH 5041, 5047); females and males, Ballina, 25.i.1999, ex F. rubiginosa (J.Y. Rasplus & S. Meusnier); 2 females, 40 S Singleton, 30.xii.1959 (E.F. Riek); 1 female, Brimbin Road, Via Taree, 5.iii.1979 (A. Postle); 1 female, Bucketts Road, Gloucester, 6.iii.1979 (C. Brennan); 2 females, Moonbi Lookout via Moonbi, 30°59'S-151°05'E, 25.ix.1995 (C.J. Burwell); females and males, Hawk's Nest, Myall Lake, 3.xi.1989, ex F. rubiginosa (J. Meyer & J.T. Wiebes) (RMNH 5006); females and males, South-west Rocks, 7.xi.1989, ex *F. rubiginosa* (J.T. Wiebes) (RMNH 5010); females and males, Evan Head, 10-11.xi.1989, ex F. rubiginosa (J. Meyer & J.T. Wiebes) (RMNH 5014); females and males, Smoky Cape, E. Kemsey, 18.xi.1989, ex F. rubiginosa (J. Meyer & J.T. Wiebes); females and males, Casino, xi.1989, ex F. rubiginosa (J. Meyer & J.T. Wiebes) (RMNH 5086); females and males, 'Hilltop' Farm, Moonbi, ex F. rubiginosa (J.F. Addicott) (RMNH 5087, 5113, 5114). QUEENSLAND: 4 females 4 males. Brisbane. 6.ii.1995, ex F. rubiginosa (J.M. Cook) (in CCLV); 4 females, Brisbane, 16.v & 23.v.1952 (F.A. Perkins); 3 females 4 males, Brisbane, 14.viii.1952 & 1.viii.1959 (E.F. Riek); 1 female, Brisbane, 31.iii.1948 (Robertson); females and males, Brisbane, ix.1978, ex F. rubiginosa (J. Galil) (RMNH 3700, 3702); 5 females, Townsville, Pallerenda, 10.ii.1999, ex F. rubiginosa (C.L. Vaamonde); females and males, Townsville, Pallerenda, 15.ii.2001, ex F. rubiginosa (J. Cook); 7 females, 2 males, Mareeba, 15.i.1999, ex F. rubiginosa (J.Y. Rasplus & S. Meusnier); females, lake Tinaroo, 500 m along Danbulla Forest Drive, Atherton Tablelands, 17°09'S-145°32'E, ex F. rubiginosa (D. Dixon PHD321); females and males, Lamington N.P., nr O'Reilly's Lookout, 3.xi.1989, ex F. platypoda [without doubt a misidentification of F. rubiginosa] (J. Meyer & J.T. Wiebes) (RMNH 5018); females and males, Queensland, between Canungra & Cummara, nr Lamington N.P., 14.xi.1989, ex F. platypoda [without doubt a misidentification of F. rubiginosa] (J.T. Wiebes & J. Meyer) (RMNH 5019); females and males, Park at Tinaroo Dam, NE. Atherton, xi.1989, ex F. platypoda [without doubt a misidentification of F. rubiginosa] (J. Meyer & J.T. Wiebes) (RMNH 5078); females and males, just N. of Bowen on A1, 19.xi.1986, ex F. platypoda [without doubt a misidentification of F. rubiginosa] (J.F. Addicott) (RMNH 5082); females and males, c. 65 km SW of Mt. Garnet on A1 in 40 Mile Scrub, 21.ii.1987, ex F. platypoda [without doubt a misidentification of F. rubiginosa] (J.F. Addicott) (RMNH 106-5109); females and males, Cape Hillsborough N.P., 20.xi.1986, ex F. platypoda [without doubt a misidentification of F. rubiginosa] (J.F. Addicott)

(RMNH 5083); females and males, Yungaburra, 15.i.1999, ex F. rubiginosa (J.Y. Rasplus & S. Meusnier); females and males, Cleveland, 23.i.1999, ex F. rubiginosa (J.Y. Rasplus & S. Meusnier); females and males, North Stradbroke Island, Amity & Dunwich, 23.i.1999, ex F. rubiginosa (J.Y. Rasplus & S. Meusnier); 1 female, N. Boonah, 25°54'S-152°41'E, 18.ix.1994 (C.J. Burwell); 1 female, Bundaberg, xi.1959, 1 female, Cunningham's Gap, 2484 ft, 1-2.vi.1966 (Z. Liepa); 1 female, Cape Hillsborough, Hidden Valley Track, 16.iv.1979 (E. Dahms); 1 female, Road to Mt Macartney, Cathu State Forest, 21.iv.1979, open forest (E. Dahms); 2 females, Granite Gorge, 17°02'S-145°21'E, 450 m, 26.xi.1997 (C.J. Burwell); 1 female, Mt Glorious, iii.1982, malaise trap (A. Hiller); 1 female, Big Mitchell Creek, 15 km S Mount Molloy, 16°48'S-145°22'E, 22.iv.1997 (C.J. Burwell); 13 females 9 males, Lake Manchester near Brisbane, 30.i.1983 (Z. & T. Boucek); 1 female, Mount Glorious near Brisbane, 17.xi.1976 (Z. Boucek); 6 females, Wethern 15.i.1957 (DPI, Brisbane, C.I.E coll. n°17044); 1 female, Gatton, v.1980 (J.S. Noyes, Brit. Mus. 1981–299): 1 female. Mount Tibrogargan. 27.xii.1976 (Z. Boucek); 1 female, Surfers Paradise, 21.xi.1976 (Z. Boucek); 1 female, Cooloola, vi.1980 (J.S. Noyes B. M. 1981-299); 1 female, Danbulla State Forest, 1.ii.1978 (D. Gibson); 1 female, nr Paradise Falls, Bunya Mountains N.P., 26°52'S-151°35'E, 6.x.1984 (I. Naumann & J. Cardale); 10 females, Childers, 10.vii.1921, ex F. obligua var. petiolaris (C.E. Pemberton) (RMNH 689). SOUTH AUSTRALIA: Adelaide Botanical Garden, 5.xii.1956, 6.ii.1957, 2.v.1957, ex F. rubiginosa (E.J.H. Corner) (RMNH 433, 434, 436). USA, HAWAII: 4 males, Manoa Oahu, H. L. Coll. B. M. 1942-95, ex F. rubiginosa (R.C.L. Perkins); CALIFOR-NIA: 2 females, San Diego, viii.1993, ex F. rubiginosa (Doyle). Material in CCLV, CJYR, QMBA. ISRAEL: 10 females, Netanya, 12.xii.1999, ex F. rubiginosa (V. Fichman).

Comments

We have found intraspecific variation in colour in this species, with specimens varying from completely yellow to completely black in syconia of a single *F. rubiginosa* tree in Pallarenda (Townsville).

Biology

Saunders' (1882) record of *P. imperialis* from *F. macrophylla* is clearly based on a misidentification of the host fig. Wiebes' citations from *F. platypoda* (from western and eastern Australia) (Wiebes, 1991) are based on misidentification of either the *Ficus* or the wasps (confusion with *P. astrabocheilus*). *F. obliqua* var. *petiolaris* Benth. (eastern Australia)

also cited as a host by Wiebes (1991), is now recognized as *F. rubiginosa* (Dixon, Jackes & Bielig, 2001). Consequently *P. imperialis* is strictly associated with *F. rubiginosa*. Zammit & Schwarz (2000) have studied interactions between males and females of *P. imperialis*. They showed that males initially make holes in seeds that contain females, in order to mate. Subsequently, they enlarge the holes so that females can emerge and disperse.

Geographical distribution

Both *P. imperialis* and its host *F. rubiginosa*, a free standing, hemi-epiphytic, or lithophytic fig, occur along the east coast of Australia from the tip of Cape York Peninsula to the Border of New South Wales and Victoria. Within Australia the distribution of *F. rubiginosa* has been extended considerably by its frequent use as an ornamental and shade tree. Both plant and pollinator have been introduced to Hawaii (Swezey, 1925), California, New Zealand (Gardner & Early, 1996; Early, 2000) and Israel (Vered Fichman, pers. comm.).

PLEISTODONTES MACROCAINUS SP. NOV. (FIGS 54, 58, 66, 73, 77, 80, 88)

Description

Female: 1.6–1.9 mm. Head, mesosoma and metasoma black; antennae, legs and mandibles brownish.

Head 1.4–1.5 × as long as wide across compound eyes (Fig. 58); eye 1.4–1.5 × as long as wide; gena 1.6 × as long as compound eye (Fig. 58); area between ocelli concave with finely engraved striation (Fig. 77); POD about 3.3 × as long as OOD; antennal scape broad and 1.4 × as long as wide (Fig. 66); third antennal segment with a long external prominence which reaches the middle of the fifth segment (Fig. 66); fifth segment twice as long as wide (Fig. 66); clypeal margin with a subtriangular median lobe shorter than the lateral lobes (Fig. 73); mandible with 8–9 ventral ridges three of which are extended into a tooth (Figs 54, 88); mandibular appendage 7 × as long as wide bearing 18–21 ventral lamellae (Fig. 54).

Mesosoma: with mesosternal pollen pockets (Fig. 80); propodeal spiracle reniform; fore coxa with a corbicula (Fig. 80); fore tibia with two spurs, one dorsal bicuspidate and one simple ventral spur; hind tibia with of two spurs, one long axial bicuspidate (the second cusp is very difficult to see unless using high magnification) and a short antiaxial tricuspidate; no pilosity on the wings; no marginal fringe on the fore wing; stigmal vein $1.1 \times$ as long as marginal; postmarginal $1.7 \times$ as long as stigmal and $1.9 \times$ as long as marginal vein.

Metasoma: hypopygium glabrous; hypopygial spine sharp and slightly curved upwards, exceeding by far the insertion of the ovipositor; spiracula of the eighth urotergite circular in shape; posterior margin of tergites smooth not subdivided; ovipositor sheaths as long as metasoma.

Measurements. Head: l = 76, w = 56; compound eye: l = 25, w = 18; length of gena = 39; POD = 20; OOD = 6; antennal scape: l = 25, w = 14; fore wing: M = 16, S = 17, PM = 30.

Male: 0.9–1.1 mm. Body whitish yellow; head orange; genae and dorsal part of eye darker; short dense setae on the frons and genae.

Head $1.2 \times$ as long as wide; temple $1.9 \times$ as long as the eye; gena short and carinated; head $2.6 \times$ as long as the antennal scrobe; antennal scrobe $3 \times$ as long as the septum; pronotum nearly as long as wide; mesoscutum $1.7 \times$ as wide as long.

Measurements. Head: l = 47, w = 40; eye: l = 13; temple: l = 25; gena: l = 5; antennal groove: l = 18; septum: l = 6; pronotum: l = 51, w = 45; mesoscutum: l = 27, w = 45; propodeum spiracle: anterior = 16, posterior = 11, interspace = 38.

Material examined

Type material. Holotype female (deposited in QMBA): AUSTRALIA, QUEENSLAND: Mount Isa, Mines Weather Station, 20°44'19"S–139°29'02"E, 12.x.1997, ex *F. cerasicarpa* D.J. Dixon (D.J. Dixon & I. Champion) (PhD 405). Paratypes: 8 females, 2 males, same data as holotype; 3 females, Julia Creek Cloncurry, 20°44'S–140°41'E, 8.x.1997, ex *F. cerasicarpa* (D.J. Dixon & I. Champion) (PhD 396).

Additional material

NORTHERN TERRITORY: 4 females 1 male, Ross Highway, East Alice Springs, 23°38'10"S-134°17'33"E, 5.x.1997, ex F. brachypoda (D.J. Dixon & I. Champion) (PhD 482; 31 females, Ross Highway. East Alice 23°44′36′S–133°57′10″E, Spring, 5.xi.1997, ex F. brachypoda (D.J. Dixon & I. Champion) (PhD 480); females, Ross Highway. East Alice Spring, 3 23°44′08″S-133°44′22″E, 4.ii.1997, ex F. brachypoda (D.J. Dixon & I. Champion) (PhD 479); 3 females, 8 km N of Kulgera, 25°46′S–133°17′E, 21.ix.1978 (J. Cardale); 3 females, 32 km WNW of Alice Springs, 8.x.1978 (J. Cardale); 3 females, 53 km E by N of Alice Springs, 6.x.1978 (J. Cardale). WESTERN AUSTRALIA: 10 females, off Great Northern Highway, 92 km SW of Fitzroy Crossing WA, 18°45'S-123°04'E, ex F. brachypoda (D.J. Dixon & I. Champion) (PhD 458).

Comments

We could not find any reliable morphological differences between the pollinators of *F. cerasicarpa* D.J. Dixon and *F. brachypoda* and consider that they probably belong to the same species. However, we used only specimens from *F. cerasicarpa* as type material. The specimens from Western Australia (PhD 458) have a shorter head than those from the Northern Territory. They could represent a different species or just geographical variation in a widespread species. Further studies and material are needed to clarify their status.

Some of the specimens collected by J. Cardale in the Northern Territory and identified by Wiebes (1991) as *P. greenwoodi*, belong in fact to *P. macrocainus*. These specimens exhibit clear differences from *P. greenwoodi* in the number of lamellae on the mandibular appendage (see table 3 in Wiebes, 1991).

Biology

The species is associated with *Ficus cerasicarpa* and *F. brachypoda*, two lithophytic figs that are easily distinguishable but closely related and partially sympatric.

Geographical distribution

Pleistodontes macrocainus has been recorded in parts of the range of both its hosts: *Ficus cerasicarpa* occurs in western Queensland and in the northern part of the Northern Territory, but is poorly known in Western Australia (Dixon, 2001a). *Ficus brachypoda* is widely distributed across the Northern Territory, northern South Australia and the northern parts of Western Australia.

Etymology

The latinized species name is derived from Greek *mac*ros (= long) and *akaina* (= spine), in reference to the elongate third antennal segment.

PLEISTODONTES XANTHOCEPHALUS SP. NOV. (FIGS 69, 82, 85, 87, 91)

Description

Female: 1.1–1.3 mm. Frons, inner orbit of compound eyes and mesosoma dorsally black, metasoma lighter; antennae, face, genae, side lobes of mesoscutum, ventral side of mesosoma and legs yellow.

Head $1.2 \times$ as long as wide across compound eyes (Fig. 85); eye $1.3 \times$ as long as wide; gena $1.3 \times$ as long as the eye (Fig. 85); median ocellus within a small triangular plate (delimited by the white membranous lines) not reaching the ocular line (Fig. 85), the limits of the triangular plate are weakly chitinized and consequently appear white on the black frons; area between ocelli smooth without markings; POD $2.3 \times$ as

long as OOD; diameter of ocelli is half the length of OOD (3:6); antennal scape $1.5 \times$ as long as wide (Fig. 69); antennal spine sharp reaching the middle of the fifth segment (Fig. 69); clypeal margin with a spiniform median lobe surrounded by weak lateral lobes (Fig. 87); mandible with nine and a half ventral ridges (there is half a ridge between the first and second teeth, see Fig. 89), four of which are extended into a tooth; mandibular appendage $3.7 \times$ as long as wide and bears 15–16 ventral lamellae.

Mesosoma: with distinct mesosternal pollen pockets (Fig. 82); propodeal spiracle reniform; fore coxa with a corbicula (Fig. 82); fore femora about $2.3 \times as$ long as wide in the middle and about the same length as the tarsi (Fig. 91); hind tibia with one tricuspidate short antiaxial spur, and one axial bicuspidate spur; fore wing pilose; marginal fringe long along the apex, absent in the anal margin; stigmal vein about $2 \times as$ long as the marginal; postmarginal vein as long as the stigmal and $2 \times as$ long as the marginal vein.

Metasoma: hypopygium glabrous; hypopygial spine straight, hardly exceeding the elongate cerci; spiracula of the eighth urotergite rounded; posterior margin of tergites smooth, not subdivided; ovipositor sheaths shorter than metasoma.

Measurements. Head: l = 50, w = 40; compound eye: l = 17, w = 13; length of the gena = 23; POD = 14; OOD = 6; antennal scape: l = 20, w = 13; fore wing: M = 7, S = 14, PM = 14.

Male: 0.8 mm. Body whitish; head orange; genae and area around eye brown; long sparse setae on the genae.

Head slightly as long as wide $(1.1 \times)$; temple $1.4 \times$ as long as the eye; gena short and carinated; head $3.4 \times$ as long as the antennal scrobe; antennal scrobe $1.6 \times$ as long as the septum; pronotum nearly as long as wide; mesoscutum $1.5 \times$ as wide as long.

Measurements. Head: l = 37, w = 33; eye: l = 12; temple: l = 17; gena: l = 3; antennal groove: l = 11; septum: l = 7; pronotum: l = 31, w = 30; mesoscutum: l = 18, w = 27; propodeum spiracle: anterior = 10, posterior = 8, interspace = 21.

Material examined

Type material. Holotype female (deposited in QMBA). AUSTRALIA, QUEENSLAND: Cooktown, i.1995, ex Ficus obliqua (J.M. Cook). Paratypes. 30 females, 14 males, same data as holotype; 3 females, Cooktown, 18.xii.1998, ex Ficus obliqua (J.M. Cook); 30 females, 30 males, Rex Lookout, 13.i.1999 ex Ficus obliqua (J.Y. Rasplus & S. Meusnier); females and males, Rex Lookout, 15.i.2001 ex Ficus obliqua (J. Cook); 30 females, 30 males, Mossman Road, 18.i.1999, ex Ficus obliqua (J.Y. Rasplus & S. Meusnier). (BMNH, ANIC, RMNH, SAMC, CCLV, CJYR).

Additional material

One female, 14 km Wby N. Hope Vale Mission, $15^{\circ}16'S-144^{\circ}39'E$, 8-10.x.1980, collected at light (J.C. Cardale).

Biology

Pleistodontes xanthocephalus is associated with *Ficus obliqua* in parts of north Queensland (see below). However, *P. greenwoodi* is the species associated with *F. obliqua* at most Australian localities. Females of *P. xanthocephalus* are easily distinguished from those of *P. greenwoodi* by their yellow coloration, and the lack of an elongate triangular sclerite on the head (Figs 83, 85).

Geographical distribution

Pleistodontes xanthocephalus is only known from three localities in north-eastern Queensland, on the coast road from Cairns to Cooktown. The host has a much wider range, all along the east coast as far south as Sydney. However, all fig material examined from south of Cairns contains only *P. greenwoodi*.

Etymology

The latinized species name is derived from Greek *xanthos* (= yellow) and *kephale* (= head) and refers to the distinctive yellow colour of the head.

Pleistodontes Greenwoodi (Grandi, 1928) (FIGS 67, 81, 83, 84, 86, 89, 90)

- Blastophaga greenwoodi Grandi, 1928a: 65–68. Holotype, female, BMNH, examined.
- Proceratosolens medionigra Girault, 1933: 3–4. Holotype, female, QMBA, examined. Syn. nov.

Other citations

Blastophaga greenwoodi Grandi – Grandi, 1931: 8. Recorded from Fiji, Mts. La[u]toka and Mts. La[m]basa, ex *Ficus obliqua* G. Forst. *Pleistodontes* greenwoodi Grandi – Wiebes, 1982: 402 (first mention in *Pleistodontes*); Boucek, 1988: 192); Wiebes, 1990: 222–223 (new record from Samoa, Wiebes, 1991: 150– 151 (description of the male, map and new host citations from Australia); Boucek, 1993: 205 (new record from USA, but based on misidentification, see under *P. imperialis*); Wiebes, 1994b: 31–32.

Pleistodontes medioniger Girault – Hill, 1967a: 92; Wiebes, 1977a: 139–140; Dahms, 1984: 804–805 (catalogue of Girault's types; Boucek, 1988: 192.

Description

Female: 1–1.3 mm. Head, mesosoma and metasoma black; antennae and legs, including coxae, yellowish; femurs dorsally greyish-black.

Head $1.6 \times$ as long as wide across the compound eves (Fig. 83), eve $1.4 \times as$ long as wide; gena $1.6 \times as$ long as the compound eye (Fig. 83); median ocellus within a long triangular plate which ends below the ocular line (Fig. 83); the limits of the triangular plate are weakly chitinized and consequently appear white on the black frons; area between ocelli slightly concave and smooth; POD 1.6 × as long as OOD; diameter of the ocelli smaller than OOD (2:7); scape $1.7 \times$ as long as wide (Fig. 67); antennal spine sharp reaching the middle of the filth segment (Fig. 67); fifth segment is $1.6 \times$ as long as wide; the three last funicular segments form a distinct club; clypeal margin with a spiniform median lobe surrounded by very shallow lateral lobes (Fig. 86); mandible with 10 and a half ventral ridges (there is half a ridge between the first and second teeth, see Fig. 89), four of which are extended into a tooth. (Fig. 84); mandibular appendage $4 \times$ as long as wide bearing 16–17 ventral lamellae (Fig. 84).

Mesosoma: with distinct mesosternal pollen pockets (Fig. 81); propodeal spiracle reniform; fore coxa with a corbicula (Fig. 81); fore femora about $4 \times$ as long as wide in the middle and clearly longer than the tarsi (Fig. 90); fore tibia with a dorsal bifid spur; hind tibia with two spurs, one slender, axial simple, and one short antiaxial, tricuspid; fore wing pilose with a long fringe shorter at the apex; stigmal vein $1.2 \times$ as long as the marginal vein; postmarginal vein $1.3 \times$ as long as stigmal and $1.2 \times$ as long as the marginal vein.

Metasoma: short and blunt hypopygial spine, hardly exceeding the elongate cerci; spiracula of the eighth urotergite rounded; posterior margin of tergites smooth and not subdivided; ovipositor sheaths longer than metasoma (70 : 60).

Measurements. Head: l = 52, w = 33); compound eye: l = 14, w = 10; length of the gena = 23; POD = 20; OOD = 5; antennal scape: l = 20, w = 13; fore wing: M = 10, S = 12, PM = 16.

Male: 0.7–0.8 mm. Body whitish, head orange; gena, mandibles and area around eye brown; short dense setae all over the head except the vertex.

Head about as long as wide $(1.1 \times)$; temple $2.3 \times$ as long as the eye; gena short and carinated; head $3.2 \times$ as long as the antennal scrobe; antennal scrobe $1.5 \times$ as long as the septum; pronotum as long as wide; mesoscutum $1.5 \times$ as wide as long.

Measurements. Head: l = 29, w = 33; eye: l = 11; temple: l = 25; gena: l = 4; antennal groove: l = 9; septum: l = 6; pronotum: l = 26, w = 26; mesoscutum: l = 18, w = 27; propodeum spiracle: anterior = 15, posterior = 7, interspace = 21.

Material examined

Type material. Blastophaga greenwoodi. We examined the female holotype which is mounted, on the same pointed card, with a female paratype (the holotype, near the point of the card, is mounted laterally and the paratype, near the pin, is mounted ventrally). The holotype is labelled 'BM TYPE HYM 5–2' 'Fiji Mts. Lautoka 26.vi.21 W. Greenwood' 'Blastophaga greenwoodi sp. nov. female det. Prof G. Grandi'. We also examined 12 females paratypes mounted on five different cards, labelled as the holotype (four cards in the BMNH and one in the RMNH).

Proceratosolens medionigra. The species was transferred to *Pleistodontes* by Hill (1967a: 92 (Wiebes, 1994b: 30). Holotype on one slide with two coverslips containing the separated head + antennae and the mesosoma (minus one pair of wings). The slide is labelled 'Ent. Division Department Ag. & Stk., Qld, *Proceratosolens medionigra* Gir., type'.

Additional material

AUSTRALIA. NEW SOUTH WALES: 64 females 11 males, Sydney, 5.iii.1921, ex F. eugenioides [= F. obliqua] (C.E. Pemberton) (RMNH 691 and dry mounted material; 21 females, Sydney, Zoo Taronga, 15.i.1999, ex F. obliqua (J.Y. Rasplus & S. Meusnier); 3 females, Sydney, 5.i.1997 (J. Cook); 135 females 9 males, Booyong Flora Reserve, c. 25 km E of Lismore, 15.xi.1989, ex F. obliqua (J. Meyer & J.T. Wiebes) (RMNH 5023); 10 females 14 males, South-west Rocks, 15.xi.1989, ex F. obliqua (J.Meyer & J.T. Wiebes) (RMNH 5032); 66 females 9 males, 7.2 km of Bellingen on NSW78, 7.i.1987, ex F. obliqua (J.F. Addicott) (RMNH 5088). QUEENSLAND: 30 females 7 males, Fong-on-Bay, Tinaroo Dam Road, NE Atherton, 11.xi.1986, ex F. obliqua (J.F. Addicott) (RMNH 5074); 75 females 9 males, 4.6 km E of Ravenshoe on Millaa Millaa Road, 21.ii.1987, ex F. obliqua (J.F. Addicott) (RMNH 5111); 12 females, 8 males, Hayman Island, on the East coast of Australia, about 300 km south of Townsville S side and to N of resort road, 24.vi.1998, ex F. obliqua (I.G. Champion) (PhD188); 52 females, Atherton Tablelands, 17°34'S-145°36'E, 19.xi.1996, ex F. obligua (D.J. Dixon) (PhD 335); 7 females, Townsville, Pallerenda, 15.ii.2001, ex F. obliqua (J. Cook); Fraser Island, National Park A. road, 12.x.1978, open forest (E. Dahms); 2 females 2 males, Lamington National Park, 25.xii.1971, ex F. obliqua (S.R. Monteith); 1 female, Danbulla State Forest, 21.ii.1978 (D. Gibson); 1 female, Russell Park near Mt Mowbullan, 7.x.1984 (I. Naumann & J. Cardale); 1 female, Kirrama State Forest, 32 km NW Cardwell, 800 m, 23.vii-8.viii.1982, SBP46 flight intercept trap rainforest (S. & J. Peck); 10 females, Rex Lookout, 15.i.2001 ex F. obliqua (J. Cook). NEW CALEDONIA: 22

females, Mont Mondoue, 110 m, Fogging, sclerophytic forest, 3.vii.1992 (Chazeau, Guilbert, Bonnet de Laroque). SAMOA: 62 females 12 males Pago Pago, 19–20.ix.1923, ex *Ficus* sp. (O.H. Swezey) (RMNH 4991 and dry mounted material).

Comments

The species is often confused with several other *Pleistodontes* species (*P. imperialis*, *P. astrabocheilus*, *P. macrocainus* and *P. proximus*); however, *P. greenwoodi* can be reliably separated from any other *Pleistodontes* species by the long triangular sclerite bearing the median ocellus. Furthermore, this area is surrounded by a V-shaped white line, which makes it easy to see.

Males of *P. greenwoodi* and *P. xanthocephalus* are very difficult to distinguish. The only character is the relative length of the eyes compared to the temple; however, this character is difficult to observe and requires high magnification.

Biology

The species is associated with *F. obliqua* along most of the eastern coast of Australia, although *P. xanthocephalus* is the recorded pollinator in a few localities in north Queensland (see below). Wiebes' records of *P. greenwoodi* from *F. rubiginosa and F. platypoda* in Western Australia are based on misidentifications of either the fig or the wasp species. For example, different specimens listed by Wiebes (1991) under *P. greenwoodi*, and re-identified by us, belong to *P. greenwoodi*, *P. macrocainus* and *P. proximus*.

Geographical distribution

P. greenwoodi is known from Australia, Fiji (both Vanua Levu and Viti Levu), Samoa and New Caledonia (new record). Boucek (1993: 205) recorded the species from California (Riverside) introduced with *F. rubiginosa*. However, we have checked specimens from USA, California, Riverside, 27.iv.90, ex *F. rubiginosa* (H. Nadel), identified by Z. Boucek as *P. greenwoodi*, and they are in fact *P. imperialis*. As mentioned by Corner (1985), the pollinator of *F. obliqua* is still unknown for a large part of its range in the Pacific Islands.

DISCUSSION

The revision of Australian malvantheran figs by Dixon (1999, 2001a,b,c; Dixon *et al.*, 2001) has clarified the species delimitation in this group and produced a workable classification. Simultaneous collection of wasps from authenticated plant specimens, along with more secure identification of *Ficus* species in other

new collections, now permits us to re-examine the host relationships of *Pleistodontes* species with much greater confidence (Table 1). In most cases there is a one-to-one correspondence of *Ficus* and pollinator species. However, there are also some notable exceptions:

- (1) F. crassipes and F. pleurocarpa both have two pollinator species. Since both fig species have very restricted ranges in the upland rainforests of north Queensland, there would appear to be little scope for geographical or habitat segregation of these pollinator species, which are sympatric. In fact, on three different occasions, at three different sites, we collected both pollinators of F. pleurocarpa from the same tree on the same day. In addition, we note that F. crassipes and F. pleurocarpa are both very distinct fig species, each with little intraspecific variation and no suggestion of distinct forms.
- (2) F. obliqua might represent a different situation. It is the most widespread of the malvantheran figs, occurring in many different regions and habitats. So far, most records show P. greenwoodi as the main pollinator. However, we recently discovered a new species, P. xanthocephalus, to be the pollinator at three coastal sites in north Queensland; in one of these localities (Rex Lookout) both pollinator species occurred sympatrically in the same tree. This case would seem more likely to show habitat or geographical segregation of the pollinator species with an area of overlap, but further data are needed. Once again, there is no suggestion of significant intraspecific variation (forms) in the host fig (Dixon et al., 2001).
- (3) We also recorded one possible instance of the reverse situation a single wasp species (*P. macrocainus*) as the sole pollinator of two distinct fig species (*F. brachypoda & F. cerasicarpa*). In this instance the fig species are distinct but partially sympatric. While we cannot find any morphological differences between the wasps from *F. brachypoda & F. cerasicarpa*, they show nontrivial DNA divergence (Lopez-Vaamonde *et al.*, 2001). Further studies are needed but it is possible that the wasps represent two distinct but morphologically cryptic species.

Molecular studies of *Pleistodontes*, using nuclear and mitochondrial DNA sequences, suggest that two of the co-pollinator pairs – those from *F. obliqua* (Lopez-Vaamonde *et al.*, 2001) and *F. pleurocarpa* (Lopez-Vaamonde unpublished data) – may be sister taxa. The third co-pollinator pair, from *F. crassipes*, may also be sister species but further phylogenetic study is required to clarify these issues.

It is clear that figs and their pollinators have coevolved to a great extent, and that patterns of coadaptation can be seen when looking across different fig-pollinator species pairs (Kjellberg *et al.*, 2001). Our descriptions of the morphology of *Pleistodontes* females reveal that there is considerable variation between species (within this genus) in the presence and size of pollen pockets, as well as the presence or absence of coxal corbiculae (Table 2). Clearly it would be valuable to have corresponding data on fig syconium morphology and live wasp behaviour to explore the evolution of pollination mechanisms in the mutualism.

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APPENDIX

LIST OF CURRENTLY VALID AUSTRALIAN PLEISTODONTES SPECIES AND THEIR SYNONYMS

Pleistodontes froggatti Mayr, 1906 Pleistodontes semirucifeps Girault, 1929: 318 Pleistodontes listzi Girault. 1932: 2 svn. nov. Pleistodontes mayri Girault, 1939: 325 Pleistodontes imperialis – Froggatt, 1901: 447–451 Pleistodontes semiruficeps - Wiebes, 1963: 96; Wiebes, 1977a: 141 Pleistodontes semiruficeps – Dahms, 1986: 521 Pleistodontes semiruficeps - Boucek, 1988: 191 Pleistodontes listzi – Wiebes, 1977a: 139 Pleistodontes listzi – Dahms, 1984: 758–759 Pleistodontes listzi - Boucek, 1988: 192 Pleistodontes mayri – Wiebes, 1963: 307; Wiebes, 1977a: 139 Pleistodontes mayri - Dahms, 1984: 802 Pleistodontes mayri – Boucek, 1988: 191 Pleistodontes deuterus Lopez-Vaamonde, Dixon, Cook, Rasplus **sp. nov**. Pleistodontes regalis Grandi, 1952 stat. rev. Pleistodontes nitens- Boucek, 1988: 192 Pleistodontes nitens - Wiebes, 1990: 225 Pleistodontes nitens – Wiebes, 1991: 141–142 Pleistodontes nitens – Wiebes, 1994b: 27 Pleistodontes nitens (Girault, 1915a) Neoceratosolens nitens Girault, 1915b: 313 Pleistodontes achorus Lopez-Vaamonde, Dixon, Cook, Rasplus **sp. nov**. Pleistodontes nigriventris (Girault, 1915a) Agaon nigriventre Girault, 1915a: 44-45 Pleistodontes addicotti Wiebes, 1991 Pleistodontes schizodontus Lopez-Vaamonde, Dixon, Cook, Rasplus sp. nov. Pleistodontes rigisamos Wiebes, 1991 Pleistodontes cuneatus Wiebes, 1990 Pleistodontes proximus Wiebes, 1990

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Pleistodontes athysanus Lopez-Vaamonde, Dixon,	Pleistodontes nigris Girault – Wiebes, 1977a: 140
Cook, Rasplus sp. nov .	Pleistodontes nigris Girault – Dahms, 1986: 341
Pleistodontes proximus Wiebes, 1991: 151	Pleistodontes nigris Girault – Boucek, 1988: 192
Pleistodontes astrabocheilus Lopez-Vaamonde,	Pleistodontes macrocainus Lopez-Vaamonde,
Dixon, Cook, Rasplus sp. nov .	Dixon, Cook, Rasplus sp. nov .
Pleistodontes imperialis Saunders, 1883	Pleistodontes xanthocephalus Lopez-Vaamonde,
Pleistodontes nigricaput Girault, 1927: 337 syn.	Dixon, Cook, Rasplus sp. nov .
nov.	Pleistodontes greenwoodi (Grandi, 1928)
Pleistodontes nigris Girault, 1925: 2 syn. nov.	Blastophaga greenwoodi Grandi, 1928: 65–68
Pleistodontes greenwoodi, Grandi – Boucek, 1993:	Proceratosolens medionigra Girault, 1933: 3–4 syn.
205	nov.
Pleistodontes greenwoodi, Grandi – Boucek in Gib-	Blastophaga greenwoodi Grandi – Grandi, 1931: 8
son <i>et al.</i> , 1997: 121	Pleistodontes medioniger Girault – Hill, 1967a: 92
Pleistodontes nigricaput Girault – Wiebes, 1977a:	Pleistodontes medioniger Girault – Wiebes, 1977a:
140	139–140
Pleistodontes nigricaput Girault – Dahms, 1986:	Pleistodontes medioniger Girault – Dahms, 1984:
332–333	804-805
Pleistodontes nigricaput Girault – Boucek, 1988:	Pleistodontes medioniger Girault – Boucek, 1988:
192	192



Figures 1–8. Head (females). (1) *P. froggatti* dorsal view; (2) *P. froggatti* mandibles; (3) *P. deuterus* **sp. nov**. dorsal view; (4) *P. regalis* dorsal view; (5) *P. froggatti* clypeus; (6) *P. deuterus* **sp. nov**. clypeus; (7) *P. regalis* clypeus; (8) *P. regalis* mandibles. Scale bar = $200 \,\mu$ m (head) and $50 \,\mu$ m (clypeus and mandibles).



Figures 9–13. Antennae (females). (9) *P. rigisamos*; (10) *P. schizodontus*; (11) *P. froggatti*; (12) *P. deuterus* sp. nov.; (13) *P. regalis*.



Figures 14–22. (14) *P. regalis* pronotum anterior part; (15) *P. nitens* metasoma; (16) *P. addicotti* head; (17) *P. nitens* head; (18) *P. nigriventris* head; (19) *P. addicotti* mandibular appendages; (20) *P. nitens* mandibular appendages; (21) *P. nitens* mandibular appendages; (22) *P. nigriventris* mandibular appendages. Scale bar = $200 \mu m$, except 14 & $22 = 100 \mu m$.



Figures 23–28. (23) *P. nigriventris* clypeus; (24) *P. addicotti* clypeus; (25) *P. nitens* clypeus; (26) *P. addicotti* fore leg; (27) *P. froggatti* fore leg and detail of protarsus; (28) *P. deuterus* **sp. nov**. fore leg. Scale bar = $50 \mu m$ (clypeus) and $100 \mu m$ (legs).



Figures 29–34. Pollen pocket. (29) *P. froggatti*; (30) *P. regalis*; (31) *P. deuterus* sp. nov.; (32) *P. nigriventris*; (33) *P. addicotti*; (34) *P. nitens*. Scale bar = $50 \mu m$.



Figures 35–39. Antenna (females). (35) P. nigriventris; (36) P. addicotti; (37) P. nitens; (38) P. achorus sp. nov.; (39) P. achorus sp. nov. head.



Figures 40–45. Head (females). (40) *P. schizodontus*; (41) *P. rigisamos*; (42) *P. schizodontus* **sp. nov.** clypeus; (43) *P. rigisamos* clypeus; (44) *P. schizodontus* **sp. nov.** mandibles; (45) *P. rigisamos* mandibles. Scale bar = 100μ m.



Figures 46–52. (46) *P. schizodontus* **sp. nov.** pollen pocket; (47) *P. rigisamos* pollen pocket; (48) *P. schizodontus* **sp. nov.** tergites; (49) *P. cuneatus* clypeus; (50) *P. cuneatus* head; (51–52) *P. cuneatus* mandibles. Scale bar = 100μ m.



Figures 53–62. Head (females). (53) *P. imperialis* mandibles; (54) *P. macrocainus* **sp. nov**. mandibles; (55) *P. proximus* mandibles; (56) *P. astrabocheilus* **sp. nov**. mandibles; (57) *P. imperialis* head; (58) *P. macrocainus* **sp. nov**. head; (59) *P. astrabocheilus* **sp. nov**. head; (60) *P. athysanus* **sp. nov**. head; (61) *P. athysanus* **sp. nov**. mandibles and gena; (62) *P. proximus* head. Scale bar = 100 μm.



Figures 63–70. Antennae (females). (63) *P. astrabocheilus* sp. nov.; (64) *P. proximus*; (65) *P. imperialis*; (66) *P. macrocainus* sp. nov.; (67) *P. greenwoodi*; (68) *P. cuneatus*; (69) *P. xanthocephalus* sp. nov.; (70) *P. athysanus* sp. nov.



Figures 71–76. Head (females). (71) *P. proximus* gena; (72) *P. imperialis* clypeus; (73) *P. macrocainus* sp. nov. clypeus; (74) *P. astrabocheilus* sp. nov. clypeus; (75) *P. athysanus* sp. nov. clypeus; (76) *P. proximus* clypeus. Scale bar = 50 μm.



Figures 77–82. Head and mesosoma (females). (77) *P. macrocainus* sp. nov. vertex; (78) *P. cuneatus* pollen pocket; (79) *P. astrabocheilus* sp. nov. pollen pocket; (80) *P. macrocainus* sp. nov. pollen pocket; (81) *P. greenwoodi* pollen pocket; (82) *P. xanthocephalus* sp. nov. pollen pocket. Scale bar = 100 μm.



Figures 83–87. (83) *P. greenwoodi* head; (84) *P. greenwoodi* mandibles; (85) *P. xanthocephalus* **sp. nov**. head. Scale bar = 100μ m; (86) *P. greenwoodi* clypeus; (87) *P. xanthocephalus* **sp. nov**. clypeus. Scale bar = 50μ m.



Figures 88–91. (88) *P. macrocainus* **sp. nov**. (ex *F. brachypoda*) mandible; (89) *P. greenwoodi* mandible; (90) *P. greenwoodi* fore leg; (91) *P. xanthocephalus* **sp. nov**. fore leg. Scale bar = 50μ m.



Figures 92–93. Meso and metasoma (Males) (92) *P. deuterus* sp. nov.; (93) *P. regalis*. Pro = Propodeum; Mt1 = Metasomal segment 1.



Figure 94. Comparison of head shape between *P. athysanus* sp. nov. (Fig. 60) and *P. proximus* Wiebes (Fig. 62).