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Whiteflies of Belize (Hemiptera: Aleyrodidae). Part 1 — introduction and account of the subfamily Aleurodicinae Quaintance & Baker

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Table of contents

Abstract	4
Introduction	5
New World to Old — the relevance of the present study	6
Whitefly natural history and morphology — a synopsis	7
Specimen depositories	9
Materials and methods	9
Terminology and scope	. 10
Systematic studies of whiteflies in the Neotropical Region - a synopsis	. 11
Subfamily ALEURODICINAE Quaintance & Baker, 1913	. 12
Key to genera of Aleurodicinae in the Neotropical Region — puparia	. 14
Genera and species of Aleurodicinae present in Belize	. 18
ALEURODICUS Douglas	. 18
Key to Aleurodicus species in Belize — puparia	. 19
Aleurodicus araujoi Sampson & Drews	. 20
Aleurodicus coccolobae Quaintance & Baker	. 21
Aleurodicus dispersus Russell	. 21
Aleurodicus dugesii Cockerell	. 22
Aleurodicus inversus sp. nov	22
Aleurodicus magnificus Costa Lima	. 24
Aleurodicus maritimus Hempel	. 24
Aleurodicus niveus sp. nov.	. 25
Aleurodicus pauciporus sp. nov	. 26
Aleurodicus pulvinatus (Maskell)	. 28
Aleurodicus rugioperculatus sp. nov	. 29
Aleurodicus vinculus sp. nov	30
ALEURONUDUS Hempel	32
Aleuronudus acapulcensis (Sampson & Drews)	. 32
Aleuronudus manni (Baker) comb. nov	. 33
AZURALEURODICUS Martin	. 33
Azuraleurodicus pentarthrus Martin	. 33
CERALEURODICUS Hempel	. 34
Ceraleurodicus keris sp. nov	35
Ceraleurodicus varus (Bondar)	. 38

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7.H H H A X A	10ALEL/NUMULI/AUDEREIEU 19
	Dialeurodicus hondariae sp. nov. 40
(681)	Dialeurodicus cohalleroi sp. nov. 41
	Dialeurodicus silvestrii (Leonardi)
	<i>I FONARDIUS</i> Quaintance & Baker 44
	Leonardius kellvae sp. nov 45
	METALEURODICUS Quaintance & Baker 47
	Key to Metaleurodicus species in Belize — nunaria 47
	Metaleurodicus arcanus species in Denie pupular function of the second sec
	Metaleurodicus griseus (Dozier) 49
	Metaleurodicus tenuis sp. nov
	Metaleurodicus variporus sp. nov
	NEALEURODICUS Hempel
	Key to <i>Nealeurodicus</i> species in Belize — puparia
	Nealeurodicus altissimus (Quaintance) comb. nov
	Nealeurodicus bakeri (Bondar) comb. nov
	<i>Nealeurodicus fallax sp. nov.</i>
	Nealeurodicus petiolaris sp. nov
	PARALEYRODES Quaintance
	Paraleyrodes ancora sp. nov
	Paraleyrodes bondari Peracchi
	Paraleyrodes cervus sp. nov
	Paraleyrodes citricolus Costa Lima
	Paraleyrodes minei Iaccarino
	Paraleyrodes perplexus sp. nov
	Paraleyrodes proximus Terán
	Paraleyrodes triungulae sp. nov
	Acknowledgements
	References
	Appendix 1 — check list of the Aleyrodidae-Aleurodicinae of Belize
	Appendix 2 — host plants of the Aleyrodidae-Aleurodicinae in Belize
	Appendix 3 — summary of taxonomic changes proposed in this work
	Appendix 4 — guide to field collection and preparation of whiteflies for microscopic examination 84
	Illustrations

Abstract

A field survey of sternorrhynchous Hemiptera in Belize, principally conducted within the Chiquibul Forest Reserve, has revealed in excess of 180 species of whiteflies, over 40 of which belong to the subfamily Aleurodicinae. Provided here are a key to all the neotropical genera of Aleurodicinae, an illustrated account of all definable Belize species of Aleurodicinae, and a review of literature that is relevant to systematic studies of New World species in both whitefly subfamilies. Four appendices provide a check list of Belize members of the Aleurodicinae, a list of their known host plants in Belize, a list of nomenclatural changes proposed by this work, and a protocol for the field collection and subsequent laboratory preparation of whitefly specimens. As detailed in Appendix 3, this account proposes one revised subfamilial placement, three new generic synonymies, six new specific synonymies and 12 new combinations; 18 new species are here described.

Key words. Whiteflies, Aleurodicinae, Belize, neotropical, key to genera, check list, illustrations, slide-preparation, literature review, host plants

Introduction

Whiteflies comprise a single family, Aleyrodidae, within the Sternorrhyncha which is one of three suborders of the Hemiptera. If the numbers of described species are an accurate guide, then whiteflies are by far the least speciose of the four groups of sternorrhynchous Hemiptera, with around 1,500 currently valid species and subspecies names listed in the fully indexed collection-catalogue of The Natural History Museum, London (BMNH). This figure may be compared with over 7,300 Coccoidea (Miller & Ben Dov, 2003), over 4,800 Aphidoidea (Remaudière & Remaudière, 1997; Eastop, 1998), and over 2,500 Psylloidea (Martin & Hollis, 1992). However, the present author's tropical field collecting of whiteflies in Asia, Australia and Central America indicates that a particularly small proportion of whitefly species have yet been described (Martin, 1999; vouchers in BMNH collection) in comparison with the other groups of Sternorrhyncha.

The common name, "whiteflies", derives from the presence of powdery secretion which is preened over the bodies and wings of the adults of almost all species. Adult whiteflies are very small insects, most measuring 1–3 mm in body length. A structure known as the vasiform orifice (Fig. A, p.17) is unique to aleyrodids, and comprises the anus, a lingula for ejecting liquid excreta, and an operculum that partially or wholly covers the orifice itself. The vasiform orifice is present in all larval stages, as well as in the adults, providing a simple character for recognising whiteflies at any stage of their life cycle.

Whiteflies are divided into two extant subfamilies, Aleurodicinae and Aleyrodinae. The Aleurodicinae is the subject of this communication, accommodating less than ten percent of known whiteflies: only 102 aleurodicine species had been described prior to the current study, all of them tropical and subtropical in distribution. Notably, most members of the Aleurodicinae are native to the Neotropical Region, with only 12 described species being palaeotropical natives. The Aleurodicinae is generally thought to be the more primitive of the two whitefly subfamilies, and undoubtedly the greatest species radiation has occurred within the Aleyrodinae, which accommodates over 1300 currently valid species. Most aleurodicine whiteflies are somewhat larger than most aleyrodine species, but males of a remarkable (undescribed and generically uncertain) species from Nicaragua have extremely long abdomens and measure up to 10.50 mm from vertex to claspers (vouchers in BMNH). Most members of the Aleurodicinae also have a more complex wing venation than is seen in most aleyrodines, but in both subfamilies there are several notable exceptions to this general rule.

In recent years, whitefly pests have become an escalating problem for agriculturalists, almost worldwide. Although a mainly tropical insect group, injurious whitefly species are found in all warmer parts of the world, and several are also serious pests in glasshouses in temperate areas. Despite this, little funding has been made available for basic systematic studies that could assist early recognition of other species suddenly attaining pest status and this trend has continued, despite the increasing economic impact caused by previously unknown or obscure whitefly species becoming established in new geographical areas (see

5

zоотаха 681

New World to Old, below). Still more species are intercepted by quarantine services, and species mobility is no doubt greatly assisted by the phenomenon of worldwide mass air travel.

Intensive sampling of whiteflies in the Chiquibul Forest Reserve (CFR), Belize, (see **Materials and methods**) has provided the first opportunity to present a substantial synopsis of the Central American whitefly fauna. This includes, here, an account of all members of the Aleurodicinae found in Belize and, in a future contribution, a synoptic study of the Belize Aleyrodinae. In its two parts, it is a particularly timely study in view of species movements discussed in more detail below.

New World to Old — the relevance of the present study

Unknown whitefly species, newly appearing as agricultural pests, may require considerable investigation to determine even their broad geographical origins, because of our rudimentary knowledge of the tropical and subtropical whitefly faunas worldwide. Most new whitefly introductions in the past 30–40 years have been from the New World into the Old World, and reasons for the disproportionate number of movements in this direction remain obscure. Whatever these reasons may be, systematic whitefly studies in the New World therefore have particular practical relevance.

Over the past quarter-century particularly, several New World members of the Aleurodicinae have caused major problems for quarantine authorities and local agricultural communities, when they have arrived in Old World countries for the first time. Some new introductions have involved species that were completely unknown (undescribed) when first encountered in pest proportions in the Old World. *Lecanoideus floccissimus* Martin *et al.* (1997) became an established pest in the Canary Islands while it was still scientifically unknown, and Hernández-Suarez *et al.* (1997) presented a Spanish-language report on the agricultural and urban problems caused by this new pest. Similarly, *Paraleyrodes minei* Iaccarino (1990), often called the "nesting whitefly", caused moderate problems for growers of citrus and other crops in California, Syria and Spain, before eventually being formally described from the introduced population in Syria. Both of these species were, fortunately, immediately recognised as being of neotropical origin, and this recognition assisted confirmation that they were not already known to science, as well as indicating likely source areas for natural enemies.

In addition to *P. minei*, discussed above, four more *Paraleyrodes* species have become established beyond their native neotropics. *P. citricolus* Costa Lima appeared in Madeira in the early 1990s (Martin, 1996), and its presence on the Azores was confirmed in 2002. *P. pseudonaranjae* Martin (2001) was described from introduced populations in Hong Kong, Hawaii and Florida, having been misidentified as *P. naranjae* Dozier for several years. *P. perseae* (Quaintance) is now reported to be present on the Hawaiian Islands (Beardsley, 1970; Paulson & Kumashiro, 1985): however, the precise identity of *P. per-*

seae remains uncertain, through conflicting published accounts and poor representation in voucher collections (personal observations; see also discussion of *P. ancora*, p. 65). Amongst the most geographically mobile of the *Paraleyrodes* species have been *P. minei* and *P. bondari* Peracchi, both of them found in Belize, with their present geographical distributions given here in the relevant species accounts. *Aleurodicus dugesii* Cockerell and *Metaleurodicus cardini* (Back) have both become established in the Hawaiian islands, with *M. cardini* subsequently reported in Guam (Marianas group) in 2004. Voucher specimens from most of the introduced populations discussed above are present in the BMNH collection.

Probably the most notorious of all aleurodicines to have escaped the confines of the neotropics is *Aleurodicus dispersus* Russell (1965), the co-called "spiralling whitefly". *A. dispersus* is now virtually pan-tropical in distribution, and initially tends to cause a significant economic impact in each new area of introduction. Certainly *A. dispersus* has proved to be the most invasive member of the Aleurodicinae, to date, but readily responds to biological control regimes.

New World members of the Aleyrodinae have also become established in the Old World in recent decades, as will be discussed in a forthcoming account of the Aleyrodinae of Belize.

Whitefly natural history and morphology — a synopsis

The whitefly life-cycle is unusual. As with all Sternorrhyncha, first-instar whitefly larvae can walk short distances to locate suitable feeding sites. However, once the first moult has taken place, the remaining three immature stages are sessile and individuals are unable to relocate themselves if feeding conditions deteriorate. The final nymphal stage is usually termed a "puparium", even when still actively feeding. This term simply reflects the extreme morphological difference between this stage and the four-winged adult, whose emergence is later facilitated by the rupturing of lines of weakness (the "transverse and longitudinal moulting sutures", Fig. A, p. 17). The vacated puparium is often referred to as a "pupal case". A detailed account of whitefly biology and morphology was provided by Gill (1990). Mound (1961) published an account of his observations on the biology of *Aleurodicus capiangae* Bondar, based on work conducted in Trinidad, and this remains the only such account of aleurodicine biology.

The eggs of many species of Aleyrodinae are laid in partial or complete circles, as the ovipositing female rotates about her rostrum while continuing to feed. Other species, particularly members of the Aleurodicinae, lay their eggs in spirals as the female wanders over leaves, and some aleurodicines commonly oviposit on non-foliar surfaces, such as fruits. A very few whitefly species, in both subfamilies, habitually develop on the upper surfaces of leaves, whilst some others readily develop on both leaf surfaces. More rarely still, the immature stages of some species develop on the petioles or woody stems of their

hosts; only one such species has been encountered in Belize (see *Nealeurodicus petiolaris*, p. 59, Figs 129–130). Ant-attendance of immature whiteflies is much less common than amongst aphids and scale insects (personal observations).

The great majority of extant whiteflies colonise dicotyledonous angiosperm hosts (Mound & Halsey, 1978). Some members of the Aleyrodinae are specialist fern (Martin & Camus, 2001) or grass-feeders. Also, some members of both subfamilies colonise other monocotyledonous hosts, especially palms (Arecaceae) and members of the families Araceae, Musaceae, Orchidaceae, Smilacaceae and Zingiberaceae (Mound & Halsey, 1978). Whilst jumping plant lice and the great majority of aphids have clear host plant preferences, the lack of such clear preferences amongst many whiteflies is equally notable.

The systematics of the Aleyrodidae are currently based almost entirely on the morphology of the puparial stage, and adults found in isolation can be identified only rarely (but see discussion of *Paraleyrodes*, p. 61). There are a number of historical and practical reasons for this curious situation, as outlined by Martin (2003). Unfortunately for systematists, whitefly puparia are notorious for displaying variation induced by environmental factors, particularly the physical characteristics of leaf surfaces, as suggested by Russell (1948) and subsequently demonstrated experimentally by Mound (1963). The phenomenon of puparial variation has become particularly well known amongst certain polyphagous species, notably in the aleyrodine genera *Bemisia* and *Trialeurodes*. In contrast, however, puparia of the highly polyphagous *A. dispersus* (Aleurodicinae) display almost no variation. Indeed, the puparia of most aleurodicine species appear much less plastic than those of many of their aleyrodine counterparts — but see description and discussion of *Metaleurodicus variporus*, p. 51.

As well as displaying the variation discussed above, many whiteflies also exhibit puparial sexual dimorphism, which in the Aleyrodinae usually manifests itself as male puparia being consistently smaller than those of females in the same colony. In the Aleurodicinae, the antennae of male puparia of some species are distinctly longer than those of females (Figs 41–42). In species without antennal or body size dimorphism, sex-determination of individual puparia is usually not possible even though Russell (1948) reported a tiny invagination, or "bifid sac", to be present between the posterior abdominal spiracles of male puparia: this was discussed by Martin (1999).

A factor that greatly favours puparial taxonomy is that colonies of immature whiteflies are frequently discovered at times when associated adults are unavailable (their emergence being seasonal or correlated with other aspects of the physiology of their host plants). The seasonal unavailability of adults was a common feature of field work in Belize, as in other tropical environments.

The third-instar whitefly larva is sometimes mistaken for the puparium, and has been erroneously described as such by several authors in the past. The third-instar larval legs of Aleurodicinae are rather triangular, with their apices laterally directed towards the margin of the specimen (Fig. 39), in contrast to the much larger and distinctly two-segmented legs

in puparia (Figs 1–24). Also, longitudinal and transverse moulting sutures have not developed in the third-instar larva.



Specimen depositories

BMNH — The Natural History Museum, London, U.K.

BZ — Belize National Plant Protection Service, Central Farm, Cayo, Belize

CDFA — California Department of Agriculture, Sacramento, U.S.A.

FDA — Florida Department of Agriculture & Consumer Services, Gainesville, U.S.A.

MZUSP — Museu de Zoologia da Universidade de São Paulo, Brazil

UCD — R.M. Bohart Museum of Entomology, University of California, Davis, U.S.A.

USNM — US Department of Agriculture, Beltsville, Maryland, U.S.A. (custodians of the Sternorrhyncha collections of the United States National Museum of Natural History, Washington DC)

ZISP — Zoological Institute, St Petersburg, Russia

Materials and methods

This study is based upon the results of five field visits, about 20 weeks in total, to Las Cuevas Research Station (LCRS) in the Chiquibul Forest Reserve (CFR), Cayo District, Belize. LCRS is a joint facility of BMNH and the Belize Forest Department, and is located at approximately 16° 43' N, 88° 58' W, 45 km south of the San Ignacio / Santa Elena conurbation. LCRS is located centrally within the Maya Mountains, an area of over half a million hectares of forested upland, approximately 400-1100 metres above sea level. The field station itself is located in a shallow hollow at approximately 600 metres altitude, in the centre of an extensive area of dense, closed-canopy secondary broadleaf forest. The forest extends towards the highest parts of the Maya Mountains to the south-east, the Guatemalan border to the west, and an east-west loop of the Macal River 13 km to the north. North of the Macal River the vegetation type changes abruptly, becoming a much drier, shrubby understorey amid expanses of Caribbean pine, rising towards a plateau known as Mountain Pine Ridge. Most sampling work was carried out in the broadleaf forest, south of the Macal River. Although the great majority of the study samples were obtained within the CFR, small numbers of samples from elsewhere in Belize have also been included in the study, to provide a preliminary account of whiteflies in the country as a whole.

Whenever practicable, leaves bearing puparia were transferred to the laboratory to await the emergence of adult whiteflies and/or hymenopterous parasitoids. Adult whiteflies, parasitoids, and some whitefly puparia and larvae were preserved in alcohol prior to return to the U.K., with the remainder of the puparia and larvae preserved dry, *in situ* on leaf tissue. Dry preservation allows any waxy secretions, as well as behavioural character-istics such as aggregation or close association with particular leaf veins, to be preserved —

information that is usually lost when specimens are selected for liquid storage. For details of preservation of material, see Appendix 4, p. 84.

Syntype slides of several species, not represented in the BMNH collection, were borrowed from collections as detailed in in **Acknowledgements**, p. 70. In some cases (particularly slides of Bondar, Hempel and Sampson & Drews species) the mountant had badly deteriorated, making examination extremely difficult. Although remounting would probably improve the material on many such slides, the custodians of these slides were understandably reluctant to take this risk. However, with perseverance much invaluable information was obtained from these slides, as is here detailed in the accounts of several genera and species.

Host plant genera and family names follow the system of Balick *et al.* (2000). Full identification of host plant voucher specimens often relies upon the presence of flowers or fruits, which are frequently not present on vegetation that is accessible from the ground. Inevitably, therefore, host data has been unavailable for many samples, and is incomplete for others. Where herbarium vouchers were preserved for this study, they reside in the Botany or Entomology Departments of BMNH.

Terminology and scope

Puparial descriptions and discussions presented here follow the terminology detailed by Russell (1965), Martin (1987) and Gill (1990), with some characters unique to the Aleurodicinae following Iaccarino (1990) and Quaintance & Baker (1913). Figure A (p. 17) depicts a typical aleurodicine puparium, *Aleurodicus pulvinatus* (Maskell), specially annotated to illustrate this terminology (modified after Martin & Watson, 1998).

The generic and species definitions within the Aleurodicinae have been reappraised as far as possible, with syntype material of several Hempel and Bondar species examined for the first time for many years. Based on conclusions thus reached, a key is provided to puparia of all neotropical aleurodicine genera. The generic key is supported by illustrations of puparia of most genera, including those not so far discovered in Belize.

As complete an account as possible of the Belize members of the Aleurodicinae is provided here. With the exception of some members of *Paraleyrodes* (q.v.), all new aleurodicine taxa revealed by the study are here described. Again excepting *Paraleyrodes*, where adult males are often needed for authoritative identification, new species descriptions here are mostly limited to the puparial stage. Other stages, available for future study, are listed in each new species account and some adult features are discussed under COMMENTS for previously described species.

Distributions of individual species, given in the accounts below, are mainly based upon Mound & Halsey (1978) and the BMNH collection. No detailed searches for other published distribution records have been carried out.

Systematic studies of whiteflies in the Neotropical Region — a synopsis

Systematic studies of whiteflies in this geographical region, which comprises South and Central America and the Caribbean islands, suffer from a paucity of published work when compared with what is available for other groups of Sternorrhyncha. This brief review covers the Aleyrodidae as a whole, with many papers being of relevance to studies of both subfamilies. It is intended that this overview of systematic literature may materially aid future systematic studies of whiteflies in this region.

Larger works, dealing with moderate numbers of taxa, were published on the Brazilian fauna by Hempel (1922a,b), Bondar (1923a, 1928) and Costa Lima (1928); and on the Mexican fauna by Baker (1937) and Sampson & Drews (1941). Several significant papers were also published by Louise Russell, mostly dealing with particular neotropical aleyrodine genera or species assemblages, particularly *Bellitudo* (1943), *Aleuroglandulus* (1944), *Crenidorsum* (1945), *Aleuroparadoxus* (1947), *Venezaleurodes* (1967), *Aleurocerus* (1986), *Disiphon* (1993) and *Paraleurolobus* (1994), but also the aleurodicine species *Aleurodicus dispersus* and its close allies (1965). A key to the Caribbean species of *Aleurodicus* was given by Martin & Watson (1998). Nakahara (1995) presented an account of *Tetraleurodes* species (Aleyrodinae), with key, based primarily on the U.S.A. and Central America: several of the species treated by Nakahara are now known to occur in Belize. A major work by Quaintance & Baker, in three parts (1913, 1914 & 1917), included a number of neotropical species decriptions as part of an overview of world whiteflies, based on the holdings of what is now the USNM collection.

There are a number of smaller works in which new taxa were described from the Neotropical Region, some of which are listed here:—

Argentina — Leonardi (1910) — 1 new species; Tapia (1970) — 1 new genus and species; Terán (1979) — 2 new species.

Brazil — Bondar (1923b) — 1 new species; Bondar (1931) — 1 new species, and adult *Paraleyrodes* characters discussed; Costa Lima (1942) — 5 new species of *Aleurothrixus*; Goeldi (1886) — 3 new species; Hempel — several minor papers between 1899 & 1938 — see bibliography of Mound & Halsey (1978); Laing (1930) — 1 new species; Penny & Arias (1980a, 1980b) — 3 new species; Peracchi (1971) — 1 new species.

Chile — Baker & Moles (1921) — 4 new species, and a synopsis of the South American fauna.

Cuba — Back (1912) — 2 new species and synopsis.

Guyana — Quaintance & Baker (1915) — 1 new genus and species.

Honduras — Baker (1923) — 1 new species.

Jamaica — Maskell (1896) — 2 new species.

Mexico — Leonardi (1910) — 1 new species; Maskell (1896) — 2 new species; Sampson (1944) — 3 new species.

Puerto Rico — Dozier (1927) — 1 new species; Dozier (1936) — 2 new species. Trinidad — Maskell (1896) — 1 new species. $\overline{681}$

With a number of Central American species also being found in the southern U.S.A., papers dealing with North American whiteflies are also of relevance. Quaintance, and Quaintance & Baker, published several papers between 1899 and 1917, some of them dealing with new species from around the Americas, including the U.S.A.; additionally, between 1893 and 1911 Cockerell published a number of short bulletins on whiteflies from Mexico and U.S.A. — see the bibliography of Mound & Halsey (1978). Russell also published on the whitefly fauna of U.S.A. (these references were listed in Mound & Halsey, 1978), while Bemis (1904) provided an early account of the whiteflies of California. Drews & Sampson (1958) described several Californian species of *Aleuropleurocelus* (Aleyrodinae), a genus found in Belize. Hamon published several individual pest introduction bulletins for Florida, including one Caribbean species of Aleurodicinae (Hamon, 1989).

Recent check lists, or accounts without descriptions of new species, have been published for Bermuda (Nakahara & Hilburn, 1989) and California (Gill, undated), Central America and Colombia (Caballero, 1992, 1994), Nicaragua (Maes & Mound, 1993), Peru (Valencia, 2000) and Venezuela (Arnal *et al.*, 1993, 2000). Hilje & Arboleda (1993) edited a compilation of reports on whiteflies in Central America and the Dominican Republic, predominantly dealing with economic species, their host plants and crop damage, but a contribution by Caballero included more general species listings based upon his (1992) thesis account.

Prior to the present study, there appear to have been only two whitefly species described from Belize — *Aleuroparadoxus sapotae* Russell (1947) (Aleyrodinae), where "British Honduras" was later mistakenly quoted as Honduras by Mound & Halsey (1978), and *Azuraleurodicus pentarthrus* Martin (in Martin & Polaszek, 1999) (Aleurodicinae). Despite historical links between Belize and Britain, whitefly material from Belize was almost unrepresented in BMNH prior to this survey.

Subfamily ALEURODICINAE Quaintance & Baker, 1913: 25

DIAGNOSIS. Puparia of all New World species with at least two of the following three characters, most having all three (see Fig. A, p. 17): lingula large, usually tongue-shaped, bearing 4 stout setae; each puparial leg with an apical claw; puparia bearing compound pores on the dorsum, usually in pairs but sometimes on one side of puparium only.

COMMENTS. Aleurodicinae is the generally accepted name for this smaller of the two extant whitefly subfamilies. An older name, Udamoselinae Enderlein (1909) was regarded as *nomen dubium* by Mound & Halsey (1978), through a combination of loss of the sole original (adult) specimen and inadequacy of its description. The history of Aleurodicinae *versus* Udamoselinae was discussed in detail by Martin & Streito (2003). Shcherbakov (2000) has proposed a further new subfamily, Bernainae, for the most primitive known whiteflies, from the fossil record in Asia. There is a misconception amongst some workers, that the genera of Aleurodicinae are better defined than are many of those within the Aleyrodinae. Examination of the generic and species synonymies within the Aleurodicinae (Mound & Halsey, 1978) reveals that redefinition of a number of genera and species combinations has occurred several times, and the situation is not stable. A particular example is *Nealeurodicus altissimus* (Quaintance), *q.v.*, p. 55.

Some nomenclatural problems have arisen because Hempel and Bondar were effectively working in parallel during the 1920s, probably with a degree of rivalry, independently describing new whitefly species from Brazil. Quite apart from inevitable species synonymies, this resulted in several genera being described twice, and even resulted in the two workers each publishing a different new genus name for the same type species within the space of one year (see synonymy of *Aleuronudus*, p. 32). Costa Lima began publishing on whiteflies towards the end of the 1920s, by which time Hempel and Bondar had almost completed their own whitefly descriptive work. Although Costa Lima sought to remedy synonymies he discovered, he gave little or no explanation for his decisions, which cannot always be easily reappraised. However, through the kind loan of original material by MZUSP, the placement of *Quaintancius* Bondar (1922) as a junior synonym of *Octaleurodicus* Hempel (1922a) by Costa Lima (1928), through synonymy of the type species, is here confirmed; some other decisions of Costa Lima are commented on under generic and species accounts, below. Costa Lima's illustrations (see Fig. 73) were a great improvement on those provided by Bondar and, very rarely, by Hempel.

Whilst a few genera, including *Paraleyrodes* and *Azuraleurodicus*, are well defined by both puparial and adult characters, it is the fact that adults of so many species remain unknown that still renders the definition of many other genera difficult. An extreme example is provided by the adults of some species, accommodated within one genus, having differing numbers of abdominal wax plates: this character was thought to be of fundamental generic importance, but a recent discovery revealed that the two known species of *Stenaleyrodes* (a palaeotropical member of the Aleurodicinae) have females with differing numbers of abdominal wax plates (Martin & Streito, 2003). It is almost certain that studying adults of a larger proportion of aleurodicine species will assist in elucidating the most important generic puparial characters, but much rearing work will be required to achieve this goal. For each genus treated here, its current interpretation by the present author is briefly stated.

As part of the Belize study, the genus *Septaleurodicus* Sampson (1943) is clearly of relevance because it was erected for a single new species, *S. mexicanus*, from neighbouring Mexico. Its description was based upon only adults. An attempt to locate original material for this study was unsuccessful, but the author considers *Septaleurodicus mexicanus* Sampson to be a member of the Aleyrodinae (**new placement**) for the following reasons. Sampson (1943) described this new genus, and he re-published the identical description in 1944, still flagged as "new genus" and "new species", but with the addition

zоотаха 681

of illustrations. Scrutiny of the description and illustrations reveals nothing to indicate that this insect belongs to the Aleurodicinae. Features that could have indicated placement in the Aleurodicinae (for example wax plate distribution; tarsal paronychium being spine-like) are not mentioned at all, nor illustrated. It is not clear why Sampson concluded that he had adults of an aleurodicine whitefly in front of him. Just as this paper went to press, syntypic slides of *S. mexicanus* were located, and examination of the very poor specimens on six slides has confirmed that this is a member of the Aleyrodinae (Raymond Gill, pers. comm.).

Perusal of the list of recorded host plants for Aleurodicinae in Belize (Appendix 2, p. 78), reveals that a high proportion of the aleurodicine whitefly species have been recorded from hosts belonging to more than one plant family. This tendency to exhibit oligophagy or polyphagy is a major reason for the impact of aleurodicine whiteflies when they become established in new geographical areas (see **New World to Old**, p. 6). Each of the aleurodicine species now established beyond its native neotropics shows a degree of polyphagy, probably reflecting the situation in its area of original occurrence. Until very recently, no member of the subfamily Aleurodicinae was thought to develop on a poaceous host, but the recent discovery of *Paraleyrodes minei* developing on a grass has obliged even this assumption to change (see p. 67).

Key to genera of Aleurodicinae in the Neotropical Region — puparia

- This key includes all New World aleurodicine genera, as understood by the present author. Genera that have been discovered in **Belize** are indicated in **bold italics**, the others in *italics* only.
- Quoted counts of submarginal setae include the nominal caudal pair, but not the anterior and posterior marginal setae.
- Submedian cephalothoracic setae are usually obvious, but they are sometimes very small.

- Cephalic pair, and 5 abdominal pairs of compound pores present, all subequal in size (40–65 µm in outer diameter), the abdominals evenly spaced on segments III–VII (Figs 16, 65); compound pores each with a protruding, dagger-shaped axial process. Submargin with large double-rimmed and 8-shaped pores..... *Azuraleurodicus* (p. 33)
- 3. Abdominal compound pores distributed in a smooth arc, almost concentric with curve

	of puparial margin, with at least posteriormost 4 pairs evenly spaced (Figs 25–32)
	Abdominal compound pores not all distributed in a smooth arc, at least 1 of the poste-
	riormost 4 pairs inset or offset; spacing between the abdominal compound pores not
	even (Figs 13, 14) Aleuronudus (p. 32)
4.	Thoracic submedian setae absent (Fig. 119). Cephalic and posterior 4 pairs of abdomi-
	nal compound pores larger than anterior abdominal pairs. With 14 pairs of submar-
	ginal setae Paraleyrodes (p. 61)
	Thoracic submedian setae present in 2 or 3 pairs (Figs 63, 68, 71, 79), cephalic pair
	present or absent. Large and small compound pores present in a different combination.
	Usually with 12, 13 or 15 pairs of submarginal setae
5.	Compound pores absent (Figs 21-23). Lingula completely included within vasiform
	orificeDialeurodicus (p. 39)
	Compound pores present, usually paired on either side of body. Lingula included
	within vasiform orifice, or variably extending beyond its boundary
6.	Paired ovoid granular areas, termed agglomerate pores, present; 1 cephalic pair and 6
	abdominal pairs (Figs 24, 91-92). Compound pores comprising a pair on each of
	abdominal segments III & IV, and sometimes also a cephalic pair, each situated within
	a larger agglomerate pore area (Figs 24, 91) <i>Leonardius</i> (p. 44)
	Agglomerate pores absent
7.	Vasiform orifice transversely elliptical and slightly elevated; lingula folded into vasi-
	form orifice and its detail not visible. A single compound pore present on one side of
	abdominal segment III; a pair of compound pores present on abdominal segment VIII,
	each possessing a seta-like axial process long enough to reach puparial margin. With
	13 pairs of submarginal setae Eudialeurodicus Quaintance & Baker, 1915
	If vasiform orifice wider than long, then lingula extending beyond orifice boundary,
	always clearly visible, bearing 4 distinct setae. Usually with at least one cephalic com-
	pound pore present. When compound pores present on abdominal segment VIII, then
	axial processes often not evident; if present, each axial process never more than twice
	pore diameter in total length. Usually with 12, or more than 13, pairs of submarginal setae
8.	Paired compound pores present on each of abdominal segments III-VI, describing an
	arc concentric with curvature of puparial margin on each side of body (Figs A, 1-12,
	15, 63, 68), these pores similar in size to the cephalic pair. With 12 pairs of submar-
	ginal setae9
	If cephalic compound pores present, paired, and similar in size to those on abdominal
	segments III-VI, then puparium with 15 pairs of submarginal setae11
9.	Cephalic pair and 6 abdominal pairs of compound pores all subequal in size, the
	abdominal pairs describing an even arc on each side of segments III-VIII (Fig. 15)
	Austroaleurodicus Tapia, 1970

- $\overline{681}$
- Cephalic pair of compound pores of similar size to the 4 pairs forming an arc on each side of abdominal segments III–VI; if present, an additional 1 or 2 pairs are much smaller, situated on abdominal segments VII and/or VIII (Figs A, 5–12, 66, 68, 70, 75)

- 10. If very small compound pores present, then located on segment VIII only (Fig. 68a). Submargin with a broad band of crowded simple pores of only the wide-rimmed type present (Fig. 68). On slide-mounted specimens, axial processes of large compound pores on abdominal segments III–VI usually all directed posteromesad; puparial margin is usually substantially deflexed *Lecanoideus* Quaintance & Baker, 1913

Areuroucus (p. 18

- -. Asymmetry (when evident) often affecting compound pore distribution as well as puparial outline (Fig. 17–20, 114). Provision of compound pores very variable, but almost always with at least one cephalic pore and one pore present posterior to vasi-

form orifice (Figs 67c, 83, 114); if compound pores present on each of abdominal seg-
ments III-VI then these not submedially situated and longitudinally aligned
Ceraleurodicus (p. 34)



Figure A. Aleurodicus pulvinatus (Maskell) — dorsal detail of puparium, annotated with anatomical terminology used in descriptions and keys.

ZOOTAXA

(681)

Genera and species of Aleurodicinae present in Belize

ALEURODICUS Douglas

ZOOTAXA

681

Aleurodicus Douglas, 1892: 32. Type species *Aleurodicus anonae* Morgan, 1892: 32, by subsequent designation by Quaintance, 1908: 8. [Synonymised with *A. cocois* (Curtis, 1846: 284–285) by Mound & Halsey, 1978: 228.]

DIAGNOSIS AND COMMENTS. As interpreted here, *Aleurodicus* comprises species with the following combination of characters: 4 pairs of large subdorsal abdominal compound pores, evenly spaced and usually each with an axial process extending well beyond the pore mouth, the anteriormost pair located on segment III (but lateral to median part of segment II, see Fig. A); most species also additionally with one or two much smaller abdominal pairs posterior to the other four; two pairs of cicatrices present on thoracic area (scars of third-instar compound pores, fig. A); 12 pairs of submarginal setae present (including the nominal caudal pair); submedian cephalothoracic setae present — some species with cephalic and three thoracic pairs, all similar to submarginal setae, others with cephalic pair wanting, and the *dispersus / flavus / coccolobae* assemblage possess only meso- and metathoracic pairs of submedian setae which are also much smaller than submarginal setae; submargin and/or dorsal disc usually punctuated by pores of several types; lingula always protrudes beyond vasiform orifice, its four subapical setae on the protruding part.

Species with the above characters, but whose puparial margins are usually substantially deflexed, the submargin punctuated by a broad band of crowded simple pores of only the wide-rimmed type (Fig. 68), and whose compound pore axial processes are usually directed mesally when slide-mounted, are currently placed in the genus *Lecanoideus* Quaintance & Baker, but a separate genus may not be justified (Martin & Watson, 1998). No member of the *Lecanoideus* assemblage has yet been seen in Belize, but *Aleurodicus inversus* (here described from Belize) is somewhat intermediate in form. However, Caballero (1992) recorded *L. giganteus* (Quaintance & Baker), the type species of *Lecanoideus*, from nearby Honduras and *L. mirabilis* (Cockerell) was described from Mexico, which borders Belize.

Quaintance & Baker (1913) distinguished *Lecanoideus mirabilis* from *L. giganteus* through the shape of the puparia, and the relative positions of the cephalic compound pores. The highly variable degree of marginal deflexion when members of this group are slide-mounted affects the puparial outline and, hence, the perceived distance of compound pores from the apparent puparial margin. Examination of type material of both species (USNM) revealed no differences considered to be of specific significance (Steve Nakahara, pers. comm.), and *L. giganteus* (Quaintance & Baker, 1913) is therefore here regarded as a junior synonym of *L. mirabilis* (Cockerell, 1898) **syn. n.**

With the revised generic definitions proposed here, *Aleurodicus bondari* Costa Lima (1928), known from Brazil and Colombia, is here transferred to *Aleuronudus* **comb. nov.**

Key to Aleurodicus species in Belize — puparia

zootaxa 681

• Note that the pair of posterior abdominal spiracles (ventral) can be mistaken for small post-vasiform orifice compound pores (dorsal). Figure 3 is a good example, being without any small compound pores, but with the spiracles clearly visible in a similar position.

1	A pair of small compound pores present on each of abdominal segments VII & VIII (Figs A, 1, 6–12, 64, 69–70, 73, 75)
-	Without small compound pores on abdominal segments VII & VIII (Figs 2–3, 55, 63)
2	Submarginal pore band continuous posterior to vasiform orifice, but such pores absent
	from median part of abdominal segment VII between pockets and segment VI/VII
	division (Fig. 63)dispersus Russell
-	Submarginal pore band interrupted posterior to lingula (Figs 2, 55), but a few such
	pores present on median part of abdominal segment VII between pockets and segment
	VI/VII division
3	Outer submargin with a very distinct, mostly-regular, row of 8-shaped pores, each less
	than a pore-length from its adjacent neighbours (Fig. 11). Dorsal disc with transverse
	"chains" of septate pores across most segments (Fig. 79) vinculus sp. nov.
-	Outer submargin may possess double-rimmed pores (Figs 69-70, 72-74), but these are
	less robust and, hence, less distinct at lower magnifications. Dorsal disc without sep-
	tate pores in distinct transverse "chains"
4	Double-rimmed pores (Figs 70, 72, 74) present in submargin, and sometimes also
	subdorsum5
-	Double-rimmed pores absent
5	Septate double-rimmed pores present in subdorsum, mesal to abdominal compound
	pores, as well as in submargin (Figs 5, 72) inversus sp. nov.
-	Double-rimmed pores, with or without septa, present only in submargin
6	Double-rimmed pores septate and exceptionally large (Fig. 7), each 30–35 μm long,
	unevenly spaced and aligned, and particularly irregular on cephalothorax (Fig. 74, to
	left). Dorsal disc septate pores also unusually large, each up to 15 μ m long (Fig. 74, to
	right). Lingula tongue-shaped and usually overlapping puparial margin in slide-
	mounted specimens (Fig. 7) maritimus Hempel
-	Double-rimmed pores each usually less than 25 μm long, often more evenly spaced
	and aligned. Dorsal disc septate pores each much smaller than 15 µm. Lingula may or
	may not overlap puparial margin
7	Anterior 4 pairs of abdominal compound pores exceptionally large, each up to 80 µm
	in diameter (Fig. 6). Double-rimmed pores septate and situated within a narrow sub-
	marginal band of crowded wide-rimmed pores (Fig. 73). Lingula narrowly acuminate
	magnificus Costa Lima

-	Anterior 4 pairs of abdominal compound pores much smaller, not attaining 50 µm in
	diameter. Double-rimmed pores not enclosed within a crowded submarginal band of
	wide-rimmed pores. Lingula apically rounded or slightly truncate
8	A cluster of bright pores present on each side of abdominal segment VII, anterior to
	small compound pores (Fig. 69). Double-rimmed pores septate and numerous, set
	close to puparial margin (Figs 1, 69); submargin with only sparse wide-rimmed pores
	(Fig. 69). Lingula slightly truncate apically, not overlapping puparial margin
	araujoi Sampson & Drews
-	Without a cluster of bright pores on each side of abdominal segment VII. Double-
	rimmed pores not septate, each with only a faint notch in inner rim, sparse, poorly
	defined and widely spaced, most alternating with submarginal setal bases, lining mesal
	boundary of submarginal band of crowded wide-rimmed pores (Fig. 70). Lingula
	tongue-shaped, usually overlapping puparial margin in slide-mounted specimens (Fig. 4)
9	A submarginal band of crowded wide-rimmed pores present, its mesal boundary
	extending at least half-way towards compound pores (Figs 8, 10, 12, 64, 66, 77–78)
-	Without a submarginal band of crowded wide-rimmed pores; dorsal pores all minute
	and very sparse, a few bright pores loosely clustered in vicinity of compound pores
	(Fig. 75) pauciporus sp. nov.
10	Lingula rounded apically (Figs A, 10, 64). Operculum surface finely spinulose but oth-
	erwise smooth pulvinatus (Maskell)
-	Lingula acute apically (Figs 8, 12, 58, 66). Operculum surface distinctly rugose or cor-
	rugate (Figs 58, 66) 11
11	Inner boundary of submarginal zone of wide-rimmed pores forming mesally-directed
	lobes (Fig. 12), the pore band interrupted immediately posterior to lingular apex
	rugioperculatus sp. nov.
-	Inner boundary of submarginal pore band concentric with curvature of puparial mar-
	gin, not lobulate, the band not interrupted posterior to vasiform orifice (Figs 8, 66)

Aleurodicus araujoi Sampson & Drews

(Figs 1, 69)

ZOOTAXA

(681)

Aleurodicus araujoi Sampson & Drews, 1941: 145-147. Syntypes, Mexico [examined].

DISTRIBUTION. Neotropical Region — Belize, Mexico.

COMMENTS. Numerous samples of Belizean material of *A. araujoi* have been identified in comparison with syntypic material loaned by UCD. In the CFR, this is one of the most common *Aleurodicus* species.

niveus sp. nov.

Aleurodicus coccolobae Quaintance & Baker

(Figs 2, 55)

Aleurodicus coccolobae Quaintance & Baker, 1913: 46-47. Syntypes, Mexico.

DISTRIBUTION. Neotropical Region — Belize, Brazil, Costa Rica, Honduras, Mexico, Panamá.

COMMENTS. A. coccolobae is one of three species that form a natural grouping within *Aleurodicus*, their puparia lacking the more usual pair of small compound pores on each of abdominal segments VII & VIII, and with particularly dense provision of dorsal disc pores of four types. This small group was discussed in detail as part of the description of *A. dispersus* Russell (1965).

Aleurodicus dispersus Russell

(Figs 3, 63, 123)

Aleurodicus dispersus Russell, 1965: 49-54. Holotype, Florida [paratypes examined].

DISTRIBUTION. Neotropical Region — widely distributed; Nearctic Region — Florida; Palaearctic Region — Canary Islands, Madeira; Ethiopian Region — Cameroun, Congo, Benin, Ghana, Nigeria, Sao Tomé, Togo; Malagasian Region — Mauritius; Oriental Region — India, Maldives, Sri Lanka, Thailand; Austro-oriental and Pacific Regions widely distributed; Australia — northern Queensland.

COMMENTS. A. dispersus is one of only two known Aleurodicus species that possess only 4 pairs of abdominal compound pores, in total, on the puparium. A third member of the same small assemblage (A. flavus Hempel) has additionally just one pair of tiny compound pores, situated on abdominal segment VII, otherwise strongly resembling A. dispersus.

A. dispersus was particularly unusual in remaining undescribed for many years, despite the accumulation of numerous samples in the USNM collection, most of them interceptions at United States port quarantine facilities; yet it is now the best-known of all *Aleurodicus* species. It is probable that *A. dispersus* (the so-called "spiralling whitefly") is native to the Caribbean and northern South America. Although many of the paratypes are from these native areas, Russell chose a sample from Florida from which to select the holotype. This curious technicality qualifies *A.dispersus* as one of several neotropical whiteflies to have been described from material sampled in an area of probable introduction. This choice of holotype may have been the result of most other specimens, then available to Russell, being isolated quarantine interceptions with imprecise originating locality data. Since its description, the spiralling whitefly has become almost pan-tropical in its distribution, its rapid radiation having begun in the 1980s (Martin & Lucas, 1984; Martin 1990).

ZOOTAXA

681

Aleurodicus dugesii Cockerell

(Figs 4, 70)

ZOOTAXA

681

Aleurodicus dugesii Cockerell, 1896: 302. Syntypes, Mexico [examined]. *Aleurodicus poriferus* Sampson & Drews, 1941: 149. Syntypes, Mexico [examined]. **Syn. nov.**

DISTRIBUTION. Neotropical Region — Belize, Guatemala, Mexico, Nicaragua, Venezuela; Nearctic Region — Arizona, California, Florida, Louisiana, Texas; Pacific Region — Hawaii.

COMMENTS. A. dugesii has recently gained similar notoriety to A. dispersus although not yet increasing its range as extensively. It causes direct feeding damage to crops, and also cosmetic problems on ornamental plants through the unsightly appearance of its own woolly-waxy secretions, its excreted honeydew and the sooty mould that grows on the honeydew. Although described from Mexico, and almost certainly a native of Central America, it is the recent movement of this species into the southern states of the U.S.A. and Hawaii that has raised its profile, provided it with a vernacular name, "giant whitefly", and gained it much coverage in contempory Internet reports.

Sampson & Drews (1941) stated that their new species, *A. poriferus*, differed from *A. dugesii* in two characters. Firstly, the puparia of *A. poriferus* were stated to have "simple pores scattered over the dorsum". Examination of two syntypes of *A. poriferus* (UCD), marked "holotype" and "paratype" (but such status not mentioned in the description), revealed septate pores scattered over the dorsal disc, with a band of crowded wide-rimmed pores occupying the submargin, the submarginal band's mesal boundary lined by poorly-defined double-rimmed pores (Fig. 70), exactly as also seen in Cockerell's type-locality (probably syntypic) material of *A. dugesii* in BMNH. Secondly, the large compound pores of *A. poriferus* were stated each to have an axial "long process" (Fig. 70) which is, in fact, a character also clearly seen in many specimens of the Cockerell material. It is clear that *A. poriferus* should be regarded as a junior synonym of *A. dugesii* syn. nov.

Aleurodicus inversus sp. nov. (Figs 5, 59, 71–72)

PUPARIUM. *Habitus*. puparial dorsum densely covered by curls of waxy secretion (which are similar to, but less distinctive than, those seen in *A. dispersus*, fig. 123), with a long, glassy filament secreted from each of the ten large compound pores and emerging through the denser wax. *Margin*. Outline 1.05–1.16 mm long, 0.65–0.77 mm wide, generally widest at abdominal segment II/III (n=17). Margin smooth but often downcurled or slightly deflexed, not modified opposite tracheal openings. *Dorsum*. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures only distinct submedially. Abdomi-

nal segment VII so reduced medially as to be difficult to discern. Vasiform orifice (Fig. 59) rounded-cordate; operculum trapezoidal, its posterior margin very shallowly "m"-shaped, bearing a pair of stout setae; lingula head tongue-shaped, densely covered by seta-like spinules, bearing the normal 4 stout setae; lingula slightly overlapping posterior puparial margin in all but the most flattened of slide-mounted specimens. Chaetotaxy. Anterior marginal setae not evident. A pair of posterior marginal setae, single pairs of submedian cephalic, pro-, meso- and metathoracic (Fig. 71), and eighth abdominal setae present, all long and hair-like; submargin with 12 pairs of similar setae (including the nominal caudal pair), the anteriormost pair inset to near cephalic submedian pair (Fig. 71). Pores. Cephalic compound pores 30-35 µm in outer diameter, abdominal compound pores often slightly decreasing in diameter from 1st pair (up to 50 µm) to 4th pair (40 µm), with 5th and 6th pairs only 10-18 µm. Axial processes of large compound pores, when present, rather short, dagger-shaped and variably curved apically (Figs 5, 72). Immediately within puparial margin lies a single row of small wide-rimmed simple pores (Fig. 72a), each pore sometimes appearing shallowly "w"-shaped if seen in lateral aspect, situated only about a pore-diameter from its neighbours and separated from each neighbour by a short cuticular fold perpendicular to puparial margin (Fig. 72a); remainder of submargin and whole of subdorsal zone densely punctuated by slightly larger wide-rimmed simple pores, this zone encompassing the large abdominal compound pores, and the zone's inner boundary developed into mesally-directed lobes that stand slightly proud of the remainder of the dorsal disc (Figs 5, 72). Large septate double-rimmed pores, up to 18 µm in diameter, present in an uneven submarginal row, with one or two also situated mesal to each large abdominal compound pore and between 4th abdominal pair of (large) compound pores and the (small) 5th and 6th abdominal compound pores (Fig. 59). Submedian area only sparsely provided with (smaller) septate pores and minute bright pores (Fig. 72, to right), these only inconsistently paired on either side of body; submedian pores usually absent from metathorax and abdominal segments I & II. Venter. Ventral abdominal setae similar to dorsal setae, their bases close-set, situated mesal to abdominal spiracles and underlying vasiform orifice. Legs typically robust and two-segmented, smooth, each with a pronounced apical claw (Fig. 5). Antennal apices extending to middle of hind legs (Fig. 5), their bases anterolateral to fore legs, the basal one-third smooth-sided but remainder finely corrugate-sided, pointed apically. Tracheal folds absent. Each abdominal segment with a median patch of very fine spinules present.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, Las Cuevas, on *Stizo-phyllum riparium* (Bignoniaceae), 25.iii.2003 (J.H.Martin #7800) (BMNH). Paratypes (all from CFR, Martin coll.): 22 puparia, 3 adult males, 7 adult females, same data as holotype (BMNH); 37 puparia, 4 third-instar larvae, 1 adult male, 1 adult female, same locality and host family, 11.ii.1996, 16.ii.1996, 04.iii.1996, 25.iii.2003, 09.vi.2004 (BMNH, USNM); 5 puparia, 1 third-instar exuviae, 1 adult male, 2 adult females, on *Paullinia pinnata* (Sapindaceae), 29.iii.2003 (BMNH); 1 puparium, same locality, on unidentified host, 06.iv.2003

zоотаха 681

(BMNH); 13 puparia (plus approximately 10 more dry, attached to leaf), on *Combretum cacoucia* (Combretaceae), 06.vi.2004 (BMNH).

ETYMOLOGY. The specific epithet is the Latin *inversus* (meaning inverted), referring to the raised-lobulate inner edge of the wide-rimmed pore band lending the submedian area the appearance of a rhachis-shaped depression.

COMMENTS. The puparial characters of *A. inversus* indicate that it is a close relative of *A. dugesii* Cockerell, sharing the characters of a submarginal zone of wide-rimmed simple and double-rimmed pores, the arrangement of its six pairs of abdominal compound pores, and submedially having only sparse septate and minute bright pores. However, *A. inversus* is immediately distinguished by the zone of wide-rimmed pores occupying the subdorsum as well as the submargin (encompassing abdominal compound pore pairs 1–4), by the pronounced lobulate inner margin of this zone, and by the presence of septate double-rimmed pores mesal to abdominal compound pore pairs 1–4 and between the 4th and 5th/6th pairs of abdominal compound pores; in contrast, the wide-rimmed pores in *A. dugesii* are not obviously septate, and are only present in the submargin. The possession of a broad zone of wide-rimmed pores and a submarginal row of double-rimmed septate pores by *A. inversus* also indicates similarity to the spiralling whitefly, *A. dispersus* Russell, but *A. dispersus* has only 4 pairs of abdominal compound pores (all large), its wide-rimmed septate pores are in a single outer submarginal row only, and its submedian area is very densely provided with smaller septate pores.

All the recorded host plants for *A. inversus* are woody forest vines, and this whitefly species displays a clear preference for such plants.

Aleurodicus magnificus Costa Lima

(Figs 6, 73)

Aleurodicus magnificus Costa Lima, 1928: 129-131. Syntypes, Brazil [examined].

DISTRIBUTION. Neotropical Region - Belize, Brazil, Panamá.

COMMENTS. This species secretes an exceptionally dense, woolly tangle, with particularly coarse strands of secretion. Colonies often appear dirty, greyish. Most commonly, puparia are aligned along the undersides of leaf midribs, rather than in broader aggregations.

Aleurodicus maritimus Hempel

(Figs 7, 74)

Aleurodicus maritimus Hempel, 1922b: 1160–1161. Syntypes, Brazil [examined].
 Aleurodicus linguosus Bondar, 1923a: 76–78. Syntypes, Brazil [examined]. [Synonymised by Costa Lima, 1928: 133.]

DISTRIBUTION. Neotropical Region — Belize, Brazil, Guyana, Mexico, Nicaragua, Panamá, Surinam, Trinidad.

COMMENTS. The author was able to examine syntypes of both *A. linguosus* and *A. maritimus* through the kindness of USNM and MZUSP, respectively. Costa Lima (1928) considered *A. linguosus* to be a junior synonym of *A. maritimus*, and his opinion is considered sound by the present author.

A. *maritimus* is one of the most frequently observed *Aleurodicus* species in the CFR, feeding on a range of host plants. Extrapolating from the recorded distribution, above, this species is certain to occur through much of the Neotropical Region.

Aleurodicus niveus sp. nov. (Figs 8, 66, 135)

PUPARIUM. Habitus. Surface of dorsal disc completely covered by opaque and exceptionally pure-white mealy secretions (Fig. 135); protruding through this opaque meal a single lustrous waxy filament issues from each of the cephalic and four abdominal pairs of large compound pores. Immediately lateral to the compound pores, submargin and puparial sides are completely hidden by dense, almost hair-like, white waxy filaments. Margin. Outline broadly ovoid, 1.28-1.41 mm long, 0.91-1.08 mm wide, generally widest at abdominal segment III (n=11). Margin smooth to broadly lobulate, dependent on degree of downcurling, lobes more often evident anteriorly. Dorsum. Cuticle dusky-brownish. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures apically curving slightly anteriorly, terminating opposite median part of metathorax, at level of submarginal setal row. Subdorsal and submedian area somewhat corrugate but without definite sculpturing. Abdominal segment VII/VIII boundary medially only marked by presence of pockets, and not by any suture; median lengths of segments VI, VII and VIII apparently similar. Vasiform orifice (Fig. 66) broadly cordate, a little wider than long, its rim thickened laterally, with a broad posterior lip that facilitates protrusion of lingula beyond operculum, the orifice situated about 0.75–0.80 times its own length from posterior margin of puparium; operculum almost completely occupies vasiform orifice, posteriorly emarginate where it overlies lingula, its margin uneven and surface shallowly rugose (Fig. 66), apparently without a posterior pair of setae; lingula head protrudes slightly beyond vasiform orifice, with an acute and finely bifid apical point, its two pairs of setae situated close to apex, the distal setal pair much stouter and longer than the proximal pair. Chaetotaxy. Anterior marginal setae not evident. With posterior marginal setae, 12 pairs of outer submarginal setae (including nominal caudal pair), and single pairs of submedian pro-, meso- and metathoracic setae, each long and hair-like; eighth abdominal setae shorter and finer, situated anterior to vasiform orifice (Fig. 66). Pores. Cephalic and anterior 4 pairs of abdominal compound pores 35–50 (usually 45–50)µm in maximum diameter, each

with a dagger-shaped axial process protruding beyond the pore rim (Fig. 66); a pair of much smaller compound pores, 15–20µm diameter, present on each of abdominal segments VII & VIII, those on segment VII about twice as long as those on segment VIII. Broad submargin defined by a zone of crowded, wide-rimmed pores that stand proud from puparial surface, inner boundary of zone closely approaching compound pores but not forming mesally-directed lobes, the pore band narrowing posterior to vasiform orifice (Figs 8, 66), but band not interrupted to form a caudal furrow. Remainder of dorsal disc with scattered pores slightly larger than those of submarginal band. Venter. Ventral abdominal setae overlain by vasiform orifice, the setae similar to dorsal submarginal setae. Legs typically robust and two-segmented, smooth, each with a pronounced apical claw, and with the distal segment bearing one or two small lateral setae. Antennae with their bases situated anterolateral to fore legs; antennae are damaged in parasitised individuals, and evidently not fully expanded in some others (see comments on Metaleurodicus variporus, p. 52); when expanded, antennae with basal one-third smooth-sided, remainder subtly corrugate-sided, apices pointed; in holotype one antenna reaches level of middle legs, the other only to fore legs. Tracheal folds absent.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, Las Cuevas forest, on *Encyclia cochleata* (Orchidaceae), 04.vi.2004, (J. H. Martin #7986) (BMNH). Paratypes: 17 puparia (7 dry on leaf), same data as holotype (BMNH, USNM).

ETYMOLOGY. The specific name is the latin adjective *niveus* (meaning snowy-white), reflecting the appearance of grouped puparia in optimum condition when first collected.

COMMENTS. This species is known from a single colony, a group under one leaf of its epiphytic orchid host (Fig. 135). Most individuals proved to be parasitised, but five undamaged specimens were preserved in alcohol as soon as this became evident: three of these show no signs of parasitism under high magnification, and it is thought unlikely that the habitus appearance of the colony was affected by the development of parasitoids.

The features of the vasiform orifice, operculum and lingula (Fig. 66) are highly characteristic, with the very large operculum and bifid apical lingular process of particular note. In other characters, *A. niveus* resembles *A. rugioperculatus*, also described in this work.

Aleurodicus pauciporus sp. nov.

(Figs 9, 75-76)

PUPARIUM. *Habitus*. Body colour yellowish, with sparse waxy secretion in the form of marginal meal, slight medial mealy dusting, and a fine filament issuing from each of the large compound pores. Cuticle pale or with submargin distinctly brownish. Individuals feed alongside the major veins, under leaves. *Margin*. Outline ovoid, slightly indented at

distal end of longitudinal moulting suture, 0.90-1.08 mm long, 0.64-0.82 mm wide, generally widest at abdominal segment I/II (n=11). Margin rather irregular (Fig. 76), not toothed, not modified at thoracic tracheal openings. Dorsum. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures curving anteriorly, closely approaching puparial margin almost opposite meso-/metathoracic division. Dorsal disc almost smooth, although somewhat irregular-corrugate between abdominal compound pores and puparial margin. Only 7 abdominal segments discernible medially, but pockets not overlapping segment VI (Fig. 75). Vasiform orifice transversely oval, smooth; operculum transversely rounded-rectangular, its posterior edge bearing a pair of fine setae; lingula head very large, rather coarsely spinulose, tongue-shaped, its apex extending over half way to the posterior margin of puparium (Figs 9, 75). Chaetotaxy. Anterior marginal setae absent. Extreme outer submargin bearing 12 pairs of hair-like setae (Figs 75–76), including the nominal caudal pair; single pairs of pro-, meso- and metathoracic and eighth abdominal setae present, similar to submarginal setae; eighth abdominal setae situated slightly anterolateral to anterior corners of operculum (Fig. 75); posterior marginal setae present, similar to caudal setae. Pores. Large compound pores (Fig. 75) 28-40 µm in diameter (size correlated with puparial size), each apparently with a truncate axial process that does not emerge beyond the pore mouth; small compound pores, on abdominal segments VII and VIII, presenting laterally, 10-14 µm wide, shape of those on segment VII reminiscent of unshelled peanuts, while those on segment VIII are distinctly mushroomshaped (Fig. 75). Outer submargin (Fig. 76) with a narrow zone of sparsely distributed tiny simple pores, probably of the minute wide-rimmed type of Russell (1965), very few extending mesad beyond the row of submarginal setae. Dorsal disc sparsely provided with septate pores, only one or two on each side of submedian part of abdominal segments II-VI (Fig. 75), and similarly scarce in subdorsum. In the vicinity of the abdominal compound pores on segments III-VII are small numbers of loosely aggregated bright pores, most highly visible mesal to the compound pores (Fig. 75). Very small numbers of other simple pores are distributed across the dorsal disc. Venter. Ventral abdominal setae similar to posterior abdominal submarginal setae, but finer. Legs each two-segmented, smooth, their distal segments usually with one or two tiny setae visible, and the usual apical claw; middle and hind legs sometimes each with a small basal seta visible. Antennal bases anteromesal to fore legs, their apices reaching mid-length of hind legs (Fig. 9). Tracheal folds absent.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, Monkey Tail track, on *Casearia tremula* (Flacourtiaceae), 04.iv.2003 (J.H.Martin #7846) (BMNH). Paratypes (all from CFR, Martin coll.): 11 puparia (1 teneral), 7 third instar larvae, 3 adult females, same data as holotype (BMNH, USNM); 8 puparia, 1 third-instar larva, 1 third-instar / puparium intermoult, 4 adult females, Las Cuevas study plots, on *Ilex belizensis* (Aquifoliaceae), 30.v.2004 & 04.vi.2004 (BMNH); 29 puparia, 3 third-instar larvae, 1 second-instar larva, 2 adult males, 6 adult females, same locality, on ?Lauraceae, 30.v.2004 &

zоотаха 681

05.vi.2004 (4 separate samples) (BMNH, BZ, USNM); approximately 20 puparia and earlier instar exuviae dry on leaf, same locality, on ?Lauraceae, 30.v.2004 (BMNH).

Other material (see discussion): 9 puparia, COSTA RICA, Guanacaste Province, Santa Rosa NP, on undetermined host, 06.iii.1990 (J.M.Cox) (BMNH); 7 puparia, COSTA RICA, northern Heredia Province, 10 km north of Puerto Viejo, on undetermined host, 02.ii.1983 (J.H.Martin) (BMNH).

ETYMOLOGY. The species name is derived from the Latin *pauci* (meaning a few), reflecting the unusually low density of simple pores in the puparia of *A. pauciporus*.

COMMENTS. The most notable feature of the puparia of this species is the paucity of dorsal simple pores, which are usually more numerous, and of more types, in species of *Aleurodicus*. The lack of simple pores is reflected in similarly sparse secretion by the immature stages, with the puparia of some colonies distinctly brownish submarginally. Nevertheless, the nature and distribution of the compound pores, and the puparial chaetot-axy, strongly indicate inclusion in *Aleurodicus*. Within the genus, *A. pauciporus* is the only described species with such scarcity of simple pores. The puparia from Costa Rica, listed above, are very similar to the type material but have a higher density of submarginal pores.

Aleurodicus pulvinatus (Maskell)

(Figs A, 10, 64, 77, 124)

Aleurodes pulvinata Maskell, 1896: 439–441. Lectotype designated by Martin & Watson (1998), Trinidad [examined].

Aleurodicus pulvinatus (Maskell); Cockerell, 1902: 280.

Aleurodicus iridescens Cockerell, 1898: 225. Lectotype designated by Martin & Watson (1998), Mexico [examined]. [Erroneously synonymised with *Aleurodicus cocois* (Curtis) by Quaintance & Baker, 1913: 47; synonymised with *A. pulvinatus* by Martin & Watson, 1998: 93.]

DISTRIBUTION. Neotropical Region — widely distributed, especially amongst the Caribbean islands.

COMMENTS. A. pulvinatus was investigated by Martin & Watson (1998), who redefined this species, concluding that puparial pigmentation varies considerably. Puparia may be completely pale, have pronounced subdorsal pigmentation in a longitudinal stripe on each side of the puparium, or possess more limited marking in the form of a pair of thoracic patches or, occasionally, a median thoracic patch (Figs 64, 124). This species is widespead in the Caribbean area, where it sometimes causes considerable damage to coconut palms, but has not been encountered in pest proportions in Belize despite being collected on many occasions.

Aleurodicus rugioperculatus sp. nov. (Figs 12, 56–58, 78)

zоотаха 681

PUPARIUM. Habitus. Colonies seen by the author were in generally poor condition, with groups of woolly-wax puparia untidily grouped under the leaves of the host. Margin. Outline oval, 0.97–1.22 mm long, 0.66–0.88 mm wide, generally widest at abdominal segment III (n=35). Margin smooth, often down-curved in slide-mounted specimens. Dorsum. Cuticle pale or with variably developed dusky coloration, especially submedially. Longitudinal and transverse moulting sutures reaching puparial margin; transverse moulting sutures apically curving slightly anteriorly, terminating opposite median part of metathorax. Dorsal disc with subtle reticulate patterning often visible across the cephalothorax (Fig. 56) and in abdominal subdorsum, and extremely fine spinulosity present along median line of abdomen (Fig. 57). Abdominal segment VII medially reduced to less than half length of segment VI. Vasiform orifice (Figs 12, 58) broadly cordate, slightly emarginate to either side of lingula; operculum broadly elliptical except for its anterior edge, ventro-basally spinulose and dorsally characteristically rugose (Fig. 58), with a pair of ventro-median fine setae; lingula head protruding beyond vasiform orifice, finely spinulose, apically acute, its four stout setae situated close to apex, which almost reaches puparial margin. Chaetotaxy. Anterior marginal setae not evident. Posterior marginal, and 12 pairs of outer submarginal setae present (including nominal caudal pair), each long and hair-like. Single submedian pairs of pro-, meso- and metathoracic and eighth abdominal setae present, finer and shorter than submarginal setae (Fig. 78); eighth abdominal setae situated fully anterior to vasiform orifice, opposite anterior corners of operculum. Pores. Cephalic and anterior 4 pairs of abdominal compound pores 30-40 µm in maximum diameter, each with a dagger-shaped axial process protruding by about one pore-diameter beyond the pore rim (Fig. 78); 2 pairs of much smaller compound pores, $10-12 \,\mu\text{m}$ diameter, present on abdominal segments VII & VIII. Immediately lining puparial margin is a narrow band of minute cellular structures (Fig. 78), ranked 2-3 deep, but their structure / function not certain. Submargin defined by a zone of crowded, wide-rimmed pores that stand proud from puparial surface, inner boundary of zone forming mesally-directed lobes, the pore band interrupted immediately posterior to lingular apex, and the zone not encompassing the compound pores (Figs 12, 78). Remainder of dorsal disc with sparsely distributed septate and tiny bright pores. Venter. Ventral abdominal setae situated mesal and slightly anterior to posterior abdominal spiracles, the setae similar to dorsal submarginal setae. Legs typically robust and two-segmented, smooth, each with a pronounced apical claw (Fig. 12), and with the distal segment bearing one or two small lateral setae. Antennae extending to basal segment of hind legs, their bases situated anterolateral to fore legs, the basal one-third smooth-sided but remainder subtly corrugate-sided, pointed apically. Tracheal folds absent.

MATERIAL EXAMINED. Holotype puparium, BELIZE, Belize City, on Cocos

nucifera (Arecaceae), 11.iii.1996 (J. H. Martin #6770) (BMNH). Paratypes: 12 puparia, 1 adult male, 1 adult female, same data as holotype (BMNH); 19 puparia, 8 third-instar larva, 9 adult females, same locality and host, 01.vii.2002 (Martin) (BMNH, USNM); 6 puparia, 5 adult females, CFR, Las Cuevas – Millionario road, on undetermined broadle-aved woody host, 03.vi.2004 (Martin) (BMNH); MEXICO, Tamaulipas, "CD: Victoria, UAT", on *Psidium guajava*, 08.xii.1995 (E. Chouvakhina) (BMNH); 2 slide-mounted, 11 dry puparia, same host and locality, 25.x.2002 (S. N. Myartseva K#392) (BMNH, ZISP).

ETYMOLOGY. The specific name describes the characteristically rugose (i.e. fluted / irregularly corrugate) appearance of the puparial operculum.

COMMENTS. The lingula apex of this species is atypically narrowly acute, its 4 setae situated very close to the apex. The lingula protrudes beyond the boundary of the vasiform orifice, as is usual in *Aleurodicus*, but otherwise is more reminiscent of species in other aleurodicine genera. The subtle reticulate patterning of the cuticle in the cephalothorax and abdominal subdorsum, seen in many specimens, is also unusual as is the sometimes extensive dark, cloudy cuticular pigmentation seen in some individuals. *A. rugioperculatus* is similar to *A. niveus*, described above, and may be distinguished by use of the key to Belize species of *Aleurodicus*, p. 19.

Aleurodicus vinculus sp. nov.

(Figs 11, 79-80)

PUPARIUM. Habitus. Unknown — only post-emergence pupal cases and one unviable puparium found. Margin. Outline broadly oval, 1.12-1.37 mm long, 0.92-1.09 mm wide, widest at abdominal segment III/IV (n=4). Margin smooth, but a row of pore-like structures present immediately inside margin lend the margin an irregular appearance when seen in relief — margin requires to be completely flattened for its true character to be visible (Fig. 80); margin not modified at tracheal openings. Dorsum. Cuticle pale. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures reaching into submargin. Dorsal disc smooth. Abdominal segment VII not discernible medially, only 7 segments visible on median line, the pockets extending into segment VI (Fig. 11). Vasiform orifice broadly cordate, smooth; operculum transversely rounded-rectangular, its posterior edge with a pair of stout setae; lingula head very large, rather coarsely spinulose, tongue-shaped, its apex almost attaining posterior margin of puparium (Fig. 11), its 4 setae conspicuously subapical in position. Chaetotaxy. Anterior marginal setae not evident in the small study sample; posterior marginal setae very stout, similar to caudal setae. Submargin with a row of 12 pairs of hair-like setae present, including the nominal caudal pair; single pairs of pro-, meso- and metathoracic and eighth abdominal setae present, similar to cephalothoracic submarginal pairs; eighth abdominal setae situated anteromesal to anterior corners of operculum. Pores. Cephalic and anterior 4 pairs of abdominal compound pores

large, 40–60 µm in diameter, size correlated with overall puparium size, their axial processes truncate and hardly protruding beyond pore mouths in the small study sample (Fig. 80); small compound pores, on abdominal segments VII and VIII (Fig. 11), presenting laterally, $\sim 16 \ \mu m$ wide, with two protuberant basal cells, the pores appearing bell-shaped, with rounded apices and smooth margins. Extreme outer submargin with a single row of dark, pore-like structures (Fig. 80), 7-10 per 0.1 mm (but see Margin, above); between puparial margin and row of submarginal setae lies a regular row of elongate 8-shaped pores (Figs 11, 80), each less than a pore-length from its adjacent neighbours, 4–5 occupying 0.1 mm, the cephalothoracic region sometimes with a few additional 8-shaped pores mesal to the main row. Dorsal disc with many septate pores present, many arranged in distinctive chain-like lines (Fig. 79); submedian areas of cephalic region, prothorax and abdominal segments II-VIII each with a single chain on either side of the median line, lying parallel to the intersegmental divisions (thus transverse on anterior abdominal segments, but almost longitudinal on abdominal segment VIII); meso- and metathorax each with a pair of chains of septate pores which converge towards the median line and forming a shallow "X" shape on each segment (Fig. 79); in the subdorsum, slightly less chain-like rows of septate pores extend between the compound pores, parallel to the transverse moulting sutures. Dorsal disc with scattered tiny pores present that are not in geminate pairs. Venter. Ventral abdominal setae similar in length to posterior abdominal submarginal setae, but finer. Legs each two-segmented, smooth, the distal segments with a small number of tiny setae and a stout apical claw; middle and hind legs each with a small basal seta; fore legs each with two closely-adjacent minute basal setae with bright bases. Antennal bases situated anteromesal to fore legs, their apices reaching mid-length of hind legs (Fig. 11). Tracheal folds absent.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, San Pastor track, from a tangle of undetermined woody vines, 20.xi.1994 (J.H.Martin #6492A) (BMNH). Paratypes: 2 puparia, same data as holotype (BMNH); 1, same locality, undetermined woody broadleaf host, 23.iii.2003 (Martin) (BMNH).

ETYMOLOGY. The specific epithet is the Latin word *vinculus* (meaning a band or chain), reflecting the chain-like lines of septate pores running across the submedian part of the dorsal disc in puparia of this species.

COMMENTS. Only a single sample comprising three puparia, and a further single specimen, are known, and these were initially tentatively identified as a variant of *A. trinidadensis* Quaintance & Baker. In comparison with study material of *A. trinidadensis* from Trinidad, the Belizean specimens have a much greater number of small septate pores on the dorsal disc, these arranged in distinct chain-like rows across the submedian areas of the cephalothorax and abdominal segments II–VIII; on the meso- and metathorax, there are two such chains of pores. Without more study samples, the degree of variation in *A. trinidadensis* is uncertain, but *A. vinculus* is considered to be distinct, defined by these chains of septate pores.

ZOOTAXA

681

ALEURONUDUS Hempel

Aleuronudus Hempel, 1922a: 5. Type species Aleuronudus induratus Hempel, by monotypy.

Pseudaleurodicus Bondar, 1923a: 85–87. Type species Aleuronudus induratus Hempel, by original designation. [Synonymised by Costa Lima, 1928: 137, through community of type species, and discussed by Mound & Halsey, 1978: 236.]

Hexaleurodicus Bondar, 1923a: 84. Type species Hexaleurodicus jaciae Bondar. Syn. nov.

DIAGNOSIS AND COMMENTS. As interpreted here, *Aleuronudus* comprises species with the following combination of characters: submedian cephalothoracic setal pairs absent; with 6 pairs of abdominal compound pores of at least two, often three, sizes present, never distributed in an even arc and never all evenly spaced (Figs 13, 14); two pairs of cicatrices (scars of third-instar compound pores) present on thoracic area; central part of each large compound pore usually occupied by bundled rods that do not protrude beyond the pore; dorsum without distinct groupings of simple pores, except sometimes in extreme outer submargin (Fig. 81); 12 pairs of submarginal setae present (including the nominal caudal pair).

The only difference between the puparia of *Hexaleurodicus jaciae* and those of *Aleuronudus* species is the displacement of the anterior two pairs of abdominal compound pores towards the median line of the body in *H. jaciae*. All other characters are entirely typical for *Aleuronudus*, and *Hexaleurodicus* is therefore considered its junior synonym (**syn. nov.**).

When the type species of *Aleuronudus* and *Metaleurodicus* are compared, the only major character that separates them, and might be considered to be of generic significance, is the unevenness of the alignment and spacing of abdominal compound pores in *Aleuro-nudus*: characters such as inclusion of lingula within vasiform orifice, and the nature of dorsal disc simple pores, are found across the assemblage of species included within these two genera. It is considered likely that future studies may indicate the synonymy of these two genera, but this character does currently provide satisfactory separation of the two assemblages. Accordingly, *Metaleurodicus jequiensis* Bondar (1928), described from Brazil, is here transferred to *Aleuronudus* comb. nov.

Aleuronudus acapulcensis (Sampson & Drews) (Fig. 13)

Pseudaleurodicus acapulcensis Sampson & Drews, 1941: 155–156. Syntypes, Mexico. *Aleuronudus acapulcensis* (Sampson & Drews) Mound & Halsey, 1978: 236.

DISTRIBUTION. Neotropical Region — Belize, Mexico, Panamá.

COMMENTS. The only Belizean representatives of this species were collected from *Citrus* sp. at the Belize Botanic Gardens, adjacent to the Macal River, near San Ignacio (BMNH).

Aleuronudus manni (Baker) comb. nov.

(Figs 14, 81, 115, 133-134)

Aleurodicus (Metaleurodicus) manni Baker, 1923: 253–254. Syntypes, Honduras. Metaleurodicus manni (Baker) Mound & Halsey, 1978: 245. Aleuronudus ferrisi (Sampson & Drews) Martin & Polaszek, 1999: 1553. Hexaleurodicus ferrisi Sampson & Drews, 1941: 154–155. Syntypes, Mexico syn. nov.

DISTRIBUTION. Neotropical Region — Belize, Costa Rica, Honduras, Mexico, Nicaragua, Panamá, Trinidad.

COMMENTS. Aleuronudus manni is frequently encountered in the CFR, especially colonising members of the Rubiaceae. Its puparia are extremely characteristic, with the anteriormost pair of abdominal compound pores much larger than the remainder (Fig. 14), each of these very large pores secreting an exceptionally long filament (Fig. 133). Initially, its adults were confused with those of the then newly discovered *Azuraleurodicus pentar-thrus* (see below), which also colonises *Guettarda combsii*, indicating the importance of rearing of adults for definite association with puparia (Martin & Polaszek, 1999). The adult females of *Al. manni* (Fig. 134) secrete exceptionally robust extrusions of wax, of brush-like appearance, from their abdominal wax plates (Fig. 115), which those of *Az. pen-tarthrus* do not.

AZURALEURODICUS Martin

DIAGNOSIS AND COMMENTS. This monobasic genus is briefly defined thus: puparia with 5 pairs of large, evenly-spaced abdominal compound pores, each with a large axial process, located on segments III–VII (Figs 16, 65); two pairs of cicatrices (scars of third-instar compound pores) present on thoracic area; puparial submargin with an uneven row of large 8-shaped pores and a row of large double-rimmed pores (Fig. 65); without submedian cephalothoracic setae, but with a row of 12 pairs of submarginal setae; adults greyish in colour, with evenly dusky wings and with only 5 evident antennal segments.

Azuraleurodicus pentarthrus Martin (Figs 16, 65)

Azuraleurodicus pentarthrus Martin, in Martin & Polaszek, 1999: 1547–1550. Holotype, Belize [examined].

DISTRIBUTION. Neotropical Region — Belize, Colombia, El Salvador.

zоотаха 681

Azuraleurodicus Martin, in Martin & Polaszek 1999: 1547. Type species Azuraleurodicus pentarthrus, by original designation and monotypy.



COMMENTS. This species is notable for the delicately bluish-iridescent filaments secreted by its yellowish immature stages. Collecting in CFR subsequent to the description of *A. pentarthrus* has revealed puparia on the following additional host plants: two species of *Inga* (Fabaceae: Mimosoideae), *Vismia camparaguey* (Clusiaceae), *?Acalypha* sp. (Euphorbiaceae) and a vine belonging to the Phaseoleae (Fabaceae: Papilionoideae). No large colonies of this species have ever been discovered, the largest group available comprising less than 30 puparia, scattered under a *Croton* leaf in CFR (BMNH).

CERALEURODICUS Hempel

Ceraleurodicus Hempel, 1922a: 6. Type species Ceraleurodicus splendidus, by monotypy. Radialeurodicus Bondar, 1922: 74. Type species Radialeurodicus cinereus, by subsequent designation. [Synonymised by Costa Lima, 1928: 137.]

Parudamoselis Visnya, 1941: 4–5. Type species Parudamoselis kesselyaki, by monotypy. [Synonymised by Mound & Halsey, 1978: 238.]

DIAGNOSIS AND COMMENTS. Amongst the genera of Aleurodicinae found in Belize, Ceraleurodicus has hitherto been particularly unsatisfactorily defined. As interpreted here, Ceraleurodicus comprises species with the following characters that separate them from species here transferred to *Nealeurodicus* Hempel (1922b): normally 15 pairs of submarginal setae present, usually situated distant from puparial margin (Figs 67a, 67c, 82, 114) or, if setal bases closer to margin, setae only slightly extending beyond margin; with submarginal area planar, true margin almost smooth but submarginal sculpture giving appearance of laterally-contiguous teeth (Figs 67c, 82), sometimes also with an apparent second rank of teeth submarginally; usually displaying marked asymmetry in puparial outline (Figs 17, 18, 20, 114) and often also in compound pore provision (Figs 17–20, 114); usually with nine pairs of rays [these were termed "peripheral intersegmental ridges" by Shcherbakov, 2000] leading mesad from puparial margin (Figs 20, 114); some rays have fine marginal serrations apically (Figs 67c, 82) and finely spinulose apparent tracheal folds underlying them, ventrally. Additionally, the following characters are shared with those species here transferred to *Nealeurodicus*: with a single pair of submedian setae present on each thoracic segment, and usually also a cephalic pair; cicatrices absent from thorax (indicates absence of compound pores in third-instar); lingula normally included within the vasiform orifice (Figs 67b, 83). See also comments on Nealeurodicus, p. 53.

The author was able to reassess the synonymy of *Radialeurodicus* with *Ceraleurodicus*, proposed by Costa Lima (1928), through the examination of original material loaned courtesy of MZUSP. Despite the poor condition of the mountant on a probable syntype slide of each species the puparia do, indeed, appear to belong to the same species. However, the adults are definitely not conspecific. Bondar's drawing of the fore wing of *R. cinereus* (1923a: 16) clearly shows almost the whole wing to be fairly evenly pigmented, with an extremely unusual trilobulate apical margin, and a darker patch on each wing-mar-

gin lobe. Hempel did not illustrate *C. splendidus* at all, but described both fore and hind wings as being "densely spotted with both large and small, irregular, fuliginous [=sooty / smutty] spots". Each author's observations on the wings are confirmed to be accurate, and the adults therefore represent two distinct species. As has happened in other whitefly descriptions (see Martin, 2001), the adults of one (possibly even both) of these two species are unlikely to be correctly associated with the puparia. It will require the rearing of adults from fresh puparia to resolve this uncertainty.

zootaxa 681

Ceraleurodicus keris sp. nov.

(Figs 17–19, 67, 136, Table 1)

PUPARIUM. Habitus. Appearance in life rather cryptic, with the only visible secretions being a long fibrous thread guided from each of the large compound pores by a long axial process (Fig. 136); puparia develop singly, typically with the body laterally adpressed to the leaf midrib or a major leaf vein. Margin. Outline usually asymmetrical (Figs 17, 18), 2.37-4.25 mm long, 0.90-1.74 mm wide, generally widest at abdominal segments II/III (n=21). Margin planar, fine and not tending to down-curl on slides, smooth but with very fine submarginal folds, lending an appearance of contiguous-sided "pseudo-teeth" (Fig. 67c); margin modified into very fine crenulations at lateral extremities of most rays (see below) and always distinctly indented at extremity of posteriormost pair of rays (Fig. 67c). Dorsum. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures, and all other intersegmental divisions, only suture-like submedially. With 9 pairs of rays leading mesad from puparial margin, all except the anteriormost and posteriormost pairs coalescing with submedian intersegmental divisions. Dorsal disc flattened, smooth; cuticle without coloration in the study samples, except for a brownish ring surrounding each large compound pore (Figs 18, 67a — but see comments, below). Abdominal segment VII distinct medially, about two-thirds as long as segment VI but longer than segment VIII anterior to vasiform orifice; paired submedian pockets pronounced, extending anteriorly about half-way towards segment VI/VII division. Vasiform orifice (Fig. 67b) elongate rounded-triangular, 0.15–0.19 mm long, about 1.5 times longer than wide basally, laterally smooth and straight, with a pair of subapical shoulders and a distinct apical boss, orifice inset from caudal margin by 3-5 times its own length; operculum ovoid and smooth, wider than long and sometimes with a pair of posterior marginal setae visible; lingula head finely spinulose, rounded-diamond shaped, exactly occupying posterior part of vasiform orifice, bearing the usual 4 subapical setae. Caudal furrow absent. Chaetotaxy. With 15 pairs (occasionally 14 on one side) of inner submarginal setae present, including nominal caudal pair, these very short and fine but with their bases rather robust in proportion, their apices not closely approaching puparial margin (Fig. 67a,c); single pairs of submedian cephalic, pro-, meso- and metathoracic setae present, similar to submarginal setae; eighth abdominal setae longer, fine, situated lateral to anteriormost point of vasiform ori-

fice (Fig. 67b). Anterior and posterior marginal setae present, similar to each other, similar to eighth abdominal setae, their bases situated ventrally, slightly away from margin. Pores. Large compound pores, 40–50 µm in diameter, usually present only on side of body furthest from adjacent leaf vein (Fig 17, 18), one cephalic pore and 2 or 3 abdominal pores on segments III-IV or III-V: occasionally puparia are more symmetrical and some large compound pores are paired on either side of body (Fig. 19, Table 1); from each large compound pore issues a long, brown, robust axial process that extends well beyond puparial margin and may reach 0.90 mm in length; axial processes approximately straight, swordlike, but often slightly "wavy" towards apex (Fig. 67a), and those of more teneral specimens tending to curl in maceration potash. All specimens with a tiny submarginal compound pore on each side of body, at distal end of posteriormost pair of rays, mesad of abdominal marginal indentations (Fig. 67c), these pores 20-25 µm in diameter. Surrounding each large compound pore is an annulus of brown-pigmented cuticle incorporating a ring of large, protuberant simple pores (Fig. 67a). Dorsal disc punctuated by fairly evenly distributed small loculate pores and simple porettes, the loculate pores each not apparently associated with a porette; a row of slightly larger simple pores is present to either side of vasiform orifice. Ventral abdominal setae almost as long as vasiform orifice, their bases underlying it. Underlying rays on pro-/mesothorax and abdominal segment VII/VIII, are subtle tracheal folds which are finely spinulose, especially distally, sometimes other rays are ventrally similarly marked; caudal tracheal fold is subtly marked by line of rather sparse tiny spinules. Legs each bisegmented, smooth, each with usual apical claw, and with small number of fine setae on distal segment and a variable small number of tiny setae on each basal segment. Antennae with basal one-third smooth-sided and remainder finely corrugate-sided, each with pronounced apical point, their apices (in all specimens) reaching articulation of middle legs, their bases situated anteromesal to fore legs. Rostrum elongate, a little longer than vasiform orifice.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, Las Cuevas study plots, on *Laetia thamnia* (Flacourtiaceae), 29.v. 2004 (J.H.Martin #7938) (BMNH). Paratypes: 1 puparium, BELIZE, CFR, Monkey Tail track, on *Protium copal* (Burseraceae), 05.vi. 2004 (Martin #7991) (BMNH); 3 puparia, NICARAGUA, Granada Province, Domitila Forest Reserve, near Nandaime, on undetermined broadleaved sapling, 13.vi.2004 (Martin #8030) (BMNH); 4 puparia, 1 third-instar / puparium intermoult, 1 third-instar larva, NICARAGUA, Rio San Juan Province, Rio San Juan / Rio Bartola confluence, on *Uncaria tomentosa* (Rubiaceae), 22.vi.2004 (Martin #8078) (BMNH); 9 puparia (2 dry on leaf), same locality, on *Lunania parviflora* (Flacourtiaceae), 24.vi.2004 (Martin #8083) (BMNH, USNM); 2 puparia, COSTA RICA, Turrialba, CATIE research centre, on *Eupatorium* sp. (Asteraceae), 01.iii.1983 (Martin #3924) (BMNH); 1 puparium, PANAMÁ, Canal Zone, Barro Colorado Island, on *Mouriri myrtilloides* (Melastomataceae), 01.i.1983 (Martin #3478) (BMNH); 1 puparium, Canal Zone, *rophylla* (Rubiaceae), 15.iii.1983 (Martin #4026) (BMNH); 1 puparium, Canal Zone,
Gamboa Hill, on *Heterocondylus vitalbae* (Asteraceae), 20.iii.1983 (Martin #4092) (BMNH).

JHM #	Puparial length	Puparial width	Large abdominal compound	Large compound pores
	mm	mm	pores on segment nos	paired on segment(s)
7938	2.87	1.29	III,IV	-
7991	2.77	1.26	III, IV	-
8030	2.65	1.10	III,IV	-
8030	2.77	1.18	III,IV	-
8030	2.68	1.09	III,IV	-
8078	2.71	1.07	III,IV	-
8078	2.47	0.92	III,IV,V	-
8078	2.61	1.00	III,IV	-
8078	2.44	0.95	III,IV	-
8083	4.00	1.66	III,IV,V	-
8083	3.95	1.65	III,IV,V	-
8083	4.21	1.70	III,IV,V	-
8083	4.22	1.73	III,IV,V	-
8083	4.25	1.74	III,IV,V	-
8083	4.08	1.72	III,IV,V	-
8083	3.90	1.48	III,IV,V	-
3924	3.63	1.38	III,IV,V	-
3924	3.62	1.53	III,IV,V	cephalic
3478	2.50	0.88	III,IV - left, IV - right	cephalic, abdom. IV
4026	2.53	0.98	III,IV	-
4092	2.37	1.05	IV	cephalic, abdom. IV

TABLE 1. Data table for puparia of Ceraleurodicus keris sp. nov.

ETYMOLOGY. The chosen species name is *keris*, a type of Malay dagger with a wavy blade, similar to the rather sinuous apical section of the axial process which issues from each of the large compound pores in this species. The word is used as noun in apposition.

COMMENTS. *C. keris* has puparia whose large compound pores each possess a very long, sword-like, axial process which extends well beyond the puparial margin, and the puparial outline is usually exaggeratedly asymmetrical. Most puparia develop parallel to, and contiguous with, the midrib or another major leaf vein, the puparia themselves then being asymmetrical, with large compound pores only on the side furthest from the adjacent leaf vein; two specimens from Panamá (on *Heterocondylus* and *Mouriri*, see material



examined, above) are symmetrical in outline, have most of their large compound pores paired on either side of the body (Fig. 19), and probably each developed away from a major vein. Variation in the number of large compound pores also occurs, with either two or three abdominal pores present (Figs 17, 18): one sample from Nicaragua includes individuals with two and with three abdominal large pores. However, all other characters remain entirely typical, and the number and degree of pairing of the large compound pores is regarded as intraspecific variation – see Table 1. There is considerable size variation amongst the study material, but there is no evidence of puparial sexual dimorphism.

All puparia occur singly, and collection of a few specimens always involves examination of the lower surfaces of many leaves. In this respect, *C. keris* is similar to several other species of *Ceraleurodicus* and *Nealeurodicus* (personal field observations).

Ceraleurodicus varus (Bondar)

(Figs 20, 82-83, 114)

Radialeurodicus varus Bondar, 1928: 1-3. Syntypes, Brazil [examined].

Ceraleurodicus varus (Bondar) Costa Lima, 1928: 137 [by inference].

Parudamoselis kesselyaki Visnya, 1941: 5–12. Syntypes, Hungary (under glass) [examined]. [Synonymised by Martin et al., 2000: 442.]

DISTRIBUTION. Neotropical Region — Belize, Brazil.

COMMENTS. When Visnya (1941) described this species, under the name Parudamoselis kesselyaki, from Hungarian glasshouse colonies he used the adjective "gigantic" in the paper's title. This was no exaggeration, C. varus and some other Ceraleurodicus species being amongst the largest known whiteflies. The series of 14 puparia of C. varus found in Belize measure 3.45-3.90 mm in length (Visnya recorded the puparial length attaining 4.3 mm), each of them extremely asymmetrical, "banana"-shaped (Figs 20, 114), the flatter side always parallel-contiguous with a major leaf vein (see also description of C. keris, above). Compound pores are unpaired, very small (the cephalic one is slightly larger than the remainder), distributed as shown in Fig. 114, always with the cephalic pore and 3rd to 6th abdominal pores on the curved side of the puparium, and the post vasiform orifice pore on the flat, leaf-vein, side. The puparia have no visible waxy secretion, develop solitarily and are exceptionally cryptic when feeding. The silvery empty pupal cases are more visible, but easily fall from the leaf, leaving faint mealy scars that can mislead the collector into thinking that a cryptic, feeding, puparium is still present. Three reared adult females have been dissected and slide-mounted for future studies, and their forewings each measure up to 2.75 mm.

C. varus and *C. keris* (described above) are the only members of this genus so far recorded from Belize. Other species found in Belize, and hitherto placed in *Ceraleurodicus*, are now accommodated in *Nealeurodicus*, as discussed below.

DIALEURODICUS Cockerell

Aleurodicus (Dialeurodicus) Cockerell, 1902: 280. Type species Aleurodicus cockerellii Quaintance, 1900: 45–46, by original designation.

Dialeurodicus Cockerell; as full genus, Quaintance & Baker, 1913: 26.

Bondaria Sampson & Drews, 1941: 149. Type species Bondaria radifera, by original designation and monotypy. Syn. nov.

DIAGNOSIS AND COMMENTS. As interpreted here, *Dialeurodicus* comprises species with the following combination of characters: compound pores completely absent, although small clusters of simple pores on tubercular elevations may be present (Figs 22, 87); cicatrices absent from thorax, indicating absence of compound pores in third-instar; single pairs of submedian cephalic, pro-, meso- and metathoracic setae almost always all present; with an outer row of 13–17 (usually 14–15) pairs of setae present — these are nominally the submarginal setae but some species have certain pairs displaced mesad into the subdorsal area; dorsal disc usually generously provided with small simple pores and porettes (Figs 23, 60–61, 84, 86), often in distinct geminate pairs (Figs 87–89); lingula included within confines of vasiform orifice (Figs 21–23, 61, 84, 89), its head bearing 4 setae; nine pairs of oblique rays lead mesally from puparial margin (Figs 22, 86–88), often better defined abdominally but sometimes difficult to observe; cuticle may be pale, patterned (Fig. 22), or evenly dark. Puparia may be almost without visible waxy secretions (e.g. *D. caballeroi*), but fields of simple pores secrete long ribbons of white secretion in at least one species (see *D. silvestrii*, below; Fig.132).

In their greatly oversimplified key to genera of Aleurodicinae, Sampson & Drews (1941) indicated that *Dialeurodicus* species do not display the character of rays leading mesally from puparial margin. Examination of ten species (BMNH, UCD) has revealed that nine pairs of such rays are always present, although often particularly subtly marked in the cephalothorax. Examination of the only known syntype specimen of Bondaria radifera revealed that its rays are not suture-like for their whole lengths, as was misleadingly illustrated by Sampson & Drews, that the cephalic / prothoracic suture is actually very subtly marked and then only distally, that the number of rays is the same as in all examined Dialeurodicus species, and that the line delineating the submargin / subdorsum division is an artifact of parasitism. This syntype is in generally very poor condition and the venter is incomplete. The dorsal surface was illustrated by Sampson & Drews as though densely porate, but few pores are visible, even though they would still be expected to be obvious on cuticle in poor condition. Its condition means that the only submedian setal pairs visible are the prothoracic, posterior marginal, eighth abdominal and caudal pairs but, importantly, the presence of prothoracic setae usually accompanies the presence of the other cephalothoracic pairs and, indeed, a single probable mesothoracic seta is just visible. A few setae are also visible in the inner submargin, fine and with their apices not reaching the puparial margin, but a full count is not possible. Bondaria is here regarded as a junior synonym of Dialeurodicus syn. nov., on the basis of the major characters discussed above.

Dialeurodicus bondariae sp. nov. (Figs 21, 84–86)

PUPARIUM. Habitus. Appearance in life rather cryptic, but only a small sample seen. Each insect feeds with its body alongside a major leaf vein. Margin. Outline somewhat asymmetrical (Fig. 21), 2.53-2.60 mm long, 1.50-1.75 mm wide, generally widest at abdominal segments III/IV (n=4). Margin planar, fine and not tending to down-curl on slides, smooth but with very fine submarginal folds, lending an appearance of contiguoussided "pseudo-teeth" (Fig. 86). Dorsum. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures, and all other intersegmental divisions, only suturelike submedially. With 9 pairs of rays (Fig. 86) leading mesad from puparial margin and meeting intersegmental divisions, but abdominal divisions I/II and II/III do not merge with rays; pro-/meso- and meso-/ metathoracic segmental rays each marked apically by a dorsal cluster of tiny roughenings that resemble radular teeth (Fig. 86), and the pair of rays dividing abdominal segments VII/VIII similar (Fig. 85) but with the posterior marginal setae located immediately proximal to these roughenings. Dorsal disc flattened, smooth and without coloration in the study sample. Abdominal segment VII distinct medially, only a little over half as long as segment VI (Fig. 21). Vasiform orifice (Fig. 84) elongate-cordate, about 1.25 times longer than wide basally, laterally smooth, inset from caudal margin by 5–6 times its own length; operculum a little wider than long, laterally rounded, bearing a pair of posteromarginal setae similar to lingular setae; lingula head finely spinulose, exposed part triangular, exactly occupying posterior part of vasiform orifice, bearing the usual 4 subapical setae. Caudal furrow absent, but see pores. Chaetotaxy. With 15 pairs of inner submarginal setae present, including nominal caudal pair, these very fine but similar in length to operculum, their apices not closely approaching puparial margin (Fig. 86); single pairs of submedian cephalic, pro-, meso- and metathoracic setae present, similar to submarginal setae; eighth abdominal setae (Fig. 84) a little more robust, situated midway between the angular abdominal VII/VIII pockets and anterior corners of vasiform orifice. Anterior and posterior marginal setae present, similar to each other, stouter than submarginal setae, their bases situated ventrally, slightly away from margin (Fig. 85). Pores. Compound pores entirely absent. Whole of dorsum, excepting the rays and the median line at anterior and posterior ends of puparium, punctuated by many small, evenly spaced, granular pores, each appearing "notched" on one side (Figs 84, 86); in outer submargin is a row of apparently similar pores, many of which have a pale "tail" leading mesad (Fig. 86). Each of the 9 pairs of rays has its length punctuated by tiny, dark 4- to 5-locular pores (Fig. 86), which continue right across each segment; similar loculate pores line the longitudinal moulting suture, mark the position of an otherwise-absent caudal furrow, and border sides of vasiform orifice (Fig 84). Each loculate pore is clearly associated with an adjacent porette, but indistinct porettes scattered amongst the notched pores are less certainly associated. Venter. Ventral abdominal setae almost as long as vasiform orifice, their bases situated just posterior to it. Anterior and posterior marginal setal bases slightly displaced from margin, ventrally (Fig. 85). Underlying the rays on pro-/meso- and meso-/metathorax, and abdominal segment VII/VIII, are subtle tracheal folds which are finely spinulose distally (Fig. 85), but caudal tracheal fold is not marked thus. Legs each bisegmented, smooth, with the usual apical claw, and with a small number of very fine setae on distal segment, middle and hind legs each with a seta on its posterior basal corner. Antennae reaching bases of middle legs (Fig. 21), their bases situated anteromesal to fore legs. Feeding rostrum (Fig. 21) elongate, almost parallel-sided, about as long as an antenna.

ADULT. The adults of *D. bondariae* feed in groups, in lines, with their heads abutting a major leaf vein, and hold their wings at right angles to the body when undisturbed: the analogy to aircraft at a terminal is unavoidable. The fore wing is rather elongate, not emarginate on its posterior margin, is punctuated by yellowish-brown clouds and by two small black spots on anterior, and two more on posterior wing margin. Ventromarginal abdominal glands not discernible, but this may be an indication of the available specimens being rather teneral. Antennae 7-segmented, apically acute, with segment III rather thickened. Posterior abdominal segment of adult male elongate cylindrical, 0.90 mm long, densely covered by simple pores all over its surface; claspers each 0.78 mm long, with a rectangular boss on its inner edge at half-length, a brownish patch on its outer side at two-thirds length and brownish apically; aedeagus simple, shallowly curved, 0.39 mm long.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, San Pastor track, on woody Lauraceae, 18 xi.1994 (J.H.Martin #6494) (BMNH). Paratypes: 4 puparia, 1 adult female, same data as holotype (BMNH); 2 adult females, 1 adult male, same host and locality, 30 xi.1994 (Martin) (BMNH).

ETYMOLOGY. The species name reflects similarities to *D. radifera* (Sampson & Drews), which was originally proposed as type species of a separate genus, *Bondaria*.

COMMENTS. *D. bondariae* differs from *D. radifera* (Sampson & Drews) principally as follows: vasiform orifice around 1.25 times longer than wide (it is more rounded, and only about as long as wide in *D. radifera*); dorsal disc densely porate (mottled markings on syntype of *D. radifera* are apparently not pores).

During an attempt to re-collect *D. bondariae*, aggregations of adult females were found, along with a few old puparia and a few 2nd/3rd-instar larvae, on *?Nectandra* (Lauraceae). However, the old puparia were *D. caballeroi*, more often associated with *Persea* (see below); the larvae belonged to two species, probably *D. caballeroi* and *Nealeurodicus* fallax (q.v.); the adults are considered likely to belong to a species of *Nealeurodicus*, but with no evidence to associate them with the larvae of *N. ?fallax*. All specimens are available in BMNH.

Dialeurodicus caballeroi sp. nov. (Figs 22, 87–89)

PUPARIUM. Habitus. Scattered on the lower surfaces of leaves, not noticeably associated

ZOOTAXA

681

with major leaf veins, without visible secretions but a translucent plate of secretion is usually revealed during slide-making: when actively feeding, immature stages extremely cryptic, with leaf tissue often visible through body; post-emergence pupal cases silvery, with rays and median line variably brownish-pigmented (Fig. 22). Margin. Outline ovoid, often slightly asymmetrical, 1.78–2.41 mm long, 1.05–1.65 mm wide, generally widest at abdominal segment III/IV (n=20). True margin diaphanous, smooth, but immediately mesad is a row of short, raised corrugations that appear as marginal crenulations in many slide-mounted specimens (Fig. 87-88), about 8-10 per 0.1 mm. Margin is sometimes very subtly modified at apex of each posteriormost and second anteriormost ray, each of which overlies a tracheal fold. Dorsum. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures resembling other intersegmental folds, all terminating in subdorsum; submedian abdominal depressions not evident. Leading mesad from puparial margin are 9 pairs of rays (Fig. 22), each terminating in a cluster of simple pores, often borne on a shallow tubercle (Fig. 87), the rays and tubercles often variably pigmented, but less distinct when not so. Abdominal segment VII about two-thirds length of segment VI medially (Fig. 22). Vasiform orifice (Fig. 89) with its sides almost straight, apically truncate and often unevenly trilobate apically, inset from caudal margin by about 3 times its own length (Fig. 22); operculum a little wider than long, laterally rounded, bearing a pair of posteromarginal setae that are finer than lingular setae; lingula head finely spinulose, slightly emarginate between bases of basal pair of setae and lingular apex, fully occupying posterior part of vasiform orifice. Chaetotaxy. With 15 pairs of fine inner submarginal setae present (Figs 87-88), including nominal caudal pair, each seta about the length of the operculum; single pairs of submedian cephalic, pro-, meso- and metathoracic present; eighth abdominal submedian setae situated lateral to anterior corners of vasiform orifice (Fig. 89); submedian setae are similar to anterior and posterior marginal setae, all somewhat longer and more robust than submarginal setae. Pores. Compound pores entirely absent. Immediately mesal to outer submarginal crenulations is a single row of dark pores (Figs 87–88), possibly modifications of the 8-shaped type, laterally presenting and appearing shallowly "w"-shaped, about one pore to each pair of crenulations. Dorsal disc with many, fairly evenly distributed, tiny pore/porette geminate pairs (Figs 87-89). Additional to the geminate pore/porette pairs, parts of the rays (mostly distal) are punctuated by somewhat larger pores that are mostly 3-locular (Figs 87-88); loose agglomerations of similar 3-locular pores cover the tubercles usually present at proximal ends of rays, and still more mark median line of the puparium, some of them each clearly with an adjacent porette. Venter. Ventral abdominal setae each longer than operculum. Caudal tracheal fold only marked distally, by a few fine spinules; a pair of tracheal folds underlie posteriormost pair of dorsal rays, and a thoracic pair underlie the second anteriormost pair of rays, both pairs of folds marked by fine spinules distally. Leg, antennal and rostral characters (Fig. 22) as in D. bondariae, above.

ADULT. Abdomen of adult female has only two pairs of ventrolateral wax glands, sit-

uated at anterior end. Posterior abdominal segment of adult male is elongate cylindrical, around 0.50 mm long, densely covered by simple pores only on dorsal surface; claspers 0.43 mm long, each with a rectangular boss on its inner edge at half-length; aedeagus simple, shallowly curved, 0.25 mm long. Adults rest with their fore wings at right-angles to the body axis, as do the adults of the other two Belizean species of *Dialeurodicus*. A field note described the living adult thus: body yellow to orangy, with bright orange flecks laterally; wings with brownish clouds and black flecks. For future studies, a few adults were slide-mounted with their wings having been removed prior to maceration, the wings then separately mounted without any chemical treatment.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, Las Cuevas clearing, on *Persea americana* (Lauraceae), 10.ii.1996 (J.H.Martin #6633) (BMNH). Paratypes, BELIZE (all Martin coll.): 76 puparia, 7 third-instar larvae, 1 second-instar larva, 10 adult males, 13 adult females, all from same individual tree as holotype, 02.xii.1994, 10.ii.1996, 02.iii.1996, 11.vi.2002, 20.iii.2003 (BMNH, BZ, CDFA, USNM); 2 puparia dry on leaf, same data as holotype; 5 puparia dry on leaf, 02.iii.1996 (BMNH); 11 puparia, 2 third-instar larvae, Las Cuevas, on *Persea americana* (different tree), 10.vi.2004 (BMNH); 3 puparia, CFR, San Pastor track, on *?Nectandra* sp. (Lauraceae), 22.iii.2003 (BMNH). Paratypes, NICARAGUA: 26 puparia (1 dry on leaf), 4 second / third-instar larvae, Rio San Juan Province, Rio San Juan / Rio Bartola confluence, on *Persea americana*, 23.vi.2004 (Martin) (BMNH).

ETYMOLOGY. This species is named for Rafael De J. Caballero, who provided (1992) a description and illustration which almost certainly represent this species, but where it was not named because of International Commission for Zoological Nomenclature rules on nomenclatural changes within a thesis.

COMMENTS. In addition to the Belizean and Nicaraguan material examined in connection with the description presented here, Caballero (1992) had studied material from Honduras, also from avocado. A small sample of puparia collected from *?Nectandra* sp. in Belize, indicates a degree of oligophagy in this species.

Dialeurodicus silvestrii (Leonardi) (Figs 23, 60–61, 90, 132)

Aleurodicus silvestrii Leonardi, 1910: 320–322. Syntypes, Mexico.
Dialeurodicus silvestrii (Leonardi) Quaintance & Baker, 1913: 28–30.
Dialeurodicus tracheiferus Sampson & Drews, 1941: 152–153. Syntypes, Mexico [examined].
Syn. nov.

DISTRIBUTION. Neotropical Region — Belize, Mexico.

COMMENTS. This species is remarkable for the secretion, by each puparium, of three pairs of very long white ribbons of waxy material (Fig. 132). This material is produced

from large fields of crowded simple pores, which define the subdorsal zone (Figs 23, 60–61). The sole colony from Belize comprised small groups under the midribs of individual leaves widely scattered on their small myrtaceous tree host, probably a species of *Eugenia*, but collectively they amounted to a substantial sample. Emergent adults of this species rested with their wings held at right angles to the body when undisturbed, a characteristic possibly of generic significance (see description of *D. bondariae*, above).

Sampson & Drews (1941) were aware of the existence of Leonardi's (1910) description of *D. silvestrii*, but considered that their new species, *D. tracheiferus*, differed from it. They described *D. tracheiferus* as having thoracic tracheal folds, which is a character not revealed by examination of syntypic material, nor seen in Belizean material. However, syntypes of *D. tracheiferus* from Mexico (UCD), and most puparia from Belize, do each have a small *dorsal* patch of cuticular roughening opposite the position of the middle legs, seen in relief on the margin as irregular tiny "teeth" (Fig. 90). No type material of *Aleurodicus silvestrii* has been traced, but it is considered that Leonardi simply omitted to mention this minor character. Leonardi provided an otherwise accurate illustration of the microscopical puparial detail, and also an excellent *habitus* drawing of the six highly characteristic and enormously long white waxy ribbons that issue from each puparium: in contrast, Sampson & Drews made no mention of *habitus* appearance of *D. tracheiferus*, and the boundary of the dense field of wax-secreting simple pores is inaccurate in their drawing. *D. tracheiferus* is considered here to be a junior synonym of *D. silvestrii* **syn. nov**.

LEONARDIUS Quaintance & Baker

Leonardius Quaintance & Baker, 1913: 33. Type species *Aleurodicus lahillei* Leonardi, 1910: 316–320, by original designation.

DIAGNOSIS AND COMMENTS. As interpreted here, *Leonardius* comprises species with the following combination of puparial characters: a subdorsal ovoid patch of porous / granular structure, termed an "agglomerate pore", present on each side of body on cephalic segment and on each of abdominal segments III–VIII (Figs 24, 91–92); two pairs of abdominal compound pores present, on segments III & IV; cephalic compound pores present or absent; the compound pores are each situated in the centre of an agglomerate pore; thoracic cicatrices absent (*i.e.* compound pores absent in third-instar larva); 4 pairs of submedian cephalothoracic setae present; normally 15 pairs of submarginal setae present, each not extending to puparial margin; with submarginal area planar, true margin almost smooth but submarginal sculpture giving appearance of laterally-contiguous teeth (Fig. 91); remainder of dorsal disc bearing only scattered simple pores.

The puparia of species of *Leonardius* and *Bakerius* in BMNH each possess only two pairs of abdominal compound pores, situated on segments III & IV. Puparia of species placed in *Bakerius* also possess a pair of cephalic compound pores, whereas those of the two hitherto described species of *Leonardius* have only agglomerate pores on the cephalic segment, a gland type not seen in the species of *Bakerius*.

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Two puparia collected from *Erythrina* from Colombia, and an extensive sample from a mistletoe in Belize, possess agglomerate pores and cephalic compound pores (Fig. 24), with abdominal pores as in the described species of *Leonardius*, thus combining the *Bakerius* compound pore arrangement with the presence of agglomerate pores that is diagnostic for *Leonardius*. Puparia-associated adults of *B. attenuatus* Bondar, *B. phrygilanthi* Bondar, *L. lahillei* and the Belizean sample are available in BMNH, and differences in such characters as wing venation, wing coloration, antennal structure, abdominal wax glands and head shape seem consistent with interspecific differences only. It is possible that future opportunities to study the puparia and associated adults of more species, in more detail, may lead to the conclusion that *Bakerius* and *Leonardius* are synonymous. However, agglomerate pores are a feature not seen in any other members of the Aleurodicinae, and it is considered that the two genera should remain separate pending further study. The Belizean sample represents a new species of *Leonardius*, which is here described.

Leonardius kellyae sp. nov.

(Figs 24, 91-92)

PUPARIUM. Habitus. The original colony had suffered abrasion of the waxy secretions, but the numerous puparia were located in whitish-mealy patches on the leathery leaves of their host, and many fragments of thickened waxy rods had clearly been secreted by the compound pores. The individual puparia appeared brownish, and quite cryptic despite their numbers. Margin. Outline elongate-ovoid, usually subtly more acute posteriorly (Fig. 24), 1.30–1.44 mm long, 0.80–0.90 mm wide, generally widest at abdominal segment I/II (n=10). Margin almost smooth but with short fine folds running mesad, giving a false impression of laterally contiguous marginal teeth (Fig. 91), about 7 occupying 0.1 mm; alternate "teeth" each with a tiny basal circular gland (similar to a simple pore); true margin sometimes very slightly modified at the tracheal openings. Dorsum. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures terminating above inner margins of apical segments of middle legs. Dorsal disc generally smooth. Abdominal segment VII subequal in length to segment VI medially. Vasiform orifice (Fig. 92) rounded-triangular, inset from posterior puparial margin by slightly less than its own length, its sides often slightly emarginate, orifice floor rugose, its posterior end bearing a distinct apical process; operculum transversely oval, dorsally faintly corrugate, with a pair of posterior marginal setae that almost exactly overlie edges of lingula; lingula occupying remainder of vasiform orifice, included within it except for the apices of its 4 setae. Caudal furrow absent. Chaetotaxy. Possessing single pairs of anterior and posterior marginal, 4 pairs of submedian cephalothoracic, single pair of eighth abdominal and 15 pairs of sub-

marginal setae, all similar and hair-like, the submarginal setae not reaching puparial margin (Fig. 91). Cephalic setae situated anterior to mouthparts, eighth abdominal setae lateral to anteriormost part of vasiform orifice. Pores. Cephalic compound pores 50-55 µm in diameter, compound pores on abdominal segments III & IV 65-75 µm in diameter, each with half its diameter comprising the central lumen, from which arises an acute axial process (Fig. 91) that extends beyond the pore by the equivalant of a pore diameter (but these processes are often missing or incomplete in slide-mounted specimens). Largest agglomerate pores are those surrounding the compound pores, 140–150 µm in diameter, each with a crescent of small bright pores in its outer zone (Fig. 91); cephalic pair (Fig. 24) less sharply defined than the abdominal agglomerate pores which are almost confluent at segment III/IV boundary; agglomerate pores on abdominal segments V-VIII much smaller (Figs 91-92), each punctuated by a few bright pores. Dorsal disc with many randomly distributed simple pores, not evidently associated with adjacent porettes. Venter. Ventral abdominal setae similar to dorsal setae, but difficult to detect in many individuals, when lying directly underneath operculum and lingula. Legs each typically smooth and bisegmented, with a single apical claw. Antennae reaching articulations of middle legs (Fig. 24), only their basal quarter to one-third laterally smooth, their bases anteromesal to fore legs.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, Las Cuevas, on Loranthaceae, 02.viii.2003 (S. Kelly & A. Polaszek) (BMNH). Paratypes: 40 puparia, 6 third-instar larvae, 3 third-instar / puparium inter-moults, 12 adult males, 11 adult females, same data as holotype (BMNH, USNM); numerous puparia dry on leaves, same data as holotype (BMNH).

ETYMOLOGY. This species is named for Suzanne Kelly, who noticed the type colony on leaves of an arboreal mistletoe.

COMMENTS. As discussed under the generic comments this species, in common with two individuals of another species from Colombia, displays a combination of compound / agglomerate pore characters that has indicated a close relationship between *Bakerius* and *Leonardius*. In possessing cephalic compound pores at the centre of larger agglomerate pores, *L. kellyae* is immediately distinguished from both described species of *Leonardius* (but see below). The Colombian specimens are presumed to represent a separate species; they have compound pores of much greater diameter, and their agglomerate pores are punctuated by many more bright pores than in *L. kellyae*.

Examination of material of five different samples in BMNH, from four countries, has led to the conclusion that Costa Lima (1928) was correct in his tentative suggestion that *L. loranthi* Bondar (1923a) is a junior synonym of *L. lahillei* (Leonardi, 1910) **syn. nov.**

METALEURODICUS Quaintance & Baker

Aleurodicus (Metaleurodicus) Quaintance & Baker, 1913: 73. Type species Aleurodicus minima Quaintance, 1900: 47–48, by original designation.

Metaleurodicus Quaintance & Baker; as full genus, Bondar, 1923a: 81.

Pseudaleurodicus Hempel, 1922a: 9. Type species Pseudaleurodicus bahiensis Hempel, 1922a: 9– 10 by monotypy. [Synonymised with Aleuronudus by Costa Lima, 1936: 146, but here regarded as a synonym of Metaleurodicus syn. nov.]

DIAGNOSIS AND COMMENTS. As interpreted here, *Metaleurodicus* comprises species with the following combination of characters: submedian cephalothoracic setal pairs absent; 4–6 pairs of abdominal compound pores present, forming a smooth arc on either side of body, without any pairs conspicuously inset mesally (Figs 25–32); if only 4 pairs present, it is anterior pairs that are lost, with a pair always present on each of segments V–VIII; two pairs of cicatrices present on thoracic area (scars of third-instar compound pores); dorsal disc without distinct groupings of simple pores, although often with large numbers evenly distributed; dorsal disc simple pores often loculate, in which case the septa may lend the pores the appearance of being cruciate or stellate (Figs 93–96); with submarginal setal row comprising 12 pairs, including the nominal caudal pair. Also, see generic discussion for *Aleuronudus*.

The puparia of *M. pigeanus* (Baker & Moles, 1921) (Fig. 15), known only from Chile, possess paired submedian cephalothoracic setae, and this species is therefore here referred to *Austroaleurodicus* Tapia (1970) **comb. nov.** — see generic key, p. 14.

Four species of *Metaleurodicus* have been discovered in Belize, and they may be distinguished by use of the key, below.

Key to *Metaleurodicus* species in Belize — puparia

Abdominal compound pores of 2 or 3 different sizes (Figs 28–32), numbering 6 pairs.
Abdominal compound pores all similar to each other (Figs 25–27), numbering 5 or 6 pairs
Abdominal compound pores numbering 5 pairs (Fig. 25) arcanus sp. nov.
Abdominal compound pores numbering 6 pairs (Figs 26, 27) 3
Abdominal compound pores presenting laterally when viewed on slides appearing
cylindrical (Figs 27, 96); tiny submarginal setae located in extreme outer submargin
Abdominal compound pores appearing circular when viewed on slides (Figs 26, 94);
submarginal setae inset further from puparial margin but longer and coarser

Metaleurodicus arcanus sp. nov. (Figs 25, 93)

PUPARIUM. Habitus. Detailed appearance of holotype sample not noted prior to preservation. Margin. Outline oval, 0.88–1.25 mm long, 0.58–0.87 mm wide (n=10), generally widest at abdominal segment II/III. Margin smooth but with short fine folds running mesad, giving a false impression of contiguous marginal teeth (Fig. 93); margin not modified at thoracic tracheal openings. Dorsum. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures terminating in inner submargin. Dorsal disc generally flat and smooth, but abdominal segments often having a slightly developed median rhachis without lateral arms (Fig. 25). Abdominal segment VII medially about one-third of length of segment VI. Submedian abdominal depressions very narrow, hardly differentiated from intersegmental divisions. Vasiform orifice (Fig. 93) cordate, very slightly emarginate at half length; operculum much wider than long, laterally rounded, posteriorly sinuate with a pair of stout marginal setae, its surface finely spinulose except anteriorly and medially; lingula head tongue-shaped, its apex (including the 4 subapical setae) slightly protruding beyond vasiform orifice. Chaetotaxy. Anterior marginal setae present, minute. Outer submargin with 12 pairs of hair-like setae, the caudal pair (Fig. 93) longer and more robust than remainder, thus similar to the posterior marginal pair; submedian pairs of cephalothoracic setae absent. Eighth abdominal setae (Fig. 93) similar to submarginal setae, located anterior to vasiform orifice, opposite anterior corners of operculum. Pores. Immediately inside puparial margin, each lying between a pair of the short marginal folds, is an even single row of black scallops (Fig. 93), probably pores seen in lateral aspect; a similar distance mesad again is a single row of bright pores, each not apparently associated with one of the scallops; both these rows lie between the submarginal setae and puparial margin (Fig. 93). Compound pores (Fig. 25), one cephalic pair and 5 abdominal pairs, present on abdominal segments IV-VIII [one specimen with the compound pore missing from abdominal segment IV on one side], all subequal in size, rather bell-shaped (Fig. 93), around 20 µm in diameter in larger puparia, only 12–16 µm in smallest examined puparia; compound pores apparently without spinneret cells in the outer zone. Dorsal disc punctuated by moderate numbers of, apparently randomly-distributed, 4- to 5-locular pores (Fig. 93), each pore appearing somewhat cruciate or stellate, and also by minute wide-rimmed bright pores. Venter. Ventral abdominal setae each longer and finer than any dorsal seta, underlying vasiform orifice to either side of lingula. Ventral abdominal spiracles lying to either side of lingular apex (Fig. 25). Middle and hind legs typically smooth and bisegmented. Antennae reaching articulations of middle legs, only their basal quarter to one-third laterally smooth, their bases anteromesal to fore legs.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, Monkey Tail track, on *Chiococca ?alba* (Rubiaceae), 04.iv.2003 (J.H.Martin #7843) (BMNH). Paratypes (all from CFR, Martin coll.): 9 puparia, 1 adult female, same data as holotype; 3 puparia, Las

Cuevas area, on undetermined host, 02.vi.2002 (BMNH); 4 puparia, 2 third-instar larvae, 1 second instar larva, Las Cuevas area, on undetermined host, 23.iii.2003 (BMNH); 11 puparia, 7 adult females, 2 adult males, Monkey Tail track, on Chiococca ?alba (Rubiaceae), 01.vi.2004; 7 puparia, 1 adult female, Las Cuevas – Millionario road, on Chiococca ?alba, 03.vi.2004 (BMNH, USNM).

ETYMOLOGY. This species bears the name arcanus (Latin, meaning hidden/concealed), reflecting the natural appearance of this species.

COMMENTS. This species most closely resembles M. cardini (Back, 1912), but M. arcanus possesses five pairs of abdominal compound pores, and M. cardini only four: also, M. cardini has a row of 8-shaped pores between the submarginal setae and the scallops / pale pore band, which *M. arcanus* lacks.

Metaleurodicus griseus (Dozier)

(Figs 26, 94)

Aleurodicus griseus Dozier, 1936: 143–144. Syntypes, Puerto Rico [examined]. Metaleurodicus griseus (Dozier) Hamon, 1989: 2.

DISTRIBUTION. Neotropical Region — Belize, Barbados, Jamaica, Puerto Rico; Nearctic Region — Florida.

COMMENTS. M. griseus is represented from Belize by a single parasitised puparium, collected from the upper midrib of an undetermined woody sapling host. Figs 26, 94 depict a complete puparium, in good condition, from Dade County, Florida, U.S.A.. Major characters are 6 pairs of abdominal compound pores, the lingula fully included within the vasiform orifice, with a pair of basal lingular shoulders, with loculate pores scattered across the dorsal disc, and with the compound pores on posterior abdominal segments presenting axially to the viewer - see key to Belize species of Metaleurodicus, above.

Metaleurodicus tenuis sp. nov. (Figs 27, 62, 95–96)

PUPARIUM. Habitus. Feeding singly or in small aggregations under the midribs of leaves, oblique to the midrib. Fine waxy filaments are secreted, but these are clear and usually only seen when light is reflected. When viable (i.e. feeding and not parasitised), the puparia and earlier instars are quite cryptic, but some specimens that were reddish in colour were later found to be parasitised. Margin. Outline ovoid, slightly narrowed anteriorly (Fig. 27), widest at abdominal segments III/IV, 1.27-1.55 mm long, 0.80-1.05 mm wide (n=19). Margin smooth but with short fine folds running mesad, giving an impression of contiguous marginal teeth, margin appearing crenulate when slightly downcurled,





about 9-11 folds / crenulations per 0.1mm, margin not modified at thoracic tracheal openings. Dorsum. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures variably discernible as far as subdorsum or submargin. Dorsal disc generally smooth but submargin, as far as arc of compound pores, with a marbled appearance (Fig. 62), possibly glandular in nature. Abdominal segment VII medially about half length of segment VI (Fig. 27). Submedian abdominal depressions (Fig. 95) well-developed and distinct from remainder of length of intersegmental divisions, which are well-defined into subdorsum. Vasiform orifice (Fig. 96) rounded-triangular, longer than wide; operculum almost straight anteriorly and posteriorly, rounded laterally, with a band of fine spinules lining its posterior margin, which also bears a pair of very fine setae; lingula head tongueshaped, finely spinulose, almost entirely included within vasiform orifice, its 4 setae subapically situated, almost completely overlapping boundary of vasiform orifice. Chaetotaxy. Anterior marginal setae present, minute. Extreme outer submargin with a row of 12 pairs of hair-like setae (Fig. 27), each similar in length to compound pore diameter, except for the caudal pair and adjacent pair (Fig. 96), which are longer and stouter, each resembling a posterior marginal seta. Paired cephalothoracic submedian setae absent. Eighth abdominal setae situated anterior to, and opposite corners of, operculum, similar to submarginal setae (Fig. 96). Pores. Immediately mesal to marginal crenulations lies a row of widely-spaced modified 8-shaped pores (Fig. 96), at least 3 crenulations present between most pairs of these pores, and bases of submarginal setae interspersed with them. Cephalic and 6 evenly-spaced abdominal pairs of compound pores, on segments III-VIII, all subequal in size (Fig. 27), each rather narrowly cylindrical, emarginate-sided, up to about 25 μ m in diameter, nearly twice as long as wide, each with axial process not protruding beyond pore mouth; outer zone of each compound pore apparently without spinneret cells. Dorsal disc with moderately numerous, randomly scattered, 4- to 5-locular pores (Figs 95– 96), and less numerous minute bright pores present. Venter. Ventral abdominal setae similar to submarginal dorsal setae, underlying posterior corners of operculum, anterior and slightly mesal to posterior abdominal spiracles. Legs bisegmented, smooth, with 1-3 tiny setae visible near bases of some or all legs. Antennae smooth-sided only in basal one-third part, curved from base to apex, reaching to bases of middle legs (Fig. 27).

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, Las Cuevas permanent study plots, on Myrtaceae, probably *Eugenia* sp., 29.iii.2003 (J.H.Martin #7827) (BMNH). Paratypes: 30 puparia, 1 third-instar larva, same data as holotype (BMNH, USNM); 1 complete puparium, 2 post-emergence parasitised puparia, dry on leaf tissue, residue of type sample (BMNH).

ETYMOLOGY. The specific epithet is the Latin, *tenuis* (meaning fine or slight), describing the sparse puparial secretion.

COMMENTS. *M. tenuis* resembles *M. griseus* (Dozier), having 6 pairs of evenlyspaced abdominal compound pores: however, *M. griseus* has compound pores little longer than wide (Fig. 26), in contrast to the emarginate-cylindrical form observed in *M. tenuis* (Fig. 27). *M. tenuis* has a row of fine setae in the extreme outer submargin (Fig. 27), whereas those in *M. griseus* are inset further mesad, and are longer and coarser (Fig. 26).

Metaleurodicus variporus sp. nov.

(Figs 28-32, 97-98)

PUPARIUM. Habitus. The immature stages develop in loose aggregations under leaves, most individuals having chosen feeding positions adjacent and nearly parallel to a major leaf vein, but not only the midrib. Visible was secretion comprises fine, transparent filaments: each of the dorsal compound pores secretes a long and rather rigid filament, and these readily break off as length increases; the filaments issuing from the largest compound pores are visibly hollow and thicker than the remainder; a short, transparent, wax rod issues from each submarginal cup-shaped pore, to give the puparium a sparse fringe. Despite wax filaments, the feeding larval and nymphal stages are extremely cryptic, the leaf tissue being visible through the body. Margin. Outline rather narrowed cephalically (Figs 28-32), 1.10-1.40 mm long, 0.68-0.90 mm wide (n=50), widest at abdominal segment IV/V. Margin smooth to slightly uneven, but may appear irregularly crenate if slightly downcurled (Fig. 98), not modified at thoracic or caudal tracheal openings. Dorsum. A series of fine lines run mesad from margin as far as the submarginal setal bases, revealed as corrugations when seen in relief through down-curling of the puparial margin (Fig. 98). Longitudinal moulting suture reaching puparial margin, transverse moulting sutures reaching submargin, the sutures sometimes difficult to discern distally. Segmentation well marked across subdorsum, from meso-/metathorax to abdominal segment VII/ VIII, with pro-/mesothoracic suture only distinct medially; abdominal segment VII half length of segment VI medially. Vasiform orifice (Figs 28-32) cordate; operculum transversely rounded-rectangular, with a pair of fine setae present on its sinuate posterior margin; lingula head tongue-shaped, extending about half way from posterior margin of vasiform orifice to puparial margin, bearing 4 stout setae. Chaetotaxy. Anterior and posterior marginal setae present, anterior pair minute but posterior pair similar to caudal pair of submarginal setae. Outer submargin with 12 pairs of hair-like setae (Fig. 98), including nominal caudal pair which are somewhat longer than remainder. Dorsal disc setae restricted to eighth abdominal pair, anterior to vasiform orifice and adjacent to anterior corners of operculum. Pores. Cephalic and 6 pairs of abdominal compound pores present, of three variants, always at least two variants present in an individual (Figs 28-32): large variant each $\sim 40 \ \mu m$ diameter (up to 50 $\ \mu m$ in one individual), robust and clearly cylindrical, usually presenting laterally or obliquely (Fig. 98) on slides; medium variant ~30 μ m, cup-shaped, often presenting axially or obliquely, when the basal loculi then resemble a stylised flower (Fig. 98); small variant ~20 μ m, usually presenting laterally. Cephalic compound pores always of the small or medium variant, 2nd and 4th abdominal pairs

always of the large variant, 6th (posteriormost) abdominal pair always small, 1st and 5th abdominal pairs large or medium, 3rd abdominal pair may be any of the three variants; commonest abdominal combinations are LLSLLS (Fig. 31, n=53) & MLMLMS (Fig. 28, n=38), total n=118. Each compound pore with a short, truncate central process which, at most, protrudes only slightly beyond the pore mouth (Fig. 98). Outer subdorsum with a single row of cup-shaped simple pores (see *habitus* description), presumed to be the 8shaped type described by Russell (1965) but with the structure indistinct, fairly evenly spaced except where submarginal setae interrupt the row (Fig. 98). Remainder of dorsal disc smooth, except for scattered tiny simple porettes and larger quadrilocular pores (Fig. 98). Venter. Ventral abdominal setae underlying vasiform orifice, of similar length to it. Legs large, each two-segmented, with a single apical claw, sometimes relatively "larviform" in appearance (Figs 97b,c) but much larger in mature specimens (Fig. 97a), see discussion below. Antennae of mature specimens reaching mid-point of middle legs (Figs 31, 97a): however those of many individuals considerably reduced, and when viewed laterally (Fig. 97c) they are much shorter than apical segment of foreleg, extremely corrugate; many others have completely vestigial antennae, appearing subcircular with only the apex distinct (Figs 28-30, 32, 97b). Rostrum acute-triangular (Figs 28-29).

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, San Pastor track, on *Lasianthaea fruticosa* (Asteraceae), 28.ii.1996 (J.H.Martin #6714) (BMNH). Paratypes (all CFR, Martin coll.): 133 puparia, 15 third-instar larvae, 2 second-instar larvae, 6 adult females, tracksides in Las Cuevas vicinity, same host as holotype, 30.xi.1994, 28.ii.1996, 06.iii.1996, 04.vi.2002, 20.iii.2003, 22.iii.2003, 24.iii.2003 (BMNH, BZ, USNM); 5 puparia, same locality, on *Urera* sp. (Urticaceae), 28.ii.1996; 7 puparia, 1 third-instar / puparial mid-moult, 1 third-instar exuviae, on ?Euphorbiaceae, 23.iii.2003; 6 puparia, 1 third-instar larva (all slide-mounted) & 5 puparia, 3 third-instar larvae (dry on leaves), same locality, undetermined host, 20.xi.1994 (all BMNH).

ETYMOLOGY. The specific epithet is derived from the Latin, *varius* (meaning changeable or variable), reflecting the pronounced variability in the dorsal compound pores of the puparium, within populations.

COMMENTS. This species exhibits unusual developmental features, affecting the puparial legs, antennae and compound pores. The marked plasticity of size and, hence, form displayed by the compound pores is a feature that is not usual, but has been observed in a few other Aleurodicinae. The reason for the vestigial nature of the puparial antennae in some samples (see *venter*, above) is not certain, but a few specimens from reduced-antenna samples have the antennae beginning to lengthen (Fig. 97c), and all post-emergence pupal cases have normal antennae (Fig. 97a). A similar phenomenon appears to affect the development of the puparial legs, with fully-developed legs only apparent in specimens that also have fully developed antennae (Figs 31, 97a). It seems likely that the antennae and legs do not begin to expand towards their full length until some time after the third/fourth instar moult. There is no obvious correlation between antennal and leg devel-

opment and the distribution of compound pore types. The holotype puparium has fully developed antennae and legs.

Caballero (1992) presented a description and puparial illustration of a species that is almost certainly *M. variporus*, from an ornamental plant in Guatemala, but listed it only as an undescribed member of the Aleurodicinae.

M. variporus may be distinguished from the other *Metaleurodicus* species known from Belize by use of the key, above.

NEALEURODICUS Hempel

Nealeurodicus Hempel, 1922b: 1134, 1170. Type species *Nealeurodicus paulistus*, by original designation and monotypy

DIAGNOSIS — PUPARIUM. Nealeurodicus comprises species with the following suite of characters that differ from those of species of Ceraleurodicus (in which genus most *Nealeurodicus* species were accommodated prior to the present work): bases of the 12–15 pairs of submarginal setae situated very close to margin, the setae themselves long and robust, with almost their entire lengths reaching beyond puparial margin, forming a distinct fringe (Figs 33, 35-37, 117); margin somewhat thickened, often down-curved, appearing crenate; puparia at most slightly asymmetrical, with compound pores always paired on each side of body (Fig. 117); a variable number of pairs of radial rays often present (Figs 33, 35, 37), sometimes indicated by pigmentation, or indistinct, but without marginal modifications at their extremities; almost always with a cephalic pair and a postvasiform orifice pair of compound pores on abdominal segment VIII, but distribution, size and structure of compound pores very variable between species. Other characters are shared with Ceraleurodicus and include: single pairs of submedian cephalic, pro-, mesoand metathoracic setae present; cicatrices absent from thorax (reflecting absence of compound pores in third-instar); lingula with 4 apical setae and normally included within the vasiform orifice. Puparia of species of Nealeurodicus typically secrete a dorsal crust of hard, waxy material that appears fibrous towards the edges of the crust (Figs 34, 38).

COMMENTS. The type species of *Ceraleurodicus*, *C. splendidus* Hempel, clearly belongs to an assemblage of species quite different from several other species that have hitherto been accommodated within the genus. As far back as 1930, Laing opined that his new species, *melzeri*, was congeneric with *octifer* and *bakeri* (both Bondar) (all three described in *Radialeurodicus*, later placed as a junior synonym of *Ceraleurodicus* by Costa Lima (1928), through synonymy of the type species of the two genera), but that these three species were only "doubtfully congeneric" with *C. splendidus*. Through the kindness of MZUSP, the author was able to study syntypic puparial material of *Nealeurodicus* melzeri. The following species are therefore here transferred to *Nealeurodicus* from *Ceraleurodicus* —



altissimus (Quaintance, 1900), *bakeri* (Bondar, 1923a), *ingae* (Baker, 1937), *melzeri* (Laing, 1930), *moreirai* (Costa Lima, 1928) and *octifer* (Bondar, 1923a) (all **comb. nov.**). Two new species of *Nealeurodicus* from Belize are here described.

In addition to the puparial characters discussed above, adult females of *C. varus* (Bondar) have only two pairs of ventro-lateral wax plates, whereas those of *N. altissimus*, *N. bakeri* and a new species, here described, have four pairs: it is unfortunate that adults are unknown for most of the species now placed in *Ceraleurodicus* and *Nealeurodicus*, so testing this character across the whole assemblage has not been possible.

During the course of study of the *Ceraleurodicus / Nealeurodicus* assemblage, the author has become convinced that the number, distribution between and within segments, and structure of compound pore pairs are of much greater importance in species definitions, than is cuticular pigmentation. *Radialeurodicus melzeri* Laing (1930) was synonymised with *Ceraleurodicus moreirai* Costa Lima (1928) by Mound & Halsey (1978: 239), presumably because of the near-identical pattern of pigmentation. However, the puparia of *N. melzeri* have a pair of compound pores on each of abdominal segments II, IV, VII and VIII, whereas puparia of *N. moreirai* only have pairs on abdominal segments II and VII, and thus *N. melzeri* should not be regarded as a synonym of *N. moreirai* (but see below).

The puparium of *N. paulistus* was described as possessing six pairs of abdominal compound pores. Examination of the two puparia present on the slide quoted as "type" by Hempel (1922b) was hampered by the presence of the dorsal wax crust on both specimens, which had clearly not received any sort of treatment prior to slide mounting. However, it can be seen that six pairs of abdominal compound pores are only present on one side of one specimen: the other side of this individual, and both sides of the other specimen, only have abdominal compound pores on segments II, IV, VII & VIII, thus matching the arrangement in *N. melzeri* (Laing). Despite the presence of secretions covering the syntype puparia of *N. paulistus*, it is possible to see that the characters of the vasiform orifice, are identical to *N. melzeri*. It is therefore considered that *N. melzeri* should be regarded as a junior synonym of *N. paulistus*, a species whose puparia are considered normally to possess abdominal compound pores on segments II, IV, VII & VIII (syn. nov.).

Key to Nealeurodicus species in Belize — puparia

- 3 Abdominal compound pores present on segments II, IV, V and VIII; without a distinct shoulder on each side of the lingula (Fig. 117)...... *petiolaris* sp. nov.

Nealeurodicus altissimus (Quaintance) comb. nov.

(Figs 33, 99-101, 128)

Aleurodes altissima Quaintance, 1900: 20–21. Syntypes, Mexico [examined]. Aleurodicus altissimus (Quaintance) Cockerell, 1902: 280 Aleurodicus (Metaleurodicus) altissimus (Quaintance) Quaintance & Baker, 1913: 73 Metaleurodicus altissimus (Quaintance) Bondar, 1923a: 81 Radialeurodicus altissimus (Quaintance) Baker, 1937: 608. Ceraleurodicus altissimus (Quaintance) Mound & Halsey, 1978: 238.

DISTRIBUTION. Neotropical Region — Belize, Colombia, Costa Rica, Mexico, Nicaragua, Panamá, Venezuela.

COMMENTS. *N. altissimus* is principally defined by the following suite of puparial characters: a row of typically 15 pairs of long outer submarginal setae present (Fig. 33); the cephalic and third abdominal pairs of compound pores are of unique structure (Figs 100, 101), the small main pore (12–20 μ m diameter) featuring a 3-spoked central opening, surrounded by an array of wide-rimmed bright simple pores; each of abdominal segments IV–VII bearing a pair of elongate compound pores that present laterally to the viewer (Fig. 99), each about 12–16 μ m in diameter; abdominal segment VIII with a pair of compound pores similar in diameter to those on segments IV–VII, but not elongate, presenting axially to the viewer; more mature puparia are rendered highly visible by secretions of characteristic spiky form (Fig. 128) which can become opaquely white but younger, actively feeding, individuals are often extremely cryptic.

There is evidence to suggest that *N. altissimus* comprises a complex of very closelyrelated species. The axial processes of the compound pores on abdominal segments IV– VII differ substantially between populations. In some samples, each process is truncate, hardly extending beyond the pore mouth (Fig. 99b); in others, the process is simply somewhat longer, but sometimes (notably on *Inga* species) the axial process of each compound pore is acute and sword-like, more than doubling the overall length of the structure (Fig. 99a). There is substantial variation in the degree and nature of puparial cuticular pigmenta-

tion, affecting the appearance of many of the simple pores, but pigmentation alone is unlikely to be a useful character (see generic discussion, above). The density of distribution of the dorsal disc simple pores, the degree of tubercle development in the outer submargin, and the position of the compound pores on abdominal segment VIII, relative to those on segment VII, also vary. Puparia-associated adults are only available for two samples, and yet one significant difference is apparent between them: females of a population from *Inga* possess a distinct cluster of bright pores on each side of the vasiform orifice, but such pores are entirely wanting in females from *Canavalia* cf. *oxyphylla*. Once again, investigation of puparia and associated adults from a wider variety of populations is desirable.

N. altissimus sensu lato is one of the most abundant members of the Aleurodicinae in the CFR, and is common elsewhere in Central America. Baker (1937) proposed a new species, *N. ingae*, for a member of the *altissimus*-group that has much broader compound pores on abdominal segments IV–VII, but specimens matching this nominal species have not been found amongst several samples taken from *Inga* in Belize. The limited available material, collected elsewhere in Central America and identified as *N. ingae*, also reveals variation in compound pore size.

To judge from the BMNH collection and the results of this study, *N. altissimus sensu lato* displays a clear preference for fabaceous [legume] hosts although, curiously, host plant data available to Mound & Halsey (1978) did not include any legumes at all. Indeed, material present in BMNH has all been collected from Fabaceae — in the genera *Canavalia*, *Cassia*, *Erythrina*, *Inga*, *Loncohcarpus*, *Machaerium*, and from one unidentified legume.

Nealeurodicus bakeri (Bondar) comb. nov.

(Figs 34-35, 116, 131)

Radialeurodicus bakeri Bondar, 1923a: 21–24. Syntypes, Brazil [probable syntypes examined]. *Ceraleurodicus bakeri* (Bondar) Costa Lima, 1928: 137 [by inference].

DISTRIBUTION. Neotropical Region — Belize, Brazil, Costa Rica, Nicaragua, Panamá, Trinidad.

COMMENTS. Although definite syntypes of this species have not been examined, four puparia on one slide were donated to BMNH by Bondar, and these are probably syntypic. The reason for making this statement is that the date borne on the slide label is "7.xii.1923", exactly the same date as is borne on the labels of a number of other slides donated to BMNH at the same time, and registered in 1924. It is likely that this is not a date of collection, but a date of selection for donation or a date of receipt at BMNH, neither precluding the material being part of Bondar's original series.

This species is distinguished from other species of Nealeurodicus by the presence of

small, circular compound pores on the cephalic segment and abdominal segments II, IV and VIII, the pair on segment IV being displaced a little further away from the median line (Fig. 35). The dorsal disc is punctuated by 4- to 5-locular simple pores, but such pores are absent from the median part of abdominal segment VIII between the vasiform orifice and the pockets (Fig. 116); additionally, there is a small cluster of bright pores present on each side of the vasiform orifice, and irregularly distributed minute composite pores (usually 2– 5 within an outer boundary) (Fig.116). The puparial secretions are robust and may be detached and slide-mounted (Fig. 34), but are not obvious to the naked eye (Fig. 131).

N. bakeri is represented in BMNH by material from the countries listed above; recorded host plants include palms and several broadleaf families (see Appendix 2), and no clear host preferences are shown.

Nealeurodicus fallax sp. nov.

(Figs 36, 102, 103)

PUPARIUM. Habitus. Little secretion evident, appearing blackish to naked eye. Margin. Overall outline elongate-oval, somewhat asymmetric with one side less curved through development alongside major leaf vein (Fig. 36), with series of shallow indentations lending margin a wavy appearance, puparium 1.75–1.90 mm long, 0.92–1.07 mm wide, widest at abdominal segment III (n=2). Margin, when not obscured by downcurling, with very small and rather irregular crenulations, about 14 occupying 0.1 mm; margin not modified at tracheal openings. Dorsum. Cuticle darkly pigmented except for a pair of pale submarginal patches on prothorax, metathorax, and abdominal segment V/VI, and a median pale patch posterior to vasiform orifice (Fig. 36). Abdominal segment VII medially slightly shorter than each of segment VI and segment VIII anterior to vasiform orifice (Fig. 102). Submedian abdominal depressions each marked as two or three contiguous subcircular markings (Fig. 102). Vasiform orifice (Fig. 102) elongate-cordate, about 0.16 mm long, 0.11 mm wide, inset from posterior margin of puparium by 0.21–0.24 mm, thickened but evenly rounded posteriorly, inner lateral margins and orifice floor finely striate; operculum laterally curved, much wider than long, occupying only basal one-third of vasiform orifice, with a very fine pair of posterior-marginal setae just discernible in holotype; lingula head finely spinulose, similar in shape to vasiform orifice, just reaching posterior rim of orifice, with a distinct basal shoulder on each side and bearing the usual 4 stout subapical setae. Chaetotaxy. With 12 pairs of robust, hair-like setae in extreme outer submargin (Fig. 36), including the nominal caudal pair, most in excess of 100 µm long; anterior and posterior marginal setae a little shorter than submarginal setae, similar to 4 paired submedian cephalothoracic and pair of eighth abdominal setae. Pores. Single pairs of compound pores present cephalically and on abdominal segments II, IV, V, VI and VIII, the pores on segment VIII situated to either side of apex of vasiform orifice and slightly smaller than remainder (Fig. 102). All compound pores ring-like, with thickened rims, each $15-20 \,\mu m$

in diameter, the axial lumen with tightly bundled rod-like structures which do not emerge beyond pores; outer torus of each compound pore (excepting those on abdominal segment VIII) with subcircular "spinneret" cells (terminology of Quaintance & Baker, 1913) forming a single ring of 12–15 cells (Fig. 103). Whole of dorsum densely punctuated by evenly-distributed, mostly quadrilocular, simple pores (Fig. 102, expanded detail); small, bright, wide-rimmed pores also occur in small aggregations of 2–5 pores bounding submedian zone; a more distinct aggregation of larger bright pores present to either side of vasiform orifice (Fig. 102, expanded detail). *Venter*. All characters as in *N. petiolaris* (below) except thoracic tracheal folds unmarked.

MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, San Pastor track, on *Sebastiania longicuspis* (Euphorbiaceae), 31.v.2004 (J.H.Martin #7963) (BMNH). Paratypes: 1 puparium, same data as holotype (BMNH); 1 third-instar / puparium intermoult, Las Cuevas, on *Persea americana* (Lauraceae), 04.xi.1994 (Martin) (BMNH). Other material: 1 third-instar larva, 1 second-instar larva, Las Cuevas, on *Nectandra* ?nitida (Lauraceae), 23.iii.2003 (Martin) (BMNH).

ETYMOLOGY. The specific epithet is the latin adjective *fallax* (meaning elusive), reflecting the difficulty in finding specimens of this species.

COMMENTS. This species is represented by only two puparia and one third-instar / puparium mid-moult specimen; there are additionally two earlier larval instars that are tentatively identified as *N. fallax*. An exhaustive search of its host plant species failed to reveal any further study material. Although the extensive dark pigmentation of the two fully developed puparia is unusual, such pigmentation is variable within *Nealeurodicus* species: however, the combination of extensive pigmentation, five pairs of abdominal compound pores, and a distinct basal shoulder on each side of the lingula (Fig. 102) serve to distinguish *N. fallax* from other members of the genus.

N. fallax shares the same distribution of compound pores as seen in *N. octifer* (Bondar). However, there are several notable differences that preclude regarding the Belize specimens as belonging to *N. octifer*. In *N. fallax*, there is a ring of bright pores within the outer torus of each of the compound pores (except those on abdominal segment VIII), whereas in *N. octifer* this ring of pores surrounds each compound pore, beyond its boundary – thereby placing *N. octifer* as a member of the *N. altissimus* group; the vasiform orifice of *N. fallax* is rather elongate, with the operculum only occupying its basal one-third part, whereas in *N. octifer* the broader vasiform orifice has half its length occupied by the operculum; the location of compound pores on abdominal segments II, IV, V and VI differs, with the anteriormost pair in *N. octifer* located much further mesad in comparison to the other pairs (as in the distribution of these pores in *N. altissimus*, fig. 33), in marked contrast to the more linear arrangement of these compound pores in *N. fallax* (Fig. 102); puparia of *N. fallax* are much more elongate (*i.e.* less broad) than the puparia of the several examined samples of *N. octifer*, which are also symmetrical in contrast to those of *N. fallax*; a single, rather linear, group of bright simple pores is present to either side of the vasiform orifice in *N. fallax* (Fig 102, expended detail), whereas in *N. octifer* there are two distinct, less numerous, groups to either side of the vasiform orifice.

The fully developed paratype puparium is most unusual, bearing both a thoracic parasitoid emergence hole (and the expected parasitoid remains) and also a clearly fullyformed adult female whitefly about to emerge. Although few characters of this adult whitefly can be discerned in detail, her abdomen clearly possesses four pairs of large ventro-lateral wax plates), a character which is mentioned because it may prove to be of generic significance in future studies.

Nealeurodicus petiolaris sp. nov.

(Figs 37–39, 117–118, 129–130)

PUPARIUM. Habitus. Immature stages of the extensive type sample all occurred on the woody petioles and young stems of their sapling host (Figs 129–130), and were vigorously attended by ants, Dolichoderus bispinosus (Olivier). A ragged marginal fringe of short waxy filaments is present, and undisturbed individuals, viewed in lateral aspect, can be seen to have a very fine secreted filament issuing from the position of each compound pore. A crust of whitish secretion covers the dorsum, of variable opacity depending (apparently) on the age of the individual, but the vasiform orifice is always uncovered, appearing black: in some individuals, the puparia appear sugary-white, and the covering may be sufficiently robust to be removed and slide-mounted (Fig. 38). In specimens that are approaching the emergence of adults, the dorsum is also raised away from the venter, supported by a vertical waxy palisade (Fig. 129), with the dorsum slightly domed; but less mature specimens are much more flattened. Margin. Outline elongate-oval, very slightly more obtuse anteriorly than posteriorly, 1.90–2.36 mm long, 1.17–1.40 mm wide, generally widest at abdominal segment III/IV (n=18). Margin with very shallowly castellate, almost contiguous, teeth, but only a slight degree of down-curling (which usually occurs in slide-mounted specimens) places outer-submarginal tubercular ridges in relief as irregular crenulations (Fig. 117a,b), fewer than 10 occupying 0.1 mm of margin at mid-length of puparium; margin modified at tracheal openings as combs of very fine, rounded teeth opposite forelegs (Fig. 117a) and between caudal setae. Dorsum. Cuticle variably pigmented, the coloration tending to indicate rays leading mesad from puparial margin, darkest cephalically, on mesothorax and on abdominal segments III/IV and VII/VIII (Fig. 37); often a pigmented longitudinal band encompassing the submedian depressions on either side of body. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures becoming indistinct subdorsally. Dorsal disc generally smooth. Abdominal segment VII medially longer than segment VIII anterior to vasiform orifice, and hardly shorter than segment VI (Fig. 117). Submedian abdominal depressions narrow but distinct from medial parts of abdominal intersegmental folds (Fig. 117); intersegmental folds becoming indistinct distal to submedian depressions. Vasiform orifice (Fig. 117) rounded-

triangular, little longer than wide, slightly raised posterolaterally where the outer margin is roughened and is apically developed into a transverse boss; inner lateral margins of vasiform orifice also roughened, and floor of orifice with reticulate patterning; operculum trapezoidal, laterally curved, with a fine pair of setae situated on its posterior margin; lingula head finely spinulose, similar in shape to vasiform orifice, just overlapping apical boss of vasiform orifice, bearing the usual 4 stout subapical setae. Chaetotaxy. With 12 pairs of robust, hair-like setae in extreme outer submargin, including the nominal caudal pair, all similar in length to vasiform orifice; posterior marginal setae often a little longer than submarginal setae (Fig. 117), but anterior marginal setae absent; single submedian pairs of cephalic, pro-, meso- and metathoracic and eighth abdominal setae present, similar to submarginal setae; eighth abdominal setae situated lateral to anterior part of operculum. *Pores.* Single pairs of compound pores present cephalically and on abdominal segments II, IV, V and VIII, the pores on segment VIII situated just posterior to apex of vasiform orifice (Fig. 117). All compound pores similar (Fig. 117c), ring-like, each 25-30 µm in diameter, the axial lumen with tightly bundled rod-like structures which hardly emerge beyond pores; outer torus of each compound pore with subcircular "spinneret" cells (terminology of Quaintance & Baker, 1913) almost always forming a single ring of 10–18 cells. Whole of dorsum densely punctuated by evenly-distributed, mostly quadrilocular, simple pores (Fig. 117d), including between vasiform orifice and pockets; small wide-rimmed pores also occur, most in small aggregations of 2-5 pores bounding submedian zone and in outer subdorsum; somewhat more numerous aggregations of these pores present lateral to abdominal pockets (segment VII/VIII boundary) and to vasiform orifice (Fig. 117d). Venter. Ventral abdominal setae underlying posterolateral margins of vasiform orifice very long, but finer than dorsal submarginal setae. Posterior abdominal spiracles almost underlying compound pores on abdominal segment VIII; anterior to these spiracles is a pair of "pads" of unknown function (Fig. 118). Legs typical for Aleurodicinae, bisegmented and smooth; a fine seta situated at base of each middle and hind leg (Fig. 117), and a few minute setae present on distal segment of each leg. Antennae typical for Aleurodicinae, their apices reaching to articulations of middle legs (Fig. 117). Caudal tracheal fold indicated by a narrow band of tiny black spinules (Fig. 118); thoracic tracheal folds much wider than marginal combs, marked by faint boundary folds but not spinulose.

ADULT FEMALE. Several adult females emerged in culture, but males remain unknown; neither is there any sign of developing males in any of the slide-mounted puparia. The females are very large, fore wings and body lengths each about 3 mm, and wings and body are unusually darkly pigmented for any aleurodicine (Fig. 130), with the fore wings being almost covered by dark clouds, and the wing margin sharply emarginate at the confluence with the anal vein; the hind wings are dusky, with the radial vein lined with darker pigment. The abdomen has four pairs of large ventro-lateral wax plates. Abdominal tergites II–VIII and all thoracic plates are darkly pigmented. Antennae 7-segmented.

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MATERIAL EXAMINED. Holotype puparium, BELIZE, CFR, Las Cuevas, Saffron trail, on *Protium glabrum* (Burseraceae), 06.iv.2003 (J.H.Martin #7857) (BMNH). Paratypes: 78 puparia, 8 third-instar larvae, 1 third-instar / puparium mid-moult, 22 adult females, same data as holotype (BMNH, CDFA, USNM); numerous puparia dry on stems, residue of type sample (BMNH).

ETYMOLOGY. The specific epithet reflects the petiole-feeding habit of the immature stages of this species.

COMMENTS. *N. petiolaris* has a similar distribution of compound pores to *Ceraleurodicus neivai* (Bondar, 1928), but *N. petiolaris* clearly belongs to *Nealeurodicus*, possessing the generic characters discussed above. Also, unlike those of *N. petiolaris*, the puparia of *C. neivai* have a pair of tiny compound pores located in the submargin that, unusually, appear to be on the same segment (VII) as the posteriormost large abdominal pair; the presence of more than one pair of compound pores per segment is abnormal [the posteriormost compound pores in *N. petiolaris* are situated closer to the median line, on segment VIII].

N. petiolaris is the only Belizean whitefly (in either subfamily) to have been found favouring the woody stems and petioles of its host. Indeed, not a single specimen was observed on a leaf, despite the extensive colony comprising several hundred individuals massed on the stems and petioles of their sapling host. Also quite unusually, this colony was vigorously attended by ants, *Dolichoderus bispinosus*. The combination of petiole-feeding, large size, strong ant-attendance and initial absence of adults led to a provisional assumption, in the field, that this was a colony of scale insects (Coccoidea). Ant-attendance may be part of the reason for a very low degree of parasitism, only one pre-emergence adult of an *Encarsia* species, belonging to the *E. luteola*-group (A. Polaszek, pers. comm.), being found while slide-mounting material, and very few of the puparia showed parasitoid emergence holes.

PARALEYRODES Quaintance

Paraleyrodes Quaintance, 1909: 169–170. Type species *Aleurodes perseae* Quaintance, 1900: 32–33, by monotypy.

DIAGNOSIS AND COMMENTS. *Paraleyrodes* comprises species that are physically much smaller than most other aleurodicines, with the following combination of puparial characters: with 5 or 6 pairs of abdominal compound pores, the anteriormost 1 or 2 pairs being much smaller than the remaining 4 abdominal pairs and the cephalic pair (Fig. 119); two pairs of cicatrices present on thorax (scars of compound pores in third-instar); a pair of submedian cephalic setae is present, but corresponding thoracic setal pairs are wanting; outer submargin with a row of 14 pairs of hair-like setae, including the nominal caudal pair. Adults of *Paraleyrodes* are unusual amongst members of the Aleurodicinae, in hav-

ing all wing veins unbranched; females have 4 articulated antennal segments; males have only 3 articulated antennal segments (Fig. 127) and also have complex aedeagal apices (Figs 106–110, 120, 122). Females usually secrete so much mealy wax around them, while ovipositing, that the common name "nesting whitefly" has been used for *P. minei* (see below), although "nesting whiteflies" is an appropriate term for the whole genus. Members of the genus have a marked propensity for ovipositing amongst the puparia or colony remains of other whitefly species, presumably taking advantage of the shelter provided, augmenting that provided by their own secretions. The larvae and puparia of *Paraleyrodes* species secrete long waxy filaments that often form an annulus surrounding the feeding insect (Figs 125–126).

Uniquely amongst known whiteflies, all species of *Paraleyrodes* are most reliably diagnosed from the structure of the male aedeagus, with the puparia of some being difficult to distinguish from those of similar species when males are not present. Approximately ten species of *Paraleyrodes* have been discovered in Belize, but numerically large colonies are rare, and this probably reflects the natural situation throughout the Neotropical Region. The absence of discrete colonies has proved to be an impediment to attempts to associate males and puparia, and adults are frequently not conspecific with puparia that happen to be nearby. Nevertheless, satisfactory association of males and puparia has enabled the description here of both the puparium and adult male of two new species (P. ancora and P. perplexus), and has confirmed the presence in Belize of some described species. Male specimens alone of two further new species are here described (P. cervus and P. triungulae), despite the absence of associated puparia, based on distinctive aedeagal characters. However, two males have been found that resemble those of *P. goyabae* (Goeldi, 1886), but with detail differences that preclude formal recording of this species from Belize. Two male specimens with the aedeagal apex closely resembling that of *P. citricolus* Costa Lima (see below) are also uncertainly identified, but more-typical males and very characteristic puparia do enable P. citricolus to be recorded for Belize.

Description here of *P. cervus* and *P. triungulae*, based only on adult males, is considered valid and important given that five species of *Paraleyrodes* have already become established beyond their native neotropics (see **New World to Old**, p. 6, and discussion by Martin, 2001). The author considers that any newly described species of *Paraleyrodes* should have an adult male holotype designated, with new species not being proposed at all in the absence of male specimens. In the meantime, it is highly desirable that attempts should continue to discover males of species where they remain unknown, or where their association with puparia is uncertain.

Many *Paraleyrodes* puparia from Belize, without associated males, cannot be identified with certainty, although some do appear to belong to the *P. proximus / goyabae* group (see discussion of *P. proximus*, below) and are so listed in Appendices 1 and 2.

Paraleyrodes ancora sp. nov.

(Figs 41-44, 104-105)



PUPARIUM. *Habitus*. Rather cryptic when feeding, but presence of puparia indicated by patches of broken white wax filaments secreted by the compound pores. Apparently never developing in crowded colonies. Margin. Puparial outline ovoid, 0.70-0.80 mm long, 0.40–0.50 mm wide, widest at about metathorax (n=20). Margin smooth to slightly irregular, not modified at thoracic tracheal openings. Dorsum. Longitudinal moulting suture reaching puparial margin; transverse moulting sutures only distinct submedially in preemergence specimens, but reaching outer edges of hind legs in post-emergence individuals. Dorsal disc surface generally smooth, but fine spinules and distinct mottling visible in many specimens (Fig. 105), possibly developing with increasing maturity. Abdominal segmentation distinct as far laterad as compound pores; meso-metathoracic division distinct submedially; abdominal segment VII only slightly shorter than segment VI medially. Abdominal segments I-IV/V submedially sclerotic, often pigmented brownish, this cuticle usually staining more darkly than remainder of puparium (Figs 41-42, 104). Vasiform orifice (Figs 41–42) straight anteriorly, remainder rounded-cordate, smooth; operculum transversely trapezoidal, its posterior margin slightly sinuate and bearing a pair of setae; lingula head finely spinulose and quadrisetose, smoothly tongue-shaped, extending beyond vasiform orifice and reaching almost to puparial margin. Chaetotaxy. Posterior marginal setae long and stout, similar to caudal setae, but anterior marginal pair very much shorter and finer; the remaining 13 pairs of submarginal setae, the cephalic and eighth abdominal setae all a little shorter and finer than posterior marginal setae and caudal pair (chaetotaxy exactly as shown for P. pseudonaranjae, fig. 119). Eighth abdominal setae situated anterior to basal corners of vasiform orifice. Pores. Cephalic and posteriormost four abdominal pairs of compound pores subequal in size and structure (Figs 41-42), each 30-40 µm in overall outer diameter; the central lumen plain; inner ring of spline-bearing spinneret cells [terminology of Quaintance & Baker, 1913, adapted by Martin, 1996] usually with splines intact and vertical to puparial surface; outer ring with cells only faintly marked as radial "spokes". Anteriormost two pairs of abdominal compound pores much smaller than remainder, each 10-13 µm in outer diameter. Two pairs of thoracic cicatrices (scars of third-instar larval compound pores) present submedially. Abdominal segments II-V/VI each with 2-5 submedian bright simple pores (Fig. 104), distributed asymmetrically, often especially visible against the sclerotic cuticle; similar pores also present subdorsally on thorax and abdomen, usually a single pair situated on each thoracic segment and abdominal segments V-VII, and with 1 or 2 on each side of abdominal segments III and IV; abdominal segment VIII normally without a pair of such bright pores. Immediately inside puparial margin is a single row of crater-like pores, usually viewed laterally because of down-curving of puparial margin (as figured for *P. perplexus*, fig. 121), about 3 pores per pair of submarginal setae. Venter. Cuticle very smooth, delicate. Ventral abdominal setae

finer than dorsal setae, underlying vasiform orifice and operculum. Legs typical for genus, each with an apical claw. Antennal bases situated anterior to fore legs, each antenna describing an arc lateral to the legs, terminating opposite basal bulge of hind leg in female puparia (Fig. 42), and reaching to between the small abdominal compound pores in male puparia (Fig. 41).

ADULT MALE. Body 1.10–1.30 mm long, including parameres (n=16). Apex of aedeagus with a pair of laterally directed apically acute processes, their bases opposite each other and arising almost at right-angles to the shaft (Fig. 44), very slightly curved; the lateral profile (Fig. 43) reveals the shaft to be almost straight for most of its length, with an apical, dorsally-recurved hook that almost reaches the height of the median section, overall aedeagal length 0.12–0.13 mm. On slides, the length of the lateral aedeagal processes results in a rather differing appearance depending on the degree of compression by the coverslip, but they are never recurved anteriad (see COMMENTS, below). Abdomen bearing three pairs of ventro-lateral wax-secreting glands, as is common in the Aleurodicinae. Last abdominal segment (Fig. 43) rather short, typically 0.14–0.15 mm long, claspers (parameres) 0.17–0.18 mm long (Figs 43–44). Single antennal flagellar segment (fused segments III–VII) measures 0.65–0.73 mm and is densely sensoriate, typical for male *Paraleyrodes* (see Fig. 1 of Iaccarino, 1990). Ultimate rostral segment 0.105–0.115 mm long.

MATERIAL EXAMINED. Holotype adult male, BELIZE, CFR, Monkey Tail track, on Asteraceae, possibly *Lasianthaea* sp., 22.vi.2002 (J.H.Martin #7701) (BMNH). Paratypes, BELIZE (all CFR, Martin coll.): 2 adult males, 3 puparia, 1 mid-emergence male/puparium (males all associated with pupal cases), same data as holotype and on same slide (BMNH); 1 puparium, San Pastor track, on *Tetracera* sp.(Dilleniaceae), 18.xi.1994; 1 male & associated pupal case, Las Cuevas, on *Brosimum* sp. (Moraceae), 03.vi.2002; 1 puparium, Monkey Tail track, on *?Trophis* sp. (Moraceae), 17.ii.1996; 1 mid-emergence male/puparium, Las Cuevas, on Arecaceae, 01.iii.1996; 1 male & associated pupal case, 1 pupal case, Las Cuevas, on *Coccoloba belizensis* (Polygonaceae), 06.vi.2002; 1 male, Monkey Tail track, on *C. belizensis*, 13.ii.1996 (all BMNH); 17 males, 14 females, 15 mid-emergence adult/puparia, 38 puparia, Las Cuevas, on *Persea americana* (Lauraceae), 02.xii.1994, 10 & 20.ii.1996, 11.vi.2002 (all from the same tree) (BMNH, CDFA, USNM, BZ). Paratypes, NICARAGUA: 3 puparia, Rio San Juan Province, Rio San Juan / Rio Bartola confluence, on *Persea americana*, 23.vi.2004 (Martin) (BMNH).

ETYMOLOGY. The specific name is the Latin word *ancora* (meaning an anchor — possibly the best description of the shape of the aedeagal apex of the male).

COMMENTS. The author had provisionally identified this species as *P. citri* Bondar (1931), on the basis of size and form of the puparial compound pores, combined with two very elongate and spine-like lateral processes on the male aedeagus. However, the opportunity to examine syntypic males of *P. citri* (courtesy of MZUSP) revealed the paired aedeagal processes in *P. citri* to be distinctly posteroventrally directed, at an acute angle to

the aedeagal shaft (as illustrated effectively by Bondar, 1931), whereas in P. ancora these processes arise almost at right-angles to the shaft (Fig. 44) and are even more slender than in *P. citri*. The aedeagal apex of *P. ancora* is also somewhat reminiscent of the drawing by Quaintance (1909), reproduced again by Quaintance & Baker (1913), accompanying a revised description of *P. perseae* (Quaintance, 1900). However, only one such male (stated on the label to be *P. perseae*, from Florida, BMNH) is available to the author, and the aedeagus differs from *P. ancora* in the bases of the two prongs not arising opposite each other as they do in *P. ancora*, and the dorsally-directed hook being vestigial in comparison with that seen in *P. ancora*. Despite the similarity of the puparia of *P. ancora* and *P. citri*, those of P. ancora have distinctive submedian sclerotisation on abdominal segments I-IV/V, often slightly pigmented (Figs 41-42, 104) and thus rendering the encompassed simple pores more visible against the dusky cuticle; also, the dorsal cuticle is distinctly spinulose and mottled in many puparia of *P. ancora* (Fig. 105). Both of these characters are unusual in puparia of *Paraleyrodes* species, although the poor state of the mountant on Bondar's slide precluded seeing whether these characters are present on the puparial surface of the syntypes of P. citri.

Paraleyrodes bondari Peracchi

(Figs 45, 108, 113)

Paraleyrodes bondari Peracchi, 1971: 146-148. Holotype (adult male), Brazil.

DISTRIBUTION. Neotropical Region — Belize, Brazil, Honduras, Venezuela; Nearctic Region — California, Florida; Palaearctic Region — Madeira; Malagasian Region — Comoro archipelago, Mauritius, Réunion; Oriental Region — Taiwan; Pacific Region — Hawaii.

COMMENTS. This species is represented from Belize (and also Honduras & Venezuela, slides in CDFA) only by small numbers of puparia. Even though the large puparial compound pores of *P. bondari* are distinctive (Fig. 113), the diagnostic male aedeagus (Fig. 108) not having been seen from Belize renders the record somewhat tentative, given the similarities between puparia of several *Paraleyrodes* species. *P. bondari* is currently one of the more mobile of *Paraleyrodes* species, as can be seen from the distribution data quoted here.

Paraleyrodes cervus sp. nov. (Figs 49–50, 106)

ADULT MALE. Body 1.18–1.23 mm long, including parametes (n=2). Aedeagus (Figs 49–50, 106) with a straight dorsal thorn at mid-length (directed about 45° posteriad), a dor-

soapical process similarly directed but less acute, and with the aedagal apex truncate and ventrally directed; the aedagal apex bears a pair of parallel posteriorly-directed acute prongs, and a pair of anteroventrally-directed spine-like processes that are almost parallel to the shaft and thus difficult to see (Fig. 106); overall aedeagal length 0.15 / 0.17 mm in the two available specimens. Last abdominal segment 0.14 / 0.16 mm long, itself also with a large, curved, posteriorly-directed thorn-like process between the vasiform orifice and articulation with the genitalia (Figs 49–50), its surface finely spinulose, as is the surface of the whole segment; claspers 0.155 / 0.18 mm long. Abdomen with the normal three pairs of ventro-lateral wax-secreting glands present. Single antennal flagellar segment (fused segments III–VII) 0.45 / 0.59 mm long, densely sensoriate, typical for male *Paraleyrodes*. Ultimate rostral segment 0.12 / 0.13 mm long.

MATERIAL EXAMINED. Holotype adult male, BELIZE, CFR, Las Cuevas study plots, on a vine, probably Bignoniaceae, 16.ii.1996 (J.H.Martin #6678) (BMNH). Paratype: 1 adult male, CFR, Las Cuevas, on *Piper* sp. (Piperaceae), 22.iii.2003 (Martin #7778) (BMNH).

ETYMOLOGY. The specific name is the Latin word *cervus* (meaning a stag), reflecting the antler-like aedeagal apex.

COMMENTS. The characters of the aedeagus, which is very reminisent of a deer's antler, are quite unlike those seen in any other *Paraleyrodes* species. With a pair of anteroventrally-directed spine-like processes that are swept back close to the shaft, the aedeagus of *P. cervus* is perhaps most similar to that of *P. minei* Iaccarino, but its other characters are very different. The presence of a pronounced dorsal thorn-like process on the terminal abdominal segment is also unique to *P. cervus*, at least amongst known *Paraleyrodes* species. Collection sample #7778 also includes one adult female and three puparia: two of the puparia may belong to *P. minei*, with slightly smaller compound pores than usual; the other resembles *P. goyabae* (Goeldi), and association of the paratype of *P. cervus* with any of these individuals is very uncertain.

Paraleyrodes citricolus Costa Lima (Figs 46–47, 109, 112, 126)

Paraleyrodes citricolus Costa Lima, 1928: 136. Holotype, presumed Brazil but not stated.

DISTRIBUTION. Neotropical Region — Belize, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Mexico, Panamá; Palaearctic Region — Azores, Madeira.

COMMENTS. *P. citricolus* is probably the *Paraleyrodes* species most frequently encountered in the CFR. The puparia have the cephalic and posterior four abdominal pairs of compound pores (Figs 46–47, 112) very large (outer diameter of each compound pore usually 45–55 μ m), its central lumen with a cellular pattern. These large compound pores secrete long filaments that are characteristically thick and frayed in appearance (Fig. 126).

The typical male aedeagus is shown in Fig. 109, but the few males seen from Belize have the ventrally directed cluster of spines somewhat reduced.

Paraleyrodes minei Iaccarino

(Figs 48, 110–111)

Paraleyrodes minei Iaccarino, 1990: 132-149. Holotype (adult male), Syria.

DISTRIBUTION. Neotropical Region — Belize, Guatemala, Mexico, Puerto Rico; Nearctic Region — Bermuda, California, Florida, Texas; Palaearctic Region — Lebanon, Morocco, Spain, Syria, Turkey; Ethiopian Region — Benin; Oriental Region — Hong Kong.

COMMENTS. Although this species was described from citrus crops in Syria, all *Paraleyrodes* species are native to the Neotropical Region. *P. minei* is now often called the nesting whitefly, but this name should be used with caution, because it describes the wax-deposition habits of females of many, possibly all, members of this genus.

As can be seen from the currently recorded distribution, above, *P. minei* is clearly a mobile species. It was discovered by the author on several host plants in Hong Kong (2003, BMNH), the first records of this species occurring in Asia. Two puparia from Hong Kong were collected from a grass blade, *Miscanthus sinensis*, and an adult female emerged from each of these. Also, further adult females were observed nearby, on the same grass, with the presence of eggs and much secreted wax indicating further colonisation. This may be the first record of any member of the Aleurodicinae developing on a poaceous host, and is most notable.

In Belize, several puparia (Fig. 48) have been studied, and the characteristic male aedeagus (Fig. 110) has been seen in one fully-developed adult male and one pre-emergence male dissected from its puparium, thereby confirming the occurrence of this species in Belize.

Paraleyrodes perplexus sp. nov.

(Figs 121–122)

PUPARIUM. *Margin*. Puparial outline ovoid, 0.68–0.90 mm long, widest at about metathorax (n=21). Margin smooth to slightly irregular, not modified at thoracic tracheal openings. *Dorsum*. Abdominal segmentation distinct almost as far laterad as compound pores; abdominal segment VII medially similar in length to segment VI. Puparial cuticle without pigmentation and without median sclerotisation that stains differentially. *Pores*. Cephalic and posteriormost four abdominal pairs of compound pores subequal in size and structure, each 20–25 μ m in overall outer diameter, outer ring with cells only faintly

marked as radial "spokes"; anteriormost two pairs of abdominal compound pores similar in outer diameter to, or a little smaller than, remainder, each 15–20 µm in outer diameter; compound pores appear as those of *P. pseudonaranjae* Martin (Fig. 119). Abdominal segment IV with 2–5 submedian bright simple pores, on each side of median line; similar pores also present subdorsally on thorax and abdomen, usually a single pore situated on each side of abdominal segments III and V–VIII. Immediately inside puparial margin is a single row of crater-like pores (Fig. 121), usually viewed laterally through down-curving of puparial margin, about 2 pores per pair of submarginal setae. Other characters typical for *Paraleyrodes* (see generic discussion, above, and fig. 119).

ADULT MALE. Body 1.02–1.17 mm long, including parameres (n=5). Aedeagal apex (Figs 122a–d) with a single dorsal, thumb-like, process and ventrally with a pair of slightly recurved prongs that appear to be variably membraneous on their posterior edges. Last abdominal segment short, only about 0.10 mm long, normal, similar in length to ultimate rostral segment; claspers 0.125–0.14 mm long.

MATERIAL EXAMINED. Holotype adult male, BELIZE, CFR, Las Cuevas forest, on *Piper yucatanense* (Piperaceae), 06.vi.2004 (J.H.Martin #8003A) (BMNH). Paratypes: 2 adult males, 15 puparia, 1 third-instar larva / puparium intermoult, same data as holotype (BMNH, USNM).

Other material: 1 adult male, San Pastor track, on undetermined Asteraceae, 14.ii.1996 (Martin #6662); 1 adult male, 1 puparium with fully developed pre-emergence female, on undetermined woody broadleaf host, Monkey Tail track, 01.vi.2004 (Martin #7972); 1 adult male, 5 puparia, Las Cuevas forest, on *Casearia sylvestris* (Flacourtiaceae), 30.v.2004 (Martin #7950) (all BMNH).

ETYMOLOGY. The specific name is the Latin adjective *perplexus* (meaning intricate or confused), reflecting the apparent plasticity of the aedeagal apex in males.

COMMENTS. This species is very similar to *P. pseudonaranjae* Martin (2001), but both the adult male and the puparium display differences. The puparial differences are more consistent: those of *P. perplexus* possess a row of rather large crater-like pores in the outer submargin (Fig. 121), whereas those of *P. pseudonaranjae* do not (Fig. 119); there is a small bright pore to either side of the vasiform orifice (abdominal segment VIII) in *P. perplexus*, but this pair of pores is wanting in *P. pseudonaranjae* (Fig. 119). All of the adult males determined as *P. perplexus* have the aegeagal apex somewhat different to those of *P. pseudonaranjae*. However, there is a degree of variation shown in the aedeagus of *P. perplexus* (Fig. 122a–d), seemingly to do with the degree of devlopment of the membraneous posterior edges of the ventral prongs.

There remains slight doubt as to whether two males, with the most acute aedeagal prongs (aedeagus of one shown in fig. 122e), are conspecific with the other specimens of *P. perplexus*. At the time of this study, no reliably identified material of *P. pseudonaranjae* has been seen from anywhere in its native Neotropical Region, and it therefore remains possible that these two individuals could be variants of *P. pseudonaranjae*, whose typical

aedeagus is also shown here (Fig. 120). The holotype and paratypes of *P. perplexus* have therefore been selected from a single sample, from which three adult males were reared in culture (see above); the other available material is not given paratype status.



Paraleyrodes proximus Terán

(Figs 51-52)

Paraleyrodes proximus Terán, 1979: 170-174. Holotype (adult male), Argentina.

DISTRIBUTION. Neotropical Region — Belize, Argentina, Guatemala, Nicaragua, Peru.

COMMENTS. This is a little-known member of the genus, but its presence in Belize is confirmed by the characteristic aedeagal apex of the male (Fig. 52), which is the least developed amongst known *Paraleyrodes* species. However, the puparia (Fig. 51) are not very distinctive, being similar to poor published descriptions of those of *P. goyabae* (Goeldi), and are unsafe to identify in isolation. Illustrated here are the aedeagus of a male and the vacated pupal case of the same individual.

Paraleyrodes triungulae sp. nov.

(Figs 53–54, 107)

ADULT MALE. Body 1.33–1.37 mm long, including parameres (n=2). Aedeagus (Figs 53–54, 107) with its main axis termination ventrally-curved and claw-like; with two smaller lateral processes, one of which is similar in shape to apex of main axis, the other more spine-like; additionally with a dorsal thumb-like protrusion; overall aedeagal length 0.13 / 0.14 mm in the two available specimens. Last abdominal segment 0.15 / 0.16 mm long, normal; claspers 0.18 mm long. Abdomen with the normal three pairs of ventro-lateral wax-secreting glands present. Single antennal flagellar segment (fused segments III–VII) measuring 0.80 / 0.84 mm, densely sensoriate, typical for male *Paraleyrodes*. Ultimate rostral segment 0.11 / 0.12 mm long.

MATERIAL EXAMINED. Holotype adult male, BELIZE, CFR, Guacamallo Bridge — Millionario road, on *Guettarda combsii* (Rubiaceae), 25.ii.1996 (J.H.Martin #6707) (BMNH). Paratype: 1 adult male, same data as holotype, on same slide (BMNH).

ETYMOLOGY. The specific name incorporates the Latin word *ungula* (meaning a talon or claw), with the name *triungulae* referring to the three ventrolateral developments of the aedeagal apex.

COMMENTS. In lateral aspect, the aedeagal apex somewhat resembles that of *P. perplexus* **sp. nov.** and *P. pseudonaranjae* Martin (Figs 122 and 120, respectively), with clawlike ventral processes, but in *P. triungulae* these are uneven in size and position, as well as being more curved and talon-like. A single puparium collected as part of this sample, and

present on the type slide, resembles *P. bondari* Peracchi but there is no evidence of association of this puparium with the holotype and paratype of *P. triungulae*.

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Fig. 63 features the work of Arthur D. Cushman, from Russell (1965), and has been reproduced in papers by the present author on several occasions through the kind permission of the editors of the *Florida Entomologist*. Fig. 73 is modified after Costa Lima (1928). All other line drawings and photographs are the work of the present author, with Figs 119–120 originally appearing in *Bulletin of Entomological Research* **91**: 105, and the following first appearing in *Journal of Natural History*: Figs A and 64 from vol. **32**: 85–98; Figs 108–113 from vol. **30**: 1849–1859; Figs 65 & 115 from vol. **33**: 1545–1559; and Fig. 68 from vol. **31**: 1261–1272.

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ZOOTAXA

681
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Appendix 1 — check list of the Aleyrodidae-Aleurodicinae of Belize

- The numbers in the left-hand column correspond with those in the right-hand column of Appendix 2
- 1. Aleurodicus araujoi Sampson & Drews, 1941
- 2. Aleurodicus coccolobae Quaintance & Baker, 1913
- 3. Aleurodicus dispersus Russell, 1965
- 4. Aleurodicus dugesii Cockerell, 1896 Aleurodicus poriferus Sampson & Drews, 1941 **syn. nov.**
- 5. Aleurodicus inversus sp. nov.
- 6. Aleurodicus magnificus Costa Lima, 1928
- 7. Aleurodicus maritimus Hempel, 1922b
- 8 Aleurodicus niveus sp. nov.
- 9. Aleurodicus pauciporus sp. nov.
- 10. Aleurodicus pulvinatus (Maskell, 1896)
- 11. Aleurodicus rugioperculatus sp. nov.
- 12. Aleurodicus vinculus sp. nov.
- 13. Aleuronudus acapulcensis (Sampson & Drews, 1941)
- Aleuronudus manni (Baker, 1923) comb. nov. Hexaleurodicus ferrisi Sampson & Drews, 1941 syn. nov.
- 15. Azuraleurodicus pentarthrus Martin, in Martin & Polaszek, 1999
- 16 Ceraleurodicus keris sp. nov.
- 17. Ceraleurodicus varus (Bondar, 1928)
- 18. Dialeurodicus bondariae sp. nov.
- 19. Dialeurodicus caballeroi sp. nov.
- 20. Dialeurodicus silvestrii (Leonardi, 1910)

Dialeurodicus tracheiferus Sampson & Drews, 1941 syn. nov.

- 21. Leonardius kellyae sp. nov.
- 22. Metaleurodicus arcanus sp. nov.
- 23. Metaleurodicus griseus (Dozier, 1936)
- 24. Metaleurodicus tenuis sp. nov.
- 25. Metaleurodicus variporus sp. nov.
- 26. Nealeurodicus altissimus (Quaintance, 1900) comb. nov.
- 27. Nealeurodicus bakeri (Bondar, 1923a) comb. nov.
- 28. Nealeurodicus fallax sp. nov.
- 29. Nealeurodicus petiolaris sp. nov.
- 30. Paraleyrodes ancora sp. nov.
- 31. Paraleyrodes bondari Peracchi, 1971
- 32. Paraleyrodes cervus sp. nov.
- 33. Paraleyrodes citricolus Costa Lima, 1928

- 34. Paraleyrodes minei Iaccarino, 1990
- 35. Paraleyrodes perplexus sp. nov.
- 36. Paraleyrodes proximus Terán, 1979
- 37. Paraleyrodes triungulae sp. nov.
- 38. Paraleyrodes sp., male only, cf. citricolus see discussion of Paraleyrodes
- 39. Paraleyrodes sp., males, cf. goyabae see discussion of Paraleyrodes
- 40. *Paraleyrodes*, species with puparia only, not identified with certainty but belonging to the *proximus / goyabae*-group.
- 41. Paraleyrodes spp, undetermined, puparia or adult females only.

zоотаха 681

Appendix 2 — host plants of the Aleyrodidae-Aleurodicinae in Belize

Nomenclature follows the system of Balick *et al.* (2000), many of these determinations having been made by Caroline Whitefoord, Department of Botany, BMNH

• The numbers in the right-hand column refer to the whitefly taxa in Appendix 1, above.

Aquifoliaceae	
Ilex belizensis	9
Araceae	
?Philodendron sp.	41
Arecaceae	
<i>Chamaedorea</i> sp.	34, 36
Cocos nucifera	11
undetermined	30
Asteraceae	
Lasianthaea fruticosa	25, 31, 33, 34
?Lasianthaea fruticosa	30
Otopappus verbesinoides	33
undetermined	1, 27, 33, 37, 40, 41
Bignoniaceae	
Arrabidaea patellifera	5
Cydista aequinoctialis	1
Stizophyllum riparium	5, 7, 14, 33
undetermined	1, 5, 32
Burseraceae	
Protium copal	16, 17, 27
Protium glabrum	29, 40
Cecropiaceae	
<i>Cecropia</i> sp.	7
Clusiaceae	
Vismia camparaguey	7, 15

Combretaceae	
Combretum cacoucia	5
Combretum laxum	7
Terminalia amazonia	1, 27
Dilleniaceae	
Tetracera volubilis	6
Tetracera sp.	30
Euphorbiaceae	
Acalypha costaricensis	25
Acalypha macrostachya	15
Croton ?billbergianus [= pyramidalis]	1, 7, 15
Sebastiania longicuspis	3, 28
Fabaceae: Caesalpinioideae	
Bauhinia sp.	31
Cassia siamea	2
Fabaceae: Mimosoideae	
<i>Inga</i> spp	15, 26, 40
undetermined	26
Fabaceae: Papilionoideae	
Canavalia cf. oxyphylla	26
<i>Erythrina standleyana</i> [= <i>rubrinervia</i>]	15
Lonchocarpus rugosus	26, 33
Machaerium riparium	26
undetermined	7, 15
Flacourtiaceae	
Casearia sylvestris	35
Casearia tremula	9
Laetia thamnia	16
Lauraceae	
Nectandra ?nitida	19, 28
?Nectandra sp.	9, 10, 40
Persea americana	2, 19, 28, 30, 34
undetermined	10, 18, 34, 40

Loganiaceae	
Strychnos sp.	14
Loranthaceae	
undetermined	21
Marantaceae	
undetermined	33, 40
Melastomataceae	
Clidemia octona	7
Miconia impetiolaris	7
undetermined	7
Meliaceae	
?Trichilia sp.	31, 36, 39, 40
Moraceae	
Brosimum sp.	30
Ficus sp.	33
Trophis racemosa	33
?Trophis sp.	30
Myrtaceae	
probably <i>Eugenia</i> sp.	20, 24, 40
Pimenta dioica	41
Psidium guajava	2, 3, 7, 10, 34
undetermined	14
Orchidaceae	
Encyclia cochleata	8
Piperaceae	
Piper ?auritum	1
Piper yucatanense	35
Piper spp	32, 33, 34, 40
Polygonaceae	
Coccoloba belizensis	4, 10, 30, 33, 36, 40, 41

Rubiaceae	
Chiococca alba	14
Chiococca ?alba	22, 41
Guettarda combsii	10, 14, 15, 33, 34, 37, 40, 41
Psychotria mexiae	14
Psychotria ?fruticetorum	14
undetermined	14, 22, 40
Rutaceae	
Citrus sinensis	34
Citrus sp.	13
Zanthoxylum juniperinum	14
Sapindaceae	
Paullinia pinnata	5
Sapotaceae	
?Pouteria reticulata	
Simaroubaceae	
?Simarouba sp.	2, 10
Solanaceae	
Lycianthes hypoleuca	4
Solanum cordovense	4
Solanum sp.	3
Styracaceae	
Styrax argenteus	7
Theophrastaceae	
Deherainia smaragdina	40
Urticaceae	
Boehmeria ramiflora	4
Urera sp.	25
Verbenaceae	
Petrea volubilis	7

Appendix 3 — summary of taxonomic changes proposed in this work

Revised generic placement

Septaleurodicus Sampson (1943) transferred from Aleurodicinae to Aleyrodinae.

New combinations.

Aleuronudus bondari (Costa Lima, 1928), transferred from Aleurodicus Aleuronudus jaciae (Bondar, 1923a), transferred from Hexaleurodicus Aleuronudus jequiensis (Bondar, 1928), transferred from Metaleurodicus Austroaleurodicus pigeanus (Baker & Moles, 1921), transferred from Metaleurodicus Aleuronudus manni (Baker, 1923), transferred from Metaleurodicus Metaleurodicus bahiensis (Hempel, 1922a), transferred from Aleuronudus Nealeurodicus altissimus (Quaintance, 1900), transferred from Ceraleurodicus Nealeurodicus bakeri (Bondar, 1923a), transferred from Ceraleurodicus Nealeurodicus ingae (Baker, 1937), transferred from Ceraleurodicus Nealeurodicus melzeri (Laing, 1930), transferred from Ceraleurodicus Nealeurodicus moreirai (Costa Lima, 1928), transferred from Ceraleurodicus Nealeurodicus octifer (Bondar, 1923a), transferred from Ceraleurodicus

New generic synonyms

- *Bondaria* Sampson & Drews (1941) becomes a junior synonym of *Dialeurodicus* Cockerell (1902)
- Hexaleurodicus Bondar (1923a) becomes a junior synonym of Aleuronudus Hempel (1922a)
- *Pseudaleurodicus* Hempel (1922a) becomes a junior synonym of *Metaleurodicus* Quaintance & Baker (1913), and is removed from synonymy with *Aleuronudus* (Hempel, 1922a)

New specific synonyms

- Aleurodicus poriferus Sampson & Drews (1941) becomes a junior synonym of A. dugesii Cockerell, (1896)
- Dialeurodicus tracheiferus Sampson & Drews (1941) becomes a junior synonym of D. silvestrii (Leonardi, 1910)
- *Hexaleurodicus ferrisi* Sampson & Drews (1941) becomes a junior synonym of *Aleuronudus manni* (Baker, 1923)
- Lecanoideus giganteus (Quaintance & Baker, 1913) becomes a junior synonym of L. mirabilis (Cockerell, 1898)

Leonardius loranthi Bondar (1923a) becomes a junior synonym of L. lahillei (Leonardi,

1910)

Nealeurodicus melzeri (Laing, 1930) becomes a junior synonym of N. paulistus Hempel (1922b), and is removed from synonymy with N. moreirai Costa Lima (1928)

zootaxa 681

New species

Aleurodicus inversus Aleurodicus niveus Aleurodicus pauciporus Aleurodicus rugioperculatus Aleurodicus vinculus Ceraleurodicus keris Dialeurodicus bondariae Dialeurodicus caballeroi Leonardius kellyae Metaleurodicus arcanus Metaleurodicus tenuis Metaleurodicus variporus Nealeurodicus fallax Nealeurodicus petiolaris Paraleyrodes ancora Paraleyrodes cervus Paraleyrodes perplexus Paraleyrodes triungulae

ZOOTAXAAppendix 4 — guide to field collection and preparation of whiteflies for microscopic681examination

Field Collection

Immature whiteflies are usually best collected whilst still attached to leaf tissue, and may be either stored dry or in strong alcohol. Adult whiteflies must be collected alive into alcohol. In Belize, as in many other countries, ethanol is extremely expensive, but rubbing alcohol (isopropyl alcohol) is a satisfactory substitute, except for molecular studies. For puparia, dry storage is usually preferable, providing the possibility of acquiring emergent adults or parasitoids; it also allows later observations to be made on the nature of puparial secretions, which may aid identification. Each field-collected sample must have its full data written in firm pencil or permanent ink included in the sample, so as to avoid data being rubbed from dry storage envelopes or dissolving in alcohol. Ballpoint pen ink invariably dissolves in alcohol and must not be used for spirit samples, even on the outside of vials (in case of leakage).

Preparation for microscopic examination

With very few exceptions whiteflies can only be accurately identified once puparia have been mounted on microscope slides, and standard 75 x 25 mm slides are used. Coverslips should be the thinnest possible, no. 0 grade, but many workers have their own preferences for coverslip dimensions: for whitefly puparia, the author prefers circular coverslips of 13 mm diameter, or 16mm diameter for adults of larger species.

Quickmounts

Quickmounts allow the rapid confirmation of the identity of a whitefly species with pale puparia, especially if it has little wax secretion. These will suffice when a permanent preparation is not required. Post-emergence pupal cases are usually needed, and may be picked carefully from the leaf, placed directly into almost any mounting medium and protected by a coverslip. Bubbles of air may be removed by warming the newly prepared slide over a light bulb, when expansion of the bubbles forces them to the edge of the coverslip. Sometimes, satisfactory quickmounts can be prepared from post-emergence parasitised puparia, or from puparia that have dried out before emergence of adult whiteflies or parasitoids. Only rarely is this method suitable with dark puparia.

Permanent mounts



In scientific surveys, a permanent record is usually desired. This is for voucher purposes and to allow subsequent taxonomic study. The current study benefitted significantly from the permanent collections of several institutions.

With health and safety issues assuming increasing importance in most laboratories, the choice of reagents may be constrained by local regulations. Also, the choice of final mountant affects the sequence and nature of reagents used. For reasons of proven permanence, **Canada balsam** is the mountant preferred by the present author. Similarly, when the insect material is to be placed in a permanent collection, labels, glues and inks should all be selected with archival quality in mind.

The method described below should be carried out under conditions of controlled ventilation and in accordance with the safety procedures of the laboratory. All stages can be carried out in a square-based solid watch glass or similar small receptacle with a wide opening and a lid. Because decanting fluids between stages of the procedure needs to be done whilst observing the pipette tip through the dissection microscope (to avoid the loss of specimens), the use of test tubes is not recommended.

1. *Maceration* of body contents is carried out by warming to about 80° C in a 10 % Potassium Hydroxide solution (an alkali) until visible body contents have become translucent. [A small puncture may be made in the ventral surface of each specimen in order to speed up this and subsequent processes.] Usually no more than 10 minutes is required, but considerably longer may be needed on occasions, and this does no harm to the cuticle if the specimens are not over-heated.

2. Decant excess macerant.

3. *De-waxing* of the cuticle is carried out by gently warming specimens in one of the following mixtures (*): carbol-xylol (Xylene with 10% dissolved Phenol), carbol-Histoclear (Histoclear with dissolved Phenol), Chloral-Phenol (equal weights of Phenol and Chloral Hydrate warmed to liquefy, remaining liquid when cooled) or a mixture of absolute alcohol and Xylene.

4. Decant de-waxing fluid.

5. a) for black puparia rinse in alcohol and then *partially bleach* cuticle by adding a few drops each of cold strong Ammonia and 30-volume Hydrogen Peroxide solutions. Bleaching should be monitored as it can be very rapid, and may be stopped quickly by adding a few drops of a water-soluble acid. [Note that domestic bleach is unsatisfactory for controlled cuticular bleaching.]

OR

b) for pale puparia *staining* may be carried out by adding an excess of Glacial Acetic Acid (**) and a few drops of Acid Fuchsin stain solution. Staining is carried out cold and usually only takes a few minutes. Failure of staining may result if de-waxing, or the neutralisation of macerant, has been inadequate (see stage 3).

6. Decant bleach or stain and rinse specimens in Glacial Acetic Acid (**) or 95% Ethanol.

7. *Final dehydration* of specimens may be carried out by soaking in Glacial Acetic Acid (**) or Absolute Ethanol for a few minutes. Decant dehydration fluid.

8. *Clear* specimens by adding a few drops of Clove Oil or Histoclear, or an appropriate product compatible with any alternative mountant.

9. Place specimen(s) on a pre-cleaned and polished slide, in a drop of Canada balsam or chosen alternative mountant and arrange specimens as required. It is a good idea to place some specimens dorsum-upwards and some venter-upwards, as this aids in the resolution of ventral characters of species with very ornate dorsa. When the mountant has partially dried, gently a lower coverslip with a small amount of fresh mountant applied to it: the drier mountant will hold the specimens in place, while the fresh mountant will spread to cover the entire lower surface of the coverslip. A little practice will be needed to perfect the amount of mountant needed to provide a preparation which does not cause distortion through over-flattening, but is also not so thick that its optical quality is impaired.

10. Slides must be adequately dried, especially if vertical storage is to be employed. With Canada balsam, slides may require up to two months at 35–45° C prior to permanent vertical storage, although they will be touch-dry after only a day or two. If each slide is provided with a pair of thick card labels, slides can then be stacked immediately, and the coverslip will also be protected throughout the life of the slide: for this reason, the use of paper labels is not recommended for permanent mounts.

- * A number of chemicals have been found to be efficacious in the removal of waxy whitefly secretions, some with more success than others. All of them should be used in conjunction with controlled ventilation, but local laboratory regulations may preclude the use of some or all of them. If all of them are disallowed, then repeated warming in clove oil will often succeed, although much more slowly.
- ** The choice between Glacial Acetic Acid and alcohols is influenced primarily by safety factors. Glacial Acetic Acid has the advantage of being a quick means of neutralising alkalis and vigorously dehydrating material, and provides the acid medium necessary for staining; it has the disadvantages of its unpleasant, breath-catching smell and ability to cause skin burns. Whilst 95% industrial-grade Ethanol (Industrial Methylated Spirit) may be cheap in some countries, Absolute (100%) Ethanol is always extremely expensive: however, both are more pleasant to work with than Acetic Acid. Ethanol is extremely hygroscopic, however, and many workers prefer 100% iso-propanol. Iso-propyl alcohol is, thus, a better choice for dehydration in humid environments, as well being cheaper than Absolute Ethanol.



FIGURES 1–4. *Aleurodicus* spp, puparia. 1, *A. araujoi* Sampson & Drews. 2, *A. coccolobae* Quaintance & Baker. 3, *A. dispersus* Russell. 4, *A. dugesii* Cockerell.





FIGURES 5–8. Aleurodicus spp, puparia. 5, A. inversus sp. nov. 6, A. magnificus Costa Lima. 7, A. maritimus Hempel. 8, A. niveus sp. nov.







FIGURES 9–12. *Aleurodicus* spp, puparia. 9, *A.* pauciporus **sp. nov.** 10, *A. pulvinatus* (Maskell). 11, *A. vinculus* **sp. nov.** 12, *A. rugioperculatus* **sp. nov.**

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zоотаха 681



FIGURES 13–16. Various, puparia. 13, *Aleuronudus acapulcensis* (Sampson & Drews), ex-Darién, Panamá. 14, *Aleuronudus manni* (Baker). 15, *Austroaleurodicus pigeanus* (Baker & Moles), ex-Santiago, Chile (genus not recorded from Belize but see generic key). 16, *Azuraleurodicus pentarthrus* Martin.





FIGURES 17–20. *Ceraleurodicus* spp. 17–19 *C. keris* sp. nov., puparia. 17, holotype ex- Belize. 18, JHM #8083 ex- Nicaragua. 19, JHM #3478 ex- Panamá. 20, *C. varus*, puparium.





FIGURES 21–24. Dialeurodicus and Leonardius spp, puparia. 21, D. bondariae sp. nov. 22, D. caballeroi sp. nov. 23, D. silvestrii (Leonardi). 24, L. kellyae sp. nov.



FIGURES 25–28. *Metaleurodicus* spp, puparia. 25, *M. arcanus* sp. nov. 26, *M. griseus* (Dozier), ex- Dade County, Florida. 27, *M. tenuis* sp. nov. 28, *M. variporus*, with abdominal compound pore combination medium/large/medium/large/medium/small (MLMLMS).





FIGURES 29-32. *Metaleurodicus variporus* **sp. nov.**, puparium, abdominal compound pore combination variants (see fig 28 for key). 29, LLLLMS. 30, LLLLLS. 31, LLSLLS. 32, MLMLMS on left, LLMLMS on right.





FIGURES 33-35. *Nealeurodicus* spp. 33, *N. altissimus* (Quaintance), puparium, ex-*Machaerium riparium*. 34, *N. bakeri* (Bondar), waxy cover of puparium. 35, *N. bakeri* (Bondar), puparium. 36, *N. fallax* **sp. nov.**, puparium.

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FIGURES 37-40. *Nealeurodicus* and *Octaleurodicus* spp. 37, *N. petiolaris* sp. nov., puparium. 38, *N. petiolaris* sp. nov., waxy cover of puparium. 39, *N. petiolaris* sp. nov., third-instar larva. 40, *Octaleurodicus* sp., ex- Darién, Panamá (genus not recorded from Belize but see generic key).



FIGURES 41–44. *Paraleyrodes ancora* **sp. nov.** 41, male puparium. 42, female puparium. 43, adult male, terminal abdominal segment and genitalia, lateral aspect. 44, adult male, genitalia, dorsal aspect.

ALEURODICINAE OF BELIZE

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FIGURES 45–48. *Paraleyrodes* spp, puparia. 45, *P. ?bondari* Peracchi. 46, *P. citricolus* Costa Lima. 47, *P. citricolus* Costa Lima, mid-moult specimen. 48, *P. minei* Iaccarino.









FIGURES 49–52. Paraleyrodes spp. 49–50, P. cervus sp. nov., males, terminal abdominal segment and genitalia, lateral aspect. 51, P. proximus Terán, post-emergence male pupal case. 52, P. proximus Terán, male, genitalia, lateral aspect.







FIGURES 53–54. *Paraleyrodes triungulae* **sp. nov.**, male, terminal abdominal segment and genitalia, with aedeagus in imperfect lateral aspect in both.





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FIGURES 55–58. *Aleurodicus* spp, puparia. 55, *A. coccolobae* Quaintance & Baker, region of vasiform orifice. 56, *A. rugioperculatus* sp. nov., cephalothoracic sculpture. 57, *A. rugioperculatus* sp. nov., median abdominal detail. 58, *A. rugioperculatus* sp. nov., operculum and lingula.





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FIGURES 59–62. Various, puparia. 59, *Aleurodicus inversus* sp. nov., vasiform orifice and posterior marginal area. 60, *Dialeurodicus silvestrii* (Leonardi), division between subdorsal abdominal fields of wax-secreting pores. 61, *D. silvestrii*, vasiform orifice and posterior submarginal area. 62, *Metaleurodicus sp.* nov., submarginal sculpturing, cephalothorax.



FIGURE 63. *Aleurodicus dispersus* Russell, puparium, after Russell (1965), with inset detail of (a) 8-shaped pore, (b) double-rimmed pore, (c) wide-rimmed pore, (d) minute wide-rimmed pore and (e) septate pore.





FIGURE 64. *Aleurodicus pulvinatus* (Maskell), puparia, showing variation of cuticular pigmentation in samples from (a) Costa Rica, *Hura crepitans*, (b) Belize, Lauraceae, (c) Belize, *Guettarda combsii*, (d) Belize, undetermined host, (e) Panamá, *Isertia hypoleuca*. The dashed line marks the boundary of the submarginal pore band.



FIGURE 65. *Azuraleurodicus pentarthrus* Martin, puparium, with expanded detail of (a) marginal glands and submarginal 8-shaped pores, (b) "hour-glass" septate pore, and (c) submarginal double-rimmed pores.





FIGURES 66–67. *Aleurodicus* and *Ceraleurodicus* spp., puparia. 66, *A. niveus* **sp. nov.**, posterior dorsal detail, with submarginal pore band detail shown as inset. 67, *C. keris* **sp. nov.**, detail of (a) margin, tiny submarginal setae, cepalic compound pore and its axial process, (b) vasiform orifice and (c) small compound pore at abdominal segment VII/VIII boundary, with posterior marginal seta and tiny submarginal seta.



FIGURE 68. *Lecanoideus floccissimus* Martin *et al.*, puparium; arrow (a) indicates tiny 8th abdominal compound pore almost underlying lingula. (Genus / species not recorded from Belize but see generic key and discussion of *Aleurodicus.*)



FIGURES 69-74. Aleurodicus spp, puparia. 69, A. araujoi Sampson & Drews, posterior dorsal detail, with inset (a) showing posterior marginal seta and down-curled margin. 70, A. dugesii Cockerell, posterior dorsal detail, with section (a) showing posterior marginal seta and down-curled margin. 71, A. inversus sp. nov., cephalothoracic chaetotaxy. 72, A. inversus sp. nov., anterior abdominal dorsal detail, with inset (a) showing margin deflexed ventrally. 73, A. magnificus Costa Lima, posterior dorsal detail, with inset (a) showing margin deflexed ventrally (after Costa Lima, 1928). 74, A. maritimus Hempel, cephalothoracic dorsal detail.

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FIGURES 75–83. Various, puparia, dorsal detail. 75, *Aleurodicus pauciporus* sp. nov., abdominal segments V–VIII. 76, *A. pauciporus* sp. n, lateral margin and submarginal detail. 77, *A. pulvinatus* (Maskell), abdominal segment IV. 78, *A. rugioperculatus* sp. nov., section of cephalothorax, with longitudinal moulting suture on right. 79, *A. vinculus* sp. nov., submedian thoracic detail, showing "chains" of septate pores. 80, *A. vinculus* sp. nov., cephalothoracic margin and submarginal detail. 81, *Aleuronudus manni* (Baker), lateral margin and submarginal detail. 82, *Ceraleurodicus varus* (Bondar), margin and submarginal detail of thoracic ray. 83, *C. varus* (Bondar), vasiform orifice and compound pore (present on one side only, posterolateral to vasiform orifice).





FIGURES 84–90. *Dialeurodicus* spp, puparia. 84, *D. bondariae* sp. nov., vasiform orifice and surrounds. 85, *D. bondariae*, ventral abdominal "ray" detail and posterior marginal seta. 86, *D. bondariae* sp. nov., margin and dorsal submarginal detail of second anteriormost "ray". 87, *D. caballeroi* sp. nov., margin and dorsal detail of abdominal "ray" and porate tubercle at its proximal end. 88, *D. caballeroi* sp. nov., margin and submarginal dorsal detail of cephalothoracic ray. 89, *D. caballeroi* sp. nov., vasiform orifice and surrounds. 90, *D. silvestrii* (Leonardi), margin and dorsal submarginal detail, opposite thoracic tracheae.



FIGURES 91–94. Various, dorsal puparial detail. 91, *Leonardius kellyae* sp. nov., abdominal segments IV–VI, with agglomerate pore areas on each segment, and compound pore on segment IV. 92, *L. kellyae* sp. nov., vasiform orifice and agglomerate pore areas on abdominal segments VII & VIII. 93, *Metaleurodicus arcanus* sp. nov., vasiform orifice and posterior marginal area. 94, *M. griseus*, ex-Dade County, Florida, vasiform orifice and posterior marginal area (to same scale as 93).





FIGURES 95–98. *Metaleurodicus* spp, puparia. 95, *M. tenuis* **sp. nov.**, dorsal submedian abdominal depressions, segment III/IV and IV/V boundaries. 96, *M. tenuis* **sp. nov.**, vasiform orifice and posterior marginal area. 97 a,b,c, *M. variporus* **sp. nov.**, fore leg and antenna (all drawn to same scale). 97a, fully developed, mature, specimen with antenna and leg fully expanded. 97b, antenna at smallest size, and leg almost larviform. 97c, antenna beginning expansion towards full development, leg still as in 97b. 98, *M. variporus*, lateral margin and dorsal submarginal abdominal detail, with large and medium compound pore types (and expanded detail of simple pores).



FIGURES 99–105. *Nealeurodicus* and *Paraleyrodes* spp., puparia. 99, *N. altissimus* (Quaintance), small cylindrical compound pore, abdominal segment VII, (a) from *Inga* sp. and (b) from *Lon-chocarpus rugosus* (both to same scale). 100, *N. altissimus* (Quaintance), left cephalic compound pore and satellite pores. 101, *N. altissimus* (Quaintance), small compound pore and satellite pores, abdominal segment III, right. 102, *N. fallax* sp. nov., dorso-median abdominal segmentation and compound pores, with expanded detail of vasiform orifice. 103, *N. fallax* sp. nov., compound pore, abdominal segment V. 104, *Paraleyrodes ancora* sp. nov., submedian dorsal abdominal detail, showing dusky coloration and simple pores. 105, *P. ancora* sp. nov., post-emergence pupal case, dorsal detail surrounding small and large abdominal compound pores.

 $\overline{681}$



FIGURES 106–116. Various. 106, Paraleyrodes cervus sp. nov., adult male aedeagus, lateral aspect. 107, P. triungulae sp. nov., adult male aedeagus, imperfect lateral aspect. 108, P. bondari Peracchi, adult male aedeagus, (a) lateral aspect and (b) oblique aspect. 109, P. citricolus Costa Lima, adult male aedeagus, (a) lateral aspect and (b) dorsal aspect. 110, P. minei Iaccarino, adult male aedeagus, (a) lateral aspect and (b) dorsal aspect. 111, P. minei Iaccarino, puparium, large compound pore (a) in natural aspect, drawn to smaller scale and (b) flattened, with chitinous splines radially arranged, drawn to larger scale. 112, P. citricolus Costa Lima, puparium, large compound pore, flattened, with chitinous splines radially arranged. 113, P. bondari Peracchi, puparium, large compound pore, flattened, with chitinous splines missing [111b–113 all to same scale]. 114, Ceraleurodicus varus (Bondar), entire puparium, dorsal, to show rays and compound pores; single dots represent the chaetotaxy. 115, Aleuronudus manni (Baker), adult female, abdomen, lateral aspect, showing robust secreted wax "brushes". 116, Nealeurodicus bakeri (Bondar), puparium, dorsal, vicinity of vasiform orifice, showing bright pores lateral to the orifice, bi- and tri-composite pores, pair of tiny compound pores on abdominal segment VIII, and remainder of pores of the loculate type.





FIGURES 117–118. *Nealeurodicus petiolaris* **sp. nov.**, puparium. 117, whole puparium, with ventral detail at left and expanded detail of (a) thoracic margin, (b) lateral margin and dorsal submargin, (c) abdominal compound pore and (d) dorsal submedian detail of abdominal segments VII and VIII, showing clusters of wide-rimmed pores and quadriloculate pores. 118, ventral pads, abdominal spiracles, ventral abdominal setae and spinulose caudal tracheal fold.



FIGURES 119–122. *Paraleyrodes* spp. 119, *P. pseudonaranjae* Martin, paratype puparium ex-Hong Kong. 120, *P. pseudonaranjae* Martin, paratype male aegeagus, lateral view. 121, *P. perplexus* **sp. nov.**, puparium, detail of anterior margin and submarginal glands. 122, *P. perplexus* **sp. nov.**, aedeagus, lateral apsect of (a–c) paratypes JHM #8003A, (d) JHM # 7972 and (e) JHM #7950.







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126



FIGURES 123–128. Habitus photographs. 123, *Aleurodicus dispersus* Russell, puparia, on undetermined host. 124, *Aleurodicus pulvinatus* (Maskell), puparia, on *Guettarda combsii*. 125, *Paraleyrodes* sp., puparium, on *Inga* sp. 126, *Paraleyrodes citricolus* Costa Lima, puparium, on *Coccoloba belizensis*. 127, *Paraleyrodes* sp., adult male and pupal case, on *Guettarda combsii*. 128, *Nealeurodicus altissimus* (Quaintance), puparium, on undetermined host.







130





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FIGURES 129-134. habitus photographs. 129-130, Nealeurodicus petiolaris sp. nov., puparia and emergent adult female, on young stem of Protium glabrum. 131, Nealeurodicus bakeri (Bondar) on undetermined Asteraceae. 132, Dialeurodicus silvestrii (Leonardi), group of eight puparia lining midrib of ?Eugenia sp. 133-134, Aleuronudus manni (Baker), on Guettarda combsii: 133, two puparia, with undamaged wax filaments issuing from the large compound pores on abdominal segment III; 134, adult female and vacated pupal cases.



135



136

FIGURES 135–136. habitus photographs. 135, *Aleurodicus niveus* sp. nov., group of puparia under leaf of *Encyclia cochleata*; 136, *Ceraleurodicus keris* sp. nov., single puparium under leaf of *Lunania parviflora*, Nicaragua, JHM #8083.