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Four new neotropical *Trioza* species associated with Loranthaceae (Santalales) and comments on mistletoe inhabiting psyllids (Hemiptera, Psylloidea)

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Abstract

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Key Words

Sternorrhyncha Triozidae systematics hemiparasitic plants phytophagy distribution Four new *Trioza* species associated with mistletoes are described, diagnosed and illustrated from Brazil and Chile. They are monophagous on the Loranthaceae *Struthanthus uraguensis* (*Trioza struthanthi* **sp. n.**), *Tripodanthus acutifolius* (*Trioza tripodanthi* **sp. n.**) and narrowly oligophagous on *Tristerix* spp. (*Trioza tristericis* **sp. n.**). For a fourth species (*Trioza vagata* **sp. n.**) host information is unavailable but its association with mistletoes is likely. The four species form a putative monophyletic group, together with three North American species (*Trioza acuminata* Tuthill, *T. incidata* Tuthill and *T. phorodendrae* Tuthill), based on the apically incised paramere, the highly modified valvulae of the female ovipositor and the host association with mistletoes. *T. acuminata* stat. n. from California is raised to species rank (originally described as subspecies of *T. phorodendrae*). The *Trioza struthanthi*-group is diagnosed and a key for the identification of its constituent members is provided. New host data are provided for *Calophya* sp. from Brazil as well as for *Notophorina fusca* Burckhardt and *Zonopelma australis* Burckhardt from Chile. Host plant and biogeographical patterns of mistletoe feeding psyllids around the world are briefly discussed.

Introduction

Psyllids or jumping plant lice are plant sap sucking insects, which are generally highly host specific, i.e. they complete their development on only one plant species or a few species of the same plant genus. In addition, related psyllid species tend to develop on related plant species, making them an interesting group for evolutionary studies (Burckhardt et al. 2014). Several studies showed that these host plant patterns are not primarily the result of cospeciation, as there is no large scale congruence of the phylogenies of the two groups, but rather host shifts within the particular host group (Ouvrard et al. 2015). Mistletoes are a particularly fascinating group to study host patterns as they themselves, by their hemiparasitic life style, depend on a host (Lázaro-Gonzales et al. 2017).

Mistletoes are members of the order Santalales which contains 13 families, 151 genera and 1992 species of hemiparasitic and non-parasitic plants (Stevens 2001). Psyllid associations have been reported from the three families Loranthaceae, Misodendraceae and Santalaceae (including Viscaceae) (Table 1). Taylor (2016), in a study of Australian *Acizzia* species from mistletoes of the genus *Amyema*, suggested that the switch of psyllids from ancestral hosts (probably Fabaceae) to mistletoes may have been mediated by their close proximity (i.e. within the same canopy).

Psyllids associated with mistletoes have been known from all biogeographical regions (except for Antarctica): Australian (12 species), Nearctic (6 species), Oriental (4 species), Afrotropical (3 species), Neotropical (1 species) and Palaearctic (1 species) realms (Table 1). Material collected during extensive field work in Brazil and Chile in the

Table 1. Psylloid associations with plants of the order Santalales reported in the literature or present in the collections of the MHNG and NHMB (* = host confirmed by the presence of immatures or skins; † = host improbable) and their distribution.

Psylloidea	Host plants	Distribution	Reference
CALOPHYIDAE			
Calophyinae			
Calophya oweni Tuthill, 1939	Phoradendron juniperinum A. Gray (Santalaceae)	USA (California, Colorado)	Burckhardt and Basset (2000)
Calophya sp.	* Phoradendron ensifolium (Pohl ex DC.) Eichler in Mart.	Brazil (Paraná)	present paper
HOMOTOMIDAE			
Macrohomotominae			
Macrohomotoma maculata Mathur, 1975	† Santalum album L. (Santalaceae)	India	Mathur (1975)
Mycopsylla indica Mathur, 1975	† Santalum album	India	Mathur (1975)
LIVIIDAE			
Euphyllurinae	* Agalanthus natalitius con zoubori (Harry) Polhill		/
Diaphorina Ioranthi Capener, 1973	and Wiens (Loranthaceae)	* Agelanthus natalitius ssp. zeyheri (Harv.) Polhill South Africa South Africa	
Diaphorina venata Mathur, 1975	Santalum album L. (Santalaceae)	India	Mathur (1975)
Diaphorina verbera Kandasamy 1986	Santalum album	India	Kandasamy (1986)
Notophorina fusca Burckhardt, 1987	* Misodendrum punctulatum Banks ex DC. (Misodendraceae)	Chile	present paper
PSYLLIDAE			
Acizziinae			
Acizzia amyemae Taylor, 1999	Amyema miquelii (Lehm. ex Miq.) Tiegh., A. pendula (Sieber ex Spreng.) Tiegh., * A. preissii (Miq.) Tiegham, A. sp. (Loranthaceae)	Australia (Australian Capital Territory, New South Wales, South Australia, Victoria, Western Australia)	Taylor (2016)
Acizzia casuarinae Taylor, 2016	* Amyema sp. Australia (New South Wales, Oueensland)		Taylor (2016)
Acizzia lanceolatae Taylor, 2016	* mistletoe Australia (South Australia)		Taylor (2016)
Acizzia loranthacae Taylor, 1999	Amyema miquelii, A. pendula, * A. sp.	Amyema miquelii, A. pendula, * A. sp. Amyema miquelii, A. pendula, * A. sp. South Australia (Australian Capital Territory, New South Wales, South Australia, Victoria)	
Acizzia maculata Taylor, 2016	mistletoe	Australia (Western Australia)	Taylor (2016)
Acizzia miraculosa Taylor, 2016	* Amyema miraculosa (Miq.) Tiegh., A. quandang Australia (New South Wald (Lindl.) Tiegh. South Australia)		Taylor (2016)
Acizzia nestor Taylor, 2016	Amyema nestor (S. Moore) Danser Australia (New South Wale Western Australia)		Taylor (2016)
Acizzia novaeguineae Taylor, 2016	unknown Papua New Guinea		Taylor (2016)
Acizzia pendulae Taylor, 1999	Amyema pendula, A. sp. Australia (Australian Capital Territory, New South Wales)		Taylor (2016)
Acizzia preissiae Taylor, 2016	Amyema preissii	Australia (Western Australia)	Taylor (2016)
Acizzia quandang Taylor, 2016	Amyema quandang	Amyema quandang Australia (New South Wales,	
Acizzia sp.	* Amyema miquelii, Amyema preissii Australia (South Australia)		Taylor (2016)
Aphalaroidinae	, my oma miquem, my oma process	/ doctronal (country doctronal)	10,101 (2020)
Freysuila phorodendrae (Tuthill, 1939)	Phoradendron leucarpum subsp. tomentosum (DC.) J.R. Abbott and R.L. Thompson, * P. villosum (Nutt.) Nutt. ex Engelm., * P. sp. [as Phoradendron "pubescens" sic!]	USA (Arizona, California)	Burckhardt and Wyniger (2007)
Zonopelma australis Burckhardt, 1987	* Misodendrum linearifolium DC., * M. punctulatum		
Zonopelma myzodendri Burckhardt, 1987	* Misodendrum linearifolium	Chile	Burckhardt (1987a)
Psyllinae	,		
Cacopsylla visci (Curtis, 1835)	* Loranthus europaeus Jacq. (Loranthaceae), * Viscum album L., V. album subsp. austriacum (Wiesb.) Vollm. (Santalaceae) (Wiesb.) Vollm. (Santalaceae) Armenia, Austria, Belgium, Bulgaria, Czech Republic, France, Georgia, Germany, Hungary, Iraq, Italy, Japan, Moldova, Morocco, Norway, Poland, Russia, Slovakia, Slovenia, Sweden, Switzer- land, UK, Ukraine		Gegechkori and Logi- nova (1990), Lauterer (1999), Baugnée et al. (2002), Inoue (2010), Ouvrard (2017)
Psylla loranthi Capener, 1973	* Agelanthus natalitius subsp. zeyheri, * Tapinanthus kraussianus subsp. kraussianus Tiegh. (Loranthaceae)	South Africa	Capener (1973)
Psylla santali Mathur, 1975	Santalum album	India	Mathur (1975)
Psylla winkleri Rübsaamen, 1910	Tapinanthus bangwensis (Engl. & K. Krause) Danser (Loranthaceae)	Cameroon	Rübsaamen (1910)
TRIOZIDAE	Dharadandranan		
Trioza acuminata Tuthill, 1943,	Phoradendron sp. [as Phoradendron "pubescens" sic!]	USA (California)	Tuthill (1943)

Psylloidea	Host plants	Distribution	Reference Tuthill (1945)	
Trioza incidata Tuthill, 1945	unknown	Mexico		
Trioza phorodendrae Tuthill, 1939	Phoradendron juniperinum A. Gray	erinum A. Gray USA (Colorado)		
Trioza struthanthi sp. n.	* Struthanthus uraguensis G. Don (Loranthaceae)	Brazil (Minas Gerais, Struthanthus uraguensis G. Don (Loranthaceae) Paraná, Rio Grande do Sul, Santa Catarina)		
Trioza tripodanthi sp. n.	* Tripodanthus acutifolius (Ruiz & Pav.) Tiegh. (Loranthaceae)	Brazil (Santa Catarina)	present paper	
Trioza tristericis sp. n.	* Tristerix corymbosus (L.) Kuijt (Loranthaceae), T. verticillatus (Ruiz & Pav.) Barlow & Wiens, T. sp. (Loranthaceae)	latus (Ruiz & Pav.) Barlow & Wiens, Chile		
Trioza vagata sp. n.	unknown; adults collected on <i>Clusia</i> sp. (Clusiaceae), an unlikely host	' Brazil (Parana)		

last three decades shows that the apparent paucity in South America is an artefact of poor knowledge on the psyllid fauna of this continent (Burckhardt and Queiroz 2012). Here we describe four new *Trioza* species from Brazil and Chile associated with Loranthaceae (confirmed for three, likely for one species), report host plants (Misodendraceae and Santalaceae) for another three species from Brazil (*Calophya* sp.) and Chile (*Notophorina fusca* Burckhardt and *Zonopelma australis* Burckhardt) and discuss the host patterns of Psylloidea developing on Santalales.

Material and methods

Material was examined or is cited from following institutions: BMNH-Natural History Museum, London, UK; MHNG-Muséum d'histoire naturelle, Genève, Switzerland; MMBC-Moravian Museum, Brno, Czech Republic; MZSP-Museu de Zoologia, Universidade de São Paulo, SP, Brazil; NHMB-Naturhistorisches Museum, Basel, Switzerland; UFPR-Coleção Entomológica Padre Jesus Santiago Moure, Centro Politécnico, Universidade Federal do Paraná, Curitiba, PR, Brazil; USNM-United States National Museum collections, Beltsville, MD, USA. Females are selected as holotypes of the four new species which is somewhat unusual in psyllid taxonomy. The four species have highly modified valvulae in the female ovipositor, a feature which is unique within the large family Triozidae, and each species is well diagnosed by the shape of the female terminalia and the valvulae. The male terminalia are also diagnostic but for T. tripodanthi sp. n. only two specimens are available, one specimens is slide mounted, the other one has abnormally developed, asymmetrical genal processes. Neither specimen is ideal as holotype.

The morphological terminology is mostly that of Hollis (1984, 2004) but see also Figs 11, 13, 32. Measurements were taken as follows: adult body length from dry mounted or ethanol preserved specimens measuring the distance between fore margin of head and tip of forewings when folded over body; body length of immatures from specimens preserved in ethanol; the other measurements were taken from slide mounted specimens. The adult body length is given as range, mean and standard deviation, the other measurements and the ratios as range.

The plant nomenclature accords with The Plant List (2013).

Results

Taxonomy

Trioza struthanthi-group

Diagnosis. Adult. Body size small, 2.3–3.2 mm long. Genal processes developed, slender, 0.7-1.0 times as long as vertex along midline. Antenna ten-segmented, 1.3–2.0 times as long as head width; with a single subapical rhinarium on each of segments 4, 6, 8 and 9. Forewing narrow, lanceolate, 2.5-3.0 times as long as wide; angular apically, with weakly curved vein Rs and small cu, cell. Metatibia with genual spine and 1+3 apical spurs. Paramere incised apically. Female terminalia subglobular, proctiger with styliform process apically. Valvulae of ovipositor highly modified: dorsal valvula stylet-shaped; ventral valvula very broad, ribbon-shaped, obliquely truncate apically; lateral valvula ribbon-shaped, with two strongly sclerotised, teeth apically. - Fifth instar immature 1.5-1.7 mm long, 1.4-1.6 times longer than wide. Antennal flagellum 1-segmented. Forewing pad with humeral lobe extending forward almost to the middle of eye. Tarsi with triangular arolium, bearing short petiole and distinct unguitractor, claws fully developed and of similar size, small, shorter than arolium. Anus ventral; outer circumanal ring transversely reniform, consisting of a single row of pores. Marginal sectasetae truncate, densely spaced; postocular seta present; sectasetae absent from dorsum. - Host plants. Santalales.

Description. Adult (Figs 1, 3, 5, 7). Body length 2.3–3.2 mm. Integument lacking macroscopic setae dorsally, mat with very fine scattered punctures. Head (Figs 2, 4, 6, 8) inclined at about 45° to longitudinal body axis; slightly wider than pronotum and about as wide as mesoscutum. Vertex trapezoidal, in the middle of each half slightly produced anteriorly; flat with weakly indented foveae; with sparse, moderately long microscopic setae; evenly curved down to genal processes; occipital margin relatively well-defined. Median suture fully developed, weakly incised in anterior half. Occiput forming narrow bands caudad of eyes, visible from above, weakly convex. Median ocellus directed forward, not visible from above, completely covering frons. Genal processes distinctly deflected from plane of vertex, 0.7–1.0 times as

long as vertex along midline, bearing a long seta at base and a few long setae apically. Eyes hemispherical. Clypeus pear-shaped, bearing a pair of setae; ultimate rostral segment with each one pair of setae basally and in the middle, respectively. Antenna 10-segmented, 1.3-2.0 times as long as head width, with a single, subapical rhinarium on each of segments 4, 6, 8 and 9; segment 9 about as long as segment 10; segment 9 bearing two thick bristles, a longer one just proximal to rhinarium and a shorter one more towards the base of the segment; segment 10 with two terminal setae, one slender, subacute and about as long as segment, and the other one thicker, truncate and half as long as segment. Pronotum strongly curved down anteriorly, weakly arcuate in dorsal view. Mesopraescutum, in dorsal view, about 1.5 as wide as long, in lateral view relatively flat; anterior margin strongly arcuate. Forewing (Figs 9–16) narrowly lanceolate, subacute or narrowly rounded apically, 2.5-3.0 times as long as wide; veins beset with fine microscopic setae which are shorter than distance between setae, slightly denser at wing base becoming sparser towards apex; R branch acutangular, vein Rs weakly curved towards fore margin in apical third, branching of M on or close to Rs-Cu_{1a} line, vein Cu 4-5 times as long as Cu_{1b}, cell m₁ value 1.1-1.6, cu, value 1.8-2.7; radular spinules covering narrowly triangular fields at the outer margins of cells m, m₂ and cu₁. Hindwing 0.7–0.8 times as long as forewing, costal margin with 0-2 setae proximal to costal break, setae distal to costal break divided into two groups with 2–4 and 3–5 setae, respectively, as well as one seta at the end of sclerotised part of C+Sc; veins M and Cu with common stem. Hind leg with metacoxa bearing relatively short horn-shaped meracanthus, hardly produced at inner anterior trochanteral insertion; metatibia 0.7-0.9 times as long as head width, not inflated basally with genual tooth and 1+3 strongly sclerotised apical spurs. Abdomen with setae present on tergite 2 in male and tergite 3 in female. Male proctiger (Figs 17, 20, 23, 26) tubular, relatively short and thick, covered in long setae in apical two thirds along posterior margin. Subgenital plate subglobular, covered in moderately long setae. Paramere (Figs 18, 21, 24, 27) in profile, lamellar; incised apically with outer and inner lobe. Aedeagus with proximal segment slender, narrowly rounded basally; distal segment (Figs 19, 22, 25, 28) long and slender, longer than proctiger, weakly expanded apically; sclerotised end tube of ductus ejaculatorius short, weakly sinuous. Female terminalia (Figs 29, 32, 36, 39) subglobular, proctiger with styliform process apically. Proctiger with a few sparse, moderately long setae at and beyond the distal end of the circumanal ring and a few long, transversely arranged setae in the middle; circumanal ring oval, consisting of two rows of unequal pores (Fig. 31). Subgenital plate shorter than proctiger, subtriangular in profile, truncate or weakly indented apically in ventral view, evenly covered in moderately long setae basally and in the middle (Figs 38, 34, 37, 40). Valvulae (Figs 32, 35, 38, 41) highly modified: dorsal valvula stylet-shaped; ventral valvula very broad, ribbon-shaped, obliquely truncate apically with each a tooth apico-dorsally and apico-ventrally, respectively; lateral valvula ribbon-shaped, with two strongly sclerotised, teeth apically.

Fifth instar immature (Figs 42, 43). Body 1.5–1.7 mm long, in dorsal view, oval, 1.4–1.6 times longer than wide. Antennal flagellum one-segmented; cephalopronotal sclerite distinctly separated from mesonotal sclerite which is also separated from metanotal sclerite. Forewing pad 0.8-0.9 mm long, 2.3–2.8 times as long as antenna; humeral lobe extending forward almost to the middle of eye. Tarsi with triangular arolium (Fig. 47), bearing short petiole and distinct unguitractor, claws fully developed and of similar size, small, shorter than arolium. Caudal plate 0.7-0.8 times as long as wide; anus ventral; outer circumanal ring (Figs 48, 49) transversely reniform, distance between posterior margins of circumanal ring and of caudal plate 1.0-1.3 times as long as circumanal ring in longitudinal body axis; consisting of a single row of oval pores. Marginal sectasetae (Figs 44-46) truncate, evenly and densely spaced; postocular seta present; sectasetae absent from dorsum.

Comments. Seven species are included: the North American *Trioza acuminata* Tuthill, 1943, stat. n., *T. incidata* Tuthill, 1945 and *T. phorodendrae* Tuthill, 1939, as well as the four South American species described below: *T. struthanthi* sp. n., *T. tripodanthi* sp. n., *T. tristericis* sp. n. and *T. vagata* sp. n. (Table 1).

Trioza acuminata Tuthill, 1943, was described as subspecies of *T. phorodendrae* Tuthill, 1939 based on a single male from California. According to Tuthill (1943) the genal processes of *T. acuminata* are distinctly longer than in *T. phorodendrae* suggesting that the two taxa are distinct. Until additional evidence becomes available, the two taxa are treated as different species and we elevate the former to species rank as *Trioza acuminata* Tuthill, 1943, stat. n.

Key to adults of the species of the Trioza struthanthi-group

3 4 Body orange red, 2.8 mm long. Paramere, in profile, straight. Dorsal outline of female proctiger between apex of circumanal ring and base of apical process, in profile, undulate. Mexico......incidata Body yellow, 2.5 mm long. Paramere, in profile, weakly curved. Dorsal outline of female proctiger between apex of circumanal ring and base of apical process, in profile, weakly convex. USA. On Phoradendronphorodendrae 5 Genal processes conspicuously dark, tubular, obtuse apically (Fig. 4). Paramere, in profile, lamellar, straight (Fig. 21). Dorsal outline of female proctiger between apex of circumanal ring and base of apical process, in profile, evenly convex, apical process straight, with dorsal teeth on its entire length (Fig. 33). Brazil. On Tripodanthus......tripodanthi Genal processes light, of same colour as vertex, conical, subacute apically (Figs 6, 8). Paramere, in profile, lamellar and weakly curved (Fig. 24) or digitiform (Fig. 27). Dorsal outline of female proctiger between apex of circumanal ring and base of apical process, in profile, almost straight with bump in the middle or irregularly convex, apical process curved, Genal processes 0.8 times as long as vertex along mid-line. Forewing wider, 2.7 times as long as wide. Paramere, in profile, lamellar, weakly curved (Fig. 24). Apical dilatation of apical segment of aedeagus gradually narrowing towards base (Fig. 25). Dorsal outline of female proctiger between apex of circumanal ring and base of apical process, in profile, almost straight with bump in the middle, apical process with dorsal teeth only near apex (Fig. 36). Chile. On Tristerix......tristericis Genal processes 0.9 times as long as long as vertex along mid-line. Forewing narrower, 2.8–2.9 times as long as wide. Paramere, in profile, digitiform, straight (Fig. 27). Apical dilatation of apical segment of aedeagus abruptly narrowing towards base (Fig. 28). Dorsal outline of female proctiger between apex of circumanal ring and base of apical process, in profile, convexly curved, apical process with dorsal teeth along its entire length (Fig. 39). Brazil. Host unknown vagata

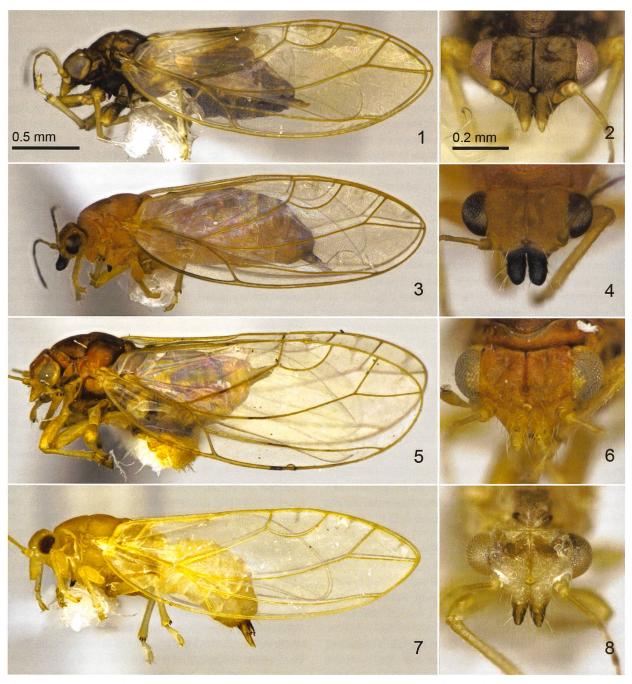
Trioza struthanthi sp. n.

http://zoobank.org/692ADAAB-50C7-4608-AA79-B969A2F569A6 Figs 1, 2, 9, 10, 17–19, 29–32, 42, 44, 47, 48

Material examined. Brazil: holotype ♀, Brazil: Paraná, Curitiba, Parque Tanguá, −25.3770 −49.2839, 870 m, 25.vi.2017, old mine redone as park with seminatural biotopes, mixed Atlantic and *Araucaria* forest, *Struthanthus uraguensis* (D. Burckhardt & D.L. Queiroz) DB&DLQ#243(2) (MZSP, dry).

Paratypes: Brazil: 1 ♀, **Minas Gerais**, Coromandel, Fazenda Lage, -18.5452 -46.9092, 1060 m, 5.iii.2014 (D. L. Queiroz) DLQ#606(-) (NHMB, ethanol 70%, NMB-PSYLL0004523); $1 \stackrel{?}{\circlearrowleft}$, $2 \stackrel{?}{\hookrightarrow}$, same but Vargem Bonita, Parque Nacional da Serra da Canastra, Cachoeira Casca d'Anta, near waterfall, -20.3083 -46.5233, 860 m, 5.ix.2014, transition from riparian to cerrado vegetation, Struthanthus uraguensis (D. Burckhardt & D.L. Queiroz) DB&DLQ#143(10) (NHMB, ethanol 70%, NMB-PSYLL0004520); 2 ♀, same but Cachoeira Casca d'Anta, plateau, -20.2967/2983 -46.5183/52833, 1160-1250 m, 6.ix.2014, degraded cerrado and riparian vegetation, Struthanthus sp., DB&DLO#144(8) (NHMB, ethanol 70%, NMB-PSYLL0004521); 5 \circlearrowleft , 7 \circlearrowleft , 6 immatures, Paraná, Antonina, Usina Parigot de Souza, -25.2438 -48.7511, 30 m, 17-20.vii.2017, roadside vegetation, Atlantic forest, Struthanthus uraguensis (D. Burckhardt & D.L. Queiroz) DB&DLQ#248(8) (NHMB, dry, ethanol 70%, NMB-PSYLL0004493-NMB-PSYLL0004497); 1 \bigcirc , same but -25.2702 -48.7322, 18.vii.2017 (I. Malenovský) (MMBC, dry); $1 \circlearrowleft$, $1 \circlearrowleft$, 1 immature, same but Bocaiuva do Sul, BR-476 km 72, -25.0800 -49.0933, 1140 m, 21.iv.2013, remnants of Atlantic forest, Struthanthus uraguensis, DB&DLQ#108(4) (NMHB, ethanol

70%, NMB-PSYLL0004518); $1 \stackrel{?}{\circ}$, $3 \stackrel{?}{\circ}$, same but Colombo, Embrapa campus, -25.3200/3350 -49.1567/1683, 920 m, 1-5.iv.2013, remnants of Atlantic forest, waste place with Baccharis spp., various plantations, Struthanthus uraguensis, DB&DLQ#96(10) (NHMB, ethanol 70%, NMB-PSYLL0004516); 3 \circlearrowleft , 5 \circlearrowleft , 1 immature, same but 24.vii.2017, Struthanthus uraguensis (I. Malenovský) (MMBC, dry, ethanol 99%); $6 \stackrel{?}{\circ}$, $11 \stackrel{?}{\circ}$, same but Curitiba, Barrio São Lourenço, -25.3925 -49.2619, 23. vii.2017, street trees and park vegetation, Struthanthus uraguensis, DB&DLQ#252(4) (NHMB, dry, ethanol 70%, NMB-PSYLL0004498-NMB-PSYLL0004501); 3 3, 2 9, 9 immatures, 2 skins, same but Boa Vista, near Parque São Lourenço, -25.3835 -49.2627, 24.vi.2017, street trees, Struthanthus uraguensis, DB&DLQ#233(1) (NHMB, dry, slide, ethanol 70%, NMB-PSYLL0004481– NMB-PSYLL0004483); 9 \circlearrowleft , 7 \circlearrowleft , 3 skins, same but Boa Vista, Rua Holanda, -25.3943 -49.2523, 830 m, 2. vii.2017, single trees and shrubs, Struthanthus uraguensis, DB&DLQ#243(2) (MZSP, NHMB, UFPR, USNM, dry, slide, ethanol 70%, NMB-PSYLL0004455-NMB-PSYLL0004458); 1 ♀, same but Centro Politécnico, UFPR, -25.4467 -49.2317, 900 m, 7.v.2014, park with planted trees, remnants of Araucaria forest, Struthanthus uraguensis, DB&DLQ#136(8) (NHMB, ethanol 70%); 2 3, 1 9, same but -25.4467, -49.2317, 890 m, 1.vii.2015, park with planted trees, remnants of Araucaria forest, Struthanthus uraguensis, DB&DLQ#173(9) (NHMB, ethanol 70%); 3 3, 1 9, same but -25.4450, -49.2345, 900 m, 15.vi.2016, park with planted trees, remnants of Araucaria forest, Struthanthus uraguensis, DB&DLQ#200(12) (NHMB, ethanol 70%, NMB-PSYLL0005998); $5 \circlearrowleft , 5 \circlearrowleft$, same but -25.4451 - 49.2341, 25-27.vii.2017 (I. Malenovský) (MMBC, dry, 99% etha-



Figures 1–8. *Trioza struthanthi*-group, adults. 1, 3, 5, 7, Habitus, scale bar = 0.5 mm; 2, 4, 6, 8, head, in dorsal view, scale bar = 0.2 mm. 1, 2, *T. struthanthi*; 3, 4, *T. tripodanthi*; 5, 6, *T. tristericis*; 7, 8, *T. vagata*.

nol); 4 ♂, 6 ♀, 3 immatures, same but −25.4466 −49.2321, 840 m, 23.vi.2017, park with planted trees, remnants of *Araucaria* forest, *Struthanthus uraguensis*, DB&DLQ#231(3) (NHMB, dry, slide, ethanol 70%, NMB-PSYLL0004477–NMB-PSYLL0004480); 1 ♂, 7 ♀, 6 immatures, same but −25.4466 −49.2321, 840 m, 23.vi.2017, park with planted trees, remnants of *Araucaria* forest, *Struthanthus uraguensis*, D. Burckhardt & D.L. Queiroz, DB&DLQ#244(5) (NHMB, dry, ethanol 70%, NMB-PSYLL0004459–NMB-PSYLL0004460); 2 ♂, same but Cidade Industrial, Parque Tropeiros, Rua Raul

Pompéia, −25.4944 −49.3527, 11.vi.2017, park with remnants of Atlantic forest, *Struthanthus uraguensis*, DB&DLQ#225(5) (NHMB, dry, NMB-PSYLL0004476); 1 ♂, same but Parque Atuba, −25.3817, −49.2033, 890 m, 12.ii.2013, planted park vegetation, river bank and remnants of Atlantic forest, DB&DLQ#92(-) (NHMB, ethanol 70%); 1 ♂, same but Parque Bacacheri, −25.3200/3350, −49.1567/1683, 920 m, 6.iv.2013, park, remnants of Atlantic forest, DB&DLQ#98(-) (NHMB, ethanol 70%, NMB-PSYLL0004517); 1 ♂, 5 ♀, same but Parque Passaúna, −25.4750 −49.3767, 940 m, 5.ii.2013, planted park

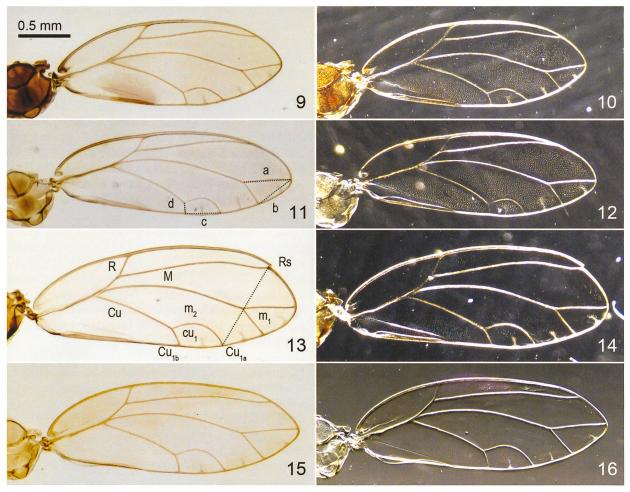
vegetation and edge of Araucaria forest remnants, Struthanthus uraguensis, DB&DLQ#89(3) (NHMB, ethanol 70%, NMB-PSYLL0004514); 1 ♀, same but -25.4750 -49.3783, 930 m, 8.ii.2016, planted park vegetation and edge of Araucaria forest remnants, Struthanthus uraguensis, DB&DLQ#195(3) (NHMB, ethanol 70%, NMB-PSYLL0004522; 3 ♂, 4 ♀, 2 immatures, same but -25.4750 -49.3783, 930 m, 30.vii.2017, planted park vegetation and edge of Araucaria forest remnants, Struthanthus uraguensis, DB&DLQ#253(5) (NHMB, 70%, NMB-PSYLL0004502-NMBethanol PSYLL0004504); 3 ♀, same but (I. Malenovský) (MMBC, dry, ethanol 99%); $3 \circlearrowleft$, $2 \circlearrowleft$, 6 immatures, same but Parque São Lourenço, -5.3817 -49.2650, 930 m, 5.xii.2012, planted park vegetation, Struthanthus uraguensis, DB&DLQ#86(6) (NHMB, ethanol 70%, Parque Tanguá, -25.3817, -49.2850, 930 m, 6.ii.2013, old mine redone as park with seminatural biotopes, mixed Atlantic Araucaria forest, Struthanthus uraguensis, DB&DLQ#90(10) (NHMB, slide, ethanol 70%, NMB-PSYLL0004506, NMB-PSYLL0004515); 3 3, 7 9, 1 immatures, same but -25.37702 -49.28393, 870 m, 25. vi.2017, old mine redone as park with seminatural biotopes, mixed Atlantic and Araucaria forest, Struthanthus uraguensis, DB&DLQ#234(4) (BMNH, NHMB, dry, NMB-PSYLL0004484-NMBethanol 70%, PSYLL0004485); $10 \, \circlearrowleft$, $15 \, \circlearrowleft$, 3 immatures, same but Parque Tingui, -25.3867/3950, -49.3067, 910-920 m, 21-24.x.2012, planted park vegetation and remnants of Araucaria forest edge, Struthanthus uraguensis, DB&DLQ#46(6) (NHMB, dry, slide, ethanol 70%, NMB-PSYLL0004461–NMB-PSYLL0004473); 1 ♂, same but -25.3950 -49.3050, 870 m, 26.xi.2012, planted park vegetation and edge of Araucaria forest remnant, Queiroz, DB&DLQ#77(-) (NHMB, ethanol 70%, NMB-PSYLL0004511); 1 \circlearrowleft , same but -25.3950 -49.3050, 870 m, 10.xii.2012, planted park vegetation and edge of remnants of Araucaria forest, Struthanthus uraguensis, 70%, DB&DLQ#88(-) (NHMB, ethanol PSYLL0004513); $3 \circlearrowleft 1$ immatures, same but -25.3950-49.3050, 890 m, 31.iii.2013, planted park vegetation and remnants of Atlantic forest, Struthanthus uraguensis, DB&DLQ#95(4) (NHMB, ethanol 70%); 9 ♂, 5 ♀, 5 immatures, 2 skins, same but -25.3953 -49.3062, 860 m, 16.vii.2017, planted park vegetation and remnants of Atlantic forest, Struthanthus uraguensis, DB&DLQ#247(2) (NHMB, dry, slide, ethanol 70%, NMB-PSYLL0004487-NMB-PSYLL0004492); 2 ♂, 1 ♀, same but (I. Malenovský) (MMBC, dry, 99% ethanol); 3 ♂, 1 ♀, same but Piraquara, Parque Estadual do Marumbi, -25.1567/1600 -48.9750/9933, 890-1170 m, 23-24.iv.2013, Atlantic forest, Struthanthus uraguensis, DB&DLQ#109(11) (NMHB, ethanol 70%); $3 \circlearrowleft$, 1 immatures, same but Ponta Grossa, Parque Estadual de Vila Velha, -25.2238/2465 -49.9927/50.0399, 750-870 m, 12-14.vii.2017, Araucaria forest, transitional forest, Baccharis scrub, Struthanthus uraguensis, DB&DLQ#246(2) (NHMB,

ethanol 70%, NMB-PSYLL0004486); 1 ♀, same but Tunas do Paraná, Parque Campinhos, -25.0367/0417 -49.0900/1000, 870 m, 8.v.2014, edges of transitional Araucaria/Atlantic forest, park, Struthanthus uraguensis, DB&DLQ#137(1) (NHMB, ethanol 70%); 1 3, Rio Grande do Sul, Passo Fundo, Brigada Militar, -28.2333 -52.3333, 640 m, 5.v.2014, remnants of degraded Atlantic forest (A. L. Marsaro Júnior) ALM#023/14 PF (NHMB, dry, NMB-PSYLL0003308); 1 ♀, Santa Catarina, Caçador, Embrapa, -26.8400/8650 -50.1017/9750, 930-1070 m, 16-17.ix.2011, Atlantic forest, Struthanthus uraguensis (D. Burckhardt & D.L. Queiroz) 70%, DB&DLQ#9(9) (NHMB, ethanol PSYLL0004510); 1 ♂, same but São Bento do Sul to Corupá, BR-280, km 102-97, -26.3500 -49.3400, 430 m, 28.iv.2013, Atlantic forest, DB&DLQ#114(-) (NMHB, ethanol 70%, NMB-PSYLL0004519); $2 \circlearrowleft$, $1 \circlearrowleft$, 1 immature, same but Urubici, Morro da Igreja, Pousada Cascata Véu de Noiva, -28.07608 -49.51567, 1360 m, 28. vi.2017, pasture with trees, degraded forest edge, sweeping vegetation, DB&DLQ#239(-) (NMHB, ethanol 70%, NMB-PSYLL000461).

Diagnosis. Member of the *Trioza struthanthi*-group. Body of adult brown to almost black. Forewing membrane with a dark brown infuscation in cell cu₂ close to anal vein. Genal processes 0.8 times as long as vertex along midline, irregularly tapering to subacute apex. Forewing subacute apically, 2.6–2.8 times as long as wide. Paramere about twice as long as broad, straight. Dorsal margin of female proctiger strongly angled; valvula ventralis lacking apico-ventral teeth. Fifth instar immature with following numbers of marginal sectasetae (one side only): head 34–36, forewing bud 90–102, hindwing bud 16–18, precaudal abdominal margin 2, caudal plate 84–87; distal portion of sectasetae on forewing bud 1.5 times as long as wide.

Description. Adult (Fig. 1). Colouration. Brown to black, intersegmental membranes red. Tips of genal processes dirty yellowish; eyes grey, ocelli yellowish to grey. Antennal segments 1 brown and 2 yellow, flagellum brown, gradually becoming darker towards apex. Tibiae entirely and basitarsi partially yellow. Veins of forewing light brown, membrane yellowish with indistinct brown patch along clavus (cell cu₂), transparent. Hindwing transparent, colourless. Male terminalia brown. Younger specimens almost entirely dirty yellow, getting gradually darker with age.

Structure. Body length $3 \cdot 2.3-2.9 \text{ mm} (2.60\pm0.17 \text{ mm})$, $2 \cdot 2.7-3.1 \text{ mm} (2.85\pm0.11 \text{ mm}) (10 3 \cdot 10 2)$. Genal processes 0.8 times as long as vertex along midline, irregularly tapering to subacute apex (Fig. 2). Antenna 1.4-1.6 times as long as head width; segments 4 and 6 distinctly inflated apically. Forewing (Fig. 9) narrowly lanceolate, subacute apically, 4.2-4.7 times as long as head width, 2.6-2.8 times as long as wide; surface spinules present in all cells, leaving spinule-free



Figures 9–16. *Trioza struthanthi*-group, forewing, scale bar = 0.5 mm. 9, 11, 13, 15, Forewing, bright field, showing venation; 11, $a/b = m_1$ cell value, $c/d = cu_1$ cell value; 13, vein and cell nomenclature; 10, 12, 14, 16, dark field, showing surface spinules. 9, 10, *T. struthanthi*; 11, 12, *T. tripodanthi*; 13, 14, *T. tristericis*; 15, 16, *T. vagata*.

stripes along the veins and reduced at the base of cells, only few or no spinules in cell c+sc, forming indistinct transverse rows (Fig. 10). Metatibia 0.8-0.9 times as long as head width, genual tooth prominent. - Terminalia as in Figs 17-19, 29-32. Male: setae on proctiger covering a wide area in apical two thirds arranged in several indistinct transverse rows. Paramere about as long as proctiger, in profile, about twice as long as broad; outer and inner lobe of about the same length; outer lobe with sclerotised tooth subapically, inner lobe with sclerotised, forward directed point; inner surface with long setae, in basal half with a group of thick bristles. Distal segment of aedeagus weakly expanded apically. Female: dorsal outline of proctiger in basal two thirds almost straight, then abruptly curved down, forming angular bump; apical process bearing five evenly spaced, dorsal teeth. Subgenital plate, in ventral view, truncate apically, with a small group of setae apically which is well separated from other setae. Oblique apex of ventral valvula smooth, lacking teeth. - Measurements see Table 2.

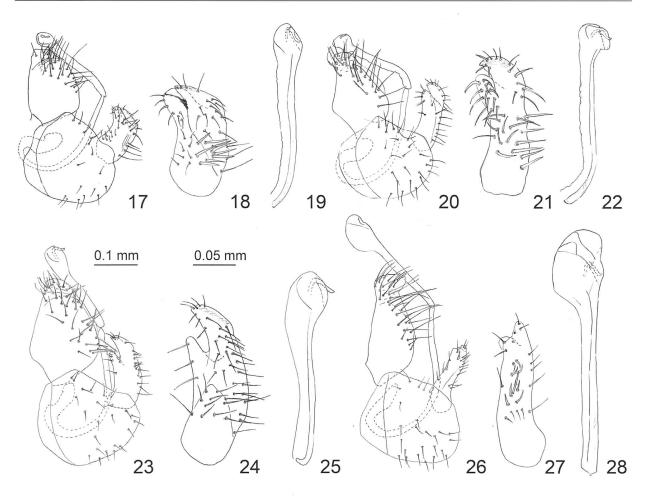
Fifth instar immature (Fig. 42). Colouration. Head and thorax yellow, wing pads and abdomen light ochreous, the latter sometimes greenish. Eyes reddish-grey. Antennae brown. Ventral body surface yellow, tips of tarsi brown.

Structure. Outer circumanal ring (Fig. 48) with a single row of 88–93 pores (one side only); distance between posterior margins of circumanal ring and of caudal plate 1.0 times as long as outer circumanal ring in longitudinal body axis. Marginal truncate sectasetae present in following numbers (one side only): head 34–36, forewing bud 90–102, hindwing bud 16–18, precaudal abdominal margin 2, caudal plate 84–87; distal portion of sectasetae on forewing bud 1.5 times as wide (Fig. 44).

Etymology. The species is named after its host plant genus *Struthanthus*; *struthanthi* is a noun in the genitive case.

Distribution. Brazil (Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina).

Host plant. Struthanthus uraguensis G. Don (Loranthaceae).



Figures 17–28. *Trioza struthanthi*-group, male terminalia. 17, 20, 23, 26, Terminalia, in profile, scale bar = 0.1 mm; 18, 21, 24, 27, inner face of paramere, scale bar = 0.05 mm; 19, 22, 25, 28, distal portion of aedeagus, scale bar = 0.05 mm. 17–19, *T. struthanthi*; 20–22, *T. tripodanthi*; 23–25, *T. tristericis*; 26–28, *T. vagata*.

Table 2. Measurements in mm of adult Trioza species.

	T. struthanthi	T. tripodanthi	T. tristericis	T. vagata
Number of measured specimens	3 ♂, 4 ♀	1 ♂, 1 ♀	1♂,1♀	1 ♂, 1 ♀
Head width	0.48-0.53	0.45-0.48	0.53-0.55	0.48-0.50
Antennal length	0.70-0.80	0.68-0.70	0.80-0.83	0.70-0.73
Forewing length	1.98-2.45	1.95-2.28	2.35-2.55	2.55-2.43
Male proctiger length	0.13-0.15	0.15	0.15	0.23
Paramere length	0.13-0.15	0.18	0.18	0.18
Length of distal segment of aedeagus	0.18-0.20	0.23	0.20	0.28
Female proctiger length	0.38-0.43	0.45	0.48	0.45

Discussion. Trioza struthanthi differs from the other six members of the T. struthanthi-group in the dark brown or almost black body colour of the adults which is yellow, orange or light brown in the other species, in the presence of a dark brown patch in cell cu_2 of the forewing, in the much broader paramere and the strongly angled dorsal

margin of the female proctiger. The fifth instar immatures of *T. struthanthi* differ from those of *T. tripodanthi* in the larger number of marginal sectasetae und from those of *T. tristericis* in the shorter and broader marginal sectasetae. The immatures of *T. vagata* and of the North American species of the *T. struthanthi*-group are unknown.

Trioza tripodanthi sp. n.

http://zoobank.org/17DB5657-552E-49B2-98DC-81F73C7D3F56 Figs 3, 4, 11, 12, 20–22, 33–35, 43, 45, 49)

Material examined. Brazil: holotype ♀, Santa Catarina, Urubici, Estrada Morro da Igreja, −28.0439 −49.4865, 950 m, 29.vi.2017, *Mimosa-Baccharis* scrub along road, *Tripodanthus acutifolius* (D. Burckhardt & D.L. Queiroz) DB&DLQ#242(4) (MZSP, dry).

Paratypes: Brazil: 1 ♀, **Paraná**, Curitiba, Centro Politécnico, UFPR, −25.4467 −49.2317, 890 m, 5–6. ii.2016, park with planted trees, remnants of *Araucaria* forest (D. Burckhardt & D.L. Queiroz) DB&DLQ#192(-) (NHMB, ethanol 70%, NMB-PSYLL0004509; 1♀, same

but Praça Brigadeiro do Ar M. C. Eppinghaus, −25.4155 −49.2531, 4.i.2012, park, DB&DLQ#28(-) (NHMB, ethanol 70%, NMB-PSYLL0004507); 1 ♂, same but Tibagi, Parque Estadual Guartelá, −24.5683 −50.2553, 940 m, 10−12. vii.2017, cerrado vegetation, DB&DLQ#245(-) (NHMB, dry, NMB-PSYLL0004505); 3 ♀, **Rio Grande do Sul**, Cambará do Sul, Parque Nacional de Aparados da Serra, Macieira, −29.1333 −50.1333, 980 m, 24−27.i.2016, edge of *Araucaria* forest, Atlantic forest, *Baccharis* scrub, swamp (D. Burckhardt & D.L. Queiroz) DB&DLQ#186(-) (NHMB, ethanol 70%, NMB-PSYLL0004508); 1 ♂, 4 ♀, 3 immatures, **Santa Catarina**, same data as holotype (NHMB, dry, slide, ethanol 70%, NMB-PSYLL0004448−NMB-PSYLL0004454).

Diagnosis. Member of the *Trioza struthanthi*-group. Body of adult orange with conspicuously black genal processes. Genal processes 0.7 times as long as vertex along mid-line, strongly tapering near base, then tubular with blunt apex. Forewing subacute apically, 2.8 times as long as wide. Paramere about three times as long as broad, straight. Dorsal margin of female proctiger distal of circumanal ring evenly curved down to process; valvula ventralis with three apico-ventral teeth. Fifth instar immature with following numbers of marginal sectasetae (one side only): head 29–31, forewing bud 86–88, hindwing bud 13–15, precaudal abdominal margin 1–2, caudal plate 79; distal portion of sectasetae on forewing bud 1.5 times as long as wide.

Description. Adult (Fig. 3). Colouration. Orange, intersegmental membranes red. Genal processes black; eyes grey, ocelli reddish. Antennal segments 1–3 yellowish, remainder of flagellum brown, gradually becoming darker towards apex. Thorax indistinctly brownish dorsally, yellow ventrally. Tibiae indistinctly brownish at base, basitarsi yellow. Veins of forewing brown basally, yellow otherwise, membrane colourless, transparent. Hindwing transparent, colourless. Abdominal tergites brown, sternites yellow, intersegmental membranes yellowish to orange.

Structure. Body length $3 \cdot 2.5-2.6 \text{ mm} (2.55\pm0.07)$ processes 0.7 times as long as vertex along mid-line, strongly tapering near base, then tubular with blunt apex (Fig. 4). Antenna 1.5 times as long as head width; segments 4 and 6 not inflated apically. Forewing (Fig. 11) narrowly lanceolate, subacute apically, 4.3-4.8 times as long as head width, 2.8 times as long as wide; surface spinules present in all cells except for cells c+sc and r₁, leaving broad spinule-free stripes along the veins, arranged in squares or rhombs (Fig. 12). Metatibia 0.7–0.8 times as long as head width, genual tooth prominent. – Terminalia as in Figs 20–22, 33–35. Male: setae on male proctiger covering a narrow stripe along posterior margin arranged in two irregular longitudinal rows as well as on apex. Paramere slightly longer than proctiger, in profile, about three times as long as broad; outer lobe distinctly shorter than inner lobe; outer lobe digitiform, lacking sclerotised subapical tooth; inner lobe with sclerotised,

forward directed point; inner surface with long setae, in basal half with a group of thick bristles. Distal segment of aedeagus with short, abruptly expanded apical dilatation. Female: dorsal outline of proctiger distal of circumanal ring evenly curved down to apical process; apical process bearing 4–5 uneven dorsal teeth. Subgenital plate, in ventral view, truncate apically, without well-separated apical group of setae. Oblique apex of ventral valvula with three large teeth. – Measurements see Table 2.

Fifth instar immature (Fig. 43). Colouration. Irregularly yellow. Eyes light reddish, antennae brown. Tips of tarsi brown. Bacteriome orange.

Structure. Outer circumanal ring (Fig. 49) with a single row of 84–87 pores (one side only); distance between posterior margins of circumanal ring and of caudal plate 1.3 times as long as outer circumanal ring in longitudinal body axis. Marginal truncate sectasetae present in following numbers (one side only): head 29–31, forewing bud 86–88, hindwing bud 13–15, precaudal abdominal margin 1–2, caudal plate 79; distal portion of sectasetae on forewing bud 1.5 times as wide (Fig. 45).

Etymology. The species is named after its host plant genus *Tripodanthus*; *tripodanthi* is a noun in the genitive case.

Distribution. Brazil (Paraná, Rio Grande do Sul, Santa Catarina).

Host plant. *Tripodanthus acutifolius* (Ruiz & Pav.) Tiegh. (Loranthaceae).

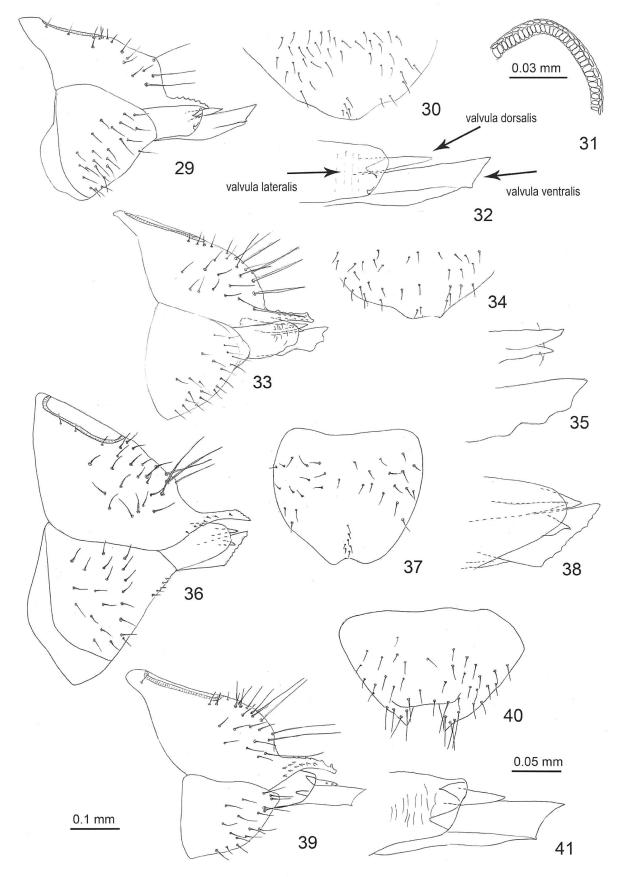
Discussion. *Trioza tripodanthi* differs from the other six members of the *T. struthanthi*-group in light body colour with the very conspicuous dark genal processes and details of the male and female terminalia. The fifth instar immatures of *T. tripodanthi* differ from those of *T. struthanthi* in the smaller number of marginal sectasetae and from those of *T. tristericis* in the shorter and broader marginal sectasetae. The immatures of *T. vagata* and of the North American species of the *T. struthanthi*-group are unknown.

Trioza tristericis sp. n.

http://zoobank.org/A5FB2318-7012-4D1B-A624-973B12965502 Figs 5, 6, 13, 14, 23–25, 36–38, 46

Material examined. Chile: holotype ♀, V Region, Province Los Andes, Aconcagua Valley, 25 km W Portillo, route 60, Valle Aconcagua, -32.8333 -70.1333, 1900-2100 m, 1.xii.1993, subalpine/alpine scrub (D. Burckhardt) DB#1(-) (MHNG, dry).

Paratypes: Chile: $10 \circlearrowleft$, $10 \circlearrowleft$, IV **Region**, Province Limarí, Hurtado, -30.2768 - 70.6660, 19.ii.1985, *Tristerix* sp. (D. Hollis) (BMNH, dry, BMNH(E)1271039); $1 \circlearrowleft$, **Region Metropolitana**, Province Santiago, between Corral Quemado and Farellones, -33.3451 - 70.3334, 1700 m, 19.v.1993, open mediterranean scrub, *Tristerix* sp. (D. Burckhardt) DB#14(4) (MHNG, dry); $1 \circlearrowleft$, $4 \circlearrowleft$,



Figures 29–41. *Trioza struthanthi*-group, female terminalia. **29**, **33**, **36**, **39**, Terminalia, in profile, scale bar = 0.1 mm; **30**, **34**, **37**, **40**, subgenital plate, ventral view, scale bar = 0.1 mm; **31**, circumanal ring, in dorsal view, scale bar = 0.03 mm; **32**, **35**, **38**, **41**, valvulae, scale bar = 0.05 mm. **29–32**, *T. struthanthi*; **33–35**, *T. tripodanthi*; **36–38**, *T. tristericis*; **39–41**, *T. vagata*.

5 immatures, same but Province Tiltil, Cuesta La Dormida, 7–10 km W Tiltil, -33.0667 -71.0333, 950–1200 m, 28.xii.1993, mediterranean sclerophyll scrub, Tristerix *corymbosus*, DB#41(5) (MHNG, dry, slide); $4 \circlearrowleft$, $8 \circlearrowleft$, V Region, same as holotype (MHNG, NHMB, dry, slide, NMB-PSYLL0004524–NMB-PSYLL0004526); 1 ♀, same but km 19 Portillo to Río Blanco, -32.8671 -70.1863, 1900 m, 23.xii.1995, subalpine scrub, Tristerix verticillatus, DB#20(6) (MHNG, dry); 1 \circlearrowleft , same but Portillo to Río Blanco, -32.8718 -70.1985, 1900 m, 24.xii.1998, gully with a few shrubs and small trees along river and subalpine scrub, Tristerix sp., DB#7(7) (NHMB, dry, NMB-PSYLL0004474); 1 ♀, same but Province Petorca, Cuesta El Melón, -32.6067 -71.2400, 600 m, 23.ii.2009, degraded Acacia caven steppe and sclerophyll scrub on slope, DB#3 (NHMB, dry, NMB-PSYLL0004475; 1 ♀, same but Province Quillota, La Campana National Park, -32.9721 -71.0735, 1100 m, 11.i.1985, Tristerix sp. (D. Hollis) (BMNH, dry, BMNH(E)-1271160); 5 ♂, 11 ♀, 2 immatures, same but -32.9721, -71.0735, 1300 m, 11.i.1985, Tristerix sp. (BMNH, dry, BMNH(E)1271051, BMNH(E)1271268).

Diagnosis. Member of the *Trioza struthanthi*-group. Body of adult orange to brown with orange to ochreous genal processes. Genal processes 0.8 times as long as vertex along mid-line, relatively evenly tapering to subacute apex. Forewing narrowly rounded, 2.7 times as long as wide. Paramere about three times as long as broad, weakly curved. Dorsal margin of female proctiger between apex of circumanal ring and base of apical process almost straight with very small bump near the middle; valvula ventralis with several small apico-ventral teeth. Fifth instar immature with distal portion of sectasetae on forewing bud 2.6 times as long as wide.

Description. Adult (Fig. 5). Colouration. Orange to brown, intersegmental membranes orange. Genal processes orange to ochreous, tips often dirty whitish; eyes and ocelli grey; head ventrally yellow. Antennal segments 1 and 2 yellowish orange, segments 4–7 pale yellowish with apices of segments 4 and 6 brown, segments 8–10 brown to black. Meso and metathorax with indistinctly delimited longitudinal dark stripe. Thoracic pleura and venter yellow. Legs yellow, femora greyish brown. Veins of forewing light brown, membrane weakly yellowish. Abdomen almost black; male terminalia light brown, female terminalia orange to brown, apex almost black. Younger specimens dirty yellow or orange, getting gradually darker with age.

Structure. Body length \circlearrowleft 2.7–2.9 mm (2.76±0.07 mm), \updownarrow 2.6–3.2 mm (2.97±0.18 mm) (8 \circlearrowleft , 10 \updownarrow). Genal processes 0.8 times as long as vertex along mid-line, relatively evenly tapering to subacute apex (Fig. 6). Antenna 1.4–1.6 times as long as head width; segments 4 and 6 not inflated apically. Forewing (Fig. 13) narrowly lanceolate, narrowly rounded apically, 4.5–4.6 times as long as head width, 2.7 times as long as wide; surface spinules strongly reduced, present at apex of cell c+sc,

base of r₁, apex of r₂, a few scattered spinules in m₁, m₂ and cu₁, covering most of cu₂, arranged in squares or rhombs (Fig. 14). Metatibia 0.8–0.9 times as long as head width, genual tooth small. – Terminalia as in Figs 23-25, 36-38. Male: setae on male proctiger covering a wide area in apical two thirds irregularly arranged. Paramere slightly longer than proctiger, in profile, about three times as long as broad, weakly curved; outer lobe distinctly shorter than inner lobe; outer lobe digitiform. without sclerotised subapical tooth; inner lobe with sclerotised, forward directed point; inner surface with long setae, those in basal half not conspicuously thicker than those in apical half. Distal segment of aedeagus with long, gradually expanded apical dilatation. Female: dorsal outline of proctiger between apex of circumanal ring and base of apical process almost straight with very small bump near the middle; apical process bearing several small dorsal teeth near apex. Subgenital plate, in ventral view, shallowly incised apically, with a longitudinal row of setae apically which is well separated from other setae. Oblique apex of ventral valvula with several small teeth. – Measurements see Table 2.

Fifth instar immature. Colouration. Head, thorax and abdomen orange or light brown, wing pads slightly lighter. Eyes reddish-grey. Antennae reddish in basal half, dark brown apically. Tips of tarsi brown.

Structure. Only one damaged specimen available. Distal portion of sectasetae on forewing bud 2.6 times as wide (Fig. 46).

Etymology. The species is named after its host plant genus *Tristerix*; *tristericis* is a noun in the genitive case.

Distribution. Chile (Regions V and Metropolitana).

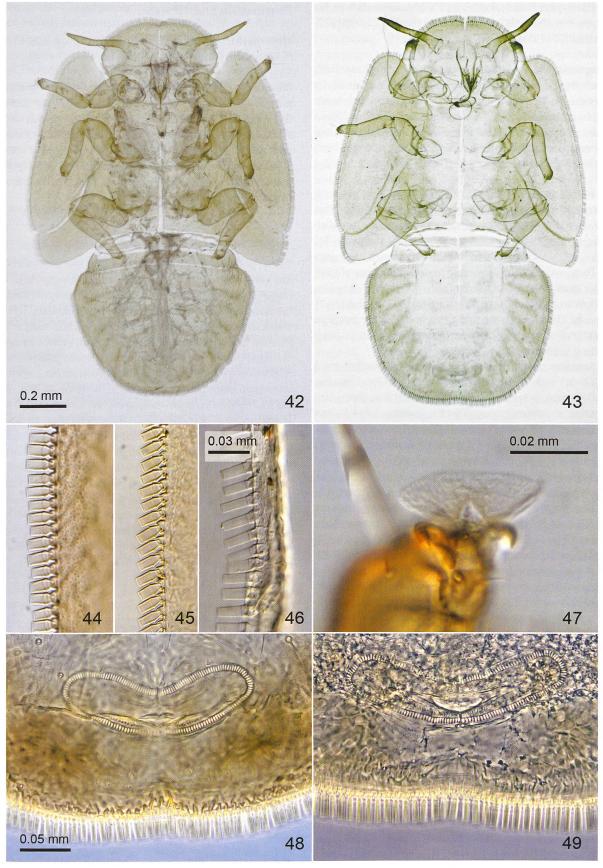
Host plants. *Tristerix corymbosus* (L.) Kuijt (Loranthaceae); adults were also collected on *Tristerix verticillatus* (Ruiz & Pav.) Barlow & Wiens and *T.* sp. which are likely hosts.

Discussion. Adult *Trioza tristericis* differ from the other six species of the *T. struthanthi*-group, apart from details of the male and female terminalia, as follows: from the North American species in the narrower forewing and from the South American species in the orange to brown body colour with concolorous genal processes. The fifth instar immatures of *T. tristericis* differ from those of *T. struthanthi* and *T. tripodanthi* in the longer and narrower marginal sectasetae. The immatures of *T. vagata* and the North American species of the *T. struthanthi*-group are unknown.

Trioza vagata sp. n.

http://zoobank.org/660C1A6E-3EF1-4D39-AC48-445CA841C48CFigs 7, 8, 15, 16, 26–28, 39–41

Material examined. Brazil: holotype ♀, Paraná, Paranaguá, Ilha do Mel, −25.5353 −48.3311, 20.xi.2013, *Clusia* sp. (D.L. Queiroz) DLQ#598(9) (MZSP, dry).



Figures 42–49. *Trioza struthanthi*-group, immatures. **42, 43,** Habitus, scale bar = 0.2 mm; **44–46,** marginal sectasetae on forewing bud, scale bar = 0.03 mm; **47,** tarsal arolium, scale bar = 0.02 mm; **48, 49,** circumanal ring, ventral view, scale bar = 0.05 mm. **42, 44, 47, 48,** *T. struthanthi*; **43, 45, 49,** *T. tripodanthi*; **46,** *T. tristericis*.

Paratypes: Brazil: $4 \circlearrowleft$, $2 \circlearrowleft$, Paraná, same data as holotype but (NHMB, dry, slide, NMB-PSYLL0004527–NMB-PSYLL0004532).

Diagnosis. Member of the *Trioza struthanthi*-group. Body of adult yellowish or orange to light brown. Genal processes 0.9 times as long as vertex along mid-line, irregularly tapering to subacute apex. Forewing subacute apically, 2.8–2.9 times as long as wide. Paramere about three times as long as broad, straight. Dorsal margin of female proctiger evenly curved; valvula ventralis lacking apico-ventral teeth.

Description. Adult (Fig. 7). Colouration. Light yellow to orange or light brown, intersegmental membranes whitish. Genal processes ochreous to brown, tips often dirty whitish; eyes dark reddish grey. Antennal segments 1–7 pale yellow with apex of segment 6 brown, segments 8–10 brown to black. Thoracic pleura and venter slightly paler than dorsum. Metacoxa brown. Veins of forewing yellow to ochreous, membrane colourless or weakly yellowish. Tip of paramere and process of female proctiger dark brown to almost black. Younger specimens paler, getting gradually darker with age.

Structure. Body length $\stackrel{\wedge}{\circ}$ 2.6–2.7 mm (2.65±0.06 mm), \bigcirc 2.8–3.1 mm (2.97±0.15 mm) (4 \bigcirc , 3 \bigcirc). Genal processes 0.9 times as long as vertex along mid-line, irregularly tapering to subacute apex (Fig. 8). Antenna 1.4-1.5 times as long as head width; segments 4 and 6 distinctly inflated apically. Forewing (Fig. 15) narrowly lanceolate, subacute apically, 4.7–4.9 times as long as head width, 2.8–2.9 times as long as wide; surface spinules present in most cells, leaving broad spinule-free stripes along the veins, forming indistinct transverse rows, in cell c+sc restricted to apex and in cell r, to base, almost completely absent from cells m, and m₂ (Fig. 16). Metatibia 0.8 times as long as head width, genual tooth prominent. – Terminalia as in Figs 26–28, 39– 41. Male: setae on male proctiger covering a narrow stripe along posterior margin arranged in two irregular longitudinal rows as well as on apex. Paramere distinctly shorter than proctiger, in profile, about three times as long as broad; outer lobe shorter than inner one; outer lobe with sclerotised tooth subapically, inner lobe with sclerotised, forward directed point; inner surface with few long setae, in middle third with a group of thick bristles. Distal segment of aedeagus strongly expanded apically. Female: dorsal outline of proctiger in basal two thirds almost straight to weakly, then evenly curved down; apical process bearing many uneven dorsal and lateral teeth. Subgenital plate, in ventral view, truncate apically bordered on either side by pointed lobes, with moderately long setae in apical two thirds except for a longitudinal stripe in the middle which is almost bare and at apex where the setae are very long. Oblique apex of ventral valvula smooth, lacking teeth. – Measurements see Table 2. Fifth instar immature unknown.

Etymology. From Latin vagare = to wander, to roam, for its discovery away from its supposed host, a mistletoe; *vagata* is the feminine form of the participle perfect passive.

Distribution. Brazil (Paraná).

Host plant. Adults have been collected on *Clusia* sp. (Clusiaceae) which is an unlikely host.

Discussion. *Trioza vagata* differs from the other six members of the *T. struthanthi*-group in the very narrow forewing (2.8–2.9 times as long as wide) which lacks surface spinules in most of cell \mathbf{r}_2 and in the digitiform paramere. The female terminalia are similar to those of *T. tripodanthi* but the dorsal margin of the proctiger is more curved and the oblique apex of the valvula ventralis lacks teeth.

Nomenclature

Tuthill (1939) described *Psylla phorodendrae* [sic!] and *Trioza phorodendrae* [sic!] naming the two species after the host *Phoradendron*. Both names are incorrectly formed as the host name is spelled with an 'a', and 'dendron' (from Greek δευδρου, noun of neuter gender) would require the genitive ending 'i'. In a later paper, Tuthill (1943) changed the names to *Psylla phoradendri* and *Trioza phoradendri*, respectively, which are grammatically correct but constitute unjustified emendations according to the ICZN (1999), article 33.2.3. For *Psylla phorodendrae*, Hodkinson (1988) and Burckhardt and Wyniger (2007) incorrectly used the spelling *Cacopsylla 'phorodendri*' and *Freysuila 'phorodendri*', respectively. In the case of *Trioza phoradendrae*, Hodkinson (1988) used Tuthill's (1943) emended name '*phoradendri*'.

Another incorrectly formed name is *Trioza incidata*, according to Tuthill (1945) the participle perfect passive of incidere, which would correctly be 'incisa'. Despite the incorrect derivation, the name *Trioza incidata* constitutes a correct original spelling according to the ICZN (1999), article 32.2.

New host records

For the following three species new host records are provided here.

Calophya sp.

Material examined. Brazil: 1 ♂, 3 ♀, 1 skin, Paraná, Curitiba, Boa Vista, Rua Holanda, −25.3943 −49.2523, 830 m, 2.vii.2017, single trees and shrubs, *Phoradendron ensifolium* (D. Burckhardt & D.L. Queiroz) DB&DLQ#243(1) (NHMB, ethanol 70%).

Distribution. Brazil (Paraná).

Host plants. *Phoradendron ensifolium* (Pohl ex DC.) Eichler in Mart. (Santalaceae).

Comment. Calophya comprises some 70 described species mostly associated with Sapindales. A notable exception is *C. oweni* Tuthill, 1939 which was described from adult specimens collected in the USA (Colorado) on *Phoradendron juniperinum* Engelm. (Santalaceae) (Burckhardt and Basset 2000; Mendez et al. 2016). Recently adults and a mummy of a similar, undescribed *Calophya* sp. were collected in Brazil on *Phoradendron ensifolium*. This find confirms *Phoradendron* as host of the Brazilian species and makes the association of the North American species with this host more likely.

Notophorina fusca Burckhardt, 1987

Material examined. Chile: 1 immatures, IX Region, Province Cautín, Parque Nacional Conguillío, Playa Linda, -38.6500 -71.6333, 1150 m,19-20.xii.1990, Nothofagus antarctica forest on volcanic soil, Misodendrum punctulatum (D. Burckhardt & D. Agosti) DB#13b (MHNG, slide); 1 &, same but Parque Nacional Conguillío, sector Laguna Conguillío, -38.6468 -71.6451, 1100 m, 30.i.1996, open Nothofagus antarctica scrub (D. Burckhardt) DB#66 (MHNG, dry); 3 immatures, same but Province Malleco, Parque Nacional Nahuelbuta, -37.8167 -73.0167, 1300 m,16-17.xii.1990, Nothofagus antarctica forest, Misodendrum punctulatum (D. Burckhardt & D. Agosti) DB#11(1) (MHNG, slide); $5 \circlearrowleft$, $3 \circlearrowleft$, 9 immatures, same but Parque Nacional Nahuelbuta, road from "Administración" to Piedra del Aguila, -37.8167 -73.0167, 1200 m, 24-25.xii.1992, open Nothofagus obliqua-antarctica forest, Misodendrum punctulatum (D. Burckhardt) DB#32(3) (MHNG, dry); $24 \stackrel{?}{\circ}$, $46 \stackrel{?}{\circ} 4$ immatures, **XII Region**, Province Magallanes, Punta Arenas, Universidad Magallanes, Parque John Fell and Jardín Botánico, -53.1167 -70.8667, 50 m, 16-19.i.1991, park, Misodendrum punctulatum, DB#42(2) (MHNG, dry, slide); $1 \circlearrowleft$, $1 \circlearrowleft$, same but Province Ultima Esperanza, Rio Rubens, -52.0167 -71.9333, 200 m, 11.i.1991, Nothofagus antarctica forest, Misodendrum punctulatum DB#32(1) (MHNG, dry).

Distribution. Chile (Regions IX and XII).

Host plants. *Misodendrum punctulatum* Banks ex DC. (Misodendraceae).

Comment. *Notophorina fusca* was described from the Far South of Chile (XII Region) but without host data (Burckhardt 1987b). Most members of the *Notophorina fusca* group are associated with Myrtaceae.

Zonopelma australis Burckhardt, 1987

Material examined. Chile: $1 \circlearrowleft , 4 \circlearrowleft , 1$ immature, 1 skin, **IX Region**, Province Cautín, Parque Nacional Conguillío, sector Laguna Arcoiris, -38.6540 -71.6178, 1100 m, 30.i.1996, mixed *Nothofagus/Araucaria* forest, *Misoden*-

drum, linearifolium (D. Burckhardt) DB#68(3), (NHMB, dry); $3 \stackrel{?}{\circ}$, $4 \stackrel{?}{\circ}$, same but Province Malleco, Parque Nacional Nahuelbuta, -37.8167 -73.0167, 1300 m, 16-17.xii.1990, Nothofagus antarctica forest, Misodendrum punctulatum (D. Burckhardt & D. Agosti) DB#11(1) (MHNG, dry); 2 ∂, 10 ♀, same but road from "Administración" to Piedra del Aguila, -37.8167 -73.0167, 1200 m, 24-25.xii.1992, open Nothofagus obliqua-antarctica forest, Misodendrum punctulatum (D. Burckhardt) DB#32(3) (NHMB, dry); 2 ♂, 3 ♀, same but Parque Nacional Tolhuaca, sector Laguna Verde, -38.2142 -71.7340, 1000-1300 m, 27.i.1996, mixed Nothofagus and Nothofagus/Araucaria forest, Misodendrum punctulatum, DB#63b(6) (NHMB, dry); $1 \, \mathcal{Q}$, X Region, Province Chiloé, Chepu, -42.0490 -74.0329, 19.ii.1991, Nothofagus antarctica (T. Cekalovic) (MHNG, dry); 2 \mathcal{J} , same but Parque Nacional Chiloé, Rancho Grande, -42.5500 -74.0333, 400 m, 8.ii.1996, degraded open Tepualia/Fitzroya scrub on peat bog, Misodendrum punctulatum (D. Burckhardt) DB#79b(3) (MHNG, dry); 1 ♂, same but Rancho Grande, Río Cypressal, –42.5882 -74.0999, 0-150 m, 8.ii.1996, Tepualia scrub and Nothofagus forest, Misodendrum punctulatum, DB#80(2) (MHNG, dry); 30 ♂, 36 ♀, XI Region, Province Capitán Prat, 20 km S Cochrane, -47.4185 -72.7351, 3.ii.1990, *Nothofagus*, antarctica (L. Peña) (MHNG, dry); 14 ♂, 12 ♀, 19 immatures, 1 skins, XII Region, Province Magallanes, Punta Arenas, Aeropuerto, Parque Chabunco, -53.0000 -70.8167, 20 m, 18.i.1991, Nothofagus antarctica forest, Misodendrum sp. (D. Burckhardt) DB#47(2) (MHNG, dry); 42 ♂, 32 ♀, 21 immatures, 2 skins, same but Punta Arenas, Universidad Magallanes, Parque John Fell and Jardín Botánico, -53.1167 -70.8667, 50 m, 16-19.i.1991, park, Misodendrum punctulatum, DB#42(2) (MHNG, dry); $5 \circlearrowleft$, $6 \circlearrowleft$, same but Río Chabunco, -53.0172 -70.8306, 11.ii.1990, Nothofagus antarctica (T. Cekalovic) (MHNG, dry); 1 ♀, same but Silla del Diablo, -51.5650 -72.6200, 14.ii.1990, Nothofagus antarctica, (MHNG, dry); $29 \stackrel{?}{\circ}$, $26 \stackrel{?}{\circ}$, 15 immatures, same but Province Ultima Esperanza, Laguna Figueroa, S Cerro Castillo, -51.3823 -72.4360, 200 m, 11-15.i.1991, Nothofagus antarctica forest with transition to pasture, Misodendrum punctulatum (D. Burckhardt) DB#35(1) (MHNG, dry); 13 3, 13 4, 1 skins, same but Monumento Natural Cueva del Milodón, -51.5656 -72.6197, 150 m, 11.i.1991, open scrub with Nothofagus, Misodendrum sp., DB#34(4) (MHNG, dry); 14 ♂, 25 ♀, same but Parque Nacional Torres del Paine, along road between Lagunas Mellizas and Lago Toro, -51.0615 -72.9661, 0-100 m, 13.i.1991, steppe with small patches of scrub, Misodendrum linearifolium, DB#38(4) (MHNG, dry); $43 \circlearrowleft$, $50 \circlearrowleft$, 13 immatures, 3 skins, same but Cascada Rio Paine, -51.1322 -72.9655, 150 m, 14.i.1991, steppe and Nothofagus antarctica scrub, Misodendrum punctulatum, DB#40(1) (MHNG, dry); $10 \, \circlearrowleft$, $14 \, \circlearrowleft$, same but Lago Grey, along Rio Pingo, -51.1183 -73.1352, 100 m, 12.i.1991, mixed *Nothofagus* forest and open scrub, *Mi*sodendrum punctulatum, DB#37b(4) (MHNG, dry); 2 ♀, immatures, same but Laguna Azul, -50.8935 -72.7819, 400 m, 14.i.1991, gully with Nothofagus antarctica and Berberis buxifolia surrounded by steppe, Misodendrum

Distribution. Argentina, Chile (Regions IX-XII).

Host plants. *Misodendrum linearifolium* DC., *M. punct-ulatum* Banks ex DC. (Misodendraceae).

Comment. Zonopelma australis was described from Southern Argentina and Far Southern Chile (XII Region) but without host data (Burckhardt 1987a). Here we provide host data and add new localities from Chile (Regions X–XII). Zonopelma contains a second species (Z. myzodendri Burckhardt) which occurs in southern Chile on Misodendrum punctulatum. A third species from Paraguay, viz. Zonopelma borealis Burckhardt, develops on mimosoid Fabaceae. Extensive material collected on Mimosa spp. in Brazil is closely related to Z. borealis but not congeneric with Z. australis, the type species of Zonopelma (Burckhardt and Queiroz, unpublished data).

Discussion

Trioza, in its present definition, is a large, artificial genus of worldwide distribution (Hollis 1984, Burckhardt and Ouvrard 2012, Ouvrard 2017). Several, probably monophyletic species-groups have been defined whose relationships to each other, however, remain uncertain (Hollis 1984, Burckhardt 1988, Brown and Hodkinson 1988). The incised paramere and the highly modified valvulae of the female ovipositor, along with the association with Santalales, strongly support the monophyly of the Trioza struthanthi-group. Tuthill (1939) noted a resemblance of T. phorodendrae, a member of the T. struthanthi-group, to T. mexicana Crawford, though without giving details. Both species bear an apical process on the female proctiger, but T. mexicana lacks the apically incised paramere and the highly modified valvulae of the T. struthanthi-group. The host of T. mexicana is unknown. A close phylogenetic relationship of the two species is, therefore, not supported. At present, no detailed synapomorphies are known linking the T. struthanthi-group to other members of *Trioza* and its phylogenetic relationships remain obscure.

Psyllids are generally highly host specific, i.e. they can complete their development only on a single (monophagous) or on several plant species of the same genus (narrowly oligophagous), family or order (widely oligophagous). Polyphagy is very rare among psyllids. Host data in the literature are, unfortunately, blurred by reports of plants on which adult psyllids have been observed or collected but on which they would be unable to complete their development (Burckhardt et al. 2014). Of the 34 psyllid species listed in Table 1, which summarises all psyllid species from Santalaceae reported in the literature or represented in the collections of the MHNG and NHMB, hosts are confirmed with immatures (or skins) for 18 and

are likely for another eight species. For three species there are no host records but an association with Santalales is likely, and for five species the host records are improbable or uncertain. Mathur (1975) described four species, collected during a survey of sandalwood in northern India. All four species were described from adults only. Macrohomotoma maculata Mathur, 1975 and Mycopsylla indica Mathur, 1975 are members of the Homotomidae, a family which is restricted to hosts within the Moraceae (Hollis and Broomfield 1989). Santalum album is, therefore, a very unlikely host. In the case of Diaphorina venata Mathur, 1975 and Psylla santali Mathur, 1975 there is no evidence for or against sandalwood being the host and the information is, therefore, uncertain. Equally uncertain is the record of *Diaphorina verbera* Kandasamy, 1986 described from two adults from southern India also on sandalwood. In terms of host specificity, 15 of the 26 species with confirmed or likely hosts are monophagous, 9 narrowly oligophagous and 2 widely oligophagous.

Taylor (2016) suggested that the switch of the Australian Acizzia species from their ancestral hosts, probably Fabaceae, to mistletoes may have been mediated by the close proximity of these plants. This may be also true for Notophorina fusca and Zonopelma from south temperate and subantarctic rain forests in southern Chile developing on Misodendrum, whose closest relatives live in the same habitats and develop mostly on Myrtaceae (Notophorina fusca-group) or on Euphorbiaceae and Rosaceae (Sphinia), respectively. The phylogenetic relationships of the other taxa developing on Santalales are unknown so that their ancestral hosts cannot be inferred. In Acizzia, the Trioza struthanthi-group, Zonopelma as well as the species pairs of Calophya and Afrotropical Psylla, probably all monophyletic, a single shift to Santalales followed by a radiation within the host group is the most likely explanation of the observed host patterns. For the other groups, there is no evidence for a radiation after the host switch.

Psyllids associated with Santalales are relatively species rich in the New World and the Australian biogeographical realm. In the Afrotropical and Palaearctic regions only three, resp. one psyllid species are known from mistletoes. There are no confirmed or likely records from the Oriental region.

Five genera with 28 species of Santalales are known from southern Brazil (Dettke and Waechter 2014a, b) but only three associated psyllid species (*Calophya* sp., *T. struthanthi* and *T. tripodanthi*) could be found, each on a different host genus and species (Table 1), despite intensive field work. A fourth species (*Trioza vagata*) was collected in a single location and without reliable host information. A similar pattern is found in Chile with 13 genera and 26 species of Santalales (Marticorena and Quezada 1985) but only one associated psyllid species. This suggests that there was only a very limited radiation after the shift to Santalales wich is in contrast to other groups of phytophygous insects. Butterflies of the family Pieridae, e.g., colonised Santalales three times, probably from ancestral Fabaceae, and then successfully radiated on this plant or-

der: about 440 of a total of about 1100 species of Pieridae develop on Santalales (Braby and Trueman 2006).

Conclusions

The present study documents that the psyllid fauna associated with mistletoes from the New World is much richer than previously estimated. On the other hand, a critical review of published data shows that the host records from the Oriental region are unlikely or, at least, questionable.

Santalales were colonised by psyllids at least nine times independently. In *Acizzia* and *Freysuila* the shift was probably from ancestral Fabaceae, in *Calophya* from Sapindales and in *Notophorina* from Myrtaceae. For the remaining groups, the plant taxon from which the psyllids colonised mistletoes remains unknown due to unsolved phylogenetic relationships of the psyllid taxa. Santalales are only sparingly used by psyllids as hosts and there seems to be no major radiation within this host taxon despite multiple colonisation events unlike some other groups of phytophygous insects, such as Pieridae which extensively exploits this plant order (Braby and Trueman 2006).

More targeted field work is necessary to confirm the host patterns described here and to examine the doubtful host records. More phylogenetic data is required to reconstruct ancestral host plants from which the psyllids colonised the mistletoes.

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