



Host–parasite relationships and life cycles of cuckoo wasps in agro-ecosystems in Argentina (Hymenoptera: Chrysididae: Chrysidini)

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Chrysididae is a diverse group of parasitoid/cleptoparasitic wasps; however, host–parasite relationships and life cycles of few species have been studied. Nests of different wasp and bee species were obtained during a trap-nesting programme, in the Pampean region. Some of these nests were parasitised by cuckoo wasps females of *Caenochrysis taschenbergi* (Mocsáry), *Chrysis boutheryi* (Brèthes), *C. saltana* Bohart, *C. sp. 1* (ignita-group), *C. sp. 2* (ignita-group), *Neochrysis lecointei* (Ducke), *Pleurochrysis ancilla* (Buysson) and *P. lynchi* (Brèthes). This paper reports new data about host–parasite relationships and life cycles for these species. Multiple parasites (from one species or from different families of insects) emerged from single cells of some parasitised nests: from each host cell parasitised by species of *Pleurochrysis*, two adults emerged successfully, information previously unknown for the genus; and in three cases of cells parasitised by *C. boutheryi*, two adults successfully emerged from a single cell; in two cases both individuals were chrysidine, and in third one was chrysidine and one *Leucospis pulchripes* (Leucospidae).

Keywords: crabronidae; cuckoo wasps; eumeninae; megachilidae; vespidae

Introduction

The family Chrysididae is a diverse group of parasitic wasps (Kimsey and Bohart 1991). Its 2500–3000 species are arranged in four subfamilies: Amiseginae, Chrysidinae, Cleptinae and Loboscelidiinae. Chrysidinae is the largest subfamily, comprising 80% of the species of this family. Within this subfamily, the tribe Chrysidini, with more than 1200 valid species, is the prevalent group (Kimsey and Bohart 1991). All species treated in this contribution belong to this tribe. In the Neotropical region, Chrysidini are represented by 110 species in nine genera: *Caenochrysis* Kimsey and Bohart, *Ceratochrysis* Cooper, *Chrysis* Linnaeus, *Exochrysis* Bohart, *Gaullea* Buysson, *Ipsiura* Linsenmaier, *Neochrysis* Linsenmaier, *Pleurochrysis* Bohart and *Pseudospinolia* Linsenmaier (Kimsey 2006).

All chrysidids are parasitoids or cleptoparasites, and the nature of the primary food source is practically a subfamilial character in these wasps (Kimsey and Bohart 1991). The chrysidine cuckoo wasps attack aculeate wasp and bee larvae, except for some species of *Praestochrysis* Linsenmaier, which attack moth larvae. In spite of this, the biology of only a small percentage of the species of this tribe has been studied (Kimsey and Bohart 1991).

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In the Pampas of Argentina, 90% of the original grasslands have been converted into fields used for crops and/or livestock, threatening native animals through habitat destruction, fragmentation and/or loss of original habitat quality, the introduction of competing animals, and direct human impact (Medan et al. 2011). Trap-nests are a good tool to get biological information on bees and wasps that nest in pre-existing cavities, and provide good evidence about parasites and/or cleptoparasites (Krombein 1967). A number of studies have examined the bees and wasps found in trap-nests in agro-ecosystems in the Pampean region, including Torretta and Durante (2011), Torretta et al. (2012) and Torretta et al. (2014), and their host–parasite interactions (Torretta 2014). Adults of different species of cuckoo wasps emerged from nests of different species of bees and wasps during distinct sample periods; therefore, the objectives of this study were: (1) to describe host–parasite relationships and (2) to study life cycles and emergence patterns of the different species. Additionally, sex ratio, associated organisms and parasitism percentage are provided for some cuckoo-wasp species.

Methods

Study sites

The trap-nests were located in four sites of the Pampean region. The sites represent different subdivisions of the Pampean grassland (Figure 1a) and have distinct main economic activities (Table 1). The Toay site is located in a xerophytic open forest system (Caldenal) which is a transitional ecosystem between the Pampas grasslands, to the east, and the dry Monte shrublands, to the west. It is dominated by the *caldén* tree (*Prosopis caldenia* Burkart), with an understory of predominantly perennial grasses (Cabrera 1994). The Hortensia site is a mosaic of crop fields and semi-natural grasslands used for livestock grazing. The Pila site is a seasonally flooded grassland dedicated to cattle breeding, and the Colonia Elía site is a mosaic of crop fields and grazing land in similar proportions.

Nest collection

Trap-nests were placed between November and March during three consecutive periods (Table 1), and were visited monthly. In Toay, trap-nests were located in two areas of forest in two (2009–2010) and in four (2010–2011) transects perpendicular to the field margin at heights of 1–2 m on trees. In Hortensia and Pila, trap-nests were placed on fence posts in field margins associated with diverse crops, semi-natural grassland and/or sown pasture. In Colonia Elía, they were located on trees and on fence rows (Figure 1b, c). Trap-nests (numbered in each sampled period from #1) were arranged in bundles (numbered with Roman numerals, from I) of 14 canes, and the bundles were placed at intervals of 50–100 m, covering areas from 3–10 ha. The number of trap-nests varied among sites and sampled periods (Table 1).

Trap-nests used in this study consisted of hollow bamboo canes (5–11 mm internal diameter), which were cut so that a nodal septum closed one end of the cane (Aguilar and Garófalo 2004). At each monthly visit, the traps with nests were removed and taken to the laboratory. There, the cells were separated in plastic vials with cotton plugs and numbered from 1 to n (starting from the innermost) and were

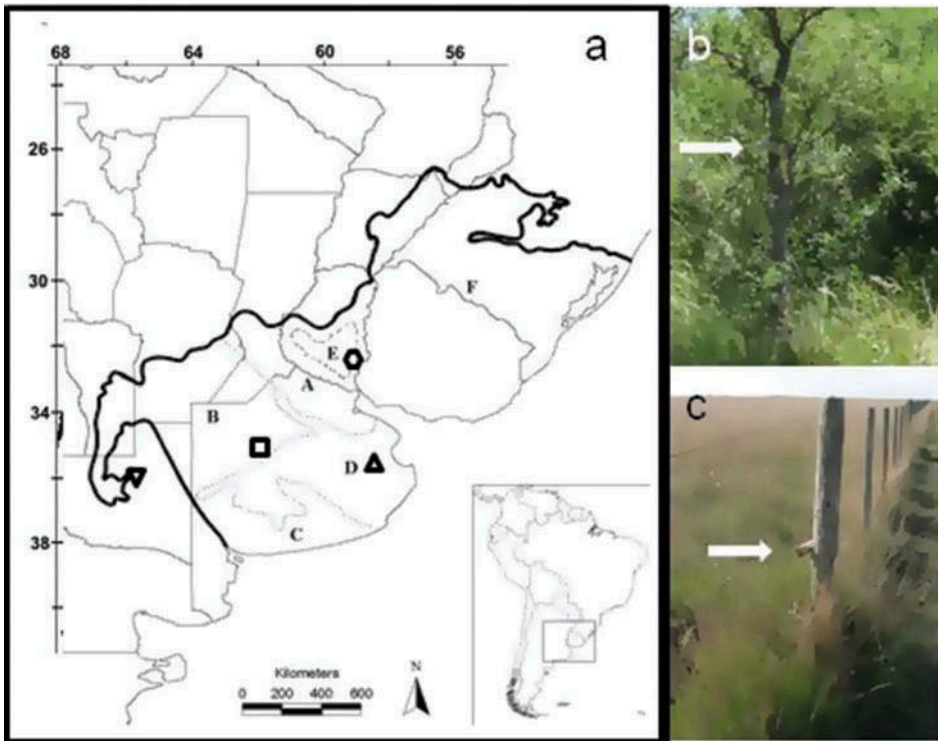


Figure 1. (a) Study sites: Toay (inverted triangle), Hortensia (square), Pila (triangle) and Colonia Elía (hexagon), situated in the Pampean region. The area encircled by thick line indicates the location of the Río de la Plata grasslands. Subdivisions are limited by dotted lines and identified by capital letters. A: Rolling Pampa; B: Inland Pampa; C: Southern Pampa; D: Flooding Pampa; E: Mesopotamic Pampa; F: Campos (modified from Medan et al.2011). (b–c) Trap-nests located in one tree and on fence posts.

kept in the laboratory at room temperature (ca. 15–25°C) until adult emergence. Since trap-nests were collected at monthly intervals, development time can only be estimated with an error of ± 15 days (Thiele 2005).

For each chrysidine species, I calculated the percentage of parasitism as [number of parasitised host(s) cells]/[total number of host(s) cells].

The material studied is deposited in the Entomological Collection of the General Botany Unit (FAUBA), Facultad de Agronomía, Universidad de Buenos Aires, Argentina, and at the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (MACN).

Determination of cuckoo wasp species

For determination of species of Chrysididae, I used Kimsey and Bohart (1980, 1991), Bohart (1985), Kimsey (1985, 2006) and Linsenmaier (1985), and I also had the opportunity to compare my specimens with those identified by Bohart deposited at the Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’ (MACN), with

Table 1. Description of the study sites in Argentina.

Sites	Toay	Hortensia	Pila	Colonia Elía
Geographic provinces	La Pampa	Buenos Aires	Buenos Aires	Entre Ríos
Geographic coordinates	S 36°22'24.3" W 64°50'29.5"	S 35°56'44.9" W 61°11'43.7"	S 36°15'41.7" W 58°16'14.2"	S 32°39'58.4" W 58°26'42.0"
Phytogeographic provinces	Ecotone Pampean Grasslands and xeric forest	Inland Pampa	Flooding Pampa	Mesopotamic Pampa
Altitude (m above sea level)	310	90	15	24
Sampling dates/number of trap-nests placed	November 2009 to March 2010/140 November 2010 to March 2011/350	November 2009 to March 2010/140 November 2010 to March 2011/350	November 2010 to March 2011/350	November 2011 to March 2012/350
Main economic activity	Cattle ranching	Agriculture	Cattle ranching	Cattle ranching/agriculture
Neighbouring crops	Pasture, Alfalfa	Soybean Wheat, maize	Pasture Clovers	Pasture Soybean

the kind collaboration of A. Roig Alsina. In general, I followed the taxonomical treatment of Kimsey and Bohart (1991).

Results

During the three sampling periods, a total of 397 traps ($n = 69$ in 2009–2010, $n = 288$ in 2010–2011 and $n = 40$ in 2011–2012) were colonised by different bee species of the family Megachilidae, and wasps of the families Crabronidae and Vespidae (Eumeninae). Of these, 32 nests ($n = 7$ in 2009–2010, $n = 21$ in 2010–2011 and $n = 4$ in 2011–2012; Table 2) were parasitised by eight species of chrysidine cuckoo wasps: *Caenochrysis taschenbergi* (Mocsáry), *Chrysis boutheryi* (Brèthes) (*nisseri* group), *C. saltana* Bohart (*comparata-gibba* group), *C. sp. 1* (*ignita* group), *C. sp. 2* (*ignita* group), *Neochrysis lecointei* (Ducke), *Pleurochrysis ancilla* (Buysson) and *P. lynchi* (Brèthes) (Table 2).

For each species, I report the number and sexes of emerged adults, estimated developmental time, host/s, material used by female host for construction of nest, provisions for larvae, the percentage of parasitism and other parasitic species associated (Table 2).

During the 2010–2011 period, I reared 20 individuals of *Chrysis boutheryi* (Brèthes) from 13 nests of vespid wasps, and a megachilid bee. Only one nest was parasitised in each bundle of canes, except one bundle with three parasitised nests. Ten nests were found and removed during early summer (January), and the remaining three during late summer (March). Adult emergence showed a clear bimodal pattern (Table 2; Figure 2a). The sex ratio was strongly female-biased (19/1). In 15 host cells, a single adult chrysidine was developed. However, in three cases, two adults successfully emerged from a single cell (Table 2), two female chrysidines from one cell of *Zethus dicomboda*, a female and a male chrysidine from one cell of one species of *Hypodynerus* de Saussure, and a female chrysidine and one female of *Leucospis pulchripes* Cameron (Hymenoptera: Leucospidae) from a cell of *Megachile catamarcensis* Schrottky.

During two consecutive years of study in Toay, 19 individuals of *Chrysis saltana* Bohart ($n = 13$ in 2009–2010 and $n = 6$ in 2010–2011) were reared from the nine nests of *Anthidium vigintipunctatum* Friese ($n = 6$ in 2009–2010 and $n = 3$ in 2010–2011). Seven nests were removed during January and one during February, and the remainder in March. Estimated emergence time showed a unimodal pattern, although one female took nearly 22 months to emerge (Figure 2b). In both sampled periods, the sex ratio was female-biased (1.2/1 and 2/1, respectively; Table 2).

Two specimens of chrysidine successfully emerged for each cell of the two species of *Pleurochrysis*. During 2010–2011, I reared two individuals of *Pleurochrysis ancilla* (Buysson) from a nest of *Hypodynerus* sp. from Toay, and six individuals of *Pleurochrysis lynchi* (Brèthes) from three nests of *Stenodynerus* sp. from Pila (Table 2).

Discussion

This paper is the first report about host–parasite relationships and life-cycle data for these eight species of chrysidine in the highly modified Pampean region.

Four species in the genus *Chrysis* were studied in this work. In two of them, the numbers of emerged adults and attacked nests provide good information about their biological traits. The females of *Chrysis boutheryi* seem to be generalist in the hosts

Table 2. Species of chrysidine cuckoo wasps (Chrysididae, Chrysidini) rearing from nests of wasps and bees obtained in trap-nests in agro-ecosystems in Argentina, during 3 years of study. f: female, m: male * denotes two chrysidines successfully emerged from a single cell, ** one chrysidine and one leucospid wasp successfully emerged from a single cell. Hym.: Hymenoptera, Dip.: Diptera and Col.: Coleoptera. CE: Colonia Elia, H: Hortensia, P: Pila, and T: Toay.

Species of Chrysididae	Nest Number	Date Nest Collection	Host cells / Chrysidine emerged (sex)	Date Chrysidine Emerged	Estimated Developmental Range (months)	Hosts	Host cell Partition	Host Provisions	Percentage parasitism: Parasitised cells / total cells of host species	Other parasitic Species associated	Site
<i>Caenochrysis taschenbergi</i>	20	19 January 2012	2/1 (m)	1 November 2012	9–10	<i>Trypoxylon</i> sp.	Mud	Spiders	2.8 (3/106)		CE
	156	19 January 2012	3/1 (m)	15 March 2012	1–2						
	610	25 March 2012	4/1 (f)	14 December 2012	8–9						
	323	16 March 2011	5/3 (3 f)	14–23 December 2011	8.5–9.5	<i>Pachodynerus argentinus</i>	Mud	Caterpillars	25 (3/12)		H
<i>Chrysis boutheryi</i>	488	10 December 2010	1/2* (f, m)	28–29 December 2010	1	<i>Hypodynerus</i> sp.	Mud	Caterpillars	4.5 (11/242)		T
	540	10 December 2010	2/1 (f)	7 January 2011	0.5–1.5					<i>Anthrax oedipus</i> (Dip.: Bombyliidae)	
	547	10 December 2010	4/1 (f)	29 December 2010	1					<i>Huarpea fallax</i> (Hym.: Sapygidae)	
	553	10 December 2010	3/1 (f)	29 December 2010	1					<i>Leucospis pulchripes</i> (Hym.: Leucospidae)	
	583	11 December 2010	8/1 (f)	27 December 2010	1					<i>Melittobia hawaiiensis</i> (Hym.: Eulophidae)	
	616	11 December 2010	5/1 (f)	31 December 2010	1					Pteromalidae sp. (Hym.)	
	702	22 January 2011	2/1 (f)	21 November 2011	9.5–10.5						
	732	4 April 2011	7/1 (f)	21 December 2011	8.5–9.5						
	371	4 April 2011	2/1 (f)	25 November 2011	7–8	<i>Zethus dicomboda</i>	Mud	Caterpillars			
	453	10 December 2010	8/2 (2 f)	26–28 November 2011	11–12						
	464	10 December 2010	7/3* (3 f)	4–7 December 2011	11–12						
	554	10 December 2010	5/2** (2 f)	2–3 November 2011	10–11	<i>Megachile catamarcensis</i>	Mud/petals	Pollen			

(Continued)

Table 2. (Continued).

<i>Chrysidsaltana</i>	209	23 March 2010	5/1 (f)	5 January 2011	9–10	<i>Anthidium</i>	Trichomes/	Pollen	2.6 (13/506)	<i>Nemognathia</i> sp.	T
	270	14 January 2010	11/4 (2 f, 2 m)	27 December 2010 to 15 January 2011	11–12	<i>viginipunctatum</i>	plant fibers			(Col.: Meloidae)	
	275	14 January 2010	5/1 (m)	26 December 2010	11–12						
	278	14 January 2010	18/1 (f)	5 January 2011	11–12						
	279	14 January 2010	24/5 (2 f, 3 m)	3–27 January 2011 to 15 November 2011	12–13 (– 22)						
	280	14 January 2010	27/1 (f)	3 January 2011	11–12						
	370	16 February 2011	3/2 (f, m)	25 November 2011 to 16 January 2012	9–12				5.6 (6/107)	<i>Huarpea fallax</i> (Hym.: Sapygidae)	
	384	22 January 2011	4/1 (f)	7 November 2011	9–10					<i>Leucospis pulchripes</i> (Hym.: Leucospidae)	
	463	22 January 2011	9/3 (2 f, m)	21 December 2011 to 8–9 February 2012	10.5–13					Eupelmidae sp. (Hym.)	
<i>Chrysid</i> sp. 1 (<i>ignita</i> -group)	98	16 March 2011	3/1 (f)	12 December 2011	8.5–9.5	<i>Trypoxylon</i> sp.	Mud	Spiders	16.7 (1/6)		H
<i>Chrysid</i> sp. 2 (<i>ignita</i> -group)	586	28 February 2011	10/1 (f)	16 April 2012	3.5–4.5	<i>Trypoxylon</i> sp.	Mud	Spiders	0.9 (1/106)		CE
<i>Neochrysis lecontei</i>	117	10 March 2010	3/1 (m)	20 November 2010	8–9	<i>Trypoxylon</i> sp.	Mud	Spiders	33.3 (1/3)		H
<i>Pleurochrysis ancilla</i>	569	11 December 2010	4/2* (f, m)	12 December 2011	11.5–12.5	<i>Hypodynerus</i> sp.	Mud	Caterpillars	0.7 (1/143)		T
<i>Pleurochrysis lynchi</i>	760	3 March 2011	1/2* (2 f)	11–15 March 2011	1	<i>Stenodynerus</i> sp.	Mud	Caterpillars	50 (3/6)		P
	761	3 March 2011	1/2* (2 f)	11–14 March 2011	1						
	765	3 March 2011	2/2* (f, m)	10 March 2011	1						

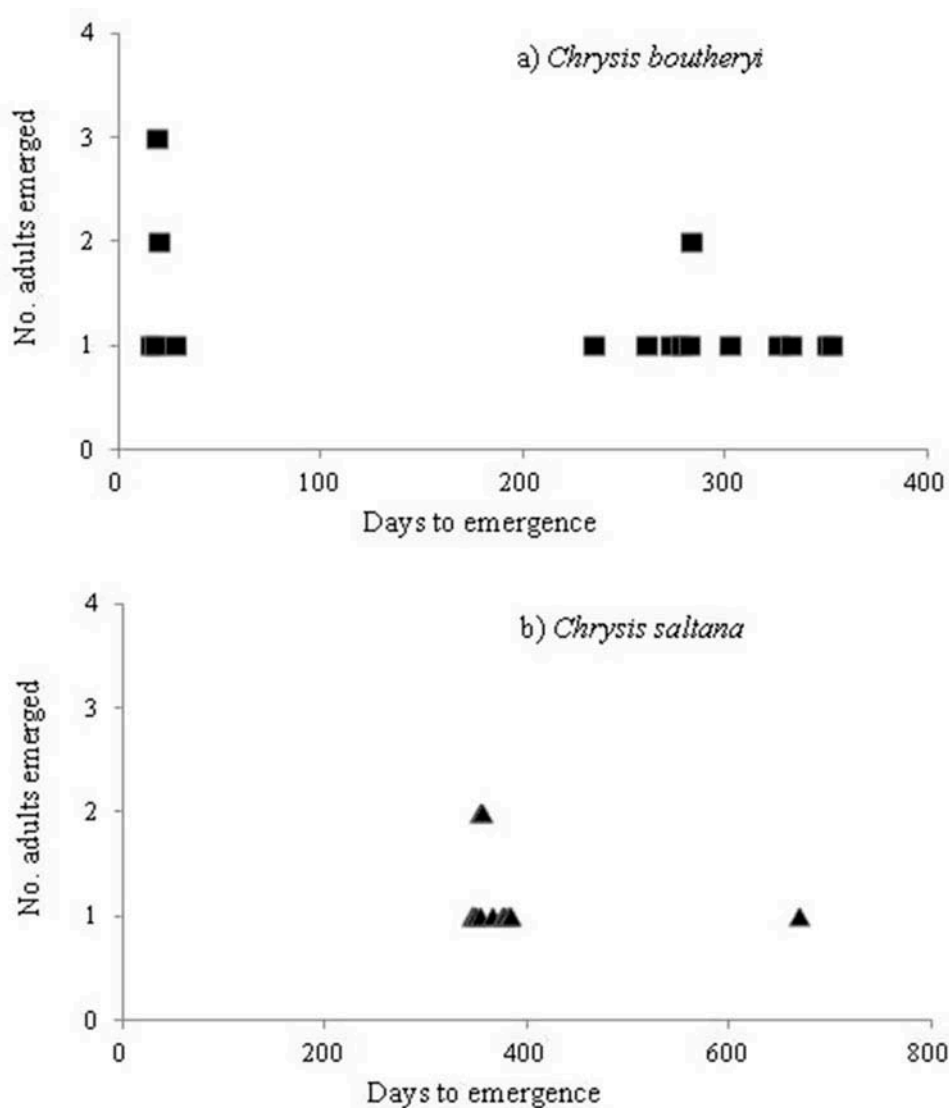


Figure 2. Emergence patterns of (a) *Chrysis boutheryi* (Brèthes) (squares; n = 20) and (b) *C. saltana* Bohart (triangles, n = 19) adults reared from trap-nests in Toay, La Pampa Province.

which they parasitise: eumenine vespids and megachilid bees. However, most parasitised nests were of mud cell-building species of the family Vespidae. Also, *Megachile catamarcensis* used mud (with flower petals and/or leaf pieces) to build their nests (Torretta et al. 2014). These are the first records about host–parasite relationships for a species of the *nisseri* species group. One cell was attacked by *C. boutheryi* and *L. pulchripes*, and both adults successfully emerged. This is an interesting finding given that there are few reported cases where two parasites emerge from a single cell. Rosenheim (1987) reported cells of the ground-nesting *Ammophila dysmica* Menke

(Sphecidae) successfully parasitised by the cuckoo wasp *Argochrysis armilla* Bohart and the miltogrammine fly *Hilarella hilarella* (Zetterstedt) (Sarcophagidae). Also, from another cell of this nest of *Hypodynerus* sp., two female of *C. boutheryi* emerged. These facts indicate that in the preimaginal stages of *Hypodynerus* sp., food was sufficient for both individuals to develop and emerge successfully in a single cell.

The bimodal emergence pattern of *Chrysis boutheryi* trait is reflected in the activity pattern of oviposition of females (note dates of nest collection in Table 2). Sex ratio was strongly female-biased. The significance of the female-biased sex ratio of emergence of this cuckoo wasp is unclear.

The females of *Chrysis saltana* seem to be host specific, only parasitising cells of the carder bee *Anthidium vigintipunctatum*. The only other record for a species of the *comparata-gibba* group is for *Chrysis tripartita* Aaron, closely related to *saltana* (Bohart 1985), which also attacks bees in the genus *Anthidium* Fabricius (Grigarick and Stange 1968). *Chrysis saltana* shows a univoltine life cycle; however, one female took about two years to emerge, suggesting parsivoltinism (Torchio and Tepedino 1982). In many species of Apoidea, the duration of the life cycle varies among individuals of the same generation (Torchio and Tepedino 1982; Weislo and Cane 1996) and may be a bet-hedging strategy related to unpredictable resource availability (Neff and Simpson 1992) or to the abundance of natural enemies (Weislo and Cane 1996). Parsivoltinism can favour the persistence of some populations by staggering the emergence of sequential generations (Torchio and Tepedino 1982). *Chrysis saltana* has been recorded from Salta, Santiago del Estero, Catamarca and La Rioja (Bohart 1985). The population studied herein is the southernmost record for this species, and temperature accumulation required for diapause termination possibly takes longer than for other populations. Therefore, at lower latitudes, this species could exhibit a bivoltine life cycle.

Two species of *Pleurochrysis* were reared in this study, both nest parasites of mud-pot nesting wasps. The host wasps of *P. ancilla* and *P. lynchi* were *Hypodynerus* sp. and *Stenodynerus* sp., respectively, species that supply their nests with numerous Lepidoptera larvae. There are few host records for other species of this genus. *Pleurochrysis bruchi* (Brèthes) was reported from *Pachodynerus gayi* (Spinola) (Janvier 1933); *P. postica* (Brullé) from *Trypoxylon rogenhoferi* Kohl (Garcia and Adis 1995), *Trypoxylon xanthandrum* Richards (Coville and Griswold 1983) and one species of *Sceliphron* Klug (Kimsey and Bohart 1991); and *P. morosa* (Buysson) from *Trypoxylon rogenhoferi* Kohl (Garcia and Adis 1995). All female wasps of these species of Vespidae: Eumeninae, Sphecidae and Crabronidae, used mud as cell partitions and captured a large number of prey for their offspring.

Possibly, the species of *Pleurochrysis* are cleptoparasitic and their larvae consume host provisions, or they are parasitoids and consume pre-imaginal instars host. The cocoons of chrysidines were formed inside the host cell, and therefore I could not see if these wasps attacked host larvae, their provisions or host prepupae/pupae. For both species of *Pleurochrysis*, two adults emerged successfully from each host cell parasitised. This information is previously unknown for the genus. While the number of obtained parasitised nests was low ($n = 4$), I suggest that it might be possible that females of this genus lay two eggs in each host cell due to a sufficient provision of caterpillars (*Hypodynerus*, *Pachodynerus* de Saussure and *Stenodynerus* de Saussure) or spiders (*Sceliphron* and *Trypoxylon* Latreille). Another explanation is that more than one female will lay eggs in the same host cell. Rosenheim (1987) found up to six

Argochrysis armilla Bohart produced from a single cell of *Ammophila dysmica* Menke (Sphecidae).

The other chrysidine species of this study were reared from diverse species of *Trypoxylon*, which build mud nests and capture spiders for larval provision. These results agree with known records for other species of these genera. The *Chrysis ignita* group has numerous species, and a wide range of hosts (Crabronidae and Vespidae: Eumeninae) has been reported (Kimsey and Bohart 1991). At the same time, the few available records about hosts of *Caenochrysis taschenbergi* and *Neochrysis lecontei* indicate a marked specialisation on *Trypoxylon* (Coville 1981; Kimsey and Bohart 1991; Garcia and Adis 1995).

Very little is known about sex ratio in chrysidine species (Yokoi et al. 2012). Highly female-biased sex ratios (as has happened in *Chrysis boutheryi*) for single batch rearing of cuckoo wasps are not uncommon (Medler 1964), and sex ratio may vary between sites and years (Krombein 1967). Therefore, more data should be obtained to clarify sex-ratio dynamics in these species.

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