RESEARCH ARTICLE



Studies on the Asian sawflies of Formosempria Takeuchi (Hymenoptera, Tenthredinidae), with notes on the suitability of F. varipes Takeuchi as a biological control agent for skunk vine, Paederia foetida L. (Rubiaceae) in Florida

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Abstract

Formosempria Takeuchi, 1929, is distributed in southeastern Asia from Taiwan and China to Vietnam, Myanmar, and possibly northern India. Three species are included: *F. crassicornis* Wei & Nie, 2002, *F. shanensis* Malaise, 1961, and *F. varipes* Takeuchi, 1929 (= *F. annamensis* Malaise, 1961, **syn. n.**; = *F. metallica* Wei, 2003, **syn. n.**). *Formosempria varipes* was reared from larvae feeding on *Paederia foetida* L. (Rubiaceae) in Hong Kong and was a potential biological agent for the invasive *P. foetida* in Florida. Larval feeding tests indicate more than one species of *Paederia* are suitable hosts for *F. varipes* and further study for use as a biological control agent in Florida is unwarranted. Descriptions and illustration of the species are given, and life history notes on *F. varipes* are presented.

Keywords

Symphyta, biological control, skunk vine

Introduction

Interest in the small and little-known genus *Formosempria* Takeuchi was prompted by discovery of larvae of a species in Hong Kong feeding on skunk vine, *Paederia foetida* L. (Rubiaceae), a target for a biological control program in Florida (Pemberton and Pratt 2002). Adults reared from these larvae were identified as a species of *Formosempria*, an Asian genus in the subfamily Allantinae. Taeger et al. (2010) listed five described species in this genus, distributed from Taiwan and western and southern mainland China to Vietnam, Myanmar, and possibly northeastern India. Very few specimens of *Formosempria* were previously available for study, most of which are types of the described species, but additional specimens from Taiwan and those reared from Hong Kong have become available. The identity of the Hong Kong species, as outlined here, is *Formosempria varipes* Takeuchi, 1929, which was described from Taiwan.

Formosempria was based on a single species, *F. varipes*, described from a single specimen (Takeuchi 1929). Malaise (1961) added two species, *F. annamensis* from Vietnam and *F. shanensis* from Myanmar, and gave a key to the three species. Wei and Nie (2002) and Wei (in Wei and Nie 2003) added *F. crassicornis* and *F. metallica* from China. Saini and Deep (1994) and Saini (2006) reported *F. shanensis* Malaise, the species described from Myanmar, from India, but this is questionable. The genus probably does not occur in India. Haris (2012) recorded *F. crassicornis* from Vietnam. Critical to the study of *Formosempria* is the identity of the type species of the genus, *F. varipes* Takeuchi. Unfortunately, the type could not be located. However, among some specimens from Taiwan we found a series identical to Takeuchi's description of *F. varipes*. We use these specimens to characterize *Formosempria* and the included species.

Discovery of *F. varipes* feeding on *Paederia* in Hong Kong initiated studies on the species as a possible biological control agent for *P. foetida* in Florida. However, host preference studies showed that several species of *Paederia* may serve as host plants, thus making it unsuitable for release as a biological control agent of *P. foetida* in Florida.

Material and methods

Figures 1-15 were obtained using an EntoVision Imaging Suite that included a firewire JVC KY-75 3CCD digital camera mounted to a Leica M16 zoom lens via a Leica z-step microscope stand. Multiple focal planes were merged using Cartograph 5.6.0 (Microvision Instruments, France) software. Figures 16–18 were prepared by PDP.

Acronyms used are: CSCS (Collection of Central South University of Forestry and Technology, Changsha, Hunan, China); FSCA (Florida State Collection of Arthropods, Gainesville, FL, USA); IPRL (Invasive Plant Research Laboratory, Agricultural Research Service, U. S. Department of Agriculture. Ft. Lauderdale, FL, USA); NHR (Naturhistoriska Riksmuseet, Stockholm, Sweden); UOP (University of Osaka Prefecture, Sakai, Japan); SDEI (Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany); USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA).

Recent surveys by JM resulted in the discovery of numerous *F. varipes* larvae feeding on the foliage of *P. foetida* in the Sham Tseng area (N 22.373, E114.064), Hong Kong. Taxonomic and biological assessments were based on *F.varipes* individuals that were shipped from Hong Kong in March 2013 and April 2014 to the quarantine facility at IPRL, under permit #P526P-12-04814. In an effort to establish a laboratory colony of *F. varipes*, 25 males and 25 females from the 2013 shipment were added to each of three screen cages $(33 \times 33 \times 61 \text{ cm})$ within the quarantine glasshouse (28 °C (±5), 85% (±10) relative humidity). Each cage contained a potted *P. foetida* plant as well as several cotton balls hydrated with dionized water, which were positioned on the top surface of each cage. Observations of these adults, the resulting eggs, and larvae were recorded.

A subset of adults arising from the 2014 shipment were incorporated into nochoice host range tests, which were designed to quantify the propensity of *F. varipes* to oviposit and feed on select *Paederia* species. Among the *Paederia*, only *Paederia ciliata* (Bartl. ex DC) Standley is native to North America and has a geographic range limited to Mexico (Puff 1991). The release of *F. varipes* as a biological control agent of *P. foetida* in Florida may pose significant risk to the Mexican endemic if female sawflies recognize *P. ciliata* as an ovipositional host and larvae complete development when feeding exclusively on the plant. To test these host use patterns, five replicate *P. ciliata* or *P. foetida* potted plants were placed in individual screen cages $(33 \times 33 \times 61 \text{ cm})$ within a quarantine glasshouse as described above. Plants were pruned to ensure a uniform height and biomass among individuals. Five malefemale pairs, each less than 24 hours old, were randomly assigned to each cage and held with the test plant until death. Each plant was reviewed for oviposition incidence 7 days following adult inoculation and larval densities per plant were noted 21 days after adult release.

Additionally, no-choice larval tests were conducted to determine if *P. ciliata* is a developmental host. Other *Paederia* species were also included to provide insights into the generic specificity of the herbivore: *Paederia bojeriana* (Rich.) Drake, *P. cruddasiana* Prain, *P. pilifera* Hook., and the target weed *P. foetida*. Tests were conducted in a single controlled environmental chamber set at 25 °C, 75% relative humidity and 14:10 light:dark. Neonate larvae (< 24 hrs old) were collected from the laboratory colony and five individuals were transferred onto a slightly moistened filter paper within individual 90 × 15 mm petri dishes. Five replicate petri dishes with the accompanying larvae were randomly assigned one of five replicated plants for each of the five host plant treatments. Leaves were excised from assigned test plant replicates and placed within the petri dish, which was sealed with parafilm and maintained at internal conditions of 25 °C and 90% relative humidity. A mixture of soft, newly developing and mature, fully expanded leaves in excess of the herbibore's daily consumption were added to each petri dish every 24 hours. Survivorship was monitored daily and larval development time to the prepupal stage was noted. The influence of host plant species on oviposition, larval survival, and development rates were compared with ANOVA followed by Tukeys HSD post hoc analysis (PROC GLM; SAS 1999). Data are presented as means (± standard error).

Results

Systematics

Formosempria Takeuchi

Formosempria Takeuchi 1929: 85. Type species: Formosempria varipes Takeuchi, original designation; Malaise 1961: 247 (diagnosis; key to 3 species); Malaise 1963: 159 (in world key); Togashi 1990: 184 (one species, Taiwan); Abe and Smith 1991: 34 (genus listed); Chou and Naito 1991: 89 (one species, Taiwan); Saini and Deep 1994: 48 (one species, India); Wei and Nie 1998: 28 (placed in Blenno-campidae, Belesesinae, Atelozini); Wei 2001: 678 (one species, Zhejiang, China); Lacourt 2003: 506 (in Allantinae, Atelozini); Wei et al. 2006: 527 (three species listed from China); Saini et al. 2006: 579 (one species, India); Xiao 2006: 192 (one species listed from China); Taeger et al. 2010: 282 (world catalog, five species listed); Haris 2012: 138 (one species, Vietnam).

Description. Antenna (Figs 3, 10) hairy, stout and slightly thickened medially; scape longer than broad; pedicel as long as broad, antennomere 3 longer than 4; apical 3 antennomeres each with ventral sensory area. Malar space linear; clypeus (Figs 4, 8) truncate or bluntly protruding anteriorly; each mandible with large subapical tooth; inner margins of eyes slightly converging below (Figs 4, 8); genal carina absent; head from above strongly narrowing behind eyes (Figs 5, 9). Epicnemium absent. Forewing (Fig. 2) with 4 cubital cells; hind wing (Fig. 2) without cells Rs and M, anal cell with short petiole. Inner fore tibial spur appearing simple but with very slight preapical projection. Tarsal claws (Fig. 11) with long inner tooth, nearly as long as outer tooth and lateral to outer tooth, with basal lobe. Pulvilli small on hind tarsomeres 3 and 4. Head and body usually with slight metallic luster.

Remarks. Species of *Formosempria* are superficially similar to species of *Empria*, being similar in size and color and similar wing venation; thus, the reason for the name. Takeuchi (1929) mentioned that they are like *Empria*, but without a malar space. *Formosempria* will key to the same couplet as *Hemibeleses* in Malaise's 1963 key, but are separated from *Hemibeleses* which has the pedicel as long or longer than the scape and the 3-toothed hind claws in the male. Males of *Formosempria* were not known at that time, but the hind claw is similar to the fore- and midclaws, not 3-toothed as in *Hemibeleses*.

Based on this study, two species of *Formosempria* are recognized, *F. varipes* from Taiwan, southeastern China, and Vietnam, and *F. shanensis* from Myanmar. *Formosem*-

pria crassicornis Wei and Nie is listed, but the type was not examined and its status cannot be determined. The record of *Formosempria* from India by Saini and Deep (1994) and Saini (2006) is questionable.

Formosempria crassicornis Wei & Nie

Formosempria crassicornis Wei and Nie 2002: 837, 839, 846, 848, figs 10, 11 (female sheath, saw on p. 848); Wei et al. 2006: 527 (listed); Haris 2012: 138 (recorded from Vietnam).

Comments. This species was described from Hainan, China. The holotype, deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing, was not examined.

The figures by Wei and Nie (2002) of the female sheath and lancet do not differ from *F. varipes*, and *F. crassicornis* may be a synonym. Even though distinguishing characters for the species are not evident in the description and the species seems to fall within the range of *F. varipes*, it is kept valid until the type can be examined. Haris (2012) recorded a female from Vietnam ("N. Vietnam, Ninh Binh, Cue Phuong NP, near centre, c. 225 m, 20.xii.1999-19.ii.2000"), but gave no discussion. This specimen was not examined.

Formosempria shanensis Malaise

Figs 1-5

Formosempria shanensis Malaise 1961: 249, fig. 8A,B,C (head front; antenna, sheath dorsal); Malaise 1963: figs 73, 131; Saini and Deep 1994: 48 (listed; first record from India); Saini 2006: 68, 152, figs 215–222 (India record; male described); Saini et al. 2006: 579 (listed).

Comments. Malaise described this species from five females from "Burmese Southern Shan States (Taunggyi at 1500 m)". The syntypes are in NHR and were examined. The lectotype, here designated, is a female labeled "S. Shan States, Burma, 1500 m, Taunggyi, 1-VIII-22.IX.34 ["22.IX" crossed out], Malaise", "TYPUS" [red], "Formosempria shanensis n. sp., R. Malaise det 1958", "NHRS-HEVA 000000834" with a lectotype label added. The other four females are paralectotypes with the same data but with the label "PARATYPUS" [in red]; three do not have dates crossed out and one has "1-VIII" crossed out.

The color and structure are very similar to *F. varipes*, but *F. shanensis* differs by its slightly larger size, the more truncate clypeus with more acute lateral corners (Fig. 4, more rounded laterally in *F. varipes*, Fig. 8), and longer antennae (Fig. 1), being more than half the length of the body (thorax and abdomen) and about 2.2× the head width. These differences seem significant to retain *F. shanensis* as a distinct species at present.



Figures 1-2. Formosempria shanensis, lectotype. I Lateral 2 Dorsal.

Saini and Deep (1994) and Saini (2006) recorded this species from five males from India: "Himachal Pradesh, Dalhousie, Kalatop, 2850 m, 29.6-30.6.1986". Saini (2006) mentioned these are the first known males of the genus, although Wei (in Wei and Nie 2003) described the male of *F. metallica*. Saini (2006) also included description of the female. These specimens have three-toothed hind claws and the genitalia figured are quite different from that of associated males of *F. varipes*. We have not seen



Figures 3-5. Formosempria shanensis, lectotype. 3 Antenna 4 Head, front 5 Head, dorsal.

specimens, but according to Saini's (2006) description, we question that these are *F. shanensis* or even a member of *Formosempria*. Thus, the India record for *Formosempria* is doubtful.

Formosempria varipes Takeuchi

Figs 6-18

Formosempria varipes Takeuchi, 1929: 85–86. Figure of wings; Malaise 1961: 249 (in key); Togashi 1990: 184, figs 46–50; Wei et al. 2006: 527 (listed).

Formosempria annamensis Malaise, 1961: 249. syn. n.

Formosempria metallica Wei, in Wei and Nie 2003: 136–137, 207, figures, male and female; Wei et al. 2006: 527 (listed). syn. n.

Description. Female: Length, 6.5–7 mm. Black, with slight metallic lustre, and following white: apices of coxae, trochanters, basal third of mid and hind femora, basal third to half of mid and hind tibiae, base of hind basitarsus, most of mid and fore basitarsi. Wings lightly, uniformly infuscated; veins and stigma black. Head and body with slight metallic luster, smooth, shiny, with short silvery hairs.

Antenna (Figs 6, 10) with scape longer than broad; pedicel about quadrate; antennomere 3 longer than 4, remaining antennomeres gradually decreasing; length less



Figures 6-9. Formosempria varipes. 6 Lateral 7 Dorsal 8 Head, front 9 Head, dorsal.

than half body length (thorax and abdomen) and about 1.7× head width. Clypeus truncate to slightly protruding anteriorly, with corners rounded (Fig. 8). Malar space linear. Hind basitarsus (Fig. 11) about equal to length of remaining tarsomeres combined. Sheath (Fig. 13) slender in dorsal view, in lateral view slightly truncate at apex, appearing slightly directed dorsally. Lancet (Fig. 12) with serrulae low, pointed at apices, each with about 6 fine anterior and posterior subbasal teeth.

Male: Length, 6.5 mm. Similar in color and structure to female. Genitalia in Figs 14, 15. Neonates (Fig. 17): Similar to late feeding stage.

Last feeding stage (Fig. 18): Length, about 12 mm. Head black with postclypeus, preclypeus, area between antacorium and clypeus and mandible, mandible except apex and mouthparts except apices of palpi whitish; labrum brownish. Thorax and abdomen entirely pale with whitish bloom. Head with long scattered setae, longer than preclypeus; preclypeus with 2 setae on each side; labrum with 3 setae on each side; right mandible with 3 small ventral teeth and 2 acute and one broad dorsal teeth; left mandible with 2 acute ventral teeth and 4 acute dorsal teeth and with inner ridge extending inward from outer dorsal tooth. Thorax with scattered long setae. Abdominal segments each with 6 dorsal annulets; 2–3 setae on each side of annulets 2 and 4; subspiracular lobe and surpedal lobe each with about 4 long setae; apical segment with about 12 long setae dorsally and with long setae on subanal area.

Prepupa: Differs from feeding stages by head, thorax, and abdomen entirely pale, whitish. Setae on head and body absent. Each mandible with 3 linear teeth; left mandible with outer tooth largest, basal 2 teeth smaller and subequal in size; right mandible with central tooth largest, outer and inner teeth smaller and subequal in size.

Type material. Takeuchi described this species from a single female "Sozan near Taihoku, Formosa" "collected by M. Kato, on May 2, 1926". The holotype should be in UOP with the Takeuchi collection. On a visit to Japan in 1979, I examined the holotype and took some brief notes. When recently requesting the type, it could not be found in the Takeuchi collection at UOP. A thorough search for the type was made by Noria Hirai (UOP) and Akihko Shinohara (National Museum of Nature and Science), but to no avail.

Formosempria annamensis was described from a single female. The holotype is at NHR, was examined and is labeled "Phuc Son, Annam, XI-XII, H Rosse, Berlin, s.w. 11", "TYPUS" [red], Formosempria annamensis n. sp., R. Malaise det 1958, "NHRS-HEVA 000000839".

Formosempria metallica was described from nine female and male specimens from Hubei, Fujian, Zhejiang, Hangzhou provinces, China. The female holotype is at CSCS, from "Maheba, Xiangeng, Hubei, 1999-VII-25" and was examined. The holotype label is in Chinese, with the same date and "450 m." and additional labels "F. metallica", "Holotype: Formosempria metallica Wei female, M. Wei 1992".

Specimens examined. CHINA: Hong Kong, Sham Tseng San Tsuen Temple, larvae, March 24, 2013, on *Paederia foetida*, adults April 2013, reared in quarantine, ARS, Ft. Lauderdale, FL by Paul Pratt ($5 \ Q$, $5 \ Z$, USNM); same data, larvae March



Figures 10–15. *Formosempria varipes*. 10 Antenna 11 Hind tarsus 12 Ovipositor 13 Female sheath, lateral 14 Male genital capsule, ventral 15 Male penis valve, lateral.

2014, pupated and adults emerged IV–V 2014 (about 7 \bigcirc , 100 \Diamond , 20 larvae, USNM, IPRL); Hubei, holotype and paratype of *F. metallica* (1 \bigcirc , 1 \Diamond , CSCS); Zhejiang, paratype; Henan (1 \bigcirc , SDEI). TAIWAN: Keelung Co., Keelung City, V.2004, Malaise trap, L. Stange and H. Wang (1 \bigcirc , 4 \Diamond , FSCA). VIETNAM: Holotype of *F. annamensis* (1 \bigcirc , NHR).

Distribution. China (Hong Kong, Hubei, Fujian, Zhejiang, Hangzhou); Taiwan; Vietnam.

Hosts. Paederia foetida, also P. ciliata, P. cruddasiana, P. bojeriana, and P. pilifera based on host testing (Rubiaceae).

Comments. The interpretations of *F. varipes* by Malaise (1961), Togashi (1990) and others were based on the original description by Takeuchi (1929), not examination of the type. The type is now presumed lost. In a collection of sawflies from Taiwan (FSCA) DRS discovered a series of four males and one female that agree with Takeuchi's description. Due to the absence of the type, we are using these specimens as representative of F. varipes. A key character used by Malaise (1961) and others to separate F. varipes is the length of the hind basitarsomere. Takeuchi (1929) stated "posterior basitarsus shorter than the following joints". In the specimens examined, the hind basitarsomere is subequal to very slightly longer than the remaining tarsomeres combined. This is the only discrepancy between the Taiwan specimens we have and Takeuchi's (1929) description. However, because of the overwhelming similarity of the Taiwan specimens with Takeuchi's description, we do not believe "shorter", "subequal", or "slightly longer", alone are sufficient to justify a separate species. This could have been misinterpreted by the authors, or it could be slightly variable in the species. The female ovipositor and male genitalia of the Taiwan and Hong Kong specimens were compared and were identical.

Togashi (1990) briefly described one female from Taiwan "Shin Bao Shi, near Liu Kui, 3.V.1986, K. Baba leg." He stated that it agrees with Takeuchi's original description. He illustrated the dorsal view of the head (fig. 46), front inner tibial spur (fig. 47), tarsal claw (fig. 48), sheath (fig. 49), and lancet (fig. 50). The front inner tibial spur was illustrated and stated to be simple; however, in specimens we have examined there is a very slight subapical projection. Otherwise, Togashi's description and illustration agree with the specimens examined from Taiwan. Togashi's specimen was not examined.

Malaise's holotype of *F. annamensis* from Vietnam is identical to specimens from Taiwan and Hong Kong; therefore, we synonymize this species.

Wei (in Wei and Nie 2003) stated that *F. metallica* "...differs from its congeners in malar space absent, lateral furrows of postocellar area very weak and shallow, antenna as long as half the body length, and mesoscutellum black". Figures in Wei and Nie (2003) of the male genitalia, tarsal claw, sheath and part of the lancet do not noticeably differ from specimens from Taiwan and Hong Kong. All of the differing characters mentioned by Wei are shared with *F. varipes*, and, upon examination of the holotype, DRS observed no differences between this and *F. varipes*. Thus, *F. metallica* is synonymized.



Figures 16–18. Formosempria varipes. 16 Eggs 17 Neonate larvae 18 Mature larva.

Biology and host specificity of Formosempria varipes

The objective of importing *F. varipes* into the IPRL quarantine facility was to determine the sawfly's host range, from which inferences can be drawn concerning the herbivore's suitability as a biological control agent of *P. foetida* in Florida. Females from the 2013 survey were observed dragging their ovipositors across the leaf surface shortly after release into the cages, creating 1-2 cm longitudinal incisions through the leaf and typically located midway between the midvein and the leaf margin. Eggs (Fig. 16) were inserted between the adaxial and abaxil leaf surfaces, usually on the leaf margin but occasionally along the leaf midribs. Oviposition was consistently adjacent to the incision created by the female. The reason for this leaf cutting behavior is unknown but may be related to assessment of host plant suitability or the disruption of host plant defenses. In an effort to force mating, the heads of several males were excised and multiple attempts were made to mate females but all efforts were unsuccessful.

Neonates (Fig. 17) exited their leaf-enclosed eggs approximately one week following oviposition. Groups of first instar larvae were observed feeding gregariously, consuming the foliage between the leaf veins. First instar larvae were transferred to small, ventilated plastic cages and fed exclusively on *P. foetida* until pupation, demonstrating that the target weed is a developmental host. Later instars consumed entire leaves. Larvae (Fig. 18) possess a black head capsule but only later instars also have a fine wax covering the thorax and abdominal integument. The last instar larvae (prepupae) were observed wandering within the cages and lacked the wax covering, possessing instead a pale colored head capsule and integument. Prepupae were transferred to plastic boxes filled with a loose sandy soil, where the larvae readily burrowed below the surface. Pupation occurred within an oblong casing (cell) constructed, in part, from the surrounding soil. Adults emerged from their pupal cells approximately two weeks following pupation and tunneled to the surface of the soil. The subsequent (F_1) generation, however, were exclusively males and the laboratory colony was lost. These observations confirm that females of *F. varipes* are arrhenotokous.

A second collection of *F. varipes* larvae in Hong Kong was made in April 2014 and efforts to colonize the species were repeated. Adults arising from this 2014 shipment were also used in no-choice host range tests, which were designed to quantify the propensity of *F. varipes* to oviposit and feed on select *Paederia* species. Oviposition was observed among all replicates of *P. ciliata* and *P. foetida* tested. There was no difference in the number of larvae recovered from the *Paederia* species used in the ovipositional test ($F_{1,9} = 3.0$; $P \le 0.1214$). From these data it is clear that *F. varipes* females readily oviposit on the Mexican endemic *P. ciliata* so no-choice larval feeding tests were conducted to determine if *P. ciliata* is also a developmental host. Survivorship varied among hosts ($F_{4,24} = 10.38$; P < 0.001), with no individuals completing development when held with *P. pilifera*. Larval survivorship did not vary when feeding on the remaining species including *P. foetida* (90.0% (±0.05)), *P. cruddasiana* (88.0% (±0.08)), *P. ciliata* (76.0% (±0.10)), or *P. bojeriana* (52% (±0.22)). Host plant species also

influenced development times ($F_{3,17} = 6.69$; P < 0.005). Development from neonate to prepupa was shortest when feeding on *P. foetida* (9.5 days (±0.3)) and *P. bojeriana* (9.8 (±0.5)) but slowest when held with *P. ciliata* (13.1 (±0.9)), with *P. cruddasiana* (11.6 (±0.6)) intermediate. Like those of 2013, all efforts to establish a laboratory colony were unsuccessful with the 2014 material.

Although *P. ciliata* may not be an optimal host based on development rates, these data demonstrate that *F. varipes* will readily oviposit and complete development on the Mexican native under no-choice conditions. The risk *F. varipes* would pose to *P. ciliata* populations is a function of 1) host use, as reported herein, but also 2) the permeability of geographic barriers that inhibit landscape level dispersal of the herbivore from its intended range (Florida) to the native range of *P. ciliata* (central Mexico). While the dispersal pathway(s) remain unknown, there are several examples of biological control agents spreading far beyond their intended geographic ranges through natural or anthropogenic means (Pratt and Center 2012). Considering the ever increasing levels of tourism and trade between Florida and Mexico, the authors consider the probability of *F. varipes* dispersing to Mexico and threatening *P. ciliata* populations too great a risk to justify its release. Therefore, additional resources dedicated to the development of this species as a biological control agent are unwarranted.

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RESEARCH ARTICLE



Sawflies (Hymenoptera, Symphyta) of three Mid-Atlantic Parks in the George Washington Memorial Parkway, U.S.A.

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Abstract

A diverse sawfly fauna of 176 species in 66 genera in 10 families occurred in three parks in the George Washington Memorial Parkway – Dyke Marsh Wildlife Preserve (DMWP), Great Falls Park (GFP), and Turkey Run Park (TRP). Adult sawflies flew from early March through mid-November. They included the rarely-collected *Kerita fidala* Ross, a leafminer of *Mertensia virginica* (L.) Pers. ex Link (Boraginaceae) and an unidentified *Caliroa* sp. which consumes *Staphylea trifolia* L. (Staphyleaceae). Nine of the collected species are alien ones in North America. Based on coefficients of community, DMWP was more similar to TRP than GFP, and GFP and TRP were more similar to one another than to DMWP. In DMWP, most species were uncommon in samples. Ninety-five percent of the reported host genera of the collected sawfly species occurred in all three of the parks.

Keywords

Survey, species list, flight periods, abundance

Introduction

Symphyta (sawflies) is a hymenopteran suborder of about 9,000 species in about 1,000 genera in 14 families (Taeger et al. 2010), which occurs in many terrestrial habitats worldwide. Sawfly larvae consume foliage, stems, and wood, and adults consume leaf pubescence, nectar, other insects, water, or a combination of these things, depending on the species (Smith 1979, 1993). Larvae are external leaf feeders, gall-formers, leaf-miners, and stem- and wood-borers of a diverse flora of mosses, ferns, conifers, and herbaceous and woody flowering plants. Most sawfly species are larval specialist feeders of one or a few plant genera, except larval Orussidae which parasitize wood-boring beetles. Some sawfly species can cause significant economic damage to agricultural crops, forests, and ornamental plants. Larvae of these species, either as defoliators, stem borers, or wood borers, can reduce growth of plants, even killing them. In the U.S. mid-Atlantic area, adults fly from March through October, with most species flying in spring and early summer.

Our goal is to ascertain sawfly species identities, flight times, and abundances in three parks within the George Washington Memorial Parkway (GWMP). Our samples are from Townes-style Malaise traps (Townes 1972) and hand-collecting in a rare, tidal, freshwater marsh; a floodplain forest; a swamp; and an upland forest in the Piedmont and Coastal Plain geological provinces – Dyke Marsh Wildlife Preserve (DMWP), Great Falls Park (GFP), and Turkey Run Park (TRP), in Fairfax County, Virginia. Our research questions include (1) which species are present in each park, (2) how similar are the species compositions among parks, (3) what are the species flight periods, and (4) more specifically, what are the species and their abundances in three habitats of DMWP? To our knowledge, this is the second-most comprehensive study of sawflies of a U.S. park administered by the National Park Service. Further, this is the first study of a park that occurs in two geological provinces or has a rare, freshwater, tidal marsh.

Methods

The GWMP comprises 2,984 ha of roads and roadsides, land, and water in the Potomac River Valley on the western side of the river from the Great Falls area south to Mt. Vernon, Virginia and on the eastern side of the river from Glen Echo, MD through Georgetown in Washington, D.C. (Fig. 1). Great Falls Park (323 ha) and TRP (312 ha) are in the northern part of GWMP in the Piedmont Province, and DMWP (154 ha) is in the southern part of GWMP in the Coastal Plain Province. Johnston (2000) described DMWP, and Steury et al. (2008) described the flora of GFP in detail. The GWMP contains many habitats including upland forest; flood-plain forest; swamp forest; freshwater, tidal marsh; mowed areas along its heavily-traveled parkway; and open park areas. This park has a rich biota of perhaps at least 20,000 species of ar-



Figure 1. Locations of sawfly sampling sites. Dyke Marsh Wildlife Preserve, Great Falls Park, and Turkey Run Park within the George Washington Memorial Parkway (GWMP) in Virginia.

chaeans, bacteria, and eukaryans, including over 1,300 vascular-plant species. (Johnston 2000, Steury 2011, Barrows and Kjar 2014, pers. obs.). Further, the GWMP has several undescribed insect species and at least 58 rare, threatened or endangered animals and plants.

We sampled DMWP from April 1998 through December 1999 with six Townesstyle Malaise traps (Townes 1972), two in each of three habitats (open marsh, floodplain forest, and ecotone) as described by Barrows et al. (2005). We sampled GFP and TRP in 2006 through 2009 from mid-March through mid-November with Townes-style Malaise traps, supplemented by hand-collecting. In GFP, we ran one trap in each of three habitats – quarry site, Great Falls Swamp, and in the upland forest by Mine Run. In TRP, we ran one trap in an upland forest and two traps in the floodplain forest near and just upstream from the mouth of Turkey Run. We ran traps long enough each year to obtain entire sawfly seasonal records. In DMWP, we ran traps in the same places in 1998 and 1999. In GFP and TRP, we moved traps within their habitats from year to year to increase the sawfly diversity in our samples and obtained about 72 samples per year for both parks combined. Although Malaise traps obtain biased samples, they are the single best method for collecting and surveying for sawflies. In the mid-Atlantic area, visual searches for sawflies in nature usually do not discover many species.

For DMWP, we extracted all sawflies from samples for quantitative analysis of numbers of adults of each species and their abundances and flight times in the three study habitats. For GFP and TRP, we extracted all sawflies from samples to determine the number of species and their flight times in both of these parks. Over 10,000 specimens were collected during this study. To calculate coefficients of community, we used the formula CC = 2c/(a + b), where c = the number of species that pairs of parks have in common, a = the species richness of park-1, and b = the species richness of park-2 of the comparison.

Voucher specimens are deposited in the GWMP Arthropod Collection at TRP and duplicate material is held in the Georgetown University Arthropod Collection and the National Museum of Natural History, Smithsonian Institution, pending cataloging in the NPS ReDiscovery database and processing of loan agreements.

Results

Species richness

We found a diverse sawfly fauna of 176 species in 66 genera in 10 families in GWMP which consume at least 57 genera of angiosperms, ferns, gymnosperms, and horsetails (Table 1). These sawflies include a rarely-collected species (*Kerita fidala* Ross) recorded as a leafminer of *Mertensia virginica* (L.) Pers. ex Link (Boraginaceae) and an unidentified *Caliroa* sp. which consumes *Staphylea trifolia* L (Staphyleaceae) and is still known only from larvae. Both sawfly species were collected in the floodplain near Turkey Run. The record of *K. fidala* is the first for Virginia (Smith 2009). Nine of the collected species are alien in North America. Ninety-five percent of the reported plant host genera of the sawfly species that we caught occurred in all three of the parks.

We found 69 species in DMWP, 134 in GFP, and 115 in TRP. Twelve species were unique to DMWP, 43 to GFP, and 22 to TRP. Forty species were found in all three parks. Coefficients of Community (CCs) for GWMP ranged from 0.49 through 0.68 (Table 2). Dyke Marsh Wildlife Preserve was more similar to TRP than GFP, and GFP and TRP were more similar to one another than to DMWP.

Table 1. An annotated list of sawfly taxa of GWMP with fight periods based on our samples, parks in which species occurred, known species host plants, and other notes[†].

Xyelidae. Larvae of *Xyela* feed in staminate cones of *Pinus* species (pines). *Xyela* are the first sawflies to fly in a given year in the mid-Atlantic Region, as early as late February, but most fly in March and April, and are found wherever pines occur.

Xyela middledauffi Burdick. TRP. May. Host: Pinus.

Xyela bakeri Konow. GFP. March-April. Host: Pinus.

Xyela minor Norton. GFP, TRP. March-April. Host: Pinus.

Xyela pini Rohwer. DMWP (E, 1), GFP, TRP. March-April. Host: Pinus.

Pamphilidae. Larvae of *Neurotoma* are gregarious and live in webs which they make on their hosts. Larvae of *Onycholyda* and *Pamphilius* are solitary and live and feed in rolled leaf margins.

Neurotoma edwardsi Liston. GFP. May-June. Host: Prunus.

Onycholyda amplecta (Fabricius). GFP. June. Host: Rubus.

Onycholyda excavata (Norton). GFP. May. Host: Cornus.

Onycholyda luteicornis (Norton). GFP. April–May. Host: Rubus.

Onycholyda quebecensis (Provancher). GFP, TRP. May-June.

Onycholyda rufofasciata (Norton). GFP, TRP. May-June.

Pamphilius middlekauffi Shinohara & Smith. TRP. May. Hosts: Corylus, possibly Cornus.

Pamphilius ochreipes (Cresson). DMWP (E, M, 3), GFP, TRP. April-May. Host: Viburnum.

Pamphilius pullatus (Cresson). GFP, TRP. April-May. Host: Viburnum.

Diprionidae. Larvae of all species feed externally on needles of conifers. Species are usually present where conifers grow, but rarely occur in Malaise traps

Monoctenus melliceps (Cresson). GFP (quarry only), a site of many J. virginiana trees. March-April. Host: Juniperus, including J. virginiana L.

Neodiprion sp. TRP. One male netted near the Potomac Heritage Trail along the Potomac River. Males cannot be identified. Host: *Pinus*.

Cimbicidae. Larvae are external feeders.

Abia lonicerae (Linnaeus)[‡]. DMWP (E, 1), GFP, TRP. March–May (most in April). Host: *Lonicera*. This introduced sawfly is now widespread in eastern U.S.

Argidae. Larvae of all species are external leaf feeders, except Schizocerella pilicornis which is a leafminer.

Arge humeralis (Beauvois), poison-ivy sawfly. DMWP (E, 1), GFP, TRP. June–August. Host: Toxicodendron radicans (L.).

Arge macleayi (Leach). GFP. May. Host: Prunus.

Arge scapularis (Klug). TRP (upland forest). June. Host: Ulmus.

Arge smithi Blank, Liston, & Taeger. GFP (quarry only). April-May.

Arge willi Smith. GFP. May. Host: Corylus.

Atomacera debilis Say. DMWP (E, M, 2). May. Host: Desmodium.

Atomacera decepta Rohwer . DMWP (E, M, 58). TRP. May–September. Host: *Hibiscus*. This sawfly is common on some *Hibiscus* cultivars and species known as rose-mallows.

Schizocerella lineata (Rohwer). DMWP (E, M, 9). September. Host: Portulaca. Larvae are external feeders.

Schizocerella pilicornis (Holmgren). DMWP (E, M, 3), TRP. September. Host: Portulaca. Larvae are leafminers.

Sphacophilus cellularis (Say). GFP, TRP. June–July. Hosts: Convolvulus, Ipomoea.

Sterictiphora sericea (Norton). GFP (quarry only). April-May.

Sterictiphora serotina Smith. DMWP (F, 2). April–June. Host: Prunus.

Sterictiphora transversa Smith. GFP (quarry only). April.

Pergidae. The larvae feed gregariously as external leaf feeders on leaf underside.

Acordulecera dorsalis Say. DMWP (E, 1), GFP, TRP. April–June. Hosts: Carya, Castanea, Juglans, Quercus.

Acordulecera mellina MacGillivray. GFP, TRP. May-September. Acordulecera mellina and

Acordulecera pellucida (Konow). GFP, TRP. May–September. Probably several generations a year (Smith and Barrows 1987).

Family Tenthredinidae. This is the largest and most diverse sawfly family in numbers of species, host plants, and habits. Larvae of most species are external leaf feeders, and a few are leafminers and gall formers, as noted below. All six tenthredinid subfamilies occurred in GWMP.

Selandriinae. Genera of this subfamily, except *Dolerus*, consume ferns. *Dolerus* larvae feed on *Carex*, *Equisetum*, and grasses.

Aneugmenus flavipes (Norton). GFP, TRP. May-July. Host: Pteridium, probably other ferns.

Dolerus apricus (Norton). GFP, TRP. April-June. Host: Equisetum.

Dolerus hebes Goulet. DMWP (M, 1), GFP. April-May. Hosts: probably grasses.

Dolerus neoagcistus MacGillivray. GFP, TRP. March-April.

Dolerus nitens Zaddach[‡]. GFP, TRP. March–April. Hosts: grasses. This introduced species is now widespread in North America and can be very common in late winter (early March) and early spring.

Dolerus tibialis Cresson. TRP. May. Host: Equisetum.

Dolerus unicolor (Beauvois). GFP, TRP. March-April. Hosts: grasses.

Dolerus versus Norton. GFP. April–May.

Heptamelus dahlbomi (Thomson)[‡]. GFP, TRP. May, July. Hosts: unknown ferns, possibly *Athyrium* as recorded in Europe. Larvae bore downward in stems.

Strongylogaster impressata Provancher. GFP, TRP. April-May. Hosts: ferns.

Strongylogaster remota Rohwer. GFP (swamp only). April-May.

Thrinax albidopicta (Norton). DMWP (F, M, 2), GFP, TRP. April–September. Hosts: ferns.

Thrinax dubitata (Norton). DMWP (F, 3), GFP, TRP. May–September. Host: Onoclea sensibilis.

Nematinae. A large and diverse subfamily, dominant in arctic and subarctic regions of the world. Nematines are external gall formers, leaf feeders, leafminers, leaf rollers, and petiole miners.

Amauronematus orbitalis Marlatt. DMWP (E, M, 2), GFP. March-April.

Caulocampus acericaulis (MacGillivray). TRP. April. Host: *Acer*. Larvae are petiole miners and can cause premature leaf dropping.

Caulocampus matthewsi Smith. TRP. April-May.

Cladius difformis (Panzer), bristly rose slug. DMWP (E, 8), GFP, TRP. March–October. Host: *Rosa*. This sawfly is common on both wild and cultivated roses and has multiple generations throughout the warm season.

Craterocercus fraternalis (Norton). GFP, TRP. March-April. Host: Quercus.

Craterocercus obtusus (Klug). GFP. March-April. Host: Quercus.

Hemichroa militaris (Cresson). TRP. April. Host: Amelanchier.

Hoplocampa marlatti Rohwer. GFP. April-May. Host: Prunus. Larvae of Hoplocampa spp. feed in the developing fruits of their hosts.

Kerita fidala Ross. TRP. March–April, when its host plant *Mertensia virginica* is flowering along the Potomac River. A leafminer.

Nematus abbotii (Kirby). DMWP (E, M, 8), GFP, TRP. April–June. Host: *Robinia pseudoacacia* L. Larvae occured on this host at the GFP quarry in April. *Nematus abbotii*, has only one generation and occurs only in spring and has black larvae. Adults of *Nematus tibialis* occur throughout most of the warm season, and this species has entirely green larvae which feed on *R. pseudoacacia*.

Nematus attus Smith. GFP. April.

Nematus carpini (Dyar). GFP, TRP. June-September. Host: Carpinus.

Nematus corylus Cresson. GFP, TRP. June-September. Host: Corylus.

Nematus erythrogaster Norton. DMWP (E, M, 7), TRP. April–June. Host: Alnus.

Nematus laticulus Norton. TRP. April. Host: Betula.

Nematus lipovskyi Smith. GFP. April–May. Host: Rhododendron.

Nematus oligospilus (Foerster). DMWP (E, M, 11), TRP. April-June. Host: Salix.

Nematus ostryae (Marlatt). GFP, June. Host: Ostrya.

Nematus tibialis Newman. DMWP (E, F, M, 4), GFP, TRP. April–October. Host: Robinia pseudoacacia. See notes under N. abbotii.

Neopareophora litura (Klug). DMWP (F, 1), GFP, TRP. March-April. Host: Vaccinium.

Pachynematus corniger (Norton). DMWP (E, M, 5), GFP, and TRP. April–September. Host: grasses. A common sp. with continuous generations during the warm season.

Pontania populi Marlatt. DMWP (M, 1). April. Host: Populus. Larvae live and feed in rolled leaf margins.

Priophorus compressicornis (Fabricius). GFP. May-June. Host: Prunus.

Pristiphora abbreviata (Hartig). DMWP (E, M, 2), GFP. April. Host: Malva.

Pristiphora acidovalva Wong. TRP. March-April.

Pristiphora appendiculata (Hartig). GFP. June. Host: Ribes.

Pristiphora banksi Marlatt. DMWP (E, 1), GFP, TRP. May–August. Host: Vaccinium.

Pristiphora chlorea (Norton). DMWP (E, 1), GFP, TRP. March-April. Host: Quercus.

Pristiphora cincta Newman. GFP. April.

Pristiphora micronematica Malaise. DMWP (E, 1). May.

Pristiphora siskiyouensis Marlatt. TRP. June.

Pristiphora sycophanta Walsh. DMWP (E, F, 5). April-June. Host: Salix.

Pristiphora zella Rohwer. DMWP (E, 1), GFP, TRP. May-June.

Pseudodineura parva (Norton). GFP, TRP. April-May. A leafminer. Host: Anemone (formerly Hepatica).

Heterarthrinae, Sluglike larvae of *Caliroa* and *Endelomyia* feed on the undersides of their host leaves. Larvae of other genera are leaf miners.

Caliroa fasciata (Norton). GFP. July-August. Host: Quercus.

Caliroa lobata MacGillivray. GFP, TRP. June-August. Host: Quercus.

Caliroa lunata MacGillivray. TRP. May-September.

Caliroa obsoleta (Norton). GFP, TRP. May-September. Host: Quercus.

Caliroa quercuscoccineae (Dyar). GFP. September. Host: Quercus.

Caliroa sp. TRP, larvae only. July. Host: Staphylea trifolia L.

Endelomyia aethiops (Fabricius), rose slug. GFP, TRP. April-May. Host: Rosa. Common on wild and cultivated roses.

Fenusa pumila Leach, birch leafminer. TRP. April–May. Host: Betula.

Metallus ochreus Smith. DMWP (E, M, 2), GFP (swamp only). September-October.

Metallus rohweri MacGillivray. A leafminer. A leafminer. DMWP (E, 1), GFP, TRP. August–September. Host: *Rubus.*

Nefusa ambigua (Norton). A leafminer. TRP. May. Host: Viola

Profenusa canadensis (Marlatt). GFP. A leafminer. April-May. Host: Crataegus.

Blennocampinae. Larvae of all species are external leaf feeders.

Eupareophora parca (Cresson). DMWP (E, M, 5), GFP, TRP. April-May. Host: Fraxinus.

Eutomostethus ephippium (Panzer)[‡]. GFP, TRP. April-May. Hosts: grasses.

Eutomostethus luteiventris (Klug)[‡]. DMWP (E, M, 2), GFP. April-May. Host: Carex.

Halidamia affinis (Fallén)[‡]. DMWP (E, F, M, 6), GFP, TRP. April-May. Host: Galium.

Monophadnoides conspiculatus MacGillivray. GFP, TRP. March-April.

Monophadnoides pauper (Provancher). GFP. March-April.

Monophadnoides rubi (Harris), raspberry sawfly. DMWP (E, 2), GFP, TRP. April-May. Host: Rubus.

Monophadnus pallescens (Gmelin)[‡]. TRP. April-May. Host: Ranunculus.

Paracharactus niger (Harrington). GFP. April-May.

Paracharactus rudis (Norton). GFP, TRP. April-May. Host: grasses.

Periclista absens Smith. DMWP (E, 1). May. Host: Quercus.

Periclista albicollis (Norton). GFP, TRP. March-May. Host: Quercus.

Periclista bipartita (Cresson). GFP. April-May. Host: Quercus.

Periclista diluta (Cresson). GFP. April-May. Host: Quercus.

Periclista inaequidens (Norton). GFP. March-April. Host: Quercus.

Periclista marginicollis (Norton). GFP, TRP. April-May. Host: Carya.

Periclista subtruncata Dyar. GFP. March-April. Host: Quercus.

Phymatocera fumipennis (Norton). GFP, TRP. May-July. Host: Maianthemum racemosum (L.) Link.

Phymatocera racemosae Smith. GFP, TRP. May-July. Host: Maianthemum racemosum.

Allantinae. Larvae are external leaf feeders.

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Allantus nigritibialis Rohwer. GFP, TRP. March–September. Host: *Rosa.* This species and *Allantus viennensis* can be common on cultivated roses, and they each have spring and fall generations (Smith and Barrows 1987).

Allantus viennensis (Schrank)[‡]. DMWP (E, 1), GFP. May. Host: Rosa.

Ametastegia aperta (Norton). GFP, TRP. April–September. Host: Rumex. Ametastegia aperta and A. articulata have continuous generations throughout the warm season.

Ametastegia articulata (Klug). DMWP (E, M, 11), GFP, TRP. April-September. Host: Rumex.

Ametastegia equiseti (Fallén)[‡]. GRP, TRP. April–September. Host: Rumex. Ametastegia equiseti, A. glabrata, A.

pulchella, and A. pallipes have continuous generations throughout the warm season.

Ametastegia glabrata (Fallén), dock sawfly[‡]. DMWP (M, 1). May. Host: Rumex.

Ametastegia pallipes (Spinola), violet sawfly[‡]. DMWP (E, 1), GFP, TRP. April–September. Host: Viola.

Ametastegia pulchella (Rohwer). GFP, TRP. April–September. Host: Polygonum.

Dimorphopteryx virginica Rohwer. TRP. May–June. Host: *Castanea*. We also found one larva, perhaps of this or another *Dimorphopteryx* sp. in the GFP swamp.

Empria maculata (Norton). DMWP (M, E, F, 20), GFP, TRP. April-May. Hosts: Fragaria, Rubus, Potentilla.

Empria multicolor (Norton). DMWP (F, 1), GFP, TRP. April-May. Host: Alnus.

Macremphytus tarsatus (Say). DMWP (F, 2). August. Host: Cornus.

Macremphytus testaceus (Norton). DMWP (M, E, F, 84), GFP, TRP. April-September. Host: Cornus.

Monostegia abdominalis (F.). DMWP (M, 1). May. Host: Lysimachia.

Monsoma inferentium (Norton). GFP. April. Host: Alnus.

Phrontosoma belfragei (Cresson). DMWP (E, 4). April. Host: possibly Cornus.

Pseudosiobla excavata (Norton). DMWP (M, E, 23), TRP. April-June. Host: Cephalanthus occidentalis L.

Taxonus epicera (Say). DMWP (M, 2), GFP, TRP. March-September.

Taxonus pallidicornis (Norton). DMWP (E, F, 2), GFP, TRP. March, May, September. Host: *Rubus*. This sp. has a large spring generation and a small, late-summer generation.

Taxonus pallipes (Say). GFP, TRP. April–September. Host: Fragaria. This sp. has continuous generations throughout the warm season.

Taxonus rufocinctus (Norton). GFP, TRP. May–June. Host: Rubus. This species has a large spring generation and a small late summer generation.

Taxonus terminalis (Say). DMWP (M, 2), GFP, TRP. May-June. Host: Rubus.

Tenthredininae, Larvae of all species are external leaf feeders.

Aglaostigma semiluteum (Norton). DMWP (E, F, M, 3), GFP, TRP. May-June. Host: Impatiens

Lagium atroviolaceum (Norton). DMWP (E, F, M, 7). GFP. May -July. Host: Sambucus.

Leucopelmonus annulicornis (Harrington). GFP, TRP. April-May.

Macrophya alba MacGillivray. GFP. May-June.

Macrophya albomaculata (Norton). DMWP (F, 1), GFP. June–July. Host: Sambucus canadensis L.

Macrophya bifasciata (Say). GFP. May

Macrophya cassandra Kirby. DMWP (M, 3), TRP. April–May.

Macrophya epinota (Say). GFP. April-May.

Macrophya flavicoxae (Norton). GFP, TRP. May–June.

Macrophya flavolineata (Norton). DMWP (M, 6), GFP, TRP. April -June.

Macrophya flicta MacGillivray. DMWP (F, M, 9), GFP, TRP. April-June.

Macrophya formosa (Klug). DMWP (F, 7), GFP, TRP. May–July.
Macrophya goniphora (Say). DMWP (F, 1), GFP, TRP. May–July.
Macrophya lineatana Rohwer. TRP. June.
Macrophya macgillivrayi Gibson. DMWP (M, 1), GFP, TRP. April–July.
Macrophya masneri Gibson. GFP. April–May.
Macrophya mensa Gibson. DMWP (E, F, M, 8), GFP, TRP. April–July.
Macrophya pannosa (Say). DMWP (E, F, M, 8), GFP, TRP. April–May. Host: Sambucus.
Macrophya phylacida Gibson. GFP, TRP. May–June.
Macrophya pulchella (Klug). GFP, TRP. April–June.
Macrophya senacca Gibson. DMWP (M, 1). April–May.
Macrophya simillima Rohwer. GFP, TRP. April–June.
Macrophya succincta Cresson. GFP. April–May.
Macrophya trisyllaba (Norton). DMWP (F, 29), GFP, TRP. May–July. Host: Sambucus canadensis L.
Macrophya varia (Norton). DMWP (F, 251), GFP. June–July.
Macrophya zoe Kirby. GFP, TRP. April–June.
Tenthredo carolina (Rohwer). TRP. June.
Tenthredo fernowi Goulet & Smith. GFP, TRP. May–June.
Tenthredo fisheri (Rohwer). TRP. May–June.
Tenthredo maculosa (Smulyan). TRP. May-June.
Tenthredo mellicoxa Provancher. GFP, TRP. April–June.
Tenthredo nimbipennis Cresson. GFP. May–June.
Tenthredo rufopectus (Norton). DMWP (F, 14), GFP, TRP. May–July.
Tenthredo verticalis Say. GFP, TRP. May–June.
Tenthredo yuasi MacGillivray. TRP. April–May.
Orussidae. This is the only parasitic symphytan family, and its larvae apparently parasitize wood-boring beetles. Most specimens are from in the GFP swamp where there were many fallen branches and trees probably harboring orussid hosts.
Orussus minutus Middlekauff. GFP. April–June.
Orussus terminalis Newman. GFP. June.
Xiphydriidae. Larvae are wood borers in small, weakened branches.
Xiphydria maculata Say. GFP, TRP. May–June. Host: Acer.
Xiphydria polia Smith. GFP. September
Xiphydria tibialis Say. DMWP (F, 2), GFP, TRP. May–August. Host: Prunus.
Siricidae. Larvae are wood borers.
Tremex columba (Linnaeus), pigeon tremex. DMWP (E, F, M, 5), GFP, TRP. August-September Hosts: Fagus and
some other angiospermous-tree species.
Cephidae. Larvae are stem borers.
Hartigia trimaculata (Say). DMWP (E, M, 3), GFP, TRP. May–June. Hosts: Rosa, Rubus.
Janus himaculatus (Norton), DMWP (E 5), GFP TRP May-June, Host: Vihurnum,

Janus integer (Norton), currant stem girdler. DMWP (F, 2), GFP, TRP. May-June. Host: Ribes.

[†]Taxon arrangement and nomenclature follows Smith (1979) and Taeger et al. (2010). Collection site abbreviations are: DMWP = Dyke Marsh Wildlife Preserve (E = ecotone; F = lowland forest; M = marsh); GFP = Great Falls Park; TRP = Turkey Run Park; and GWMP = George Washington Memorial Parkway which contains DMWP, GFP, and TRP. Dates of collections of adults are given by month for all three parks combined. Numbers listed for DMWP indicate the number of individuals of a taxon for 1998 and 1999 combined. Recorded host(s), if known, are mostly from Smith (1979), and for most sawfly species only host plant genera are cited. [‡]An alien species in North America.

Table 2. Coefficients of community (CC) of sawflies between pairs of three parks of George Washington Memorial Parkway. DMWP = Dyke Marsh Wildlife Preserve; GFP = Great Falls Park; TRP = Turkey Run Park. Sawfly species numbers for each park are within parentheses.



Figure 2. Number of sawfly species versus month in the GWMP, Virginia. Diamonds represent sawfly numbers in DMWP; squares, GFP; triangles, TRP; and circles, all three parks combined.

Flight periods

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As a group, GWMP sawflies flew from early March through mid-November. With regard to species richness and month, more species occurred in April through June than in other months, with species numbers peaking in May in each of the three parks and for all parks combined (Fig. 2). In DMWP, the number of individuals peaked in early June 1998 and early May 1999.

Of the 176 species collected, 138 have a single emergence period in the spring, March through June, indicting a single generation a year. Another 12 species apparently with only a single generation fly only from mid-summer through October, with only 3, both species of *Metallus* and *Tremex*, occurring as late as September and October. The remaining 26 species occur through much of March or April through September and are probably multivoltine. Species of two genera, *Allantus* and *Taxonus* are apparently bivoltine, with a large emergence in the spring and a small emergence in late summer or early autumn.



Figure 3. Sawfly abundances (mean per day per sampling period) varied over their flight periods in 1998 and 1999 in Dyke Marsh Wildlife Preserve, Virginia. Diamonds represent sawfly numbers in the ecotone; squares, forest; triangles, marsh; and circles, all three habitats combined. In 1998, sampling interval A1 was from 12-19 April; A2, 19-28 April; M1, 28 April - 10 May; M2, 10-17 May; M3, 17-28 May; J1, 28 May - 6 June; J1, 6-14 June; J3, 14-24 June; J1, 24 June - 7 July; J2, 7-19 July; 1J3, 19-30 July; A1, 30 July – 9 August; A2, 9–12 August; A3, 12–28 August; S1, 28 August – 11 September; S2, 11–26 September; O1, and 26 September - 11 October. No sawflies were in the samples from 11-26 October and 26 October - 6 November; 6-22 November, 22 November - 6 December, and 6-20 December, which are not shown on this graph. In 1999, sampling interval F1 was from 24 January - 15 February; M1; 15 February - 6 March; M2, 6-20 March; A1, 20 March - 3 April; A2, 3-11 April; A3, 11-25 April; M1, 25 April - 8 May; M2, 8-23 May; J1, 23 May - 6 June; J2, 6-20 June; J1, 20 June - 2 July; J2, 2-18 July; J3, 18–23 July; A1, 23 July – 8 August; A2, 8–15 August; A3, 15–29 August; S1, 29 August – 12 September; S2, 12–26 September; O1, 26 September – 11 October; O2, 11–24 October; 16, N1, 24 October - 8 November; and N2, 8-21 November. There were no sawflies in samples J1, 20 December -3 January; J2; 3-24 January; D1, 21 November - 5 December; and D2, 5-19 December which are not shown on this graph.

Sawfly abundance and distribution in DMWP

Of the 695 sawfly specimens trapped in DMWP 73% were from 1998, and 27% were from 1999. In both years combined, 42% were in the ecotone; 39%, forest; and 19%, marsh (Fig. 3). A plot of frequency of specimens versus species (Fig. 4) indicates that only a few species were present in large numbers; 71% of the 69 species had 9 or fewer individuals in our sample.



Figure 4. Number of species versus number of individuals captured in the DMWP sample. In addition, one species had 58, one had 84, and one had 251 individuals which are not shown on this graph to conserve space.

Discussion

Our GWMP sawfly survey is the second largest survey of a U.S. park administered by the U.S. National Park Service. Smith (2008) reported on the largest such survey in the Great Smoky Mountains National Park.

Species richness

We found 176 sawfly species in the GWMP; however, this biotically-rich location might harbor over 200 species. A similar study of species abundance and diversity in two oak-pine forests in Virginia and West Virginia using Malaise traps estimated that 81% of the actual species present were captured over a five-year period (Braud et al. 2003, Strazanac et al. 2003). We expected to find more diprionid species and species of conifer-feeding siricids. We found three *Acordulecera* species, but more are expected once taxonomic problems are resolved. There are several reasons why we did not find more species in our survey. Malaise traps are biased toward strong flying species such as *Taxonus* and *Macrophya*; species that are weak flyers or stay close to their host plant are not often collected in traps. Some mid-Atlantic species are rare or not expected in GWPM. Immature stages of many species are very difficult to find in nature. Adults of some species tend to be in places such as near their hosts or in treetops where we did not site our traps. More intense sampling in already-sampled habitats and sampling of additional unsampled GWMP habitats could obtain more species. Unsampled GWMP sites include areas in Montgomery Co., Maryland, and the District of Colum-

bia, as well as sites with *Pinus* and *Salix*, the floodplain forest of Theodore Roosevelt Island, the Clara Barton Parkway in Maryland, and the George Washington Memorial Parkway in Virginia, where these roads border and run through the GWMP.

The GWMP sawfly fauna is 50% of the 351 sawfly species recorded for the entire state of Virginia (Smith 2006, 2013). In comparison, Smith and Barrows (1987) found 85 species in samples from less natural Maryland habitats using two sets of Malaise traps 0.8 and 1.5 km from TRP. Seventy percent of these species are also in our samples from the three GWMP parks. There are 91 recorded species for Plummers Island, Maryland, located across the Potomac River from TRP (Smith 2008). In another Virginia Coastal Plain site, D. R. Smith (unpublished) found 175 species in Essex Co. based on 10 years of sampling. In other Virginia Piedmont sites, he found about 200 species in the University of Virginia Blandy Experimental Farm and State Arboretum of Virginia, Clarke Co., based on 6 years of sampling; 175 species in Bull Run Mountains Conservancy, Prince William Co., in 3 years; and 125 species in a his suburban yard in Fairfax Co. in 33 years.

Abundance, distribution, and flight periods

Flight times and numbers of adult sawflies can vary from year to year as occurred in the DMWP samples. Factors including distribution of host plants, adult foods, and mates; drying winds; natural enemies; soil moisture and temperature; and weather affect adult abundances, distributions, and flight periods (Wallace and McNeal 1966), subjects not yet studied in DMWP.

Sawfly abundance and distribution in DMWP

The causes of the sawfly abundance and distribution in DMWP are not yet studied. Our plot of frequency of specimens versus species (Fig. 4) shows that the majority of species were not common in our samples. Smith and Barrows (1987) found a similar relationship in their sample from a less natural area and a yard in the Washington, D.C., area. Low numbers of specimens of many species may have occurred in our sample because of factors such as a species' being rare, rare individual's of more common species straying into our study site from elsewhere, and a species' flight habit precluding our trapping the species. In DMWP, adult sawflies were more common in 1998 than in 1999 based on trap samples, as also occurred in other DMWP insects such as fireflies (Barrows et al. 2008) and mecopterans (Barrows and Flint 2009). In contrast, DMWP rhopalosomatids (Barrows 2013) and sialids (Barrows et al. 2005) were more frequently captured in 1999 than in 1998.

In summary, we found a rich fauna of 176 sawfly species which feed on many plant genera in the GWMP, and as a group, the sawflies flew from early March through November. Sawfly species in DMWP were most common in its ecotone, followed by its

forest and marsh, and these species greatly varied in abundance. In this time of worrisome, rapid global change, threats to the GWMP include air, soil, and water pollution; many alien, invasive species; flooding; and erosion (Litwin et al. 2013, pers. obs.). In fact, DMWP is losing about 0.6–0.8 hectare per year due to erosion. The National Park Service may restore the marsh to some extent in this decade. Increased marshland from restoration could change the mean population sizes of some the DMWP sawfly species. Since Symphyta is a species-rich, GWMP taxon, it is an appropriate one for monitoring GWMP's health in forthcoming years. This large, wasp suborder is an understudied animal taxon, and myriad aspects of the biologies of GWMP and other species are ripe for investigation.

Acknowledgments

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RESEARCH ARTICLE



The Encarsia noyesi species-group (Hymenoptera, Chalcidoidea, Aphelinidae) in the Neotropical region, with a key and description of the male of E. andrewi from Mexico

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Abstract

The *Encarsia noyesi* group species known to occur in the Neotropical region are reviewed. Taxonomic, host and distribution information for these eight species, and a key to females and males are provided. The male of *E. andrewi* (Myartseva and Coronado-Blanco) is described from Mexico. *Aleurodicus dugesii* Cockerell is reported as a new host record for *E. andrewi*.

Keywords

Aphelinidae, Encarsia, Neotropical, noyesi species-group

Introduction

The Aphelinidae is a moderately sized family of the Chalcidoidea with currently about 1350 species in 36 genera (Noyes 2013). The known fauna occurring in Mexico consists of 189 species representing 13 genera (Myartseva et al. 2012, 2013a, 2013b, Kim and Heraty 2012). Many of the species that have been used successfully in classical biological control

projects directed against major diaspidid and aleyrodid pests around the world, have been aphelinids (Greathead 1986, Rosen and DeBach 1990, Arredondo-Bernal et al. 2008).

The genus *Encarsia* Förster consists of about 400 known species (Noyes 2013), and is by far the most diverse group within the subfamily Coccophaginae. Females of nearly all of the species are primary endoparasitoids of Aleyrodidae or Diaspididae. A few species have been recorded from soft scales, hormaphidine aphids, psyllids and eggs of various insect orders. Males are generally known to be hyperparasitoids. In Mexico, 99 species of *Encarsia* are known (Evans 2008, Myartseva et al. 2012, 2013a, 2013b).

Various authors have designated species groups for Encarsia species which share a combination of morphological characters (Viggiani and Mazzone 1979, Hayat 1989, 1998, Heraty and Polaszek 2000, Polaszek et al. 2004, Schmidt and Polaszek 2007). In the last catalog of Encarsia of the world, Heraty et al. (2007) listed 344 species of Encarsia known worldwide of which all but 80 species were placed in one of 30 species-groups. Many species clearly belong to one of these defined groups; however, the placement of some species remains tentative until more information on the world fauna and the degree of interspecific variation in some morphological structures and coloration is known. The genus Encarsia is represented in Mexico by 20 species-groups, including five species in the noyesi group (Myartseva and Evans 2008). The noyesi species-group was established by Schmidt and Polaszek (2007) for a number of species which were formerly placed in the genus Encarsiella Hayat, and appears to be monophyletic. The genus Encarsiella was erected by Hayat (1983) for one described (E. noyesi Hayat) and two undescribed species. Since then, nine new species have been described, including three species from Mexico (Myartseva and Coronado-Blanco 2002, 2004, Myartseva et al. 2013a), and four species that were transferred from other genera to *Encarsiella*. Polaszek and Hayat (1992) provided a key to the species of *Encarsiella*, and diagnoses, illustrations and other data for the species known at that time. Later the genus Encarsiella was synonymized with Encarsia on the basis of molecular and morphological characters (Schmidt and Polaszek 2007). A total of 14 species of the noyesi species-group are currently known and occur in Central, South America, Australasian and Oriental regions. Most of the species are associated with hosts of the whitefly subfamily Aleurodicinae of family Aleyrodidae, which is primarily distributed in the Neotropical region (Schmidt and Polaszek 2007).

Some species of the *Encarsia noyesi* species-group have been studied as natural enemies of whitefly pests and have been used successfully for biological control of whiteflies in Central America. *Encarsia aleurodici* (Girault) and *E. noyesi* (Hayat) have been used against *Aleurodicus cocois* (Curtis) (Cock 1985) and an undescribed *Encarsia* species was introduced into Nevis (Caribbean Islands) for the biological control of *Aleurodicus pulvinatus* (Maskell), a serious pest of coconuts and many ornamental plants, and appears to have become established (Kairo et al. 2001). Currently, *Encarsia noyesi* has been studied as a potential biological control agent of *Aleurodicus dugesii* (Cockerell) in ornamental plants in California, USA (Dreistadt et al. 2001), and also attacks *Aleurodicus rugioperculatus* Martin, a recently introduced invasive whitefly in Florida. The goals of this work are to review the eight species of *Encarsia* that belong to the *Encarsia noyesi* species-group in the Neotropical region, provide taxonomic, biological and distribution data and a key to the females and males of these eight species.

Abbreviations

BMNH The Natural History Museum, Department of Entomology, London, UK.
NRCBC National Reference Centre for Biological Control, Colima, Mexico.
UCRC University of California, Riverside, California, Entomological Museum, USA.
USNM U.S. National Museum of Natural History, Washington D.C., USA.

Results

Encarsia noyesi species-group (Aphelinidae, Coccophaginae)

Diagnosis. Maxillary palp 2-segmented. Pronotum medially narrow and membranous. Antenna 8-segmented in both sexes, female antennal clava with sensory complex, oblique suture between fifth and sixth flagellar segments and the obliquely truncate apical segment. Mid lobe of mesoscutum with more than 30 setae. Axilla large, strongly projecting forwards and separated medially by less than the maximum length of one axilla. Fore wing hyaline or infuscate, with weakly developed stigmal vein, marginal fringe very short. Basitarsus of mid leg with a variable number of robust, spine-like setae.

Encarsia noyesi species-group is the sister group of the *E. smithi* species group, but the latter has 10 or fewer setae on mid lobe of mesoscutum, the apical segment of the antenna is not obliquely truncate, and the first segment of funicle is quadrate to slightly longer than wide, about 0.5 times as long as second segment.

Key to females and males of Neotropical species of Encarsia noyesi group

1	Female2
_	Male9
2	Fore wing infuscate below marginal vein andrewi
_	Fore wing hyaline
3	Scutellum entirely black
_	Scutellum yellow
4	Ovipositor as long as mid tibiaaleurodici
_	Ovipositor 1.3 times as long as mid tibia
5	Gaster orange yellow at base and with yellow tip. Legs white. Fore wing with
	two large setae and 2-4 small setae on submarginal vein magniclava
_	Gaster brownish black. Legs partly brownish. Fore wing with two long setae
	on submarginal vein
6	Base of fore wing with an infuscate area basally. Pedicel entirely pale pithecura
_	Base of fore wing hyaline. Pedicel infuscate partly or entirely dark7
7	Second segment of funicle white, with black apical 1/3–1/2. First segment of
	funicle slightly shorter than pedicel and without sensilla. Ovipositor longer
	than mid tibia. Third valvula 0.7 times as long as second valvifer nayarita

_	Second segment of funicle completely yellow. First segment of funicle about
	as long as pedicel and with sensilla. Ovipositor shorter than mid tibia8
8	Fore wing with a long band bare of setae along anterior margin and with-
	out asetose area below stigmal vein. Second segment of funicle somewhat
	longer than first and third segments. Mid tibial spur 0.9 times as long as
	basitarsus noyesi
_	Fore wing without a long band bare of setae along anterior margin and with
	asetose area below stigmal vein. Second and third segments of funicle sub-
	equal in length and shorter than first segment. Mid tibial spur 0.7 times as
	long as basitarsusnarroi
9	Pedicel globular, as long as wide10
_	Pedicel longer than wide
10	Flagellum unicolored, yellow. Scutellum yellowish medially andrewi
_	Flagellum bicolored, with some dark segments. Scutellum completely dark
	brown
11	Club longer than two preceding funicular segments combined. Mid lobe of
	mesoscutum with strong imbricate/reticulate sculpturealeurodici
_	Club as long as two preceding funicular segments combined. Mid lobe of
	mesoscutum with elongate/reticulate sculpture tamaulipeca

Review of Neotropical species of the Encarsia noyesi group

Encarsia aleurodici (Girault, 1916)

Coccophagus aleurodici Girault, 1916: 401. Syntype females and male. Trinidad: British West Indies, xii.1914, F. W. Urich, ex. Aleurodicus on Theobroma bicolor, in USNM. Prospaltella aleurodici (Girault); Compere 1931: 11.
Dirphys aleurodici (Girault); Hayat 1989: 59.
Encarsiella aleurodici (Girault); Viggiani 1986: 59.
Encarsia aleurodici (Girault); Schmidt and Polaszek 2007: 81.

Diagnosis. This species was redescribed by Viggiani (1986) and Polaszek and Hayat (1992). Female: body entirely dark brown. Fore wing hyaline. Legs dark brown except as follow: distal half of femur and tibia of fore leg, distal half of tibia of mid leg pale, hind tibia brown-yellow, all tarsi pale. Antennal (Fig. 1) radicle, pedicel, first segment of funicle and club dark brown, scape light yellow with brown dorsal margin of distal half, second segment pale brown, third segment yellow. Third valvula pale yellow. Mouth fossa narrower than width of frontovertex at front ocellus. Mid lobe of mesoscutum, scutellum and axillae with strong imbricate/reticulate sculpture. Ovipositor about as long as mid tibia. Male with pedicel of antenna (Fig. 2) longer than wide and slightly shorter than first funicle segment.


Figures 1–6. Antennae of *Encarsia* spp.: 1 *aleurodici*, female 2 male 3 *andrewi*, female 4 male 5 *magniclava*, female 6 *narroi*, female.

Distribution. Bahamas, Barbados, Bermuda, Brazil, Costa Rica, Ecuador, Trinidad and Tobago (Noyes 2013).

Hosts. Aleurodicus sp., A. capiangae Bondar, A. cocois (Curtis), A. dispersus Russell.

Comments. Notes on the biology of *A. capiangae* (host selection, oviposition) were published by Mound (1961). In 1966, this parasitoid was introduced into Brazil from Trinidad against *Aleurodicus cocois* (Carvalho et al. 1971).

Encarsia andrewi Myartseva & Coronado-Blanco, 2008

- *Encarsiella polaszeki* Myartseva & Coronado-Blanco, 2004: 229. Holotype female. Mexico: Tamaulipas, Jaumave, 30.IV.2000, S. Myartseva, ex. Aleurodicinae, in UCRC.
- *Encarsia polaszeki* (Myartseva & Coronado-Blanco, 2004); Schmidt and Polaszek 2007: 81.
- *Encarsia andrewi* Myartseva & Coronado-Blanco, 2008: 67, previous name preoccupied by *Encarsia polaszeki* Evans, 1997.

Diagnosis. Female: head yellow, frontovertex orange. Antenna (Fig. 3) yellow, first and second segments of club brown, pedicel and first segment of funicle infuscate. Meso-soma yellow, pronotum, mid lobe of mesoscutum and axillae dark orange or fuscous. Legs light yellow. Fore wings infuscate below marginal vein. Gaster dark brown, third valvula light yellow. Eye more than 1.5 times as long as cheek. Antennal scape 4.0–4.2 times as long as wide, pedicel 1.7 times as long as wide, segments of funicle about twice as long as wide each, club slightly shorter than funicle. All flagellar segments with longitudinal sensilla. Fore wing twice as long as wide. Mid tibial spur 0.8 times as long as basitarsus. Ovipositor exserted, 1.2 times as long as mid tibia, third valvula 0.7 times as long as second valvifer.

Male (first description). Length of body: 0.7 mm. Head coloration as in female, antenna uniformly dark yellow with sensilla brown. Mesosoma dark brown, side lobes yellow with dark spot apically, scutellum light brown laterally and yellow medially. Fore wing hyaline. Legs yellow; hind coxa, femur and base of tibia infuscate. Gaster brownish black. Eye 1.6 times as long as cheek. Antennal scape 4.0 times as long as wide, pedicel very slightly longer than wide (15:13). First segment of funicle slightly shorter than second segment (6:7) and about 3 times as long as wide; second to sixth segments about 4 times as long as wide each. Club not expressed (Fig. 4). All flagellar segments with 4 linear sensilla each. Fore wing 2.4–2.7 times as long as wide, base with 4 setae, marginal vein with 8–9 setae along anterior margin. Hind wing 8.0 times as long as maximum width of wing, its marginal fringe 0.8 times as long as wide. Genitalia 0.8 times as long as mid tibia.

Material. Mexico: Tamaulipas, Altamira, ex *Aleurodicus dugesii* Cockerell on epiphyte plant *Struthanthus* sp. (Loranthaceae) on unknown tree, 4 males, 23.V.2013 (coll. E. Ruíz-Cancino).

Distribution. Mexico (Querétaro, Tamaulipas).

Hosts. Aleurodicinae unspecified sp. (possibly *Aleurodicus* sp.), *Aleurodicus dugesii* Cockerell. First record of epiphyte plant *Struthanthus* sp. as host for *A. dugesii*.

Comments. A new name *Encarsia andrewi* nom. nov. was proposed by Myartseva et al. (2008) for *E. polaszeki* (Myartseva and Coronado-Blanco 2004), which was pre-occupied by *E. polaszeki* Evans, 1997, a species described from Brazil.

Encarsia magniclava (Girault, 1915)

Coccophagus magniclavus Girault, 1915: 33. Syntype females. British Guiana (=Guyana): Berbice, Demarara, iii.1993, G. E. Bodkin, ex. Aleurochiton sp., in USNM.
Prospaltella magniclava (Girault); Compere 1931: 31.
Encarsiella magniclava (Girault); Viggiani 1986: 66.
Dirphys magniclavus (Girault); Hayat 1989: 288.
Encarsia magniclava (Girault); Schmidt and Polaszek 2007: 81.

Diagnosis. This species was briefly redescribed by Viggiani (1986); Polaszek and Hayat (1992) provided a more complete redescription of the species. Female: body deep orange yellow, the following parts black: head around occiput, pronotum, antennal club, apex of axillae, suture along apical margin of scutellum. Gaster orange yellow at base and black dorsally. Legs white. Fore wing hyaline. Third valvula yellow. Antennal (Fig. 5) pedicel very slightly longer than wide; first and second segments of funicle subequal in length, each 2.4 times as long as wide and 1.5 times as long as pedicel; third segment as long as pedicel. Segments of club wider than long. Fore wing with two large setae and 2–4 smaller setae on submarginal vein, marginal vein with 14-16 setae along anterior margin. Ovipositor about as long as mid tibia. Male: unknown.

Distribution. Guyana, Panama (Noyes 2013). **Hosts.** *Aleurochiton* sp., *Eudialeurodicus bodkini* Quaintance & Baker (Noyes 2013).

Encarsia narroi Gómez & García, 2000

Encarsia narroi Gómez & García, 2000: 49. Holotype female. Mexico: Parras, Coahuila, 1500 masl, 11.ii.1995, Gómez and García, ex. *Aleurodicus* sp., on *Bauhinia variegata*, in NRCBC; Schmidt and Polaszek 2007: 81.

Encarsiella narroi (Gómez & García); Myartseva and Coronado-Blanco 2004: 624.

Diagnosis. Female: body brown, scutellum pale yellow, antennal funicle and legs pale yellow, hind femora infuscate. Pedicel subequal in length to first segment of funicle (Fig. 6). Fore wing hyaline, with small asetose area below stigmal vein, about 2.3 times as long as wide, with 10 basal group setae. Mid tibial spur 0.7 times as long as basitarsus. Male: unknown.

Distribution. Mexico (Coahuila).

Hosts. Aleurodicus sp.

Encarsia nayarita Myartseva, 2013

Encarsia nayarita Myartseva, 2013b: 646–649. Holotype female. Mexico: Nayarit, Jalisco, Universidad Autonoma de Nayarit, 18.IX.2012, S. Myartseva, ex. *Aleurodicus coccolobae* on *Myrtus communis*, in UCRC.

Diagnosis. Female: head yellow, face and orbits of eyes white, in living female pearlish-bluish-white, occiput black. Antenna white, scape and pedicel dorsally black, first segment of funicle completely, third to half of second segment black, upper part of third segment slightly infuscate. Club, excluding whitish base and third segment, black. Mesosoma black, scutellum light yellow, in living female pearlishbluish-white, side lobes light yellow, with dark spot on apical part. Fore wing hyaline. Legs white, basal part of mid coxae, hind coxae and half basal part of femora dorsally black. Gaster black, third valvula white. Eye slightly longer than cheek. Mandible 3-dentate. Antennal scape (Fig. 7) 4.6 times as long as wide, pedicel 1.8 times as long as wide. First segment of funicle 0.6 times as long as second segment and 1.7 times as long as wide; second segment 2.5 times as long as wide; third segment twice as long as wide. First segment of funicle without sensilla. Sculpture of mesoscutum longitudinally reticulate. Fore wing twice as long as wide, its base with 10-14 short setae. Mid tibial spur slightly longer than basitarsus. Ovipositor exserted, 1.1 times as long as mid tibia, third valvula 0.7 times as long as second valvifer. Male: unknown.

Distribution. Mexico (Nayarit). **Hosts.** *Aleurodicus coccolobae* Quaintance & Baker.

Encarsia noyesi (Hayat, 1983)

Encarsiella noyesi Hayat, 1983: 85. Holotype female. Trinidad: St. George, St. Augustine, xi.1976, F. D. Bennett, in BMNH; Polaszek and Hayat 1992: 195; Myartseva and Coronado 2002: 623.

Dirphys noyesi (Hayat); Hayat 1989: 7.

Encarsia noyesi (Hayat); Schmidt and Polaszek 2007: 81.

Diagnosis. Female: head with frontovertex orange, face pale, occiput brownish. Antenna (Fig. 8) with second and third segments of funicle yellow, club dark brown. Body brownish-black, scutellum pale yellow, in living female pearlish-bluish-white. Legs pale yellow, mid and hind coxae and hind femora infuscate. Third valvula pale, with black apices. Fore wing hyaline, with a long bare band along wing margin, 8–10 basal group setae, 9 setae on marginal vein. Mid tibial spur 0.9 times as long as basitarsus. Ovipositor as long as mid tibia, third valvula 0.6 times as long as second valvifer. Male similar to female, except for darker coloration and structure of antenna (Fig. 9) and genitalia.



Figures 7–12. Antennae of *Encarsia* spp.: 7 *nayarita*, female 8 *noyesi*, female 9 male 10 *pithecura*, female 11 *tamaulipeca*, female 12 male.

Distribution. Anguilla, Antigua, Barbados, Bermuda, Costa Rica, Grenada, Mexico, Peru, St. Vincent and Grenadines, Trinidad and Tobago, USA (California, Florida) (Noyes 2013). In Mexico, this species has been found in Jalisco, San Luis Potosí, Tamaulipas, Yucatán (Myartseva and Evans 2008).

Hosts. Aleurodicus chirripoensis Martin, A. cocois, A. dispersus, A. dugesii Cockerell, A. maritimus Hempel, A. rugioperculatus Martin, and Aleurothrixus floccosus (Maskell). It has been reported from Nipaecoccus aurilanatus (Maskell), Puto barberi (Cockerell) (Pseudococcidae), probably as a hyperparasitoid (Noyes 2013).

Comments. *Encarsia noyesi* has been used to control *Aleurodicus dugesii* in Florida (Nguyen and Hamon 2002) and also attacks *Aleurodicus rugioperculatus*, a newly introduced, invasive whitefly in Florida (Taravati et al. 2013), and *A. chirripoensis*, new pest of banana in Costa Rica (Sánchez and Laprade 2013).

Encarsia pithecura (Polaszek, 1999)

Encarsiella pithecura Polaszek, in Martin and Polaszek 1999: 1557-1558. Holotype female. Belize: Cayo District, Chiquibul Forest Reserve, Las Cuevas-Monkey Tail trail, 5.iii.1996, J.H. Martin, ex. *Azuraleurodicus pentarthus*, in BMNH; Myartseva and Coronado-Blanco 2002: 624.

Encarsia pithecura (Polaszek, 1999); Schmidt and Polaszek 2007: 81.

Diagnosis. Female: head and body largely brownish-black. Antennal scape, pedicel and third segment of funicle pale, first, fourth to sixth segments brown, second segment pale brown; face, scrobes and clypeus pale. Mesosoma and gaster brownish black, scutellum, tip of seventh tergite and third valvula entirely pale. Legs pale yellow/brown except all coxae and hind femora brown. Fore wing hyaline, except for a small circular patch basally, faintly infuscate. Antennal scape (Fig. 10) very slightly expanded, about 2.5 times as long as pedicel. First segment of funicle shorter than pedicel and without sensilla; fifth and sixth segments partly fused, claval sensorial complex developed, the oblique suture dividing these segments absent on part of the ventral surface. Fore wing with 6-8 setae in basal cell. Ovipositor slightly shorter than mid tibia, second valvifer 2.5 times as long as third valvula. Male: unknown.

Distribution. Belize.

Hosts. Azuraleurodicus pentarthus Martin (Martin and Polaszek 1999).

Encarsia tamaulipeca (Myartseva & Coronado-Blanco, 2002)

- *Encarsiella tamaulipeca* Myartseva & Coronado-Blanco, 2002: 621. Holotype female. Mexico: Tamaulipas, Ciudad Victoria, 7-8.xii.1995, S. Myartseva, ex. Aleyrodidae on *Psidium guajava*, in USNM.
- *Encarsia tamaulipeca* (Myartseva & Coronado-Blanco, 2002); Schmidt and Polaszek 2007: 81.

Diagnosis. Female: head black, face ferrugineous from anterior ocellus to interantennal prominence and whitish below (except upper margin of mouth, hind part of cheeks and

antennal scrobes). Pedicel and club brown, scape (except distal half dorsally) and third funicular segment whitish, first and second segments pale brown. Mesosoma and gaster black. Fore wings hyaline. Legs yellowish-white, mid and hind coxae, hind femora black, mid femora and hind tibiae infuscate. Third valvula whitish. Eye 2 times as long as cheek. Antennal scape (Fig. 11) 4 times as long as wide; pedicel 1.7 times as long as wide and slightly longer than first segment of funicle; first to third segments of funicle 1.5, 1.8 and 1.3 times as long as wide, respectively. Club slightly longer than funicle. First segment of funicle without sensilla. Fore wing more than twice as long as wide, its base with 7-10 setae, marginal fringe very short. Hind wing more than 4.5 times as long as wide. Mid tibial spur slightly shorter than basitarsus. Ovipositor exserted, longer than mid tibia (14:11), third valvula 0.5 times as long as second valvifer. Male differs by head and body more dark coloration, and structure of antenna (Fig. 12) and genitalia.

Distribution. Mexico (Tamaulipas).

Hosts. Aleurodicinae unspecified sp. (possibly Aleurodicus sp.).

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RESEARCH ARTICLE



Description of two new Chinese Subancistrocerus de Saussure (Hymenoptera, Vespidae, Eumeninae), with a key to the Chinese species

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Abstract

Two new species from Yunnan, China are described and illustrated, namely *Subancistrocerus compressus* and *Subancistrocerus jinghongensis*. In addition, *S. camicrus* (Cameron) and *S. sichelii* (de Saussure) are newly recorded from China. A key to the Chinese species of *Subancistrocerus* is provided. Type specimens of the new species are deposited in Chongqing Normal University and Yunnan Agricultural University.

Keywords

Hymenoptera, Vespidae, Eumeninae, Subancistrocerus, new species, China

Introduction

De Saussure (1855) provided the name *Subancistrocerus* for his division I of the subgenus *Ancistrocerus* Wesmael of the genus *Odynerus* Latreille. This genus contains 29 species with three subspecies, and is mainly distributed in the Oriental Region (Giordani Soika 1994; Gusenleitner 2000; Kumar 2013). The Ethiopian Region has five species with one subspecies, and there are two in the Australian Region (Giordani Soika 1961, 1993; Carpenter et al. 2010). In addition, two species occur in more than one Region (Giordani Soika 1994; Madl et al. 1996; Giordani Soika and Kojima 1988). Only *S. kankauensis* (von Schulthess) was recorded from China so far (Schulthess 1934; Giordani Soika 1994). In our study of the eumenine wasps of China, five species of *Subancistrocerus* have been collected and recognized, of which two are new to science and two are newly recorded from China. In the present paper, the two new species are described and illustrated in detail, and a key to the Chinese species of *Subancistrocerus* is provided. In addition, we also provide the taxonomic information and global distributions for these five species. The key and distributions were produced based on both the examination of specimens and the information extracted from the literature.

Materials and methods

The specimens examined are deposited in the Institute of Entomology and Molecular Biology, Chongqing Normal University, Chongqing, China (CQNU) and Department of Entomology, College of Plant Protection, Yunnan Agricultural University, Kunming (YNAU), respectively. Descriptions and measurements were made under a stereomicroscope (Nikon SMZ1500), and all figures were taken with a stereomicroscope (LEICA EZ4HD) attached to a computer using Leica Application Suite version 2.1.0 software. The ratios used throughout the descriptions were measured in the same amplifying multiple of stereomicroscope. All measurements were taken as the maximal length of body parts measured. Body length was measured from the anterior margin of the head to the posterior margin of metasomal tergum 2. For the density description of punctures, "sparsely" means that the interspaces are larger than one puncture diameter, "moderately" means equal to the diameter, and "densely" means less than one diameter. The abbreviations used in the text are as follows: A1 for antennal segment 1, A2 for antennal segment 2, T1 for metasomal tergum 1, T2 for metasomal tergum 2, S1 for metasomal sternum 1, S2 for metasomal sternum 2, and so on. Terminology principally follows Carpenter (1982) and Carpenter and Cumming (1985).

Taxonomy

Subancistrocerus de Saussure, 1855

Subancistrocerus de Saussure, 1855: 206; Bequaert 1925: 61; Carpenter 1986: 83–85; van der Vecht and Carpenter 1990: 56; Giordani Soika 1994: 4,11–48.

Type species. Odynerus sichelii de Saussure, 1855, by subsequent designation of Bequaert 1925.

Diagnosis. This genus is related to some of *Pseudonortonia* Giordani Soika, with which it shares metasomal tergum 1 with two transverse carinae. However, *Subancis*-

trocerus differs from *Pseudonortonia* in haveing tergum 1 wider than long in dorsal view and both transverse carinae close to each other at the crest of the declivity (Carpenter et al. 2009).

Distribution. China (Sichuan, Chongqing, Yunnan, Taiwan); Oriental, Ethiopian and Australian Regions.

Subancistrocerus compressus Li & Chen, sp. n.

http://zoobank.org/F0649BD5-4E1F-4700-9015-7720E0ADA8B5 Figs 1–11

Material examined. Holotype, ♀, China, Yunnan Province, Xishuangbanna State, Jinghong City, Ancient Forest Park, 22°01'49.76"N, 100°52'25.27"E, 758 m, 31.VII.2003, Zhenshan Geng, No. 1004039 (CQNU). Paratypes: 3 ♂♂, same data as holotype, Nos. 1004040, 1004041, 1004042 (CQNU); 1 ♂, China, Yunnan Province, Xishuangbanna State, Mengla County, Shangyong Town, Longmen Village, 21°16'50.65"N, 101°32'19.44"E, 922.03m, 9. V. 2008, Fangzhou Ma, No. 1004043 (CQNU).

Description. Female (Figs 1, 3): body length 5.0 mm, forewing length 5.5 mm. Black, with the following parts yellow: apex of ocular sinus, postocular spot, interantennal spot, scape ventrally, clypeus except medial dark brown spot (Fig. 3), contiguous triangular pronotal spots, parategula, nearly coterminous spots of metanotum, and apical bands of T1 and T2; antennae ventrally except scape yellow to brown; mandible basally white and apically dark ferruginous; tegula and tibiae outside brownish yellow; apical margin of fore femur to apex of tarsi largely brown, and other parts of legs dark brown.

Head. Frons densely punctate and reticulate; clypeus with silvery setae, sparsely punctate and medially with longitudinal depression, length of clypeus: width = 29:34, clypeal margin emarginate, laterally angulate, and apical width: depth of emargination = 1:0.1; length of A3: width = 4:3, length of A4 equal to width, length of A5: width = 6:7.

Mesosoma. Length of mesosoma: width = 19:12; pronotal carina somewhat rounded laterally; pronotum, scutum, scutellum and mesopleuron except posteriorly densely punctate, the punctures obviously larger and deeper than those on head; punctures on metanotum sparser than those on other parts of thorax, left and right parts of metanotum contiguously tiled, metapleuron impunctate and somewhat coriaceous; propodeum coarse, with lateral carina and densely reticulate ridges, side somewhat coriaceous.

Metasoma. Width of T1: length = 7.1:5.0, T1 and T2 densely punctate, S1 impunctate and coriaceous, punctures on S2 sparser than those on T1, T2 subapically somewhat depressed, T1, T2 and S2 with lamellate apical margin, respectively.

Male. Body length 5.0 mm, forewing length 6.0 mm. Sculpture, punctuation, setae, and coloration similar to those of female except as follows: clypeus entirely whitish yellow (Figs 3–4); mandible largely whitish yellow; spots on pronotum and metanotum smaller and separated (Fig. 2); mid tarsomere 1 and hind tarsomere 1 whitish yellow,



Figures 1–11. Subancistrocerus compressus sp. n. I habitus of holotype (dorsal view), \bigcirc 2 habitus of one paratype (dorsal view), \bigcirc 3 clypeus, \bigcirc 4 clypeus, \bigcirc 5 antennae (lateral view), \bigcirc 6 antennae (ventral view), \bigcirc 7 fore tarsus (lateral view), \bigcirc 8 fore tarsus (dorsal view), \bigcirc 9 fore femur (ventral view), \bigcirc 10 fore femur (lateral view), \bigcirc 11 mid tarsomere 1, \bigcirc . Scale bar for 1–10 = 1.0 mm; for 11 = 0.1 mm.

remaining tarsi ferruginous, mid tibia and base of hind tibia with one long whitish yellow elliptic spot, respectively; clypeus medially convex and without depression, length equal to width; length of A4: width = 5:4, length of A5: width = 8:9, A4–A9 laterally with carina-like prominences and ventrally without concavities, A11–A12 ventrally concave, length of A11: width = 17:15, A13 broad, foliaceous, its apex rounded and reaching the basis of A11 and not covering A10 (Figs 5–6), length of A13: width = 18:11; punctures on frons deeper than those in female; metanotum narrower than that in female; fore femur basally with anteroventral compression (Figs 9–10); fore tarsomere 1 longer than the following segments together (Figs 7–8); mid fore tarsomere 1 curved downward (Fig. 11); width of T1: length = 7.6:5.5, S1 basally depressed, apical depression of T2 less obvious than in female.

Recognition. The species resembles *S. indochinensis* Gusenleitner, 2000 from Laos in having male A4–A9 ventrally without concavities, A13 broad, foliaceous and not covering A10 (Figs 5–6). It differs from *S. indochinensis* and all other members of the genus by the following character combination: the male fore femur basally with an anteroventral compression (Figs 9–10), fore tarsomere 1 longer than the following segments together, not curved or arched (Figs 7–8), and the mid tarsomere 1 curved (Fig. 11).

Distribution. China (Yunnan).

Etymology. The specific name is derived from the Latin word: *compressus* (compressed), with reference to the male fore femur with an anteroventral compression basally.

Subancistrocerus jinghongensis Li & Chen, sp. n.

http://zoobank.org/00005ACB-87EC-47A2-A34B-E56411D1997B Figs 12–19

Material examined. Holotype, ♀, China, Yunnan Province, Xishuangbanna State, Jinghong City, Ancient Forest Park, 22°01'49.76"N, 100°52'25.27"E, 758 m, 31.VII.2003, Qian Jiang, No. 1004044 (CQNU). Paratype: 1 ♂, same data as holotype, No. 1004045 (CQNU).

Description. Female (Figs 12, 17): body length 6.0 mm, forewing length 5.5.0 mm. Body black; with the following parts whitish yellow to yellow: apex of ocular sinus, interantennal spot, postocular spot, scape ventrally, clypeus except medial spot and apical margin, contiguous triangular pronotal spots, parategula, spots on metanotum, apex of fore femur and fore tibia outside, spots of apex of mid femur and tibia outside, and apical bands of T1, T2 and S2; antennae ventrally except scape yellow to brown; apical margin and medial spot of clypeus dark brown; mandible basally white yellow and apically ferruginous to dark brown; tegula brownish yellow; fore tibia inside to tarsal apex largely ferruginous, and other tarsi brownish yellow to brown; other parts of mid leg dark brown.

Head. Frons densely punctate and reticulate; clypeus sparsely punctate and setose, medially with wide longitudinal spade-formed depression, and clypeal margin bluntly angulate (Fig. 17), length of clypeus: width = 32:35, apical width: depth of emargination = 1:0.1, clypeal margin laterally angulate (Fig. 17), antennae lacking.

Mesosoma. Length: width = 25:16; pronotal carina laterally somewhat rounded; pronotum, scutum, scutellum and mesopleuron except posteriorly densely punctate, punctures obviously larger and deeper than those on head, interspaces with ridges; punctures on metanotum sparser than those above, left and right parts of metanotum uncomtoguously tiled (Fig. 12); metapleuron impunctate and somewhat rugose; propodeum coarse, with lateral carina and densely reticulate ridges, side somewhat coriaceous.



Figures 12–19. *Subancistrocerus jinghongensis* sp. n. **12** habitus of holotype (dorsal view), \bigcirc **13** habitus of paratype (dorsal view), \bigcirc **14** antennae (ventral view), \bigcirc **15** antennae (lateral view), \bigcirc **16** clypeus, \bigcirc **17** clypeus, \bigcirc **18** fore tarsus (dorsal view), \bigcirc **19** mid tarsomere 1, \bigcirc . Scale bar for **10–18** = 1.0 mm; for **19** = 0.1 mm.

Metasoma. Width of T1: length = 6.3:4.5, T1 and T2 densely punctate, S1 impunctate and coriaceous; punctures on S2 sparser than those on T1 and T2; T1, T2 and S2 with thin lamellate apical margin, respectively, in front view, the lamellate apical margin invisible, T2 subapically somewhat depressed.

Male (Figs 13–16, 18–19). Body length 5.5 mm, forewing length 5.5.0 mm. Sculpture, punctuation, setae, and coloration as in female except as follows: clypeus entirely whitish yellow (Fig. 16); parategula brownish yellow; two spots on metanotum smaller than those in female; fore and mid tarsomere I with long whitish spot, respectively (Figs 18–19), other parts of mid leg dark ferruginous; clypeus medially somewhat convex and without depression, length: width=15:13 (Fig. 16); length of A4: width = 6:7, length of A5: width = 7:8, A4–A9 outside with prominent carina, respectively, A10 apically to A12 ventrally concave, length of A11: width = 19:17, A13 foliaceous, from base to apex gradually narrowing and its apex reaching the base of A10 (Figs 14–15), length of A13: width = 2:1; transverse ridges on metapleuron and side of propodeum more obvious and denser than those in female; metanotum narrower than that in female (Fig. 13); fore femur normal, fore tarsomere 1 arched, and almost equal to the following segments together (Fig. 18); mid tarsomere 1 curved and short, much shorter than the following segments together (Fig. 19); width of T1: length = 6.4:4.3, S1 normal; T2 medially somewhat convex, its apical margin normal, with a regular series of big punctures, not reflected, and its apex more depressed than that in female.

Recognition. The species is similar to *S. reflexus* Giordani Soika, 1994 from Philippines in mid tarsomere 1 in male curved and short, much shorter than the following segments together (Fig. 19), and A13 foliaceous, gradually narrowing from base to apex, and its apex reaching the base of A10 (Figs 14–15). It differs from that species and all other members of the genus by the following character combination: apical margin of T2 normal, not reflected; fore tarsomere 1 arched, and almost equal to the following segments together (Fig. 18); and body length obviously smaller than in *reflexus*.

Distribution. China (Yunnan).

Etymology. The specific name is the Latined adjective *jinghongensis*, with reference to the region from which the type–specimens were collected.

Subancistrocerus camicrus (Cameron, 1904), new record

Odynerus camicrus Cameron, 1904: 259.

Ancistrocerus camicrus (Cameron): Giordani Soika 1941: 241, fig. 20.

Subancistrocerus camicrus(Cameron): Gusenleitner 1988: 178; Giordani Soika 1994: 14 (key), 46, Figs 10, 19; Gusenleitner 2006: 689.

Subancistrocerus obscuripennis Gusenleitner, 1987: 263, fig. 6; 1988: 178.

Material examined. 2 \Im , China, Sichuan Province, Liangshan State, Minsheng Town, 5. VIII. 2011, Tingjing Li; 3 \Im , China, Sichuan Prov., Liangshan State, Xide County, Hongmo Town, 4.VIII. 2011, Tingjing Li & Yuan Bai; 1 \bigcirc , China, Chongqing, Beibei County, Jinyun Mountain, 20.V. 2006, Yin Li; 1 \Im , China, Yunnan Province, Wenshan State, Qiubei County, Chalukou, 3. V. 2004, Peng Wang; 1 \bigcirc , China, Yunnan, Zhaotong State, Yongshan County, Huanghua Town, 16. IX. 2005, Hesheng Wang; 1 \bigcirc , China, Yunnan Province, Xishuangbanna State, Jinghong City, Mengyang Town, Mansahao, 28. VII.2011, Xin Zhou; 1 \bigcirc 2 \Im , China, Yunnan Province, Xishuangbanna State, Jinghong City, Ancient Forest Park, 31.VII.2003, Tingjing Li & Qian Jiang; 1 \bigcirc , China, Yunnan Province, Lincang State, Linxiang County, Fengxiang Town, 5. X. 2004, Kai Wu.

Distribution. China (Sichuan, Chongqing, Yunnan); India; Nepal; Thailand; Burma; Laos; Malaysia.

Subancistrocerus kankauensis (von Schulthess, 1934)

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Odynerus kankauensis von Schulthess, 1934: 69.
Nortonia kankauensis(von Schulthess): Iwata 1939: 71–72 (ethology).
Ancistrocerus kankauensis (von Schulthess): Giordani Soika 1941: 241.
Subancistrocerus kankauensis(von Schulthess): Giordani Soika 1981: 170, Figs 3–4; 1994: 14 (key), 44, Figs 7, 16.

Material examined. $2 \Leftrightarrow \diamondsuit$, China, Jiangxi Province, Xingangshan Site A, 1171-216 m, 25.V.2013, Michael Staab.

Distribution. China (Jiangxi, Taiwan).

Subancistrocerus sichelii (de Saussure, 1855), new record

Odynerus sichelii de Saussure, 1855: 206, pl. X fig. 6; Dalla Torre 1894: 96 (catalog); Bingham 1897: 361 (key), 363; Rothney 1903: 107; Dover 1925: 299; Dusmet 1930: 104.
Odynerus intendens Walker, 1860: 304; Dalla Torre 1894: 449; Bingham 1897: 363 (key), 373; Dover 1925: 299; Giordani Soika 1941: 243.

Ancistrocerus intendens (Walker): 304; Motschoulsky 1863: 23 (catalog).

Ancistrocerus sichelii (de Saussure): Giordani Soika 1941: 242.

Subancistrocerus sichelii (de Saussure): Iwata 1965: 105; van der Vecht 1967: 31, 33; Gusenleitner 1987: 263, fig. 7; 1988: 177; Giordani Soika 1994: 13 (key), 33, Figs 4, 13; Madl et al. 1996: 831; Gusenleitner 2006: 689; Gusenleitner and Madl 2009: 468.

Subancistrocerus tristis Giordani Soika, 1991: 41, 50; Gusenleitner and Madl 2009: 468.

Material examined. 2 ♀♀ 1 ♂, China, Sichuan Province, Panzhihua State, Miyi County, Baima Town, 30. VII. 2011, Tingjing Li & Zhenhu Wu; 1 ♀, China, Yunnan Province, Dehong State, Longchuan County, North Outskirts, 17. VIII. 2005, Kai Wu; 1 ♀, China, Yunnan Province, Dehong State, Yinjiang County, Taiping Town, 15. VIII. 2005, Kai Wu; 1 ♂, China, Yunnan Province, Baoshan State, Lujiang Town, 20. VII. 2006, Rui Zhang; 1 ♂, China, Yunnan Province, Lincang State, Shuangjiang County, Mengmeng Town, 22. VII. 2011, Xin Zhou.

Distribution. China (Sichuan, Yunnan); Mauritius; Seychelles; India; Sri Lanka; Chagos Archipelago; Nepal; Burma; Thailand; Cambodia; Vietnam; Malaysia; Singapore.

Key to the Chinese species of Subancistrocerus de Saussure

Females

1	Body black, with white spots and bands S. sichelii (de Saussure)
_	Body black, with yellow or red-orange spots and bands2

2	Clypeus almost yellow except margin, without black spots
	S. kankauensis (Schulthess)
_	Clypeus at least medially with black spots
3	Scutum coarsely punctate, interspaces with obvious longitudinal strips
	S. camicrus (Cameron)
_	Scutum punctate and interspaces without or with indistinct longitudinal
	strips4
4	Clypeus medially with narrower longitudinal depression, (Fig. 3)
	S. compressus sp. n.
_	Clypeus medially with wider and rounder longitudinal depression (Fig. 17)
	S. jinghongensis sp. n.

Males

1	Fore femur ventrally compressed in basal half (Fig. 9–10)S. compressus sp. n.
_	Fore femur normal, not compressed in basal half2
2	First tarsomere on average straight or very slightly curved, cylindrical and
	long, its length 7 × width
_	First tarsomere on average more arched dorsally and often depressed, its
	length less than 7 × width
3	Mid tarsomere 1 very short, much shorter than the following segments to-
	gether, markedly curved (Fig. 19) S. jinghongensis sp. n.
_	Mid tarsomere 1 different from above4
4	Flagellomeres 6-8 ventrally not concave, only 9 and 10 ventrally widely and
	deeply concave
_	Flagellomeres 6-8 ventrally deeply concaveS. camicrus (Cameron)

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RESEARCH ARTICLE



Nest architecture of Oxaea austera (Andrenidae, Oxaeinae) and its significance for the interpretation of Uruguayan fossil bee cells

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Abstract

Oxaea austera nests in hard, red lateritic soils with dense grass cover. Some characters of *Oxaea austera* nests conform to the known architecture of the oxaeine nests such as the long, vertical shaft and the radiating, horizontal tunnels connected to vertical cells. The presence of more than one cell per lateral, cells at different depths containing larvae at different stages, and discrete walls in the main and laterals are described for the first time for Oxaeinae. One cell was located at the end of each lateral with others (2–4) near them, in some cases arranged in a row just beneath the lateral. Cells are oriented vertically and consist of a chamber, a spiral closure and an antechamber connected with a lateral. The chamber and antechamber are surrounded by a thick discrete wall. Each nest was occupied by at least two active females indicating communal nesting. They also contained older cells, suggesting the reutilization of the nests by successive generations. Both behaviors may be a response to the difficulties of excavation in hard soils. Communal nesting may be also a defensive behavior against nest cleptoparasites. The shape, size, discrete walls of lateritic soil material, spiral closure, and antechamber of *O. austera* cells closely resemble the fossil bee cells included in the ichnogenus *Palmiraichnus* from the early Eocene Asencio Formation of Uruguay. This new evidence reinforces the proposal of extinct representatives of Oxaeinae as it constructor.

Keywords

Oxaea austera, Andrenidae, Oxaeinae, nest architecture, communal nesting, nest reutilization, fossil bee cells

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Introduction

The subfamily Oxaeinae is a small group of 22 species of large, robust, hairy bees distributed from southern USA to northern Argentina (Ascher et al. 2006; Michener 2007; Graf and Moure 2012). With eleven species, *Oxaea* is the most species of the four genera of Oxaeinae. A distinctive character of some species of *Oxaea*, including *O. austera*, is having the metasoma bright metallic green or blue (Engel 2006). Most species inhabit tropical or subtropical areas of America (Hurd and Linsley 1976). The nesting behavior of the Oxaeinae is poorly known. Bertoni (1911) made some brief observations on *Oxaea austera* in Paraguay, Roberts (1973) described the nest architecture of *Oxaea flavescens* from Colombia, and Linsley and Michener (1962) described a nest of *Mesoxaea nigerrima* from México.

Data on the nest architecture of the Oxaeinae has been reviewed and compared with that of other soil-nesting bees such as the Diphaglossinae (Hurd and Linsley 1976). The nests described to date consist of a single, vertical main shaft and several horizontal laterals, each terminating in a single vertical cell. In particular, the morphology of the cells is distinctive because of the presence of a discrete wall separable from the substrate, their large size, and the presence of an antechamber (Rozen 1992; 1993; Genise and Hazeldine 1998). These two features suggested that the fossil bee cells included in *Palmiraichnus castellanosi* from the Early Eocene Asencio Formation of Uruguay were produced by the Oxaeinae as originally proposed by Genise and Hazeldine (1998).

The objectives of this contribution are: 1. to describe the nest architecture of *Oxaea austera* and some aspects of its nesting behavior; 2. to compare its nest architecture and behavior with other species of Oxaeinae, and: 3. to present new evidence supporting the Oxaeinae as potential constructors of *Palmiraichnus castellanosi* from the Asencio Formation.

Material and methods

Excavations of nests were performed using plastic tubes to trace the shaft while exposing a vertical section of the soil with the nest. The measures taken were: width and height of the tumulus; number, diameter and length of the shaft and laterals; and number of cells per nest. The measures taken from the cells were: the maximum diameter and length of the cell chamber, width of walls and the width and length of the antechamber. The larvae were boiled in water and maintained in 70% alcohol. Collected bees and larvae were deposited in the entomological collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-En), Buenos Aires, Argentina. Cells and parts of tunnels were deposited in the ichnological collection of the same museum (MACN-Icn). Drs. Arturo Roig-Alsina and Luis Compagnucci identified the bees.

Results

Nesting site and daily activity. The study was carried out from March 10 to 18, 2012 in the Karadya Bioreserve (25°52.233'S, 53°58.167'W), southwards of Andresito, Misiones, Argentina, in the Upper Paraná Atlantic Forest Region (Galindo-Leal and Câmara 2003). The climate is warm, non-seasonal subtropical with a mean annual temperature around 20 °C and a mean annual precipitation around 2000 mm (Servicio Meteorológico Nacional 2012).

The nests were found in a flat, open, grassy area of 25 m \times 20 m near a house (Fig. 1). The soil was red, lateritic, and devoid of rocks or large roots. The upper horizon (30 cm) was extremely hard, probably because of an unusual lack of precipitation during the previous four months. The vegetation consisted of a dense cover of short grasses and a few isolated trees of *Solanum granuloso-leprosum* (Solanaceae).

A total of four active nests were located from 4 m to 18 m away from each other (Fig. 1). One of them was not excavated with the purpose of studying it the next season. However, in a second field trip during December 2012, there was no activity of *Oxaea austera* at the nesting site, nor was this detected during the rest of the season (Julián Baigorria, pers. comm. 2013). Females were observed outside nests from 6:15 am with daylight to 3:00 pm when the entrances were closed from inside. During this period, females completed from 8 to 14 trips, remaining for 2-8 minutes inside the nests between trips. Two females were observed entering the nest that was not excavated. Different conditions were observed in the three excavated nests. In nest 1 (Fig. 18) one active female was collected while leaving the nest and six other females and a single male were collected in the shaft during the excavation of the nest. The six females were found at a depth of about 50 cm, while the male was found deeper at 90 cm. Two active females showed little to no wing wear. Both females of the unexcavated nest and one female in nest 1 and nest 2 showed some wing wear.

Nest Architecture. Nests entrances were circular with a maximum diameter of 0.9 cm. Each was surrounded by an unconsolidated tumulus, 4.5 cm in maximum diameter and less than 1 cm high (Fig. 2). The nests consisted of one, mostly straight, vertical main shaft, 0.90–1.10 m long and 0.9 cm in diameter, which was circular in cross section (Fig. 3). The main burrow wall consisted of a 2 mm thick layer of packed soil (Fig. 5). The inner surface of the main shaft showed overlapping circular to ovoid concave marks 1.4 mm in maximum diameter (Fig. 4). Horizontal laterals, 10 cm to 37 cm long, radiated from the main shaft at depths ranging from 59 cm to 92 cm (Fig. 6). They had also a discrete 1 mm wall of packed soil (Fig. 7). Laterals were filled with soil after cell closure. Cells appeared at depths from 59 cm to 1.10 m in the different nests. Among the three studied nests, only one (nest 2) (Fig. 19) had lateral tunnels connected to the already filled antechambers of closed cells. Two of them ended in a cell (Fig. 8), whereas a third extended beyond the connected cell (Fig. 19). Other cells (2–4) were present near the tunnels, some arranged in a row just beneath them. The cells, oval and



Figures 1–8. I General view of the nesting site of *Oxaea austera* at Karadya Bioreserve **2** Tumulus and open nest entrance, scale: 1 cm **3** Main shaft **4** Surface texture of the first portion of the shaft showing marks, scale: 0.5 cm **5** Cross section of the shaft showing the discrete wall (arrow), scale: 0.5 cm **6** Curved portion of the main tunnel (left) with a lateral one (right) of nest 1 scale: 1 cm **7** A portion of the lateral tunnel showing the discrete wall (arrow), scale: 0.5 cm **6** Curved portion of the lateral (arrow), scale: 0.5 cm **7** A portion of the lateral tunnel showing the discrete wall (arrow), scale: 0.5 cm **8** The antechamber (arrow) connected to the end of the lateral tunnel, scale: 1 cm.



Figures 9–17. 9 Three individual *Oxaea austera* cells removed from soil, scale: 1 cm **10** Black manganese mottles on the inner surface of the chamber (arrow), scale: 0.5 cm **11** Closed cell showing the antechamber filled with unconsolidated soil, scale: 0. 5 cm **12** Internal view of a closed cell showing the spiral closure, scale: 0.5 cm **13** Cellophane-like lining **14** Radial arrangement of fecal pellets in contact with the spiral closure, scale: 0.5 cm **15** Longitudinal section of a cell showing the semiliquid provisions, scale: 1 cm **16** Cell with a post-defecating larva, the mass of fecal pellets in the upper part and a mesh of rootlets originally developed between the lining and the soil wall, scale: 0.5 cm. **17** Post-defecating larva inside another cell showing remains of the antechamber, spiral closure and fecal pellets, scale: 0.5 cm.



Figures 18–20. General view of the three excavated *Oxaea austera* nests 18 nest 1 19 nest 2. 20 nest 3, scales: 5 cm.

elongate, were vertical with the lower end rounded and the upper flat. The chamber was 2.4 cm long and 1.2 cm in maximum diameter (n = 15) and the discrete wall 2.3–3.5 mm thick (Fig. 9). The cylindrical antechambers were 1.7 cm long and 1.2 cm in maximum diameter (n = 15). The antechamber connected the chamber with the lateral and was filled with unconsolidated, unsorted soil material in closed cells (Fig. 11). The cells (including antechambers) were 4.7 cm long and 2.7 cm in maximum diameter (n = 15) and they were easily removable from the soil once dry (Figs 9, 11, 12). The inner surface of the cell chamber was smooth, and except for the closure, it was lined with a shiny semitransparent cellophane-like film (Fig. 13). The spiral cell closure, which separates the chamber from the antechamber, was composed of six whorls of soil material (Fig. 12). Cells contained eggs, pre-defecating and post-defecating larvae. Nest 1 contained 28 cells. The shallowest level with 6 old cells filled with soil was located at a depth of 59 cm. The second level at 90-93 cm had 5 more old cells filled with soil and fecal pellets and 9 new cells containing eggs and young larvae (Fig. 18). At 1.10 m, the lowest level at the opposite side of the shaft, 6 old cells filled with soil and 2 cells containing post-defecating larvae were found. Nest 2 was composed of 22 cells containing eggs or larvae in different stages distributed from 94 cm to 1.10 m (Fig. 19). Nest 3 contained 15 cells at a depth around 76 cm, 13 with mature larvae and two old ones filled with soil (Fig. 20).

Cells with eggs and larvae were less than half filled with whitish yellow semi-liquid provisions (Fig. 15). No bees were observed foraging at flowers. Analysis of pollen from the provisions under SEM showed that it belonged to Fabaceae and Solanaceae. The whitish, elongate eggs were 5 mm long and 1 mm wide and floated horizontally on the provisions. The pre-defecating larvae were curved and white and were mostly submerged in the provisions. The post-defecating larvae, curved and yellowish, were located head up in cells devoid of provisions (Figs 16 and 17). Cells containing post-defecating larvae showed elongate, dark green 1 mm long and 0.5 mm wide fecal pellets with rounded ends. They were disposed radially close to the cell closure and attached to the cell wall (Fig. 14), and in other cases forming a compact green mass on the inner surface of the cell closure (Figs 16 and 17). Some cells with post-defecating larvae show a mesh of rootlets between the soil wall and the lining (Fig. 16). Other cells show black mottles, probably of manganese, on the walls beneath the lining (Fig. 10).

Parasites. Females of *Thalestria spinosa* (Apidae: Nomadinae) were observed flying around and entering the nests of *Oxaea austera*. One cell contained the egg of *O. austera* and a young larva probably of a parasitic bee according with their different morphology. Bertoni (1911) also described the presence of *T. spinosa* (as *T. smaragdina*) near the nests of *O. austera* in Paraguay.

Discussion

The nest architecture of Oxaeinae is scarcely documented in the literature. Most of the knowledge about the biology of Oxaeinae is restricted to descriptions of the immature

stages of certain species (Rozen 1964; Rozen and Rozen 2010) and habits other than nesting such as mating behavior, aggressive territoriality near the nests and flowers, and male aggregations in some *Protoxaea* and *Oxaea* species (Linsley and Michener 1962; Cazier and Linsley 1963; Linsley and Cazier 1972; Hurd and Linsley 1976; Alcock 1990; Oliveira and Castro 2002). Birkmann (1932) (reproduced in Hurd and Linsley 1976 and summarized in Cockerell 1933) mentioned that *Mesoxaea texana* nests in large aggregations. Hurd and Linsley (1976) believed that high concentration of nests observed in *Protoxaea gloriosa* might reflect the scarcity of suitable soil to nest instead of gregarious tendencies. Linsley and Michener (1962) found an isolated nest of *Mesoxaea nigerrima* and Roberts (1973) observed two nests of *Oxaea flavescens* situated ten meters apart. In the studied locality, the nests of *Oxaea austera* were found sparsely distributed over the nesting site. These data suggest that gregariousness in Oxaeinae may depend on the species considered.

Nest entrances of *Oxaea austera* in Paraguay (Bertoni 1911) and of *O. flavescens* in Colombia (Roberts 1973) were concealed by clumps of grass, which was also the case of the *O. austera* nests here studied. *O. flavescens* nested in red-compacted soil (Roberts 1973) and the nest of *Mesoxaea nigerrima* was found in hard soil as well (Linsley and Michener 1962). These records suggest that the Oxaeinae prefer to nest in hard soils with grasses, although observations remain sparse.

Two nests of *Oxaea austera* showed evidence of communal nesting. In both, nest 2 and the unexcavated one, two females were collected while leaving each nest. In the latter case, both females were observed over three days while entering and leaving the nest, and remaining inside together. The evidence provided by nest 1, despite hosting 7 females, is weaker since only one was collected leaving the nest. The remaining 6 females, whose wings showed no evident wear, could have been either females involved in nesting activities or more probably individuals recently emerged from their natal cells, as was probably the case of the male. The presence of cells with eggs indicates that at least one female was actively nesting, and the presence of post-defecating larvae demonstrates that the same or other(s) female(s) had been active for an extended period. Two females entering the same nest was a condition previously mentioned for this species in Paraguay by Bertoni (1911). The occurrence of more than one female of *O. austera* active in the same nest could discourage parasites when one of the females is in the shaft. The cleptoparasitic bee *Thalestria spinosa* was observed entering open entrances of *Oxaea* nests as is typical for Nomadinae (Rozen 1992).

The observations partly confirm those of Roberts (1973) on *Oxaea flavescens*. He studied a single nest with only one active female, and assumed that nests were perennial (i.e. that were used by successive generations of bees for years) based on the long length of the shaft, the estimated large number of cells in a single nest, the slight wing and mandibular wear of the active female, and the presence of mummified larvae, which he attributed to a previous generation. Alternatively, the long shafts and large number of cells can be also explained by communal nesting (i.e. more than one female nesting simultaneously in the same nest) as shown here for *O. austera*, although Roberts (1973) found only a single female in the nest. According to Michener (2007) one

of the conditions that promote communal behavior is very hard soil, because it is much easier to join other bees in a pre-existing nest than to excavate a new nest starting at the surface. At the same time, the presence of old cells containing fecal pellets associated with the main shaft of an active nest in *O. austera* confirms that nests may be used for more than one generation of bees. The upper 1/3 of the main tunnel of *O. austera* was highly packed resulting in discrete walls that were 2 mm thick. These could be the result of intensive trampling by multiple females of the same or successive generations.

Roberts (1973) assumed that nests were deepened by successive generations until females were forced to excavate new ones because of increasing soil moisture or for discouraging cleptoparasites. In nest 1 of *Oxaea austera*, the newest cells were in the intermediate level, neither the shallowest nor the deepest one. In Misiones, under a non-seasonal climate, fluctuations of soil moisture, either by rainfall or changes in water table, might alternatively favor the deepening of nests or the construction of shallower cells. Such fluctuations could be reflected in the different levels containing old as well as new cells in reused nests of *O. austera*.

The nest architecture of *Oxaea austera* is similar to that of many other ground nesting Andrenidae in that it consists of a long, straight, vertical, main shaft and several horizontal laterals ones ending in a single cell (Michener and Lange 1957; Hurd and Linsley 1976). This seems to be a common feature of oxaeine nests as it was observed previously in *Mesoxaea nigerrima* (Linsley & Michener, 1962) and *Oxaea flavescens* Roberts (1973). A major difference between oxaeine nests and nests of other andrenids is that cells are vertically oriented in the former and horizontally oriented in the latter (Rozen 1992).

The number of vertical cells in the nests of *Oxaea austera* ranged from 15 to 28, disposed not only at the end of laterals but also up to 3 in a row beneath them (Fig. 19). This location and the proximity with the tunnel suggest that these cells were formerly connected with the tunnel, which would be extended along with the construction of new cells. This arrangement is different from those previously described for oxaeine nests, where only one cell is located at the end of each lateral (Roberts 1973; Linsley and Michener 1962). The presence of well differentiated levels at different depths showing cells in similar stages (i.e. old and new with eggs, pre and post-defecating larvae) was not described previously in Oxaeinae. In addition, the discrete walls observed in the main and lateral tunnels of *O. austera* are also described for the first time for Oxaeinae. Roberts (1973) described the provisions of *O. flavescens* as "unconsolidated mass of pollen" or "pollen mass". In *O. austera* the provisions are semiliquid as described for *Mesoxaea nigerrima* and *P. gloriosa* (Linsley & Michener, 1962).

The cells of *Oxaea austera* are elongated structures composed of a hard discrete wall and an antechamber, which connects the cell to the lateral tunnel. These cells closely resemble those of *Protoxaea gloriosa* described by Rozen (1993) and illustrated by Genise and Hazeldine (1998). These characters may have been overlooked in described cells of other species of Oxaeinae. Other Andrenidae and the Stenotritidae also construct cells with discrete walls and antechambers (Houston 1984; Rozen 1992, 1993, 1994). The cells of *Protoxaea gloriosa* may show septa in the



Figures 21–22. Fossil bee cells from the early Eocene Asencio Formation of Uruguay **21** external aspect of *Palmiraichnus castellanosi*, scale: 1 cm **22** longitudinal section of *P. castellanosi* showing the chamber and the filled antechamber, scale: 1 cm.

antechamber (Rozen 1993). The females of *Ancylandrena larreae* excavate horizontal lateral tunnels that widen to form an antechamber with discrete walls. The chamber is separated from the antechamber by the spiral closure and the antechamber also contains an external septum and filling (Rozen 1992). The cells of *Ctenocolletes ordensis* (Stenotritidae) are ovoid chambers with discrete walls and a shorter septate antechamber (Houston 1984). Antechambers of these species differ each other in the arrangement and material of their fillings. The cells of *Ancylandrena larreae* and *C. ordensis*, which are filled with solid provisions, are oriented horizontally whereas the cells of *O. austera* and other Oxaeinae, filled with semiliquid provisions are oriented vertically. The discrete wall of *Oxaea austera* cells may be the result of an active building behavior with soil pellets, whereas the wall of tunnels could be more likely the byproduct of packing soil against walls due to repeated trampling or active compression during excavation.

The characters found in cells of *Oxaea austera*, particularly the shape, size, discrete wall, and antechamber, also described for *Protoxaea gloriosa* (Genise & Hazeldine, 1998), supports the proposal that the fossil bee cell *Palmiraichnus castellanosi* (Figs 21 and 22), from the early Eocene Asencio Formation of Uruguay, could be produced by Oxaeinae (Genise and Hazeldine 1998). Reinforcing this hypothesis, *Oxaea austera* and *Oxaea flavescens* (Roberts, 1973) nest in red lateritic, tropical and subtropical soils, the same as the paleosols from the Asencio formation are interpreted to be (González 1999; Bellosi et al. 2004).

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RESEARCH ARTICLE



On the spider parasitoids Polysphincta longa Kasparyan and P. boops Tschek (Hymenoptera, Ichneumonidae, Pimplinae), with the first host records of P. longa

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Abstract

The rarely recorded *Polysphincta longa* is probably widely overlooked in Europe as a result of confusion with the morphologically similar *P. boops*. Characters for the separation of these species are given, and host and distribution records, largely based on recent fieldwork, are presented. *Araneus angulatus* is shown to be the hitherto unknown host of *P. longa*, while all rearing records for *P. boops* are from *Araniella* species. *P. longa* is reported as new to the fauna of the United Kingdom and *P. boops* as new to Estonia.

Keywords

Araniella, Araneus angulatus, cocoon, Poland, Finland, rearing

Introduction

The description of *Polysphincta longa* Kasparyan, 1976 was based on 10 females from Azerbaijan (holotype), Armenia and Primorsky Krai (Kasparyan 1976). The original description (Kasparyan 1976) and the only keys including this species (Kasparyan 1981, Kasparyan and Khalaim 2007) are in the Russian language, and the species has

not been treated in any other work on European species. It has subsequently been recorded in Germany (Walter 1991, Schmidt and Zmudzinski 2003), Bulgaria (Ivanov 2002) and Poland (Kasparyan and Khalaim 2007, Horstmann and Floren 2008). In the papers giving records from Bulgaria and Germany it is not indicated how the specimens were distinguished from the very similar *P. boops* Tschek, 1869, nor is it stated that the records were the first for those countries, or indeed for Europe. The literature also seems to lack records of males of *P. longa. Polysphincta boops* is known to be a parasitoid of *Araniella* spp. (Hudson 1988, Jones 1988, Fitton et al. 1988, Shaw 1994) but the host of *P. longa* has hitherto been unknown (Yu et al. 2012).

The main purpose of this paper is to give diagnoses of *P. boops* and *P. longa* in English to facilitate the recognition of *P. longa* in Europe, as it seems to occur in large parts of central Europe but is apparently overlooked because of its similarity to *P. boops*. This is indicated by a misidentified 80-year-old specimen in the collection of BMNH and the very few literature records of the species in Europe. Two males of *P. longa* are included in our material. We give new notes on the hosts of *P. boops* and present the first host records for *P. longa*.

Material and methods

The material examined is based on mainly reared specimens of *P. boops* in the collections of NRF from Finland and NMS from Britain, as well as some specimens collected within the Swedish Malaise trap project (SMTP). Apart from the paratype and a German and a British specimen in BMNH, the examined specimens of *P. longa* have been collected in Poland, either with yellow pan traps in *Quercus* canopy or on their hosts in spruce canopy.

The hosts of *P. longa* were immature and were determined by their overall habitus. The *Araniella* hosts of *P. boops* were determined based on their habitus and mainly to genus level only, but a single specimen was determined to species level based on its copulatory organ. Any uncertainty is indicated with a "?" in the material examined.

The measurements were made using an ocular micrometer with an accuracy of 0.1 mm. Abbreviations used in the text: coll. refers to the date when the parasitised spider was collected; coc. refers to the date of finishing the construction of the cocoon; em. to the date of emergence.

Figures 1–5 were made using an Olympus E-520 DSLR attached to an Olympus SZX16 stereomicroscope and composed using CombineZM image stacking software at the Zoological Museum, University of Turku. Figures 6–8 were made with Olympus E-300 and E-3 DSLR with a twin flash.

Depositories: NRF = Private collection of the first author, FI; NRM = Swedish Museum of Natural History, Stockholm, SE; ZISP = Zoological Institute of the Russian Academy of Sciences, St. Petersburg, RU; NMS = National Museums of Scotland, Edinburgh, UK; BMNH = The Natural History Museum, London, UK; RJ = Private collection of Reijo Jussila, FI.
Species survey

Polysphincta longa Kasparyan, 1976

Figures 1-3, 8

Material examined. AZERBAIJAN: **Paratype** \bigcirc (ZISP) Kalaybugurt forest 22.vii.1971 (Kuslicky); POLAND: Białowieża, west of the village: $1 \bigcirc$ (NRF) 52.7128°N; 23.7151°E, old forest with *Quercus, Betula, Fraxinus* and sparse spruce trees (*Picea abies*), beaten from spruce branches, ex *Araneus angulatus*, coll. 9.vii.2010, coc. 12.vii.2010, em. 20.vii.2010 (N. R. Fritzén) (Figure 8); $1 \bigcirc$ (NRF) 52.7190°N; 23.7871°E, old mixed forest with *Picea abies, Quercus, Betula* and *Populus*, beaten from spruce branches, ex *Araneus angulatus*, coll. 10.vii.2010, coc. 15.vii.2010, em. 24.vii.2010 (N. R. Fritzén) (Figure 1); $1 \bigcirc$ (NMS) Krotoszyn, yellow pan trap in *Quercus* canopy, vi.2009 (J. Hilszczanski); GERMANY: $1 \bigcirc$ (BMNH) labelled "59·101 Germany", "*P. eximia*", "Ruthe coll. 59.101", and "*Polysphincta boops* Tschek \bigcirc , J. F. Perkins det ix-1934" (det. N. R. Fritzén 2013); WALES: $1 \bigcirc$ (BMNH) Denbighshire SJ365548, Horsley Hall, beech log, 20.ix.2010 (J. B. Formstone) (det. G. R. Broad 2014, not examined by us).

Distribution. Azerbaijan, Armenia, Primorsky Krai, Poland, Germany, Bulgaria (Kasparyan 1976, Kasparyan and Khalaim 2007, Horstmann and Floren 2008, Walter 1991, Ivanov 2002) and United Kingdom (the present paper).

Biological notes. Koinobiont ectoparasitoid of *Araneus angulatus* Clerck, 1757. Both reared specimens were on juvenile hosts. Based on the collecting and rearing data the species is at least bivoltine, with one generation in June and a second one from late July. The larva is positioned in the typical *Polysphincta* manner, transversely at the anterior apex of the spider's opisthosoma just above the pedicel, with the anterior end moving laterally towards the posterior part of the opisthosoma while growing. Before their death the spiders did not spin any "death chamber" (see discussion) or any other distinctly modified web construction for the larva to cocoon in. Only some additional droplets and threads of silk were attached to the wall of the rearing vial onto which the larva attached when making its cocoon. The cocoon (Figure 8) is diaphanous, fulvous, and fusiform with an open and springy construction of irregular silk, and with a size of 11.8 × 6.3 mm for the reared larger female. The species is arboreal, perhaps in long established forests.

Polysphincta boops Tschek, 1869

Figures 4–7

Material examined. FINLAND: 1° (NRF) ex *Araniella* sp., *Al*, Sund, Kulla, open moist grassland, coll. vi.2003, (N. R. Fritzén); 1° (NRF) ex *Araniella* sp., *Al*, Lemland, Jungfruskär (nature reserve), edge between spruce forest and seashore, coll. 26.v.2006, coc. 1.vi.2006, em. 11.vi.2006 (N. R. Fritzén); 1° (NRF) ex *Araniella* sp.,



Figure 1. Polysphincta longa, habitus in lateral view.

Ab: Kaarina, Kuusisto, garden close to forest, beaten from *Abies* sp., coll. 26.ix.2006, coc. 19.xi.2006, em. 30.xi.2006 (N. R. Fritzén) (Figure 7); 1 $\stackrel{\circ}{\bigcirc}$ (NRF) ex *Araniella* sp., *Al*, Hammarland, Ängessjö (nature reserve), sweeping of vegetation at rich fen, coll. 19.v.2007, coc. 23.v.2007 (N. R. Fritzén); 1 $\stackrel{\circ}{\bigcirc}$ (NRF) ex *Araniella* sp., *Ta*, Lammi biol. st., mixed grove at lake shore, beaten from spruce, coll. 5.iv.2008, em. <6.v.2008 (I. Österblad); 1 $\stackrel{\circ}{\bigcirc}$ (NRF) ex *Araniella* sp., *Obu*, Keminmaa, Helkkusenvaara, sweeping of *Betula nana* at edge of small open bog, coll. 3.vi.2007, 10.vi.2007, em. 20.vi.2007 (N. R. Fritzén) (Figure 6); 1 $\stackrel{\circ}{\bigcirc}$ (NRF) ex adult $\stackrel{\circ}{\bigcirc}$ *Araniella cucurbitina*, *Ta*, Iitti, Radansuu, in hotel room, coll. 5.vii.2010, coc. <10.vii.2010, em. ~17.vii.2010 (R. Pajarre); 1 $\stackrel{\circ}{\bigcirc}$ (NRF) ex *Araniella* sp., *N*, Hangö, Tvärminne zool. st., in *Artemisia vulgaris* at open parking place, coll. 24.vii.2007, coc. 27.vii.2008, em. viii.2008 (I. Österblad); SWEDEN: 1 $\stackrel{\circ}{\bigcirc}$ (NRM) Sm, Nybro, Bäckebo, Grytsjön (nature reserve), Malaise trap



Figures 2–5. Head in anterior view (**2**, **4**) and anterior part of mesosoma in dorsolateral view (**3**, **5**) of *Polysphincta longa* (**2–3**) and *P. boops* (**4–5**). Scale bars 0.2 mm.

in old moist haymaking meadow at forest edge (=Trap ID 1001), 12.ix–10.x.2005 (=coll. event ID 1366) (SMTP); 1 \bigcirc (NRM) Sm, Gränna, Lönnemålen, Malaise trap in Norway spruce forest with big harvested ashes (= Trap ID 17), 13.vii–20.viii.2004 (=coll. event ID 968) (SMTP); 1 \bigcirc (NRM) Bh, Stenungsund, Kolhättan, Malaise trap in broad-leaved deciduous forest (=Trap ID 31), 29.vi–14.vii.2004 (=coll. event ID 1059) (SMTP); 1 \bigcirc (NRF) ex *Araniella* sp. Hls, Söderhamn, *Sphagnum*-bog, coll.



Figures 6-7. Araniella sp. with larva of Polysphincta boops. Scale bars 1 mm.



Figure 8. Cocoon of *Polysphincta longa*. Scale bar 1 mm.

26.iv.2009 (I. Österblad); POLAND: 2° (NMS) Biebrza National Park, Kopciowe, Yellow pan, vii-ix.2002 (J. Hilszczanski); ENGLAND: Surrey, Box Hill, TQ 1852: 1° (NMS) ex *Araniella* [?]*cucurbitina*, coll. 25.vi.1989, coc. ca 4.vii.1989, em.16.

vii.1989 (M. Askins); 1 (MMS) ex *Araniella* sp., *Taxus*, coll. 25.vi.1989, em. vii/ viii.1989 (E. E. Emmett); 1 (MMS) ex *Araniella* sp., bushes, coll. 2.vii.1989, em 1989 (F. M. Murphy); 1 (MMS) ex *Araniella* [?]*cucurbitina*, Devon, Horrobridge, Denham Wood, SX 475674, coll. 2.v.1990, em. 1990 (P. Smithers); Cumbria, Whitbarrow: 1 (MMS) ex *Araniella* [?]*cucurbitina*, *Corylus*, coll. 22.ix.1985, coc. (indoors) 8.iii.1986, em. 4.iv.1986 (M. R. Shaw); 1 (MMS) ex *Araniella* [?]*cucurbitina*, *Taxus*, coll. 11.v.1986, coc. 13.vi.1986, em. 4.vii.1986 (M. R. Shaw); 1 (MMS) ex *Araniella* sp., *Quercus*, Berkshire, Ascot, Silwood Park, coll.29.iv.1994, coc. 30.iv.1994, em. 23.v.1994 (M. R. Shaw); 1 (MMS) ex unspecified spider, Leicestershire, Buddon Wood, coll. 13.vii.2011, em. 2011 (A. Godfrey); 1 (MMS) ex cocoon on *Quercus*, Northamptonshire, Castor Hanglands, TF 1201, coll. 17.v.2009, em. 16.vii.2009 (M. R. Shaw); 1 (MMS) ex cocoon on *Rosa*, Warwickshire, Snitterfield, SP 2060, coll. 21.v.1988, em. 30.v.1988 (J. Robbins); 1 (MMS) Huntingdonshire, Monks Wood, Rothamsted light trap 17.viii.2005 (G. R. Broad); ESTONIA: 1 (RJ) Ösel (Saaremaa), Kaali, 15.viii.1997 (H. Silfverberg).

Distribution. Trans-Palaearctic (Yu et al. 2012), reported as new to Estonia in the present paper.

Biological notes. Koinobiont ectoparasitoid of *Araniella* spp. (Figures 6–7), mainly on immatures but occasionally on adult specimens, with the only reliable records of host species based on adult hosts or adult specimens collected together with the parasitised specimen seemingly *Araniella cucurbitina* (Clerck, 1757) (this study) and *A. opisthographa* (Kulczyn'ski, 1905) (Jones 1988). It overwinters as a minute larva on the host in a position similar to *P. longa*. The cocoon is similar to that of *P. longa*, with no distinctly modified web construction made by the spider prior to death. The species seems to be mostly arboreal (trees and bushes) in a wide range of habitats.

Discussion

Polysphincta boops and *P. longa* are among the largest species in the *Polysphincta* genusgroup in Europe and, based on the specimens we have seen, *P. longa* exceeds the size of *P. boops*. Further, with an ovipositor length of 4.3–5.0 mm (based on the reared Polish female and the larger paratype from Azerbaijan), *P. longa* has a longer ovipositor than any other European species of the *Polysphincta* genus-group. The two species are morphologically very similar and form a distinct group within the European *Polysphincta*, characterised by the yellow colour of the scutellum, postscutellum, mandibles, tegulum and subtegular ridge contrasting with the otherwise black body colour (Figure 1). They are also characterised by the very long ovipositor; ovipositor-hind tibia index about 1.7 in both species in this study. They have the submetapleural carina present and complete (this character varies within the genus).

According to the original description (Kasparyan 1976) and the keys in Kasparyan (1981) and Kasparyan and Khalaim (2007), *P. longa* is distinguished from *P. boops* by its longer antenna (antennal flagellum longer than front wing in *P. longa* and shorter

in *P. boops*), the greater number of antennal flagellomeres (28–33 in *P. longa* and 25–28 in *P. boops*) and the more pubescent mesoscutum. In addition *P. boops* has a slightly shorter malar space ($0.6 \times$ basal mandibular width) than *P. longa* ($0.8 \times$ basal mandibular width).

When we examined the material of *P. longa* and *P. boops* we also found the pubescence of the mesoscutum (Figures 3, 5) and the number of flagellomeres the most useful characters to distinguish the two species. In addition we found that the eye in P. longa is a little larger than in P. boops, and the shape of the cheeks viewed from in front is different in that they are slightly convex in *P. longa* whereas they are slightly concave in *P.* boops (Figures 2, 4). Further, in P. longa, the scape of the antenna is distinctly broader compared to the flagellomeres (Figures 2, 4). According to Kasparyan (1976, 1981) and Kasparyan and Khalaim (2007) there seems to be some overlap in the number of flagellomeres between the two species. In our rather limited material there is no overlap between the species when males and females are considered separately. An overlap seems only to exist between the usually larger sex (females) of P. boops and the usually smaller sex (males) of *P. longa*. The number of flagellomeres in our material of *P. boops* is 23-27 in males (n=17) and 26-28 in females (n=7), while the number in P. longa is 28-31 in males (n=2) and 31-33 in females (n=3; the German female in BMNH has broken antennae). The two largest males of P. boops have longer wings (but slightly shorter hind tibia) than the reared male of *P. longa*, and the greater number of flagellomeres in *P. lon*ga seem thus not a consequence of greater body size alone. In P. longa the pubescence of the mesoscutum is moderately dense and covers most of it apart from its posteromedian 0.20–0.25 (Figure 3). In P. boops the mesoscutum is mostly bare apart from the anterior part of the median lobe, which is pubescent, and there are also sparse isolated setae on the lateral parts of the lateral lobes of the mesoscutum as well as along the notauli (Figure 5). Taking the observations of Kasparyan into account, the number of flagellomeres should not be used as a single character if they are near 28, but the combination of the pubescence of the mesoscutum, the number of flagellomeres, and the shape of the cheeks will allow for easy identification of both males and females of P. longa.

In our rearing projects *P. boops* has been reared only from *Araniella* species (n=16). The only host determined to species level based on the genitalia is a single female *A. cucurbitina*. The single record of *A. opisthographa* (Jones 1988, Hudson 1988, Fitton et al. 1988) as host species was based on circumstantial evidence, i.e. adult males collected together with the parasitised juvenile specimen (Jones 1988). There is a single rearing record of *P. boops* from *Theridion* sp. in Brischke (1877), a record frequently referred to (Dalla Torre 1902, Aubert 1969) or apparently cited without reference (Šedivý 1963, Kasparyan 1981, Kolarov 1997). On the basis of what is known about the host specificity of the species of the *Polysphincta* genus-group (see Shaw 1994, Matsumoto and Takasuka 2010, Fritzén 2010, Fritzén and Fjellberg 2014), we consider such old, aberrant and unrepeated records (in this case from another host family) in the literature to be probably misidentifications of either the parasitoid or the host species. In our projects 14 males and 2 females have been reared successfully. We are unable to explain this odd sex ratio. Taking into account that the two reared females

also were from *Araniella* species, the use of a different (and to us unknown) host for fertilized (female) eggs seems extremely unlikely. The only reasons we can think of is that either the species is so rare that females often fail to be mated (in which case they may still lay male-producing eggs), or that female mortality tends to be higher in immature stages, perhaps especially in captivity. However, neither is supported by any evidence in our projects.

The host of *P. longa* has hitherto been unknown. Through beating spruce branches in old forests at Białowieża (Poland) outside the national park in July 2010 the first author obtained only two specimens of A. angulatus, and both were parasitised by P. longa. In the same forest several juvenile Araneus nordmanni (Thorell, 1870) and also a few A. diadematus Clerck, 1757 were seen but were not parasitised. Juveniles of Gibbaranea omoeda (Thorell, 1870) were also numerous in the forests, but this species was not found to be parasitised either. The determination of the juveniles of A. angulatus was based on their habitus, including eye size and the light median area on the sternum (which separates the species from Gibbaranea), the dorsal pattern and the ventral marks of the abdomen. The only species in Europe sharing these features and the overall habitus of A. angulatus is A. circe (Audouin, 1826) (Šestáková et al. 2009), a rare species that hitherto has not been recorded in Poland (van Helsdingen 2013). Although the reared material is small, the results indicate that *P. longa* is not a generalist on Araneidae, and not even on the genus Araneus, but might be restricted to the A. angulatus group (Simon 1929), comprising A. angulatus, A. circe and A. grossus (C. L. Koch, 1844) in Europe, or to A. angulatus alone. There are no other records of A. angulatus as host for any species of the Polysphincta genus-group (Yu et al. 2012).

When collected in July, the larvae on *A. angulatus* were large and they soon killed the spiders and made cocoons. Since *P. boops* and most other Palaearctic species of the *Polysphincta* group (though not *Megaetaira madida* (Haliday) (Fitton et al. 1988) and *Zatypota maculata* Matsumoto and Takasuka (Matsumoto and Takasuka 2010)) overwinter as minute larvae on their hosts (e.g. Fitton et al. 1988, Fritzén 2010, Matsumoto and Takasuka 2010), with the larvae subsequently developing rapidly in spring, this is probably the case with *P. longa* as well. The collection date of the parasitised *A. angulatus* with large larvae indicate a second generation and that *P. longa* is at least bivoltine.

In some species of the *Polysphincta* genus-group the parasitoid larva manipulates the spider hosts to make different kinds of silk structures for the larva to cocoon in, e.g. "cocoon webs" (*sensu* Eberhard 2000, see also Nielsen 1923, Matsumoto and Konishi 2007), which are often found in the species attacking orb-weaving spiders. In some species of the *Polysphincta* genus-group, the spider host spins only a less sophisticated silken structure in the form of a "death chamber" for the parasitoid to cocoon in, prior to being killed by the parasitoid. In these cases, e.g. *Polysphincta rufipes* (Gravenhorst) on its host *Larinioides cornutus* (Clerck) (Araneidae), the spider remains will also be found inside the silken chamber (personal observations). In the cases of *P. longa* and *P. boops* the spider (though orb-weavers) do not make "cocoon webs" or "death chambers" and the spider remains are, at least *in vitro*, dropped to the bottom of the rearing vial. In the wild, unparasitised specimens of *A. angulatus* and *Araniella* spp. (the hosts of *P. longa* and *P.* *boops* respectively) do not make any silken retreats, whereas *L. cornutus* usually hides in a silken retreat. Whether the behaviour of making a death chamber, probably induced by the parasitoid larva, invariably correlates with a species-specific use of a silken retreat by the spider needs further study, but we have noted that the remains of *Araniella* sp. also fall when parasitised by *Polysphincta tuberosa* Gravenhorst (see also Matsumoto 2009 for a different kind of silken retreat made by a parasitised non orb-weaving spider).

Since the original description (Kasparyan 1976) and the keys in Kasparyan (1981) and Kasparyan and Khalaim (2007) are all in Russian and have been the only publications giving diagnostics for *P. longa*, the species has probably been overlooked in Europe and can presumably be found in entomological collections under *P. boops*. This was the case with the German specimen of *P. longa* in BMNH (from the Ruthe collection), a specimen originally determined as "*P. eximia*" (=*Zatypota albicoxa* (Walker)) but later determined as *P. boops* by Perkins in 1934. This is probably the first specimen of *P. longa* was brought to our attention, another specimen originally determined as *P. boops* by its collector. Since *P. longa* would "end up" as *P. boops* with the most commonly used keys in Europe (e.g. Fitton et al. 1988, not treating *P. longa*) we encourage curators of European ichneumonid collections to check the specimens standing as *P. boops* for the characters of *P. longa. Araneus angulatus*, the host of *P. longa*, occurs in most European countries and its parasitoid can therefore be expected to occur in several countries from which it has not yet been reported.

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RESEARCH ARTICLE



Sampling Buprestidae (Coleoptera) in Washington state with Cerceris californica Cresson (Hymenoptera, Crabronidae)

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Abstract

The beetle-hunting habits of ground nesting wasps in the genus *Cerceris* Latreille have been recently exploited as a survey technique for exotic and native Buprestidae, particularly *Agrilus planipennis* Fairmaire (the emerald ash-borer). While such methods have been developed for the wide-ranging eastern *Cerceris fumipennis* Say, the survey potential of western buprestid-hunting *Cerceris spp*. has not been explored. *Cerceris californica* Cresson is the most well-studied of the western buprestid feeders, and the only one known to occur in Washington state. Here we report the results of surveys conducted in Washington in 2012–2013 for *C. californica* colonies, and numbers of buprestid beetles collected from monitored colonies. Eight *C. californica* colonies were found through visual search of 228 baseball fields and sandy clearings, but only four were large enough to monitor. Fifty-four beetles were recovered from the four colonies, comprising five native species. Four of these are new prey records for *C. californica* colonies do not appear to be large or common enough in Washington to be a significant exotic buprestid survey strategy. However, even the limited monitoring resulted in more buprestid captures than nearby purple sticky traps, and monitoring *C. californica* nests may be a locally useful supplement for general buprestid surveys.

Keywords

Exotic species, survey

Introduction

The recent spread of two exotic metallic woodboring beetle species (Coleoptera, Buprestidae) in parts of North America has resulted in widespread tree mortality and looming long-term changes in ecological communities. Both are in the speciose genus Agrilus, which includes species capable of feeding upon and potentially killing live, healthy trees. The emerald ash borer (EAB), A. planipennis Fairmaire, 1888, was first detected in North America in 2002 (Cappaert et al. 2005, Poland and McCullough 2006), although it may have been present for many years prior (Kovacs et al. 2009). To date, the beetle has been detected in 23 states and two provinces in the northeastern United States and Canada (http://tinyurl.com/lyaka3y, accessed April 18, 2014). The congener goldspotted oak borer, A. auroguttatus Schaeffer, 1905, (in some past literature treated under A. coxalis Waterhouse, 1889, a Mexican and Central American species) has been introduced into southern California from its native range, probably from southeastern Arizona or northern Mexico, although in Mexico it has been recorded only from Baja California Sur. It has caused extensive mortality among oak species and has been steadily expanding its range northward since 2002 (Coleman and Seybold 2008, Coleman et al. 2012).

There is considerable need to effectively monitor for these species and other exotic woodborers to maximize the possibility of early detection and eradication of newly established populations. Methods for detecting and monitoring *Agrilus planipennis* and *A. auroguttatus* include visual survey for impacted trees, use of trap trees, twig sampling, sticky ash leaves, and large sticky traps baited with plant volatiles or beetle decoys (Francese et al. 2008, Poland et al. 2010, McCollough et al. 2010, McCollough et al. 2011, Ryall et al. 2011, Crook et al. 2012, Domingue et al. 2012). Developing lures and traps that are effective at detecting *A. planipennis* at low densities has been an ongoing challenge, and an ideal trap design remains elusive. The current USDA-APHIS EAB trapping protocols employ large prismatic purple sticky traps and a sampling map derived from a risk-based model emphasizing high-risk locations. Traps are armed with volatile lures and deployed in the canopy of appropriately sized *Fraxinus* trees, ideally within the model-generated trapping cells (USDA-APHIS 2013).

An alternative buprestid survey and monitoring method developed in the eastern states and provinces exploits the biology of a ground-nesting wasp in the family Crabronidae, *Cerceris fumipennis* Say, 1837. The genus *Cerceris* includes hundreds of species worldwide, adults of which hunt and collect various beetle groups as a larval food source (Bohart and Menke 1976). The majority of species for which prey data are known target Curculionidae, with fewer species preying upon Tenebrionidae, Bruchidae, Chrysomelidae, and Buprestidae. In North America, Buprestidae are the primary prey items for the five species in Scullen's (1965) Group II. *Cerceris fumipennis* is the most thoroughly studied of this group, occurring from Ontario to Florida and west into Texas and Wyoming. More than 100 species of buprestids have been recorded as prey items, including adventitious species with which it shares no evolutionary history (Scullen and Wold 1969, Rutledge et al. 2011, Swink et al. 2013, Hellman and Fierke 2014).



Figure I. A Cerceris californica nest B Adjacent Philanthus gibbosus (left) and C. californica (right) nests.

In 2005, new provincial distribution records for several buprestid species collected from foraging *Cerceris fumipennis* in Ontario launched a research program to develop a buprestid detection and monitoring tool using the wasp, sometimes dubbed "biosurveillance" (Careless et al. 2014). The beetle-hunting habits of the wasp were already well known, but it had not previously been used to investigate the occurrence, distribution, or spread of buprestid species. Careless et al. (2014) developed a thorough methodology for using *C. fumipennis* to detect *A. planipennis*, which are readily captured by the wasps, and several eastern states and provinces have successfully implemented wasp-based monitoring programs. The first *A. planipennis* recorded in Connecticut was collected from a foraging wasp in 2012, concurrent with a capture on a purple sticky trap (Rutledge et al. 2013).

The other four North American *Cerceris* species known or presumed to prey upon Buprestidae occur in the western states and provinces, and northern Mexico (Scullen 1965, Bohart and Grissell 1975). Of these, *C. californica* Cresson, 1865, ranges from British Columbia south into Mexico, and east to Texas (where it occurs with *C. fumipennis*). Females are active from at least mid-June through August, when they construct simple nests in compacted sandy soil (Fig. 1) and provision them with paralyzed buprestid beetles. Although less studied than *C. fumipennis*, it remains one of the better understood *Cerceris* species in North America, with 29 recorded prey species (Linsley and MacSwain 1956, Evans and Rubink 1978, Nelson and Westcott 1991, Davidson 2003). By comparison, few prey records are documented for the other three species attacking Buprestidae (Davidson 2003, Looney and Westcott unpublished data).

This project explored adapting the eastern sampling methodology to *Cerceris californica* in Washington to examine the potential utility of this survey method. We report on survey results for *C. californica* nest sites in Washington and new buprestid prey records from monitored nests. Data are limited, but we also compare the location of monitored nests and beetles recovered from *C. californica* with the location and results of 2013 EAB trapping with purple sticky traps. The potential contribution of *C. californica* to exotic buprestid monitoring is evaluated in the context of the *C. fumipennis* program in the east, using criteria described in Careless et al. (2014).

Methods

There are no published locations of *Cerceris californica* nest sites in Washington. Potential wasp range was inferred from Scullen (1965) and specimens housed at Washington State University, the University of Idaho, the University of California, Riverside, and Oregon State University. In Washington, wasps have been collected only east of the Cascade Range, from localities such as White Swan, Prosser, Moses Lake, Buena, Wawawai, and Lake Paha. All of these specimens were collected from flowers or at large, not from nesting sites. Surveys for *C. californica* nesting aggregations were made in Washington between July 7–25 2012, and May through July 2013 (Fig. 2). Possible *C. californica* burrows can be identified by an evenly distributed ring of excavated soil, or tumulus (Linsley and MacSwain 1956; Fig. 1).

Following Careless et al. (2014) and Nalepa et al. (2012), nest search concentrated primarily on baseball diamonds in hope of maximizing opportunities to find large colonies that would lend themselves to buprestid monitoring. Baseball diamonds are often occupied by *Cerceris* colonies, and offer several benefits for *Cerceris* survey. They represent large areas of consistent habitat for wasps and are easily located using online satellite imagery (Nalepa et al. 2012). Baseball diamonds may not be the only occupied habitat in a region, but when wasps are locally present in an area they are more easily found in ball fields than other habitat (e.g. dirt roads/trails, exposed earth) (Careless et al. 2014, Hellman and Fierke 2014). By focusing on easily-located baseball diamonds, towns may be relatively quickly surveyed for wasps. Baseball diamonds are typically



Figure 2. Cerceris californica survey sites, 2012–2013.

located on public land (schools, parks) and are therefore usually accessible to government and citizen surveyors. Since they are located in parks, there are often numerous tree species planted relatively close, which provide good habitat for buprestid beetles. Drawbacks to focusing on baseball fields include potentially high levels of maintenance and disturbance, which may deter *Cerceris* nesting, and unfavorable soil formulations (Nalepa et al. 2012). Some campgrounds, dirt roads, and vacant lots were also included in the survey.

Beetle collection followed the methodology described in Careless et al. (2014) for *Cerceris fumipennis*. First, aggregations were censused and the location of all *Cerceris* nests was mapped. The threshold for monitoring was set at ~15 burrows (Table 1). Any beetles found on the ground while surveying were collected. "Careless collars", plastic tabs with holes, were placed over each nest to mark location and impede entry by wasps returning with beetle prey (Careless et al. 2014). Frequency of wasps returning with

Site	Date	Duration (hrs)	Num. of Nests	Buprestids Recovered	
Yakima, Franklin Park				Wasp	Ground
	5 Jul 2012	1	8	0	0
	12 Jul 2012	2	21	5	2
	26 Jul 2012	3.5	13	8	0
	2 Aug 2012	2.5	1	1	1
	15 Aug 2012	4	1	0	0
	14 May 2013	_	0	_	_
	17 Jun 2013	2	8	0	0
	3 Jul 2013	2	33	14	1
	9 Jul 2013	2	16	1	0
	25 Jul 13	2	7	1	0
	29 Jul 2013	2	10	0	0
	2 Aug 2013	1	0	0	0
Yakima, Lewis & Clark	Middle School				
	6 Jul 2012	2	15	2	2
	12 Jul 2012	3	24	8	3
	2 Aug 2012	2	2	0	0
	16 Aug 2012	1	0	0	0
	14 May 2013	_	0	_	_
	17 Jun 2013	1	6	0	0
	3 Jul 2013	2	18	0	0
	9 Jul 2013	2	10	0	0
	25 Jul 2013	1	12	0	1
	29 Jul 2013	1	11	0	0
	2 Aug 2013	1	4	0	0
Wenatchee, Eastmont	Community Park	-			
	1 Aug 2012	3	7	3	0
Walla Walla, Roosevelt Park					
	19 Jul 2012	1	>20	1	0
	22 Aug 2012	3	5	0	0

Table 1. Monitoring dates, wasp colony size, and beetles capture (- indicates no monitoring).



Figure 3. Monitored *Cerceris californica* colony locations compared with 2013 EAB grids and purple prism trap locations.

and without beetle prey was recorded. Beetles were collected from wasps returning to the nest primarily by capturing them with a net. Wasps occasionally dropped the beetle they were carrying, and it was retrieved at that time. All buprestid specimens were retained. Beetles collected in 2012 were weighed and their length measured on the collection day, or immediately frozen and weighed soon after. All buprestid specimens were identified by one of us (RLW). The locations of confirmed colonies were compared with the 2013 USDA-APHIS EAB trapping cells and purple prism trap locations in 2013 (Fig. 3). Beetles retrieved in 2013 were also compared with beetles captured on four purple prism traps nearby, which were deployed from June 28 until 25 September, 2013. Three traps were located in Yakima, and one near Ellensburg (Fig. 3).

Results

In total, 228 baseball diamonds or sandy clearings were inspected for *Cerceris californica* in 2012 and 2013 (Fig. 2). Survey during 2012 detected eight *C. californica* colonies. Of these, only four (located in the cities of Yakima, Wenatchee, and Walla Walla) were robust enough to support monitoring in 2012 (Fig 2). One of these had only seven burrows, but was included due to the general paucity of colonies (Table 1). Only the two large colonies located in Yakima were monitored in 2013. Observed nest density ranged from 1–24 nests in 2012, and from 1–34 in 2013 (Table 2). No colonies

Beetle Species	Number captured / Percent of total prey	State Record	Prey Record
Agrilus granulatus (Say, 1823)	1 / 1.9		+
Agrilus politus (Say, 1825)	7 / 13		
Chrysobothris nixa Horn, 1886	4 / 7.4		+
Chrysobothris quadriimpressa Gory & Laporte, 1837	4 / 7.4	+	+
Phaenops intrusa (Horn, 1882)	38 / 70.3		+

Table 2. Species of Buprestidae collected from Cerceris californica during July-August 2012, and July 2013

were located within one of the 2013 EAB trapping cells. The colony in Wenatchee was within a few hundred meters of the nearest trapping cell, and the colonies in Yakima within 10 km (Fig 4). Although not located within a cell, one purple prism trap in Yakima was located within 1.6 km of two *C. californica* colonies.

Cerceris californica activity varied widely between sites and days, from a low of zero wasps observed to a returning wasp observed every 4 minutes. Beetles collected from foraging wasps varied similarly, from 0–7 beetles recovered per hour of monitoring. In 2012, 36 beetles were collected during 28 hours of monitoring; 7 dropped beetles and 29 taken from wasps. In 2013, 18 beetles were collected over 19 hours of monitoring; 2 dropped beetles and 16 taken from wasps. No Buprestidae were captured on purple prism traps in the Yakima or Wenatchee area in 2013.

Beetle weights in 2012 ranged from 5.2 mg to 52.3 mg, and length between 5.21 mm and 10.4 mm. The lightest beetle was a dropped specimen, which appeared to be desiccated. Excluding this specimen, average weight was 19.0 mg, and the average length was 7.80 mm. Over both years five buprestid species were collected in Washington, four of which are new prey records for *Cerceris californica* (Table 2). One of these, *Chrysobothris quadriimpressa* Gory & Laporte, 1837, is newly recorded from Washington.

Prey records

- Agrilus granulatus populi Fisher, 1928: Yakima Co., Yakima, Lewis and Clark Middle School, 46.575°, -120.522°, 12-VII-2012, W. Hellman, 1 specimen. This subspecies is widespread in the western U.S. and Canada and, as its name suggests, utilizes Populus spp. (primarily Populus trichocarpa) as hosts (Fisher 1928, Barr 1971).
- Agrilus politus (Say, 1825): Yakima Co., Yakima, Franklin Park, 46.5953°, -120.5347°, 26-VII-2012, W. Hellman, 2 specimens; 3-VII-2013, C. Looney & A. Pelegrin, 3 specimens; 3-VII-2013, Y. Inguanzo & C. Looney, 1 specimen. Yakima, Lewis and Clark Middle School, 46.575°, -120.522°, 12-VII-2012, W. Hellman, 1 specimen. This is probably the most widespread species of the genus in North America, likely occurring in every state and province (Nelson et al. 2008). Its primary hosts are *Salix* and *Acer* (Nelson et al. 2008). This species is also taken by *C. fumipennis* (Swink et al. 2013).

- Chrysobothris nixa Horn, 1886: Yakima Co., Franklin Park, 46.5953°, -120.5347°, 3-VII-2013, C. Looney & A. Pelegrin, 2 specimens; 9-VII-2013, A. Kopit & A. Pelegrin, 1 specimen. Yakima, Lewis and Clark Middle School, 46.575°, -120.522°, 25-VII-2013, Y. Inguanzo & C. Looney, 1 specimen. Occurring from British Columbia to California, east to Montana and Wyoming, the larvae of this species feed on various cupressaceous trees and shrubs (Nelson et al. 2008) and can be a pest in nursery plantings (Burke 1917, Furniss and Carolin 1977).
- Chrysobothris quadriimpressa Gory & Laporte, 1837: Walla Walla Co., Walla Walla, Roosevelt Park, 46.064387°, -118.313896°, 19-VII-2012, W. Hellman, 1 specimen. Yakima Co., Yakima, Franklin Park, 46.5953°, -120.5347°, 3-VII-2013, C. Looney & A. Pelegrin, 3 specimens. Formerly listed as a synonym of *C. femorata* (Olivier, 1790) this species has a wide distribution, but mostly in the East. It was first recorded in the Pacific Northwest from southwestern Idaho reared from ornamental black walnut (Westcott 2005), and considered to be introduced, although it was collected from more than one site. A single specimen was later collected in Oregon, near the border with Idaho (Wellso and Manley 2007). Hosts are trees and shrubs in various genera, but the beetle is most often collected on *Quercus* (Wellso and Manley 2007, MacRae and Basham 2013). This species has been recorded as prey of *C. fumipennis* (Hook and Evans 1991, Swink et al. 2013).
- Phaenops intrusa (Horn, 1882): Chelan Co., Wenatchee, Eastmont Community Park, 47.417 -120.284, 1-VIII-2012, W. Hellman, 3 specimens. Yakima Co., Yakima, Franklin Park, 46.5953°, -120.5347°, 12-VII-2012, W. Hellman, 7 specimens; 26-VII-2012, W. Hellman, 6 specimens; 2-VIII-2012, W. Hellman, 2 specimens; 3-VII-2013, C. Looney and A. Pelegrin, 7 specimens. Yakima, Lewis and Clark Middle School, 46.5736°, -120.5221°, 6-VII-2013, W. Hellman, 4 specimens; 12-VII-2012 W. Hellman, 9 specimens. This is a widespread western species most commonly taken by beating *Pinus* spp., its most common hosts (Burke 1917 [as *Melanophila*], Nelson et al. 2008), although it has also been reared from *Larix occidentalis* (Nelson and Westcott 1976). Nelson et al. (2008) erroneously listed it from "NB" instead of NE (c.f. Nelson and Westcott 1976).

Discussion

The percentage of search sites occupied by *Cerceris californica* observed in Washington appears to be much lower than for *C. fumipennis* in several eastern states. Nalepa et al. (2012) report that positive ball fields comprised approximately 22% of those surveyed in Maine, Connecticut, and North Carolina, ranging from 9.9% in Maine to 39.3% in Connecticut. Approximately 9% of the fields had large enough colonies (\geq 15 nests) to monitor, 4.7% in North Carolina and Maine, and 21.8% in Connecticut. This differed sharply from Washington, where in 2012 only about 3.5% of search sites were occupied. More critically, only 1.7% had colonies robust enough to support monitoring (Table 1). Colony size was also smaller than generally reported for *C. fumipennis*.

The largest colony located and monitored in this study included 33 burrows. In contrast, *C. fumipennis* colonies in the northeastern states and provinces could contain hundreds of burrows (Nalepa et al. 2012, Careless et al. 2014). It was expected but still disheartening to find no *C. californica* colonies west of the Cascade Range, where native ash and oak species are found in Washington.

Activity at wasp colonies was rare by August in 2012, suggesting wasps may have been primarily foraging earlier in the season than indicated by museum records and published studies. In 2013, visits to the two largest colonies (in Yakima) began in May. Wasp activity was not observed until mid-June, and appeared to peak in early July; by August almost no wasp activity was observed. This phenology is shorter than that observed for *Cerceris fumipennis*, which displays active enough foraging to enable monitoring through at least mid-August, and sometimes into September (Careless et al. 2014, Hellman and Fierke 2014).

The number of wasps observed and the number of beetles collected per colony were both much smaller than anticipated based on work with Cerceris fumipennis. Careless et al. (2014), Hellman and Fierke (2014), and Swink et al. (2013) recovered hundreds of beetles per year, from multiple colonies, compared with the 54 beetles collected in this study. The comparatively abbreviated collecting period in this study may account for part of this difference. Even so, wasp colonies were consistently smaller and less frequent, limiting the potential gains from C. californica monitoring. Dropped beetles were seldom found, which presents a challenge to locating colonies since the presence of dropped beetles is a useful indicator (Careless et al. 2014). It also limits the amount of survey data gleaned from each colony, since even damaged beetles collected from the ground can be informative (e.g. Grossbeck 1912, Swink et al. 2013). It is not clear whether the lack of dropped beetles reflects differences in biology or behavior between Cerceris congeners, or if it is characteristic of the environment near monitored colonies-low numbers of dropped and captured beetles could simply be a function of low buprestid density near the colonies monitored in this study.

The fairly small pool of prey species observed in this study may similarly derive from relatively poor buprestid habitat located near the study sites. Only five beetle species were retrieved from *Cerceris californica*, although existing literature indicates they prey upon many more species of appropriately sized buprestids given the opportunity. This species-depauperate catch also must be a product of lower abundance and diversity of Buprestidae in WA generally (Barr 1971), particularly compared to the Southwest where most of the *C. californica* prey records originate. For instance, the majority of the recorded prey (60%) of *C. californica* are of *Acmaeodera* spp., which is species-poor in WA and much more diverse in the southwestern USA.

The beetle species captured were not dissimilar in weight and size to *Agrilus planipennis* and *A. auroguttatus*. Since buprestid prey selection appears to be a function of availability and size (Hellman and Fierke 2014), *Cerceris californica* foraging habits observed here and described in other reports indicate that the species has the potential to be an effective monitoring tool if large enough colonies can be located. It is notable

that, although the beetle diversity and numbers retrieved from *Cerceris* were low in each year, the purple prism traps placed in Yakima in 2013–which ran for approximately three months in the same general location–captured no buprestids. In contrast, even the limited *C. californica* monitoring in 2013 resulted in the capture of 18 beetles in four species. Although EAB purple prism traps are hung in ash tree canopies, potentially biasing the available species pool towards ash-feeding buprestids, other species are captured. For example, *Buprestis aurulenta* L., 1767, and *Phaenops drummondi* (Kirby, 1837), were recovered from purple prism traps in western Washington in 2012 and 2013 (J. Cena, personal communication), and detections of other adventive *Agrilus* spp. have come from purple sticky trap captures in other regions (Westcott 2007, Jendek and Grebennikov 2009).

Numerous other wasps and bees were common at baseball diamonds, both occupied and un-occupied by Cerceris. Common Hymenoptera genera observed during the survey included other Cerceris, Eucerceris, Philanthus, Bembix, Halictus, and Polistes (Fig. 4). Some of these species are similar in outward appearance to C. californica, and confusing them could lead to lost time or other complications. Polistes dominulus (Christ), 1791, has somewhat similar coloring and size to C. californica and flies relatively slowly. Mistaking these two species could lead to a nasty sting. Discriminating between nests of ground-dwelling species may also be confusing for the novice. Halictus farinosus Smith, 1853 (Halictidae) was collected from one of the ballfields with an active Cerceris colony. This bee makes nests with a tumulus similar to those of C. *californica*, although the species within can be determined by gently agitating the nest entrance with a stick and eliciting a defensive showing from the occupant. Of the species commonly encountered with C. californica, Philanthus gibbosus Fabricius, 1775, was the most similar in appearance and behavior. It can be distinguished by its irregular tumulus (Fig. 1) and its bee prey. A colony of Eucerceris flavocincta Cresson, 1865, was found at a survey site west of the Cascade Range, where C. californica is not known to occur. However, the known range of E. flavocincta includes much of C. californica's range (Scullen 1968, Bohart and Grissell 1975). While similar to C. californica in color and behavior, E. flavocinta preys upon Curculionidae (Bohart and Grissell 1975, Scullen 1968). Cerceris nigrescens Smith, 1856 was also found at one site; it too preys upon weevils (Bohart and Grissell 1975).

Following the novel suggestion that beetle-hunting *Cerceris* wasps could be a viable tool in buprestid surveys (Marshall et al. 2005), significant effort has been made to develop and prescribe useful methods of exploiting this phenomenon. Careless et al. (2014) identified three general considerations for evaluating the potential effectiveness of *Cerceris* as a buprestid survey tool: accessibility, productivity, and sustainability. "Accessibility" refers to the temporal, geographic, and behavioral occurrence of the wasp species of interest. *Cerceris californica* nests located in this study were rare, and did not seem to occur in enough sampling locations to be a major source of buprestid survey records. Large colonies were even rarer, limiting effectiveness of this monitoring tool. Colonies of *C. californica* were fairly active during the day, although their seasonal activity may be abbreviated when compared with *C. fumipennis*.



Figure 4. Hymenoptera species commonly found at *Cerceris californica* colonies. The non-*Cerceris* species were observed at the majority of surveyed sites, irrespective of *C. californica*'s presence. *Philanthus gibbosus* was the most notable and similar species likely to be found with *C. californica*.

While far fewer beetles were recovered in this survey than most utilizing Cerceris fumipennis, C. californica was still relatively "productive", i.e. collected beetles at a rate that equals or exceeds other methods (Careless et al. 2014). We cannot address how effective hand sampling or beating might have been for buprestids, but in 2013, more beetles were recovered from C. californica colonies than nearby purple sticky traps. The sticky traps were sited to maximize opportunity to catch EAB - in the upper canopy of ash trees - so this comparison doesn't directly address their targeted effectiveness for Agrilus planipennis. Even so, the discrepancy in 2013 between beetles captured on traps (0) and those collected in only 19 hours of buprestid monitoring (18) suggests that C. californica could play at least a small role in Washington as a supplemental survey technique. Linsley and MacSwain (1956) report hundreds of buprestids recovered from 25 C. californica wasps and excavated burrows, indicating that with greater monitoring effort in the right habitat this wasp is productive indeed. No doubt more species and individuals would have been recovered from even the few sites monitored here had there been more collecting time. The last of the effectiveness criteria, "sustainability", concerns the ability of a Cerceris species to tolerate repeated interference by humans. This aspect of *C. californica* biology was not directly examined in this study, although Linsley and MacSwain (1956) report that females would continue to embark upon foraging flights, even after having five beetles in a row removed. We can only add the general observation that in this study individual wasps also embarked upon a foraging flight after having a beetle removed.

Ultimately, developing a *Cerceris* monitoring program for exotic buprestids in the western states may be more productive in Oregon or California, where host plant (e.g. *Fraxinus*, *Quercus*) habitat and buprestid-hunting wasp habitat overlap. However, as was the case for Washington before this study, no significant efforts have been made to locate and map colonies of *C. californica* or buprestid-feeding *Cerceris*. This would be a critical first step to monitoring with this species in the western states, particularly since colony frequency and size seem to be the major limiting factors in Washington.

Conclusions

Washington *Cerceris californica* colonies are less common and smaller than *C. fumipennis* colonies in the eastern states. Colonies of *C. californica* appear to be restricted to east of the Cascade Range in Washington state, and were seldom located near EAB trapping sites. *Cerceris californica* captures beetles within the size and weight range of target *Agrilus* spp. Despite low total numbers, *C. californica* wasps were more effective tools for general buprestid sampling in the Yakima area when compared with nearby EAB purple traps, and citizen monitoring may be a useful supplemental monitoring program in select cities in eastern Washington given such effective foraging. The monitoring potential of buprestid-hunting *Cerceris* spp. may be greater in other western states and should be studied.

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RESEARCH ARTICLE



Updates to the Nomenclature of Platygastroidea in the Zoological Institute of the Russian Academy of Sciences

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Abstract

Parabaryconus Kozlov & Kononova, syn. n. is treated as a junior synonym of Cremastobaeus Ashmead; Cremastobaeus artus (Kozlov & Kononova), comb. n. is transferred from Parabaryconus; Paridris macrurous Kozlov & Lê, syn. n. and P. taekuli Talamas & Masner, syn. n. are treated as junior synonyms of P. bispores Kozlov & Lê; Leptoteleia japonica (Kozlov & Kononova), comb. n. is transferred from Triteleia Kieffer; Leptoteleia striola Talamas & Buffington, name n. is provided as a replacement name for Leptoteleia japonica Yamagishi; Dvivarnus punctatus Rajmohana & Veenakumari, syn. n. is treated as a junior synonym of Gryonoides agamades Kozlov & Lê; Dvivarnus agamades comb. n. is transferred from Gryonoides Dodd; Anirama Kozlov, syn. n., Criomica Kozlov, syn. n. and Pyrgaspis Kozlov, syn. n. are treated as junior synonyms of Platygaster Latreille; Platygaster marikovskii Kozlov, comb. rev. and P. semiclavata (Buhl), comb. n. are transferred from Anirama; Platygaster viktorovi (Kozlov), comb. n. is transferred from Criomica; Platygaster haloxylonomyiae (Kozlov), comb. n. and P. striativentris (Buhl), comb. n. are transferred from Pyrgaspis; Stosta Kozlov, syn. n. is treated as a junior synonym of Synopeas Förster; Synopeas tosticola (Kozlov), comb. n. is transferred from Stosta.

Keywords

Platygastroidea, Platygastrinae, Scelioninae, Teleasinae, taxonomy

Introduction

The Zoological Institute of the Russian Academy of Sciences serves as the repository for a large number of primary and secondary types of species described by the late Mikhail Kozlov. Recent travel to this museum to study Kozlov's primary types of *Trissolcus* Ashmead offered the opportunity to assess type material for all of Platygastroidea in the Zoological Institute, revealing that the classification for a modest number of taxa requires adjustment. Revisionary work on *Trissolcus* will occur in a future monograph, and we here treat Platygastroidea exclusive of this genus. For completeness, the holotypes of species subsequently described by Peter Buhl in two of Kozlov's genera, *Pyrgaspis* and *Anirama*, were examined and Buhl's diagnostic characters are here photographically illustrated.

Two of Kozlov's platygastrine genera, *Pyrgaspsis* and *Stosta*, were established for species with atypical shapes of the mesoscutellum, whereas these species otherwise fit easily into the broad concepts of *Platygaster* and *Synopeas*, respectively. Similarly, *Anirama* was described for a species in which the apical male antennomere is elongate and *Criomica* for a species with a slightly unusual head shape. Such description of genera for apomorphic species brings attention to unusual morphologies, but is detrimental to the construction of a natural classification if it renders other taxa polyphyletic.

In our perspective, the most needed contribution to classification in the Platygastrinae is detailed character analysis, evaluation of monophyly for existing genera, and placement of species into monophyletic species-groups. We do not consider the characters that Kozlov used to designate new platygastrine genera to indicate lineages separate from *Platygaster* and *Synopeas*, but they are potentially useful for speciesgroup classification. It is our hope that the characters, treatments and illustrations presented here will contribute to this cause.

Examination of Kozlov's specimens revealed him to be, in our opinion, a "splitter" as opposed to a "lumper," that is, he tended not to treat morphological differences as intraspecific or intrageneric variation. A benefit of Kozlov's species concepts is that series identified by him are morphologically uniform. Because of this, we are confident that the paratypes and holotypes of Kozlov and Lê are conspecific. We here treat one of their species, *Paridris macrurous*, as a junior synonym of *Paridris bispores* based on a paratype specimen.

Materials and methods

Collections

This work is based on specimens deposited in the following repositories with abbreviations used in the text:

- **BLGA** Burgenlandisches Landesmuseum, Eisenstadt, Austria
- **BPBM** Bishop Museum, Honolulu, USA

MNHN	Muséum National d'Histoire Naturelle, Paris, France
OSUC	C.A. Triplehorn Insect Collection, Columbus, USA
USNM	Smithsonian National Museum of Natural History, Washington DC, USA
ZIN (ZMA	S) Zoological Institute of the Russian Academy of Sciences, St. Petersburg,
	Russia
ZMUC	Zoological Museum, University of Copenhagen, Copenhagen, Denmark

Informatics

Collection data for all specimens are available in the Hymenoptera Online Database (http://purl.oclc.org/NET/hymenoptera/hol) by entering the specimen identifier (CUID) in the search form. CUIDs for all specimens are presented in the material examined section of each taxonomic treatment and may be identified as a collection coden followed by a number (note capitalization and the space that follows some acronyms). The locality data reported for primary types are not literal transcriptions of the labels: some abbreviations are expanded and additional data from the collectors may be included.

Photography

Images were produced using a Microvision Instruments imaging system with Cartograph software, a Z16 Leica lens and a JVC KY-F75U digital camera. Single montage images were produced from image stacks with the program CombineZP. In some cases, multiple montaged images were stitched together in Photoshop to produce larger images at high resolution and magnification. Full resolution images, and additional photographs of the specimens treated here, are archived in the Hymenoptera Online Database (http://purl.oclc.org/NET/hymenoptera/specimage) and MorphBank (http:// www.morphbank.net).

Morphological terms

The following terms are used in the text and are active links to anatomical concepts in the Hymenoptera Anatomy Ontology (Yoder et al. 2010)

antennomere axillula clava frontal depression lateral propodeal carina (lpc: Figs 18, 26) mediotergite http://purl.obolibrary.org/obo/HAO_0000107 http://purl.obolibrary.org/obo/HAO_0000160 http://purl.obolibrary.org/obo/HAO_0000203 http://purl.obolibrary.org/obo/HAO_0000911 http://purl.obolibrary.org/obo/HAO_0001919 http://purl.obolibrary.org/obo/HAO_0001860 mesoscutellar disc posterior mesoscutellar carina (pmc: Figs 18, 21–22, 25–26) posterior mesoscutellar area (pma: Figs 18, 25–26) posterolateral mesoscutellar carina (plmc: Fig. 26) posterolateral mesoscutellar area (plma: Fig. 26) scutoscutellar sulcus http://purl.obolibrary.org/obo/HAO_0000915

http://purl.obolibrary.org/obo/HAO_0002278

http://purl.obolibrary.org/obo/HAO_0002277 http://purl.obolibrary.org/obo/HAO_0002280 http://purl.obolibrary.org/obo/HAO_0002279 http://purl.obolibrary.org/obo/HAO_0000919

Scelioninae

Cremastobaeus Ashmead

Parabaryconus Kozlov & Kononova, syn. n. http://bioguid.osu.edu/osuc_concepts:154388

Cremastobaeus artus (Kozlov & Kononova), comb. n.

http://bioguid.osu.edu/osuc_concepts:154389 Figures 1–3; Morphbank¹

Parabaryconus artus Kozlov & Kononova, 2000: 32 (original description); Kononova and Kozlov 2008: 217 (description).

Link to distribution map.²

Material examined. Holotype, male: JAPAN: Aichi Pref., Honshu Isl., 40km NW Nagoya, Inuyama City, 4.X.1981, E. Sugonyaev, ZMAS 0136 (ZIN).

Comments. The transverse carinae above the frontal depression, setose eyes, serrate A2–A3, and shape of the metasoma in lateral view unequivocally place this species in *Cremastobaeus* according to the concept of this genus established by Masner (1976) and Galloway and Austin (1984).

Paridris Kieffer

Paridris bispores Kozlov & Lê

http://bioguid.osu.edu/osuc_concepts:179766

Paridris bispores Kozlov & Lê, 2000: 65, 335 (original description, keyed).

Paridris macrurous Kozlov & Lê, 2000: 65, 69, 337 (original description, keyed). syn. n. http://bioguid.osu.edu/osuc_concepts:179769

Paridris taekuli Talamas & Masner, 2013: 13, 14, 29, 30, 43 (original description, diagnosis, keyed). syn. n.

http://bioguid.osu.edu/osuc_concepts:303974



Figures 1–3.³⁶ *Cremastobaeus artus* (Kozlov & Kononova), male holotype (ZMAS 0136) I Lateral habitus 2 Head and mesosoma, dorsal view 3 Head and mesosoma, ventrolateral view. Scale bars in millimeters.

Link to distribution map.³

Material examined. Holotype of *P. bispores*: VIETNAM: OSUC 184371 (ZIN); Paratype of *P. macrurous*: VIETNAM: 1 female, OSUC 184373 (ZIN); Holotype of *P. taekuli*: NEW CALEDONIA: Nord Prov., Pouembout Commune, Tiéa Forest, 7.XII-14.XII.2000, malaise trap, M. E. Irwin, OSUC 266150 (MNHN).

Leptoteleia Kieffer

Leptoteleia japonica Kozlov & Kononova, comb. n.

- http://bioguid.osu.edu/osuc_concepts:5560
- *Triteleia japonica* Kozlov & Kononova, 1990: 174, 176 (original description); Kononova 1995: 69 (keyed); Kononova and Petrov 2000: 28 (keyed); Kononova and Kozlov 2008: 223, 225 (description, keyed).

Link to distribution map.⁴

Material examined. Holotype, female, *T. japonica*: JAPAN: Aichi Pref., Honshu Isl., Inuyama City, 6.X.1981, E. Sugonyaev, ZIN 0012 (ZIN).

Leptoteleia striola Talamas & Buffington, name n.

http://bioguid.osu.edu/osuc_concepts:4740

Leptoteleia japonica Yamagishi, 1993: 812 (original description); Kononova and Kozlov 2008: 302 (description).

Comments. The transfer of *Triteleia japonica* to *Leptoteleia renders*, *L. japonica* Yamagishi as a junior objective homonym. We hereby provide a replacement name in the interest of nomenclatural clarity.

Etymology. The Latin adjectival epithet "striola," meaning "furrow" or "line", refers to the longitudinal costae mentioned by Yamagishi (1993) as a character useful for the diagnosis for this species.

Teleasinae

Dvivarnus Rajmohana & Veenakumari

Dvivarnus agamades (Kozlov & Lê), comb. n.

http://bioguid.osu.edu/osuc_concepts:343746 Figure 6; Morphbank⁵

Gryonoides agamades Kozlov & Lê, 1986: 100 (original description); Lê 2000: 218 (description, type information).

Dvivarnus punctatus Rajmohana & Veenakumari, 2011: 44 (original description). syn. n.

Link to distribution map.⁶

Associations. collected on *co*: [Cyperales: Poaceae]

Material examined. *Paratype*: **VIETNAM:** 1 male, OSUC 184258 (ZIN). *Other material*: **INDIA:** 2 males, OSUC 230647, 59262 (OSUC). **LAOS:** 1 female, USN-MENT00877588 (BPBM). **THAILAND:** 4 females, OSUC 284994, 342789, 374197-374198 (OSUC).

Comments. Rajmohana and Veenakumari (2011) stated that the mesoscutellar spines of *Dvivarnus punctatus* differ from those of *Gryonoides* based on their location on the mesoscutellum. We agree, and more specifically, the mesoscutellar spines of *Gryonoides* proximally abut the axillula and are derived at least in part from striations of the scutoscutellar sulcus (Fig. 5) whereas those of *Dvivarnus* are derived entirely from the mesoscutellar disc (Fig. 6). Rajmohana and Veenakumari asserted that the presence of punctation throughout T3 is unique to *D. agamades*. This character is indeed rare among teleasines, but it may also be found in *Trimorus* (Fig. 4) and *Xenomerus* (*X. spinosus* Mikó & Masner, *X. comatus* Mikó & Masner) (Mikó et al 2007). The biogeographical records published by Rajmohana and Veekakumari (2011) led them to suggest that this species was limited to semi-arid habitats. A broader geographic sampling has revealed that this species also inhabits the tropical rainforests of Southeast Asia.

Platygastrinae

Platygaster Latreille

Anirama Kozlov, syn. n.

http://bioguid.osu.edu/osuc_concepts:7822

Comments. Kozlov described *Anirama* as a genus separate from *Platygaster* because the apical antennomere of the male is elongate. There are otherwise no characters to indicate that this lineage is distinct from *Platygaster* and we consider this antennal morphology to be apomorphic within *Platygaster*.

Platygaster marikovskii Kozlov, comb. rev.

http://bioguid.osu.edu/osuc_concepts:11460 Figures 7–9, 11; Morphbank⁷

Platygaster marikovskii Kozlov, 1967: 717 (original description). *Anirama marikovskii* (Kozlov): Kozlov 1970: 224 (generic transfer).

Diagnosis. Buhl (2007) used the relative lengths of males antennomeres to distinguish *P. semiclavata* from *P. marikovskii*: A10 as long as A6-A9 in *P. semiclavata* and A10 twice as long as A6-A9 in *P. marikovskii*. This character is illustrated in Figures 10–11.

Link to distribution map.⁸

Associations. emerged from *Haloxylonomyia deformans solitaria* Marikovskij: [Diptera: Nematocera: Bibionomorpha: Cecidomyioidea: Cecidomyiidae]

Material examined. Holotype, female, *P. marikovskii*: KAZAKHSTAN: Almaty Reg., secondary stream, Ili River, no date, P. Marikovskij, ZMAS 0115 (ZIN). *Paratypes*: KAZAKHSTAN: 4 females, 1 male, USNMENT00764942, USNMENT00872134, USNMENT00872136, USNMENT00872137, USNMENT00896493 (ZIN).

Platygaster semiclavata (Buhl), comb. n.

http://bioguid.osu.edu/osuc_concepts:236452 Figure 10; Morphbank⁹

Anirama semiclavata Buhl, 2007: 329 (original description).

Diagnosis. See diagnosis of of *P. marikovskii*.

Link to distribution map.¹⁰

Material examined. Holotype, male: UNITED ARAB EMIRATES: al-Ajban, 7.XII-28.XII.2006, malaise trap/light trap, A. v. H., zmuc00036868 (deposited in ZMUC). *Paratypes*: UNITED ARAB EMIRATES: 4 females, 1 male, USNMENT00979300, USNMENT00979301, USNMENT00979302, USN-MENT00979303, USNMENT00979304 (ZMUC).



Figures 4–6.³⁷ **4** *Trimorus* sp., Dorsal habitus, female (OSUC 334274) **5** *Gryonoides* sp., scutellar-axillar complex, lateral view, male (USNMENT00872152) **6** *Dvivarnus agamades* (Kozlov & Lê), scutellar-axillar complex, lateral view, male (USNMENT00872152). Scale bars in millimeters.

Criomica Kozlov, syn. n.

http://bioguid.osu.edu/osuc_concepts:7825

Comments. The separation of *Criomica* from *Platygaster* was justified on the basis of the shape and proportions of the head. The eyes are somewhat triangular, but otherwise the cephalic shape of *Criomica* is unremarkable. The 3-merous clava in the female of this species is notable and may be a useful character for future species-group placement.

Platygaster viktorovi (Kozlov), comb. n. http://bioguid.osu.edu/osuc_concepts:11471 Figures 12–14; Morphbank¹¹

Criomica viktorovi Kozlov, 1975: 965 (original description).

Link to distribution map.¹²

Material examined. Holotype, female: MONGOLIA: Övörhangay Prov., E coast of Taatsïn Tsagaan Nuur Lake, 2.VIII-4.VIII.1969, M. Kozlov, ZMAS 0114



Figures 7–9.³⁸ *Platygaster marikovskii* Kozlov, female paratype (USNMENT00872137) **7** Lateral habitus **8** Head and mesosoma, dorsal view **9** head and mesosoma, ventral view. Scale bars in millimeters.

(ZIN). *Paratypes*: **MONGOLIA:** 6 females, 1 male, USNMENT00916649, USNMENT00916650, USNMENT00916651, USNMENT00916652, USNMENT00916653, USNMENT00916654, USNMENT00916655 (ZIN).

Pyrgaspis Kozlov, syn. n.

http://bioguid.osu.edu/osuc_concepts:7847

Comments. Kozlov considered *Pyrgaspis* to be closest to *Synopeas*, presumably because of the pointed mesoscutellum, and he separated these genera based on



Figures 10–11.³⁹ 10 *Platygaster semiclavata* (Buhl), male holotype (zmuc00036868), head, mesosoma, antennae, dorsal view **11** *Platygaster marikovskii* Kozlov, male paratype (USNMENT00872134), head and antennae, ventral view. Scale bars in millimeters.

the orientation and height of the mesoscutellar spine. However, the widely separated lateral propodeal carinae (propodeal keels) (Fig.18) indicate that *Pyrgaspis haloxylonomiae* does not belong in or near *Synopeas*. In the context of the gamut of mesoscutellar morphology within *Platygaster* (Figs 19–24), the dorsally pointed mesoscutellum alone does not warrant placement in a separate genus. Evaluation of this character revealed that the mesoscutellar points in *P. haloxylonomyiae* and *P. striativentris* are formed by a carina on the posterior surface of this sclerite (Figs 18, 21–22, 25). Examination of *Platygaster* from the eastern United States yielded a specimen that has a similar, but more pronounced, carina on the posterior surface of the mesoscutellum which does not form a point dorsally (Fig. 26). The mesoscutellum of this specimen also bears a character that is new to us, the posterolateral mesoscutellar carina (Figs 23–26).

Platygaster haloxylonomyiae (Kozlov), comb. n.

http://bioguid.osu.edu/osuc_concepts:12098 Figures 15–18, 21, 28; Morphbank¹³

Pyrgaspis haloxylonomyiae Kozlov, 1967: 716 (original description).

Diagnosis. Buhl (2009) distinguished *Platygaster striativentris* from *P. haloxylonomyiae* on the basis of shorter striae on T2 and a more pronounced point on the mesoscutel-


Figures 12–14.⁴⁰ *Platygaster viktorovi* (Kozlov), female paratype (USNMENT00916654) **12** Dorsal habitus **13** Ventral habitus **14** Lateral habitus. Scale bar in millimeters.

lum in the latter. These characters are illustrated in Figures 21–22 and Figures 27–28, respectively.

Link to distribution map.¹⁴

Associations. emerged from *Haloxylonomyia deformans solitaria* Marikovskij: [Diptera: Nematocera: Bibionomorpha: Cecidomyioidea: Cecidomyiidae]

Material examined. Holotype, female: KAZAKHSTAN: Almaty Reg., secondary stream, Ili River, 14.III.1952, Marikovskij, ZMAS 0116 (ZIN). *Paratypes*: KAZAKH-STAN: 1 female, 1 male, USNMENT00872138, USNMENT00872149 (ZIN).



Figures 15–18.⁴¹ *Platygaster haloxylonomyiae* (Kozlov), female paratype (USNMENT00872149) **15** Lateral habitus **16** Dorsal habitus **17** Head, anterior view **18** Mesosoma, posterior view. Scale bars in millimeters.

Platygaster striativentris (Buhl), comb. n.

http://bioguid.osu.edu/osuc_concepts:250131 Figures 22, 25, 27; Morphbank¹⁵

Pyrgaspis striativentris Buhl, 2009: 76 (original description).



Figures 19–24.⁴² **19** *Platygaster* sp., dorsal mesosoma, lateral view (USNMENT00877276) **20** *Platygaster* sp., dorsal mesosoma, lateral view, male (USNMENT00872147) **21** *Platygaster haloxylonomyiae* (Kozlov), dorsal mesosoma, lateral view, female paratype (USNMENT00872149) **22** *Platygaster striativentris* (Buhl), dorsal mesosoma, lateral view, male paratype (USNMENT00872149) **23** *Platygaster sp.*, dorsal mesosoma, lateral view, female (USNMENT00877259) **24** *Platygaster* sp., dorsal mesosoma, lateral view, female (USNMENT00877259) **24** *Platygaster* sp., dorsal mesosoma, lateral view, female bars in millimeters.

Diagnosis. See diagnosis of P. haloxylonomiae.

Link to distribution map.¹⁶

Material examined. Holotype, male: MONGOLIA: Bayanhongor Prov., 1240m, 45°03'N 100°59'E, 130km S Bayanhongor (Bayankhongor), 6.VII.2004, J. Halada, BLGA 0001 (deposited in BLGA). *Paratypes*: MONGOLIA: 3 males, USN-MENT00979420, USNMENT00979421, USNMENT00979422 (BLGA).



Figures 25–28.⁴³ **25** *Platygaster striativentris* (Buhl), mesosoma, posterolateral view, male paratype (US-NMENT00979421) **26** *Platygaster* sp., mesosoma, posterolateral view, male (USNMENT00877259) **27** *Platygaster striativentris* (Buhl), metasoma, dorsolateral view, male holotype (BLGA 0001) **28** *Platygaster haloxylonomyiae* Kozlov, metasoma, dorsolateral view, male paratype (USNMENT00872138). Scale bars in millimeters.

Synopeas Förster

Stosta Kozlov, syn. n.

http://bioguid.osu.edu/osuc_concepts:7850

Synopeas tosticola (Kozlov), comb. n.

http://bioguid.osu.edu/osuc_concepts:12103 Figures 29–32; Morphbank¹⁷

Stosta tosticola Kozlov, 1975: 311 (original description).

Link to distribution map.¹⁸

Associations. collected on *Brachanthemum gobium* Krasch.: [Asterales: Asteraceae] Material examined. Holotype, male: MONGOLIA: Ömnögovi Prov., 35km NNE Bulgan, sandy desert, N edge of Bayan Dzaan (Bain-Dzag) Mountain,



Figures 29–31.⁴⁴ *Synopeas tosticola* (Kozlov), male paratype (USNMENT00872135) **29** Lateral habitus **30** Head and mesosoma, dorsal view **31** Head, anterior view. Scale bars in millimeters.

31.VIII.1969, M. Kozlov, ZMAS 0137 (ZIN). *Paratype*: MONGOLIA: 1 male, US-NMENT00872135 (ZIN).

Comments. Kozlov's treatment of *Stosta* was essentially identical to that of *Pyrg-aspis* in that the description of a new genus was performed to accommodate the shape of the mesoscutellum. As in *Platygaster*, a broad range of mesoscutellar forms can be found in *Synopeas* (Figs 27–30) and we do not consider this character to be useful to indicate a lineage separate from *Synopeas*.



Figures 32–35.⁴⁵ **32** *Synopeas tosticola*, dorsal mesosoma, lateral view, female paratype (USN-MENT00872135) **33** *Synopeas* sp., dorsal mesosoma, lateral view, female (OSUC 266261) **34** *Synopeas* sp., dorsal mesosoma, lateral view, female (OSUC 334240) **30** *Synopeas* sp., dorsal mesosoma, lateral view, female (USNMENT00877326). Scale bars in millimeters.

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Endnotes

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- 3 http://hol.osu.edu/map-large.html?id=179766
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- 5 http://morphbank.net/?id=835897
- 6 http://hol.osu.edu/map-large.html?id=343746
- 7 http://morphbank.net/?id=835906
- 8 http://hol.osu.edu/map-large.html?id=11460
- 9 http://morphbank.net/?id=835914
- 10 http://hol.osu.edu/map-large.html?id=236452
- 11 http://morphbank.net/?id=835921
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- 17 http://morphbank.net/?id=835964
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RESEARCH ARTICLE



First contribution to the bionomics of the pollen wasp Celonites fischeri Spinola, 1838 (Hymenoptera, Vespidae, Masarinae) in Cyprus

In memory of Friedrich W. Gess

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Abstract

Celonites fischeri was recorded from ten localities in various open, disturbed habitats in North-West Cyprus. The species is probably narrowly oligolectic exploiting exclusively flowers of *Echium* (Boraginaceae) as the sole pollen and nectar source. Females perform a pollen collecting strategy hitherto unknown in pollen wasps; they ingest pollen from fresh anthers of *Echium* flowers that have just started to open by forcing their head into the only slightly opened corolla. Males patrol along *Echium* plants in search for females. Mating was mainly observed at *Echium* flowers but also occurred in the area of a male sleeping aggregation. The aerial nest, consisting of 2–5 earthen cells sometimes covered with an additional thin layer of earth, is attached to stones or plants. Nest building and soil collection behaviour are described and an ethogram of a nesting female observed during three consecutive days is given. Males form sleeping aggregations at particular sites that are continuously used over at least eleven consecutive nights, even though the size of the male groups may vary from day to day. During sleeping, the males characteristically curl their bodies around withered stems.

Keywords

Palaearctic, Echium, flower association, oligolecty, mating behaviour, nest construction, sleeping aggregation

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Introduction

The knowledge of the bionomics of Palaearctic species of the pollen wasp genus *Celonites* is still very limited. Hitherto, forty-six species of *Celonites* have been recorded in the Palaearctic region (Carpenter 2001; Gusenleitner 2002, 2007, 2012; Mauss 2013), but detailed bionomical information has been published only for *Celonites abbreviatus* (Villers, 1789). Studies on this species refer to mating (Mauss 2006), nesting behaviour (Lichtenstein 1869; Ferton 1901, 1910; Bellmann 1984, 1995), flower association and flower visiting behaviour (Bequaert 1940; Schremmer 1959; Blüthgen 1961; Bellmann 1995; Müller 1996; Mauss 2006) and male sleeping aggregations (Amiet and Mauss 2003). Further information is restricted to a few flower visiting records for *Celonites mayeti* Richards, 1962, *C. andreasmuelleri* Mauss, 2013). Moreover, Lichtenstein (1875) published a short and fragmentary description of a nest of *C. mayeti* (erroneously named as *C. fischeri*).

Bionomical information about Celonites fischeri is lacking, despite a short, unconfirmed note of Bingham (1898), who stated that this species had been reared from cylindrical mud nests in Aden (Yemen). The geographic range of C. fischeri extends over North Africa, Cyprus, the Middle East and the Arabian Peninsula (Richards 1962, 1984; Carpenter 2001). Together with C. afer the species belongs to the C. fischeri-complex. The C. fischeri-complex and the C. abbreviatus-complex form the C. abbreviatus-group within the subgenus Celonites s. str. (Mauss 2013). The C. fischeri-complex is characterized by a normal facial pilosity thereby differing from species of the closely related C. abbreviatuscomplex, which are equipped with a specialised pollen collecting apparatus on the frons consisting of knobbed setae (Mauss 2013). In C. abbreviatus, these knobbed setae serve to remove pollen from the nototribic anthers of various species of Lamiaceae (Schremmer 1959; Bellmann 1995; Müller 1996; Mauss 2006). Other members of the C. abbreviatuscomplex like C. mayeti and C. andreasmuelleri were also observed to visit flowers of this plant family (Bequaert 1940; Mauss 2013). Due to this difference in facial pilosity, host plant choice and flower visiting behaviour are expected to differ between the members of the two closely related Palaearctic species complexes of the C. abbreviatus-group.

The aim of this study is to perform a detailed investigation of flower association and flower visiting behaviour, mating, female brood care and male behaviour in *Celonites fischeri* and to compare the biology of this species with that of other members of the *C. abbreviatus*-group, some Ethiopian species of *Celonites* as well as other aerial nesting members of the Masarini.

Material and methods

Investigations were carried out from 20 May to 30 May 2013 in the vicinity of Paphos in north-western Cyprus. The study area has a Mediterranean climate with hot, dry

summers and mild, rainy and rather changeable winters (Meteorological Service 2014). The average annual precipitation in Paphos is about 370 mm (Baier et al. 2009). The mean temperature in the hottest (August) and coldest month (February) is 26 °C and 13 °C, respectively (Flint and Stewart 1992). During the study period, the weather was mainly sunny and warm with maximum air temperatures above 25 °C, reaching 30 °C on three days (suboptimal conditions with clouds or haze predominated in the afternoon of 24 May and in the morning of 26 May and 29 May). On 22 May and 24 May, *Celonites fischeri* was searched for systematically in the vicinity of Paphos by checking promising sites with large *Echium* populations. Geographic coordinates (WGS 84) were measured using a Garmin GPS 12.

Celonites fischeri was found at 10 localities [I Kato Paphos 34°44.495'N 32°26.004'E; II 0.5 km north of Agios Georgios 34°54.528'N 32°19.606'E; III 1 km south-east of Coral Bay 34°50.582'N 32°23.232'E; IV 1.5km south-east of Drousia 34°57.683'N 32°24.834'E; V Prodromi 35°01.779'N 32°24.798'E; VI 3 km south-west of Prodromi 35°00.760'N 32°23.584'E; VII 2 km south-west of Nikoklia 34°43.007'N 32°32.956'E; VIII 1 km north of Choletria 34°46.462'N 32°36.448'E; IX 0.5 km south-south-west of Praitori 34°50.672'N 32°44.500'E; X 0.5 km south of Pachna 34°46.120'N 32°47.334'E]. Most studies were conducted at locality II at the northern periphery of Agios Georgios, a disturbed Phrygana fragment of about 900 m², which was irregularly grazed by goats and rarely also by donkeys (Fig. 3). The area was delimited in the east by large thick bushes and in the south by a small track and an adjoining banana plantation. To the west and the north, the area was separated from the adjacent costal Phrygana of the Akámas Peninsula by two small tarred roads. In the area, 26 richly flowering patches of Echium angustifolium Mill. (Boraginaceae) were present varying in size between 0.25 to 2 m² (Fig. 46). In addition, fifteen other plant species were in flower [Asteraceae: Calendula arvensis L., Carduus nutans L., Centaurea hyalolepis Boiss., Chrysanthemum coronarium L., Pallenis spinosa (L.) Cass, Scolymus hispanicus L., Asteraceae spec.; Boraginaceae: Heliotropium hirsutissimum Grau.; Brassicaceae: Sisymbrium irio L.; Fabaceae: cf. Lotus spec.; Lamiaceae: Ajuga chamaepitys (L.) Schreb. palaestina (Boiss.) Bornm., Teucrium micropodioides Rouy; Malvaceae: Malva cretica Cav.; Primulaceae: Anagallis foemina Mill.; Ranunculaceae: Delphinium peregrinum L.].

For all documentations of observations the local time (= Greenwich Mean Time + 3h) was used. Sunrise was approximately at 5h35, sun's zenith at 12h45 and sunset at 19h50. Time intervals were measured using a digital stop-watch. Observations were made with a close-up binocular (Pentax Papilio 8.5×21) and documented by using a Canon EOS camera with a 180 mm or 100 mm macro-lens (scale up to 1:1, resolution 18 mega pixel) and macro flash-lights.

Specimens of all plant species flowering at locality II were collected and preserved dried. The material was placed in the herbarium of the Staatliches Museum für Naturkunde Stuttgart (Herbarium STU). The plant taxa were identified following Meikle (1977–1985) and Tutin et al. (1964–1980). Flower preferences of imagines were studied by counting the number of sightings (= first observations) of flower visiting



Figures 1–5. Habitat of *Celonites fischeri* at locality II 0.5 km north of Agios Georgios, Cyprus: **I** Nest site of nest F attached to a dwarf shrub (Asteraceae) **2** Bare area in the centre used by females of *C. fischeri* as a quarry site (qs) **3** Disturbed Phrygana (viewed from the south-west; with patches of *Echium angusti-folium* (E), sites of three nests (D, F, S), quarry site (qs) and male sleeping aggregation m₁) **4** Nest D and nest S attached to the same stone (viewed from the north, nest S not visible behind the side of the stone) **5** Nest GB attached to stone.

individuals while walking randomly across the area at all localities (total investigation time 18.25 h). Flower visiting behaviour of *Celonites fischeri* at *Echium angustifolium* was investigated at various patches of this plant at the localities I and II for 15 h in total. Pollen samples from two brood cell provisions of nest F (see below) from locality II were prepared using the method outlined by Westrich and Schmidt (1986). In addition, pooled pollen samples from four localities (II, III, VI and IX) were prepared each with pollen from the crops of five females previously fixed in Duboscq-Brasil solution (Romeis 1989). The different pollen types were ascertained under a light microscope at magnifications of 400× or 1000× and determined to generic level with the aid of a reference collection consisting of pollen samples of 500 mainly Mediterranean plant species.

The behaviour of a female at one of the nests (nest F; see below) was continuously investigated from 27 May until 30 May except for the individual's resting period during the night (total observation time 27.5 h). Spatial and temporal behavioural patterns were reconstructed in more detail by analysis of sequences of photographies repeatedly taken during the observation period. Activities inside the cell were observed with the aid of a magnifying hand mirror.

The nests were marked in the field with little ice-cream national flags and named after the country code of the flag used (Fig. 5). Nest GB was removed on 26 May, nest S and D on 27 May, and nest F on 30 May. In the field, cell dimensions were measured using a strip of millimetre paper (accuracy 1 mm). The brood cells were opened on June 1 and investigated under a stereomicroscope (Wild M3, magnification up to 40x, ocular micrometer with a maximum accuracy of 0.024 mm). The remnants of the nests as well as dry specimens of males and females from all localities were placed in the collection of Volker Mauss.

Behaviour and activity of males at sleeping aggregations were recorded at locality I both by point observations and during random searching on 20 May between 15h00 and 17h30, and at locality II by short observations on eight days. The number of males in each group (defined as all males sleeping together on the same stem end for a night) and the number of male groups were systematically counted in the evening, when male activity had completely stopped and all males remained motionless in sleeping position (at locality I from 20 to 30 May between 19h20 and 20h00; at locality II on 21, 23 and from 25 to 30 May between 17h40 and 19h00).

Results

Habitat

Celonites fischeri was found in various open and disturbed areas, including Phrygana fragments, coastal dunes, abandoned building areas and olive groves, as well as road sides. The localities were situated at altitudes between 10 m and 660 m above sea level. They were characterized by a considerable quantity of *Echium angustifolium*. Open water sources were always lacking.

Flower association

During random searching, all 46 sightings of flower visiting females and all 8 sightings of flower visiting males of *Celonites fischeri* were exclusively recorded at *Echium angustifolium*. Likewise, 68 females and 13 males recorded during point observations visited flowers of *E. angustifolium*. Visits to flowers of other plant species were not observed.

Both males and females showed two different types of behaviour at the flowers. The first behaviour served presumably for nectar uptake. The wasp alighted on the upper margin of the corolla and moved quickly head first deep into the corolla tube so that only distal parts of the metasoma remained visible in the flower opening (Figs 6, 8). Within the flower, the ventral side of the wasp was always orientated towards the upper wall of the corolla and its dorsal side towards the filaments and the style (Fig. 8). The wasp stayed in this position for a moment before it moved backwards out of the corolla tube and flew off. On a few occasions, when the wasp was leaving the flower, distal parts of the protruded proboscis were visible for a moment before the proboscis was completely retracted, indicating nectar uptake (Fig. 7). The median duration of nectar uptake by females was 3.2 s (range 1.6-9.8 s, n = 18). Nectar uptake was observed only at completely open flowers in full blossom. The second behaviour served apparently for pollen collection. The wasp alighted on the corolla and worked an anther with mandibles and maxillae (Figs 9, 13), while the proboscis remained retracted. At the same time, the fore legs made brushing movements from the anther towards the mouth and were repeatedly moved between the moving mouthparts. During the whole process the wasp held on only with its mid and hind legs with the meso- and metasoma remaining outside the corolla. The median duration of pollen uptake by females was 79.6 s (range 5.1–229.9 s, n = 15), which is significantly longer than the time for nectar uptake (Mann-Whitney Test: p (2-tailed) < 0.001). Pollen uptake by females was recorded at flowers with open (Fig. 13), half opened (Fig. 12) and only slightly opened corollae (Fig. 11), depending on the age of the flowers. In the latter case, the females forced their head into the only slightly opened corolla of flowers that had just started to open (Fig. 10, 11). The median duration of pollen uptake by the females did not differ significantly between flowers in different phases of corolla opening (Fig. 47; Kruskal-Wallis Test: Chi² = 0.72, df = 2, p = 0.70). On a single occasion a male was also observed to take up pollen from a flower with only slightly opened corolla tube while all other visits took place at open flowers.

Females were often observed to fly slowly past many flowers within an *Echium* patch before finally alighting on a particular flower where they started to take up pollen. During such an "inspection flight", a female sequentially approached flowers, but shortly before she came into contact with the corolla she changed the course and directed her flight towards another flower where the whole process started anew. Inspection flights were infrequently interrupted by perching on twigs or dry leaves, which was accompanied by cleaning behaviour in two instances. Foraging females were occasionally observed to switch from nectar uptake to pollen uptake or vice versa during a single flower visit as well as on consecutive visits to different flowers.

The crop content of all females investigated and the two brood cell provisions from the same nest consisted exclusively of pollen from *Echium* (more than 99%).



Figures 6–13. Flower visiting behaviour of *Celonites fischeri* at *Echium angustifolium*: **6** Female entering flower head first for nectar uptake **7** Female leaving flower after nectar uptake with proboscis still protruding **8** Male deeply inside corolla tube during nectar uptake **9** Male feeding on pollen directly from an anther **10–11** Female taking up pollen from flower with only slightly opened corolla tube **10** from anther accessible from outside **11** after forcing her head into the corolla tube from anthers inside the corolla tube **12–13** Females taking up pollen from the same flower at different stages of corolla opening **12** corolla half open **13** 9.5 min later corolla completely open.

Mating

Mating behaviour was observed both at flowering patches of *Echium angustifolium* and in the area of a male sleeping aggregation.

Males were frequently observed to patrol in a constant flight slightly above the *Echium* plants, sporadically interrupted by perching on inflorescences or on dry, horizontal stems near *Echium* plants (Fig. 21). Patrolling males sometimes approached each other over a short distance, but then continued their flights without any further interaction. On one occasion, two patrolling males flew towards each other, hovered face to face at a distance of about 1 cm and soared up in this position for approximately 5 cm, before they flew off in different directions. Patrolling males were observed several times to pounce on a flower visiting or perching male and, in a few incidents, they performed mating movements (Fig. 19) before flying off.

The behavioural sequence during copulation can be subdivided into three phases: 1. initiation, 2. insertion, 3. separation. At flowers, initiation always started by a patrolling male pouncing on a flower visiting female. In 12 out of a total of 16 cases, this was unsuccessful, since the female fell to the ground or flew off, remained on the flower without further interaction with the male or the male turned away before reaching the female (Fig. 14). In four cases, pouncing was successful and initiation behaviour was continued. After alighting on the dorsal mesosoma of the female the male held on to it (Fig. 15) and orientated his body axis parallel to hers. This resulted in a position, in which the head of the male was slightly anterior to the female's head with the male antennae orientated downwards and his fore legs placed on frontal parts of the female's head (Fig. 16). Then the male protruded the distal end of his proboscis at least for a short moment, raised his antennae and moved backwards on the back of the female (Fig. 20). During this process, the male antennae were orientated obliquely upwards and the male genitalia were already visible in the opening of the genital chamber. Finally, the head of the male was positioned above the posterior half of the female mesosoma and the basal parts of his fore legs were placed over the base of her wings and tegulae along with the fore tarsi on the sides of her mesosoma (Fig. 17). His mid and hind legs held laterally on to the anterior segments of her metasoma. The posterior end of the male metasoma was well behind the tip of the metasoma of the female (Fig. 18). The male genital chamber remained open and the genitalia were somewhat protruded. The mouthparts of the male were retracted with one exception when the distal end of the proboscis was still in a protruded position. The female usually continued pollen uptake. During the following insertion phase the male genitalia were inserted into the female genital chamber. This was observed only once with certainty at flowers and lasted for about 10 s. Separation was a short process in which the male genitalia were removed from the genital chamber of the female and both partners flew off directly. On two occasions it was observed that a second male alighted on the back of a copulating male (during initiation and insertion respectively) for a few seconds (Fig. 20).

Mating behaviour away from flowers was only observed once: At the male sleeping aggregation m_2 on 21 May at 15h49 a female alighted on a fine, dry twig where



Figures 14–21. Mating behaviour of *Celonites fischeri*: **14** Pouncing male turning off before reaching a flower visiting female **15** Male alighting on the mesosoma of flower visiting female, trying to hold on **16** Anterior position of the male during initiation, in which his head is a little anterior to the head of the female **17** Posterior position of the male during initiation, in which the head of the male is positioned above the posterior half of the mesosoma of the female **18** Male in posterior position during initiation, trying to insert genitalia into the genital chamber of the female. Note protruded male proboscis **19** Male performing mating movements after pouncing on a perching male **20** Male alighting on a pair in initiation phase. Note protruded proboscis of primary male **21** Male perching on dry stem of perennial herbaceous plant.

she remained for 7 min, while males were absent. In the beginning the female folded her wings under her metasoma. Later on she slightly opened her wings and spread her antennae. Then a flying male appeared and alighted directly on the mesosoma of the female, moved backwards on her back and inserted his genitalia into her genital chamber for 8.1 s before the partners separated and flew off.

Female brood care

Nest structure: Four nests were discovered at locality II (Table 1). All nest sites were less than 5 m away from patches of *Echium angustifolium* (Fig. 46). Three nests (GB, D and S) were attached to medium sized stones less than 10 cm above the ground. The nests were on oblique to nearly vertical lateral parts of the stones exposed to the west or north and were more or less hidden by vegetation (Fig. 4, 5). A fourth nest (F) was placed approximately 25 cm above the ground on a narrow, almost vertical stem about 10 cm inside of a dwarf shrub of the family Asteraceae, which was situated on the south-western margin of a patch of bushes (Fig. 1).

The nests were made of fine clayey soil with a small but variable proportion of tiny stones. The nests consisted of 2.5 cells in the median (n= 4) (Table 1). All the cells were orientated almost vertically with the opening directed towards the ground, but the arrangement of the cells was variable. In three nests, the cells were abutted only longitudinally (Figs 24, 25). In nest F, the third cell was also attached to the first cell longitudinally but the second cell was constructed with its closed end abutting the seal of the completed first cell resulting in a linear arrangement of these cells (Fig. 26). A nest covering was only present in nest GB (Fig. 22). The covering consisted of a smooth, thin layer of the same fine clayey earth as the brood cells and covered the cells completely. The material of the covering could be separated from the cell walls without difficulty indicating that it had been applied after the cells had been finished. The covering was only attached to the outer curves of the cells and to the adjacent substrate thus stretching over medial and lateral hollow spaces between the cells and the cell walls and the underlying stone respectively (Fig. 23).

The brood cells were cylindrical, rounded at the closed (basal) and truncate at the open (apical) end (Fig. 25). The median dimensions of the cells were: length of completed cells 10.5 mm (n = 10); outer diameter 4.4 mm (n = 4); and inner diameter at the cell opening 3.5 mm (n = 9) (Table 2). The median thickness of the cell wall was 0.29 mm (n = 11), becoming somewhat wider at the basal end of the cell. The outer cell surface showed a distinct "fish scale" pattern while the inner surface was smooth. The cell seal was positioned about 1 mm inwards from the edge of the cell opening. The thickness of the seal varied slightly over its diameter and measured in the median 0.23 mm (n = 8) at the thinnest part. Sealed cells of old nests mainly had a large frontal or lateral opening that covered the apical third of the cell and had probably been made by an emerging imago of *Celonites fischeri* (Figs 22, 25, Table 2).

Brood cell content: The content of the brood cells is summarized in Table 2.



Figures 22–26. Nest structure of *Celonites fischeri*: **22–24** Nest GB **22** Original condition on 26 May with frontal emergence hole probably made by *C. fischeri*. **23** Nest covering partly removed to show hollow spaces underneath; cell GB₁ opened containing meconium of *C. fischeri* at basal end **24** Cell GB₂ opened, showing brittle brown cocoon of unidentified holometabolic insect in basal half and small emergence hole apical in the cell wall **25** Nest S on 27 May. Cells S₁, S₃, S₄, S₅ (ordered from the left) with frontal emergence holes probably made by *C. fischeri* **26** Nest F on 1 June after dissection of cells F₁ and F₂ (cell content summarized in Table 2).

The provision was a purple, firm, but somewhat viscous pollen mass with shining surface. Contact of the provision with the cell walls was variable: In cell F_1 the surface of the pollen mass was characteristically papillated (Fig. 26), so that it barely touched

Nest	Condition	Height above ground (mm) ¹	Orientation to the North (°)	Nest substrate	Inclination of nest substrate (°)	Σ cells	Contact between adjacent cells	Nest covering
GB	old	43	20	stone (base 38×31 cm, height 19 cm)	60	2	longitudinal	present
D	old	77	20	stone (base 40×29 cm, height 24 cm)	85	2	longitudinal	absent
S	old	90	280	stone (base 40×29 cm, height 24 cm)	95	5	longitudinal	absent
F	under construction	243	70	plant (narrow stem of Asteraceae scrub)	100	3	linear or longitudinal	absent

Table 1. Parameters of four nests of *Celonites fischeri* recorded at locality II 0.5 km north of AgiosGeorgios, Cyprus.

¹measured from the lowest part of the nest

the cell walls. In cell F_2 the provision broadly adhered to the wall and apparently moistened it. However, this could have been an artefact, since the cell had to be removed and transported only a few hours after provisioning had been completed. The outer cell surface appeared to be dry when the cell was removed but was wet two days later, when the cell was opened, suggesting an artificial situation.

The egg of *Celonites fischeri* from cell F₂ was whitish, curved and measured 1.88 mm in length. It was situated on top of the provision close to the basal end of the cell (Fig. 26). Remnants of fibrous material were attached to one pole of the egg indicating that it had been fixed to the original cell wall before this had been removed during the dissection of the cell. In the same way the small larva from cell F₁ was also situated basally on top of the pollen mass, where it fed on the provision (Fig. 26). As in the egg there was some light fibrous material adhering to the posterior end of the larva that was distally fixed to the cell wall. The cocoon of C. fischeri consisted of whitish to yellowwhitish shining threads thinly covering the inner cell walls and the seal (Fig. 23). The threads became more sparse towards the basal end of the cell and in 50% of the cases (n = 6) threads were completely lacking at the basal end of the cell. The meconium was situated at the basal end more or less inside the cocoon. The cocoon threads were more brownish in this part of the cell indicating the secretion of a fluid component during the discharge of the meconium (Fig. 24). The solid fraction of the meconium comprised about 50 little, spherical, blackish packs containing pollen exines. The packs were loosely connected to each other by short threads.

Behaviour at the nest: The temporal pattern of the behaviour of the focally observed female at nest F is summarized in Fig. 48. The behavioural sequence during brood cell preparation can be subdivided into four phases: 1. cell building, 2. oviposition, 3. provisioning, 4. sealing.

At the beginning of the construction of a new brood cell, when already one or more cells had been constructed, the female alighted without a soil pellet on the stem just below the nest. Then she walked upwards and downwards, randomly across the cell(s) and also back on the stem again for approximately 1–2 min. Finally she

Nest	Cell no.	l Condition	Cell length (mm-below)	Inner cell width ¹ (mm-below)	Outer cell width (mm)	Thickness of cell wall (mm)	Thickness of seal (mm)	Content	Succeeding organisms
Ę	1	complete: sealed; large emergence hole, apical laterally in cell wall, directing away from stone edge	10	ю		0.38		cell walls and seal covered with thin whitish cocoon, a bit more brownish at basal 1/4 of cell where meconium had been placed; blackish meconium at basal end of cell inside cocoon comprising about 50 little spherical packs containing pollen exines	remnants of little spider (Salticidae spec.) and small gossamer
3	7	complete: sealed; small emergence hole, apical laterally in cell wall, directing towards stone edge	6	ŝ		0.31		reddish-brown, brittle cocoon in basal half of cell, cocoon cap loosely in the cell, threads inside of cocoon covered with a solid, brownish translucent secretion, apical of initial position of cocoon cap some brownish cocoon threads fixed on cell wall forming a thin incomplete layer	
D	1	complete; sealed; large emergence hole, apical obliquely downwards, mainly in seal but slightly extending into adjacent cell wall	10	Э	4.2	0.29	0.24	yellow-whitish, somewhat shining threads of cocoon on apical cell walls and seal, lacking at basal end of cell; blackish meconium at basal end of cell comprising about 50 little spherical packs containing pollen exines	remnants of little spider (Salticidae spec.), cell filled with gossamer
	7	incomplete; open	4	3		0.36			
\sim		complete; sealed; large emergence hole, apical anteriorly in cell wall; with a droplet of translucent yellowish, highly viscous liquid	10	n		0.24	0.24	cell walls and seal thinly covered with whitish, somewhat shining cocoon threads, becoming less dense towards basal end and a bit more brownish at basal 2/5 of cell where meconium had been placed; blackish meconium at basal end of cell inside of cocoon, comprising little spherical packs containing pollen exines, a few of these packs also in gossamer at apical end of cell	little spider (Salticidae spec.), cell filled with gossamer

Table 2. Measurements and condition of brood cells from four nests of Celonites fischeri recorded at locality II 0.5 km north of Agios Georgios, Cyprus.

	Condition	Cell length (mm-below)	Inner cell width ¹ (mm-below)	Outer cell width (mm)	Thickness of cell wall (mm)	Thickness of seal (mm)	Content	Succeeding organisms
comple small emer apical e	tte; sealed; gence hole, at nd in seal	10	ĸ		0.29	0.14		remaants of little spider (Salticidae spec.), cell filled with gossamer; cluster of little, brown, hard-shelled globes (eggs?)
comp large em apical an wall; coa with transl highly v	lete; sealed; ergence hole, teriorly in cell ted all around ucent yellowish, iscous liquid	11	ŝ		0.24	0.22	cell walls and seal thinly covered with whitish, somewhat shining cocoon threads, blackish meconium at basal end of cell inside of cocoon, comprising about 50 little spherical packs containing pollen exines	highly viscous cell provision (probably of bee); cluster of little, brown, hard-shelled globes (eggs?)
comp large em apical an	lete; sealed; ergence hole, teriorly in cell wall	11	n		0.24	0.17	cell walls and seal very thinly covered with yellow- whitish, somewhat shining cocoon threads, becoming less dense and a bit more brownish basally, completely lacking at basal end; two little spherical packs of blackish meconium fixed at basal end of cell, about 50 of these packs that probably had fallen down from basal end form blackish mass on seal	
comp large en apical ar	olete; sealed; nergence hole, nteriorly in cell wall	11	ŝ		0.29	0.24	cell walls and seal very thinly covered with yellow- whitish, somewhat shining cocoon threads, completely lacking at basal 1/2 of cell; six little spherical packs of blackish meconium fixed at basal end of cell, about 50 of these packs that probably had fallen down from basal end form blackish mass on seal	

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Succeeding organisms			
Content	firm but somewhat viscous, purple pollen mass with shining, papillate surface, barely rouching cell walls over large area making contact only by papillae, at two spots sticking broadly to cell wall; small larva feeding on basal end of pollen loaf; larva at posterior end with adhering light fibrous material distally fixed to cell wall	firm, purple pollen mass, less viscous as in cell F1, without papillae on surface, making complete contact to cell wall (artefact?), with central cavity continuing from apical to basal end; egg basally on top of provision with one end inside pollen mass and remnants of fibrous material adhering to opposite end (probably egg had been fixed with this material to part of cell wall that had been removed); egg whitish, curved, 1.88 mm long	
Thickness of seal (mm)	0.22	0.24	
Thickness of cell wall (mm)	0.26	0.24	
Outer cell width (mm)	4.3	4.6	4.5
Inner cell width ¹ (mm-below)	n	ςΩ.	
Cell length (mm-below)	=	10	6
Condition	complete; sealed	complete; sealed; cell wall appeared wet in section containing pollen mass (artrefact due to removal and transport a few hours after cell completion?)	incomplete; open
Cell no.	-	7	3
Nest		Ц	

measured at the cell opening

stopped and remained at a certain point head upwards with her body axis orientated in vertical direction (Fig. 27). Then she brought her mouthparts into contact with the substrate and moved slowly downwards (Fig. 28). After contact with the mouthparts the surface had a wet appearance with only very few or completely without adhering soil particles, indicating the application of a fluid. The process took approximately 30-40 s until the female flew off. She returned after 3 to 4 min, with a soil pellet held between her mandibles and labial palpi and alighted on the stem shortly below the nest (Fig. 35). She moved upwards to the point where she had started to apply liquid during the previous visit and began to add the moist soil to the substrate. During the first two or three visits, the female stood on the substrate while building parts of the basal cell wall connecting the cell with the underlying material, i.e. the stem or the wall of the previously build cell F, (Fig. 29). Then she changed her position and held on to the developing basal end of the cell (Fig. 30). Each load of soil was added to the cell in the form of a semi-circular plate, except for material directly applied to the underlying substrate. When building a semicircular plate the female positioned herself with her head and fore legs inside the cell, her metasoma curved around on the outside and her mid and hind legs holding on to the outer surface of the cell wall (Figs 31, 32). The mid legs were placed laterally, while the tarsi of the hind legs were positioned medially on the outside in front of the mandibles and the clypeus of the female working as an abutment during the application of the building material from the inside.

The building material was always applied through the moderately opened mandibles supported posterior-laterally by the labial palpi and posterior-medially also by the maxillary palpi (Figs 29, 31). Since the material appeared more shining and runny close to and in front of the mandibles (Fig. 32), it is likely that further liquid was added. The applied material was smoothed and formed with parts of the clypeus and mandibles (Figs 29, 30) by rubbing movements of the head accompanied by body vibrations. In addition the female infrequently slightly turned her body along the cell margin.

Each period in which building material was added to the cell under construction took between 30-50 s. These material-adding periods regularly alternated with periods during which the female was absent from the nest to collect soil. The median length of soil collection flights was 71 s (range 53-125 s; n = 6). The complete sequence of soil collection flight and material application took 119 s in the median (range 90-137 s; n = 5). Alternating with a cycle of cell construction and soil collection were longer intervals during which the female was away from the nest probably for refilling her crop with liquid. As in the area there was no source of water it seems probable that the female collected nectar. Absence for liquid collection took 23 min in the median (range 17-29 min; n = 9).

After the building of cell F_2 had been completed, the female flew off and was absent from the nest for 28 min. She returned at 16h58, alighted on the stem shortly below the nest and entered the new cell head first. Inside the cell she remained active and the tip of her metasoma became repeatedly visible in the cell opening performing vigorous transverse contractions with high frequency (Fig. 37). Occasionally, in addition, she turned slightly around her longitudinal axis. At 17h16 she was deep inside the



Figures 27–33. Nest building behaviour of *Celonites fischeri* at nest F: **27** Following the orientation walk the female has stopped and is touching the substrate with her mouthparts at the place where she will later construct the basal end of the new cell during the subsequent visits. Note that she is not carrying a soil pellet **28** The female has moved slowly downwards keeping her mouthparts into contact with the outer surface of cell F_1 **29** The female is building parts of the basal cell wall of cell F_3 standing on the surface of cell F_1 **30–32** The female holds on to the wall of the cell F_3 adding soil pellets in the form of semi-circular plates. The hind legs are used as abutment while the material is applied with the mouthparts from the inside **33** The female is sealing cell F_2 .



Figures 34–39. Behaviour associated with female brood care in *Celonites fischeri*: **34** Female taking up soil at a quarry site **35** After alighting on the stem below nest F the female is moving upwards to the nest with a soil pellet held between her mouthparts **36** Female resting in cell F_1 in the evening. Note that her wings are folded underneath her metasoma and that she probably could not move deeper inside the partly provisioned cell **37** Female remaining active inside cell F_2 . Note that her wings are in their normal dorsal position **38** Female depositing a portion of the provision of cell F_1 after a pollen collecting trip **39** On a subsequent visit the female has to stay further outside the cell than before during provisioning due to the increased volume of the provision inside the cell.

cell, with her still contracting metasoma directed towards the cell opening (observed with a mirror). On the following inspection at 17h29 the female remained motionless in a curled position in the lower part of the cell with her head close to the entrance. This was the only occasion in which the female was observed with her genital chamber directing towards the basal end of the cell indicating that oviposition had taken place. At 17h32 the female appeared in the entrance head first, left the cell, turned around and re-entered the cell head first directly thereafter and finally remained motionless deeply inside the cell with her wings folded in resting position underneath the metasoma directed towards the cell opening.

Throughout the provisioning phase the female regularly alternated between periods in which she was absent from the nest to perform provisioning flights and visits to the nest to deposit a portion of larval provision. A provisioning flight took 37 min in the median (range 24-73 min; n = 20). On return the female always alighted on the stem shortly below the nest and moved upwards directly into the cell head first. Within the cell the female gradually turned around her longitudinal axis, regularly interrupted by short periods during which she remained in her attained position. The direction of the rotations was either clockwise or counter clockwise and sometimes the female changed the direction within a single visit. At the same time her metasoma performed vigorous transverse contractions with high frequency. Sometimes telescopic contractions in longitudinal direction occurred in addition. On subsequent visits the wasp could move less and less deeply into the cell, since the volume of the provision increased with each deposit. Therefore, whereas at the beginning of the provisioning phase only the tip of her metasoma remained visible in the cell entrance, later on the metasoma and parts of the mesosoma protruded more and more from the cell. At this stage the female held onto the margin of the cell opening or the stem with her hind legs and finally also her mid legs bending her metasoma ventrad at an angle of approximately 60° against the longitudinal axis (Figs 38, 39). Leaving the nest the female backed out of the cell holding on to the opening and the outer cell wall with her hind and mid legs thus turning her longitudinal axis obliquely downwards. In this position she removed her head and fore legs from the cell entrance, turned her body upwards around the cell margin and walked at least a few steps on the outer surface towards the upper half of the cell. Here the female often remained for a few seconds until she flew away (Fig. 40). Visits to the cell for provisioning took 4 min in the median (range 2-7 min; n = 22).

The sealing phase started with the absence of the female from the nest for 7 to 17 min respectively. She returned with a soil pellet, alighted on the stem shortly below the nest and walked upwards. The female positioned herself directly below the cell entrance holding on to the apical margin of the cell with her mid and hind legs (Fig. 33) or to the stem just below it, while her head and fore legs were inside of the cell opening (Fig. 41). She applied the building material with her mouthparts sometimes accompanied by nodding movements of her head turning gradually around the cell opening. Sealing of a brood cell required 3 to 6 visits respectively, each lasting 30–50 s. The visits were regularly interrupted by soil collection flights taking 64 s in the median (range 26-164 s; n = 7).



Figures 40–45. 40 Female of *Celonites fischeri* remaining briefly on top of cell F_1 before taking off. **41** Female of *C. fischeri* sealing cell F_2 holding onto the stem below it **42–45** Behaviour of *C. fischeri* males at locality I Kato Paphos **42** Males aggregated in groups at withered stem ends of a dwarf shrub **43** Group of three males in sleeping position **44** A late arriving male has alighted on the male at the top of the group and is walking over it **45** Male in sleeping posture (viewed from the right).

Altogether the construction of brood cell F_2 required seven cycles of cell construction and soil collection in connection with seven preceding liquid collection flights taking 247 min in total (Fig. 48). Oviposition took place within less than 15 minutes. The provisioning phase included 14 provisioning flights and visits to the cell lasting 707 min in total. Finally the cell was sealed within 27 min. The cell building rate can be roughly estimated as one completed cell per two days. Cell building was initiated around midday and was finished by the end of the flight period of the same day and was followed by oviposition in the late afternoon. Provisioning took the second day and the morning of the third. Finally the cell was sealed around midday of the third day. Shortly thereafter the female started again with the building phase of another brood cell.

In all visits to the nest the female followed a characteristic pattern of orientation. On return she always alighted on the stem shortly below the nest and walked upwards to the cell (Fig. 35). On departure she walked upwards on the outer surface of the cell where she often remained for a moment before she flew off (Fig. 40). During the night the female always remained motionless in the cell in a characteristic posture with her wings folded underneath her metasoma (Fig. 36).

Soil collection: Two females of Celonites fischeri were observed to collect soil at a quarry site, which was a bare area with fine clayey soil measuring approximately 30×30 cm (Fig. 2). During consecutive visits each female always alighted on the same spot of the quarry site with identical orientation of her body axis. Within a soil collecting cycle a female arrived every 2–3 minutes at the quarry site. Soil uptake took 20.7 s in the median (range 20.6–21.6 s; n = 3). For soil collection a female stood on the ground with her mid and hind legs moving her head vigorously in a high frequency in dorso-anterior and ventro-posterior direction while scraping up a load of soil with opened mandibles which were moving inwards and outwards (Fig. 34). The process was supported by irregular movements of the forelegs with lower frequency. The removed soil had a wet appearance indicating that liquid was used during soil uptake. The moist soil particles accumulated behind the mouthparts forming a pellet that was held with the aid of the labial palpi. Finally, held securely in this position by the mandibles and labial palpi the soil pellet was carried in flight to the nest.

Male sleeping aggregations

One male sleeping aggregation was recorded at locality I and two separate aggregations at locality II (Fig. 46). The males aggregated for the night in small areas of less than 0.1 m^2 where they slept together in groups curled up around fine, withered stem ends of herbaceous plants or dwarf shrubs (Figs 42, 43). The males used the same sites over a period of at least 10 to 11 days, but there was some variation regarding the particular stems used. Moreover, the total number of males and the number and size of male groups within an aggregation varied noticeably over the observation period (Fig. 49). The median number of males per aggregation and night was 7 (range 0–13; n = 27)



Figure 46. Schematic map of the main study area of *Celonites fischeri* at locality II 0.5 km north of Agios Georgios, Cyprus.

divided into 3 groups (range 0–6; n = 27). Stem ends used by male groups were about 5–30 cm away from each other and about 20–40 cm above the ground. Group size varied from 1–5 males (median number = 2; n = 83) (Fig. 50). The distance between neighbouring males within a group varied between 0 mm (i.e., in physical contact with

duration of pollen uptake (s)



Figure 47. Correlation between the duration of pollen uptake by flower visiting females of *Celonites fischeri* and the stage of corolla opening of the visited flower of *Echium angustifolium* (median marked with line).

each other) and 7 mm, in one instance it was 50 mm. All males adopted the same typical posture; the bodies were curled clockwise or anticlockwise around the stem so that the tip of the metasoma covered the ventral part of the head. Antennae and legs were pulled up under the mesosoma, and the wings were folded underneath the metasoma (Fig. 45).

Formation of the sleeping aggregations started in the afternoon between 15h00 and 16h00, when males began to alight and perch frequently on fine, withered stem ends in the area of the aggregation. Some of the males also started to adopt the sleeping posture and curled their bodies part way around the end of a stem. However, group formation led to a lot of interactions and disturbance, since newly arriving males repeatedly alighted on males that had already occupied a sleeping position (Fig. 44). Later appearing males often tried to reach a position at the top of the group or between two other males. This sometimes resulted in a few or all of the males flying up and immediately returning thereafter, even though not always to the same stem. The last male interactions were recorded between 17h00 and 18h00. After that all males remained motionless at their final position in sleeping posture until the end of the observation period in the evening. In the morning males were observed to leave the sleeping aggregation before 9h00 at locality I and between 9h30 and 10h00 at locality II respectively.



Figure 48. Ethogram of female brood care behaviour of *Celonites fischeri* based on continuous focal observation of nest F from 27 May until 30 May 2013 (interrupted only during the resting period of the female during the night; total observation time 27.5 h).



total number of sleeping males

Figure 49. Total number of males, the number of male groups and size of male groups within three male sleeping aggregations of *Celonites fischeri* from 20 to 30 May 2013 based on counts made in the evenings.



Figure 50. Range and frequency of group size in male sleeping aggregations of *Celonites fischeri* based on 83 registered male groups from three aggregations at two different localities in Cyprus from 20 to 30 May 2013.

Associated organisms

A single brood cell had been parasitized by an unknown holometabolic insect (Fig. 24, Table 2).

After emergence of the imagines the old cells of *Celonites fischeri* were regularly inhabited by little jumping spiders (Salticidae). Old cells were also used by solitary bees as pre-existing cavities for nesting (Fig. 25, Table 2).

Discussion

Flower association

At all Cyprian localities, males and females of *Celonites fischeri* were observed to visit only flowers of *Echium angustifolium* for nectar and pollen uptake. Likewise, the content of the female alimentary tracts and the two brood cell provisions investigated exclusively consisted of *Echium* pollen. This is in accordance with the only flower visiting record published for *C. fischeri*, i.e. a photo of a pollen collecting female at an *Echium* flower taken by Weinstein (2008) in Israel. Therefore, *C. fischeri* is most prob-
ably narrowly oligolectic, using flowers of *Echium* as the sole pollen source. Oligolecty or narrow polylecty are the rule for many species of the Masarinae and are common in Celonites (Gess 1996; Gess and Gess 2010). An association with flowers of Boraginaceae has also been established for Celonites heliotropii Gess, 2007 in the Afrotropical region (Gess 2007) and may also exist in eight additional Celonites species from the Palaearctic, which were observed to visit plants of this family (summarized in Gess 1996). Interestingly, C. afer, which is the closest relative of C. fischeri, has also been recorded from four North African species of *Echium* (Bequaert 1940), suggesting that both species of the C. fischeri-complex are associated with this plant genus. This flower specialisation might explain the absence of knobbed setae on frons and clypeus of C. fischeri and C. afer, since Echium flowers are sternotribic. In contrast, the knobbed setae of the species of the C. abbreviatus-complex serve to harvest pollen from nototribic flowers of the Lamiaceae (Schremmer 1959; Müller 1996). Females of C. abbreviatus collect pollen from Lamiaceae species by rubbing the knobbed setae over the anthers so that pollen grains accumulate on the frons. Afterwards, the pollen is transferred from the head to the mouthparts by brushing movements of the fore legs (Schremmer 1959; Bellmann 1995; Müller 1996; Mauss 2006). In contrast, pollen gathering females of C. fischeri ingest pollen directly from the anthers of the Echium flowers with the aid of the fore tarsi. This corresponds closely to the pollen collecting behaviour of most other Masarinae, which either ingest pollen directly from the anthers or use their fore legs to work the anthers and draw the pollen towards their mouthparts (Gess and Gess 1989; 1990; cf Gess 2004; cf Neff and Simpson 1985; cf Torchio 1970). Interestingly, the females of C. fischeri perform a remarkable pollen collecting strategy, which has never been described in pollen wasps before in that they gather pollen from *Echium* flowers that have just started to open by forcing their heads into the only slightly opened corolla. The regularly observed "inspection flights" of the females (see Results) may serve to increase the probability of locating flowers in an early stage of flowering, which are expected to offer higher amounts of pollen in comparison with older flowers, in which the pollen has already been depleted by other flower visitors. At least some of these competitors are not able to collect pollen from the flowers before the anthers are accessible for regular flower visits. This pertains for instance to oligolectic megachilid bees of the genus Osmia (subgenus Hoplitis), which take up pollen from Echium flowers with a scopa on the underside of the metasoma. Despite its distinct pollen collecting strategy, Celonites fischeri seems to collect pollen less efficiently than C. abbreviatus as indicated by significantly longer provisioning trips performed by the female from nest F in comparison with the C. abbreviatus female studied by Bellmann (1984) (Table 3; Mann-Whitney Test: p (2-tailed) < 0.001). The difference could be related to the specialized pollen collecting apparatus of C. abbreviatus. However, the hypothesis that indirect pollen uptake with knobbed setae is more efficient than direct pollen uptake from the anthers should be tested in more detail at different localities and with a higher sample size.

During nectar uptake the body of *Celonites fischeri* is inverted by 180° so that the dorsal side of the wasp projects towards the reproductive organs of the *Echium* flower

	total time for brood cell provisioning [min]	707	220	۸.
	mean length of provisioning trips [min]	41.9 (± 12.7)	17.3 (± 3.4)	۸.
	Σ provisioning trips per brood cell	14	11	۸.
4	total time for brood cell construction [min]	247	194	128
,	(mean) length of liquid collection trips during construction phase [min]	22.8 (± 3.8)	$19.3 (\pm 3.8)$	10-20
	Σ construction cycles per brood cell	7	8	
4	Σ soil adding periods per brood cell	47	41	36
4	Species	Celonites fischeri	Celonites abbreviatus ¹	Celonites latitarsis ²

Table 3. Comparison of various parameters of brood care behaviour between C. fischeri and other species of Celonites and Pseudomasaris.

Data source: ¹ Bellmann 1984, ² Gess and Gess 1992, ³ Neff and Hook 2007, ⁴ Torchio 1970

520 265

 $\frac{31.5 (\pm 7.1)}{31.3 (\pm 2.4)}$

2 8

389

20-30 19.5 (± 8.0)

13

~ 22

Pseudomasaris phaceliae³ Pseudomasaris edwardsii⁴

n.

without coming into contact with the stigma. Therefore nectar visits of *C. fischeri* to *Echium* flowers have to be regarded as illegitimate visits and *C. fischeri* is probably not an efficient pollinator of the plant.

Mating

Males of *Celonites fischeri* regularly seek for mates patrolling *Echium* patches. This is in congruence with the behaviour of *C. abbreviatus* and several Afrotropical species of *Celonites* that also search for females at floral resources (Mauss 2006; Gess and Gess 2010). However, the single copulation of *C. fischeri* observed in the area of a sleeping aggregation indicates that further mating strategies exist, independent of flowers.

The general behaviour during copulation is similar in *Celonites fischeri* and *C. ab-breviatus*. In both species the initiation starts with a patrolling male pouncing on a female and the position of the male on the female during the insertion phase is quite similar (cf Mauss 2006). Insertion length is similar among the species and takes only about 10 s (cf Mauss 2006). However, the initial anterior position of the male on the female and the short protrusion of the distal end of the proboscis in *C. fischeri* were not described for *C. abbreviatus* (Mauss 2006). This could be due to the less complete photographic documentation of copulation behaviour in *C. abbreviatus* that did not allow more detailed analysis of "grappling" (Mauss 2006) between both partners in this phase. For other species of *Celonites* actual copulation has not been observed (Gess and Gess 2010). A comparable movement of the male backwards on the female's back has also been observed in the copulation of *Pseudomasaris* where it is combined with a series of strokes with the elongated male antennae on the head of the female (Longair 1987).

Female brood care

The recorded nests of *Celonites fischeri* were aerial and completely exposed although somewhat hidden by vegetation. This is quite similar to nest sites of *C. abbreviatus* with the exception that in *C. abbreviatus* nests are located exceptionally in pre-existing cavities on the underside of stones in addition (Bellmann 1984). Nests of Afrotropical species of *Celonites* are mainly in protected situations (Gess and Gess 2010) apart from a putative nest of *C. promontorii* Brauns, 1905 that was completely aerial, exposed on a stem of a dwarf shrub (Gess and Gess 1989). Nests of *C. fischeri* were built on stones or plants. The same variability regarding the nest substrate has been reported for *C. abbreviatus* (on a dry stem Lichtenstein 1869, on stones Ferton 1901, 1910; Bellmann, 1984, 1995) and *C. andrei* Brauns, 1905 (Brauns 1913) and is also present in *Pseudomasaris phaceliae* Rohwer, 1912 (Neff and Hook 2007) and *P. edwardsii* (Cresson, 1872) (Torchio 1970). The single known nest of *C. mayeti* described by Lichtenstein (1875) was attached to a stone. The nests of *C. fischeri* in Cyprus were not orientated towards the south, probably to avoid strong irradiation by the sun that may cause over-

heating in the hot Mediterranean summer. In contrast the majority of the nests of *C. abbreviatus* from Central Europe are exposed to the sun (Bellmann 1995).

The covering of a nest of *Celonites fischeri* with a thin layer of earth is similar to the observed nest covering in *C. abbreviatus* (Bellmann 1984). However, in two out of three old nests of *C. fischeri* a nest covering was lacking. Variation in the presence and degree of development of a nest covering has also been reported for *C. abbreviatus* (Bellmann 1995) as well as for *Pseudomasaris edwardsii* (Torchio 1970) and *P. phace-liae* (Neff and Hook 2007). It is unknown whether this is caused by external disruption of nest construction behaviour or by behavioural variance.

In the recorded nests of Celonites fischeri the average number of cells was 3.0 (± 2.7; n = 4). This is within the range of the number of cells in nests of *C. abbreviatus* recorded by Bellmann (1984), although his average number of cells per nest was slightly higher, 4.1 (± 2.7; n = 11). In nests of C. fischeri the brood cells are attached to each other both longitudinally and linearly. This variable arrangement of the brood cells is also present in C. abbreviatus (cf Lichtenstein 1869; Ferton 1901; Bellmann 1984) and C. michaelseni Schulthess, 1923 (Gess et al. 1997) but it seems to be absent in C. andrei (Brauns 1913) and species of Pseudomasaris (Neff and Hook 2007; Torchio 1970) in which the cells are only longitudinally attached to each other. The brood cells of the single nest of C. mayeti (Lichtenstein 1875) and a single putative nest of C. promontorii (illustrated in Gess 1996) were also connected longitudinally. The linear arrangement of cells in nests of *Celonites* may be associated with the characteristic frontal or lateral situation of the emergence hole in the wall of the brood cells of C. fischeri and also C. abbreviatus (Bellmann 1995). Emerging through the cell wall instead of the original cell opening is possibly a precondition for a linear cell arrangement. Otherwise the emerging wasp would have to break at least through one adjacent cell. In contrast the adults of Pseudomasaris phaceliae remove the old seal and emerge through the original apical cell opening (Neff and Hook 2007).

The brood cells of *Celonites fischeri* correspond well to the cells of all other *Celonites* species in the distinct "fish scale" pattern on the outer surface, the smooth inner surface of the constructed earthen cell and the construction of the seal just inside the cell opening (Bellmann 1984; Gess and Gess 2010). These characters are also present in the aerial brood cells of *Pseudomasaris* (Neff and Hook 2007; Torchio 1970). However, the cells of *C. fischeri* are almost parallel sided, as in *C. abbreviatus* (Bellmann 1984), while the cells of Afrotropical species of *Celonites* are more ovoid (Gess and Gess 1989, 1992, 2010; Gess et al. 1997).

The cocoon of *Celonites fischeri* is whitish to yellow-whitish and thin becoming more sparsely or even completely absent towards the basal end of the cell. This is in congruence with the cocoon of *C. abbreviatus* that has been described as white and very thin (Bellmann 1984). The meconium of *C. fischeri* looks similar to the fecal mass of *Pseudomasaris edwardsii* figured by Torchio (1970: Fig. 21) consisting of compressed fecal pellets. Comparable smooth, flattened semicircular pellets have been described for *P. phaceliae* (Neff and Hook 2007). This is the first documentation of the meconium of a *Celonites* species.

The behavioural sequence and specific manners of the *Celonites fischeri* female during nest construction generally resembles the nest building behaviour of *C. abbreviatus* (Table 3, cf Bellmann 1984, 1995).

In *Celonites fischeri* the cell building phase was always initiated by the female walking randomly over the brood cells and finally adding some fluid without or nearly without soil particles to the substrate at the future site of the new cell. This preparation of the new starting point seems to serve as some kind of marking, since afterwards the female always moved directly towards the new construction site. It is unclear whether a similar orientation and initiation sequence is present in *C. abbreviatus*, since Bellmann (1984) started his focal observation only when the female was already building the second segment of the brood cell. A comparable initiation behaviour at the beginning of the cell building phase has been described in *Pseudomasaris edwardsii* (Torchio 1970).

During cell building the female of *Celonites fischeri* always placed the tarsi of her hind legs on the outside of the cell immediately in front of her head working as an abutment while she was applying material with her mouthparts from the inside. This characteristic posture is also adopted by *C. abbreviatus* during cell building (Bellmann 1984). However, in 1995 Bellmann stated that the tip of the metasoma is used as a "trowel" during the application of soil, but this is in contradiction to all of his published figures (Bellmann 1984: Fig. 2, 1995: p. 150) and to his particular emphasis from 1984 that the metasoma of the female did not come into contact with the cell wall. In contrast, in *Pseudomasaris* use of the posterior metasomal sterna in nest building has been proven in *P. edwardsii* (Torchio 1970) and *P. phaceliae* (Neff and Hook 2007) and soil application to the cell wall occurs without direct involvement of the hindlegs that are situated more laterally.

The soil collection behaviour of *Celonites fischeri* is similar to soil uptake of *C. lati-tarsis* Gess, 1992 and *C. wahlenbergiae* Gess, 1989 (Gess and Gess 1992). These species use also defined quarry sites on small bare areas, here stabilized molerat "hillocks", where the females vibrate up and down vigorously apparently loosening sand with their mandibles (Gess and Gess 1992). *Celonites latitarsis* visits to the quarry site take an average of 29 s (Gess and Gess 1992) which is comparable with 21 s taken by *C. fischeri*.

The temporal pattern of cell building behaviour is rather similar in *Celonites fischeri* and *C. abbreviatus* (cf Bellmann 1984). In both species cell construction is initiated in the middle of the day, is finished in the late afternoon and is immediately followed by egg-laying. Afterwards the female spends the night inside the new cell and starts to provision it in the morning of the following day. However, the length of the provisioning phase seems to differ lasting one and a half day in *C. fischeri*, but only a half day in *C. abbreviatus*. Despite this difference provisioning is finished in both species at the end of the morning and is directly followed by sealing the cell. The focally observed female of *C. fischeri* completed about half a brood cell within 24 hours whereas a female of *C. abbreviatus* (Table 3) indicating once more that *C. abbreviatus* may collect pollen more efficiently than *C. fischeri* (see above).

The reproductive success of *Celonites fischeri* at the time and place of the present study can be estimated from the content of the old brood cells; from nine old brood cells six showed signs of successful development of *Celonites* offspring while three failed (Table 2). Therefore two-thirds of the completed brood cells of a female develop successfully. Success rate can be expected to vary from year to year and place to place, depending upon e.g. weather conditions, availability of provision and occurrence of nest parasites. The total number of cells that a female may construct has yet to be established.

Male sleeping aggregations

The formation of male sleeping aggregations in *Celonites fischeri* is in congruence with the behaviour of *C. abbreviatus* the only member of the Masarinae in which male sleeping aggregations have been recorded previously (Amiet and Mauss 2003). In both species the characteristic sleeping posture of the males is identical (cf Bischoff 1927; cf Amiet and Mauss 2003) and the males start to aggregate early in the afternoon. As in *C. abbreviatus*, the males of *C. fischeri* use the same site over several consecutive nights. In *C. fischeri* it has been observed for the first time that number and size of the male groups vary partly between successive nights, indicating some variance in the composition of the male groups. During formation of the aggregation in the afternoon there are several interactions between the males that often try to reach a position at the top of the group. According to Freemann and Johnston (1978) in male sleeping aggregations of various Aculeata roosting in a more apical position is frequently preferred, since it may offer better protection against walking predators that have to approach from the basal or central regions of the plant.

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