

Nesting Biology and Social Behavior of *Xenochlora* Bees (Hymenoptera: Halictidae: Augochlorini) from Perú

SIMON M. TIERNEY,^{1,*} THERANY GONZALES-OJEDA,^{1,2} AND WILLIAM T. WCISLO^{1,†}

ABSTRACT: The augochlorine (Halictidae) bee genus *Xenochlora* is the diurnal sister group to the nocturnal *Megalopta*, both of which are stem-nesting halictid bees. Here we present notes on the nesting biology and social behavior in four nests of *Xenochlora nigrofemorata* and one nest of *X. ianthina* from Madre de Dios, Perú. All nests contained multiple females and dissections of *X. nigrofemorata* indicated within nest reproductive differentiation among females that is associated with body size. Size variation among females is conspicuous and a variety of morphometrics are examined to document it. A genal index is used to describe cephalic variation, and results are compared with seven other halictine bees. All morphometrics were investigated for measurement error. Nests of *Xenochlora* appear to be founded by single females and multifemale nests clearly exhibit parasocial behavior and we hypothesize that they temporally switch between semisocial, eusocial and possibly communal phases.

KEY WORDS: Halictidae, Augochlorini, *Xenochlora*, social evolution, size variation, stem nest

RESUMEN: El género de abejas *Xenochlora* (Augochlorini, Halictidae) es el grupo hermano diurno del género nocturno *Megalopta*. Ambos grupos son abejas que construyen sus nidos en madera en descomposición. Aquí presentamos anotaciones sobre la biología de anidación y comportamiento social en cuatro nidos de *Xenochlora nigrofemorata* y un nido de *X. ianthina* en Madre de Dios, Perú. Todos los nidos contenían múltiples hembras y las disecciones de *X. nigrofemorata* indican que hay diferenciación reproductiva entre las hembras de un nido, asociada con el tamaño del cuerpo. El polimorfismo entre las hembras es evidente y una serie de mediciones morfométricas son examinadas para documentar la variación en tamaño. Un índice genal es utilizado para describir el polimorfismo cefálico y los resultados son comparados con otras especies de abejas halictidas. Todas las mediciones morfométricas fueron analizadas para determinar el error de medición. Los nidos de *Xenochlora* parecen ser fundados por hembras solitarias y los nidos con hembras múltiples exhiben claramente un comportamiento parasocial y es posible que temporalmente intercambien entre fases semisocial, eusocial y posiblemente comunal.

PALABRAS CLAVE: Halictidae, Augochlorini, *Xenochlora*, evolución social, polimorfismo, nido en tallos

Extrinsic factors (both physical and biological) help shape the expression of social behavior in many insects, whether their influence be constraining or liberating; and sweat bees (Hymenoptera: Halictidae) as a group are well suited to addressing the role of such factors (Wcislo, 1997; Schwarz *et al.*, 2007). Additionally, there is great variation in nest architecture within this taxon, but it has been the subject of far fewer studies (e.g., see reviews by Sakagami and Michener, 1962; Eickwort and Sakagami, 1979; Wcislo and Engel, 1996). The co-occurrence of social and architectural diversity is unusual among bees, and was the impetus for comparative studies assessing the behavior of nest construction with social organization, as well

¹ Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, República de Panamá, email: *TierneyS@si.edu; †WcisloW@si.edu

² Facultad de Ciencias Forestales y Medio Ambiente, Universidad Nacional de San Antonio Abad del Cusco - Sede Puerto Maldonado, Jr. San Martín 451, Puerto Maldonado, Madre de Dios, Perú.

as characters for systematic analyses (Sakagami and Michener, 1962; Michener, 1974). Bees of the tribe Augochlorini, like the remaining Halictidae, are largely comprised of ground nesting taxa. Bees in some genera, however, excavate burrows and construct brood cells within dead or decaying plant matter including trunks, branches, stems, vines and rosettes of bromeliads: *Augochlora* (Stockhammer, 1966; Eickwort and Eickwort, 1973; Eickwort, 1979; Zillikens *et al.*, 2001; Wcislo *et al.*, 2003); *Megalopta* (Sakagami, 1964; Sakagami and Moure, 1967; Janzen, 1968; Wcislo *et al.*, 2004); *Neocorynura* (Lüderwaldt, 1911; Schremmer, 1979; Brosi *et al.*, 2006); and *Xenochlora* (Smith, 1861).

Xenochlora and *Megalopta* are an unusual monophyletic group within the Augochlorini, firstly because the former are diurnal and the latter nocturnal, enabling studies of an evolutionary transition into a novel temporal environment (Wcislo and Tierney, in prep.). Secondly, both genera nest in stems, lianas and vines in the same habitats. Use of these substrates may constrain the upper limits of colony size, as suggested for stenogastrine (Vespidae) wasps (Hansell, 1984), but few data are available to test this hypothesis for bees. Likewise, no data are available to assess whether the availability of suitable nest substrates is limiting, but if so it would put additional constraints on solitary nesting. As noted by Danforth and Eickwort (1997), the importance of twigs and branches in the forest canopy for the stem nesting augochlorines is still relatively unexplored.

Recently *Megalopta* has received considerable attention with regard to social behavior (Arneson and Wcislo, 2003; Smith *et al.*, 2003, 2007; Wcislo *et al.*, 2004; Wcislo and Gonzalez, 2006), and sensory ecology, because they forage at very low light levels (e.g., Warrant *et al.*, 2004; Kelber *et al.*, 2006; Theobald *et al.*, 2007). Basic life history information for numerous halictine bees is lacking, even though such data are vital for comparative studies. Given that *Xenochlora* is likely the sister clade to *Megalopta* (Engel, 2000; Michener, 2007), and is also a stem nesting bee, behavioral data on these bees will provide valuable insights for broader evolutionary studies.

Females of *Xenochlora* closely resemble the nocturnal *Megalopta*, with the exceptions of the black setae of the hind legs; the less densely packed hamuli at irregular spacing; and regular sized ocelli (Engel *et al.*, 1997). *Xenochlora* is assumed to be diurnal based on morphology, yet nothing is known of its biology outside of the observations of Henry Walter Bates, as transcribed by Smith (1861):

“A most lovely species of bee, exhaling a very powerful aroma months after death. One day, on breaking a piece of dead branch to pieces, I came upon a row of cells containing these bees, already enclosed and ready to escape. There were about a dozen cells placed end to end, of which two contained pupae; most of them escaped: I could only secure four or five.”

Xenochlora is distributed throughout the Guyana Shield to the Amazonian basin (Brazil, Ecuador, Perú) and consists of four species (Engel *et al.*, 1997), two of which, *X. ianthina* (Smith, 1861) and *X. nigrofemorata* (Smith, 1879), were previously placed in *Megalopta* (Moure and Hurd, 1987). Both Moure (1958) and Eickwort (1969) noted the normal sized ocelli of these species as an exception to the remaining *Megalopta*. Here we present an account of *Xenochlora* nesting biology and sociality.

Methods

Study Site

Bees were studied at the Centro de Investigacion y Capacitacion Rio los Amigos, Madre de Dios, Perú, ~90 km West of Puerto Maldonado (12°34'07"S, 70°05'57"W; ~268 m elevation) near the confluence of the Madre de Dios and los Amigos rivers (see Pitman, 2006).

Collections were made at the end of the dry (low river) season from 23–26 September 2006. Intact nests of *Xenochlora* were located by searching for circular entrance collars constructed from the pith of branches, lianas and vines suspended in the forest under-story. Nest entrances were plugged with cotton wool and nests were then refrigerated for ~4–8 hrs before being opened by splitting the wood longitudinally with a knife, being careful to avoid damaging brood cells. Adults were removed and preserved in either Kahle's solution for dissection or 95% ethanol for an associated phylogenetic study. Brood cells were removed intact and maintained in cell culture trays to rear as many adults as possible. Voucher specimens are deposited in the Dry Reference Collection of the Smithsonian Tropical Research Institute, Balboa, Ancón, Republic of Panamá.

Dissections and Morphometrics

Reproductive activity of adult females was inferred by dissection following Schwarz (1986). Ovarian development was measured as the sum length of the three largest terminal oocytes under slide mount. To account for possible scaling effects on ovary development, due to body size variation, an ovarian index was calculated as the sum of oocyte lengths divided by intertegular distance. Mating status was identified by the presence or absence of sperm in the spermatheca.

Various head measurements were taken: *head width* as maximal width from the outer edge of each compound eye (dorsal view); *head length 1* as the distance from the base of the clypeus to the top of the vertex (anterior view); *head length 2* from the base of the clypeus to the base of the median ocellus (anterior view); *ocellar size* as width of the median ocellus (dorsal view); *interocular distance* as the maximal distance between compound eyes (anterior view); *intermandibular distance* (anterior view) as maximal distance from condyle to condyle; *eye length* as the longest row of ommatidia (Blackith, 1958); maximal *eye width* (left lateral view); and, maximal *genal width* (left lateral view). A measure of cephalic polymorphism was the *genal index* (per Sakagami and Moure, 1965), calculated as the division of the genal width by eye width. Due to the striking variation in head size, we also used a number of other measurements to assess overall body size including: *intertegular distance*, which reliably correlates with body weight in a variety of bees (Cane, 1987); *hind tibia length* (per Danforth and Desjardins, 1999); and the *wing length* of one randomly chosen forewing, measured as the distance from the axillary sclerites to the base of the stigma. The number of nicks and tears along the distal margin of this wing was taken as a measure of wing wear.

All linear measurements were taken 5 times for each specimen, to assess which morphometrics are most susceptible to recording error (e.g., Danforth and Desjardins, 1999). The standard error of the mean of each morphometric was recorded per individual bee; these standard errors were then averaged across all individuals for each morphometric to give an indication of the most reliable linear measurements.

All statistical analyses were calculated with SPSS® version 11 for Mac OS X.

Table 1. *Xenochlora* nest census data. Physical nest properties and the number of adults and brood of four *X. nigrofemorata* nests (6, 7, 12, 13) and one *X. ianthina* nest (11). Legend: F – female; M – male; S – small larvae; L – large larvae.

Nest	<i>X. nigrofemorata</i>				<i>X. ianthina</i>
	6	7	12	13	11
Nest length (mm)	187	93	173	405	302
Tunnel width (mm)	6	6	6	8	8
Adults	3 F	2 F	2 F	6 F	3 F
Total brood	2	0	2	11	3
Callows				1 F	
Pupae	1 F		1 M	3 F, 1 M	
Larvae			1 S	1 S, 2 L	1 S, 1 L
Eggs	1			3	1
Total brood cells (sealed cells)	4 (2)	1 (0)	3 (2)	16 (11)	5 (3)

Results and Discussion

Collections

Four nests of *Xenochlora nigrofemorata* and one nest of *X. ianthina* were collected. Nest architecture does not appear to be different from that of *Megalopta* (see Weislo *et al.*, 2004), which also nest in dead wood suspended in the forest understory; both create linear tunnels within these substrates and construct a restricted collar at the nest entrance. Tunnel diameter for *Xenochlora* nests ranged from 6–8 mm. Brood cells are constructed from excavated pith, and their interior walls are lined with a hydrophobic coating secreted from the Dufour's gland, as typical for halictids (see Cane, 1983). Members of four augochlorine genera nest in wood, and morphological features shared among these taxa (e.g., robust mandibles) were hypothesized by Eickwort (1979) as evidence of convergent evolution associated with wood nesting. In a comparison of nest architecture among the Augochlorini Eickwort and Sakagami (1979) concluded that there was no clear relationship between nest architecture and social behavior, although nesting substrate may impose an upper limit to group size (see Introduction).

Details of nest contents are presented in Table 1. Brood of all stages was present in this sample and all nests were multi-female, ranging from two to six individuals. No adult males were present, but of the six pupae found in *X. nigrofemorata* nests, two were males. The largest nest (nest 13: 6 adults; 11 brood) contained brood of all stages and considerably more brood compared to all other nests (2–3 adult females; ≤3 brood); only nest 7 contained no brood at all.

Dissections

Bees from only two nests (12 and 13) of *X. nigrofemorata* were dissected (Table 2), because the remaining adults were required as voucher specimens for a separate phylogenetic study. Nest 12 contained two adults of similar size, one female (12*b*) was inseminated and exhibited a nearly five fold higher ovarian index (2.14) compared to her uninseminated nestmate 12*a* (0.45). The putative reproductively active female (12*b*) was also slightly larger in body size (intertegular width) and head size (interocular width) compared to female 12*a*. Nest 13 contained six females; the

Table 2. Mean morphometric measurements and reproductive status of female *Xenochlora nigrofemorata*. Each female was measured 5 times and means calculated. The within-nest rank of each individual is given in brackets for each measurement or index. Body size is contrasted with measurements of head size (interocular width, genal width and the genal index) and degree of wing wear. For nests 12 and 13 these morphometrics are compared with reproductive status. The sample range of each measurements is noted at the bottom of the table.

Nest	Female	Wing wear	Reproductive status			Body size		Head size	
			Inseminated	Sum oocyte length (mm)	Ovarian index	Intertegular width (mm)	Interocular width (mm)	Eye width (mm)	Genal index
6	a	2	-	-	-	2.77 [1]	2.67 [1]	0.74 [1]	1.62 [1]
6	b	0	-	-	-	2.17 [2]	2.00 [2]	0.65 [2]	1.05 [3]
6	c	0	-	-	-	2.02 [3]	1.80 [3]	0.57 [3]	1.21 [2]
7	b	3	-	-	-	2.42 [1]	2.22 [1]	0.64 [2]	1.31 [1]
7	a	0	-	-	-	2.20 [2]	2.06 [2]	0.69 [1]	1.22 [2]
12	b	0	Y	4.54 [1]	2.14 [1]	2.12 [1]	2.05 [1]	0.62 [1]	1.33 [1]
12	a	0	N	0.93 [2]	0.45 [2]	2.06 [2]	1.98 [2]	0.57 [2]	1.45 [2]
13	f	9	Y	5.64 [2]	2.16 [2]	2.61 [1]	2.84 [1]	0.70 [2]	1.91 [1]
13	a	1	?	7.04 [1]	2.42 [1]	2.42 [2]	2.37 [3]	0.73 [1]	1.32 [5]
13	d	0	N	0.36 [6]	0.15 [6]	2.41 [3]	2.43 [2]	0.70 [2]	1.43 [3]
13	e	0	N	1.08 [4]	0.45 [4]	2.40 [4]	2.18 [4]	0.62 [5]	1.44 [2]
13	c	0	Y	2.92 [3]	1.27 [3]	2.30 [5]	2.12 [5]	0.64 [4]	1.31 [6]
13	b	3	N	0.80 [5]	0.35 [5]	2.26 [6]	2.08 [6]	0.60 [6]	1.42 [4]
Sample range:				6.68	2.27	0.75	1.04	0.17	0.86

two females with the highest ovarian index rank (13a = 2.42; 13f = 2.16) were also the two largest in terms of body size. Female 13f was inseminated and possessed the most wing wear (9 nicks) of any individual in this study, and is the likely foundress of this nest. Interestingly, the female with the highest ovarian index (13a = 2.42) possessed minimal wing wear; the insemination status of this female was undetermined. The third female ranked by ovarian index (13c = 1.27) was also inseminated but was the second smallest female in the nest. The smallest female (13b) possessed some wing wear (3 nicks) and had the second lowest ovarian index rank (0.35).

Based on this sample it would appear that *X. nigrofemorata* forms parasocial groups that are likely semisocial, and perhaps even eusocial (terminology *per* Michener, 1974, 2007). Uninseminated females tended to have a low ovarian index (<0.45) and were of medium to small body size (intertegular width <2.41 mm). The sample range in body size (intertegular width) was 0.74 mm and the two extremes in body size existed within the same nest (nest 6). The largest female in each dissected nest was inseminated and in nests 6, 7 and 13 the largest female also possessed the most wing wear (see Fig. 1), except for nest 12 in which neither female had worn wings.

Morphometrics

Mean standard errors for the 12 morphometric measurements are presented in Fig. 2. Ocellus width is the least prone to recorder error; however there is little variance of this character and hence it is not really suitable for describing the range of overall head/body size. Interocular distance appears to be the most repeatable of the head measurements.

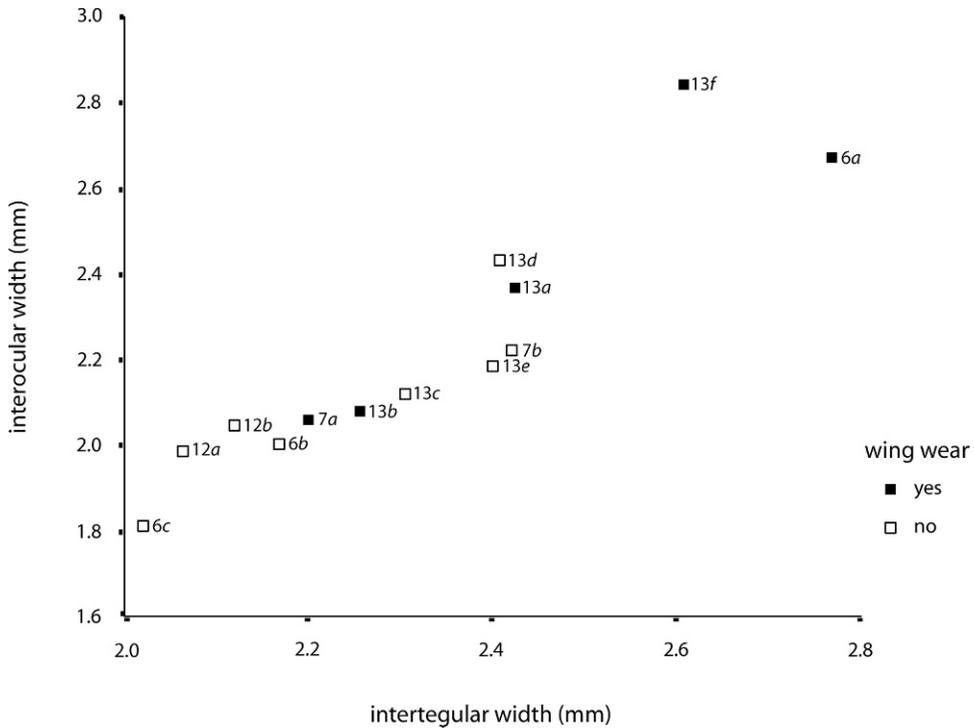


Fig. 1. Size variation in *X. nigrofemorata*. Scattergram of thorax (intertegular width, mm) and head (interocular width, mm) size. Individual females are denoted by the presence (closed square) or absence (open square) of wing wear.

Intermandibular width, head length 2 and maximal head width are typically used as metrics for head size, although these measurements were less repeatable here. Wing length had the most error in measurement, presumably because we chose to take measurements from intact bees, due to the small sample size and the need to preserve some specimens as vouchers. Head length 1 was the next least repeatable metric in terms of recorder error, closely followed by hind tibia length and this is likely due to variations in the plane of orientation when repeatedly recording this metric.

As a metric for body size, intertegular width is as repeatable a measure as interocular width. The mean values of these metrics for each *X. nigrofemorata* individual are plotted in Fig. 1, and the two measures are highly correlated (Pearson's $r = 0.925$, $P < 0.001$). Given the reliability of intertegular width as a gauge of body weight across a broad range of bee taxa (Cane, 1987), we suggest it is the most appropriate indicator of body size in these bees. Intertegular width also correlates well with genal width ($r = 0.855$, $P < 0.001$), and eye width ($r = 0.784$, $P = 0.002$), both which are used to calculate the genal index, used to assess macrocephaly.

Compared to the largely Brazilian augochlorine species examined by Sakagami and Moure (1965), *X. nigrofemorata* displays a very high range in genal index. This variation could be interpreted as evidence for the likelihood of eusocial cooperation, but without additional longer term collections of this species throughout an annual cycle, it is inappropriate to directly equate differences in body size with any social

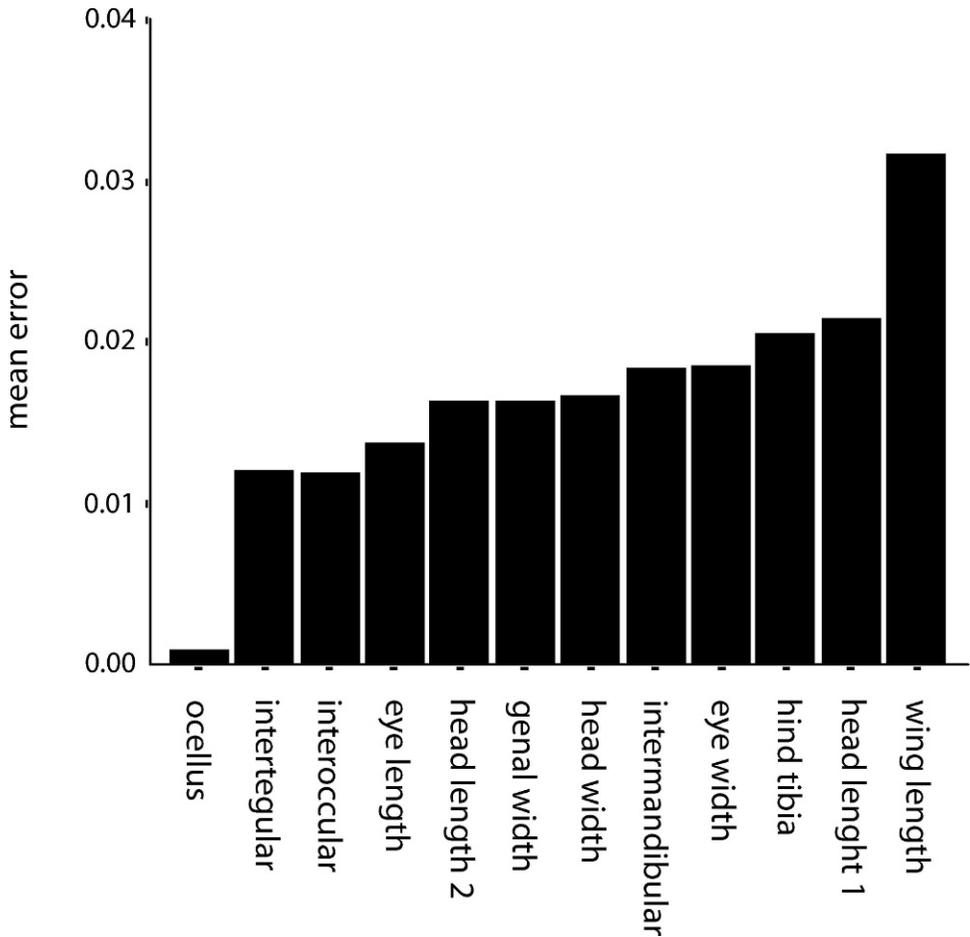


Fig. 2. Repeatability of morphometrics. Shown by the average standard error of the mean for each metric.

tendencies per se. Moure (1958) mentioned the conspicuous allometry in *Xenochlora ianthina*, and there is a noticeable difference in size among members of nest 11 collected in this study, suggesting that conspicuous allometry may be characteristic of the genus.

Our limited data suggest that larger *X. nigrofemorata* females have undergone allometric growth. Sakagami and Moure (1965) comment on the general features common to macrocephalic augochlorine females, such as modified proportions of the upper head and vertex, more robust mandibles, and in some taxa processes of the clypeus and genae become more prominent; in some species pronotal lobes become more acute, as known for parasitic bees with enlarged heads (Weislo, 1999). In the two largest *X. nigrofemorata* females (6a and 13f), a large projection from the lower gena is obvious and the dorsolateral angle of the pronotum is also enlarged (Fig. 3).

Sakagami and Moure (1965) highlight the dangers and inappropriate use of metrics of morphological features (especially of the head) in the taxonomic designation of augochlorine and other halictine species where size variation is clearly present. For example, Moure's (1958) description of *X. nigrofemorata* is largely based on head measurements.

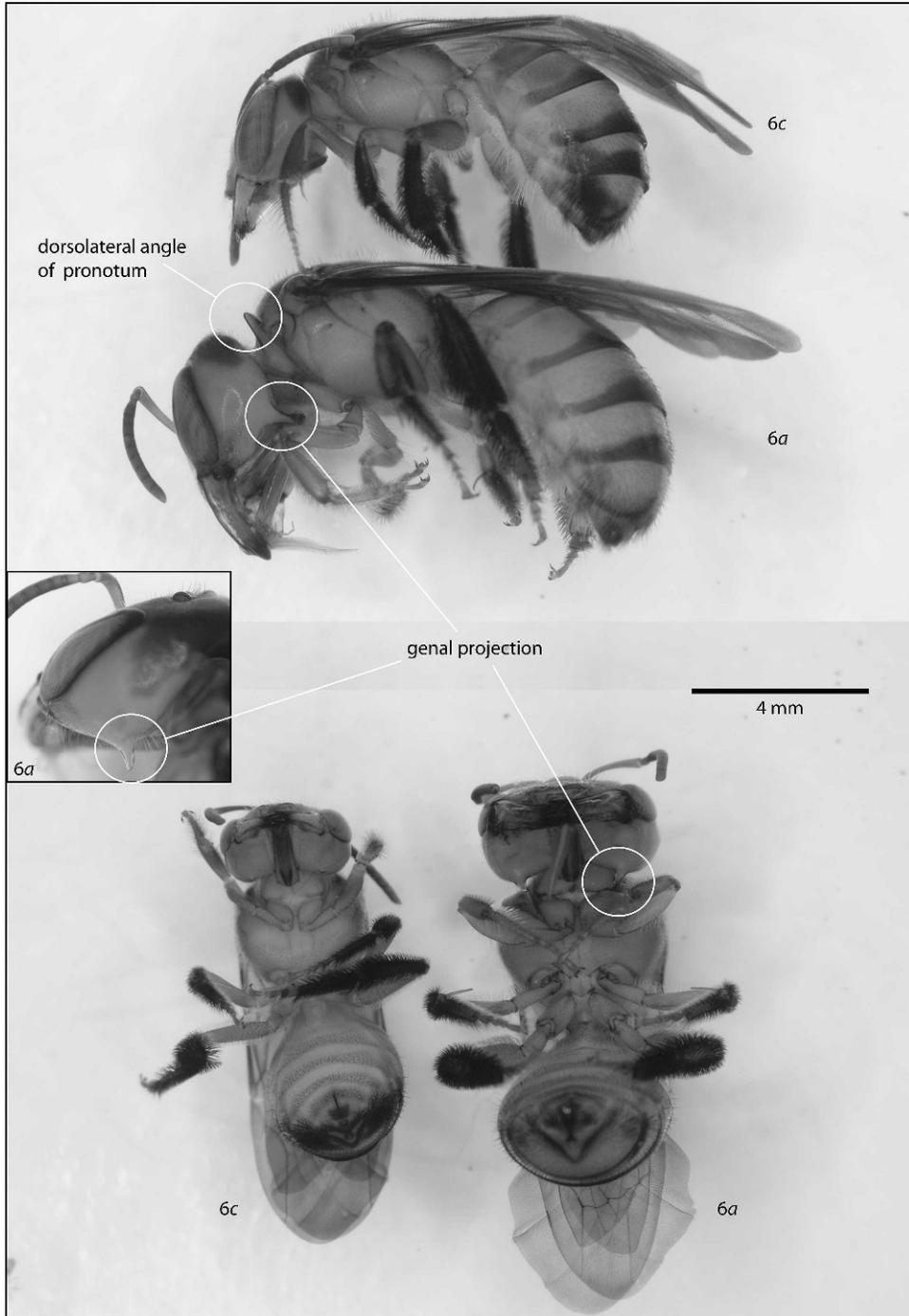


Fig. 3. Polymorphism and body size variation in *X. nigrofemorata*. Two female nestmates (6a and 6c) exemplify the range in body size and female 6a shows the pronounced genal projections and dorsolateral angle of the pronotum found in larger females.

Social Organization

Wing wear has been shown to be associated with both foraging activity and age in megachilid and allodapine bees (Mueller and Wolf-Mueller, 1993; Tierney and Schwarz, in prep.). Under the assumption that *Xenochlora* initiates nests with a single foundress, as in *Megalopta* and most augochlorines, one would expect the foundress to exhibit both a higher ovarian index as well as more wing wear than nest mates, from having to forage for the first brood. The smallest female in nest 13 (female 13*b*) also displayed wing wear and yet had the second lowest ovarian index of the nest and was uninseminated. Such observations raise the possibility that there is co-operative brood provisioning by a non-reproductive individual from a different generation.

New nests of *Xenochlora* are probably solitary until the first brood eclose, based on the numbers of brood cells and tunnel lengths of nests 6, 7 and 12 (Table 1). For example, nest 6 contained four brood cells (two open) and three adult females, and only one female (6*b*) had worn wings, though we cannot distinguish whether the two un-worn females (6*a* and 6*c*) had recently eclosed from the two open brood cells, or emerged earlier and helped construct them. Nest 7 contained only one brood cell, which was open, and two adult females, one (7*b*) with wing wear, the other (7*a*) was unworn. Nest 12 had three brood cells (one open) and although neither of the two females had wing wear, female 12*b* was inseminated, possessed a relatively high ovarian index and was not recently eclosed; female 12*a* was uninseminated, with a relatively low ovarian index and was likely to be recently eclosed. Nest 13 was likely older and contained members from multiple generations, as indicated by the nest length, which was more than double that of all other *X. nigrofemorata* nests. This nest was likely semisocial due to the broader association of reproductive activity with body size (females 13*a* and 13*f*) suggesting some degree of caste development, but we cannot rule out the possibility that this may be a communal nest, based on female 13*c*.

Obligate sociality is known in some species of seven genera of Halictinae: *Halictus* (*Halictus*), *Halictus* (*Seladonia*), *Lasioglossum* (*Evyllaes*), *Lasioglossum* (*Dialictus*), *Augochlora*, *Augochlorella*, and *Augochloropsis*. However, more recent studies suggest social nesting is more widespread than hitherto thought, which is likely a consequence of the general lack of in-depth behavioral knowledge for all taxa, compounded by the fact that many existing accounts of species' biology are based on minimal data - including the current study (see Danforth and Eickwort, 1997; Wcislo, 1997). Among the augochlorines, social nesting is now known to also occur in *Augochloropsis* (Coelho, 2002), *Xenochlora* based on the findings from this study, and *Megalopta*. Only three species of *Megalopta*, all from Panama (*M. genalis* Meade-Waldo, *M. ecuadoria* Friese and *M. atra* Engel), have been examined in any detail. Colony size ranges from 1–11 females. Nests are largely solitary at the beginning of dry season (December–January) and brood rearing and social nesting increases as the season progresses; females enter a quiescent phase toward the end of the wet season (June–November), presumably due to a scarcity of floral resources (e.g., Arneson and Wcislo, 2003; Smith *et al.*, 2003, 2006, 2007; Wcislo *et al.*, 2004; Tierney *et al.*, in press).

The phylogeny of Augochlorini was revised by Danforth and Eickwort (1997), based on Eickwort's (1969) comprehensive morphological data set; supplemented by evidence from fossil specimens and additional characters the tribe was re-analyzed

more recently by Engel (2000). Based on Engel's (2000) hypothesis, *Xenochlora* forms a monophyletic clade with *Megalopta* and its associated parasitic derivative *Megalopta* (*Noctoraptor*) (Engel *et al.*, 1997). This group is sister clade to ((*Caenaugochlora*, *Ctenaugochlora*), (*Augochloropsis*, *Paraugochloropsis*, *Glyptochlora*)); the only member of the latter clade in which eusociality is known is *Augochloropsis* (Coelho, 2002). The sister clade to both these monophyletic clades is (*Oligochlora*, *Thectochlora*); the former is extinct and the latter consists of a single species, *Thectochlora alaris* (Vachal), whose social habits are unknown (Danforth and Eickwort, 1997).

A wide range of Halictinae exhibit reproductive hierarchies based on age, and secondarily on body size relative to nest-mates (reviewed by Michener, 1990; Packer, 1993; Danforth and Eickwort, 1997; Wcislo, 1997; Schwarz *et al.*, 2007; Smith *et al.*, 2007). However, most of this research involves temperate species. Studies of *Lasioglossum* sociality have implied that a large queen-worker body size difference may typify the eusocial colonies (Breed, 1976; Packer and Knerer, 1985; Wyman and Richards, 2003). The conspicuous variation in body size among nest-mates of *Xenochlora* likewise implies that size differences may be associated with social roles, but additional studies are needed.

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