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RESEARCH ARTICLE

A single origin of large colony size in allodapine bees suggests a threshold event among 50 million years of evolutionary tinkering

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Abstract Evolutionary origins of highly eusocial organization involving morphological castes have been very rare, yet these origins have often led to enormous diversification and ecological success. This suggests that once an apparently severe selective barrier to highly eusocial behaviour is overcome, major new adaptive landscapes open up. One would therefore expect a discontinuity in patterns of evolutionary change across this barrier. However, we do not know if highly eusocial organization has evolved incrementally from less complex societies, or if it has involved some kind of evolutionary leap. Our study examines this issue using colony size data from 33 allodapine bee species, with a crown age of ca. 47 Mya. Our species cover all major allodapine clades, and include *Exoneurella tridentata*, the only known allodapine with morphologically discrete castes. Phylogenetic analyses indicate a strong effect of phylogeny on the evolution of maximum brood size, but the effect of phylogeny on maximum colony size (number of adults) depends on whether *E. tridentata* is excluded or included in analyses. We found no evidence of punctuational change in maximum colony or brood sizes over the phylogeny as a whole, but colony and brood sizes in *E. tridentata* fall well beyond variation among the other allodapines. Colony size in *E. tridentata* therefore represents an evolutionary outcome that does not fit within the kinds of incremental changes found in other allodapines. We propose that *E. tridentata* indicates the crossing of an important threshold, and this has entailed some very unusual ecological circumstances.

Keywords Eusociality · Morphological castes · Social evolution · Allodapini · Bees

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Introduction

The evolution of eusociality represents one of the major transitions in the history of life (Szathmary and Maynard-Smith, 1995), whereby previously independent units evolve inter-dependencies, where levels of organization between units increase dramatically, and where the ability for independent reproduction is often lost. Many highly eusocial insects, such as honeybees, ants and termites, lack close phylogenetic relatives that are solitary or exhibit only simple social organization. For these 'advanced' groups it can be very difficult, if not impossible, to determine whether highly eusocial organization evolved as a gradual increase in colony size and complexity, or whether it represents the crossing of a discrete threshold, as is often implied though

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perhaps not formally stated (e.g. Oster and Wilson, 1978; Wilson, 2008).

Using fossils to identify whether such a threshold in highly eusocial organization exists is very difficult, if not impossible, because identifying discontinuities in evolutionary change is confounded by incompleteness in the fossil record. However, identifying such events may be possible with the use of phylogenetic analyses of extant insect groups, provided that they exhibit wide variation in the traits of interest and that phylogenetic relationships are reasonably well established. Inferring the tempo of past evolutionary change when such change is influenced by phylogeny is possible using both maximum likelihood and Bayesian techniques (e.g. Pagel et al., 2004; Pagel and Meade, 2006).

Bees in the tribe Allodapini (family Apidae) exhibit wide variation in forms of sociality, ranging from predominantly subsocial to highly eusocial. Maximum colony sizes also vary widely, from 2–3 females to >35 females during brood-rearing periods. Allodapines rear their brood in a nest that is comprised of a single unbranched and undivided tunnel in the dead stem of a plant. Brood are not enclosed within cells and this means that in the absence of adult females, they are highly vulnerable to enemies at-the-nest such as parasites and predators (Schwarz et al., 2007; Zammit et al., 2008). Studies across a wide range of allodapine genera indicate that multi-female colonies often have much higher per capita numbers of brood, and much lower rates of total brood loss, than solitary nesting females (Schwarz et al., 2007). It is thought that for this reason, social nesting has never been entirely lost in the tribe, despite sociality being facultative in all extant species (Chenoweth et al., 2007).

Phylogenetic analyses indicate that the ancestral form of sociality in allodapines did not involve differentiation into reproductive queens and foraging workers. Instead, colonies comprised totipotent females in reproductive queues, with reproductives also performing foraging tasks (Schwarz et al., 2011). The existence of a foraging worker caste arose at least twice in allodapines, but only one of those origins led to a species, *Exoneurella tridentata*, with morphologically discrete reproductive and non-reproductive castes and with comparatively large colony sizes. Queens in this species have greatly enlarged metasomas with different morphology from workers, and they are often unable to fly (Houston, 1976; Hurst, 2001). Workers carry out all foraging (Houston, 1976), they very rarely lay eggs and when they do so, these are haploid (Hurst, 2001). New nests are established solitarily by females with morphology intermediate between queens and workers, and approximately 18% of actively brood-rearing colonies contain solitary nesting females (Hurst, 2001).

Given the ubiquity of sociality in allodapines (Schwarz et al., 2007), the ancient origin of this tribe (>40 mya; Chenoweth et al., 2007) and the large number of species (approximately 350), the origin of discrete castes leading to *Exoneurella tridentata* appears to represent a very unusual event. This raises the question of whether this species simply represents an extreme case of the social variation occurring more widely in allodapines, or whether it represents a qualitatively different evolutionary endpoint.

Here, we use a molecular phylogeny of 33 allodapine species, covering nearly all extant genera, to examine the tempo of evolutionary change in three key social traits: maximum colony size, maximum brood size, and the proportion of colonies that are either social or solitary. We use three key parameters, λ, κ and δ (Pagel et al., 2004; Pagel and Meade, 2006) that can be derived from a combination of phylogeny and extant character states, to explore three important issues: (a) are these different metrics of social living associated with phylogenetic history? (b) If so, do they show signs of adaptive radiation? And (c) are evolutionary changes in these parameters associated with speciation events, or do they accumulate in a more gradual fashion?

Methods

Choice of taxa

Our approach was to maximise the number of species for which we had both sequence and social data. We included some species for which DNA sequences have been published, but for which previously unpublished social data were available from field collections associated with published studies on allodapine species. We also included some species in our phylogenetic analyses for which we had sequence data, but no social data, to avoid long branch attraction problems for thinly sampled clades (Schwarz et al., 2004). These latter species were pruned from chronograms before analyses of social traits. The species for which we retrieved unpublished life history data are listed in the electronic supplementary material, along with sample sizes, localities, and references to publications that describe the relevant collecting protocols.

Our pruned phylogeny comprised at least two species of each non-parasitic allodapine genus except *Exoneuridia* and *Compsomelissa,* for which we have no detailed social data. All of the allodapine taxa used in our study had been used in previous phylogenetic analyses (Bull et al. 2003; Chenoweth et al., 2007; Schwarz et al., 2005, 2011).

We included eight non-allodapine bee species to help root the allodapine clade: *Apis mellifera* (Apini), *Liotrigona*

sp. (Meliponini), *Bombus* sp. (Bombini), *Bombus terrestris* (Bombini), *Xylocopa violacea* (Xylocopini), *Ceratina australensis*, *C. japonica* and *C. malindae* (Ceratinini).

Phylogenetic analyses

Phylogenetic analyses were based on previously published sequence data for fragments of three genes, cytochrome oxidase I (COI), cytochrome *b* (cytb), and the F2 copy of elongation factor 1α (EF-1α), comprising a total of 2,479 nucleotides. We lacked some gene fragments for some species and not all species had the same number of sequenced nucleotides for each gene fragment. Sequences were aligned using SeqEd version 1.0.3 (ABI), and we excluded the intron from EF-1α, because it was largely unalignable for many species.

Phylogenetic reconstruction was carried out using Bayesian analysis implemented in MrBayes version 3.1.2 (Huelsenbeck and Ronquist, 2001). We followed the same partitioning scheme as the most recent phylogenetic studies on allodapines (Schwarz et al., 2011). This involved combining the two mitochondrial genes, whilst keeping the nuclear genes separate, and further partitioning both mitochondrial and nuclear genes into 1st + 2nd and 3rd codon partitions. This gave us a total of four partitions for the entire sequence data set, with all partitions unlinked for model parameters and using default priors as described in Schwarz et al. (2006).

Three Bayesian runs were conducted to check that runs consistently converged on similar patterns. Stationarity was assessed by plotting log likelihood (LnL) values over generational time; the average standard deviation of split frequencies gave an indication of convergence within runs. Analyses were run for 20 million generations, with a burnin of 10 million generations (well after stationarity was reached) and post-burnin trees were combined across runs. Trees were sampled every 1000th generation.

The resulting consensus phylogram was transformed into a chronogram using the same fossil calibration points and penalised likelihood method for estimating divergence dates as in Chenoweth et al. (2007). The root node was set at 50 Mya in accordance with the findings of previous studies (Cardinal et al., 2010; Chenoweth et al., 2007). Allodapine species for which we did not have life history data were pruned from the tree before further analyses.

Patterns of evolutionary change in social traits and their ancestral values

We investigated the evolution of three key traits:

1. Maximum colony size. This was measured as the largest number of adult females from sampled colonies that also contained immatures being actively reared.
2. Maximum brood size. This was measured as the total number of immatures, based on eggs, larvae and pupae, but not including callow adults.
3. Proportion of social colonies. This was the proportion of colonies with more than one adult female (not including callow females) and based only on colonies containing immatures.

We used a maximum likelihood method, implemented in BayesTraits (Pagel et al., 2004; www.evolution.rdg.ac.uk) to explore the tempo of evolutionary change in the three key traits mentioned above and whether or not these traits were correlated when phylogenetic structure was taken into account. For each trait, we estimated three parameters: λ, κ and δ. Lambda (λ) is a measure of the influence of phylogeny on character variation, with a value of zero indicating no influence (effectively a star phylogeny with respect to the character of interest) and a value of one indicating a strong phylogenetic influence. Kappa (κ) is a measure of whether changes in a trait are proportional to branch length. Values <1 indicate relative stasis in longer branches, values close to zero suggest punctuated evolution, and values >1 indicate accelerating changes in longer branches. Delta (δ) provides a measure of whether rates of evolutionary change vary with path length from the root. Values <1 suggest early adaptive radiation, values >1 indicate a greater role for lineage-specific change, and values close to one suggest constant root-to-tip change.

We used several approaches to explore λ, κ and δ. The significance of each parameter in these analyses was assessed using likelihood ratio (LR) tests where more complex models (more parameter rich) were nested within simpler models. We also examined whether the three traits showed evidence of correlation when phylogenetic structure was taken into account, using a ML phylogenetic contrasts approach implemented in BayesTraits.

Because some nodes in our phylogeny had weak support it was necessary to estimate λ, κ and δ whilst taking phylogenetic uncertainty into account. In order to do this we began by using a single phylogeny (our Bayesian consensus phylogeny, transformed into a chronogram) to explore these values separately for each of the three social parameters. For these we also explored the effect of including or excluding a key species, *Exoneurella tridentata*, on parameter estimates and their significance. We then estimated these same parameters using the same taxon inclusion/exclusion procedure as above, for 250 randomly chosen, post-burnin phylograms converted into chronograms. Analyses of these post-burnin chronograms cannot be naturally combined to provide measures of statistical support for our parameters. However, ranges of these parameters across post-burnin trees give an indication of whether estimates are sensitive to varying topology.

Results

Phylogenetic analyses

Our initial phylogenetic analyses contained a total of 82 species, including eight outgroup species. Consensus phylogenies from the three replicate Bayesian analyses of sequence data all had identical topologies and almost identical branch lengths. A consensus phylogram, generated from the first Bayesian run is shown in Figure A1 (Supplementary Online Material), along with posterior probability (PP) support values. PP values are only shown for nodes where support was less than 97%. The tree topology is consistent with previous phylogenetic studies on allodapines, except for the node connecting *Brevineura* to *Exoneurella* + *Exoneura*, which differs from Chenoweth and Schwarz (2011) in which *Brevineura* was recovered as the sister clade to *Exoneur*a. The chronogram resulting from our penalised likelihood analysis is given in Fig. 1, where the root node is set at 50 Mya.

Analysis of social traits

Variation for our three social traits is graphically summarized in Fig. 1 using horizontal bar charts. Maximum brood

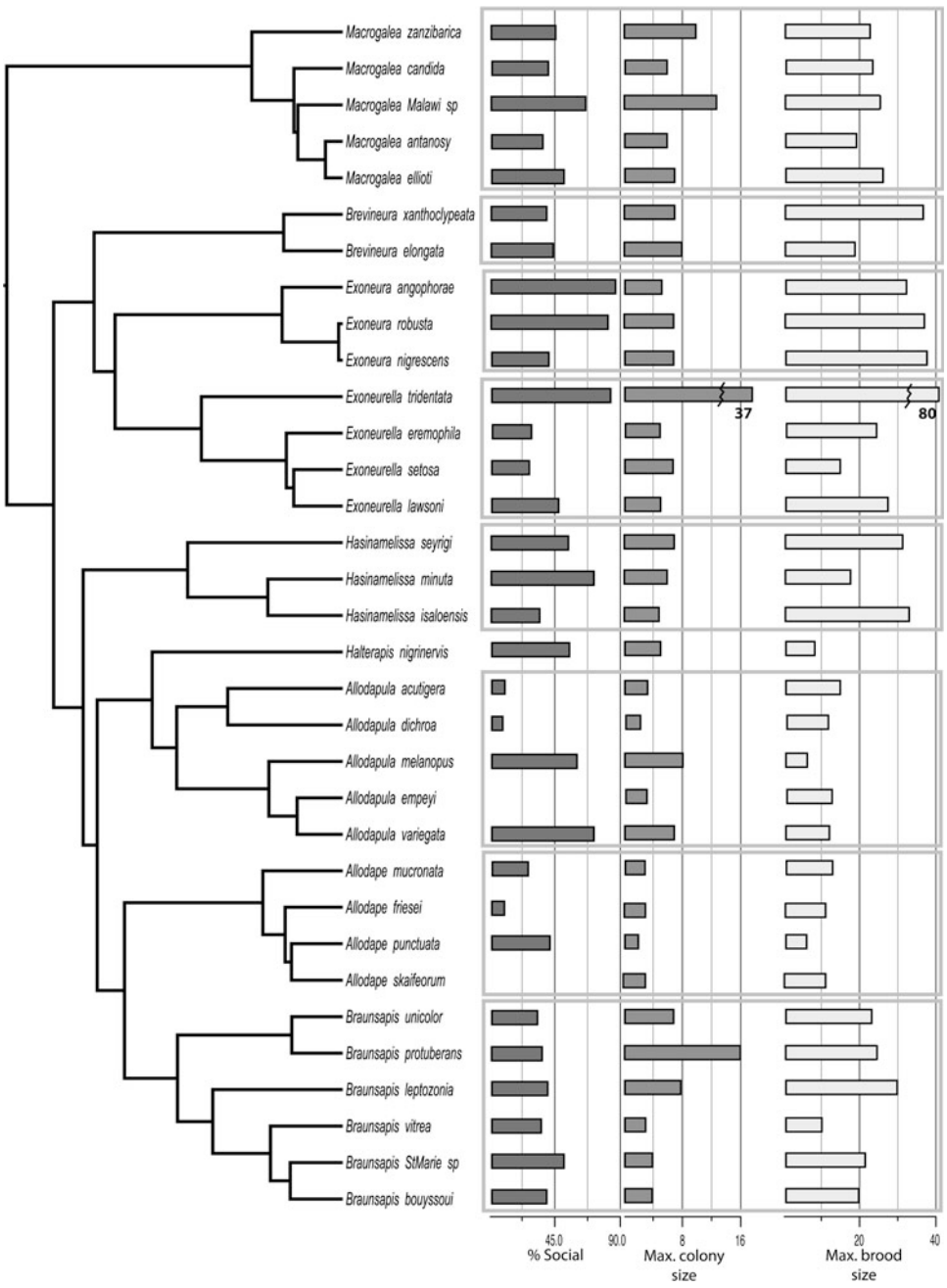

Fig. 1 Chronogram of allodapine species with demographic data. Bars represent the percentage of social colonies, maximum colony and brood size for each species. For *E. tridentata* the maximum colony and brood size exceeded the scale and actual values are indicated by numerals

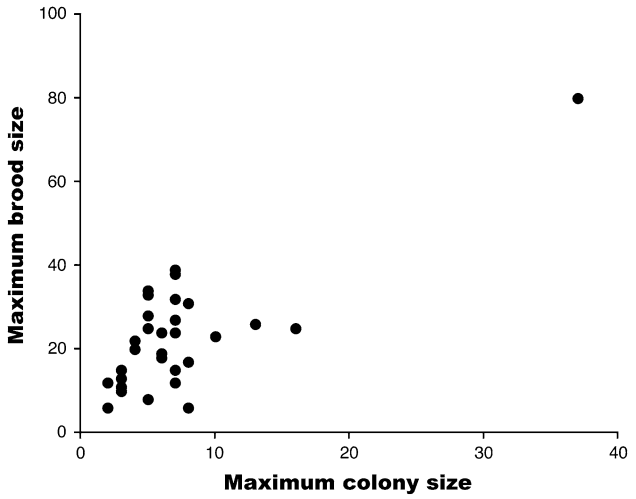

Fig. 2 Maximum colony size versus maximum brood size for allodapine species. The outlying point represents *E. tridentata*

size is plotted against maximum colony size in Fig. 2, suggesting a positive correlation, which was expected because larger colonies should have larger broods. A maximum likelihood analysis of correlation between maximum colony size and maximum brood size indicated a correlation coefficient using phylogenetic contrasts of 0.680 ($P < 0.001$, d.f. $= 32$). However, the significance of this correlation could be influenced by the outlier (*Exoneurella tridentata)*, which displays markedly larger values of both maximum brood and colony sizes than the other species (Fig. 2; Table A3). We therefore performed additional analyses with *E. tridentata* excluded. For this we performed two analyses, one in which λ was set at zero (no influence of phylogeny), and one in which λ was estimated. A likelihood ratio (LR) test indicated no significant improvement in the model by estimating λ (LR $= 0.034$, $P = 0.85$). We therefore conclude that when *E. tridentata* is excluded and phylogenetic contrasts are taken into account, there is no correlation between maximum brood and colony sizes.

We examined maximum brood size, maximum colony size, and proportion of social nests separately. When *Exoneurella tridentata* was included in ML analyses based on the consensus chronogram, we found λ values significantly different from zero for maximum colony and brood size, but not for the percentage of colonies that were social (Table 1). When estimated λ values were included in subsequent ML analyses, we found significant support for $\kappa > 1$ for maximum colony size, whereas δ was not significantly different from 1.0 for any variable. We also estimated the ancestral states for maximum colony size and maximum brood size using $\lambda = 1$ for both variables, and $\kappa = 2.35$ for colony size (κ for maximum brood size was not significant). These suggested an ancestral maximum colony size of 6.6 and maximum brood size of 25.7. When we also included estimated but non-significant δ and κ values, these estimated ancestral values changed only marginally (5.7 and 23.5, respectively). Because there was no significant support for $\lambda > 0$ for proportion of social nests, it is meaningless to estimate δ, κ or ancestral values for this trait.

Table 1 Summary of maximum likelihood analyses

Social trait	Estimated ancestral value	λ (LR) [Range] *Sig.*	δ (LR) [Range] *Sig.*	κ (LR) [Range] *Sig.*
Max. colony size (all taxa)	6.56	**1.0** (17.117) [1.00–1.06] $P < 0.0001$	**1.936** (0.943) [0.69–2.97] $P = 0.33$	**2.350** (8.902) [1.74–3.00] *$P = 0.003$*
Max. colony size (*E. tridentata* excluded)	6.36	**0.412** (1.626) [0.28–0.55] $P = 0.2$	NA	NA
Max. brood size (all taxa)	25.68	**1.0** (167) [1.0–1.05] $P < 0.0001$	**1.512** (0.437) [0.85–2.22] $P = 0.51$	**1.564** (3.101) [1.13–1.88] $P = 0.08$
Max. brood size (*E. tridentata* excluded)	22.75	**1.0** (12.600) [0.73–1.01] $P = 0.0004$	**2.419** (2.400) [1.87–3.0] $P = 0.12$	**0.779** (0.283) [0.24–1.04] $P = 0.59$
Percent social nests (all taxa)	NA	**0.262** (0.306) [0.06–0.48] *$P = 0.580$*	NA	NA
Percent social nests (*E. tridentata* excluded)	NA	**0.343** (0.540) [0.18–0.47] $P = 0.46$	NA	NA

Estimated λ, δ and κ values for three social traits (in bold), likelihood ratios (LR) and their significances. The ranges of these parameters from 250 random post-burnin chronograms are given in square brackets. LR tests for λ were against a null hypothesis value of 0.0 (no phylogenetic signature), and default values of 1.0 for δ (rates of evolutionary change independent of distance from root) and κ (evolutionary change proportional to branch lengths). δ and κ could not be estimated when $\lambda = 0$ since there is no influence of phylogeny on the trait

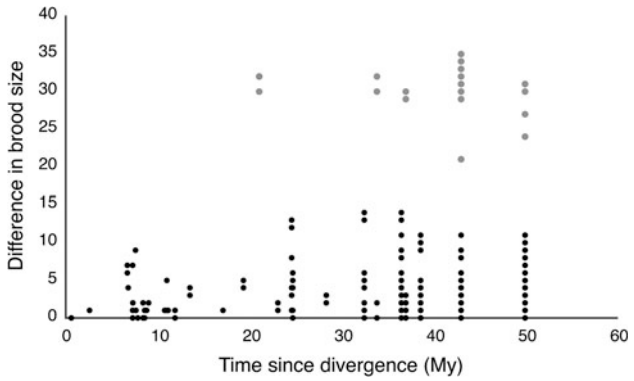

Fig. 3 Pairwise brood size differences versus time since divergence. *Grey dots* represent differences between *E. tridentata* and the other allodapine species, *black dots* represent all other pairwise values

Ranges in estimates of λ, κ and δ for the random post-burnin chronograms are given in Table 1. Ranges for the statistically significant parameters were extremely narrow, but ranges for the non-significant parameters were much larger. Combined, these results indicate that our likelihood ratio test results, both significant and non-significant, are robust to the phylogenetic uncertainty in our tree.

The analyses above included *E. tridentata*, but the extreme outlier nature of this species, along with the long branch leading to it, have the potential to produce misleading results if λ, δ and κ are based on the full-evidence data matrix. We therefore repeated the above analyses with *E. tridentata* excluded, which led to very different outcomes compared to inclusion of *E. tridentata*. We recovered a non-significant λ value for maximum colony size, but a λ value significantly >0 ($P = 0.004$) for maximum brood size (Table 1). Neither δ nor κ values were significant for either brood or colony size.

Lastly, we examined whether or not the extreme maximum colony and brood size in *E. tridentata* are consistent with a model of gradual change in the lineage leading to this species. To examine this, we plotted pairwise differences in brood sizes between all species in our sample against their estimated times since divergence. If brood sizes in *E. tridentata* are the result of gradual change we would expect to see a correlation between size differences and divergence time for data points involving *E. tridentata*. This plot is given in Fig. 3 and does not suggest any such trend.

Discussion

Exoneurella tridentata is highly unusual among allodapines in terms of both its colony size and in exhibiting morphologically discrete queen and worker castes. Interpretation of our results is not straightforward, given the conflicting outcomes stemming from inclusion versus exclusion of *E. tridentata* in our analyses. However, these differing outcomes suggest that this species' social evolution is unique in comparison to the rest of the phylogeny. With *Exoneurella tridentata* removed from analyses, we found no evidence that phylogenetic structure influenced either maximum colony size or the percentage of social nests within a population, and no evidence for a correlation between maximum colony and brood sizes. However, we did find that maximum brood size was influenced by phylogeny. The lack of phylogenetic influence on percentage of social colonies is not surprising. All allodapine species are facultatively social and we would expect the propensity of females to either (i) remain in a colony, or (ii) nest solitarily, would respond rapidly to environmental conditions. We predicted a priori that maximum colony size would be less evolutionarily labile, since larger colony size should necessitate substantial adaptations for life in a complex social construct.

The lack of significant phylogenetic effect on colony size may be related to the generally low maximum colony sizes in allodapines. Our estimated maximum ancestral colony size (when excluding *E. tridentata* from analyses) was about 5–6 females per nest, suggesting that the ability to live in moderately sized colonies had evolved before divergence of the extant lineages. The very small maximum colony sizes (<3) in some of our taxa, such as some *Allodapula* and *Halterapis* species, may therefore not have required substantial genetic change from an ancestral condition and, in this sense, decreases in colony size from the ancestral value would have been small and may be evolutionarily labile. Indeed, with the exception of *E. tridentata,* most allodapine species in our study do not have maximum colony sizes substantially greater than the ancestral estimates, and it is possible that these minor changes from the ancestral value have not required substantial genetic change.

The lack of phylogenetic influence on colony size is very interesting given the crown age of this tribe, estimated at about 47 Mya, and its biogeographical history (Schwarz et al., 2006; Chenoweth and Schwarz, 2011). Following an African origin, the Allodapini now ranges throughout the tropical and temperate Old World and occupies ecosystems in zones ranging from wet tropical to xeric temperate (Michener, 2007; Tierney et al., 2008). Although our study included only 33 species, an earlier study of African allodapine nesting biology (Michener, 1971), covering a larger sample of species (approximately 40 species, most of which do not overlap with our study), reported colonies of similar size to our data set. Allodapines have therefore experienced a geographically and ecologically very diverse evolutionary history, yet colony size has rarely exceeded the inferred ancestral values. Variation in allodapine colony sizes therefore seems to represent small 'tinkerings' around an ancestral value, with no clear phylogenetic trends towards either smaller or larger colony sizes. On the other hand,

maximum colony and brood sizes for *E. tridentata* are much larger than for other allodapines. Our plot of brood size differences versus time since divergence do not indicate that this species represents the end point of a gradual and directional deviation from ancestral values. Instead, *E. tridentata* represents a unique clade that exhibits a very different tempo of evolutionary change in relation to colony size, compared to other allodapine bees analysed in this study. This species is also unique in having morphologically discrete queen and worker castes (Houston, 1976; Hurst, 2001), raising the question of whether these combined features are associated with unusual selective environments.

We now present the hypothesis that the extreme colony sizes of *E. tridentata* and the existence of morphologically discrete castes coincide with two ecological factors, namely a xeric habitat and durable nesting substrates. *Exoneurella tridentata* nests in the dead branches of two hardwood trees, *Acacia papyrocarpa* and *Alectryon olieofolium* (Hurst, 2001). Individual nests can persist for >10 years because of the timber density and its slow rate of decomposition in a semi-arid desert (Hurst, 2001). Availability of suitable nest sites is dependent on weevil excavation of tunnels and nesting habitat is further limited by the slow growth of host trees. In these habitats mean annual rainfall is both minimal and seasonally restrictive (Kimba, South Australia mean annual precipitation = 346 mm; mean days per year with >10 mm precipitation = 8.0; Australian Bureau of Meteorology, 2011). This combination of harsh habitat and durable but scarce nesting substrate may help explain the origin of both large colony sizes and discrete castes. In particular, scarcity of nesting substrates would select against dispersal from natal nests, and durability of those nests would permit large colony sizes to accumulate over time.

One congener of *E. tridentata, E. eremophila*, also occurs in harsh xeric environments with a range overlapping that of *E. tridentata* (Houston, 1976), yet it is predominantly subsocial with no evidence of caste-like behaviour (Hogendoorn et al., 2001). *Exoneurella eremophila* lives in herbaceous nesting substrates that are much more abundant than those of *E. tridentata*, but which are also much less durable and unlikely to persist for more than a year or two (Watiniasih, 1998). The two remaining species of *Exoneurella*, *E. setosa* and *E. lawsoni*, are also predominantly subsocial, and also live in herbaceous stems that do not well persist over time (Michener, 1971; Neville et al., 1998). One Malagasy allodapine, *Hasinamelissa minuta*, lives in a xeric environment and exhibits highly eusocial behaviour, but colony sizes are small (maximum of 6 adult females per nest), and whilst queens and workers differ in body size, discrete morphological castes are absent (Schwarz et al., 2005). Interestingly, the nesting substrate of this bee is rare, as in *E. tridentata,* but the stems are friable and do not persist well over time.

It therefore appears that a unique combination of ecological and nesting substrate traits distinguish *E. tridentata* from other allodapines: harsh and xeric ecological conditions, scarcity of available nesting sites, and a nesting substrate that can be used over many generations. This raises the question of whether other evolutionary origins of complex eusociality in insects also required very particular conditions, and whether these were much more restrictive than the pre-adaptations that are currently regarded (e.g. Wilson, 2008) as important for explaining eusociality.

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References

Australian Bureau of Meteorology. 2011. Climate statistics for Australian locations, accessed 14 July 2011: http://www.bom.gov.au/climate/averages/tables/cw_018040_All.shtml

Bull N.J., Schwarz M.P. and Cooper S.J.B. 2003. Phylogenetic divergence of the Australian allodapine bees (Hymenoptera: Apidae). *Mol. Phyl. Evol.* **27**: 212-222

Cardinal S., Straka J. and Danforth B.N. 2010. Comprehensive phylogeny of apid bees reveals the evolutionary origins and antiquity of cleptoparasitism. *Proc. Natl Acad. Sci. USA* **107**: 16207-16211

Chenoweth L.B. and Schwarz M.P. 2011. Insights into the biogeographical origins and speciation history of the exoneurine Allodapine bees of Australia (Hymenoptera, Apidae). *J. Biogeogr.* doi:10.1111/j.1365-2699.2011.02488

Chenoweth L.B., Tierney S.M., Smith J.A., Cooper S.J.B. and Schwarz M.P. 2007. Social complexity in bees is not sufficient to explain lack of reversions to sociality living over long time scales. *BMC Evol. Biol.* **7**: 246-255

Hogendoorn K., Watiniasih N.L. and Schwarz M.P. 2001. Extended alloparental care in the almost solitary bee *Exoneurella eremophila. Behav. Ecol. Sociobiol.* **50**: 275-282

Houston T.F. 1976. New Australian allodapine bees (subgenus *Exoneurella* Michener) and their immatures (Hymenoptera: Anthophoridae). *Trans. R. Soc. S. Aust.* **100**: 15-28

Huelsenbeck J.P. and Ronquist F. 2001. MRBAYES: Baysesian inference of phylogenetic trees. *Bioinforma.* **17**: 754-755

Hurst P.S. 2001. Social biology of *Exoneurella tridentata*, an allodapine with morphological castes and perennial colonies. PhD thesis, School of Biological Sciences, The Flinders University of South Australia, Adelaide, Australia

Michener C.D. 2007. *Bees of the World*. Johns Hopkins University Press, Baltimore London

Michener C.D. 1971. Biologies of African allodapine bees (Hymenoptera, Xylocopinae). *Bull. Am. Mus. Nat. Hist.* **145**: 117-301

Neville T., Schwarz M.P. and Tierney S.M. 1998. Biology of a weakly social bee, *Exoneura (Exoneurella) setosa* (Hymenoptera: Apidae) and implications for social evolution in Australian allodapine bees. *Aust. J. Zool.* **46**: 221-234

Oster G.F. and Wilson E.O. 1978. *Caste and Ecology in the Social Insects*. Princeton University Press

Pagel M. and Meade A. 2006. Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am. Nat.* **167**: 808-825

Pagel M., Meade A. and Baker D. 2004. Bayesian estimation of ancestral character states on phylogenies. *Syst. Biol.* **53**: 673-684

Schwarz M.P., Fuller S., Tierney S.M. and Cooper S.J.B. 2006. Molecular phylogenetics of the exoneurine allodapine bees reveal an ancient and puzzling divergence from Africa to Australia. *Syst. Biol.* **55**: 31-45

Schwarz M.P., Richards M.H. and Danforth B.N. 2007. Changing paradigms in insect social evolution: new insights from halictine and allodapine bees. *Annu. Rev. Entomol.* **52**: 127-150

Schwarz M.P., Tierney S.M., Cooper S.J.B. and Bull N.J. 2004. Molecular phylogenetics of the allodapine bee genus *Braunsapis*: A-T bias and heterogenous substitution parameters. *Mol. Phyl. Evol.* **32**: 110-122

Schwarz M.P., Tierney S., Rehan S., Chenoweth L. and Cooper S. 2011. The evolution of eusociality in bees: workers began by waiting. *Biol. Lett.* **7**: 277-280

Schwarz M.P., Tierney S.M., Zammit J., Schwarz M.P. and Fuller S. 2005. Brood provisioning and colony composition of a malagasy species of *Halterapis*: implications for social evolution in the allodapine bees (Hymenoptera: Apidae: Xylocopinae). *Ann. Entomol. Soc. Am.* **98**: 126-133

Szathmary E. and Maynard-Smith J. 1995. The major evolutionary transitions. *Nature* **374**: 227-232

Tierney S.M., Smith J.A., Chenoweth L. and Schwarz M.P. 2008. Phylogenetics of allodapine bees: a review of social evolution, parasitism and biogeography. *Apidologie* **39**: 3-15

Watiniasih N.L. 1998. Life cycle and social behaviour of an Australian allodapine bee *Exoneurella eremophila* Houston (Apidae: Allodapini). MSc thesis, School of Biological Sciences, The Flinders University of South Australia, Adelaide

Wilson E.O. 2008. One giant leap: How insects achieved altruism and colonial life. *BioScience* **58**: 17-25

Zammit J., Hogendoorn K. and Schwarz M.P. 2008. Strong constraints to independent nesting in a facultatively social bee: quantifying the pressure posed by enemies-at-the-nest. *Insect. Soc.* **55**: 74-78