

Phylogenetics of allodapine bees: a review of social evolution, parasitism and biogeography*

Simon M. TIERNEY^{1,2}, Jaclyn A. SMITH¹, Luke CHENOWETH¹, Michael P. SCHWARZ¹

¹ School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, S.A. 5001, Australia

² Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Republic of Panama

Received 15 November 2006 – Revised 3 October 2007 – Accepted 3 October 2007

Abstract – It has been assumed that allodapine bees represent early stages in the evolution of social behaviour. Early studies suggested that sociality evolved from solitary forms, and that the solitary to social transition coincided with a transition from mass to progressive provisioning of brood. Recent studies challenge both of these assumptions, they suggest that: (i) *Macrogalea* replaces *Halterapis* + *Compsomelissa* as the sister group to all other genera; (ii) sociality is plesiomorphic for the tribe; and based on extended *Halterapis* research, (iii) there are no strictly solitary allodapine species and, therefore, no reversals to solitary living. Penalised likelihood dating of Bayesian inferred phylograms show allodapine lineages have an origin older than 40 Mya. The early origin of sociality in this tribe may explain the diverse array of social organization (and social parasitism) found in species across a range of clades, and the age of the group raises curious biogeographic scenarios.

social evolution / phylogenetics / alloparental care / brood provisioning / allodapine bees

1. INTRODUCTION

The Allodapini comprise one of four tribes in the Xylocopinae (Apidae). Allodapines are unusual among bees in rearing their brood in an open burrow (with no brood cells) excavated in dead plant stems and branches, and the majority of species progressively feed their brood. This extended contact between mothers and their offspring and the array of facultative social nesting species, that appeared to vary from simple (subsocial) to more sophisticated (eusocial) levels of organisation, made the allodapines seem particularly useful for uncovering the earliest steps in social evolution. In this sense, they were similar to the facultatively social halictine bees that showed a range from solitary to eusocial, and histori-

cally these two bee groups have provided insights on the evolution of social behaviour that studies of more advanced obligate caste-based insect societies are unable to address (reviewed in Schwarz et al., 2007).

The first detailed studies of allodapines were carried out by Charles Michener who examined a large number of species from both Africa and Australia and published a wide variety of monographs and papers covering nesting and social biology (e.g. Michener, 1965, 1971), social parasitism (Michener, 1970b), nesting substrates (Michener, 1970a), adult and immature morphology (eg. Michener, 1975a, b, c, d, 1976), and egg-size variation (Michener, 1973). Michener (1977) also carried out the first phenetic classification of allodapines, and contrasted the discordant relationships suggested by larval, pupal and adult characters. This body of work greatly influenced studies of insect social evolution (e.g. Michener, 1974), and allodapines were

Corresponding author: S.M. Tierney,
tierneys@si.edu

* Manuscript editor: Eduardo A.B. Almeida

thought to comprise one of the best examples of the ‘subsocial route’ to eusociality whereby advanced sociality is thought to have been derived from the extended contact between mothers and their immature offspring (Lin and Michener, 1972).

A second period of allodapine research began in the 1980s with a series of within-nest ethological studies by Maeta and co-workers (Maeta et al., 1992; and references therein) focussing on Asian *Braunsapis* species, and later studies by Australian researchers investigating colony life-cycles, sex allocation and intra-colony relatedness of Australian and African species (reviewed in Schwarz et al., 1997, 1998, 2007). More recently, allodapine research has focused on molecular phylogenetics and inference of ancestral characteristics arising from changes in the understanding of generic relationships. The molecular phylogenetic studies, combined with detailed social data on species from a wide range of genera, are leading to a very different interpretation of social evolution in the Allodapini.

2. PRE-MOLECULAR THEORIES ON ALLODAPINE PHYLOGENY

Behavioural traits, have played an influential role on allodapine phylogenetics, and for this reason a brief summary of their importance in inferring social evolution is helpful for understanding more recent outcomes. The paradigm of how insect societies evolved has historically revolved around the concept of a progression from simple to more complex forms – subsocial nests gradually attaining caste based eusocial organization via a directional ‘step-wise’ trajectory.

Initial systematic analyses of the Allodapini based on adult or immature morphological and behavioural character sets resulted in disparate phylogenetic arrangements (Michener, 1977). Allodapine larvae show greater morphological diversity than all other bees combined (Michener, 1977, p. 38), and the contrast in form is so distinct between genera that identification is often more easily keyed by larval traits, and taxonomic classification of adults without con-specific larvae can be problematic

(Michener, 1977; Reyes and Michener, 1992). Contradictions between data sets led to the formation of a consensus phylogeny based on a combination of all data sets, and a heavily weighted reliance on a small number of behavioural traits (e.g. egg laying and brood provisioning) at crucial nodes of the tree (for a subsequent cladistic revision see Reyes, 1998).

These studies suggested *Halterapis* + *Compsomelissa* as a holophyletic group that formed a sister clade to all other allodapines (based on brood provisioning, male genitalia, female terga and larval antennae), and retained some ancestral traits found in the other tribes of Xylocopinae. Based on knowledge of *Halterapis* natural history at the time (the only genus to mass provision brood and subsocial colonies, Michener, 1971), the logical inference was that progressive provisioning arose from an ancestral allodapine lineage that was mass provisioning. Furthermore, it seemed reasonable to suggest that allodapine social behaviour was ‘primitive’ – of relatively recent origin. Given that sociality was largely associated with the progressive provisioning taxa it was postulated that true social behaviour might have arisen from within the extant lineages of the tribe. See Figure 1 for representation of the generic phylogenetic arrangement as per Michener (1977) and Reyes (1998).

3. CURRENT UNDERSTANDING OF PHYLOGENY: RELATIONSHIPS AMONG MAJOR CLADES

A series of molecular phylogenetic studies (Schwarz et al., 2003; Bull et al., 2003; Tierney, 2004; Fuller et al., 2005; Schwarz et al., 2006) present consistent phylogenetic hypotheses that re-order relationships among the main clades, and counter arguments for the holophyly of *Halterapis* + *Compsomelissa* (Schwarz et al., 2003; Tierney, 2004). To highlight these differences we include a consensus Bayesian chronogram, from a recent study (Schwarz et al., 2006), in Figure 2 for comparison with the generic relationships in Figure 1. The main points to note are that: (i) *Macrogalea* is a monophyletic clade that is

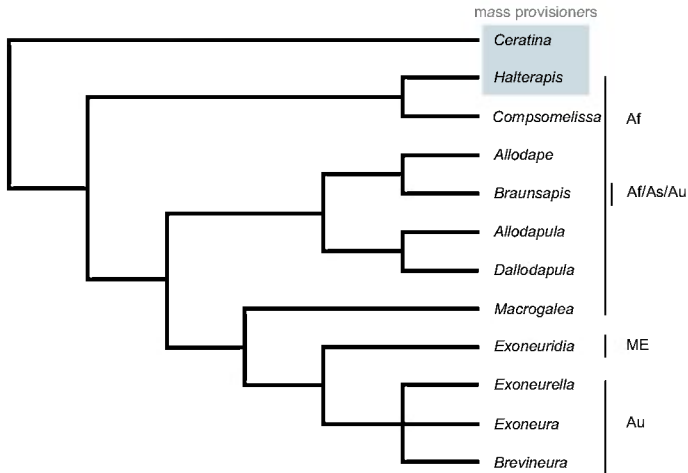


Figure 1. Genus level cladogram of Allodapini adapted from Michener (1977) and Reyes (1988). Mass provisioning taxa highlighted in grey box. Biogeographic distribution of taxa denoted at terminal branches: Af – Afrotropical; As – Asia (Indomalaya); Au – Australasia; ME – Middle East (Palearctic).

sister group to all other allodapines. Both larval and adult forms display unique characters among the tribe that add credibility to this rearrangement. Larvae of *Macrogalea* are generally simple, showing none of the elaborate setae or tubercle projections of other genera, and more closely resemble larvae of the sister tribe Ceratinini and the ancestral tribes Manueliini and Xylocopini. The remaining allodapines then form two further clades, consisting of (ii) the endemic Australian exoneurine genera; and (iii) the African genera from which the Middle Eastern *Exoneuridia* and the widespread *Braunsapis* are derived.

What is also surprising from molecular phylogenies is the point of the tree at which the exoneurines (*Exoneurella*, *Brevineura*, *Exoneura*, *Inquilina*) diverge from the other taxa. Given the geographic restriction of this clade to southern Australia, a position at the most distal end of the tree as suggested by Michener (1977) and Reyes (1998) might be expected (Fig. 1). Yet molecular results suggest a much earlier divergence from the African clades – which raises a difficult biogeographic problem with regard to when and how these bees actually got to the Australian landmass.

Molecular data sets have also improved our understanding of relationships among the most diverse African taxa, and the inclusion

of Madagascan taxa (not available to Michener (1977) or Reyes (1998)) raises new questions. An additional molecular phylogeny from a study by Smith et al. (2007) is presented, largely to examine the relationships of social parasites to their hosts (Fig. 3 – discussed below), however this work also includes African and Madagascan taxa absent from Figure 2, that are of relevance to the current discussion. Species of *Halterapis* occur in southern Africa and Madagascar, but molecular studies show this is a paraphyletic arrangement.

Madagascan species form a separate clade that is sister group to all other African (non-*Macrogalea*) genera (Fig. 2), whereas the mainland African *H. nigrinervis* is nested within a clade containing *Compsomelissa*, *Allodapula*, and *Exoneuridia* (Fig. 3). The remaining clade contains the southern African genus *Allodape* and the most widely distributed genus, *Braunsapis*. The latter most likely arose in tropical Africa, the central east African species *B. trochanterata* shows both adult and larval morphological traits that are intermediate between the two genera (Michener, 1975a, b, d), and molecular studies (Fig. 3) place this species as the sister taxon to all other *Braunsapis* (Tierney, 2004; Fuller et al., 2005).

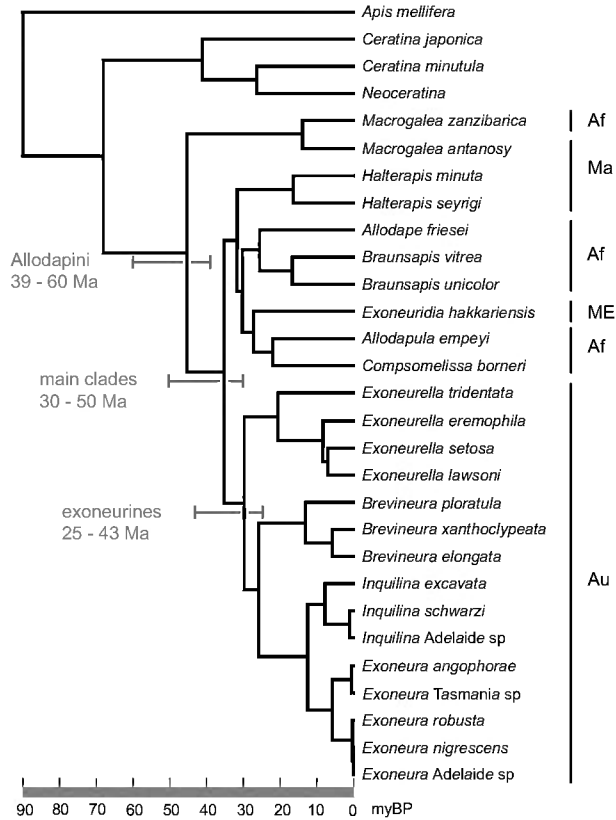


Figure 2. Chronogram derived from penalized likelihood estimation based on a Bayesian consensus phylogram, modified from Schwarz et al. (2006); see this reference for node support. Range (95% central distribution intervals) of age estimates for nodes of interest are highlighted in grey. Biogeographic distribution of taxa denoted at terminal branches: Af – Afrotropical; Au – Australasia; Ma – Madagascar; ME – Middle East (Palaearctic).

4. IMPACTS OF THE NEW PHYLOGENIES FOR UNDERSTANDING SOCIAL EVOLUTION

4.1. Social origins

Investigations of life history among the African clades (undertaken concurrently with phylogenetic work) revealed previously unexpected levels of sociality in the genus *Macrogalea*, which molecular data suggests is the sister group all other allodapines. *Macrogalea* progressively provision their brood and studies of two species (*Macrogalea zanzibarica* – Tierney et al., 2002; *M. Malawi* sp. – Thompson and Schwarz, 2006) show that

approximately half of all nests are multifemale (44% and 65% respectively) with maximum colony sizes of up to 10–13 females. Brood production is asynchronous and continuous, providing many opportunities for alloparental care because larvae constantly require defence and a progressive food supply. However, there are no clear reproductive castes – most colonies have more than one reproductive female and there are no signs that any females are permanently non-reproductive. Multifemale nesting shows significant benefits over solitary nesting in terms of the simple presence of brood as well as increases in productivity on a *per capita* basis as colony size increases, up to a certain level – implying evidence of benefits to cooperative nesting. Sex allocation is

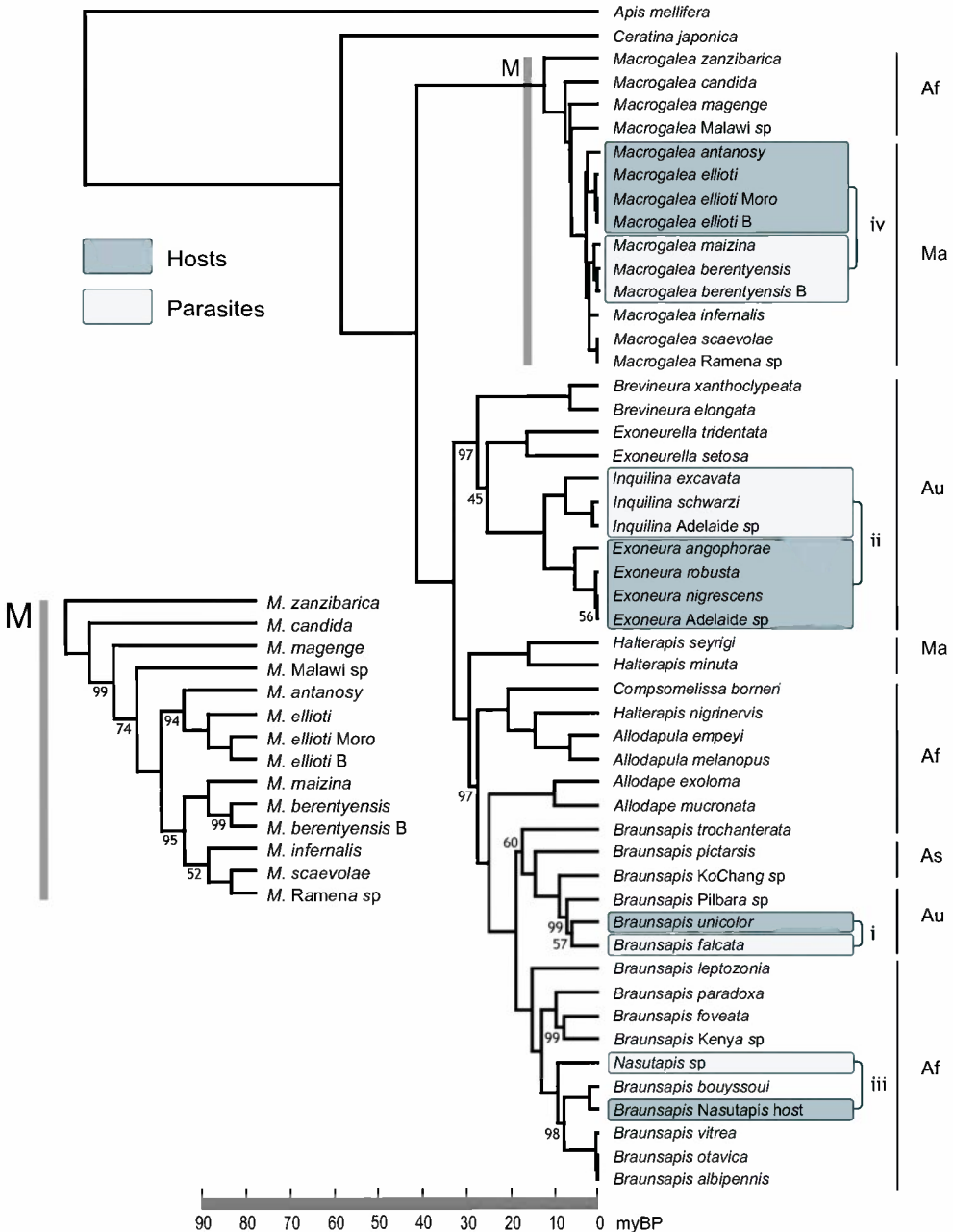


Figure 3. Chronogram of parasite – host relationships derived from penalized likelihood estimation based on a Bayesian consensus phylogram, modified from Smith et al. (2007). Posterior probability values are shown for nodes with < 100% support. Parasite (dark grey boxes) and host (light grey boxes) associations are linked and numbered as discussed in the text. A cladogram of the *Macrogalea* clade (M) is included separately as bifurcations are obscured by the scale of the main tree. The genus name *Braunsapis* is abbreviated to Br. Biogeographic distribution of taxa denoted at terminal branches: Af – Afrotropical; As – Asia (Indomalaya); Au – Australasia; Ma – Madagascar.

highly female biased, with a population-level of $r < 0.16$ for both species. Since sociality is also widespread in the Australian exoneurines (reviews in Schwarz et al., 1997, 1998; including one case of morphological caste distinction – Hurst, 2002), as well as in *Braunsapis* and *Allodapula*, the finding of sociality in *Macrogalea* made it apparent that the origin of sociality predates divergence of the extant allodapine clades. The realisation that sociality is the *bauplan* for allodapines is undoubtedly the most prominent outcome of recent phylogenetics and quite a departure from interpretations that assumed sociality arose from within existing lineages.

This finding also requires reinterpretation of the hypothesis that social origins were linked to a change in brood rearing tactics (from mass provisioning to progressive provisioning). *Halterapis* oviposit before acquiring the pollen store, which is the reverse order to all other mass provisioning bees, so that the form of mass provisioning in *Halterapis* is unlikely to represent retention of a plesiomorphic trait (Schwarz et al., 2003). In addition, molecular data place African species of *Halterapis* within a clade of partial mass provisioning genera (*Compsomelissa*, *Allodapula*), suggesting it is simply a further elaboration of brood provisioning found in this clade (Tierney, 2004). Until very recently the biology of Madagascan *Halterapis* species were unknown (Pauly et al., 2001) but two subsequent studies (Schwarz et al., 2005; Chenoweth and Schwarz, 2007), display yet another style of partial mass provisioning, which is most similar to some species of *Allodapula* – whereby eggs and early larval instars are initially mass provisioned as a group (common pollen source), and latter instars are progressively provisioned.

Both African and Madagascan *Halterapis* species are now known to nest in social groups. Chenoweth et al. (in press) re-examined African *H. nigrinervis* over different stages of the life cycle and found approximately half of collected nests to be social (up to 5 females) with generally only one reproductive in a nest. During the main brood rearing season brood production increases on a *per capita* basis, and sex allocation was female

biased across samples ($r \leq 0.18$). The first species studied from Madagascar, *H. minuta* (Schwarz et al., 2005), exhibits a high level of multifemale nesting (70%), with eusocial assemblages containing effectively sterile workers and the most distinct body size based reproductive differentiation among allodapines. Multifemale colonies are more productive than solitary nesting females in terms of absolute numbers of brood, but not on a *per capita* basis, and no male brood were found (single sample $N = 23$ colonies). Chenoweth and Schwarz (2007) also found eusocial organization in two additional Madagascan species, *H. isaloensis* and *H. seyrigi*, which closely resembles sociality found in *H. minuta*: around one half of nests were social, with no evidence of supernumerary reproductive females, no *per capita* increases in brood rearing efficiency, and highly female biased sex allocation (population $r < 0.14$).

The above considerations mean that there are currently no known 'strictly solitary' nesting allodapine lineages. The majority of species solitary found nests and ~ 50% of nests collected (from various taxa and populations) are occupied by a single female at the time of census, but there is no evidence of obligate reversals to solitary nesting in any taxa. The major eusocial insect groups (termites, ants, paper wasps and corbiculate bees) also show no reversals to solitary living from within eusocial clades, which has been interpreted as evidence that eusocial organization is an irreversible evolutionary endpoint (*sensu* Wilson, 1971). However, this contrasts with other facultatively social halictine bee groups that display few origins of eusocial behaviour, but multiple reversions back to solitary living (Danforth and Eickwort, 1997; Danforth et al., 1999, 2003). Weislo and Danforth (1997) have argued that such reversals among halictines provide evidence against a 'Dollo's law' interpretation of social evolution and that there is no reason to categorize eusocial behaviour as being more sophisticated than communal or solitary lifestyles. Rather, that these could just be alternative ways of solving the same environmental problems encountered by sterile caste based societies (reviewed in Weislo and Tierney, in press).

It is now apparent that allodapine sociality is generally associated with highly female biased sex allocation at the population level, which is widespread throughout all major clades (Schwarz et al., 1998; Tierney et al., 2000; 2002; Bull and Schwarz, 2001; Hogendoorn et al., 2001; Aenmey et al., 2006; Smith and Schwarz, 2006; Thompson and Schwarz, 2006; Joyce and Schwarz, 2006; Chenoweth and Schwarz, 2007; Chenoweth et al., in press). It is unusual to find such widespread bias among any animal group, and the only other group to display female biased allocation to this degree are the diplodiploid social spiders (reviewed Aviles, 1997) and the fig wasps (Herre, 1985; West and Herre, 1998). Whilst the mechanism for controlling sex determination in social spiders remains unknown (Aviles et al., 2000), these spiders are highly inbred and female biased sex ratios are posited to play a role in social evolution.

4.2. Social parasite evolution

There are at least eleven independent origins of social parasitism within Allodapini, most of which are host specific and range in the degree of morphological adaptations commonly associated with parasitic taxa (Michener, 1970b, 1975a, 2000). Müller (1872) was the first to propose that bee parasites speciate directly from their host and that this explained their frequent similarities (e.g. *Psithyrus c.f. Bombus*) – ‘the rule of Hermann-Müller’ (Popov, 1945). The general idea that social parasites usually parasitise hosts (species or genera) that they are closely related to, was later popularised by Emery (1909) with examples from Formicidae, and is now commonly referred to as ‘Emery’s rule’. Whilst various hymenopteran taxa exemplify a loose form of Emery’s rule (a relatively close phylogenetic association between host and parasite), evidence for the strict interpretation of the rule (sympatric speciation of intra-specific facultative parasites) is restricted to the myrmicine and attine ants (Savolainen and Vepsäläinen, 2003) and wasps (Sumner et al., 2004). However, other findings suggest more distant genealogies separating parasite and

host (e.g. paper wasps: Carpenter et al., 1993; Choudhary et al., 1994; ants: Ward, 1996).

In addition to the numerous origins of social parasitism, allodapines also display variation in the evolutionary age of these parasitic lineages (within the last 10 My Fig. 3). A recent study (Smith et al., 2007) examined four origins of parasitism, including secondary speciation within two parasitic lineages, suggesting a range of host-parasite relationships that are relevant for understanding the origin of social parasitism, namely: (i) evidence for the *strict form of Emery’s rule* – the parasite (*Braunsapis falcata*) was the closest relative to its host species (*B. unicolor*); (ii) *loose form of Emery’s rule* – one parasitic clade (*Inquilina excavata*, *I. schwarzi*, *I. Adelaide* sp.) was sister group to the clade containing their respective host species (*Exoneura angophorae*, *E. robusta*, *E. nigrescens*, *E. Adelaide* sp.); (iii) another parasite *Nasutapis* was most closely related to a clade of free-living *Braunsapis* species that contained its host; (iv) hetero-specific association – one parasitic clade of *Macrogalea* (*M. maizina*, *M. berentyensis*, *M. berentyensis b*) was the sister group to a clade of free-living species (*M. infernalis*, *M. scaevolea*, *M. Ramena* sp.) that were not their hosts, a relationship that is not consistent with Emery’s rule. Evidence suggests *M. maizina* and *M. berentyensis* are facultative parasites capable of independent nesting (Smith and Schwarz, 2006; Smith, 2007), a situation that may also be paralleled in the *Braunsapis paradoxa* group (Michener, 1975a). The range in allodapine social parasitism described here implies that these sorts of relationships are capable of developing in a number of different ways, and warrant further research.

4.3. Age of allodapine social forms

Bayesian and penalised likelihood dating analyses suggest divergence of the allodapine lineages occurred at least 39 Ma, and possibly as early as 80 Ma (Fig. 2 – Schwarz et al., 2006). The age of the tribe may account for the development of social behaviour now evident across clades, as well as the extreme diversity in larval form and methods of provisioning

them. So whilst it is clear that the Allodapini now appear to lack utility as a model system for exploring the origin of sterile-caste based eusocial behaviour, their plasticity in degrees of social organization (within and across species and genera) still provide a valuable resource for looking at transitions between levels of organization.

Eusocial and semisocial colonies are temporally dependant on alloparents, whose presence is influenced by both the environment and brood ontogeny (Tierney, 2004). Climate clearly influences voltinism in allodapines generally and in some species decreasing latitude extends brood rearing periods that allow for more generations to be reared (Cronin and Schwarz, 2001). Perhaps of greater relevance to alloparental care is the timing of oviposition, of which there are two general temporal modes: synchronous and protracted (with some variation). *Allodapula*, *Exoneura* and Madagascan *Halterapis* lay eggs in a pulse, so that eusociality is dependant on having enough time to rear through a second brood pulse for the first cohort to rear. In contrast, *Macrogalea*, *Allodape*, *Braunsapis*, *Compsomelissa*, African *Halterapis*, *Brevineura*, and *Exoneurella* tend to lay fewer eggs at a time but lay them over a protracted period – creating multiple and extended opportunities for alloparental care. The result is that variation in allodapine sociality appears to be phylogenetically constrained within genera, according to differential brood rearing tactics (Tierney et al., 1997). Empirical evidence for constraints on social nesting based on environmental pressures from either (i) the presence of predators and parasites, or (ii) floral or nest substrate availability have not yet proven to be widely influential.

In an examination of social evolution in ceratinine bees (sister tribe to Allodapini), Michener (1985) argued that there was no need for a series of intervening species; rather that eusocial behaviour could develop directly from solitary forms. Ceratinines are unusually long-lived for bees, which should increase opportunities for generation overlap to occur, however a perceived lessened threat of predation in stem nesting cf. ground nesting (3D vs. 2D space) seemed to explain why

caste development was not required in this group – in terms of parasitic invasion there is a general lack of data to support this hypothesis, but see Wcislo (1996). A similar line of argument has been put forth for communal wasps and bees (reviewed in Wcislo and Tierney, in press), in that perhaps communal living is simply an alternate means of solving the same problems that eusocial taxa face – finding a protected space to raise brood. In this light, if communal groups have already attained this goal, they need not represent a mid-point on path to eusocial organization. However, whilst communal taxa are clearly useful for addressing issues concerned with the origins of social living there still remains a noticeable lack of empirical information (West-Eberhard, 1978; Cowan, 1991; Matthews, 1991; Wcislo and Engel, 1996). Allodapine bees are also relatively long lived (up to 18 months – Schwarz unpublished) and commonly use the same nesting substrates as *Ceratina*. A decreased predation risk in 3D space, *as per* Michener (1985), may well explain why allodapines have discarded the use of brood cells. However, we lack empirical evidence to test this hypothesis and the majority of stem nesting bees and wasps construct cells and are solitary, and the only sphecid wasp that disassembles it's brood cell partitions is also solitary (Matthews, 1991; Michener, 2000). Given our current interpretation, that social behaviour has persisted for significant periods of time, perhaps similar arguments can be drawn for allodapine bees as representing yet another independent means of solving the same problems encountered by communal bees and wasps, sterile caste based eusocial insect societies and the facultative eusocial halictines.

4.4. Historical biogeography

Although molecular phylogenetic studies of allodapines have largely been driven by questions on social evolution, they have revealed some interesting patterns in historical biogeography. Dispersal-vicariance analyses indicate an African origin for the Allodapini with a dispersal of the relatively derived genus *Braunsapis* from Africa to southern

Asia ~16 Ma, and then into Australia ~9 Ma (Fuller et al., 2005). This dispersal route and divergence time is fairly typical of Indian Ocean Rim dispersal events for many taxa, which coincides with the Australian-Laurasian interchange of flora and fauna in mid-Miocene (Raven and Axelrod, 1972). However, divergences among the Madagascan *Halterapis* clade, the Australian exoneurine clade and the remaining African clade (~30–50 Ma) and radiation of the exoneurines within Australia (~25–43 Ma) predate the collision of the Australian-Laurasian plates and there are no remnant lineages in Asia; thus the current exoneurine taxa (restricted to southern semi-arid and temperate Australia) do not appear to have involved dispersal through Asia.

Schwarz et al. (2006) propose that this dispersal may have involved a southern route via either Antarctica or currently submerged landmasses of the southern Indian Ocean – e.g. the Kerguelan Plateau, an igneous province intermittently above sea level ~100–20 Mya (Frey et al., 2000; Duncan, 2002). This latter theory has been posited as a possible explanation for southern hemispheric dispersal in the Cretaceous (early Cretaceous to Cenomanian) of some Diptera, bird groups and angiosperms (reviewed in: McLoughlin, 2001; Sanmartín and Ronquist, 2004). More recently a late Cretaceous Antarctic land bridge (including the Kerguelan Plateau and Gunnerus Ridge) has been implicated in the vicariant origin of various Madagascan taxa including teleost rainbowfishes (Sparks and Smith, 2004), boid snakes, podocnemid turtles and iguanid lizards (Noonan and Chippendale, 2006). Whilst it is generally accepted that biotic exchange between Australia and Antarctica persisted until ~35–50 Mya (Woodburne and Case, 1996; Li and Powell, 2001) the cessation of interchange between India/Madagascar – Antarctica is less concrete: current palaeogeographical and palaeontologic evidence suggests the two landmasses remained contiguous until ~80–90 Mya (Smith et al., 1994; Krause et al., 1997; Sampson et al., 1998; Hay et al., 1999; Reeves and de Wit, 2000; Rage, 2003; Sereno et al., 2004). Like the freshwater rainbowfishes (Vari, 1992; Sparks and Smith, 2004, 2005) some closely related allodapine genera

are present in Madagascar (*Macrogalea*) and Australia (the exoneurines) with no representative taxa in the Mascarene isles or Asia, which would favour vicariance rather than dispersal of these taxa. However, biogeographic scenarios for the Allodapini are more complicated and could well involve both vicariant and multiple dispersal events.

Phylogenetic data suggests that the tribe originated in Africa (Schwarz et al., 2006). *Macrogalea* is sister group to all remaining genera and is restricted to tropical Africa and Madagascar, however their arrival in Madagascar appears to be very recent (~4.7–3.5 Mya) and thus can only be explained by dispersal (Tierney, 2004; see Fig. 3 also). The allodapine node after divergence from the *Macrogalea* lineages gives rise to two major clades: (i) the remaining Madagascan and African taxa (from which the Middle Eastern *Exoneuridia* and the cosmopolitan *Braunsapis* are derived); and, (ii) the exoneurines which are endemic to southern Australia. Based on current molecular dating estimates the extant allodapines arose and began diverging a minimum of ~39–60 Mya (Tierney, 2004; Fuller et al., 2005; Schwarz et al., 2006), thus the distribution of all clades except the exoneurines can be attributed to dispersal events:

Africa – Madagascar (*Halterapis*; *Braunsapis* twice; *Macrogalea*)

Afrotropic – Palaearctic (*Exoneuridia*)

Afrotropic – Indomalaya (*Braunsapis*)

Indomalaya – Australasia (*Braunsapis*)

However, it needs to be stressed that the minimum ages used to root trees in our dating analyses (amber fossils and the branch within Apidae) are likely to produce overly conservative divergence ages (see Schwarz et al., 2006); therefore the vicariance of Madagascan/southern Australian allodapines and/or dispersal involving late Cretaceous Antarctic land bridges is not implausible.

5. FUTURE AREAS FOR RESEARCH

Molecular phylogenetic studies of allodapines have altered our understanding of divergence among the major clades, historical biogeography of the tribe and combined with

recent discoveries in life history clarify our view of social evolution. However, they have also raised a number of new questions that require resolution. It now appears that allodapines cannot be used to infer origins of sociality *de novo*, but they can be used to infer key transitions among forms of sociality. However, this requires more detailed descriptions of sociality in extant species that are still poorly understood, such as *Exoneuridia* and *Compsomelissa*, furthering our understanding of behavioural traits (brood ontogeny and provisioning) and possible environmental constraints that are influential to understanding broad aspects of social evolution. Social biology of the rare Middle Eastern genus *Exoneuridia* is completely unknown, although personal observations of *E. hakkariensis* (Schwarz, unpublished) indicate that this species nests in rock cavities of cliff-faces. The traffic of bees observed coming in and out of these cavities was extremely high, suggesting very large colony sizes. Future research would examine whether sociality in these bees may be linked to relaxation of colony size constraints and nesting site persistence, if so we would expect them to be highly eusocial. Empirical evidence regarding constraints to social nesting based on pressures from either (i) the presence of predators and parasites, (ii) floral resources, (iii) nest site availability, or (iv) substrate longevity are lacking across the phylogeny and thus have not yet proven to be widely influential.

ACKNOWLEDGEMENTS

We thank Bill Wcislo and two anonymous reviewers for vibrant correspondence on earlier versions of this manuscript. This research has been supported by Australian Research Council grants to M. Schwarz, B. Crespi and S. Cooper.

Phylogénétique des abeilles de la tribu des Allostapini (Apidae, Xylocopinae) : le point sur l'évolution sociale, le parasitisme et la biogéographie.

Allodapini / abeille / évolution sociale / phylogénétique / soin alloparental / approvisionnement du couvain

Zusammenfassung – Phylogenetik allostapiner Bienen: ein Review über soziale Evolution, Parasitismus und Biogeographie. Einige Bienen und Wespen sind fakultativ sozial. Anders als Honigbienen, Ameisen und Termiten sind ihre reproduktiven Rollen nicht durch morphologische Kasten eingeschränkt. Alle Weibchen sind daher in der Lage ihre eigene Brut unabhängig aufzuziehen. Daher ist die entstehende Gruppendynamik (soziale Organisation) hoch flexibel und reicht von der solitären Lebensweise bis zu hochorganisierten (eusozialen) Gemeinwesen, wobei diese Unterschiede sowohl innerhalb einer Art als auch zwischen nahverwandten Arten auftreten.

Aus diesem Grund sind solche Organismen sehr gut für vergleichende Untersuchungen über altruistisches Verhalten und dessen Entstehung geeignet. Warum sollte ein Individuum die Gelegenheit zu eigener Reproduktion auslassen und anstelle dessen anderen helfen, deren Brut großzuziehen? Die fakultativ sozialen allostapinen Bienen ziehen ihre Brut in offenen linearen Stengelsystemen auf (i.e. nicht in von der äußeren Umgebung abgeschirmten Brutzellen), dies erzeugt unter sozialen Insekten einzigartige Lebensgeschichten und haben sie über die vergangenen mehr als 40 Jahre zu einem wichtigen Modellsystem gemacht.

Vergleichende evolutionäre Forschung benötigt einen gesicherten Stammbaum (einen Baum der evolutionären Geschichte, der die Abstammungslinien sichtbar macht), aus dem dann die Entwicklung eines spezifischen Charakteristikums hergeleitet werden kann. Anfängliche Versuche, die Phylogenie der Allostapinen aufzulösen waren problematisch, vor allem da unabhängige auf Eigenschaften der Larven, Puppen oder Adulten beruhende Studien zu widersprüchlichen Ergebnissen geführt hatten. Analysen von DNA Sequenzen unterstützen eine sehr unterschiedliche Phylogenie, die zu einer Umordnung der Beziehungen zwischen den Gattungen führt. Das hauptsächliche Ergebnis ist, dass alle Gattungen sozial sind. Es widerspricht damit früheren Interpretationen, nach denen die soziale Evolution innerhalb der noch bestehenden Linien eingesetzt hat. Die Sozialität entwickelte sich eindeutig vor den heute lebenden Arten des Stammes zurück.

Anhand von baltischen Bernsteinfossilien eines ausgestorbenen Geschwisterstammes haben die Untersucher die Zeiträume der Entstehung dieser Bienen und ihrer Auseinanderentwicklung sowie des Bestehens ihrer sozialen Organisation einzuschätzen versucht. Nach diesen Analysen ist der Tribus vor etwa 39–80 Millionen Jahren entstanden, obwohl diese Schätzungen zurückhaltend sind und die tatsächliche Entstehungszeit vermutlich etwas früher war. Dies legt nahe, dass die Art des in dem Tribus gezeigten Sozialverhaltens keineswegs primitiv ist. Soziales Verhalten tritt in allen größeren phylogenetischen Abzweigungen auf und ist mit einer hochgradig zur weiblichen Seite neigenden

Geschlechtszuweisung verbunden – eine von der Verwandtenselektion, der dominanten Theorie der letzten 30 Jahre zur Entstehung altruistischen Verhaltens nahegelegten Schlüsselgröße. Eine datierte Phylogenie ermöglicht darüber hinaus eine Untersuchung der biogeographischen Theorie. Die hier zusammengefassten Ergebnisse ergeben überraschende Einsichten über die Verbreitungsfähigkeit dieser Bienen als auch über die Rolle der nun überfluteten Landmassen im biotischen Austausch zwischen Madagaskar, Antarktis, und zuletzt auch Australien.

Sozialevolution / Phylogenetik / Alloparentale Pflege / Brutversorgung / Allodapine Bienen

REFERENCES

- Aenmey T., Tierney S.M., Pillay N., Schwarz M.P. (2006) Nesting biology of an African allodapine bee *Braunsapis vitrea*: female biased sex allocation in the absence of worker-like behavioural castes, *Ethol. Ecol. Evol.* 18, 205–220.
- Aviles L. (1997) Causes and consequences of cooperation and permanent-sociality in spiders, in: Choe J., Crespi B. (Eds.), *Evolution of Social Behaviour in Insects and Arachnids*, Cambridge University Press, Cambridge, pp. 476–498.
- Aviles L., McCormack J., Cutter A., Bukowski T. (2000) Precise highly female-biased sex ratios in a social spider, *Proc. R. Soc. Lond. B.* 267, 1445–1449.
- Bull N.J., Schwarz M.P. (2001) Brood insurance via protogyny: a source of female biased sex allocation, *Proc. R. Soc. Lond. B Biol. Sci.* 268, 1869–1874.
- Bull N.J., Schwarz M.P., Cooper S.J.B. (2003) Phylogenetic divergence of the Australian allodapine bees, *Mol. Phylogenet. Evol.* 27, 212–222.
- Carpenter J.M., Strassmann J.E., Turillazzi S., Hughes C.R., Solís C.R., Cervo R. (1993) Phylogenetic relationships among paper wasp social parasites and their hosts (Hymenoptera: Vespidae; Polistinae), *Cladistics* 9, 129–146.
- Chenoweth L.B., Tierney S.M., Smith J.A., Cooper S.J.B., Schwarz M.P. (in press) Social Complexity in bees is not sufficient to explain lack of reversions to solitary living over long time scales, *BMC Evol. Biol.* 7, 246.
- Chenoweth L.B., Schwarz M.P. (2007) Social Biology of two Madagascan *Halterapis*: Evidence that Eusociality is Plesiomorphic for an Ancient Allodapine Lineage, *Ann. Entomol. Soc. Am.* 100, 311–319.
- Choudhary M., Strassmann J.E., Queller D.C., Turillazzi S., Cervo R. (1994) Social parasites in polistine wasps are monophyletic: Implications for sympatric speciation, *Proc. R. Soc. Lond. B* 257, 31–35.
- Cowan D.P. (1991) The solitary and presocial Vespidae, in: Ross K.G., Matthews R.W. (Eds.), *The Social Biology of Wasps*, Cornell University Press, New York, pp. 33–73.
- Cronin A.L., Schwarz M.P. (2001) Latitudinal variation in the sociality of allodapine bees: sex ratios, relatedness and reproductive differentiation, *Aust. J. Zool.* 49, 1–16.
- Danforth B.N., Eickwort G.C. (1997) Evolution of social behavior in the augochlorine sweat bees (Hymenoptera: Halictidae) based on a phylogenetic analysis of the genera, in: Choe J.C., Crespi B.J. (Eds.), *The Evolution of Social Behaviour in Insects and Arachnids*, Cambridge University Press, Cambridge, pp. 270–292.
- Danforth B.N., Sauquet H., Packer L. (1999) Phylogeny of the bee genus *Halictus* (Hymenoptera: Halictidae) based on parsimony and likelihood analyses of nuclear EF-1 α sequence data, *Mol. Phylogenet. Evol.* 13, 605–618.
- Danforth B.N., Conway L., Ji S. (2003) Phylogeny of eusocial *Lasioglossum* reveals multiple losses of eusociality within a primitively eusocial clade of bees, *Syst. Biol.* 52, 23–36.
- Duncan R.A. (2002) A time frame for construction of the Kerguelen Plateau and Broken Ridge, *J. Petrology* 43, 1109–1119.
- Emery C. (1909) Über der Ursprung der dulotischen, parasitischen und myrmekophilen Ameisen, *Biol. Centralbl.* 29, 352–362.
- Frey F.A., Coffin M.F., Wallace P.J., Weis D., Zhao X., Wise S.W. et al. (2000) Origin and evolution of a submarine large igneous province: the Kerguelen Plateau and Broken Ridge, southern Indian Ocean, *Earth Planetary Sci. Lett.* 176, 73–89.
- Fuller S., Schwarz M.P., Tierney S.M. (2005) Phylogenetics of the allodapine bee genus *Braunsapis*: historical biogeography and long-range dispersal over water, *J. Biogeogr.* 32, 2135–2144.
- Hay W.W., DeConto R.M., Wold C.N., Wilson K.M., Voigt S., Schulz M., Rossby-Wold A., Dullo W.-Chr., Ronov A.B., Balukhovskiy A. (1999) An alternative global Cretaceous paleogeography, in: Barrera E., Johnson C. (Eds.), *The Evolution of Cretaceous Ocean/Climate Systems*, Geological Society of America Special Paper 332.
- Herre E.A. (1985) Sex ratio adjustment in fig wasps, *Science* 228, 896–898.
- Hogendoorn K., Watiniasih N.L., Schwarz M.P. (2001) Extended alloparental care in the almost solitary bee *Exoneurella eremophila*, *Behav. Ecol. Sociobiol.* 50, 275–282.
- Hurst P.S. (2002) Social biology of *Exoneurella tridentata*, an Australian allodapine bee with

- morphological castes and perennial colonies, Flinders University, PhD Thesis, Adelaide.
- Joyce N., Schwarz M.P. (2006) Sociality in the Australian allodapine bee *Brevineura elongata*: small colony sizes despite large benefits to group living, *J. Insect Behav.* 19, 45–61.
- Krause D.W., Prasad G.V.R., von Koenigswald W., Sahni A., Grine F.E. (1997) Cosmopolitanism among Gondwanan Late Cretaceous mammals, *Nature* 390, 504–507.
- Li Z.X., Powell C.McA. (2001) An outline of palaeogeographic evolution of the Australian region since the beginning of the Neoproterozoic Earth, *Earth Sci. Rev.* 53, 237–277.
- Lin N., Michener C.D. (1972) Evolution of sociality in insects, *Q. Rev. Biol.* 47, 131–159.
- McLoughlin S. (2001) The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism, *Aust. J. Bot.* 49, 271–300.
- Maeta Y., Sakagami S.F., Michener C.D. (1992) Laboratory studies on the behavior and colony structure of *Braunsapis hewitti*, a xylocopine bee from Taiwan (Hymenoptera: Anthophoridae), *Kans. Univ. Sci. Bull.* 54, 289–333.
- Matthews R.W. (1991) Evolution of social behavior in sphecid wasps, in: Ross K.G., Matthews R.W. (Eds.), *The Social Biology of Wasps*, Cornell University Press, New York, pp. 570–602.
- Michener C.D. (1965) A classification of the bees of the Australian and South Pacific regions, *Bull. Am. Mus. Nat. Hist.* 130, 1–362.
- Michener C.D. (1970a) Nest sites of stem and twig inhabiting African bees, *J. Entomol. Soc. S. Afr.* 33, 1–22.
- Michener C.D. (1970b) Social parasites among African allodapine bees (Hymenoptera, Anthophoridae, Ceratinini), *Zool. J. Linn. Soc.* 49, 199–215.
- Michener C.D. (1971) Biologies of African allodapine bees, *Bull. Am. Mus. Nat. Hist.* 145, 219–302.
- Michener C.D. (1973) Size and form of eggs of allodapine bees, *J. Entomol. Soc. S. Afr.* 36, 281–285.
- Michener C.D. (1974) *The Social Behavior of the Bees*, Harvard University Press, Cambridge.
- Michener C.D. (1975a) A taxonomic study of African allodapine bees, *Bull. Am. Mus. Nat. Hist.* 155, 67–240.
- Michener C.D. (1975b) Larvae of African allodapine bees. 1. The genus *Allodape*, *J. Entomol. Soc. S. Afr.* 38, 1–12.
- Michener C.D. (1975c) Larvae of African allodapine bees. 2. *Braunsapis* and *Nasutapis*, *J. Entomol. Soc. S. Afr.* 38, 223–242.
- Michener C.D. (1975d) Larvae of African allodapine bees. 3. The genera *Allodapula* and *Eucondylops*, *J. Entomol. Soc. S. Afr.* 38, 243–250.
- Michener C.D. (1976) Larvae of African allodapine bees. 4. *Halterapis*, *Compsomelissa*, *Macrogalea*, and a key to African genera, *J. Entomol. Soc. S. Afr.* 39, 33–37.
- Michener C.D. (1977) Discordant evolution and the classification of allodapine bees, *Syst. Zool.* 26, 32–56.
- Michener C.D. (1985) From solitary to eusocial: need there be a series of intervening species? in: Hölldobler B., Lindauer M. (Eds.), *Experimental behavioral ecology and sociobiology*, Gustav Fischer Verlag, Stuttgart, pp. 293–305.
- Michener C.D. (2000) *Bees of the world*, Johns Hopkins University Press, Baltimore.
- Müller H. (1872) Anwendung der Darwinischen Lehre auf Bienen, *Verh. Natur. Ver. Preuss. Rheinl. U. Westf.* 6, 1.
- Noonan B.P., Chippendale P.T. (2006) Vicariant origin of Madagascan Reptiles supports late Cretaceous Antarctic land bridge, *Am. Nat.* 168, 730–741.
- Pauly A., Brooks R.W., Nilsson A., Pesenko Y.A., Eardley C.D., Terzo M., Griswold T., Schwarz M., Patiny S., Munzinger J., Barbier Y. (2001) Hymenoptera Apoidea de Madagascar et des îles voisines, *Ann. Sci. Zool.* 286, 1–390.
- Popov V.B. (1945) Parazitizm pchelinykh ego osobennosti i evolyutsiya, *Zhurnal Obschei* 6, 183–203.
- Rage J.-C. (2003) Relationships of the Madagascan fauna during the Late Cretaceous: Northern or Southern routes? *Acta Palaeontologica Polonica* 48, 661–662.
- Raven P.H., Axelrod D.I. (1972) Plate tectonics and Australasian paleobiogeography, *Science* 176, 1379–1386.
- Reeves C., de Wit M. (2000) Making ends meet in Gondwana: retracing the transforms of the Indian Ocean and reconnecting continental shear zones, *Terra Nova* 12, 272–280.
- Reyes S.G. (1998) A cladistic analysis of the bee tribe Allodapini (Hymenoptera: Apidae: Xylocopinae), *Philipp. Entomol.* 12, 55–84.
- Reyes S.G., Michener C.D. (1992) The genus *Halterapis* Michener (1969) in Madagascar, *Trop. Zool.* 5, 249–253.
- Sampson S.D., Witmer L.M., Forster C.A., Krause D.W., O'Connor P.M., Dodson P., Ravoavy F. (1998) Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana, *Science* 280, 1048–1051.
- Sanmartín I., Ronquist F. (2004) Southern Hemisphere biogeography inferred by event-based models: plant versus animal patterns, *Syst. Biol.* 53, 216–243.
- Savolainen R., Vepsäläinen K. (2003) Sympatric speciation through intraspecific social parasitism, *Proc. Natl. Acad. Sci. USA* 100, 7169–7174.
- Schwarz M.P., Silberbauer L.X., Hurst P.S. (1997) Intrinsic and extrinsic factors associated with social evolution in allodapine bees, in: Choe

- J.C., Crespi B.J. (Eds.), *The Evolution of Social Behaviour in Insects and Arachnids*, Cambridge University Press, Cambridge, pp. 333–346.
- Schwarz M.P., Bull N.J., Hogendoorn K. (1998) Evolution of sociality in the allodapine bees: a review of sex allocation, ecology and evolution, *Insectes Soc.* 45, 349–368.
- Schwarz M.P., Bull N.J., Cooper S.J.B. (2003) The molecular phylogenetics of allodapine bees, with implications for the evolution of sociality and progressive rearing, *Syst. Biol.* 52, 1–14
- Schwarz M.P., Tierney S.M., Zammit J., Schwarz P.M., Fuller S. (2005) Brood provisioning and colony composition of a Madagascan species of *Halterapis*: implications for social evolution in the allodapine bees, *Ann. Entomol. Soc. Am.* 98, 126–133
- Schwarz M.P., Fuller S., Tierney S.M., Cooper S.J.B. (2006) Molecular phylogenetics of the exoneurine allodapine bees reveal an ancient and puzzling dispersal from Africa to Australia, *Syst. Biol.* 55, 31–45.
- Schwarz M.P., Richards M.H., Danforth B.N. (2007) Changing paradigms in insect social evolution: new insights from halictine and allodapine bees, *Annu. Rev. Entomol.* 52, 127–150.
- Sereno P.C., Wilson J.A., Conrad J.L. (2004) New dinosaurs link southern land mass in the Mid-Cretaceous, *Proc. R. Soc. Lond. B*, 271, 1325–1330.
- Smith A.G., Smith D.G., Funnell B.M. (1994) *Atlas of Mesozoic and Cenozoic coastlines*, Cambridge University Press, Cambridge.
- Smith J.A. (2007) Facultative social parasitism in the allodapine bee *Macrogalea berentyensis*, *Insect Sci.* 14, 65–69.
- Smith J.A., Schwarz M.P. (2006) Sociality in a Madagascan allodapine bee, *Macrogalea antanosy*, and the impacts of the facultative social parasite, *Macrogalea maizina*, *Insectes Soc.* 53, 101–107.
- Smith J.A., Tierney S.M., Park Y.C., Fuller S., Schwarz M.P. (2007) Origins of social parasitism: The importance of divergence ages in phylogenetic studies, *Mol. Phylogen. Evol.* (in press).
- Sparks J.S., Smith W.L. (2004) Phylogeny and biogeography of the Madagascan and Australasian rainbowfishes (Teleostei: Melanotaenioidae): Gondwanan vicariance and evolution in freshwater, *Mol. Phylogen. Evol.* 33, 719–734.
- Sparks J.S., Smith W.L. (2005) *Freshwater Fishes, Dispersal Ability, and Nonevidence: "Gondwana Life Rafts" to the Rescue*, *Syst. Biol.* 54, 158–165.
- Sumner S., Aanen D.K., Delabie J., Boomsma J.J. (2004) The evolution of social parasitism in *Acromyrmex* leaf-cutting ants: A test of Emery's rule, *Insectes Soc.* 51, 37–42.
- Thompson S., Schwarz M.P. (2006) Cooperative nesting and complex female-biased sex allocation in a tropical allodapine bee, *Biol. J. Linn. Soc.* 89, 355–364.
- Tierney S.M. (2004) *The evolution of African allodapine bees*, Flinders University, PhD Thesis, Adelaide.
- Tierney S.M., Schwarz M.P., Adams M. (1997) Social behaviour in an Australian allodapine bee *Exoneura (Brevineura) xanthoclypeata*, *Aust. J. Zool.* 45, 385–398.
- Tierney S.M., Cronin A.L., Loussert N., Schwarz M.P. (2000) The biology of *Brevineura froggatti* and phylogenetic conservatism in Australian allodapine bees, *Insectes Soc.* 47, 96–97.
- Tierney S.M., Schwarz M.P., Neville T., Schwarz P.M. (2002) Sociality in the phylogenetically basal allodapine bee genus *Macrogalea* (Apidae: Xylocopinae): implications for social evolution in the tribe Allodapini, *Biol. J. Linn. Soc.* 76, 211–224.
- Vari R.P. (1992) Redescription of *Mesopristes elongatus* (Guichenot, 1866), an endemic Malagasy fish species (Pisces, Terapontidae), *Am. Mus. Novit.* 3039, 1–7.
- Ward P.S. (1996) A new workerless social parasite in the ant genus *Pseudomyrmex* (Hymenoptera: Formicidae), with a discussion of the origin of social parasitism in ants, *Syst. Entomol.* 21, 253–263.
- Weislo W.T. (1996) Parasitism rates in relation to nest site in bees and wasps, *J. Insect Behav.* 9, 643–656.
- Weislo W.T., Danforth B.N. (1997) Secondly solitary: the evolutionary loss of social behavior, *Trends Ecol. Evol.* 12, 468–474.
- Weislo W.T., Engel M.S. (1996) Social behavior and nest architecture of nomiine bees (Hymenoptera: Halictidae; Nomiinae), *J. Kans. Entomol. Soc.* 69 (Suppl.), 158–167.
- Weislo W.T., Tierney S.M. (in press) Evolution of communal behavior in bees and wasps: an alternative to eusociality, in: Gadau J., Fewel J. (Eds.), *Organization of Insect Societies: from genomes to socio-complexity*, Harvard University Press, Massachusetts.
- West S.A., Herre E.A. (1998) Stabilizing selection and variance in fig wasp sex ratios, *Evolution* 52, 475–485.
- West-Eberhard M.J. (1978) Polygyny and the evolution of social behavior in wasps, *J. Kans. Entomol. Soc.* 51, 832–856.
- Wilson E.O. (1971) *The Insect Societies*, Harvard University Press, Massachusetts.
- Woodburne M.O., Case J.A. (1996) Dispersal, vicariance, and the late Cretaceous to early Tertiary land mammal biogeography from South America to Australia, *J. Mammal. Evol.* 3, 121–161.