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

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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) Macrogastra replaces Halterapis + Compsometissa 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 phylogenograms 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 Allozapiini 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 historically these two bee groups have provided insights on the evolution of social behavior that studies of more advanced obligate caste-based insect societies are unable to address (reviewed in Schwarzer 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 (e.g. 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
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 (Liu 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) focusing on Asian Braunsaptis species, and later studies by Australian researchers investigating colony life-cycles, sex allocation and intracolony 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 Alldopini.

2. PRE-MOLECULAR THEORIES ON ALLODAPINE PHYLOGENY

Behavioural traits, have played an influential role on alldapine 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 Alldopini based on adult or immature morphological and behavioural character sets resulted in disparate phylogenetic arrangements (Michener, 1977). Alldapine 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 + Compsonomis as a holophyletic group that formed a sister clade to all other alldapines (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 alldapine lineage that was mass provisioning. Furthermore, it seemed reasonable to suggest that alldapine 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 + Compsonomiada (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
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 Ceratini and the ancestral tribes Manuelini 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 *Halorapis* 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, Alloidapula, and Exoneuridia* (Fig. 3). The remaining clade contains the southern African genus *Alloidape* 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 Brauniaspis 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 Brownapis and Alloropina, the finding of sociality in Macro- galea made it apparent that the origin of sociality predates divergence of the extant allo- daphine clades. The realisation that sociality is the baseplan 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 oviposits 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 pleiomorphic trait (Schwarz et al., 2003). In addition, molecular data place African species of Halterapis within a clade of partial mass provisioning genera (Compsonomelissa, Allo- dapina), suggesting it is simply a further elaboration of brood provisioning found in this clade (Tierney, 2004). Until very recently the biology of Malagasy 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 Al- lodapina – 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 Malagasy Halter- apis species are now known to nest in so- cial 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 repro- ductive 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 ($r < 0.18$). The first species studied from Madagascar, H. minuta (Schwarz et al., 2005), exhibits a high level of multifemale nesting (70%), with eusocial as- semblages containing effectively sterile work- ers and the most distinct body size based re- productive 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 Madagascar 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 solitarily found nests and ~ 50% of nests collected (from various taxa and popu- lations) 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 (ter- mites, 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). Wcislo and Danforth (1997) have argued that such reversals among halictines provide evidence against a 'Dollo's law' inter- pretation 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 en- vironmental problems encountered by sterile caste based societies (reviewed in Wcislo 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 phylegnetic 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 atine ants (Savolainen and Vepsälläinen, 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 angophora, 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. berenstyensis, M. berentynensis b) was the sister group to a clade of free-living species (M. infernalis, M. scruvola, M. Ramena sp.) that were not their hosts, a relationship that is not consistent with Emery’s rule. Evidence suggests M. maizina and M. berentynensis are facultative parasites capable of independent nesting (Smith and Schwarz, 2006; Smith, 2007), a situation that may also be paralleled in the Braunsapis paradoxo 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 dependent on alloparents, whose presence is influenced by both the environment and brood ontogeny (Tierney, 2004). Climate clearly influences volitnism in allodapines generally and in some species decreasing latitude extends brood rearing periods that allow for more generations to be reared (Crornin 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). Allolepula, Exoneura and Madagascan Halterapis lay eggs in a pulse, so that eusociality is dependent on having enough time to rear through a second brood pulse for the first cohort to rear. In contrast, Macroagalae, Alloleppe, Braunsapis, Compasomelissa, 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 allolepine 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 Allolepina), 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 rear 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). Allolepine 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 allolepines 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 allolepine 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 alldapines 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 Allolepini 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 Kerguelen 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; Sammartin and Ronquist, 2004). More recently a late Cretaceous Antarctic land bridge (including the Kerguelen Plateau and Gnumerus 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 (Vai, 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 Ma) 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 – Palearctic (Exoneuridia)
- Afrotrropic – 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 allo-
dapines cannot be used to infer origins of so-
ciality de novo, but they can be used to in-
fer key transitions among forms of sociality.
However, this requires more detailed descrip-
tions of sociality in extant species that are
still poorly understood, such as Exoneuridia
and Compsoanelia, furthering our under-
standing of behavioural traits (brood ontogeny
and provisioning) and possible environmental
constraints that are influential to under-
standing broad aspects of social evolution.
Social biology of the rare Middle Eastern
genus Exoneuridia is completely unknown,
although personal observations of E. harkarien-
sis (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 con-
straints and nesting site persistence, if so we
would expect them to be highly eusocial. Em-
pirical evidence regarding constraints to so-
cial 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.

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Phylogénétique des abeilles de la tribu des Al-
loidapini (Apidae, Xylocopinae) : le point sur
l'évolution sociale, le parasitisme et la biogéogra-
phie.

Alloldapini / abeille / évolution sociale / phylogén-
étique / soin alloparental / approvisionnement
du couvain

Zusammenfassung – Phylogenetik alloldapiner
Bienen: ein Review über soziale Evolution, Para-
sitismus und Biogeographie. Einige Bienen und
Wespen sind fakultativ sozial. Anders als Honig-
bienen, Ameisen und Termiten sind ihre reprodukti-
ven Rollen nicht durch morphologische Kasten ein-
geschränkt. Alle Waben sind daher in der La-
ge ihre eigene Brut unabhängig aufzuziehen. Da-
er ist die entstehende Gruppendynamik (soziale
Organisation) hoch flexibel und reicht von der so-
litären Lebensweise bis zu hochorganisierten (eu-
sozialen) Gemeinwesen, wobei diese Unterschiede
sowohl innerhalb einer Art als auch zwischen nah-
verwandten Arten auftreten.
Aus diesem Grund sind solche Organismen sehr
gut für vergleichende Untersuchungen über altrui-
stisches Verhalten und dessen Entstehung geeignet.
Warum sollte ein Individuum die Gelegenheit zu
eigner Reproduktion auslassen und anstelle des-
en anderen helfen, deren Brut großzuziehen? Die
fakultativ sozialen alloldapinen Bienen ziehen ihre
Brut in offenen linearen Stengelsystemen auf (i.e.
ment in von der äußeren Umgebung abgeschir-
men Brutzellen), dies erzeugt unter sozialen Insekten
einzigartige Lebensgeschichten und haben sich über
die vergangenen mehr als 40 Jahre zu einem wich-
tigen Modellsystem gemacht.
Vergleichende evolutionäre Forschung benötigt
einen gesicherten Stammbaum (einen Baum der
evolutionären Geschichte, der die Abstammungs-
linien sichtbar macht), aus dem dann die Ent-
wicklung eines spezifischen Charakteristikums
hergeleitet werden kann. Anfängliche Versuche,
die Phylogenie der Alloldapinen aufzuklären waren
problematisch, vor allem da unabhängige auf Ei-
genschaften der Larven, Puppen oder Adulten be-
rührende Studien zu widersprüchlichen Ergebnissen
geführt hatten. Analysen von DNA Sequenzen un-
terstützen 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 so-
ziale Evolution innerhalb der noch bestehenden Li-
nien eingesetzt hat. Die Sozialität entwickelte sich
eindeutig vor den heute lebenden Arten des Stamm-
es zurück.
Anhand von baltischen Bernsteinfossilien eines
ausgestorbenen Geschwisterstammes haben die Un-
tersucher die Zeiträume der Entstehung dieser Bie-
nen und ihrer Auseinanderentwicklung sowie des
Bestehens ihrer sozialen Organisation einzuschät-
zen versucht. Nach diesen Analysen ist der Tribus
vor etwa 39–80 Millionen Jahren entstanden, ob-
wohl diese Schätzungen zurückhaltend sind und die
tatsächliche Entstehungszeit vermutlich etwas frü-
her war. Dies legt nahe, dass die Art des in dem
Tribus gezeigten Sozialverhaltens keineswegs prin-
mittiv ist. Soziales Verhalten tritt in allen größe-
ren phylogenetischen Abweichungen auf und ist mit
einer hochgradig zur weiblichen Seite neigenden
Phylogenetics of allopatine bees


Sozialevolution / Phylogenetik / Allopantale Pflege / Brutversorgung / Allopatine Bienen

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