

Evolutionary trends in derelomine flower weevils (Coleoptera: Curculionidae): from associations to homology

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Abstract. The host-plant associations and life histories of weevils in the pantropical tribe Derelomini are reviewed in light of new phylogenetic insights. The most immediate derelomine ancestor likely had a ‘special association’ with the inflorescences of palms (Arecaceae) involving pollination and oviposition into dispensable male flowers. Case studies of select genus groups show multiple historical forces driving their diversification. In the South and Central American genus *Celetes*, abundant host shifts are important, though clearly not enough to account for the existence of all species. Females of the Neotropical genus *Staminodeus* have remarkable morphological and behavioural modifications for exploiting the staminodes of cyclanth (Cyclanthaceae) inflorescences. The evolution of males in this genus is mostly explained by sexual selection. *Cyclanthura* illustrates the potential of the weevils for colonising hosts with widely divergent inflorescence biologies, including arums (Araceae) in the genus *Anthurium*. Members of the *Ganglionus*–*Systemotelus* clade, in turn, are exclusively associated with the cyclanth genus *Carludovica*. A phylogenetic trend in this group to attack the plants’ seeds has led to a series of counteracting transformations in inflorescence morphology. Overall there were at least three independent secondary host shifts to dicots, including one in the taxonomically complex genus *Phyllotrox*. The results suggest that in this particular tribe of weevils, focusing on the homology of specific biological traits in individual lineages is more likely to produce new knowledge than a formalistic, large-scale approach.

Introduction

Weevils represent the most diverse lineage of herbivorous beetles. Their host-plant associations are typically regarded as the primary correlates for evolutionary success (Anderson 1995; Farrell 1998; Marvaldi *et al.* 2002). Discussions of weevil diversity tend to be framed within the appealing context of insect/plant coevolution (Ehrlich and Raven 1964). Yet too often the information necessary for adequate tests of coevolutionary predictions is lacking (Anderson 1993). Either the host-plant records are not comprehensive enough, or a robust phylogenetic classification is unavailable, or both. Ongoing analyses of the evolution of certain weevils associated with cycads (the so-called ‘cycad weevils’, a non-monophyletic group) are a notable exception to this pattern (Donaldson 1992; Oberprieler 2004; Terry *et al.* 2004).

Here we discuss how recent phylogenetic and natural history studies of derelomine flower weevils have advanced our understanding of their interactions with plants. The Derelomini Larcordaire (1866) form a diverse tribe of smallish brown, overwhelmingly pantropical weevils. At present, more than 265 species are recognised in 40 genera (Franz 2005a). They convergently share with some ‘cycad weevils’

the ability to pollinate their host plants and oviposit into specific floral organs where the larvae develop. Unlike the former, however, derelomines in the new sense (Franz 2005a) are only found on angiosperms. Most species visit the inflorescences of palms (Arecaceae) and of the unrelated, exclusively Neotropical Cyclanthaceae (see Chase 2004 for a summary of the current state of monocot phylogeny). These associations are specialised, ranging from mutually beneficial to detrimental, e.g. when the plants’ fruiting prevents larval development or the weevils act as seed predators (Dufaÿ and Anstett 2004; Franz 2004). Based on the widespread distribution of derelomines and their limited fossil record, the interactions may date back to the origins of the two plant families (Henderson 1986; Kuschel 1992; Anderson and Gómez 1997). Their special character was noted early on in the palm literature (von Martius 1823).

Our purpose here is to analyse the natural history of the derelomine/host-plant associations from a systematic point of view. Emphasis is placed on aligning available host records with the relationships of the weevils. This approach will allow us to approximate the evolutionary sequence of the presumed colonisations and specialisations. The natural history data are drawn from a wide range of publications,

specimen labels and field observations. They are linked to insights from two cladistic analyses; one concerning the South and Central American genus *Celetes* Schoenherr (Valente 2005) and the other providing a phylogenetic system for the entire tribe (Franz 2005a). The overall character of the paper is that of a review with new evolutionary analysis and synthesis.

We deliberately refrain from asking specific questions in the introduction. For instance, one could ask whether switches to a particular host family or the acquisition of certain life history traits have significantly increased derelomine diversification. Such an approach is attractive in part because it lends itself to statistical analyses (Wenzel and Carpenter 1994; Pagel 1999). But the danger lies in comparing the associations too coarsely. Weevils have evolved thousands of reproductive strategies. A wide conception of similarity among their interactions with plants will raise the number of independent replications across the sampled phylogeny, yet this may come at the cost of lumping together taxa whose biological histories and functions are no longer homologous.

Instead of focusing on the broader similarities among derelomine life histories, we attempt to characterise them as precisely as any other source of attributes used for phylogenetic analysis. The objective is to translate labels such as 'on palms' or 'ex araucaria cones' into suitable homology statements that contribute to the phylogenetic picture (Wenzel 1992; Wcislo 1997). The number of traits that can or cannot be aligned with the weevil phylogeny is in itself significant. It is a reflection of the extent to which the host-plant associations have shaped their evolutionary relationships.

Material and methods

The analysis synthesises efforts over the past ten years to understand the systematics and biology of derelomines. Several studies are already published (Franz 2001, 2003a, 2003b, 2004, 2005a, 2005b; Franz and O'Brien 2001a, 2001b; Valente 2000, 2002; Valente and Almeida 2001, 2002; Valente and Vanin 2002). It is appropriate to refer to these works for further detail on methods of phylogenetic inference, field observations and deposited specimens.

In spite of their small size – typically only 1–8 mm – natural history studies of derelomines are often rewarding because of their fidelity to particular hosts. Opportunities for quantitative samples and careful observations exist whenever inflorescences are open and accessible. The number of adults pertaining to one or more species can reach several hundreds on a single plant. They will typically remain for many hours spanning both the pistillate (♀) and staminate (♂) phase of flowering. Video recordings help distinguish species-specific feeding and reproductive behaviours that take place on the floral organs. Later on the immature stages of the weevils can be collected by dissecting fruits or by searching through detached inflorescence tissue in the leaf litter. A few days of informed and focused fieldwork may thus produce a wealth of reliable natural history data.

We will first review the latest phylogenetic results on derelomines and align them with host plant records at higher levels. In keeping with the phylogenetic arrangement, individual sections will then 'zoom in' to examine the history of select weevil/plant associations more closely. At

the end we will mount these accounts into a comprehensive coevolutionary picture of the interactions between derelomines and their hosts.

Derelomine phylogeny

A phylogenetic analysis of 115 exemplar taxa and 155 predominantly morphological characters has brought forth new definitions for the tribe Derelomini and its component lineages (Franz 2005a; Fig. 1). A heterogeneous clade comprising the Juanorhinini Aurivillius and the Trypetidini Lacordaire was identified as their closest relative. Derelomines are distinguished by a lack of central setae on the maxillary palpomeres I and II and by unarmed tibial apices, as well as their unique life habits (see details below). Several genera, such as *Eisingius* Kuschel (Molytinae: Trypetidini), *Pedetinus* Faust (Curculioninae: Eugnomini) and *Neopsilorhinus* Bovie (Erihrinidae: Erihrininae) are now placed outside the Derelomini. Five monophyletic subtribes are recognised within the tribe: Derelomina Lacordaire, Acalyptina Thomson, Staminodeina Franz, Notolomina Franz and Phyllostrogina Franz. Seven genera, totalling nine species, were not examined and therefore not assigned to any of the subtribes. Some of them may not be derelomines in the new sense of Franz (Franz 2005a; R. Oberprieler, personal communication). In accordance with Alonso-Zarazaga and Lyal (1999), they are listed here as Derelomini *incertae sedis*.

Within the tribe there is considerable support for many generic groupings (Fig. 1). The monophyly of nearly all of the smaller genera has been reconfirmed. In the subtribe Derelomina, the primarily African type genus *Derelomus* Schoenherr and the South American *Anchylorhynchus* Schoenherr are both diverse and have many undescribed species but are otherwise well defined. A revision of the species-rich *Celetes* is now nearing publication, although resolving the phylogenetic complex it forms with *Phytotribus* Schoenherr will require further work. All the aforementioned genera are associated with palms. The same is true for the mostly Asian Acalyptina (H. Kojima and K. Morimoto, unpublished data).

Probably the greatest taxonomic challenges lie within the subtribe Phyllostrogina. The difficult genus *Phyllostrox* Schoenherr (*sensu lato*) occurs throughout the subtropical and tropical pre-/montane regions of the Americas. At present, 48 species are described (O'Brien and Wibmer 1982; Wibmer and O'Brien 1986), but as many, or more, undescribed species reside in collections as '*Phyllostrox* spp.'. Some of these species are palm associates, whereas others feed and reproduce on a wide range of dicotyledonous herbs or shrubs (see e.g. Voss 1954). Still other members of *Phyllostrox* in the wider sense live on Cyclanthaceae. In recognition of their distinct morphology and biology they were treated as Derelomini gen. 2 in Franz (2005a). The lack of resolution and varying associations in the *Phyllostrox* complex are the two factors most likely to alter the following analysis.

Host associations at higher levels

All derelomines and their most closely related outgroups feed on and oviposit into seed plants (Fig. 2; see also Appendix 1). The larvae hatch and begin their development inside living plant tissue. The later stages of development and pupation may take place in detached plant organs or in the soil. Derelomine weevils are furthermore plesiomorphically asso-

ciated with angiosperms. In the Trypetidini, members of a small clade including *Araucarietus* Kuschel, *Eisingius* and *Planus* Kuschel reproduce in the cones of the South American monkey puzzle tree *Araucaria araucana* (Molina) K. Koch (Kuschel 1952, 2000). Their apomorphic interactions with a gymnosperm taxon stand in contrast to the more common pattern in the Phytophaga, where associations with araucarias

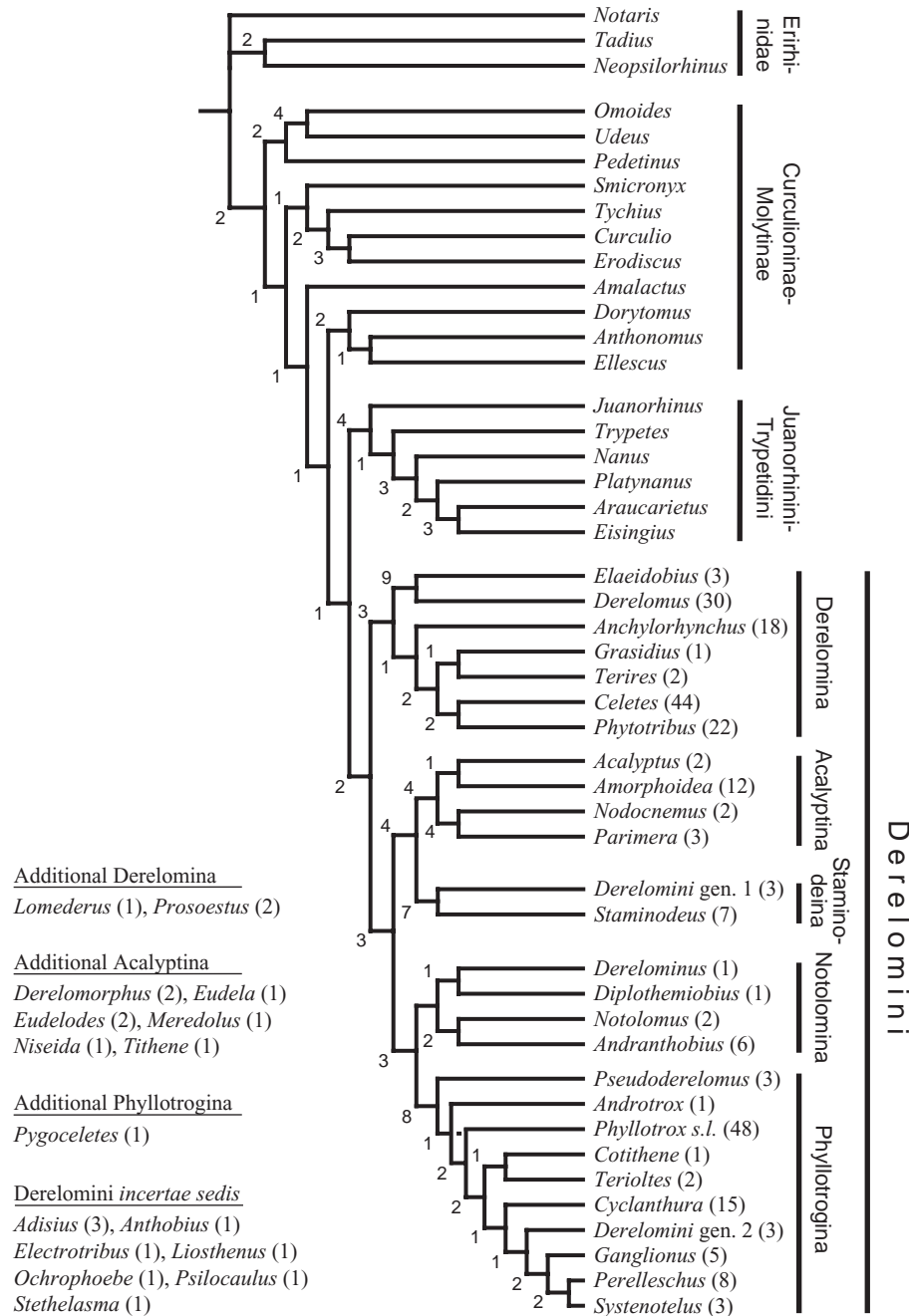


Fig. 1. Genus-level phylogeny and classification of derelomine flower weevils and select outgroups. Species numbers for the ingroup taxa are listed in parentheses (i.e. number of described species, or number of putative examined species for undescribed genera). Bremer support values are provided for the internal branches. For details of the analysis see Franz (2005a).

are typically very old (Sequeira and Farrell 2001; though see Marvaldi *et al.* 2002). Most derelomines live on monocots; this is presumably the ancestral condition for the tribe. There are independent colonisations of dicot hosts in the clade comprising *Acalyptus* Schoenherr and *Amorphoidea* Motschulsky and in the more diverse *Phyllotrox*. Multiple independent dicot and monocot associations have also been formed in the sampled outgroups.

The picture then becomes more detailed at the plant family level. Most derelomine genera are restricted to palms. In addition to the two host switches to dicots, there at least two other colonisations of cyclanths and one of the (again unrelated) Araceae (Fig. 2). Associations with palms occur in the outgroups as well. The two described species of *Pedetinus* and one undescribed species from Costa Rica have been found feeding both on palms and on flowers of dicot trees (e.g.

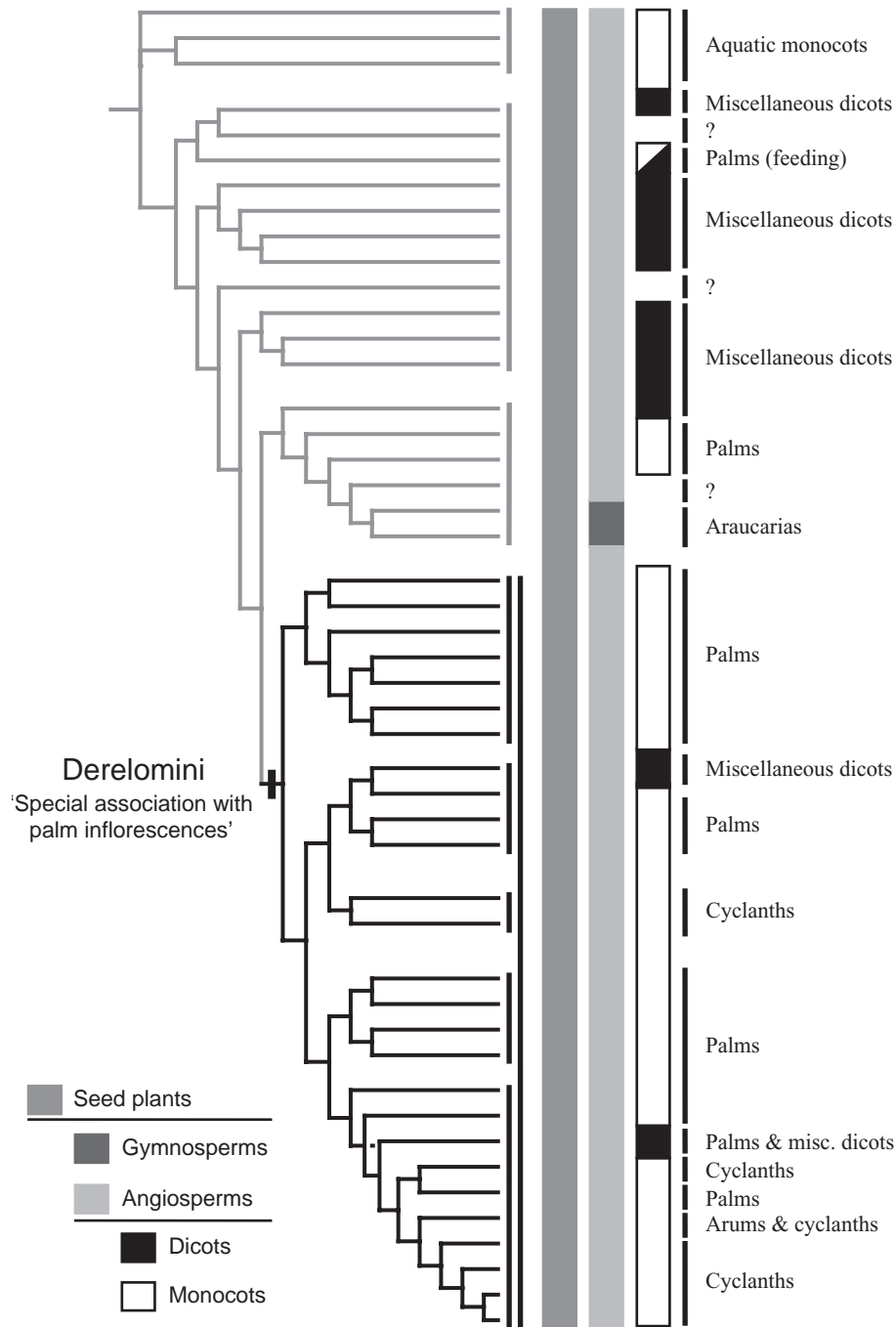


Fig. 2. Associations of derelomine flower weevils and select outgroups (see Fig. 1) at higher levels. See text for further details.

Saurauia sp., Actinidiaceae; N. Franz, personal observation). Their oviposition behaviours and larval substrates are unknown except for a new record for *Pedetinus halticoides* (Champion), which has been reared from the fruits of *Miconia calvescens* DC. (Melastomataceae; K. Nishida, unpublished data). On the other hand, *Nanus* Schoenherr and *Platynanus* Aurivillius occur exclusively on palms. However, their behaviour is more similar to that of members of the Baridinae (Eberhard and García 2000; Barbosa and Valente 2003). They are dorsoventrally flattened and reproduce in the large inflorescence spathes of, e.g. the Royal Palm *Roystonea regia* (Kunth) O. F. Cook (C. W. O'Brien, unpublished data). Neither of these outgroup life histories is directly homologous to the ancestral state in derelomines. Finally, species in the *Planus*–*Eisingius* clade share with many derelomines the ability to pollinate their host plants (Kuschel 2000). The unrelated 'cycad weevils' have similar habits (see above).

Palm associations and pollination have evolved multiple times in the weevils. It is nevertheless possible to define the original biology of derelomines in a unique, synapomorphic way. Clues for the ancestral condition come from the extant Derelomina, Acalyptina and Notolomina. The relative

homogeneity of their life habits, combined with their position in the phylogeny, suggest that the first derelomines behaved much like *Derelomus*, *Amorphoidea* or *Notolomus* LeConte (Vaurie 1954; Brown 1976; H. Kojima and K. Morimoto, unpublished data). Members of these clades are attracted to a relatively small range of palm hosts, which they locate primarily via olfactory stimuli. Adults arrive in large numbers during the peak of fragrance production. They stay on the inflorescences for several hours up to days, feeding on various floral organs without fatally damaging them (Fig. 3). In the process they transfer pollen from the same or from a previously visited palm onto the floral stigmata. They also mate on the inflorescence and eventually oviposit into structures not vital to the plant's reproductive success, e.g. detaching male flowers. The eggs hatch in these structures and thus complete their cycle either in tissues separate from the seed pockets or entirely removed from the host plant. This combination of life history traits captures the 'special association with palms' that was likely present in the most immediate derelomine ancestor (Fig. 2). We shall now examine the specialisations of several constituent lineages more closely.

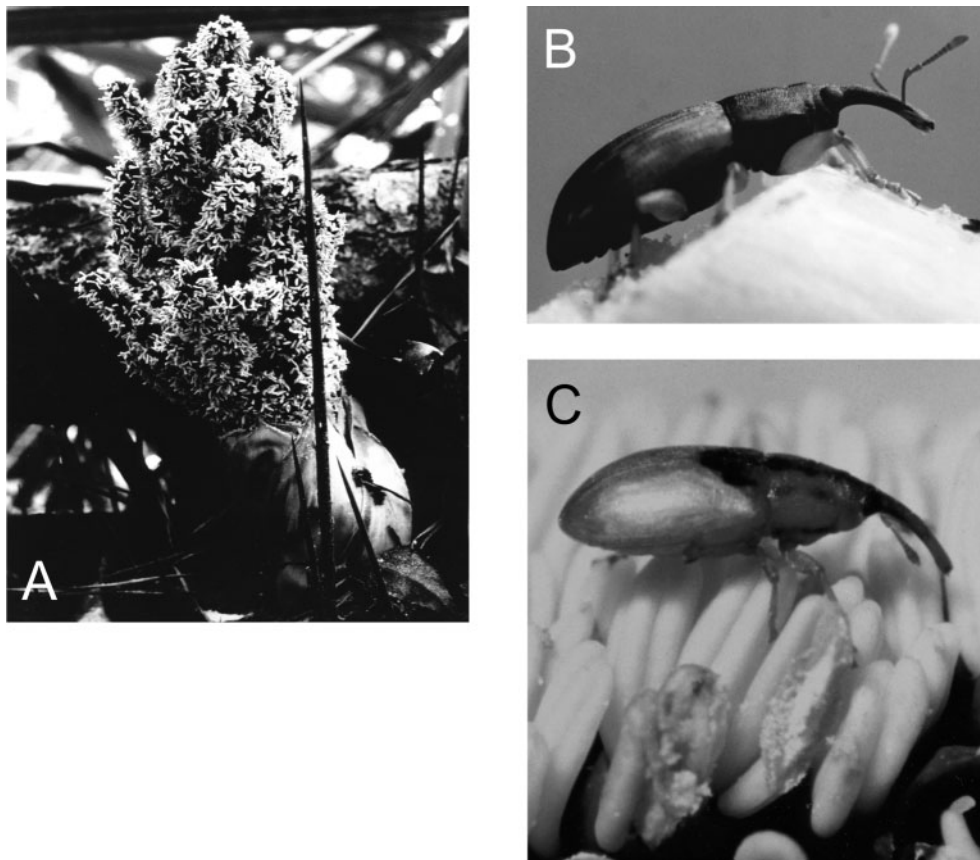


Fig. 3. The cabbage palm *Sabal palmetto* and its weevil pollinators. *A*, Opening inflorescence in Florida, USA. *B*, Adult of *Notolomus bicolor* on an inflorescence peduncle. *C*, Adult of *Notolus basalis* on male flowers. Photos courtesy of C. W. O'Brien.

'Zooming in' on specific derelomine/host-plant associations

Case 1: evolution of *Celetes* species on palm hosts

Celetes, a member of the subtribe Derelomina, is at present the second most species-rich genus of derelomines after *Phyllotrox*. The majority of its species occur in South America; only six species reach into Central America. They are medium-sized to large for derelomines (length 4–12 mm) and elongate in shape (Fig. 4). Among their diagnostic features are: a separate basal seta on the lateral margin of the labial prementum; a relative reduction in the length of the rostral carinae in females; the presence of suberect, elongate scales covering parts of the head, pronotum, and elytra; and a distinct triangular tooth on the ventral sides of the femora (Franz 2005a). Several species are recognisable by their unique elytral colour patterns.

Valente (2005) included 50 terminal taxa (43 ingroup, 7 outgroup) in a phylogenetic analysis of *Celetes*. As it turns out, the existing conception of *Celetes* is not sufficient to separate it from *Phytotribus*. Nevertheless there are two monophyletic clades within *Celetes* that merit recognition (Fig. 5). The *binotatus*-group includes the type species *C. binotatus* Gyllenhal and three other species. The *faldermanni*-group is much larger, with 19 described species and 15 additional species new to science.

The life histories of *Celetes* species are relatively uniform. The adults are, without exception, associated with palm inflorescences, where they feed on pollen and on the epidermal tissues of the floral petals and peduncles (Champion 1909; Bondar 1940, 1941, 1942, 1943, 1949; Hustache 1940; Valente 2000; Valente and Vanin 2002).

Bondar was able to rear larvae of various species in the laboratory, including *C. bipunctatus* (Hustache), *C. copiobae* (Bondar), *C. impar* Voss, and *C. testaceus* (Hustache). He observed the following pattern. The adult females oviposit into recently opened inflorescence spathes, typically in the internal areas that are in close contact with the individual flowers. The eggs hatch and the larvae drill apically directed galleries, feeding on the tissues of the spathes. They eventually pupate in small enclosures made of adhesive material. The entire life cycle is completed in 3–4 months and runs parallel to the maturation process of the palm fruits. The larval infestations are apparently not detrimental to the plants. The adults function as pollinators (Silberbauer-Gottsberger 1990).

The degree of specificity is higher in the weevils than in the palm hosts. Throughout its range of distribution a single palm species can support multiple species of *Celetes* (Appendix 1). Conversely, the weevil species are either monophagous or narrowly oligophagous, i.e. visiting related species of palms within the same genus. The only exception is *C. faldermanni* (Boheman), which occurs on two palm genera.

The new phylogenetic hypothesis for the species of *Celetes* makes it possible to reconstruct the evolutionary sequence of host-plant associations within the two major clades (Fig. 5). For this purpose the associations with palms were coded as a single, multi-state, non-additive character at the level of genus, and then optimised parsimoniously along the tree (Farris 1970). Weevil species without available host records were coded as '?'. The analysis postulates a plesiomorphic association of the *binotatus*-group with either *Attalea* Kunth (Cocoeae: Attaleinae: 29 species) or *Syagrus*

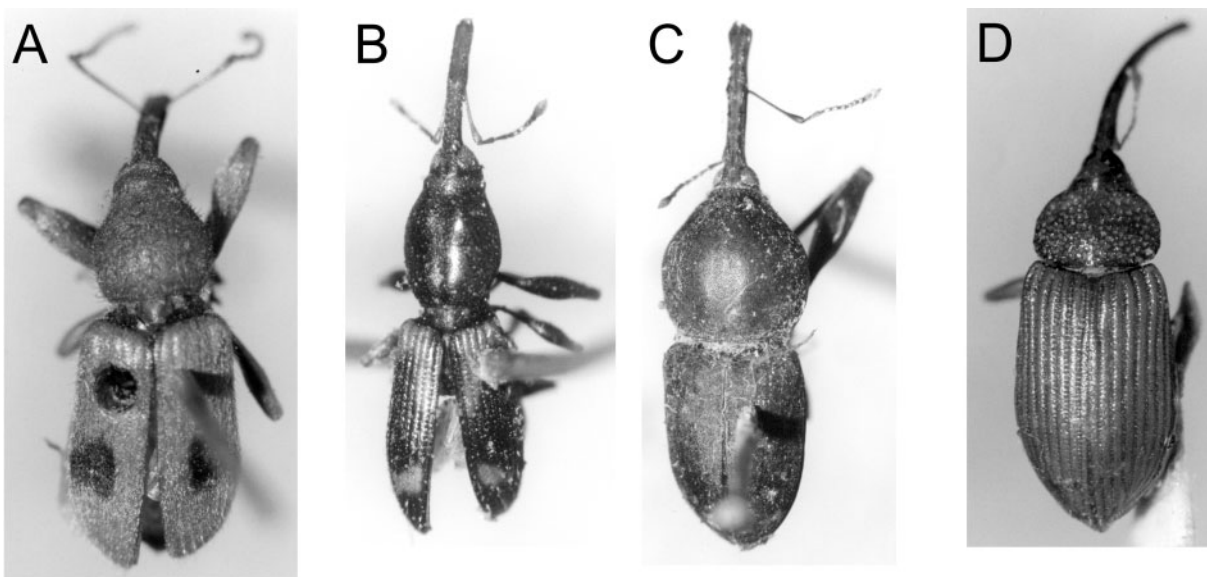


Fig. 4. Habitus of *Celetes* adults in dorsal view. A, *C. binotatus*, holotype male. B, *C. faldermanni*, holotype male. C, *C. carbonarius*, male. D, *C. planithorax*, female.

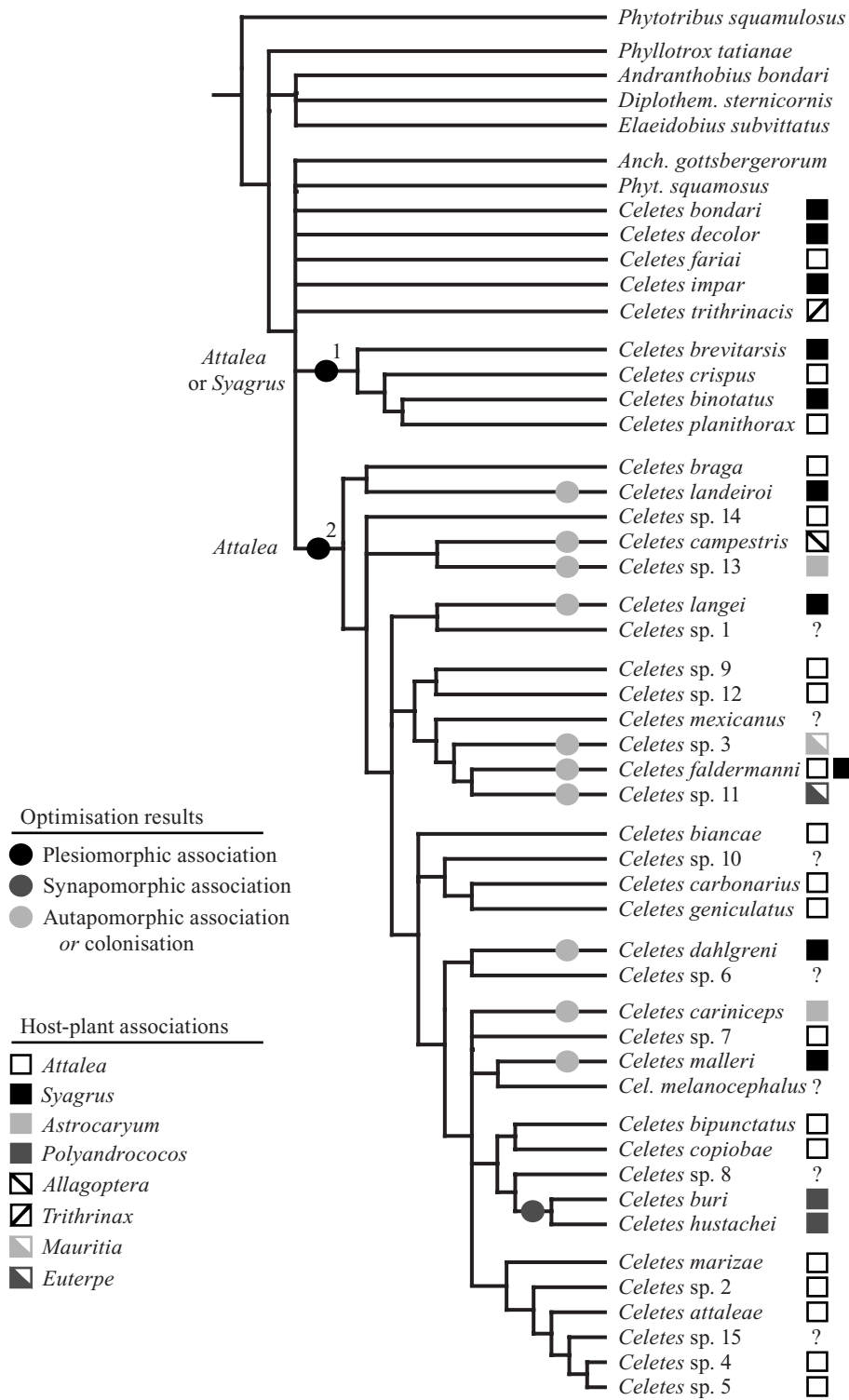


Fig. 5. Phylogeny and evolutionary sequence of host-plant associations of *Celetes* (unambiguous optimisation), according to Valente (2005). 1 = *binotatus*-group; 2 = *faldermanni*-group; ? = host association unknown.

Mart. (Coccoeae:Butinae: 30 species; tribal/subtribal classification and species numbers according to Henderson *et al.* 1995). It is likely that the discovery of additional species in this group will lead to a more definitive answer.

The *faldermanni*-group is plesiomorphically associated with *Attalea* – regardless of how the trichotomy including *Celetes* sp. 14, the *C. campestris*–*Celetes* sp. 13 clade, and the *C. langei*–*Celetes* sp. 5 clade is resolved (Fig. 5). This condition is conserved without exception in species of the apical *C. marizae*–*Celetes* sp. 5 clade. It is further retained in at least 11 species of the *faldermanni*-group. On the other hand, the association of *C. buri* (Bondar) and *C. hustachei* (Bondar) with *Polyandrococos* Brab. Rodr. (Coccoeae:Butinae: 1 species) is a synapomorphic derivation that might also include *Celetes* sp. 8. The associations of other *Celetes* species appear to have been produced by individual colonisation events. For instance, *Celetes* sp. 13 and *C. cariniceps* (Hustache) independently colonised the inflorescences of *Astrocaryum* G. Mey. (Coccoeae:Bactridinae: 13 species). Five species reproduce on *Syagrus*; each represents a distinct host switch. Three additional species have separately colonised *Allagoptera* Nees (Coccoeae:Butinae: 4 species), *Euterpe* Mart. (Areceae:Euterpiinae: 7 species), and *Mauritia* L. f. (subfamily Calamoideae: 2 species; all other genera are part of the subfamily Arecoideae). Three *Celetes* species placed outside the two monophyletic groups reproduce on *Attalea*, *Syagrus* and *Trithrinax* Mart. (subfamily Coryphoideae: 3 species). The weevils are therefore associated with nine different palm genera.

In spite of the considerable amount of host switching, the associations of *Celetes* weevils and their hosts often have a strong phylogenetic component. In some instances the historical link is preserved down to the level of host plant species, e.g. in the sister-species pairs *Celetes* sp. 9 and *Celetes* sp. 12, *C. carbonarius* (Faust) and *C. geniculatus* (Chevrolat), *C. bipunctatus* and *C. copiobae*, and *C. buri* and *C. hustachei* (Appendix 1). Narrowly framed natural history studies should lead to the discovery of additional homologous features among species of *Celetes*.

Case 2: specialised oviposition and fighting behaviours in *Staminodeus*

Staminodeus Franz has seven described species and is placed in the Neotropical subtribe Staminodeina. These weevils are only 1–3 mm long and dark reddish-brown in colour (Fig. 6). They are characterised by a unique arrangement of larger and smaller carinae on the rostrum, as well as several sexually dimorphic features (Franz 2001). The adults are exclusively associated with the inflorescences of Cyclanthaceae (Appendix 1).

The evolution of *Staminodeus* is a shining example of morphological and behavioural specialisation in weevils. The mating behaviour of *S. vectoris* Franz was described in detail in Franz (2003b). Since that publication another

species, *S. curvittibialis* Franz, has been studied at Rancho Grande, Maracay, Venezuela. The latest observations confirm the general pattern, which will now be reviewed.

At a particular site the adults of *Staminodeus* may visit and feed on multiple species of cyclanths. A subset of these represent the actual oviposition substrates. The weevils find the inflorescences in large numbers at the break of dawn when the latter begin to disperse their fragrances (Fig. 6A). The adults are specialised to feed, mate and reproduce on the female flowers' staminodes, i.e. modified, long and whitish 'spaghetti-like' stamens that produce the floral attractants. Unlike other derelomines visiting at the same time, *Staminodeus* weevils remain on the surface of the inflorescence and never reach the hidden female flowers. Therefore they do not function as pollinators of their host plants. To the contrary, the hosts' potential to attract pollinators is reduced by their attack on the ephemeral staminodes.

Upon arriving on the inflorescence, a female will move quickly up and down numerous staminodes. Females that are ready to mate and oviposit will further search for a suitable piece of staminode, then move to its base and begin to detach it with their mandibles (Fig. 6B). There is strong competition for access to these organs at La Selva, Costa Rica, where *Staminodeus* co-occurs with members of the closely related *Derelomini* gen. 1. The adults of the latter are able to locate and oviposit into the staminodes days before the inflorescences open. In that case, the females of *Staminodeus* merely feed on the previously infested substrates. When fresh pieces are still available, however, they fully detach them until both weevil and staminode fall down to the soil. At this point the female starts using the small, anteriorly directed spine on her frons (Fig. 6D) to transport the detached piece of staminode to the eventual oviposition site, located in the top layers of the leaf litter (Figs 6B, 6C). She crawls underneath the staminode at the end that faces the direction of transport. She then lies on her dorsal side – between the staminode and the soil – and faces the other end. As she pushes the staminode away from her with her legs, the frontal spine functions as a 'barb' or point of resistance that maintains her position. Once at the other end of the staminode she then repeats the entire process. In the course of 30–90 min, the staminode is thereby moved up to 1.5 m.

While transporting the staminode, the females of *Staminodeus* display an amazing ability to overcome surface obstacles (Franz 2003b). Eventually they move to a cryptic location and lay (most likely) a single egg into it. They then await the opening of a new inflorescence on the following day. The eggs hatch soon thereafter and the entire life cycle is completed in less than two weeks. Because of the ephemerality of the thin staminodes, the larvae are detritivorous (i.e. feeding on decaying plant material) during the latter stages of development.

The actual mating takes place just before oviposition. The behavioural strategy of males is best explained by postu-

lating sperm precedence (Simmons 2000): the male that copulates last has the highest probability of contributing to the progeny. This phenomenon has been observed in several weevil species (Harari *et al.* 2003). In the case of *Staminodeus*, then, males search for individual active females as soon as they arrive on the open inflorescences. Once a male locates a female detaching a staminode, he attempts to remain associated with her until she arrives at the oviposition site. Males therefore guard the staminodes during the period of detachment and transport by the females. Male-male conflicts are very frequent during this limited period of time. Guarding males show an escalating repertoire of behaviours to defend the female and staminode against as of yet unassociated opponents. In the last instance they use their long and ventrally armed prothoracic legs in

short but intense fights to physically displace one another from the moving staminode (Fig. 6B, C). The remaining male is then transported along by the female until mating takes place.

The evolution of behavioural specialisation in *Staminodeus* matches up well with the morphology-based phylogeny for the genus (Fig. 7). The females of all seven species have the distinct frontal spine and – one may infer – the ability to detach and transport the staminodes of cyclanth inflorescences. However, the males of *S. inermis* Franz lack any morphological adaptations for fighting. The adults of this species closely resemble those of the undescribed sister-genus. On the other hand, all males of the *S. curvitibialis*–*S. vectoris* clade have prothoracic legs with species-specific patterns of teeth. Optimisation of these features suggests that



Fig. 6. Mating activities of *Staminodeus* weevils on *Asplundia* staminodes. *A*, *S. vectoris* on *A. uncinata* at La Selva, Costa Rica, at 0600 hours. Mating pairs are forming as the females begin to detach suitable staminodes. *B*, *S. curvitibialis* on *A. caput-medusae* at Rancho Grande, Venezuela, at 0645 hours. Two males (arrows) associated with a staminode are fighting to displace the opponent as a female situated above detaches the staminode. *C*, *S. curvitibialis* at the same location at 0700 hours. Various male–male confrontations continue as two females (arrows) move underneath their respective staminodes to transport them to the oviposition site. *D*, Head of a female of *S. vectoris* in lateral view, with frontal spine used during the transport of staminodes.

the unique male-male fighting behaviour was developed in the ancestor of this clade. The fights among *S. curvitibialis* males are slower and more extended than in *S. vectoris*. In the former species, males position themselves almost side-by-side and attempt to ‘haul’ the opponent away from the staminode surface by hitting his supporting legs. In the latter species the fights are more frontal. The males’ up-and-down leg movements occur at a rate of up to ten blows per second. Whenever the protibial teeth interlock, the inferior male is rapidly dislodged from the staminode. Thus, the morphological features and fighting strategies appear to correlate well in the species of *Staminodeus*. They allow them to exploit the hosts’ resources, which evolved in another, pollinator-attracting context.

Case 3: pollination of arums in Cyclanthura

Cyclanthura Franz is a member of the Neotropical subtribe Phyllotrogina. Its 15 described species resemble *Phyllotrox sensu lato* (see above) but are distinguished from it by a slight elevation/impression along the anterior 1/4 of the elytra (Fig. 8C) and several genital characters (Franz 2003a).

The combination of phylogenetic and natural history studies of *Cyclanthura* species has produced interesting results. Whereas *Cyclanthura* as a whole and its closest relatives (such as *Cotithene* Voss and *Ganglionus* Franz & O’Brien) are plesiomorphically associated with cyclanths, a clade of considerable size *within* the genus has colonised arums, particularly species of the diverse Neotropical genus *Anthurium* Schott (Fig. 9). Our knowledge of the pollination ecology of arums is spotty in comparison with palms and cyclanths. *Anthurium* has more than 800 described species

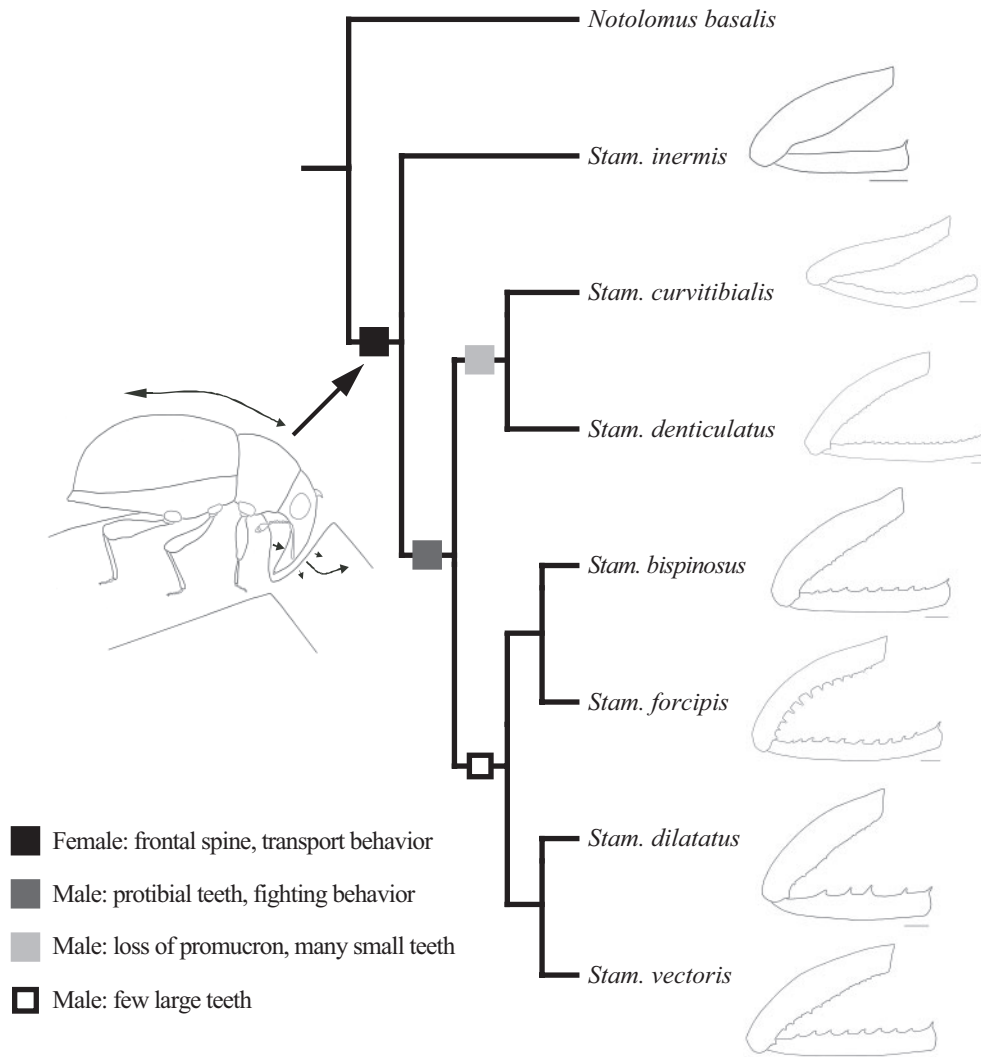


Fig. 7. Phylogeny, morphology and behavioural evolution of *Staminodeus*. The line drawing near the root of the tree depicts a female of *S. vectoris* detaching a staminode. Those to the right correspond to each species’ male profemora and protibiae. See text for further details.

(Mayo *et al.* 1997), yet there are only very few detailed studies of inflorescence development and pollinator visitation (Croat 1980; Grayum 1990; Schwerdtfeger *et al.* 2002). Many additional species of *Cyclanthura* are presumed to exist in Central and South America. In other words, the taxonomic extent and ecological significance of this phenomenon is unclear. Based on the limited data the associations do not appear to be species-specific (Appendix 1).

Observations on *A. formosum* Schott at Las Cruces, Costa Rica, revealed that only 2–18 individuals of *C. carinata* Franz are present on an inflorescence during its 8–15-day-long period of flowering (Franz 2005b). The plants' strategy to attract and host visitors presents a stark contrast with the short-lived, high-energy anthesis of cyclanths. The adult weevils arrive and leave at various times during the day. They stay for several days and rest most of the time in areas protected by the spathe, giving the inflorescence an 'empty' appearance (Fig. 8A). They do on occasion reach the open flowers to feed on pollen and parts of the pistils and triangular tepals. In the process the pollen attached to their rostrum, sterna, legs and venter is transferred from flower to flower.

The adults of *C. carinata* also mate on the inflorescences of *A. formosum* (Fig. 8B). Oviposition events are rare, however. A male can remain on top of the same female for hours without any discernable mating activity. This position appears advantageous whenever conflicts among males occur. It is assumed that the larvae develop in the maturing infructescences.

The phylogenetic hypothesis for *Cyclanthura* posits a single colonisation event of arums. There is a remarkable reversal in (at least) *C. sphaerata* Franz to an association

with the epiphytic, pre-montane cyclanth genus *Sphaeradenia* Harling (Fig. 9). The larvae of this species are pulp feeders. The life histories of *Cyclanthura* species in the sister-clade are heterogeneous as well: the closely related *C. bipartita* Franz, *C. crepidula* Franz and *C. palmata* Franz reproduce on three different plant genera. The occurrence of *C. bipartita* on *Cyclanthus bipartitus* Poit. is noteworthy because previous reports indicated that this phylogenetically distinctive species (Eriksson 1994a) is pollinated by scarabs (Beach 1982; Seres and Ramirez 1995). Weevil pollination may be a recent phenomenon in *C. bipartitus*. Its floral biology is more similar to arums like *Dieffenbachia longispatha* Engler & K. Krause (Young 1986) than to other cyclanths. If so, this example would illustrate the high degree of historical plasticity and adaptability in derelomines.

Case 4: reciprocal adaptation in the *Ganglionus*–*Systemotelus* clade

Our last singled-out account reviews the evolution of the *Ganglionus*–*Systemotelus* clade, a monophyletic lineage placed in the subtribe Phyllostrogina. The adults of *Ganglionus* (five species) are again similar to *Phyllostrox* and only 1.5–2.5 mm long (Fig. 10D). The males in this genus have a characteristically tuberculate rostrum (Franz and O'Brien 2001a). *Perelleschus* Wibmer & O'Brien (eight species) has slightly larger, less dorsoventrally compressed, reddish-coloured adults (Fig. 10B). It is diagnosed by a distinct appendix on the female spermatheca (Franz and O'Brien 2001b). The adults of *Systemotelus* Anderson & Gómez (three species) are much larger, ranging from 5 mm length in males of *S. stockwelli* Anderson & Gómez to

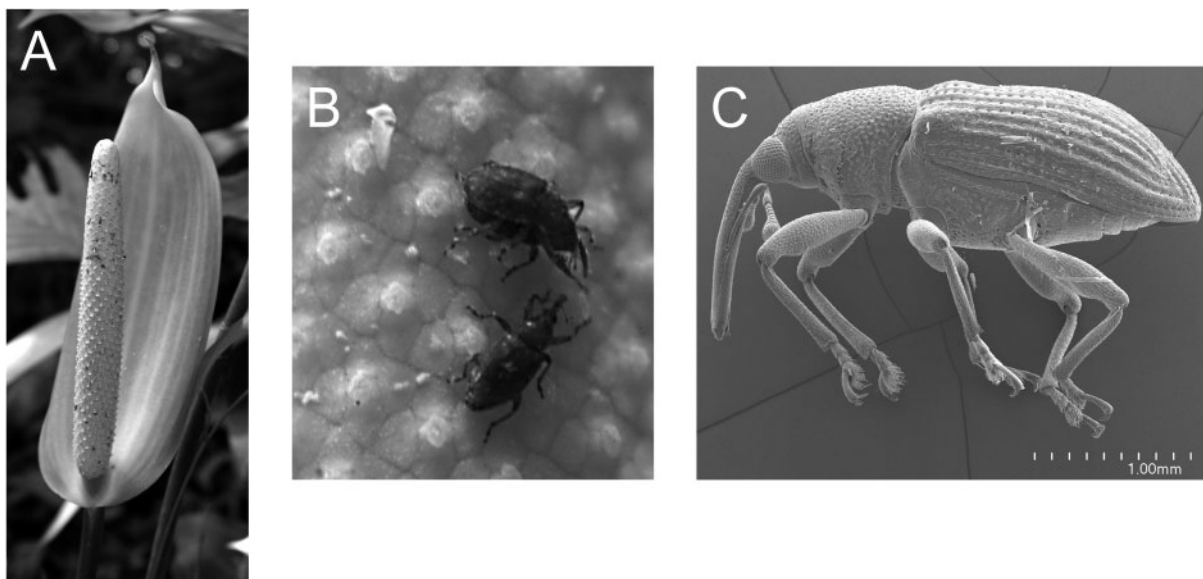


Fig. 8. *Cyclanthura* weevils on *Anthurium* inflorescences. *A*, Open inflorescence of *A. formosum* at Las Cruces, Costa Rica, at 1000 hours. *B*, A single male and a copulating pair (above) of *C. carinata* on *A. formosum*. The whitish spots on the legs and elytra are indicative of pollen released from the anthers. *C*, Habitus of a female of *C. carinata* in lateral view.

12 mm length in the anteriorly and posteriorly tapered females of *S. carludovicae* Anderson & Gómez (Fig. 10C). In addition to length-related modifications in the male and female reproductive organs, *Systemotelus* is characterised by a large lobe-like projection ventrally on the mesosternum (Anderson and Gómez 1997). All 16 species of the *Ganglionus*–*Systemotelus* clade occur in the Neotropics (Appendix 1).

The aforementioned three genera are exclusively associated with species in the cyclanth genus *Carludovica* Ruiz & Pavón (Fig. 10A). Four species of these ‘Panama-hat palms’ are recognised (Harling 1958; Hammel 1986). Only *C. palmata* Ruiz & Pavón extends to South America; the remaining species are restricted to Central America.

This weevil–plant interaction challenges a commonly held position about coevolution (Ehrlich and Raven 1964), i.e. the view that it is sufficient to test for or against coevolution by matching the phylogenetic topologies of the interacting taxa (cf. Page 2003). With the respective phylogenies at hand, Franz (2004) used three complementary methods to maximise the congruence among the patterns of speciation in *Carludovica* and its associates. Under each type of analysis, abundant host switching and non-reciprocal speciation in the weevils led to a rejection of the coevolutionary hypothesis when covevolution is equated with cospeciation. This outcome is almost expected given the mismatch in

species numbers (4 v. 16). The widespread *C. palmata* alone hosts 11 species of weevils (Fig. 11). In short, either none of the weevil subclades have come into association with their hosts through cospeciation events, or subsequent colonisations of other *Carludovica* species have obscured the historical signal. A notable exception to the unordered pattern is the absence of any species of *Systemotelus* on *C. sulcata* Hammel.

Although the topology-matching approach yielded a negative answer, closer examination of morphological reproductive traits in *Carludovica* and its associated weevils provides compelling evidence for coevolution as reciprocal adaptation (Fig. 11). The history of these traits is best developed from the perspective of the derelomines. Phylogenetic optimisation of the weevils’ host-plant associations indicates that the ancestor of the *Ganglionus*–*Systemotelus* clade established an initial association with the ancestor of *Carludovica*. The likely place and timing for this event are northern South America and the Middle Miocene, before the closing of the Central American Isthmus. *Ganglionus* comes closest to the clade’s ancestral life history. The smallish adults arrive at the *Carludovica* inflorescences in large numbers (up to 200–300 individuals) during the peak of fragrance production. Typically they are covered with pollen stemming from another conspecific inflorescence. They search for the small openings left between the male flowers in order to reach the

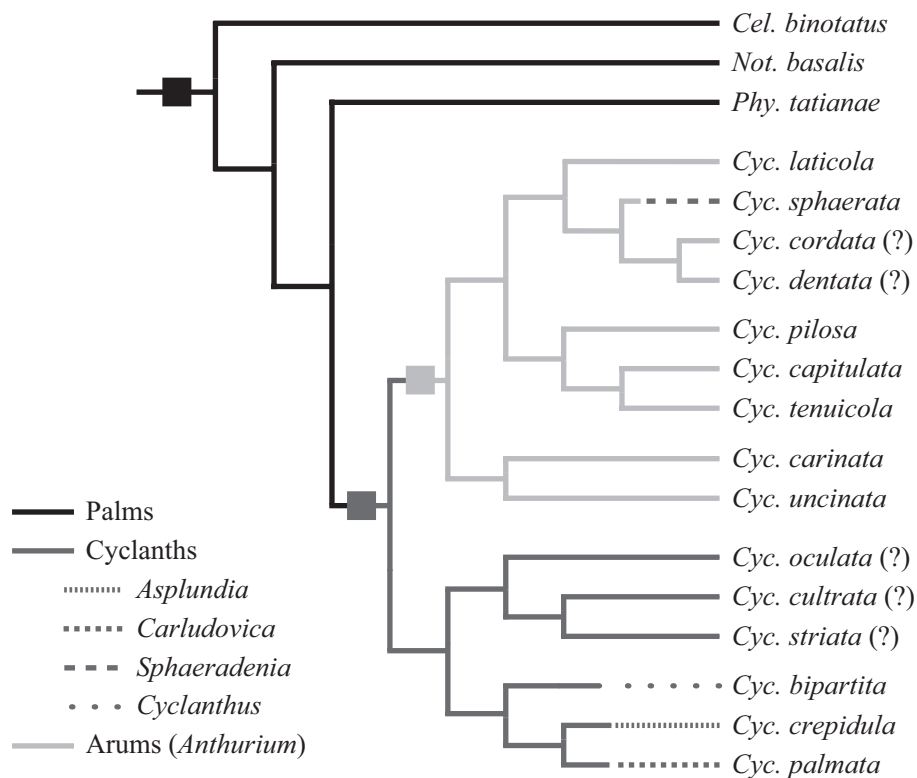


Fig. 9. Phylogeny and evolution of host-plant associations of *Cyclanthura*. ? = Host association unknown. See text for further details.

inflorescence's inside layer and the 'hidden' female flowers therein (Fig. 10C). While feeding on various floral tissues, they transfer much of the carried pollen load onto the receptive stigmata in the course of the next 24 h. After mating, the females oviposit into the bases of the male flowers. The latter become detached from the host plant as soon as the fruiting process begins. The larvae therefore finish their development as detritivores in the leaf litter. The ecological role

played by *Ganglionus* weevils is beneficial, if not essential, to the reproductive success of *Carludovica* plants.

The pattern of arrival and departure of *Perellesschus* individuals is similar to that of *Ganglionus*, although members of the former tend to be less abundant on the inflorescences (Franz 2004). Their larger size makes it more difficult for them to penetrate the outer layer of male flowers and access the female flowers. Often the adults have to 'chew' their way

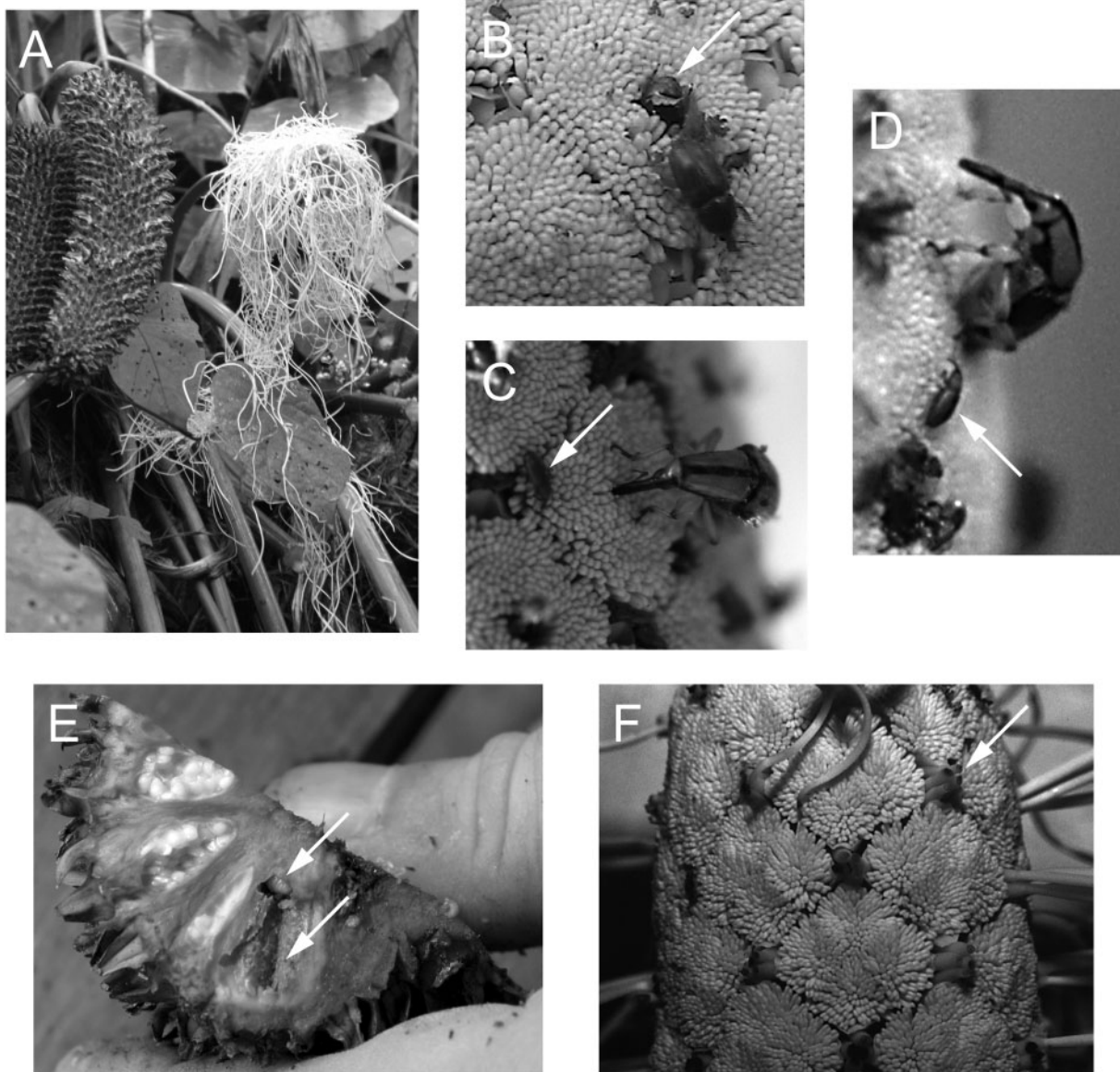


Fig. 10. Natural history of derelomine flower weevils – *Ganglionus*, *Perellesschus* and *Systenotelus* – on *Carludovica* inflorescences. *A*, Open inflorescence of *C. drudei* during the female phase at Las Cruces, Costa Rica, at 0700 hours. *B*, Associated pair of *P. splendidus* weevils, with the female (arrow) drilling an oviposition hole into the female flowers (note the narrowly arranged apices of the tepals), while the male is nearby and feeding. *C*, Pollinating female of *G. catenatus* (arrow) entering the inner layer of the inflorescence, and a much larger female of *S. carludovicae* feeding on the male flower's anthers. *D*, Female of *G. catenatus* (arrow) feeding on pollen, and a female of *S. carludovicae* ovipositing from the outside into a female flower after drilling an oviposition hole. *E*, Larva of *S. carludovicae* (arrow) feeding in the space where the seeds had developed (arrow). *F*, Opening inflorescence of *C. sulcata* at La Selva, Costa Rica, at 0715 hours. Note the fibrous, non-detaching bases of the staminodes (arrow) 'blocking' the entrance to the female flowers.

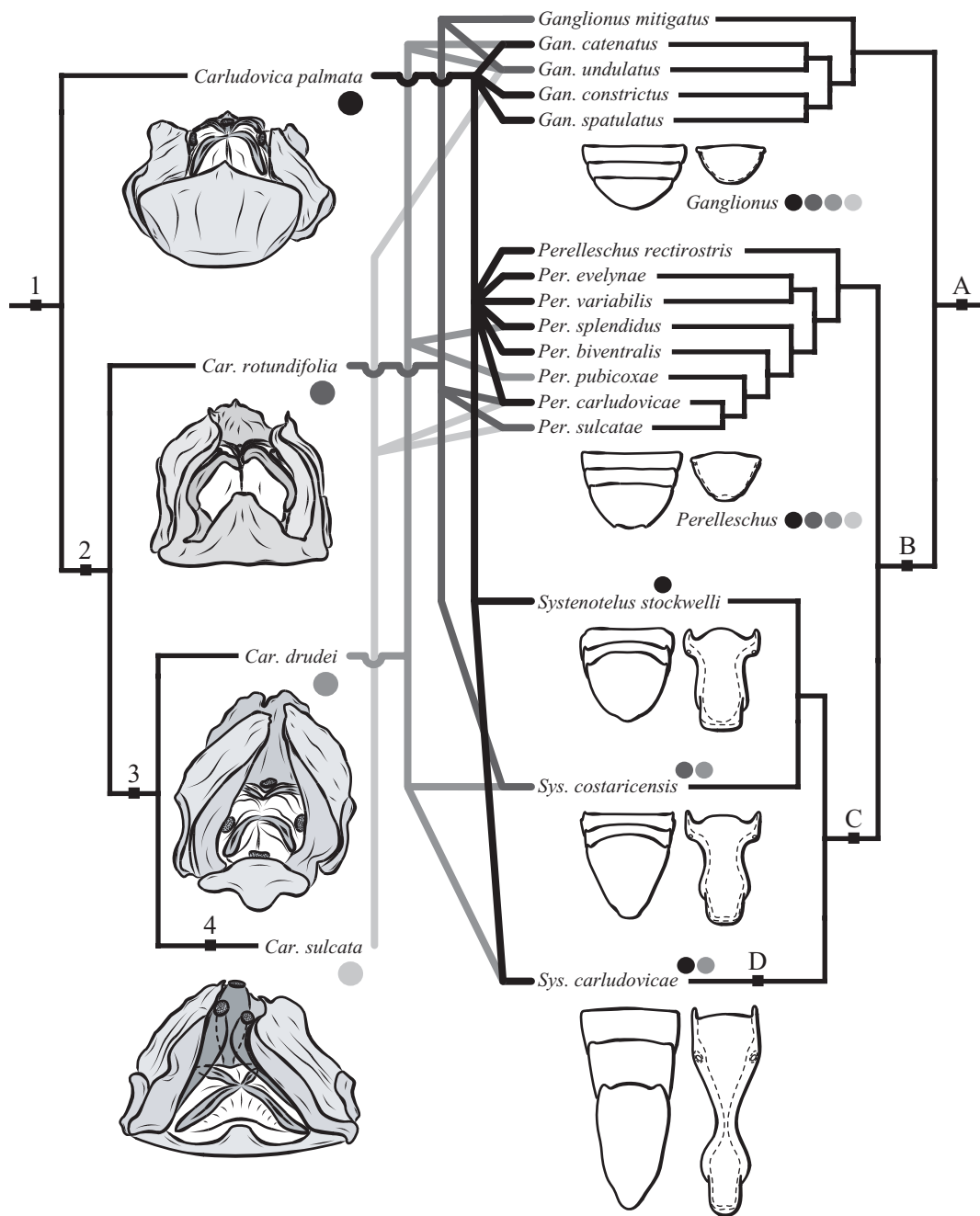


Fig. 11. Phylogeny, patterns of association and reciprocal morphological adaptation of members of the *Ganglionus*–*Systemotelus* clade and *Carludovida*. Each plant species has its own colour code. Also depicted are line drawings of the plants' female flowers (left) and the three posterior ventral segments and pygidium of the weevils (right). Note the absence of any species of *Systemotelus* on *C. sulcata*. The relevant apomorphies for the interactors are as follows. Plants: 1 = irregularly splitting infructescence; 2 = narrowed and lengthened tepals, lanceolate stigmata; 3 = tepals forming space above sessile stigmata; and 4 = basally fibrous and persistent staminodes. Weevils: A = association with *Carludovica*; B = oviposition into female flowers (tepals), herbivorous larvae feeding on pulp; C = size > 5 mm, elongate reproductive organs, larvae feeding on seeds; and D = females with centrally constricted pygidium. See text for further details.

to the inside, a process that may take up to three hours (Fig. 10B). It is conceivable that some of the pollen carried is thereby lost. Nevertheless the adults of *Perellesschus* are considered co-pollinators of *Carludovica*. The most significant difference to *Ganglionus* is that the female oviposits into the tepals of the female flowers. These remain on the host, and therefore the larvae are strictly herbivorous (i.e. using living plant material) as they feed on the reddish pulp of the maturing infructescence (this was not accurately represented in Marvaldi *et al.* 2002). They tend to avoid the seeds. Following the pupal stage, the teneral adults of *Perellesschus* leave the plant as the fruit splits open.

The transformation from a beneficial to a detrimental life habit has been taken further in *Systemotelus*. These weevils are too large to enter the inner spaces of the *Carludovica* inflorescences. Upon arriving they stay on the outer surface and feed mostly on the male flowers. Furthermore, their reproductive behaviours are not well synchronised with the flowering process. Typically fewer than ten individuals are present on an inflorescence when the female flowers are receptive. They leave before the pollen is released during the next morning. The adults of *Systemotelus* no longer function as pollinators of their hosts.

In spite of their size the females of *Systemotelus* are able to oviposit directly into the hidden female flowers (Fig. 10D). They achieve this by using their elongate and posteriorly constricted abdomen and reproductive organs. There is a clear and quantitative phylogenetic trend within the *Ganglionus*–*Systemotelus* clade towards longer and narrower oviposition structures (Fig. 11). For instance, the length-to-width ratio of the three terminal segments of the venter increases from 0.60 in *G. undulatus* Franz & O'Brien and 0.62 in *P. carludovicae* (Günther) to 0.98 in *S. stockwelli*, then 1.28 in *S. costaricensis* Anderson & Gómez, and finally 1.85 in *S. carludovicae*. In contrast to *Ganglionus* and *Perellesschus*, the larvae of *Systemotelus* are near-exclusive seed predators. Throughout their development they may destroy all the seeds developing in a single berry (Fig. 10E). The reproductive potential of their host plant is thereby directly reduced. The young adults emerge with the splitting of the mature infructescence.

The overall phylogenetic trend in the *Ganglionus*–*Systemotelus* clade is adequately summarised as (1) a loss of the ability to pollinate and (2) an attack on the seeds of *Carludovica*. The most apomorphic condition is manifested in *S. carludovicae*.

The transformations of the weevils are correlated with several morphological characteristics in the species of *Carludovica*. They should be viewed as successive adaptations towards protecting the infructescences from seed predation (Fig. 11). The 'easy-to-access' inflorescences of *C. palmata* resemble those of the most closely related out-group taxa. The stigmata of the female flowers are protruded and exposed by the short and wide tepals. Several apo-

morphies evolved in the sister-clade containing *C. rotundifolia* H. Wendl. ex Hook. fil. These include a lengthening and narrowing of the female tepals and lanceolate (apically acute) stigmata. In *C. drudei* Mast., the stigmata are sessile, i.e. inserted into the central axis of the inflorescence. The tepals form a space above the female flowers. The tips of the surrounding male flowers are further broadened, reducing the size of the entrance above the stigmata. An additional apomorphy is present in the related *C. sulcata*; here the staminodes are fibrous and strengthened at the base (Fig. 10E). Unlike in any other species of cyclanth, they continue to crowd the already small openings to the stigmata throughout the period of flowering and fruiting. The female flowers of this species are hard to access even for weevils less than 3.5 mm long, such as *P. carludovicae*. As mentioned above, no species of *Systemotelus* visit *C. sulcata*.

To sum up, the associations of members of the *Ganglionus*–*Systemotelus* clade and *Carludovica* are exclusive, longstanding, and essential to the interactors' reproductive success. In spite of the lack of congruence in the patterns of speciations, there are correlated morphological adaptations towards attacking and protecting the host plants' seeds. The evolution of the three younger species of *Carludovica* in Central America is directly linked to the apomorphic and detrimental life histories of *Systemotelus* weevils.

Other notable trends in derelomine host-plant associations

To complete the existing picture of derelomine biology, the subsequent information is summarised from the literature and personal observations. The accounts are ordered in phylogenetic sequence from subtribe to genus (Fig. 1).

Subtribe Derelomina

The adults of *Elaeidobius* Kuschel are specialised and efficient pollinators of the African oil palm *Elaeis guineensis* Jacq. (Syed 1979; Kevan *et al.* 1986). These weevils reproduce in the male inflorescences and therefore do not damage the fruits. Bondar (1941) discovered 1–5 variably sized larvae of *E. subvittatus* (Faust) per male flower. *Elaeidobius* weevils were introduced with great success in commercial plantations in South-East Asia and America (Syed *et al.* 1982; O'Brien and Woodruff 1986). The positive effect on crop yield of the largest species *E. kamerunicus* (Faust) is such that it has been named the 'multi-million dollar weevil' (Greathead 1983). Studies of this species have revealed interesting interactions with phoretic mites and nematodes (Krantz and Poinar 2004). The closely related *Prosoestus* Faust is reported to infest the female inflorescences of *E. guineensis* (Philippe 1993). A sclerotised layer of plant tissue separates the fruits from the developing larvae.

The biology of the diverse Old World genus *Derelomus* is for the most part unknown. The available observations suggest interactions with palms involving pollination and

relatively non-detrimental larval habits. The life histories of two predominantly European species have been studied in detail. The first species, *Derelomus chamaeropsis* (Fabricius), is the primary pollinator of the palm species *Chamaerops humilis* L. (von Martius 1823; Anstett 1999). The weevils visit and oviposit on all plants; however, the larvae survive and pupate only in the male inflorescences. Eggs laid into the female inflorescences are aborted owing to processes associated with the fruit development (Dufaÿ and Anstett 2004). Furthermore the palms' advertisement of a pollinator recompensation and the recompensation itself are spatially separated, i.e. the attracting floral fragrances are produced by sinuses of the palm leaves, whereas the inflorescences represent the actual nutrition and oviposition sites (Dufaÿ *et al.* 2003). The interaction exemplifies a high level of specialisation attained on each side, with the palms 'cheating' the pollinators into visiting unsuitable larval substrates. The second species, *Derelomus piriformis* (Hoffmann), was previously assigned to a separate genus *Neoderelomus* Hoffmann, but is phylogenetically nested within *Derelomus* (Franz 2005a). The adults are efficient pollinators of *Phoenix canariensis* Hort. ex Chabaud (Meekijjaroenroj and Anstett 2003). As described by Piry and Gompel (2002), the larvae develop in the male inflorescences.

The South American species of *Anchylorhynchus* are conspicuous and abundant visitors of palms, particularly members of the genera *Butia* (Becc.) Becc., *Oenocarpus* Mart. and *Syagrus* Bondar (1940, 1941, 1942, 1943, 1950; summarised in Vaurie 1954) discovered many of these associations. It is unclear where the larvae develop on their hosts. The adult colouration of several species resembles that of the palm inflorescences. Finally, the natural history of *Phytotribus* species appears similar to *Celetes* (see above). The adults oviposit and the herbivorous larvae develop in the large inflorescences spathes (e.g. Bondar 1943), without attacking the maturing fruits.

Subtribe Acalyptina

Acalyptus weevils occur in wet habitats of the northern hemisphere. They feed on and breed in the inflorescence tissues of various species of *Salix* L. (Dieckmann 1988; Topp *et al.* 2002; Nozawa and Inari 2005). Several species of the related *Amorphoidea* are observed on Malvaceae in Asia; some are considered pests attacking the flowers of cultivated cotton (Rheinheimer 1991; David and Medina 1993; H. Kojima and K. Morimoto, unpublished data). Other species are (plesiomorphically) associated with palms, but their biology is not well understood. This is true for many acalyptine taxa. Members of such genera as *Derelomorphus* Marshall, *Meredolus* Marshall and *Nodocnemus* Marshall are reported pests of the coconut palm *Cocos nucifera* L. (e.g. Ramamurthy and Ghai 1989).

Subtribe Staminodeina

The natural history of the two respective genera was recounted above. Derelomini gen. 1 is likely more diverse than *Staminodeus*. The adults of several undescribed species vary significantly in their rostral morphology, yet all oviposit into the ephemeral staminodes of cyclanths (Franz 1999). Fighting may take place during the mating phase. The males display no morphological or distinct behavioural transformations similar to those of *Staminodeus*.

Subtribe Notolomina

All members of this subtribe are associated with palms. They function as pollinators and breed in the hosts' male inflorescence structures without damaging the developing fruits. There are no detailed reports on *Derelominus* Champion. Bondar (1941) observed the sexually dimorphic *Diplothemiobius* Kuschel on *Polyandrococos caudescens* (Mart.) Barb. Rodr. The males of this species have a very large, acute, anteriorly directed projection on the prosternum whose function is unknown. *Notolomus* occurs in North America and the Caribbean (C. W. O'Brien, unpublished data). Brown (1976) suggested that the two described species are secondary pollinators of *Sabal palmetto* (Walt.) Lodd. ex Schult. & Schult. f. (see also Fig. 3). Zona (1987) failed to find any *Notolomus* individuals on the related palm *Sabal etonia* Swingle ex Nash. Finally, several species of *Andranthobius* Kuschel were shown to be significant pollinators of palms, including *A. bondari* (Hustache; see Bondar 1940), *A. mucugensis* (Bondar; see Bondar 1949), *A. palmarum* (Champion; see Mora-Urpí and Solís 1980) and several unidentified species from Brazil (e.g. Kùchmeister *et al.* 1998).

Subtribe Phyllotrogina

The relatively small and distinct genera *Pseudoderelomus* Champion and *Androtrox* Franz are presumed palm associates. An undescribed species of the former has been found on flowers of *Saurauia* sp. (N. Franz, personal observation). The adults are likely just pollen feeders there, but the observation illustrates their potential for visiting non-monocot plants. Within the taxonomically complex *Phyllotrox*, an entire subclade – named *Phyllotrox sensu stricto* herein – is associated with the flowers or inflorescences of miscellaneous dicot taxa (Appendix 1; see also Franz 2005a). These weevils tend to live in (pre)montane or temperate habitats of the New World where no palms exist. Therefore they are not reproducing on palms. For instance, Warner (1976; see also Barker 1974) observed the adults of *P. canyonaceris* Warner on the inflorescences of *Acer grandidentatum* Nutt., where they fed, mated and oviposited into the incipient seeds. The larvae first develop in the seeds but later break through the fruit shell and drop below the host tree. They continue to grow there and eventually pupate. A similar life history is

suspected for the type species *P. semirufus* Boheman, which occurs on *Rubus* (Rosaceae) at an altitude of 2000 m in Venezuela (Franz 2003a). Other species in this narrowly circumscribed group are associated with various genera of Asteraceae (e.g. Voss 1954; Voisin 1986, 1989). Field studies are needed to determine where they breed. On the other hand, members of more widely circumscribed *Phyllotrox sensu lato* have remained on palms. They are often referenced in the palm pollination literature (see Henderson 1986). Listabarth (1996) offered a detailed account of three species pollinating *Bactris* Jacq. ex Scop. palms in Peru. The adults mate and oviposit multiple times into the detaching male flowers from which the larvae move on to the soil after only 2–4 days. The entire life cycle lasts up to 14 days, and no more than 18% of the ultimately dispensable male flowers are infested. The author speculated that the larvae are ‘programmed’ by the specific floral fragrances of their hosts to later visit conspecifics, thereby increasing pollinator efficiency. Voeks’ (2002) account of the interaction of *P. tatianae* (Bondar) with *Attalea funifera* Mart. ex Spreng. contains many similarities. The associations of palm-visiting *Phyllotrox* species are specialised and of considerable ecological significance (e.g. Wolda *et al.* 1998; though see Listabarth 2001).

Cotithene and *Terioltes* Champion are small and somewhat obscure genera. The latter has been observed on palms in Costa Rica. If confirmed, this would constitute a reversal from the supposed original association of the *Cotithene*–*Systemotelus* clade with cyclanths (Fig. 2; the enigmatic *Pygocetes* Kuschel might fit in here as well). Meanwhile, the weevils of *C. globucollis* Voss and related species show life habits similar to those of *Systemotelus*. In particular, the females are larger than any of the closest relatives, with lengths up to 6–7 mm. They visit their cyclanth hosts in small numbers (Franz 1999). The patterns of arrival and departure are not well synchronised with the flowering period, which means that they do not function as pollinators. Females oviposit directly into the rachis of an inflorescence. The larvae are herbivorous throughout the entire life cycle. *Cotithene* thus presents a striking example of evolutionary convergence. In contrast to *Systemotelus*, their feeding may lead to the full destruction of an infructescence.

The many undescribed species of Derelomini gen. 2 are the exclusive pollinators of nearly all Cyclanthaceae, with the exception of *Carludovica* and *Cyclanthus* (see above). Their biological function has been discussed in several publications, sometimes under the name ‘*Phyllotrox* sp.’ (e.g. Harling 1958; Gottsberger 1991; Eriksson 1994b; Seres and Ramirez 1995; Franz 1999). It appears that the ancestors of this clade were already associated with the earliest cyclanth representatives some 40–60 million years ago (see Franz 2004). They have continued to evolve within this interaction until the present time. Typically the adults of a single species visit many cyclanths species at a given locality. If the latter

overlap in their flowering period then reproductive isolation must be upheld by processes other than pollinator specificity. The behaviour of Derelomini gen. 2 weevils is relatively uniform. Upon arrival on the fragrant staminodes they locate the access holes to the female flowers, move to the inner layer of the inflorescence, and remain there until the next morning when the pollen is released. Feeding and mating takes place in these protected areas. Eggs are laid into both male and female flowers, although the relative frequency may vary with the particular interactors. Apparently many (though not all) species of cyclanths have evolved physiological mechanisms that hinder larval development. Soon after opening, the male flowers start to deteriorate and detach from the host plant. Just as their relatives in palms, the larvae of Derelomini gen. 2 then feed as detritivores and pupate in the top layers of the soil. There is much evidence that they visit only cyclanths.

Derelomini incertae sedis

Almost nothing has been published on the natural history of the seven unplaced genera (Fig. 1). Kuschel (1992) considered the extinct Oligocene amber-preserved *Electrotribus theryi* Hustache (see also Hustache 1942) similar to *Celetes*, which would imply an association with palms.

Conclusions

Synthesis of major evolutionary trends

Our synthesis indicates that the ancestral condition – that of relatively innocuous palm pollinators (# 1) – was still present at the origin of all subtribes except the Staminodeina (Table 1; Fig. 12). This description of life habit remains accurate for the majority of derelomine species today, and in particular for those living in the Old World. However, switching from one palm host to another has been frequent throughout the history of the tribe. The case of *Celetes* illustrates to what extent narrower homology statements may be possible on the basis of detailed studies (Fig. 5). There is little reason to suspect a higher degree of host fidelity in the less well studied *Anchylorhynchus*, *Derelomus* or *Phytotribus*. Palms are a diverse family of angiosperms, and overall it seems that unambiguous apomorphies are more readily identified in smaller and younger weevil clades. The *C. buri*–*C. hustachei* clade, *Diplothemiobius* (# 10), *Elaeidobius* (# 2) and *Grasidius* (# 4) are suitable examples. Notably, the shift in the *Celetes*–*Phytotribus* clade to reproduce in the inflorescence spathes (# 5) is an innovation preserved in more than 65 species.

There were at least three independent host switches to dicots in *Acalyptus* (# 6), *Amorphoidea* (# 7) and in *Phyllotrox* (# 11) respectively. Members of the latter have colonised the widest taxonomic range of plants. In addition there were two independent shifts to cyclanth inflorescences, *viz.* in the Staminodeina (# 9) and in the *Cotithene*–*Systemotelus* clade

(# 12). Weevils pertaining to these distinct taxa may simultaneously arrive at the same host, yet their subsequent behaviours reflect their very different phylogenetic histories. The staminode-infesting *Derelomini* gen. 1 and *Staminodeus* are considered much younger. The supposedly older association with cyclanths led to one major secondary shift to arums in *Cyclanthura* (# 15) and one apparent reversal to palms in *Terioltes* (# 14).

In parallel to the colonisation events, the weevils' ecological roles have sometimes changed from beneficial to detrimental. The pollinator function has been lost on at least three independent occasions (#8, 13 and 18). The present data indicate that oviposition into non-detaching floral organs – and therefore also an herbivorous larval habit – has had five independent origins (#3, 6, 13, 15, 17). All respective clades are relatively small in their number of species.

Lessons learned

Above all, our review indicates that narrowly scoped phylogenetic and natural history studies of derelomines are rewarding, often more so than looking at the full-scale picture. Each of the four detailed analyses sends a different message in terms of mechanisms leading to the diversification of derelomines. In *Celetes*, host shifts are important, though clearly not enough to account for the existence of nearly 45 species. The evolution of *Staminodeus* is mostly explained by sexual selection. *Cyclanthura* illustrates the weevils' ability to colonise hosts with widely divergent inflorescence biologies. The *Ganglionus*–*Systemotelus* clade, in turn, showcases their potential to specialize on select floral organs along with the plants' evolutionary capacity to respond to such attacks. We often see an informative phylogenetic signal in the ecology and behaviour all the way down to the level of species. As is further suggested by the dynamic interaction of *D. chamaeropsis* and its host (Dufaÿ and

Anstett 2004), the approach to 'zoom in' pays off in terms of discovering new forms of specialisation in derelomines.

In light of the frequent host switching over time, there may be fewer unambiguous non-morphological homologies assignable to higher levels in the weevil phylogeny (i.e. multi-genus groups, subtribes, etc.; see also the extent of grey lines in Fig. 12). There is little purpose in subjecting coarse judgments of similarity to statistical tests. Whatever specialisations manifested themselves early on apparently developed further so as to obscure the original states. One-to-one cospeciation events and exclusive long-standing associations are either very rare or non-existent. In *Celetes*, for instance, it is not unusual for sister-species to reproduce in palm hosts classified in separate tribes, as in *C. faldermanni* and *Celetes* sp. 11 (Fig. 5). This also means that we should not expect radically new insights from improved phylogenetic studies of the host plants (see Anderson (1993) for a similar conclusion in a review of many weevil/plant associations). Even when the system under study is 'hand-picked' like *Systemotelus*, the topology-matching approach (Page 2003) might lead to a rejection of the coevolutionary hypothesis. Focusing on the history of biological specialisations in individual derelomine lineages is a more fruitful strategy.

Future directions

We shall end this review with an outlook. What are the most urgent and effective ways to improve our knowledge of the evolution and ecology of derelomine flower weevils? First of all we need to resolve the taxonomy and phylogeny of the following major assemblages: (1) the *Celetes*–*Phytotribus* clade; (2) the Old World (Australoasian) derelomines; (3) *Phyllotrox sensu lato*; and (4) *Derelomini* gen. 2. Each of these projects will add significantly to the phylogenetic estimate and classification for the weevils. A reliable taxonomy and identification literature for the *Phyllotrox* complex is

Table 1. Evolutionary transformations in the life histories of derelomine flower weevils (see also Fig. 12)

Number	Description of apomorphic state(s)
1	(a) Association with palm inflorescences; (b) pollinators; (c) oviposition into male flowers/ inflorescences; (d) larvae partly detritivorous
2	(a) Association with <i>Elaeis</i> palms
3	(a) In <i>Prosoestus</i> (not shown): oviposition and development in female inflorescences
4	(a) Association with <i>Bactris</i> palms
5	(a) Oviposition and development in palm inflorescence spathes
6	(a) Association with <i>Salix</i> trees and inflorescences; (b) larvae herbivorous
7	(a) In part: association with Malvaceae flowers (including <i>Derelomorphus</i> , possibly other genera)
8	(a) Association with cyclanth inflorescences, oviposition into staminodes; (b) loss of pollinator function
9	(a) Female frontal spine and staminode transporting behaviour; (b) male fighting behaviour and modifications of prothoracic legs
10	(a) Association with <i>Diplothemium</i> palms
11	(a) In part: association with flowers/inflorescences of miscellaneous dicot plants
12	(a) Association with cyclanth inflorescences, oviposition into male and female flowers but (mostly) developing in detaching male flowers
13	(a) Oviposition into female flowers; (b) larvae herbivorous, feeding along inflorescence rachis; (c) loss of pollinator function
14	(a) Likely reversal to palm inflorescences (may also include <i>Pygocetes</i>)
15	(a) In part: association with arum inflorescences (<i>Anthurium</i>); (b) larvae most likely herbivorous
16	(a) Association with <i>Carludovica</i> inflorescences
17	(a) Oviposition into female flowers (tepals); (b) larvae herbivorous, feeding on pulp
18	(a) Oviposition into stigmata; (b) larvae feeding on seeds; (c) loss of pollinator function

still lacking yet indispensable for precise evolutionary interpretations of palm pollination studies. In addition we should aim to clarify the age of the tribe, including using molecular techniques. This will answer several important questions, i.e. whether derelomines were present at the origin of palms some 100 million years ago (Bremer 2000), what their closest relatives are, and what life history transformations occurred in the process of colonising palms. Derelomines

may indeed represent one of the older lineages of weevils in the strict sense (see Kuschel 1995; Alonso-Zarazaga and Lyal 1999). A resemblance to members of the Molytinae–Trypetidini suggests that ‘proto-derelomines’ had a wood-boring habit before switching to palms (Oberprieler 2004). These propositions need testing.

Another major requirement is to close the gaps in our knowledge of derelomine reproductive biology. In accor-

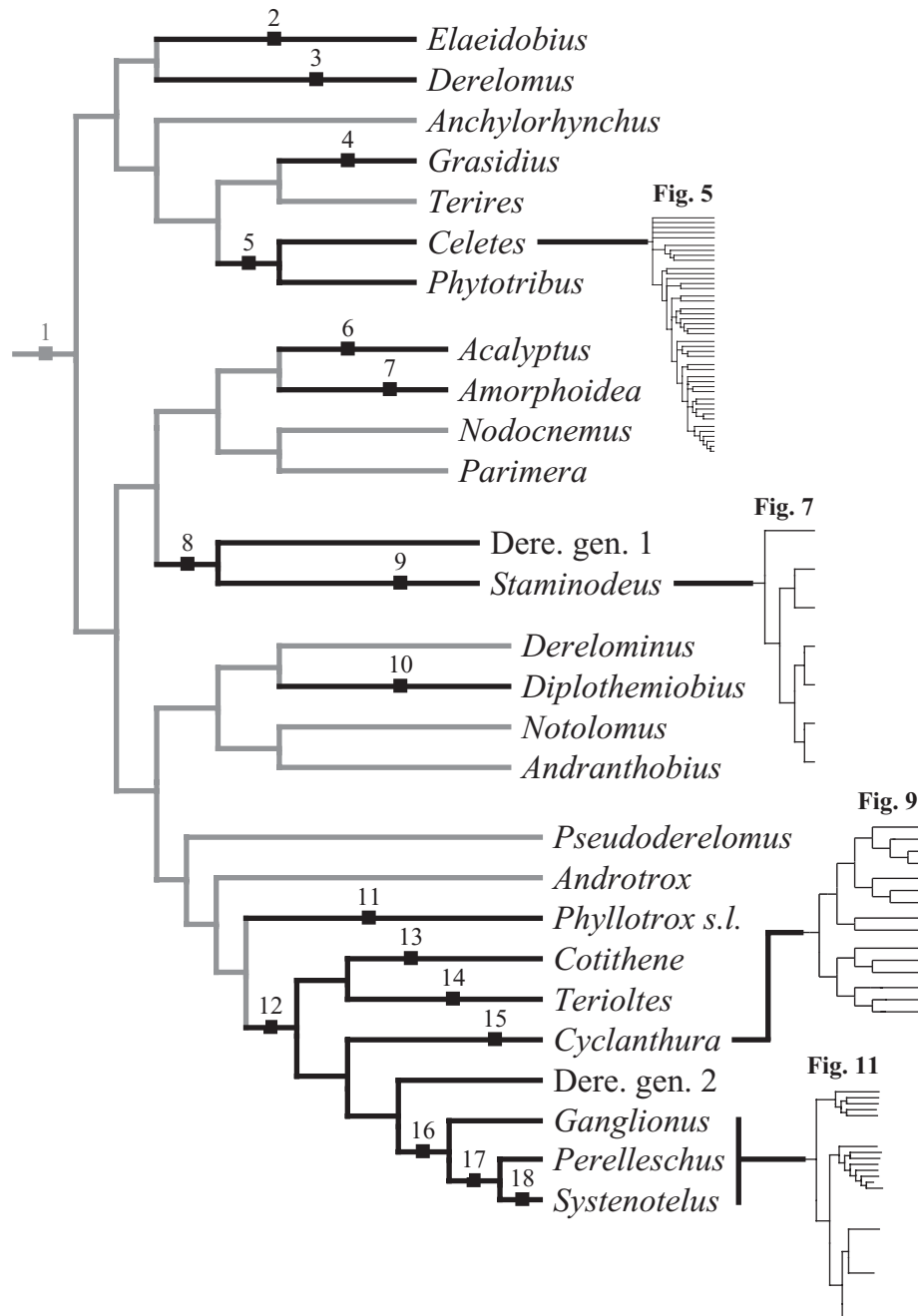


Fig. 12. Phylogenetic representation of significant life-history transformations in derelomine flower weevils. The grey colour represents the presumed ancestral condition for the tribe. See Table 1 and Figs 5, 7, 9, and 11 for further details.

dance with the theme of the paper, it is critical to continue efforts to translate field data into homology statements. What plant species are visited? Are the adults effective pollinators? In what structures do the larvae develop? Are there specialised mating behaviours or plant defenses? Answering these questions for such taxa as *Terires* Champion, *Derelominus* or *Pygoceletes* will help assign transformations to the proper evolutionary nodes and thereby refine the current picture (Fig. 12). If open inflorescences are within reach we recommend the use of video equipment to further distinguish the behaviours of individual species and sexes. This information may be produced by a wide range of ecological and evolutionary researchers.

Lastly, pollination specialists studying palms, cyclanths and arums are now prepared to explore the chemical and physiological aspects of derelomine/host-plant associations. Substantial progress has been made in identifying the floral fragrances of select members from all respective plant families (e.g. Schultz *et al.* 1999; Knudsen *et al.* 2001; Schwerdtfeger *et al.* 2002). In many hosts the fragrances alone are sufficient to attract a specific subset of derelomines from among those living in the habitat. We therefore have abundant (though merely indirect) evidence that the chemical interactions played a large role in the specialisation of each group. The sampling, analysis and synthesis of the attractants can lead to powerful *in situ* tests of homologous traits in the weevils. As an example, the absence of any species of *Systemotelus* on *C. sulcata* signifies at least two things: (1) the fragrance profile of this well protected species (Fig. 10F) differs from its immediate relatives; and (2) the weevils have subsequently lost their attractiveness to the transformed profile. *Carludovica* plants are special because floral morphology is a significant part of their defensive strategy. In most other cases the plants' means of chemical protection should prove more critical. These issues must be tackled in order to fully understand the oviposition and larval feeding habits in derelomines. Similar kinds of analyses in the unrelated yet convergent 'cycad weevils' have yielded exciting results (Pellmyr *et al.* 1991; Schneider *et al.* 2002; Terry *et al.* 2004). In the near future we hope to see such research develop on derelomines and their hosts.

Acknowledgments

The authors would like to thank Rolf Oberprieler and Catherine Duckett, the organisers of the Phytophaga Symposium at the XXII International Congress of Entomology (August 2004, Brisbane, Australia), for the opportunity to present the paper motivating this publication. We are also grateful to the Editor for her interest in publishing papers related to the Phytophaga Symposium. The first author thanks Charles O'Brien and Robert Anderson for invaluable support in terms of facilitating access to specimens and other information; Rolf Oberprieler for insightful views about weevil evolution; and Quentin Wheeler for helpful advice on a range of topics. Funding was obtained in

part through a Doctoral Dissertation Improvement Grant (DEB-0206093, with Bryan Danforth) from the National Science Foundation. The second author thanks Sergio Vanin for scientific mentoring; and financial support was provided by the Museu Paraense Emílio Goeldi as well as the Programa Norte de Pesquisa e Pós-graduação (PNOGP), through the Conselho Nacional de Desenvolvimento Científico e Tecnológico, Governo do Brasil.

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Appendix 1. Summary table of host associations for derelomine flower weevils, based either on published records, specimen labels or personal observations.
 Taxonomy and nomenclature for New World palms according to Henderson *et al.* (1995; the names may therefore differ from the original records). NA = locality information not available.

Weevil taxon	Host plant taxon	Family	Locality	Source
1. <i>Acalyptus carpinii</i> (Fabricius)	<i>Salix</i> spp.	Salicaceae	Asia, Europe, USA	Dieckmann (1988); Nozawa and Inari (2005)
<i>Acalyptus sericeus</i> Gyllenhal	<i>Salix cinerea</i> L.	Salicaceae	Europe	Topp <i>et al.</i> (2002)
2. <i>Amorphoidea coimbatorensis</i> Subramanian	<i>Cocos nucifera</i> L.	Arecaceae	India	Subramanian <i>et al.</i> (1975)
<i>Amorphoidea gossypii</i> (Pierce)	<i>Gossypium</i> sp.	Malvaceae	Philippines	H. Kojima and K. Morimoto, unpublished data
<i>Amorphoidea lata</i> Motschulsky	<i>Gossypium</i> sp.	Malvaceae	Philippines	H. Kojima and K. Morimoto, unpublished data
	<i>Hibiscus tiliaceus</i> L.	Malvaceae	Japan	H. Kojima and K. Morimoto, unpublished data
	<i>Thespesia lampas</i> Dalzell ex Dalzell & Gibson	Malvaceae	India	H. Kojima and K. Morimoto, unpublished data
	<i>Thespesia populnea</i> Sol. ex Correa	Malvaceae	Guam	H. Kojima and K. Morimoto, unpublished data
<i>Amorphoidea linospadicis</i> Rheinheimer	<i>Linospadix monostachyos</i> H. Wendl. & Drude	Arecaceae	Australia	Rheinheimer (1991)
<i>Amorphoidea</i> sp.	<i>Gossypium</i> sp.	Malvaceae	Asia	H. Kojima and K. Morimoto, unpublished data
3. <i>Anchylorhynchus aegrotus</i> Fähræus	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943)
<i>Anchylorhynchus albidus</i> (Bondar)	<i>Syagrus coronata</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1943)
<i>Anchylorhynchus amazonicus</i> (Voss)	<i>Syagrus cocoides</i> Mart.	Arecaceae	Brazil	R.M. Valente, unpublished data
<i>Anchylorhynchus bicarinatus</i> O'Brien	Arecaceae sp.	Arecaceae	Panama	O'Brien (1981)
<i>Anchylorhynchus bicolor</i> (Voss)	<i>Butia yatay</i> (Mart.) Becc.	Arecaceae	Paraguay	Vaurie (1954)
	<i>Cocos leiospatha</i> Barb. Rodr.	Arecaceae	Brazil	Vaurie (1954)
	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1950)
<i>Anchylorhynchus bucki</i> Vanin	<i>Butia</i> sp.	Arecaceae	Brazil	Vanin (1973)
	<i>Cocos</i> sp.	Arecaceae	Brazil	Vanin (1973)
<i>Anchylorhynchus burmeisteri</i> Faust	<i>Butia yatay</i> (Mart.) Becc.	Arecaceae	Argentina	Lanteri <i>et al.</i> (2004)
<i>Anchylorhynchus camposi</i> (Bondar)	<i>Syagrus flexuosa</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1943)
	<i>Syagrus loefgrenii</i> Glassman	Arecaceae	Brazil	Silberbauer-Gottsberger (1990)
<i>Anchylorhynchus eriospathae</i> (Bondar)	<i>Butia eriospatha</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1943)
<i>Anchylorhynchus gottsbergerorum</i> Vanin	<i>Oenocarpus bacaba</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Oenocarpus distichus</i> Mart.	Arecaceae	Brazil	Valente (2000)
	<i>Oenocarpus minor</i> Mart.	Arecaceae	Brazil	Vanin (1973); Küchmeister <i>et al.</i> (1998)
<i>Anchylorhynchus hatschbachi</i> (Bondar)	<i>Butia eriospatha</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1943)
<i>Anchylorhynchus minimus</i> (Bondar)	<i>Euterpe edulis</i> Mart.	Arecaceae	Argentina	Lanteri <i>et al.</i> (2004)
	<i>Oenocarpus</i> sp.	Arecaceae	Brazil	C. W. O'Brien, unpublished data
<i>Anchylorhynchus parvus</i> Fähræus	Arecaceae sp.	Arecaceae	Brazil	Bondar (1943)
<i>Anchylorhynchus pictipennis</i> (Hustache)	<i>Butia capitata</i> (Mart.) Becc.	Arecaceae	Brazil, Uruguay	Bondar (1943); C.W. O'Brien, unpublished data
<i>Anchylorhynchus pictipennis</i> (Hustache)	<i>Phoenix canariensis</i> Hort. ex Chabaud	Arecaceae	Argentina	Lanteri <i>et al.</i> (2004)
<i>Anchylorhynchus trapezicollis</i> (Hustache)	<i>Butia capitata</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1940)
	<i>Cocos nucifera</i> L.	Arecaceae	Brazil	Hustache (1940)
	<i>Syagrus botryophora</i> (Mart.) Mart.	Arecaceae	Brazil	Bondar (1943)
	<i>Syagrus coronata</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1940)
	<i>Syagrus picrophylla</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1941)
<i>Anchylorhynchus tremolerasi</i> (Hustache)	<i>Butia capitata</i> (Mart.) Becc.	Arecaceae	Brazil, Uruguay	Bondar (1943); C.W. O'Brien, unpublished data
<i>Anchylorhynchus tricarinatus</i> Vaurie	<i>Oenocarpus bataua</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Oenocarpus</i> sp.	Arecaceae	Brazil	C.W. O'Brien, unpublished data
<i>Anchylorhynchus variabilis</i> Gyllenhal	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943)
<i>Anchylorhynchus vittipennis</i> (Voss)	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943)
4. <i>Andranthobius argentinensis</i> (Hustache)	<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	Arecaceae	Argentina	C.W. O'Brien, unpublished data
	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Argentina	Lanteri <i>et al.</i> (2004)

Appendix 1. (continued)

Weevil taxon	Host plant taxon	Family	Locality	Source
<i>Andranthobius bondari</i> (Hustache)	<i>Cocos nucifera</i> L.	Arecaceae	Brazil	Hustache (1940)
	<i>Syagrus botryophora</i> (Mart.) Mart.	Arecaceae	Brazil	Hustache (1940)
	<i>Syagrus coronata</i> (Mart.) Becc.	Arecaceae	Brazil	Hustache (1940)
	Arecaceae sp.	Arecaceae	Mexico	C. W. O'Brien, unpublished data
<i>Andranthobius estriatus</i> (Champion)	<i>Butia eriospatha</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1941)
<i>Andranthobius mariahelena</i> (Bondar)	<i>Cocos</i> sp.	Arecaceae	Brazil	Bondar (1949)
<i>Andranthobius mucugensis</i> (Bondar)	<i>Acrocomia</i> sp.	Arecaceae	Brazil	D.R. Whitehead, unpublished data
<i>Andranthobius palmarum</i> (Champion)	<i>Bacris gasipaes</i> Kunth	Arecaceae	Costa Rica	Mora-Urpi and Solís (1980); Henderson (1986)
<i>Andranthobius</i> sp.	<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	Arecaceae	Costa Rica	Valente (2000)
	<i>Acrocomia hassleri</i> (Barb. Rodr.) Hahn	Arecaceae	Brazil	Silberbauer-Gottsberger (1990)
	<i>Mauritia flexuosa</i> L. f.	Arecaceae	Brazil	C. W. O'Brien, unpublished data
	<i>Oenocarpus bacaba</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Oenocarpus bataua</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998); C. W. O'Brien, unpublished data
	<i>Oenocarpus distichus</i> Mart.	Arecaceae	Brazil	Valente (2000)
	<i>Oenocarpus minor</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Phytelephas seemannii</i> O.F. Cook	Arecaceae	Brazil	C. W. O'Brien, unpublished data
	<i>Sabal mexicana</i> Mart.	Arecaceae	USA	R.S. Anderson, unpublished data
	Arecaceae sp.	Arecaceae	Panama	C. W. O'Brien, unpublished data
5. <i>Androtrox megalops</i> (Champion)	<i>Attalea cohune</i> Mart.	Arecaceae	Brazil, Guatemala	Champion (1909); Valente (2005)
6. <i>Celetes attaleae</i> (Champion)	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes biancae</i> (Bondar)	<i>Attalea humilis</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1943)
<i>Celetes bifasciatus</i> (Bondar)	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Bolivia, Brazil	Bondar (1941); Valente (2005)
<i>Celetes binotatus</i> Gyllenhal	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Bolivia, Brazil	Bondar (1942); Valente (2005)
	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1940); Valente (2005)
<i>Celetes bipunctatus</i> (Hustache)	<i>Attalea funifera</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1941); Valente (2005)
	<i>Attalea humilis</i> Mart. ex Spreng.	Arecaceae	Brazil	Valente (2005)
<i>Celetes bondari</i> Kuschel	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Valente (2005)
<i>Celetes braga</i> Bondar	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes brevitarsis</i> (Hustache)	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Argentina, Brazil, Uruguay	Bondar (1943); Valente (2005)
<i>Celetes buri</i> (Bondar)	<i>Polyandrococos caudescens</i> (Mart.) Barb. Rodr.	Arecaceae	Brazil	Bondar (1942; 1943); Valente (2005)
<i>Celetes campestris</i> Bondar	<i>Allagoptera campestris</i> (Mart.) Kuntze	Arecaceae	Brazil	Bondar (1949); Valente (2005)
<i>Celetes carbonarius</i> (Faust)	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1942, 1943); Valente (2005)
<i>Celetes cariniceps</i> (Hustache)	<i>Astrocaryum murumuru</i> Mart.	Arecaceae	Bolivia, Brazil, Peru	Valente (2005)
	<i>Astrocaryum murumuru</i> var. <i>huicungo</i> (Kahn & Millán) Henderson	Arecaceae	Bolivia, Brazil, Peru	C. W. O'Brien, unpublished data
	<i>Astrocaryum murumuru</i> var. <i>macrocalyx</i> (Kahn & Millán) Henderson	Arecaceae	Bolivia, Brazil, Peru	C. W. O'Brien, unpublished data
	<i>Astrocaryum murumuru</i> var. <i>urostachys</i> (Kahn & Millán) Henderson	Arecaceae	Bolivia, Brazil, Peru	C. W. O'Brien, unpublished data
<i>Celetes copiobae</i> (Bondar)	<i>Attalea funifera</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1941); Valente (2005)
	<i>Attalea humilis</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1941); Valente (2005)
	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1941); Valente (2005)
	<i>Attalea piassabossu</i> Bondar	Arecaceae	Brazil	Bondar (1943); Valente (2005)

(continued next page)

Appendix 1. (continued)

Weevil taxon	Host plant taxon	Family	Locality	Source
<i>Celetes crispus</i> (Champion)	<i>Attalea</i> sp.	Arecaceae	Belize, Brazil, Guatemala	Valente (2005)
<i>Celetes dahlgreni</i> (Bondar)	<i>Syagrus botryophora</i> (Mart.) Mart.	Arecaceae	Brazil	Bondar (1941, 1943); Valente (2005)
<i>Celetes decolor</i> Bondar	<i>Syagrus coronata</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes faldermanni</i> (Boheman)	<i>Attalea</i> sp.	Arecaceae	Argentina, Brazil	Valente (2005)
<i>Celetes fariati</i> (Bondar)	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Argentina, Brazil	Bondar (1941, 1943); Valente (2005)
<i>Celetes geniculatus</i> (Chevrolat)	<i>Attalea humilis</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes humilis</i> (Bondar)	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes hustachei</i> (Bondar)	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1942); Valente (2005)
<i>Celetes impar</i> Voss	<i>Polyandrococos caudescens</i> (Mart.) Barb. Rodr.	Arecaceae	Brazil	Bondar (1941, 1943); Valente (2005)
<i>Celetes landeiroi</i> (Bondar)	<i>Syagrus coronata</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1940, 1941, 1943); Valente (2005)
<i>Celetes langei</i> Bondar	<i>Syagrus botryophora</i> (Mart.) Mart.	Arecaceae	Brazil	Bondar (1941); Valente (2005)
<i>Celetes malleri</i> Bondar	<i>Syagrus picrophylla</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes marizae</i> (Bondar)	<i>Syagrus picrophylla</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes melanocephalus</i> (Chevrolat)	<i>Syagrus picrophylla</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes pallidus</i> (Champion)	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes palmarum</i> (Voss)	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes planithorax</i> (Bondar)	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes similis</i> (Bondar)	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes spinosus</i> (Bondar)	<i>Polyandrococos caudescens</i> (Mart.) Barb. Rodr.	Arecaceae	Brazil	Bondar (1942, 1943); Valente (2005)
<i>Celetes tarsalis</i> (Hustache)	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943); Valente (2005)
	Arecaceae sp.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Voss (1921); Valente (2005)
	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1941, 1943); Valente (2005)
	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1942, 1943); Valente (2005)
	<i>Polyandrococos caudescens</i> (Mart.) Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
	<i>Astrocaryum murumuru</i> var. <i>macrocalyx</i> (Kahn & Millán) Henderson	Arecaceae	Brazil	C. W. O'Brien, unpublished data
	<i>Astrocaryum murumuru</i> var. <i>urostachys</i> (Kahn & Millán) Henderson	Arecaceae	Brazil	C. W. O'Brien, unpublished data
	<i>Attalea funifera</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1940, 1943); Valente (2005)
	<i>Attalea humilis</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1940); Valente (2005)
	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1940); Valente (2005)
	<i>Syagrus coronata</i> (Mart.) Becc.	Arecaceae	Brazil	Hustache (1940); Bondar (1943); Valente (2005)
<i>Celetes triithrinacis</i> Bondar	<i>Triithrinax campestris</i> (Burmeister) Drude & Griseb. ex Griseb.	Arecaceae	Brazil	Bondar (1943); Valente (2005)
<i>Celetes</i> sp. nov. 2 s. Valente	<i>Attalea maripa</i> (Aubl.) Mart.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 3 s. Valente	<i>Mauritia flexuosa</i> L. f.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 4 s. Valente	<i>Attalea maripa</i> (Aubl.) Mart.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 5 s. Valente	<i>Attalea speciosa</i> Mart. ex Spreng.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 7 s. Valente	<i>Attalea speciosa</i> Mart. ex Spreng.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 9 s. Valente	<i>Attalea speciosa</i> Mart. ex Spreng.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 11 s. Valente	<i>Euterpe edulis</i> Mart.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 12 s. Valente	<i>Attalea speciosa</i> Mart. ex Spreng.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 13 s. Valente	<i>Astrocaryum paramaca</i> Mart.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 14 s. Valente	<i>Attalea maripa</i> (Aubl.) Mart.	Arecaceae	Brazil	Valente (2005)
<i>Celetes</i> sp. nov. 15 s. Valente	Arecaceae sp.	Arecaceae	Brazil, Ecuador	Valente (2005)

Appendix 1. (continued)

Weevil taxon	Host plant taxon	Family	Locality	Source
	<i>Asplundia uncinata</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia utilis</i> (Oerst.) Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia vagans</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Carludovica drudei</i> Mast.	Cyclanthaceae	Costa Rica	N.M. Franz, unpublished data.
	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Costa Rica	N.M. Franz, unpublished data
	<i>Carludovica rotundifolia</i> H. Wendl. ex Hook. fil.	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Carludovica sulcata</i> Hammel	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Chorogyne pendula</i> (Hammel) R. Eriksson	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Dicropygium wedelii</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Evodanthus funifer</i> Lindm.	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia aulacostigma</i> Harling	Cyclanthaceae	NA	Harling (1958)
	<i>Asplundia brachyphylla</i> Harling	Cyclanthaceae	French Guyana	L. Barrabé, unpublished data
	<i>Asplundia caput-medusae</i> (Hooker fil.) Harling	Cyclanthaceae	Venezuela	Seres and Ramirez (1995)
	<i>Asplundia euryspatha</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia fendleri</i> Harling	Cyclanthaceae	Venezuela	Seres and Ramirez (1995)
	<i>Asplundia microphylla</i> (Oerst.) Harling	Cyclanthaceae	NA	Harling (1958)
	<i>Asplundia moritziana</i> (Klotzsch) Harling	Cyclanthaceae	Venezuela	Seres and Ramirez (1995)
	<i>Asplundia peruviana</i> Harling	Cyclanthaceae	Peru	Gottsberger (1991)
	<i>Asplundia platanthera</i> Harling	Cyclanthaceae	NA	Harling (1958)
	<i>Asplundia ponderosa</i> R.E. Schult. ex Harling	Cyclanthaceae	NA	Harling (1958)
	<i>Asplundia quinindensis</i> Harling	Cyclanthaceae	NA	Harling (1958)
	<i>Asplundia rhodea</i> R.E. Schult. ex Harling	Cyclanthaceae	NA	Harling (1958)
	<i>Asplundia rigida</i> (Aubl.) Harling	Cyclanthaceae	NA	Harling (1958)
	<i>Asplundia sleeperae</i> Grayum & Hammel	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia ulei</i> Harling	Cyclanthaceae	Peru	Gottsberger (1991)
	<i>Asplundia uncinata</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia utilis</i> (Oerst.) Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia vagans</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Carludovica rotundifolia</i> H. Wendl. ex Hook. fil.	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Carludovica sulcata</i> Hammel	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Chorogyne pendula</i> (Hammel) R. Eriksson	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Dicranopygium mirabile</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Dicranopygium stenophyllum</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Dicropygium umbrophilum</i> Hammel	Cyclanthaceae	Costa Rica	Harling (1958)
	<i>Dicropygium wedelii</i> Harling	Cyclanthaceae	NA	Harling (1958)
	<i>Evodanthus funifer</i> Lindm.	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Sphaeradenia hamata</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Thoracocarpus bissectus</i> (Vell.) Harling	Cyclanthaceae	Colombia	R. Eriksson (1994b)
	Areaceae sp.	Areaceae	NA	Harling (1958)
	<i>Cocos nucifera</i> L.	Areaceae	Belize	C.W. O'Brien, unpublished data
		Areaceae	Malaysia, Java	Henderson (1986), R. Oberprieler, unpublished data
11. <i>Derelomimus piceus</i> Champion		Malvaceae	Sri Lanka	Ramamurthy and Ghai (1989)
12. <i>Derelomorphus eburneus</i> (Marshall)		Areaceae	Philippines	R. Oberprieler, unpublished data
<i>Derelomorphus subfulvus</i> Ramamurthy & Ghai		Areaceae	South Africa	C.W. O'Brien, unpublished data
<i>Derelomorphus</i> sp.		Areaceae	Taiwan	Kojima <i>et al.</i> (1995); C.W. O'Brien, unpublished data
13. <i>Derelomus auberti</i> Hustache		Areaceae		
<i>Derelomus bicarinatus</i> Marshall		Areaceae		

Appendix 1. (continued)

Weevil taxon	Host plant taxon	Family	Locality	Source
<i>Derelomus chamaeropsis</i> Fabricius	<i>Chamaerops humilis</i> L.	Arecaceae	Europe	Henderson (1986)
<i>Derelomus piriformis</i> (Hoffmann)	<i>Phoenix canariensis</i> Hort. ex Chabaud	Arecaceae	France	Piry and Gompel (2002)
<i>Derelomus singularis</i> Faust	<i>Elaeis</i> sp.	Arecaceae	Congo	R. Oberprieler, unpublished data
<i>Derelomus subcostatus</i> Boheman	<i>Chamaerops humilis</i> L.	Arecaceae	Europe	Henderson (1986)
<i>Derelomus 'ueoni'</i>	<i>Trachycarpus excelsus</i> H. Wendl.	Arecaceae	Japan	Henderson (1986)
<i>Derelomus</i> spp.	<i>Phoenix reclinata</i> Jacq.	Arecaceae	South Africa	R. Oberprieler, unpublished data
	<i>Salacca edulis</i> Reinw.	Arecaceae	Java	Henderson (1986)
14. <i>Diplothemiobius sternicornis</i> Kuschel	<i>Polyandrococos caudescens</i> (Mart.) Barb. Rodr.	Arecaceae	Brazil	Bondar (1941)
15. <i>Elaeidobius kamerunicus</i> (Faust)	<i>Elaeis guineensis</i> Jacq.	Arecaceae	Costa Rica, Zaire	C. W. O'Brien, unpublished data; R. Oberprieler, unpublished data
<i>Elaeidobius plagiatius</i> (Fähræus)	<i>Elaeis guineensis</i> Jacq.	Arecaceae	Cameroon	Syed (1979)
<i>Elaeidobius subvittatus</i> (Faust)	<i>Elaeis guineensis</i> Jacq.	Arecaceae	Brazil, Sierra Leone, Uganda	Bondar (1941) R. Oberprieler, unpublished data
<i>Elaeidobius</i> sp.	<i>Elaeis oleifera</i> (Kunth) Cortés	Arecaceae	South America	Henderson (1986)
16. <i>Eudela</i> sp.	<i>Normanbya normanbyi</i> L.H. Bailey	Arecaceae	Australia	R. Oberprieler, unpublished data
17. <i>Eudelodes bicolor</i> (Faust)	<i>Hibiscus tiliaceus</i> L.	Malvaceae	Australia, P. New Guinea	Rheinheimer (1991)
<i>Eudelodes</i> spp.	<i>Gossypium</i> sp.	Malvaceae	Asia	R. Oberprieler, unpublished data
	<i>Hibiscus tiliaceus</i> L.	Malvaceae	Australia	H. Kojima and K. Morimoto, unpublished data
18. <i>Ganglionus catenatus</i> Franz & O'Brien	<i>Carludovica drudei</i> Mast.	Cyclanthaceae	Costa Rica	A. Howden, unpublished data
<i>Ganglionus strictus</i> Franz & O'Brien	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Costa Rica, Panama	Franz and O'Brien (2001a)
<i>Ganglionus mitigatus</i> Franz & O'Brien	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001a)
<i>Ganglionus spatulatus</i> Franz & O'Brien	<i>Carludovica rotundifolia</i> H. Wendl. ex Hook. fil.	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001a)
<i>Ganglionus undulatus</i> Franz & O'Brien	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Colombia	Franz and O'Brien (2001a)
	<i>Carludovica drudei</i> Mast.	Cyclanthaceae	Panama	Franz and O'Brien (2001a)
	<i>Carludovica rotundifolia</i> H. Wendl. ex Hook. fil.	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001a)
19. <i>Grasidius</i> spp.	<i>Carludovica sulcata</i> Hammel	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001a)
	<i>Bactris guineensis</i> (L.) H.E. Moore	Arecaceae	Costa Rica	Henderson (1986)
	<i>Bactris major</i> Jacq.	Arecaceae	Costa Rica	Henderson (1986)
	<i>Elaeis guineensis</i> Jacq.	Arecaceae	Brazil	G. Couturier, unpublished data
20. <i>Lomederus ghesquierei</i> Marshall	<i>Baikiaea insignis</i> Benth.	Fabaceae	Congo	Marshall (1932)
21. <i>Meredolus cocotis</i> Marshall	<i>Cocos nucifera</i> L.	Arecaceae	Solomon Islands	Lepesme (1947); R. Oberprieler, unpublished data
22. <i>Nodocnemus subfasciatus</i> Marshall	Arecaceae sp.	Arecaceae	Samoa	H. Kojima and K. Morimoto, unpublished data
<i>Nodocnemus uniformis</i> Marshall	<i>Cocos nucifera</i> L.	Arecaceae	New Hebrides	H. Kojima and K. Morimoto, unpublished data
<i>Nodocnemus</i> spp.	<i>Hydriastele microspadix</i> (Becc.) Burret	Arecaceae	New Guinea	Henderson (1986)
	<i>Normanbya normanbyi</i> L.H. Bailey	Arecaceae	Australia	S. Boulter, unpublished data
23. <i>Notolomus basalis</i> LeConte	<i>Rhapidophyllum hystrix</i> (Pursh) H. Wendl. & Drude	Arecaceae	USA	Henderson (1986)
	<i>Sabal palmetto</i> (Walt.) Lodd. ex Schult. & Schult. f.	Arecaceae	USA	Henderson (1986)
	<i>Serenoa repens</i> (Bartram) Small	Arecaceae	USA	Anderson (2002)
	<i>Sabal palmetto</i> (Walt.) Lodd. ex Schult. & Schult. f.	Arecaceae	USA	Anderson (2002)
	<i>Serenoa repens</i> (Bartram) Small	Arecaceae	USA	Anderson (2002)
<i>Notolomus</i> sp.	<i>Copernicia macroglossa</i> H. Wendl. ex Becc.	Arecaceae	Cuba	B.E. Dahlgren, unpublished data
24. <i>Parimera fusca</i> Voss	<i>Salacca edulis</i> Reinw.	Arecaceae	NA	H. Kojima and K. Morimoto, unpublished data
<i>Parimera palmarum</i> Voss	<i>Allagoptera arenaria</i> (Gomes) Kuntze	Arecaceae	NA	H. Kojima and K. Morimoto, unpublished data

(continued next page)

Appendix 1. (continued)

Weevil taxon	Host plant taxon	Family	Locality	Source
<i>Perellesschus biventralis</i> Franz & O'Brien	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Ecuador	Franz and O'Brien (2001b)
<i>Perellesschus carludoviccae</i> (Günther)	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001b)
	<i>Carludovica rotundifolia</i> H. Wendl. ex Hook. fil.	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001b)
	<i>Carludovica sulcata</i> Hammel	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001b)
<i>Perellesschus evelynae</i> Franz & O'Brien	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Colombia, Panama	Franz and O'Brien (2001b)
<i>Perellesschus pubicoxae</i> Franz & O'Brien	<i>Carludovica drudei</i> Mast.	Cyclanthaceae	Panama	Franz and O'Brien (2001b)
<i>Perellesschus rectirostris</i> Voss	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Peru	Franz and O'Brien (2001b)
<i>Perellesschus splendidus</i> Franz & O'Brien	<i>Carludovica drudei</i> Mast.	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001b)
<i>Perellesschus splendidius</i> Franz & O'Brien	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Costa Rica, Panama	Franz and O'Brien (2001b)
<i>Perellesschus sulcatae</i> Franz & O'Brien	<i>Carludovica rotundifolia</i> H. Wendl. ex Hook. fil.	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001b)
	<i>Carludovica sulcata</i> Hammel	Cyclanthaceae	Costa Rica	Franz and O'Brien (2001b)
	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Ecuador	Franz and O'Brien (2001b)
<i>Perellesschus variabilis</i> Franz & O'Brien	<i>Espeletia timotensis</i> Cuatrec.	Asteraceae	Venezuela	Voisin (1986)
26. <i>Phyllotrx aristidis</i> Voisin (s.s.)	<i>Geranium</i> sp.	Geraniaceae	USA	Anderson (2002)
<i>Phyllotrx atratus</i> (Fall) (s.s.)	<i>Acer grandidentatum</i> Nutt.	Aceraceae	USA	Warner (1976)
<i>Phyllotrx canyonacensis</i> Warner (s.s.)	<i>Eupatorium cremulatum</i> Gardner	Asteraceae	Peru	Voss (1954)
<i>Phyllotrx eupatorii</i> Voss (s.s.)	<i>Espeletia timotensis</i> Cuatrec.	Asteraceae	Venezuela	Voisin (1989)
<i>Phyllotrx lamottei</i> Viosin (s.s.)	<i>Cirsium niveale</i> Sch. Bip.	Asteraceae	Mexico	C.W. O'Brien, unpublished data
<i>Phyllotrx mecinoides</i> Champion (s.s.)	Melastomataceae sp.	Melastomataceae	Peru	Voss (1954)
<i>Phyllotrx melastomataceae</i> Voss (s.s.)	<i>Ceanothus sanguineus</i> Pursh	Rhamnaceae	USA	Fall (1913)
<i>Phyllotrx rutilus</i> (Fall) (s.s.)	<i>Rubus</i> sp.	Rosaceae	Venezuela	N.M. Franz, unpublished data.
<i>Phyllotrx semirufus</i> Boheman (s.s.)	<i>Cirsium jorullense</i> Spreng.	Asteraceae	Mexico	C.W. O'Brien, unpublished data
<i>Phyllotrx suturalis</i> (Boheman) (s.s.)	<i>Senecio peltiferus</i> Hemsf.	Asteraceae	Mexico	C.W. O'Brien, unpublished data
	<i>Abutilon</i> sp.	Malvaceae	Bolivia	Kuschel (1952)
<i>Phyllotrx</i> sp. (s.s.)	<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	Arecaceae	Puerto Rico	C.W. O'Brien, unpublished data
<i>Phyllotrx pallidus</i> Fähræus (s.l.)	<i>Atalea funifera</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1941); Voeks (2002)
<i>Phyllotrx tatanæ</i> (Bondar) (s.l.)	<i>Thrynax</i> sp.	Arecaceae	Cuba	Suffrian (1871)
<i>Phyllotrx variegatus</i> Suffrian (s.l.)	<i>Acrocomia globosa</i> Lodd. ex Mart.	Arecaceae	NA	C. W. O'Brien, unpublished data
<i>Phyllotrx</i> spp. (s.l.)	<i>Aiphanes</i> sp.	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Ammannia decasperma</i> O.F. Cook	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Asterogyne martiana</i> (H. Wendl.) H. Wendl. ex Hemsf.	Arecaceae	Costa Rica	N.M. Franz, unpublished data
	<i>Astrocaryum mexicanum</i> Liebm. ex Mart.	Arecaceae	Mexico	Listabarth (1992)
	<i>Astrocaryum murumuru</i> var. <i>macrocalyx</i> (Kahn & Millán) Henderson	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Atalea microcarpa</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Bactris bifida</i> Mart.	Arecaceae	Peru	Listabarth (1996)
	<i>Bactris gasipaes</i> Kunth	Arecaceae	Costa Rica	Henderson (1986)
	<i>Bactris guineensis</i> (L.) H.E. Moore	Arecaceae	Costa Rica	Henderson (1986)
	<i>Bactris hirta</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Bactris macroacantha</i> Mart.	Arecaceae	Peru	Listabarth (1996)
	<i>Bactris major</i> Jacq.	Arecaceae	Costa Rica	Henderson (1986)
	<i>Bactris maraja</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Bactris maraja</i> Mart. (var. <i>maraja</i>)	Arecaceae	Peru	Listabarth (1996)
	<i>Bactris simplicifrons</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Cheilocarpus repens</i> F. Kahn & K. Mejia	Arecaceae	NA	C. W. O'Brien, unpublished data

Appendix 1. (continued)

Weevil taxon	Host plant taxon	Family	Locality	Source
	<i>Cryosophila albida</i> Bartlett	Arecaceae	Costa Rica	Henderson (1986)
	<i>Desmoncus mitis</i> Mart.	Arecaceae	Peru	Listabarth (1992)
	<i>Desmoncus polyacanthos</i> Mart.	Arecaceae	Peru	Listabarth (1994)
	<i>Euterpe precatoria</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Euterpe</i> sp.	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Geonoma</i> sp.	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Iriartella setigera</i> (Mart.) H. Wendl.	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Iriartella stenocarpa</i> Burret	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Mauritia flexuosa</i> L. f.	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Oenocarpus bacaba</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Oenocarpus bataua</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Oenocarpus minor</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Oenocarpus</i> sp.	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Phytelephas aequatorialis</i> Spruce	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Phytelephas macrocarpa</i> Ruiz & Pavón	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Phytelephas seemannii</i> O.F. Cook	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Phytelephas</i> sp.	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Prestoea decurrens</i> (H. Wendl. ex Burret) H.E. Moore	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Prestoea schultzeana</i> (Burret) H.E. Moore	Arecaceae	NA	C. W. O'Brien, unpublished data
	<i>Socratea exorrhiza</i> (Mart.) H. Wendl.	Arecaceae	Venezuela	Henderson (1986)
	<i>Wettinia hirsuta</i> Burret	Arecaceae	Colombia	Henderson (1986)
	<i>Wettinia kalbreyeri</i> (Burret) R. Bernal	Arecaceae	Colombia	Henderson (1986)
27. <i>Phytotribus andaitae</i> Bondar	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2002)
<i>Phytotribus attaleae</i> Hustache	<i>Attalea funifera</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1943)
<i>Phytotribus cachoeranus</i> Bondar	<i>Attalea humilis</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1943); Valente (2002)
<i>Phytotribus cocosae</i> Bondar	<i>Syagrus botryophora</i> (Mart.) Mart.	Arecaceae	Brazil	Bondar (1943); Valente (2002)
<i>Phytotribus curtus</i> Bondar	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943); Valente (2002)
<i>Phytotribus jiquiensis</i> Bondar	<i>Syagrus flexuosa</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1943); Valente (2002)
<i>Phytotribus minor</i> Bondar	<i>Attalea oleifera</i> Barb. Rodr.	Arecaceae	Brazil	Bondar (1943)
<i>Phytotribus palmarum</i> Bondar	<i>Attalea</i> sp.	Arecaceae	Brazil	Bondar (1943)
<i>Phytotribus pindobae</i> Bondar	<i>Attalea humilis</i> Mart. ex Spreng.	Arecaceae	Brazil	Bondar (1943)
<i>Phytotribus platyrhinus</i> Hustache	<i>Syagrus coronata</i> (Mart.) Becc.	Arecaceae	Brazil	Bondar (1943)
<i>Phytotribus romanzoffianae</i> Bondar	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943)
<i>Phytotribus squamosus</i> Bondar	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943)
<i>Phytotribus squamulosus</i> Bondar	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Arecaceae	Brazil	Bondar (1943)
<i>Phytotribus unicolor</i> Boheman	<i>Syagrus coronata</i> (Mart.) Becc.	Arecaceae	Brazil	Hustache (1940)
<i>Phytotribus</i> spp.	<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	Arecaceae	Brazil	Valente (2000)
	<i>Astrocaryum aculeatum</i> Mart.	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Astrocaryum gymnacanthum</i> Mart.	Arecaceae	Brazil	Valente (2000)
	<i>Astrocaryum murumuru</i> Mart.	Arecaceae	Brazil	Valente (2000)
	<i>Astrocaryum murumuru</i> var. <i>urostachys</i> (Kahn & Millán) Henderson	Arecaceae	Brazil	C. W. O'Brien, unpublished data
	<i>Astrocaryum paramaca</i> Mart.	Arecaceae	Brazil	Valente (2000)
	<i>Attalea attaleoides</i> (Barb. Rodr.) Wess. Boer	Arecaceae	Brazil	Küchmeister <i>et al.</i> (1998)
	<i>Attalea gernaensis</i> Barb. Rodr.	Arecaceae	Brazil	Silberbauer-Gottsberger (1990)

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Appendix 1. (continued)

Weevil taxon	Host plant taxon	Family	Locality	Source
	<i>Attalea maripa</i> (Aubl.) Mart.	Areaceae	Brazil, Peru	Valente (2000); G. Couturier, unpublished data
	<i>Bactris acanthocarpa</i> Mart.	Areaceae	Brazil	Valente (2000)
	<i>Bactris brongniartii</i> Mart.	Areaceae	Brazil	Valente (2000)
	<i>Bactris campestris</i> Poepp. ex Mart.	Areaceae	Brazil	Valente (2000)
	<i>Euterpe oleracea</i> Mart.	Areaceae	Brazil	Valente (2000)
	<i>Geonoma maxima</i> Kunth	Areaceae	Brazil	Valente (2000)
	<i>Mauritia flexuosa</i> L. f.	Areaceae	Brazil	Valente (2000)
	<i>Maurititia armata</i> (Mart.) Burret	Areaceae	Brazil	Valente (2000)
	<i>Oenocarpus distichus</i> Mart.	Areaceae	Brazil	Valente (2000)
	<i>Oenocarpus</i> sp.	Areaceae	Brazil	C. W. O'Brien, unpublished data
	<i>Syagrus inajai</i> (Spruce) Becc.	Areaceae	Brazil	Valente (2000)
28. <i>Prosoestus bilineatus</i> (Hustache)	<i>Elaeis guineensis</i> Jacq.	Areaceae	Sierra Leone	R. Oberprieler, unpublished data
<i>Prosoestus sculptilis</i> Faust	<i>Elaeis guineensis</i> Jacq.	Areaceae	Africa	Moore (2001)
<i>Prosoestus</i> sp. 'minor'	<i>Elaeis guineensis</i> Jacq.	Areaceae	Cameroon	Syed (1979)
29. <i>Pseudodelomus subopacus</i> (Schaufuss)	<i>Phytelephas</i> sp.	Areaceae	NA	C. W. O'Brien, unpublished data
30. <i>Pygocelates</i> sp.	<i>Prestoea decurrens</i> (H. Wendl. ex Burret) H.E. Moore	Areaceae	Colombia	R. Bernal, unpublished data
31. <i>Staminodeus curvibialis</i> Franz	<i>Asplundia caput-medusae</i> (Hooker fil.) Harling	Cyclanthaceae	Venezuela	Franz (2001)
	<i>Sphaeradenia hamata</i> Harling	Cyclanthaceae	Colombia	Franz (2001)
<i>Staminodeus denticulatus</i> Franz	<i>Asplundia</i> sp.	Cyclanthaceae	Panama	Franz (2001)
	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Costa Rica	Franz (2001)
	<i>Evodanthus funifer</i> (Poit.) Lindman	Cyclanthaceae	Costa Rica	Franz (2001)
	<i>Asplundia euryspatha</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia steperae</i> Grayum & Hammel	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia uncinata</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia utilis</i> (Oerst.) Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Asplundia vagans</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Carludovica rotundifolia</i> H. Wendl. ex Hook. fil.	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Carludovica sulcata</i> Hammel	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Chorogyne pendula</i> (Hammel) R. Eriksson	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Dicranopygium umbrophilum</i> Hammel	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Dicranopygium weddellii</i> Harling	Cyclanthaceae	Costa Rica	Franz (1999)
	<i>Evodanthus funifer</i> (Poit.) Lindman	Cyclanthaceae	Costa Rica	Franz (1999)
32. <i>Systemotelus carludovicae</i> Anderson & Gómez	<i>Carludovica drudei</i> Mast.	Cyclanthaceae	Costa Rica	Anderson and Gómez (1997)
	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Costa Rica	Anderson and Gómez (1997)
	<i>Carludovica drudei</i> Mast.	Cyclanthaceae	Panama	Anderson and Gómez (1997)
<i>Systemotelus costaricensis</i> Anderson & Gómez	<i>Carludovica rotundifolia</i> H. Wendl. ex Hook. fil.	Cyclanthaceae	Costa Rica	Franz (1999)
<i>Systemotelus stockwelli</i> Anderson & Gómez	<i>Carludovica palmata</i> Ruiz & Pavón	Cyclanthaceae	Panama	Anderson and Gómez (1997)
	<i>Astrocaryum</i> sp.	Areaceae	Costa Rica	N.M. Franz, unpublished data
<i>Teriolites nigripennis</i> Champion	<i>Iriartea deltoidea</i> Ruiz & Pavón	Areaceae	Costa Rica	S.H. Bullock, unpublished data
34. <i>Terites pilosus</i> Champion	<i>Attalea butyracea</i> (Multis ex L. f.) Wess. Boer	Areaceae	Panama	C. W. O'Brien, unpublished data
<i>Terites</i> sp. 'minusculus'	<i>Astrocaryum vulgare</i> Mart.	Areaceae	Brazil	G. Couturier, unpublished data
<i>Terites</i> spp.	<i>Astrocaryum murumuru</i> var. <i>macrocalyx</i> (Kahn & Millán) Henderson	Areaceae	NA	C. W. O'Brien, unpublished data
	<i>Elaeis guineensis</i> Jacq.	Areaceae	NA	C. W. O'Brien, unpublished data
	<i>Mauritia flexuosa</i> L. f.	Areaceae	NA	C. W. O'Brien, unpublished data