

Analysing the history of the derelomine flower weevil–*Carludovica* association (Coleoptera: Curculionidae; Cyclanthaceae)

NICO M. FRANZ*

Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria 'Rodrigo Facio', Costa Rica

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The evolutionary history of the interaction among species of derelomine flower weevils (Coleoptera: Curculionidae: Derelomini) and the Panama-hat palm *Carludovica* (Cyclanthaceae) is analysed with emphasis on the congruence of (1) topologies and (2) character state transformations in each of the Neotropical clades. For this purpose cladistic analyses are complemented with host plant records, natural history information and selected morphological studies of the associated taxa. The interaction is specialized, involving pollination, oviposition into the inflorescences and the predation of seeds (particularly within *Systenotelus*). As results from a range of standard coevolutionary methods of analysis indicate, however, events of colonization, extinction and independent (non-reciprocal) speciation have been abundant throughout the history of the association. At the same time it is possible to specify the homology and succession of characters among species of derelomines and *Carludovica* and interpret them as reciprocal adaptations to attack and protect the seeds, respectively. It is argued that – in light of the limited evolutionary stability of many insect–plant interactions – the question of coevolution is most effectively addressed by combining information from the character- and topology-based approaches. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, 81, 483–517.

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'The result is variously termed phylogenetic tracking, parallel cladogenesis or Fahrenheit's Rule (or sometimes coevolution by biologists who disregard the central point that coevolution involves reciprocal evolutionary change)'.

(Thompson, 1994a: 70)

INTRODUCTION

In proposing their plausible hypothesis of biochemical coevolution among butterflies and plants, Ehrlich & Raven (1964) illustrated how knowledge of phylogeny might be used in evolutionary analyses of ecological interactions. The integration of evidence for reciprocal (contemporary or historical) adaptations from experiments, natural history information, and systematics

was ambitious and attractive at the same time. Nevertheless, the process of refining the hypothesis and testing it in particular situations has been problematic. Consider, for example, the task of translating biochemical characteristics – some of which have been documented in insects and plants for over 100 years (e.g. Stahl, 1888; Verschaffelt, 1910; Dethier, 1954) – into the language of phylogeny (e.g. Barkman, 2001a). One can also argue that no specific pattern of relationships must be associated with the hypothesis of escape-and-radiation (Thompson, 1989). It is therefore not testable by some phylogenetic methods, at least not in isolation. Many empirical analyses of insect–plant interactions did not generate the kind of congruence expected in the case of coevolution (Mitter & Farrell, 1991). Gradually, the initial period of coevolutionary enthusiasm has been succeeded by more precise studies and less general conclusions (e.g. Berenbaum, 1983; Miller, 1987; Becerra, 1997).

*Current address: Department of Entomology, Comstock Hall, Cornell University, Ithaca, NY 14853, USA.
E-mail: nmf2@cornell.edu

At the level of populations, recent progress has been achieved in light of the geographical mosaic theory of coevolution (Thompson, 1994, 1997, 1999). Briefly, suppose that ecological interactions vary in space and time in such a way that there are (1) hot spots where strong reciprocal selection occurs for particular reproductive traits, and (2) cold spots with weak (or even antagonistic) selection among populations of the same or of different interacting species. If these spatiotemporal dynamics of specialization can be documented, then we have evidence for coevolution that is neither 'diffuse' nor present in all populations of the species under study. Once the respective characters are fixated at the level of species, this would presumably enable us to infer the presence of coevolution in the past. However, the fixation of locally evolving adaptations is by no means 'necessary'. Traits might become extinct or continue to vary in space and time. The geographical mosaic theory of coevolution is plausible because it facilitates hypothesis testing in ecological time while preserving the traditional conception of coevolution as reciprocal adaptation (Darwin, 1859; but see also Darwin, 1877).

Phylogenetic analyses contribute to this methodological approach by assessing the extent to which the observed spatiotemporal variation in interactions can be explained by adaptations at the level of populations, species or more inclusive taxa (Thompson, 1994a: 59–76). Yet this contribution differs from standard systematic studies in which tests for coevolution focus on the congruence among the topologies of hosts and parasites or insects and plants (e.g. Fahrenholz, 1913; Eichler, 1941; Hennig, 1966; Brooks, 1981, 1990; Miller, 1987; Page, 1994a, b; Ronquist, 1995; Schuh, 2000). In the latter case, inferences regarding the evolution of characters as adaptations among the interactors are typically not emphasized.

Here we illustrate why the topology-centred approach should be complemented by one that accommodates historical inferences of reciprocal adaptation. In a sense, the plausibility of geographical mosaic theory of coevolution will be assessed (and also confirmed) in situations going beyond its original scope. For this purpose, the history of the Neotropical association of derelomine flower weevils (Coleoptera: Curculionidae) with species of the monocot host plant *Carludovica* (Cyclanthaceae) is analysed. The interaction is characterized by relatively high levels of specialization, involving pollination as well as the predation and protection of seeds. Phylogenetic studies facilitate inferences of the behavioural, ecological and morphological adaptations among the interactors. An interesting conclusion of the present study is that the congruence among the characters and topologies of insect and plants is not necessarily correlated. Whether one accepts or rejects the hypothesis of coevolution for the

derelomine–*Carludovica* association is contingent upon the preferred method for testing. This conclusion has potential implications for many coevolved insect–plant associations. To put it into perspective, an evaluation of the achievements and limitations of the character- and topology-based approaches to historical coevolutionary studies precedes the actual analysis.

HISTORICAL COEVOLUTIONARY STUDIES: CONGRUENCE AMONG CHARACTERS 'VERSUS' TOPOLOGIES

Although Darwin regarded coevolution as the process of reciprocal adaptation among interacting species (Thompson, 1994a: 7–22), systematists have been cautious to adopt this criterion, focusing primarily on the congruence among topologies. As reviewed by Schuh (2000: 194): '[t]he observation that hosts and their parasites have evolved in concert is long-standing, and was discussed extensively by Hennig (1966) under the heading of 'Fahrenholz's rule.' The development of improved techniques for determining to what degree 'co-evolution' has actually occurred, however, has gone hand-in-hand with the development of biogeographical methods.' Systematists have no 'direct' access to analyses of adaptations in the past. Instead, the historical functions of character state transformations on the cladogram(s) must be inferred, partly on the basis of the contemporary functions of the respective traits (Coddington, 1988; Harvey & Pagel, 1991; Wenzel & Carpenter, 1994). This can be problematic in practice. At the same time, information about observed host associations comes with the specimens one collects, along with the standard distributional information. Historical analyses of biogeography and coevolution could be based on distributional records and host records, respectively. The conceptual analogies continue from this stage on.

Historically, systematists had already established some kind of coevolutionary research paradigm at least 50 years before Ehrlich & Raven (1964) published on the coevolution among insects and plants (e.g. Fahrenholz, 1913; Eichler, 1941; Stammer, 1957). These investigations were based on distributional records for associations among hosts and parasites, vertebrates and lice in particular. Hennig (1966: 106–113, 174–180) began to adopt such concepts as colonization, cospeciation, exclusion, extinction and asymmetries in speciation into the graphical language of phylogeny reconstruction. In doing so, he did not display the characters of hosts and parasites on the topologies. Brooks (1979) must be credited with developing a more formalistic approach to historical analyses of associations among taxa. Specifically, he differentiated between (1) co-accommodation (i.e. reciprocal adaptation) and (2) cospeciation (i.e. parallel cladogenesis) as complementary phenomena of coevolution. His

method focuses on the latter phenomenon (Brooks, 1979: 300): '[o]f the mechanisms described above, cospeciation clearly represents allopatric speciation phenomena best described by the vicariance biogeography model [...].' Subsequently, the analogies of cospeciation and vicariance vs. colonization and dispersal have been translated into a series of increasingly sophisticated methods conceived to test for the congruence among the topologies of areas and taxa or hosts and parasites (e.g. Brooks, 1981, 1988, 1990; Page, 1990, 1994a, b, 1995; Ronquist, 1995, 1996, 1998; Charleston, 1998; for review see Page, 2003). All of them reconcile the topologies of hosts and parasites in such a way that the number of cospeciations is maximized whereas the number of colonizations is minimized. Thus, host taxa have been interpreted just as if they were areas of endemism where the parasite taxa occur. Questions regarding adaptations among them are typically not addressed.

The topology-based approach to coevolution has been used with limited success in tests of the escape-and-radiation hypothesis among insects and plants (e.g. Mitter & Brooks, 1983; Miller, 1987; Farrell & Mitter, 1990, 1998; Futuyma & McCafferty, 1990; Becerra, 1997; and references therein). Arguably, the limitations are related to its inability to evaluate an impressive range of adaptations evolved by the plants in response to the insects. To the extent that reciprocal adaptations are important phenomena in the evolutionary history of such associations (as proposed by Ehrlich & Raven, 1964), the methods of systematics should be employed to analyse them. They cannot do so by focusing exclusively on the process of speciation.

Formulated more precisely, the problem is that the historical distribution of events of colonization, extinction and speciation within associations of taxa is not necessarily congruent with that of adaptations among them (e.g. Mitter & Brooks, 1983; Miller, 1987; Ronquist & Nylin, 1990; Thompson, 1994; Miller & Wenzel, 1995). Taken in isolation, the congruence of topologies is neither necessary nor sufficient to accept or reject the hypothesis of reciprocal adaptation. One does not know, for example, whether this reflects (1) the succession of reciprocal specializations by insects and plants, (2) the unidirectional specialization by insects to plants (or vice versa, yet without response), or (3) the absence of specialization, because insects colonize plants without evolving specializations in the process.

The situation is worse if there is incongruence. First, Ehrlich & Raven (1964) did not expect clades with comparable numbers of species to result from the process of escape-and-radiation. Insect species can evidently colonize new plants and speciate – without corresponding speciations by the host taxa. If, for example, 15 insect species are associated with five

plant species, then there are maximally four events of cospeciation in the larger insect clade. At the same time, there could be 'any number' of reciprocal adaptations among insects and plants, e.g. eight adaptations in each clade. Inequalities in the numbers of species among cladograms can therefore compromise tests for coevolution. Second, in the majority of cases, the clades of insects and plants reflect an evolutionary history comprising (tens of) millions of years (e.g. Mitter & Brooks, 1983; Mitter & Farrell, 1991; Thompson, 1994). In analogy to the geographical mosaic theory of coevolution (Thompson, 1994), they do not have to interact exclusively for the entire period in order to coevolve during parts of it. An ancestral association can plausibly involve the evolution of reciprocal specializations for some time until at one moment the insect taxon colonizes another host. Additional reciprocal adaptations could then evolve in one or more descendant associations (or perhaps not), and so on. Consequently, coevolution will be local and unstable over longer periods. The topologies of insects and plants will be increasingly more incongruent with evolutionary time. Resting on an assumption of stability, the topology-based approach will probably reject the hypothesis of coevolution.

The congruence among characters is potentially less affected by the instability of associations generated by events of colonization, extinction and speciation. Even when faced with incongruent topologies, it might be possible to infer the phylogeny of characters in insects and plants and reconstruct the temporal succession of descendant associations. Within empirical limitations, specialization vis-à-vis selection 'inside' and 'outside' of an interaction can be identified in spite of topological incongruence. However, some kind of pragmatic conception of scientific enquiry must be adopted to achieve progress in this context.

Whenever reciprocal adaptations are proposed, it is necessary to generate evidence indicating that the respective taxa interacted at the same time. This signifies that the homology of ancestral insect-plant associations must be specified. If the contemporary associations do not facilitate such assessments, e.g. because of subsequent 'excessive' colonizations, then it will be impossible to assign character state transformations in the insect clade to particular branches in the plant clade, and vice versa. Associations, characters and taxa are historically situated kinds with beginnings and endings. The delimitation of their spatiotemporal occurrence is essential to the objective of reconstructing the succession among them. Any efforts to differentiate between reciprocal vs. unidirectional adaptations are thus directly related to the precision of homology assessments of historical associations. When this becomes difficult, i.e. in the case of 'diffuse coevolution' among 'evolutionary com-

munities' (Ehrlich & Raven, 1964), the reliability of tests of coevolution decreases as well. So here again, the analogy between contemporary and historical coevolutionary analyses appears to be adequate.

To infer the homology relations of insect–plant associations with the methods of systematics, the observed ecological interactions should be included as characters in the analyses of phylogeny (Freudenstein *et al.*, 2003). Such a practice is plausible so long as the associations can be interpreted as discrete, heritable, independent and appropriately weighted indicators of phylogenetic relationships (e.g. Hennig, 1966; but see also Miller & Wenzel, 1995; Nixon & Carpenter, 1996; Grandcolas *et al.*, 2001; and references therein). In many situations, it will be sufficient to code the associations with the plant taxa as characters in the matrix of the insect taxa, although in principle the reverse is possible as well (e.g. if the plants are unable to reproduce without the insects).

To paraphrase Janzen (1980) one might justifiably ask: when was it coevolution among insect and plants? According to the approach outlined above, historical coevolution as reciprocal adaptation is evidenced by character state transformations along the branches of the cladograms of the associated taxa. Their phylogenetic congruence in space, time and evolutionary function is tested (inductively) with the methods of systematics. Imprecision in assessments of the homology and succession of associations represents an important limitation to such tests. Nevertheless, the character-based approach can potentially succeed where the topology-based approach fails. These preliminary conclusions will be supported by an analysis of the history of the derelomine–*Carludovica* association.

INTRODUCTION TO THE DERELOMINE–*CARLUDOVICA* ASSOCIATION

Research on the particularities of the derelomine–*Carludovica* association has been initiated relatively recently (e.g. Gottsberger, 1990). Derelomine flower weevils (Coleoptera: Curculionidae: Curculioninae: Derelomini; in the sense of Alonso-Zarazaga & Lyal, 1999) are small, elongate, brownish weevils. They have received attention as economically important pollinators of, for example, the African oil palm (Syed, 1979). Presently, 40 genera and 235 species are recognized within the tribe. The majority of them are pantropical and associated with the inflorescences of Cyclanthaceae, Arecaceae and Araceae. The palaeontological record of derelomines appears to indicate an interaction with some of these monocot hosts for more than 40 million years (Anderson & Gómez, 1997). The evolution of this long association has generated diverse feeding specializations, reproductive behaviours, life histories and sexual dimorphisms (e.g.

Henderson, 1986; Franz & O'Brien, 2001a, b; Franz, 2003a, b). Many species of derelomines are specialized to visit (and also pollinate) only a few, closely related species of monocots. Frequently, the adults feed on and oviposit into particular organs of the inflorescences, which constitute the substrate for the subsequent larval development. Dichogamy and monoecy predominate in the host plant taxa (Henderson, 1986; Eriksson, 1994a; Mayo, Bognor & Boyce, 1997). Accordingly, those species whose behaviours are not precisely synchronized with the spatiotemporal expression of the inflorescences do not function as pollinators. Furthermore, if oviposition occurs into caducous floral organs such as staminodes (i.e. ephemeral stamens whose primary function is olfactory attraction), then the final larval stages will be detritivorous (rather than herbivorous). Reconstructing the succession of these life histories will be relevant to the coevolutionary analysis.

Here we focus on the taxa associated with the inflorescences of *Carludovica* Ruiz & Pavón (Cyclanthaceae), particularly the species of *Ganglionus* Franz & O'Brien, *Perelleschus* Wibmer & O'Brien and *Systenotelus* Anderson & Gómez. The interaction involves pollination as well as the predation of seeds, thus being similar to some of the already classical examples of coevolution among insects and plants (Pellmyr, 1997; note, however, that active pollination does not occur in derelomines). In order to comprehend the differences it is necessary to review the biology and taxonomy of the interactors.

Carludovica, the Panama-hat palm, is an herbaceous perennial plant with palm-like habitus (Fig. 1A). It has been placed within the exclusively Neotropical monocot family Cyclanthaceae (Harling, 1958; Eriksson, 1994b; Harling, Wilder & Eriksson, 1998). All four species of *Carludovica* are diagnosed by four-segmented leaf blades, an end-situated pollen aperture and an irregularly splitting infructescence. The complex inflorescences are monoecious spadices (Fig. 1B) and covered by several spathes until the beginning of the anthesis. Their unisexual flowers are arranged in a regular chessboard mosaic (Fig. 1C) forming a spiral along the central rachis. Four staminate flowers (♂) surround each pistillate flower (♀) and project beyond it in such a way that there are reticulate spaces above the stigmata. Perhaps the filiform staminodes of the pistillate flowers are the most noticeable organs during the anthesis (Fig. 1B). As in the majority of species of Cyclanthaceae the inflorescences are protogynous yet display facultative geitonogamy (Eriksson, 1994a). The distribution of *Carludovica* ranges from Mexico to Bolivia. The plants occur in low to mid elevation wet forests and *C. palmata* Ruiz & Pavón is cultivated for fibre throughout northern South America (Harling, 1958).

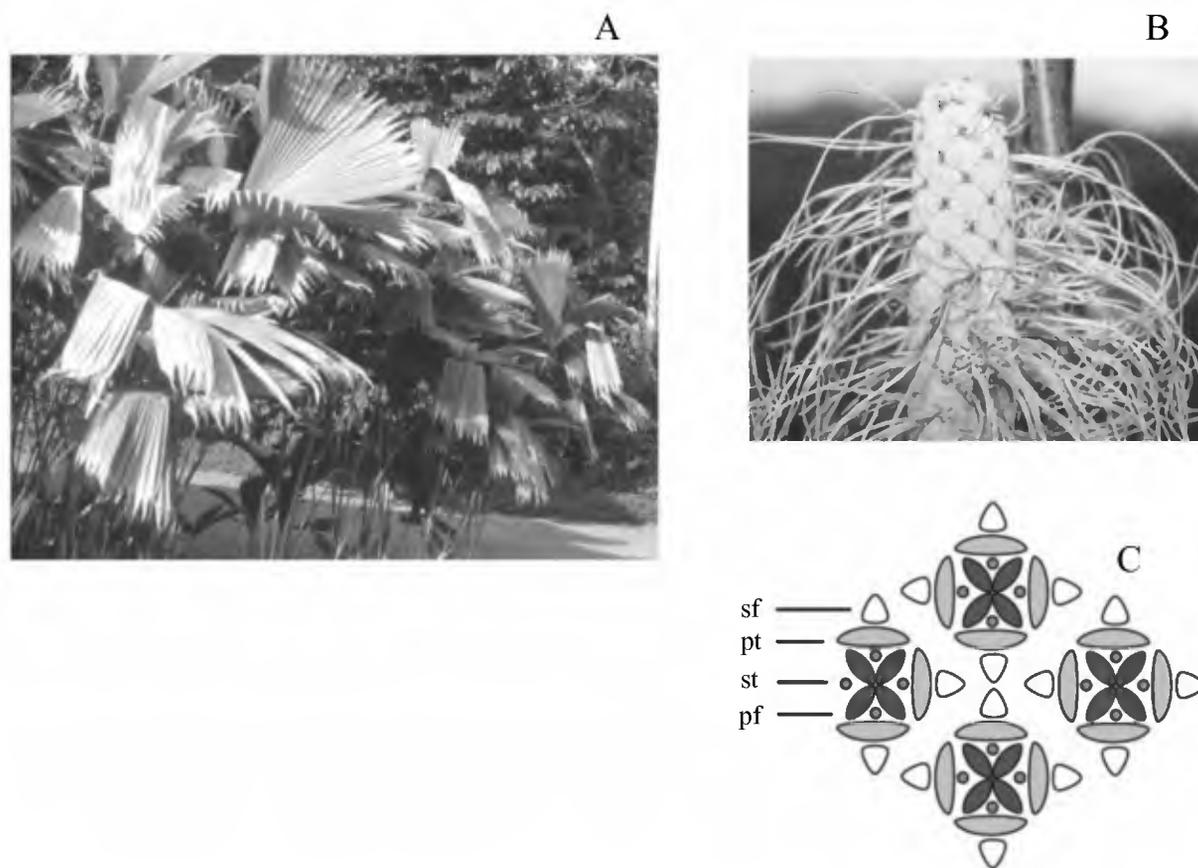


Figure 1. Habitus and inflorescence morphology of *Carludovica*. (A) Habitus of *C. sulcata* at La Selva. (B) Inflorescence of *C. sulcata* during the pistillate phase with extended staminodes projecting from 'internal' pistillate flowers between 'external' staminate flowers with densely grouped anthers. (C) Representation of 4 + 1 floral arrangement along the central axis of the inflorescence of *Carludovica*. sf: staminate (♂) flower; pt: pistillate tepal; st: staminode; pf: pistillate (♀) flower, with lobes of the four-segmented stigmata.

With respect to the derelomines, it appears that the species of *Ganglionus* (Fig. 2A, with five species), *Perelleschus* (Fig. 2B, with eight species) and *Systemotelus* (Fig. 2C–E, with three species) reproduce in exclusive association with the inflorescences of *Carludovica* (Anderson & Gómez, 1997; Franz & O'Brien, 2001a, b; see also below). Interestingly, *Systemotelus* is distributed in Costa Rica and Panama, whereas *Ganglionus* and *Perelleschus* occur south of the Central American Isthmus as well. The adults of the species of the two latter genera function as the primary pollinators of *Carludovica*. Their larvae inflict relatively little damage upon the inflorescences and infructescences of the host plant taxa. This contrasts with the species of *Systemotelus* whose adults do not pollinate the flowers of *Carludovica* and whose larvae consume the seeds of the berries. These differences in ecological functions – ranging from beneficial to detrimental – are also considered critical in the context of coevolution.

MATERIAL AND METHODS

The arrangement of the methods, results and discussion emphasizes the complementarity of the character- and topology-based approaches. Initially, hypotheses of the phylogenies for the respective species of *Carludovica* and derelomines are presented in combination with the host plant records. Then the congruence among their topologies is tested using various standard methods. Finally, detailed accounts of the natural history (biology and morphology) of the interacting taxa form the basis of the subsequent character analysis.

ANALYSES OF PHYLOGENY

The analyses of phylogeny are based on information from traditional (non-molecular) characters. Cladistic methods are considered adequate for reconstructing

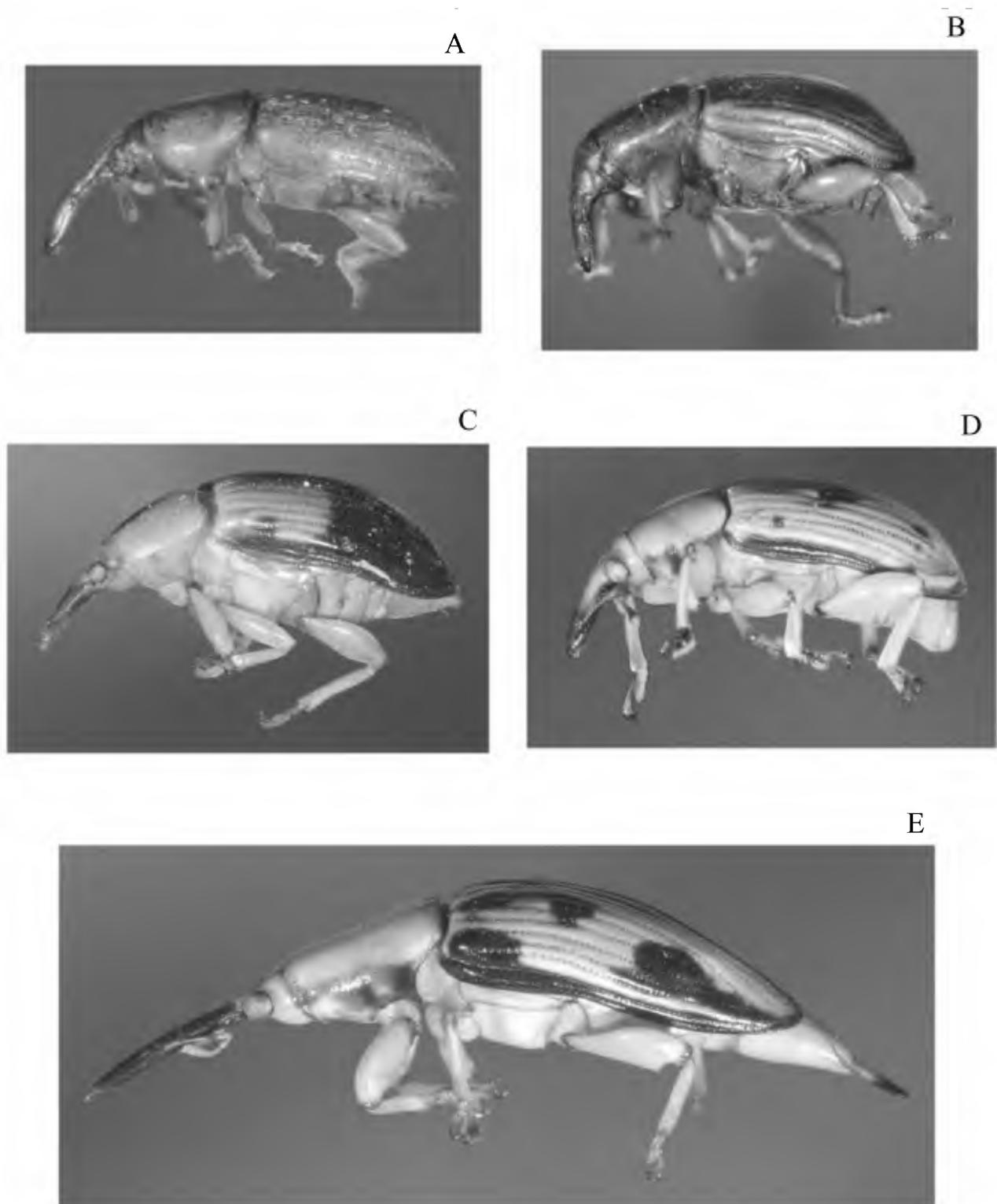


Figure 2. Habitus of species of (adult) derelomine flower weevils associated with *Carludovica*. (A) Female of *G. undulatus* (length: 1.9 mm). (B) Female of *P. carludovicae* (length: 3.1 mm). (C) Female of *S. stockwelli* (length: 5.5 mm). (D) Male of *S. costaricensis* (length: 7.0 mm). (E) Female of *S. carludovicae* (length: 10.2 mm).

the historical succession of these characters (Farris, 1983). Both cladistic analyses were conducted by complementing previous studies.

The character matrix for the species of *Carludovica* was constructed with information from the morphological cladistic analysis of all Cyclanthaceae genera by Eriksson (1994b). In order to infer the phylogeny among species, characters were extracted from available diagnostic keys (Harling, 1958: 128; Hammel, 1986: 9; and an unpublished manuscript on the Cyclanthaceae of Costa Rica by B. E. Hammel, 1995). Some of the autapomorphies were included in the analysis (for discussion see Yeates, 1992) because of their relevance to the hypothesis of coevolution. To represent the 12 genera of Cyclanthaceae (Eriksson, 1994b), the following species were selected as outgroup taxa: *Cyclanthus bipartitus* Poiteau, *Asplundia uncinata* Harling, *Dicranopygium wedelii* Harling and *Evodianthus funifer* (Poiteau) Lindman. All *Carludovica* species were included as well.

For the cladistic analysis of the derelomines, character information was combined from recent studies on the phylogeny of the species of *Ganglionus*, *Perelleschus* and *Systemotelus* (Anderson & Gómez, 1997; Franz & O'Brien, 2001a, b). Again, autapomorphies that appear to function as adaptations to *Carludovica* were coded in the character matrix. Additional evidence for the relationships among the three respective genera was adopted from an analysis of all derelomine genera (N. M. Franz, unpubl. data). Behavioural as well as ecological character information was used to the extent that the characters complied with the necessary criteria for phylogenetic inference (Wenzel, 1992; Nixon & Carpenter, 1996; Grandcolas *et al.*, 2001). Additive binary coding was performed to represent the applicability of this kind of evidence (and some of the characters for the male genital complex) as precisely as possible (Strong & Lipscomb, 1999). In accordance with previous cladistic analyses (Franz, 2003b), the following species of derelomine flower weevils were selected as outgroup taxa (with host plant records in parentheses): *Derelomus chamaeropsis* Fabricius (pollinator of the dwarf palm *Chamaerops humilis* Linnaeus; Anstett, 1999), *Elaeidobius subvittatus* (Faust) (pollinator of the oil palm *Elaeis guineensis* Jacquin; Syed, 1979), *Notolomus basalis* LeConte (pollinator of the cabbage palm *Sabal palmetto* (Walt.) Lodd. ex Schultes; Brown, 1976), *Staminodeus vectoris* Franz (associated with the staminodes of *Asplundia* sp.; Franz, 2003a); *Phyllotrox semirufus* Schönherr (associated with the flowers of *Rubus* sp.; Franz, 2003b); and *Cyclanthura laticola* Franz (pollinator of the inflorescences of *Anthurium* sp.; Franz, 2003b). All described species of *Ganglionus*, *Perelleschus* and *Systemotelus* were included in the cladistic analysis.

The character matrices were edited in WINCLADA (Nixon, 2002) and the cladistic analyses were computed with NONA (Goloboff, 1999). For the *Carludovica* matrix an exhaustive search was conducted using the commands 'whennig' and 'mswap+'. An initial search for the most parsimonious cladograms of the derelomine matrix was performed with the parsimony ratchet (Nixon, 1999; as implemented in WINCLADA), computing 500 iterations per replication, with two trees held per iteration and sampling eight characters (out of 50). Subsequently, all shortest trees were submitted to NONA to identify additional islands of equally parsimonious cladograms (Maddison, 1991), under the commands 'hold 20000', 'amb=', 'poly', 'max*' and 'amb-', 'poly=', and 'best'. Finally, by entering the commands 'ksave' and 'inters' the consensus of all shortest trees was computed. The resulting topologies and optimizations of character state transformations were edited and examined in WINCLADA. The character polarities were determined after the analyses by rooting the cladograms with the species of *Cyclanthus* and *Derelomus*, respectively (for discussion see Nixon & Carpenter, 1993). Branch support values (Bremer, 1994) were calculated in NONA with 'hold 20000', 'suboptimal 20' and 'bsupport 20'. The arrangement of the characters follows the sequence of description.

TESTING FOR THE CONGRUENCE AMONG TOPOLOGIES

The majority of host plant records for the species of derelomines were extracted from previous studies (Anderson & Gómez, 1997; Franz, 1999, 2003a, b; Franz & O'Brien, 2001a, b). The reliability of this information is variable, ranging from notes on the collecting labels of specimens to direct observations of the reproductive biology of adults, larvae and pupae of derelomines in the field.

Three standard methods were used to assess the congruence among the most parsimonious topologies for the species of *Carludovica* and derelomines. For the purpose of computing the analyses, one ambiguous clade within *Perelleschus* had to be resolved arbitrarily. This process did not affect any of the conclusions because the two respective species are associated with *C. palmata*.

Brooks Parsimony Analysis is based on the method of coding the relationships among insects as components (character state trees), replacing the names of the insects with those of the associated plant taxa, and optimizing the components as additive binary characters on the phylogeny of the plants (Brooks, 1981). Incongruence is indicated by 'homoplasy', i.e. the presence of events of colonization, extinction or (non-reciprocal) independent speciation in the insects. Systematists have recently differentiated between pri-

mary and secondary Brooks Parsimony Analyses (Brooks, van Veller & McLennan, 2001), which confer the ability to accommodate the assumption of hierarchy vs. reticulation among host plant species, respectively. In the case of *Carludovica*, hierarchy was assumed. The objective of specifying the historical succession of non-cospeciating events was considered less critical than the identification of incongruence in general. Therefore, only primary Brooks Parsimony Analyses were performed. All component matrices were generated in WINCLADA. Inclusive ORing was used to code the host plants with multiple species of associated insects (O'Grady & Deets, 1987). However, no '?' coding was applied to represent the absence of one derelomine genus from one plant species (for discussion see Brooks, 1990; Brooks *et al.*, 2001; Dowling, 2002). NONA was employed to display the additive binary characters on the phylogeny of *Carludovica* under (ACCTRAN) fast optimization. Two kinds of primary analyses were performed: (1) three separate analyses for each genus of derelomines and (2) one combined analysis for the entire clade, taking into account the relationships among genera.

Reconciled Tree Analysis proposes events of colonization, extinction and speciation in order to reconcile the insect phylogeny with the plant phylogeny (Page, 1994a,b). The computer program TREEMAP has been developed to associate the internal nodes of the insect and plant phylogenies with each other while maximizing the number of cospeciations among them (Page, 1995). Initially, the reconstructions do not introduce colonization events. If the number of cospeciations can be increased, however, then the algorithm will subsequently propose colonization and extinction events until the 'best' possible reconstruction has been achieved. Randomization procedures test the significance of the number of cospeciations in the reconstruction (Page, 1995), although the results must be interpreted critically (Siddall, 2001). The Reconciled Tree Analyses were conducted in TREEMAP 1.0 (Page, 1995). Nexus files were generated to represent information on the phylogeny of the species of derelomines and *Carludovica* as well as the associations among them. Again, two kinds of reconciliation analyses were performed, focusing (1) on each genus individually and (2) on the entire derelomine clade. In both cases the initial reconstructions were subjected to exact searches under the TREEMAP algorithm. To explore the significance of the number of cospeciations in the reconstructions, randomization tests were used. Holding the phylogeny of *Carludovica* as a constant, 10 000 random trees for the insects were generated under the proportional-to-distinguishable model, and the frequencies of events of cospeciation in the histograms were compared with those for the reconstructions.

Finally, Dispersal Vicariance Analysis implements a three-dimensional step matrix – with exact costs assigned to coevolutionary events – for the purpose of reconstructing the historical interactions among insects and plants (Ronquist, 1995, 1998). DIVA, the corresponding computer program (Ronquist, 1996), interprets events of speciation throughout the evolution of the insects as having the cost of '0', whereas colonizations and extinctions have the cost of '1'. Dispersal Vicariance Analysis does not assume hierarchy among the species of plants that are optimized on the internal nodes of the insect phylogeny in accordance with the algorithm. Nexus files were compiled for submission to DIVA 1.1 (Ronquist, 1996), specifying information on the phylogeny of the species of derelomines and their host associations. Reconstructions were computed (1) for each genus as well as (2) for all genera, using the command 'optimize' and holding the number of associations to '4' (maximally). The results were displayed on the corresponding derelomine cladograms in combination with the proposed numbers of colonization events.

FIELD OBSERVATIONS AND MORPHOLOGICAL ANALYSES

Field observations on the natural history of derelomines on all *Carludovica* species were made at the following locations (in chronological sequence): (1) Estación Biológica La Selva (Organización para Estudios Tropicales), Provincia de Heredia, Costa Rica (10°26'N, 83°59'W, c. 40 m above sea-level), from December 1996 to October 1998 (*C. rotundifolia* H. Wendl. ex Hook. fil. and *C. sulcata* Hammel); (2) Isla de Barro Colorado (Smithsonian Tropical Research Institute), Provincia de Colón, Panama (09°09'N, 79°51'W, 50 m), from May 1999 to July 1999 (*C. palmata*); (3) at El Centro Juvenil Tropical (Fundación Neotrópica), Provincia de Puntarenas, Costa Rica (08°42'N, 83°31'W, 80 m), in June 2001 (*C. drudei* Masters); (4) Estación Biológica Las Cruces (Organización para Estudios Tropicales), Provincia de Puntarenas, Costa Rica (08°47'N, 82°57'W, 1200 m), in May 2003 (*C. drudei* and *C. palmata*); and (5) Reserva Biológica Hitoy Cerere (La Amistad Caribe), Provincia de Limón, Costa Rica (09°40'N, 83°02'W, 100 m), in June 2003 (*C. palmata*). Additional information, especially for derelomines on *C. palmata* throughout northern South America, was extracted from the literature (e.g. Anderson & Gómez, 1997; Franz & O'Brien, 2001a, b), specimen label data and various personal communications.

The behaviour of adult derelomine weevils was studied during all phases of the anthesis, under moderate lighting conditions (thus minimizing disturbance; Franz, 2003a). In order to identify and sex the individuals in the field, a 10× hand lens was used in combination

with a 3× headband magnifier. Some of the ‘external’ staminate flowers had to be removed with forceps to observe the oviposition by females into the ‘internal’ pistillate flowers. Using a Sony CCD-FX 230 camcorder, approximately 2 h of the behaviour of *G. undulatus* Franz & O’Brien, *P. carludovicae* (Günther) and *P. sulcatae* Franz & O’Brien were recorded on video during observations on *C. sulcata* at La Selva, and analysed frame by frame in the laboratory.

The abundance of adults on the inflorescences of *Carludovica* was sampled by detaching entire inflorescences, collecting them into zip-loc bags and transferring the individuals into ethanol at 95%. The abundance of larvae, pupae and recently emerged adults of *Perelleschus* and *Systemotelus* was sampled by dissecting the infructescences of *Carludovica* during various stages of maturation.

Selective morphological analyses were conducted on specimens in the laboratory. Specifically, length-to-width relations were measured for the abdomens of females of *Systemotelus* and for the tepals of the pistillate flowers of *Carludovica*, using a digital micrometer (Lasico XD) on a dissecting microscope (Wild M5A) at a magnification of 25–50×. The drawings of external morphology were prepared under similar conditions and edited with an illustration software program. Finally, the derelomine habitus pictures were taken with the Macroptics photographic system at the Department of Entomology, American Museum of Natural History.

RESULTS

PHYLOGENY OF *CARLUDOVICA* AND DERELOMINES

The character matrix for the species of *Carludovica* comprised eight taxa (including four outgroups) and 23 characters, the majority of which have been proposed by Eriksson (1994b). The codings and descriptions are represented in Table 1 and Appendix 1,

Table 1. Character matrix for the cladistic analysis of the species of *Carludovica* with selected outgroup taxa. Inapplicable characters are denoted with ‘-’ (see Appendix 1 for details)

Taxon/character	5	10	15	20	
<i>Cyc. bipartitus</i>	00000	0000-	-----	-0000	000
<i>Dic. wedelii</i>	10011	01000	00-10	01000	000
<i>Asp. uncinata</i>	10010	01000	00-01	01110	111
<i>Evo. funifer</i>	00001	00011	10-00	00110	111
<i>Car. palmata</i>	01101	10111	00-00	01111	100
<i>Car. rotundifolia</i>	01101	10100	11001	01111	100
<i>Car. drudei</i>	01101	10100	11111	01111	100
<i>Car. sulcata</i>	01101	10100	11111	11111	100

respectively. An exhaustive search yielded one most parsimonious cladogram, with L = 33, CI = 69 and RI = 71 (Fig. 3). In accordance with previous studies (Harling, 1958; Hammel & Wilder, 1989; Eriksson, 1994b), the monophyly of *Carludovica* is indicated by various synapomorphic characters, e.g. the four-segmented leaf blades (character 2) and an irregularly splitting infructescence (character 6). Within the genus, the predominantly South American *C. palmata* is sister to the remaining three species, which do not occur south of Panama. The phylogenetic resolution among *C. drudei*, *C. rotundifolia* and *C. sulcata* is based on characters of the inflorescences, especially the morphology of the pistillate flowers (characters 9–16). The presence of basally persistent staminodes is an autapomorphy for *C. sulcata* (character 16).

The character matrix for the species of derelomines comprised 22 taxa (including six outgroups) and 50 characters (Table 2). Most of them have been elaborated in previous studies (Appendix 2). The heuristic search yielded one most parsimonious cladogram, with L = 66, RI = 78 and RI = 92 (Fig. 4). The phylogenetic position of the outgroup taxa reflects both their distributions and interactions with host plants. The placement of *Staminodeus* indicates that derelomines must have colonized the inflorescences of Cyclanthaceae more than once, because neither *Phyllotrox* nor *Cyclanthura* occur on this monocot family (at least not plesiomorphically; Franz, 2003b). According to the cladogram, *Ganglionus*, *Perelleschus* and *Systemotelus* form one clade with the latter genera being sister taxa, although

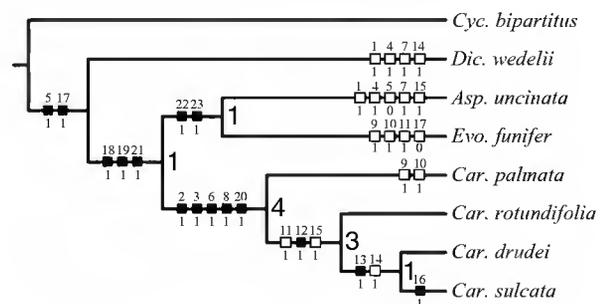


Figure 3. Phylogeny of the species of *Carludovica*, with selected outgroup taxa, according to the most parsimonious cladogram (L = 33, CI = 69, RI = 71). All characters have unambiguous optimizations. The black rectangles indicate non-homoplasious character state transformations whereas the white rectangles indicate homoplasious character state transformations. The numbers above and below each rectangle correspond to the characters and states, respectively (see Appendix 1 and Table 1 for details). Bremer support values are displayed at the right end of each node.

Table 2. Character matrix for the cladistic analysis of the species of *Ganglionus*, *Perelleschus* and *Systemotelus* with selected outgroup taxa. The two multistate characters 32 and 50 were coded as non-additive. Inapplicable characters are denoted with '-' (see Appendix 2 for details)

Taxon/character	5	10	15	20	25	30	35	40	45	50
<i>Der. chamaeropsis</i>	00000	00--0	00000	00-00	00000	00000	0-0--	--000	000-0	0--0-
<i>Ela. subvittatus</i>	00000	00--0	00000	00-00	00000	10001	0-0--	--000	000-0	0--0-
<i>Not. basalis</i>	00000	00--0	10000	00-01	00000	00000	0-0--	--000	000-0	0--0-
<i>Sta. vectoris</i>	00100	00--0	10010	00-01	00100	00000	0-0--	--000	000-0	10-0-
<i>Phy. semirufus</i>	01010	00--0	10110	00-10	10100	00001	0-0--	--000	000-0	0--0-
<i>Cyc. laticola</i>	01011	00--0	10110	00-10	10100	10000	0-0--	--000	000-0	00-0-
<i>Gan. mitigatus</i>	01010	10000	10110	11010	10000	10000	100--	--000	010-0	11000
<i>Gan. catenatus</i>	01010	11010	10110	11010	10000	10000	110--	--000	010-0	11000
<i>Gan. undulatus</i>	01010	11010	10110	11010	10000	10000	110--	--000	010-0	11000
<i>Gan. constrictus</i>	01010	11101	10110	11010	10000	10000	120--	--000	010-0	11000
<i>Gan. spatulatus</i>	01010	11101	10110	11010	10000	10000	120--	--000	010-0	11000
<i>Per. rectirostris</i>	01001	00--0	10110	11110	10100	11001	0-100	0-000	01100	11111
<i>Per. evelynae</i>	01001	00--0	10110	11110	10100	11001	0-110	0-100	01101	11111
<i>Per. variabilis</i>	01001	00--0	10110	11110	10100	11001	0-110	0-100	01101	11111
<i>Per. biventralis</i>	01001	00--0	10110	11110	10100	11001	0-111	10100	01100	11111
<i>Per. splendidus</i>	01001	00--0	10110	11110	10100	11001	0-101	10100	01100	11111
<i>Per. pubicoxae</i>	01001	00--0	10110	11110	10110	11001	0-111	11100	01100	11111
<i>Per. carludovicae</i>	01001	00--0	10110	11110	10110	11001	0-111	11100	01110	11111
<i>Per. sulcatae</i>	01001	00--0	10110	11110	10110	11001	0-101	11100	01110	11111
<i>Sys. costaricensis</i>	11101	00--0	11111	01010	11101	01111	0-0--	--010	100-0	11112
<i>Sys. stockwelli</i>	11101	00--0	11111	01010	11101	01111	0-0--	--010	100-0	11112
<i>Sys. carludovicae</i>	11101	00--0	11111	01010	10101	01001	0-0--	--011	100-0	11112

the support for this result could be better. The monophyly of each of the genera is confirmed as well, with the highest support values for the distinctly modified species of *Systemotelus*. With regard to resolution among species within genera, only the arrangement of the three *Systemotelus* species adds information to previously published results (Anderson & Gómez, 1997; Franz & O'Brien, 2001a,b). Of all 50 characters, eight characters had ambiguous optimizations. In congruence with (what are considered) the most precise statements of homology, characters 5, 16, 20, 34, 42 and 50 are displayed under (ACCTRAN) fast optimization, whereas characters 32 and 47 are displayed under (DELTRAN) slow optimization. One interesting autapomorphy has been included: the centrally narrowed pygidium in females of *S. carludovicae* Anderson & Gómez (character 40).

COEVOLUTION AS CONGRUENCE AMONG TOPOLOGIES

The host plant records for 22 species of derelomines, particularly those associated with the species of *Carludovica*, are listed in Table 3. In particular cases this information might be imprecise, e.g. it is not necessarily evident that the adults of *G. undulatus* interact in

similar ways with the different species of *Carludovica* on which they have been collected. It is critical, however, that various independent accounts have confirmed an exclusive association of the species of *Ganglionus*, *Perelleschus* and *Systemotelus* with those of *Carludovica*. This is so in spite of the observation that broader host ranges should be possible – in the sense that the species of *Carludovica* neither occur nor flower in spatiotemporal isolation from additional Cyclanthaceae species. Furthermore, larvae and pupae of more than half of the species of derelomines have been collected on the inflorescences and infructescences of *Carludovica* in the field, predominantly in Costa Rica. The host plant records in South America are not as complete and reliable, yet *C. palmata* is the only member within this genus throughout most of the region (Harling, 1958). Thus, we have to consider the information in Table 3 as the best currently available hypothesis regarding the actual ecological interactions among the species of derelomines and *Carludovica*.

To facilitate the interpretation of the Brooks Parsimony Analyses, the component matrix codings for clades and species of the exclusively *Carludovica*-associated derelomines are displayed in Figure 5. The results of the combined and separate analyses are

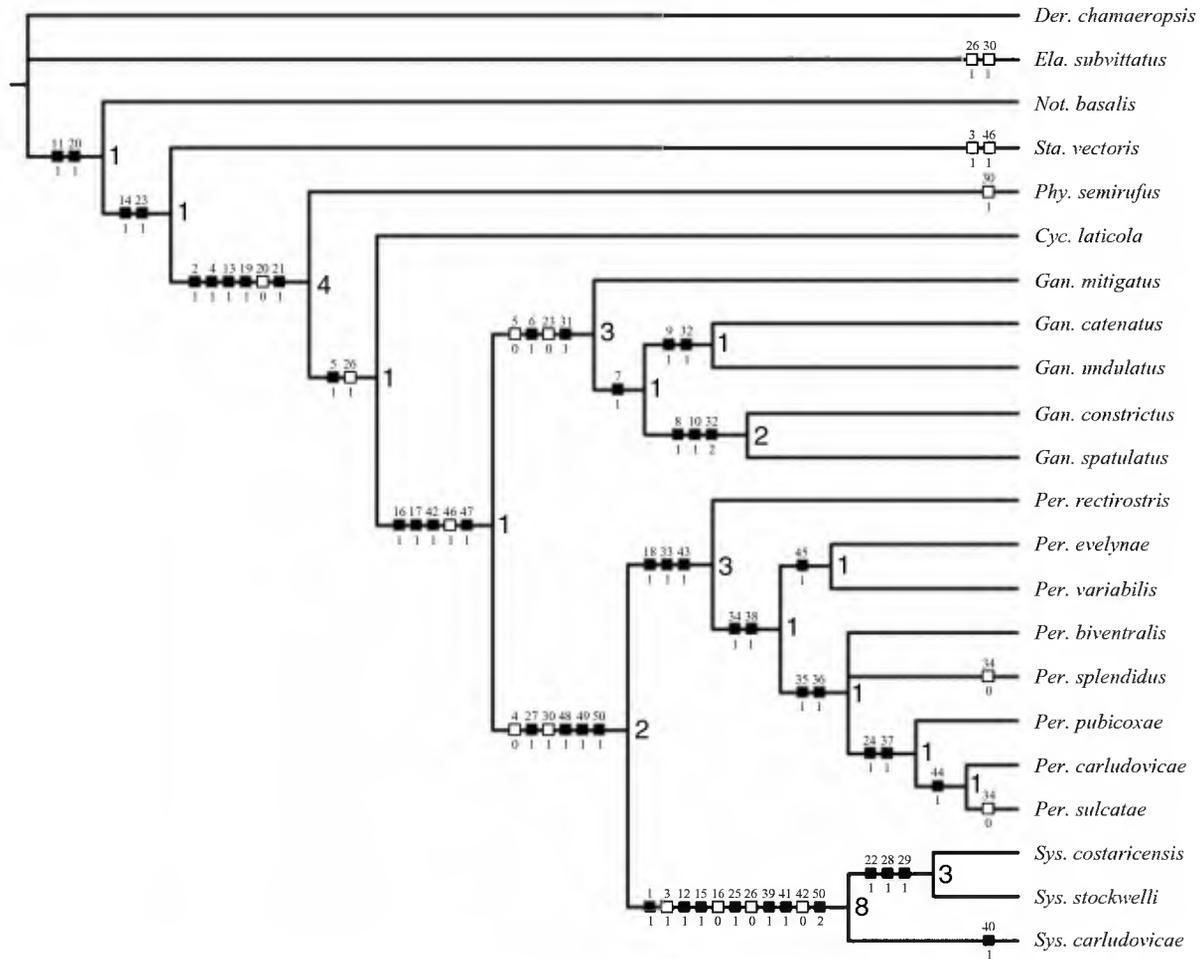


Figure 4. Phylogeny of the species of *Ganglionus*, *Perellesschus*, and *Systemotelus* with selected outgroup taxa, according to the most parsimonious cladogram ($L = 66$, $CI = 78$, $RI = 92$). Characters 5, 16, 20, 34, 42 and 50 are displayed under (ACCTRAN) fast optimization; characters 32 and 47 are displayed under (DELTRAN) slow optimization; and the remaining characters have unambiguous optimizations (see Appendix 2 and Table 2 for details). The denotation of non-/homoplasy, characters, states and Bremer support values is specified in Figure 3.

presented in Figure 6. Although the abundance of 'homoplasy' (colonization and extinction) might be overestimated in the reconstructions (Dowling, 2002), it is important to observe that none of the clades of derelomines (as represented by components 17–31) is congruent with any of the clades within *Carludovica*. In the case of component 23 (*P. evelynae* Franz & O'Brien and *P. variabilis* Franz & O'Brien; Fig. 6B) and component 26 (*G. constrictus* Franz & O'Brien and *G. spatulatus* Franz & O'Brien; Fig. 6B) there must have been (non-reciprocal) independent speciations according to the reconstruction, after an initial (plesiomorphic) colonization of *C. palmata*. However, neither the clade of *C. drudei* and *C. sulcata* nor the more inclusive clade that comprises *C. rotundifolia* can be reconstructed on the basis of the relationships among derelomines (Fig. 6D). As for species, the codings for

G. undulatus (component 3), *P. sulcatae* (component 13) and *S. costaricensis* Anderson & Gómez (component 14) appear to be congruent with the latter (inclusive) clade, yet *P. sulcatae* is absent from *C. drudei* (Fig. 6B) and none of the species of *Systemotelus* occurs on *C. sulcata* (Fig. 6C). Thus, in general, both the combined and the separate Brooks Parsimony Analyses indicate that events of colonization, extinction and spatiotemporally independent speciation have predominated throughout the history of the derelomine–*Carludovica* association. The majority of clades and species of derelomines interact with *Carludovica* at the 'level' of genus, or occur on only one species (Fig. 6D). The hypothesis of coevolution as cospeciation would be rejected in light of such an analysis.

The visual results for the Reconciled Tree Analyses, i.e. the phylogenetic tanglegram of the derelo-

Table 3. Host plant record for 22 species of derelomines, including those in association with the species of *Carludovica*: *Ganglionus*, *Perelleschus* and *Systemotelus*. The presence of “*” indicates that larvae and/or pupae have been collected on the respective species in the field (for details see text)

Derelomine species	Host species (collecting locality)	Reference
<i>Derelomus chamaeropsis</i>	<i>Chamaerops humilis</i> * (Arecaceae; Spain)	Anstett (1999)
<i>Elaeidobius subvittatus</i>	<i>Elaeis guineensis</i> * (Arecaceae; Cameroon)	Syed (1979)
<i>Notolomus basalis</i>	<i>Sabal palmetto</i> * (Arecaceae; USA)	Brown (1976)
<i>Phyllotrox semirufus</i>	<i>Rubus</i> sp. (Rosaceae; Brazil, Venezuela)	Franz (2003b)
<i>Cyclanthura laticola</i>	<i>Anthurium</i> sp. (Araceae; Costa Rica, Mexico, Panama)	Franz (2003b)
<i>Staminodeus vectoris</i>	<i>Asplundia uncinata</i> * (Cyclanthaceae; Costa Rica)	Franz (2003a)
<i>Ganglionus mitigatus</i>	<i>C. rotundifolia</i> * (Costa Rica)	Franz & O’Brien (2001b)
<i>Ganglionus catenatus</i>	<i>C. drudei</i> * (Costa Rica), <i>C. palmata</i> (Costa Rica, Panama)	Franz, 2001 ¹ ; Franz & O’Brien (2001b)
<i>Ganglionus undulatus</i>	<i>C. drudei</i> (Panama), <i>C. rotundifolia</i> * (Costa Rica), <i>C. sulcata</i> * (Costa Rica)	Franz & O’Brien (2001b)
<i>Ganglionus constrictus</i>	<i>C. palmata</i> (Ecuador)	Franz & O’Brien (2001b)
<i>Ganglionus spatulatus</i>	<i>C. palmata</i> (Colombia)	Franz & O’Brien (2001b)
<i>Perelleschus rectirostris</i>	<i>C. palmata</i> (Peru)	Franz & O’Brien (2001a)
<i>Perelleschus evelynae</i>	<i>C. palmata</i> * (Colombia, Panama)	Franz & O’Brien (2001a)
<i>Perelleschus variabilis</i>	<i>C. palmata</i> (Ecuador)	Franz & O’Brien (2001a)
<i>Perelleschus biventralis</i>	<i>C. palmata</i> (Ecuador)	Franz & O’Brien (2001a)
<i>Perelleschus splendidus</i>	<i>C. drudei</i> * (Costa Rica), <i>C. palmata</i> (Costa Rica, Panama)	Franz, 2001 ¹ ; Franz & O’Brien (2001a)
<i>Perelleschus pubicoxae</i>	<i>C. drudei</i> (Panama)	Franz & O’Brien (2001a)
<i>Perelleschus carludovicae</i>	<i>C. palmata</i> * (Costa Rica), <i>C. rotundifolia</i> * (Costa Rica), <i>C. sulcata</i> * (Costa Rica)	Franz, 2001 ¹ ; Franz & O’Brien (2001a)
<i>Perelleschus sulcatae</i>	<i>C. rotundifolia</i> * (Costa Rica), <i>C. sulcata</i> * (Costa Rica)	Franz & O’Brien (2001a)
<i>Systemotelus costaricensis</i>	<i>C. drudei</i> (Panama), <i>C. rotundifolia</i> * (Costa Rica)	Anderson & Gómez (1997); Franz (1999)
<i>Systemotelus stockwelli</i>	<i>C. palmata</i> (Panama)	Anderson & Gómez (1997)
<i>Systemotelus carludovicae</i>	<i>C. drudei</i> * (Costa Rica), <i>C. palmata</i> * (Costa Rica)	Anderson & Gómez (1997)

¹Personal observation.

mine–*Carludovica* association and the algorithmic reconstructions (as generated by TREEMAP), are displayed in Figures 7 and 8, respectively. The numerical equivalents are presented in Table 4. All confirm the previous conclusions. With 11 species of derelomines (out of 16) occurring on *C. palmata* and each genus having species with multiple host associations, there is little congruence among topologies visible in the phylogenetic tanglegram (Fig. 7). The absence of any of the species of *Systemotelus* from *C. sulcata* is the most notable observation. Furthermore, in each of the reconstructions it is impossible to increase the number of cospeciations by proposing events of colonization and extinction. The ‘best’ possible reconstructions with the algorithm do not involve colonizations, but only duplications (Table 4). Consequently, TREEMAP identifies four (non-reciprocal) independent events of speciation within *Ganglionus* (out of four; Fig. 8A) and seven similarly incongruent speciations within *Perelleschus* (out of seven; Fig. 8B). However, in the case of *Systemotelus*

there is one congruent speciation event (out of two), i.e. *S. costaricensis* cospeciating with the clade that comprises *C. rotundifolia* to *C. sulcata*. The immediate sister taxon *S. stockwelli* Anderson & Gómez is (apparently) plesiomorphically associated with *C. palmata* (Fig. 8C). This particular hypothesis of cospeciation is based on the assumption that *S. carludovicae* as well as *S. costaricensis* have become extinct on *C. sulcata*. This is interesting, particularly in light of the absence of congruence among topologies throughout much of the derelomine–*Carludovica* association. Whereas the cospeciation of *S. costaricensis* might be explicable in terms of coevolution, neither the numbers of cospeciations in *Systemotelus* nor those for all derelomine genera differ significantly from what could be expected by randomizing the topologies (Table 4). Again, the hypothesis of coevolution cannot be accepted.

Finally, the results from the Dispersal Vicariance Analyses – displayed in Figure 9 – concur with the previously established conclusions. The reconstruc-

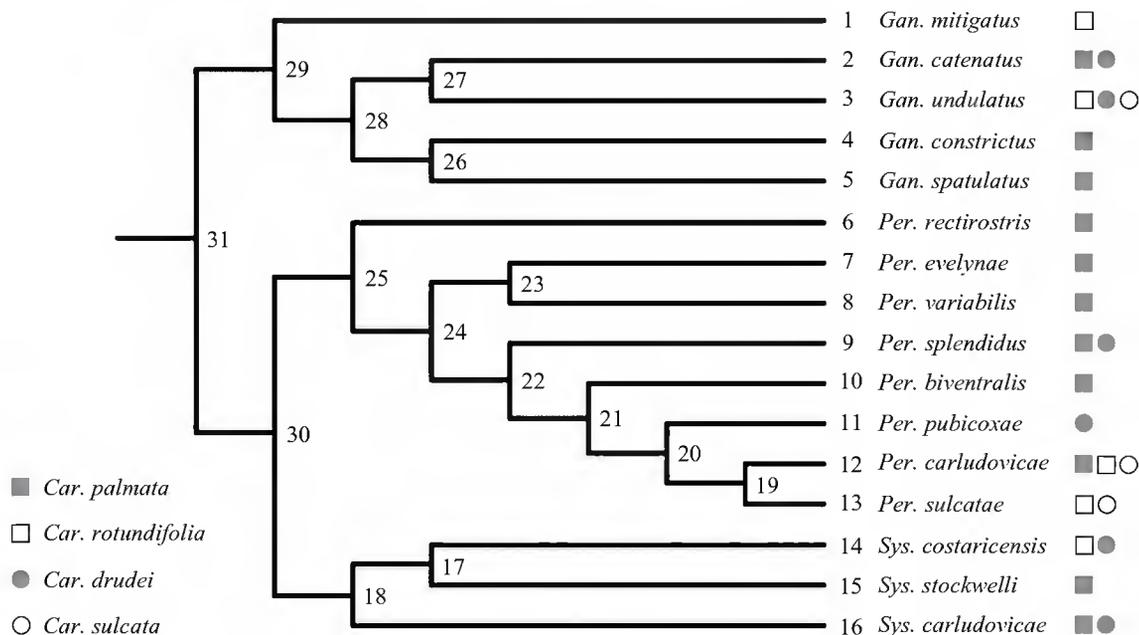


Figure 5. Phylogeny of the species of *Ganglionus*, *Perelleschus* and *Systemotelus* (according to Fig. 4), with component matrix codings of clades (right of node) and species (left of name) for the Brooks Parsimony Analyses. The host plant records are displayed at the right of each species.

tions with DIVA assign 13 events of colonization to the entire derelomine clade, three within *Ganglionus*, six within *Perelleschus* and two within *Systemotelus*. Plesiomorphically, both the clade of all derelomine genera and *Ganglionus* appear to be associated with more than one species of *Carludovica*, whereas *Perelleschus* and *Systemotelus* occur on *C. palmata*, especially throughout the South American region. Because of ambiguity in the optimal reconstructions of historical interactions on the internal nodes of the derelomine phylogeny, it is difficult to specify whether and where cospeciations should be hypothesized (Fig. 9). In addition, the clades with ambiguous host optimizations are those in which colonizations and extinction must be assumed, e.g. in the case of the three *Systemotelus* species. Thus, any kind of coevolutionary hypotheses are either not supported by the reconstructions with DIVA or not sufficiently precise.

It appears that events of colonization, extinction and (non-reciprocal) independent speciation have been abundant throughout the history of the association. Because of this, the proposition of coevolution as cospeciation has little (if any) empirical plausibility, perhaps with the exception of *Systemotelus*. However, unless observations of host plant records are eliminated *ad hoc*, it is impossible to refine this particular hypothesis of coevolution under the topology-based approach.

NATURAL HISTORY OF THE DERELOMINE–*CARLUDOVICA* ASSOCIATION

At this stage the natural history of the derelomine–*Carludovica* association must be examined in more detail, beginning with accounts of the reproductive biology and continuing with the morphological particularities of the interacting species.

Field observations indicate that all species of *Carludovica* have similar floral biologies (Schremmer, 1982; Gottsberger, 1990; Anderson & Gómez, 1997), rendering the subsequent report on *C. sulcata* (Fig. 1) representative of the genus (but see below). At La Selva, *C. sulcata* flowers for an extended period of time during the year, from March to October. The intensity of flowering varies, however, because individual plants tend to produce larger numbers of inflorescences under stronger lighting conditions. For each inflorescence the duration of the anthesis is approximately 24 h. As in the majority of Cyclanthaceae (Eriksson, 1994a, b), the inflorescences of *C. sulcata* are protogynous: the pistillate flowers will open before the staminate flowers. Yet they display facultative geitonogamy, i.e. the selfing of flowers within an inflorescence, towards the end of anthesis. Typically, the pistillate phase (♀) begins at 05:20–05:40 h of the first day, lasting 5–24 h ($N = 5$), whereas the staminate phase (♂) begins at 03:20–04:00 h of the second day, lasting 1–3 h ($N = 5$). Thermogenesis – the production

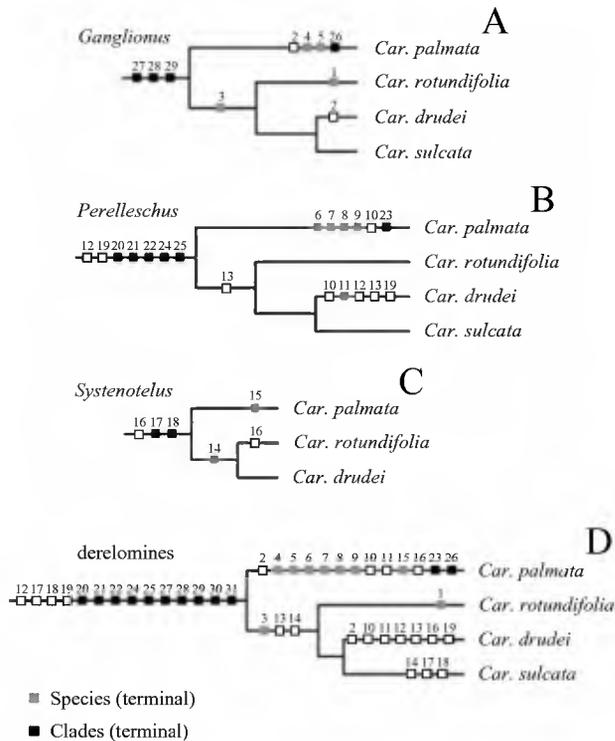


Figure 6. Combined and separate Brooks Parsimony Analyses for the *Carludovica*-associated derelomines (component matrix codings of clades and species according to Fig. 4). The black colour indicates codings for clades, whereas the grey colour indicates codings for species. The codings are displayed under (ACCTRAN) fast optimization: filled rectangles indicate non-homoplasy (i.e. congruence), and empty rectangles indicate homoplasy (i.e. congruence). *Systemotelus* is absent from *C. sulcata* (see text for details). (A) *Ganglionus*. (B) *Perelleschus*. (C) *Systemotelus*. (D) Combined analysis for the entire *Ganglionus*–*Systemotelus* clade.

of heat by the inflorescence – occurs during both phases. It is synchronized (1) with the volatilization of the fragrances that attract the pollinators (pistillate phase; maximum: $3.5 \pm 1.5^\circ\text{C}$ above ambient temperature; time of maximum: 04:30–04:50 h; $N = 3$), and (2) with the release of pollen (staminate phase; maximum: $8.2 \pm 3.4^\circ\text{C}$ above ambient temperature; time of maximum: 03:30–04:40 h; $N = 3$). The intensity of the volatilization appears to be correlated with that of the thermogenesis (as measured in the centre of the spadix; Franz, 1999), with the maximum at 05:00–06:00 h. The fragrances are reminiscent of papaya. The inside of the spathes as well as the staminate flowers are white whereas the externally visible staminate flowers are pale yellow. Experiments with three species of derelomines on *A. uncinata* indicate that olfaction facilitates long-distance attraction to

the inflorescences, although vision, thermoreception or pheromones cannot be excluded as an explanation in this context. The staminodes are ephemeral, losing their initial turgescence within a few hours after the first thermogenesis. The staminate flowers decay and detach from the inflorescence within 1 day after the second thermogenesis (Fig. 10A). The duration of the (usually successful) process of maturation is approximately 30–45 days ($N = 35$). An irregularly splitting infructescence is characteristic for *Carludovica*. The sequentially exposed orange–red berries are most likely dispersed by birds.

The adults of ten species of derelomines can be observed on the inflorescences of *C. sulcata*. They arrive in large numbers at 05.20–06.00 h during the pistillate phase (average: 560 ± 360 , range: 130–970; $N = 5$). Of these ten species, five are associated with the staminodes, representing 34–62% of the individuals. With the exception of *S. vectoris*, all of the latter are undescribed but similar to the extent that they are specialized to feed on and oviposit into the staminodes. Because they do not enter the (epistigmatic) reticulate spaces between the staminate flowers, they do not contact the stigmata of the pistillate flowers during the period of receptivity. In the course of the first day of anthesis, virtually all adults of these species fall (with the staminodes) to the ground. This signifies that they are absent from the inflorescences when the pollen is released ($N = 5$). Therefore, none of them functions as a pollinator of *C. sulcata*. Their larvae are detritivorous and develop in the leaf litter without affecting the process of maturation of the infructescences. Although over 60 individuals of *S. vectoris* have been collected on an inflorescence of *C. sulcata*, this species does not oviposit into the respective staminodes. The females display their characteristic behaviour of cutting and transporting staminodes in association with the species of *Asplundia* and *Evodianthus* but not on *Carludovica* (Franz, 2003a).

In contrast to the five previous taxa, all *Ganglionus* and *Perelleschus* species are pollinators of *Carludovica*. This is reflected in differences in the behaviour of the adults. According to the observations at La Selva, the individuals of *G. undulatus*, *P. carludovicae* and *P. sulcatae* represent 26–54% of the total of derelomines on the inflorescences of *C. sulcata* ($N = 5$). Typically, the adults of *G. undulatus* (average: 108 ± 80 , range: 15–222) are slightly more abundant than those of *P. sulcatae* (average: 85 ± 45 , range: 40–158), whereas the individuals of *P. carludovicae* are significantly less abundant (average: 28 ± 15 , range: 12–52). After arriving on the staminodes during the pistillate phase, they move towards the centre of the inflorescence and enter the spaces between the staminate flowers (Fig. 10B). In the process, some of the staminodes are detached (i.e. cut with the mandibles)

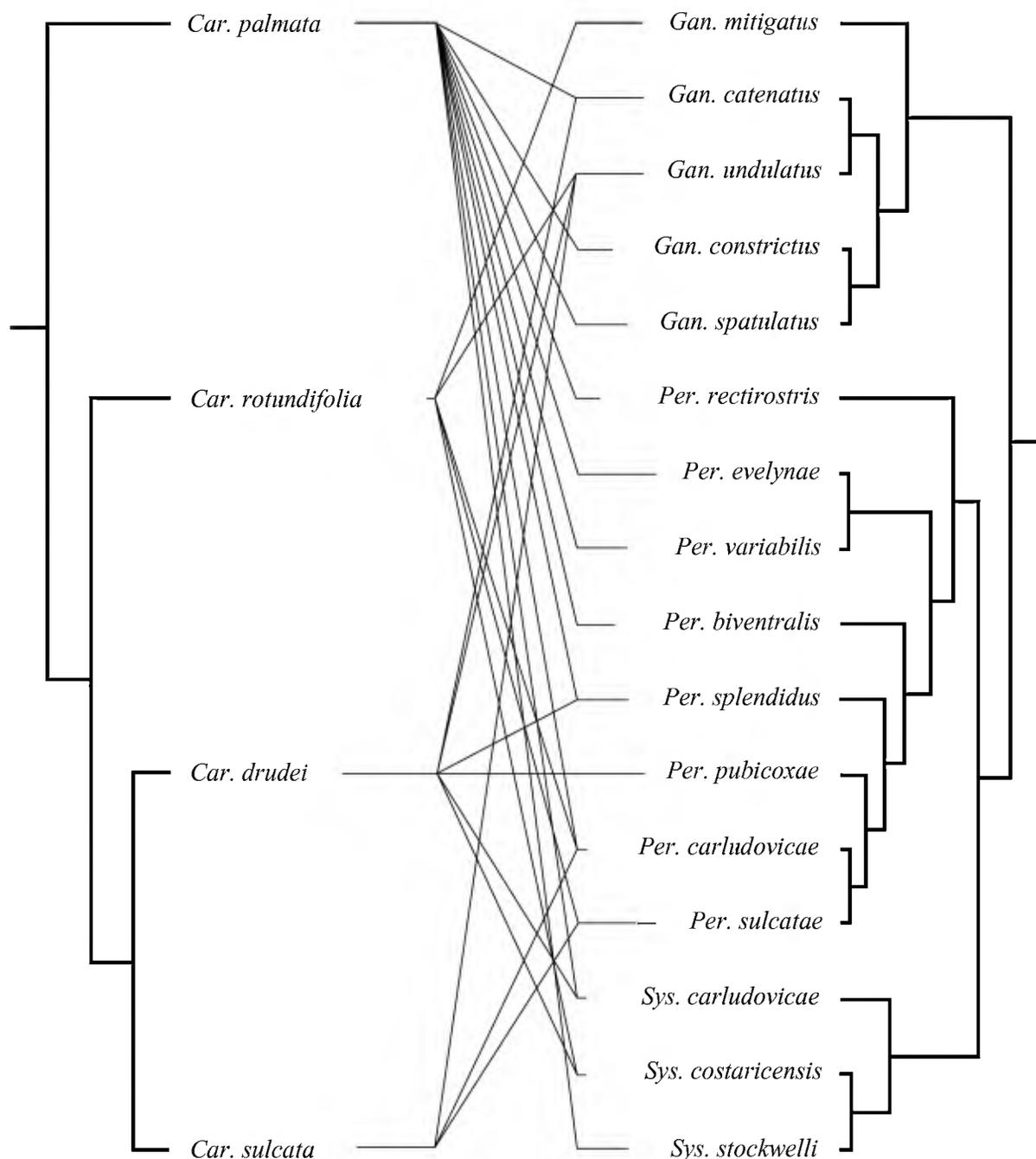


Figure 7. Phylogenetic tanglegram with associations among the species of derelomines and *Carludovica* as generated by TREEMAP.

at various (sub)basal positions. None of the species appears to have adaptations in morphology to function as pollinators, e.g. modifications in sculpture or vestiture. However, the timing of their reproductive biology is remarkably well synchronized with the anthesis of *C. sulcata*. When arriving at the fragrant inflorescences, the majority of individuals are covered on their

entire body with pollen originating from plants with inflorescences that are in their staminate phase. They will then remain on the inside of the inflorescence (i.e. above the stigmata) for the duration of anthesis – until the ‘old’ pollen is transferred and the ‘new’ pollen is released. Presumably, the second thermogenesis increases the efficiency of pollen transfer from

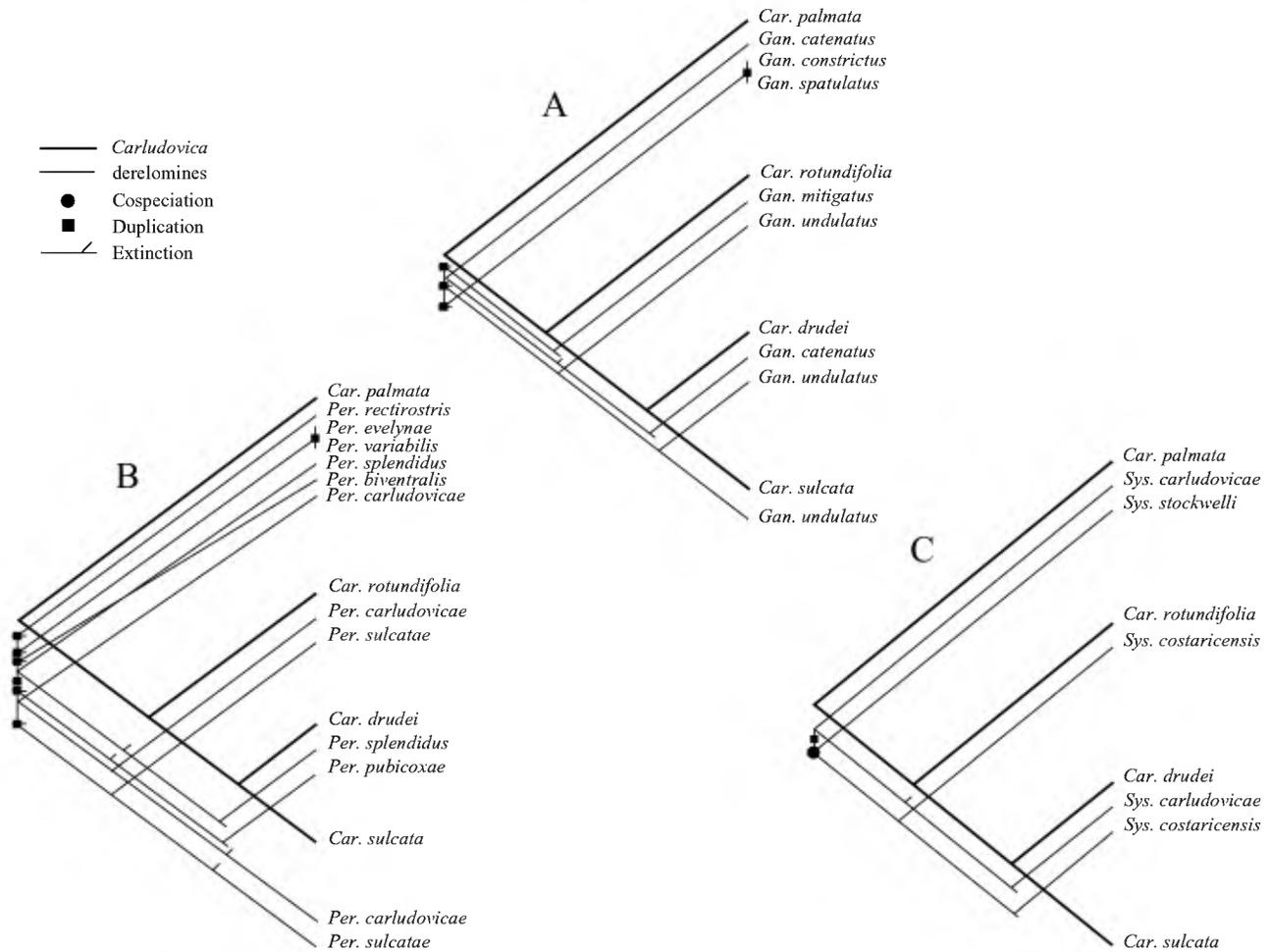


Figure 8. Reconstructions of events of (co)speciation, extinction and colonization (here not proposed) among the genera and species of derelomines and *Carludovica*, according to TREEMAP (see Tables 3 and 4 for details). (A) *Ganglionus*. (B) *Perelleschus*. (C) *Systemotelus*, with one cospeciation event.

Table 4. Numerical results for TREEMAP analyses of the derelomine–*Carludovica* association, as presented in Figures 7 and 8. The presence of ‘*’ indicates that the hypothesis of coevolution as cospeciation would be rejected (for details see text)

Association	No. of species ¹	Cospeciations	Duplications ²	Colonizations	Extinctions	Reconstruction	Significance ³
<i>Ganglionus</i>	5/4	0	4	0	6	No	1.0*
<i>Perelleschus</i>	8/4	0	7	0	11	No	1.0*
<i>Systemotelus</i>	3/4	1	1	0	3	No	1.0*
derelomines	16/4	1	14	0	20	No ⁴	0.8*

¹The numbers refer to the species of derelomines/*Carludovica*, respectively.

²In the language of TREEMAP, duplications correspond to (non-reciprocal) independent events of speciation within the insect clade.

³The numerical value, ranging from 0 to 1, equals the probability of generating just as much or more events of cospeciation than present in the reconstruction under the model for randomization (for details see text).

⁴The exact search was terminated after approximately 40 h while testing reconstructions with 14 colonizations.

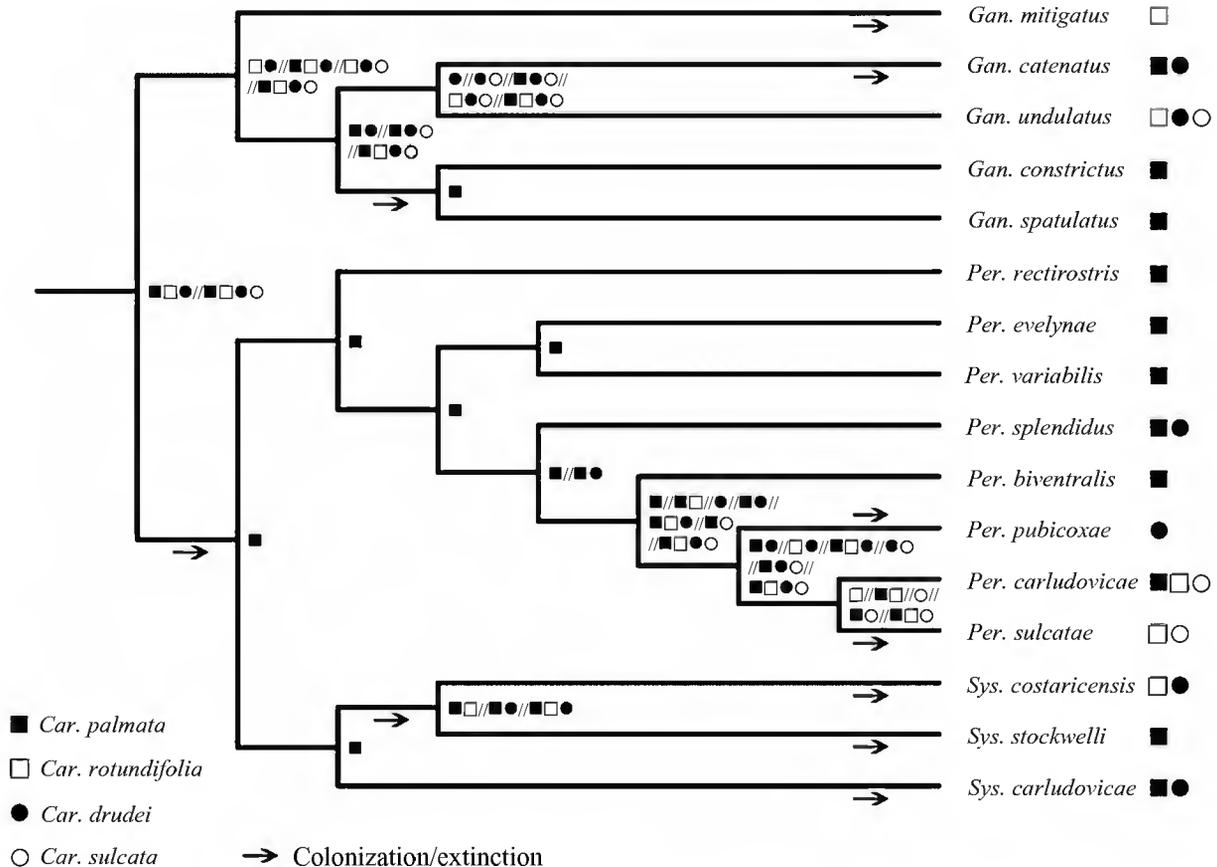


Figure 9. Dispersal Vicariance Analysis of the derelomine–*Carludovica* association. The optimized historical interactions are displayed at the right of each node. Double slash marks (//) indicate multiple optimizations whereas arrows (→) indicate one event of colonization or extinction (minimally).

inflorescence to inflorescence by inducing the individuals to be active and have abundant contacts with the anthers of the staminate flowers before they leave. Little is known about the capabilities of flight in derelomines, although the adults of one pollinating species of *A. uncinata* have been observed to fly distances of over 200 m from plant to plant, carrying an average of 82 ± 85 grains of pollen per individual (range: 10–480; $N = 65$; Franz, 1999). Because the species of *Ganglionus* and *Perellesschus* are specific to *Carludovica*, it can be assumed that they transfer pollen from donor inflorescences to receptor inflorescences with considerable efficiency. After entering the spaces between the staminate flowers, they deposit pollen on to the four-segmented stigmata, which secrete adhesive exudates. Because all behaviours associated with mating and oviposition occur on the inside of the inflorescence, the adults are likely to contact the receptive stigmata with all parts of their body during the following 24 h. Therefore, the timing of arrival and departure as well as activities on the plant facilitate the pollination of the species of *Carludovica*.

Inside the inflorescences of *C. sulcata*, the adults of *G. undulatus*, *P. carludovicae* and *P. sulcatae* feed on floral organs, e.g. the bases of the staminodes, the tepals and the stigmata of the pistillate flowers. In the process, they move between the basally narrowed pedicels of the staminate flowers. They will thus contact many stigmata within an inflorescence. Extensive periods of resting can be observed as well, particularly during the day. In addition, many of the individuals are engaged in activities of mating with the male positioned on top of the female. They can be associated in this way for minutes to hours, occasionally *in copula*, and frequently without displaying behaviours for mating. Nevertheless, the male will normally defend his position with success against competitors by pushing them away with the legs and rostrum. Eventually, the female initiates oviposition by drilling with the rostrum into the floral organs of the inflorescence. She will then rotate to lay an egg and cover the hole with masticated plant tissue. While this occurs the male continues to defend the female against competitors. On many occasions he remains with her until the sub-

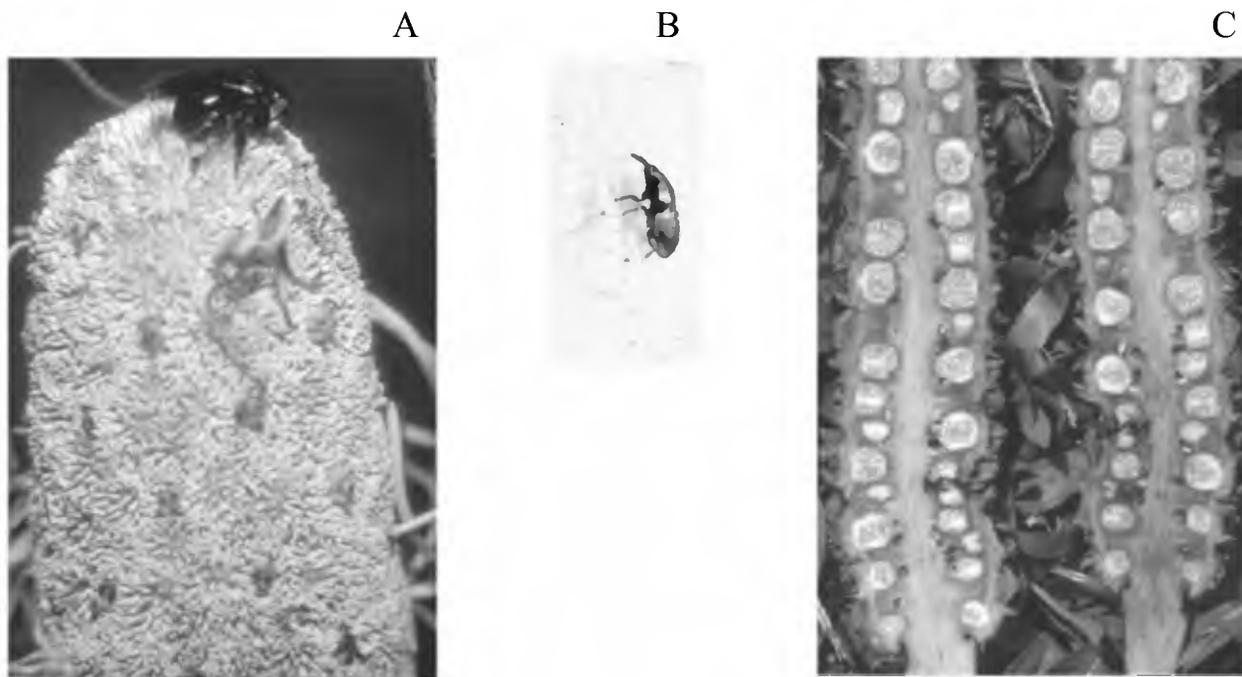


Figure 10. Anthesis, pollination and reproduction of derelomines on *C. sulcata* (see text for details). (A) Inflorescence during the staminate phase with staminodes detached and one meliponine bee collecting the pollen from the anthers. The staminate flowers detach as well in the following 24 h. (B) Male of *G. undulatus* on an inflorescence during the pistillate phase before entering the spaces between the staminate flowers to affect pollination. (C) Dissected infructescence, approximately 3 weeks after anthesis. The staminate flowers have been detached and the berries are filled with seeds. Larvae and pupae of *P. carludovicae* and *P. sulcatae* are present in the pulp, typically on the 'inside' of the berries (i.e. distad of the central axis).

sequent oviposition event. Only few activities of mating or oviposition can be observed at any particular time, yet it appears that they extend for the entire period of anthesis, i.e. as long as the adults are on an inflorescence.

The behaviour of the species of *Ganglionus* and *Perelleschus* differs with respect to the substrate used by the females for oviposition. Specifically, the females of *G. undulatus* oviposit into the basal regions of the staminate flowers of *C. sulcata*. This is where the eggs hatch. Because the staminate flowers detach from the inflorescence during the day after anthesis, the larvae do not complete the final stages of their development inside the infructescence. Instead, they develop and pupate on the ground in decaying plant tissue in the leaf litter. They are detritivorous for the latter parts of this period. Following the stage of pupation, the adults emerge from the surface of the ground after 2–4 weeks. In the case of *P. carludovicae* and *P. sulcatae*, the females oviposit into the peripheral regions of the pistillate flowers: either proximad or distad of the tepals. Less than half of the infructescences of *C. sulcata* appear to be

infested by the immature stages of these species ($N = 20$; range: 10–50 individuals per infructescence). The exclusively herbivorous larvae develop in the pulp located along the central axis and around the globular berries (Fig. 10C). Typically, they will not attack the seeds, which are characterized by sclerotized outer layers. Smaller portions of the seed packages (i.e. 5–25%) might be consumed by larvae hatching in the vicinity of the berries and penetrating them in the process of development. The pupation occurs in the pulp as well, with the adults emerging after 3–7 weeks. As observed by Anderson & Gómez (1997: 895) on *C. palmata*, the majority of them remain inside the pulp as adults until the berries are exposed through the irregular splitting of the mature infructescence. Some of them can evidently drill their way to the outside before the infructescence splits by itself, leaving circular exit holes on its surface. Interestingly, and in contrast to *A. uncinata*, all observed infructescences of *C. sulcata* matured with success ($N = 35$) in spite of the infestation with immature stages of *P. carludovicae* and *P. sulcatae* (Franz, 1999).

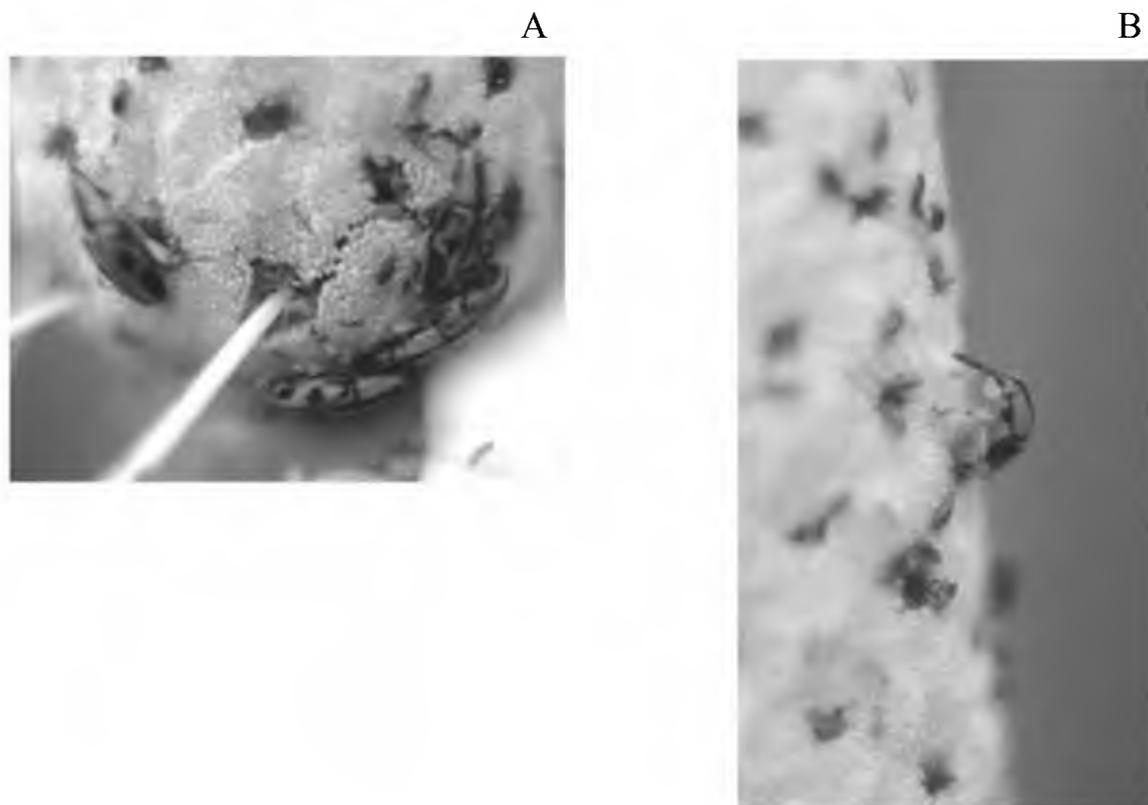


Figure 11. Reproductive behaviour of *S. carludovicae* on an inflorescence of *C. drudei* during the pistillate phase at El Centro Juvenil Tropical. (A) Adults mating and resting near the base of the inflorescence while one female of *G. catenatus* enters the spaces between the pistillate flowers. The apices of the elongate pistillate tepals are visible from the outside. (B) Female ovipositing into the pistillate flower from the outside (see text for details).

In addition to the species mentioned above, the adults of two undescribed species of derelomines visit the inflorescences of *C. sulcata*, representing 10–15% of the total of individuals (average: 65 ± 42 , range: 18–112; $N = 5$). They constitute the primary pollinators of other species of Cyclanthaceae at La Selva, including those of genera like *Asplundia*, *Chorigyne*, *Dicranopygium* and *Evodianthus* (Franz, 1999). Their feeding behaviour is similar to that of *Ganglionus*; however, considering the differences in abundance and specificity they contribute less to pollination. Furthermore, they do not reproduce on the inflorescences of *C. sulcata*. These ecological characteristics render them irrelevant to the subsequent analysis.

Finally, none of the species of *Systemotelus* can be observed on the inflorescences of *C. sulcata*. The following account of *S. costaricensis* on *C. rotundifolia* introduces the reproductive biology of this taxon. At La Selva, an average of 4 ± 3 individuals arrive at the fragrant inflorescences (range: 0–8; $N = 5$). They are twice as large as the adults of the largest pollinating species (i.e. 6–8 mm length vs. 2.5–3.5 mm length in

P. carludovicae). Because of this they are unable to enter the spaces between the staminate flowers and contact the stigmata of the pistillate flowers in the same way as the species mentioned above. Their timing of arrival and departure is also not synchronized with the anthesis of the inflorescence, because all individuals leave during the day before the pollen is released. Therefore, they do not function as pollinators of *Carludovica*. Instead, the adults feed on the surface of the inflorescence (i.e. primarily on the staminate flowers). They tend to rest near the basal pedicel for extended periods of time (Fig. 11A). Few of the individuals can be observed *in copula* with the male positioned on top of the female. Changes among pairs are frequent as the males do not appear to defend the females against competitors as efficiently as those of *Ganglionus* and *Perelleschus*. To initiate oviposition from the outside, the female probes the inside of the inflorescence by inserting her long rostrum between the staminate flowers, staminodes and tepals of the pistillate flowers. Then she drills centrally into the stigmata of the pistillate flowers while

her entire body is positioned at an angle of 60–90° to the surface of the inflorescence. After 1–5 min ($N = 3$) she rotates by 180° to insert the abdomen into the hole. With her head orientated to the outside she will then remain this way for 3–5 min while laying an egg (Fig. 11B). The characteristically elongate abdomen and corresponding genital structures enable her to oviposit deep into the ovary of the pistillate flower. After retracting the abdomen she will immediately abandon the site. Although not documented, additional events of oviposition are likely to occur. In accordance with the observations by Anderson & Gómez (1997: 895), the larvae of *S. costaricensis* develop in the centre of the ovaries of *C. rotundifolia*, consuming the entire package of seeds in the process. Thus, they are herbivorous, exclusive seed predators. Eventually, they pupate in the empty pockets and emerge with the irregular splitting of the mature infructescences. Relatively low abundances of larvae and pupae can be located in each of these (range: 0–50 individuals per infructescence; $N \sim 15$). In spite of the damage inflicted on the seeds and the associated decrease in the reproductive success of *C. rotundifolia*, the infructescences do not appear to abort in response to the infestation by immature stages of *S. costaricensis*.

VARIATION AMONG SPECIES IN BEHAVIOUR AND MORPHOLOGY

As indicated by the phylogenies of insects and plants (Figs 3 and 4), the species vary with respect to characters that are relevant to the analysis of coevolution. In the case of *Carludovica* this variation is related to the morphology of the inflorescences. Specifically, there are transformations in the length and shape of the tepals, in the position of the stigmata of the pistillate flowers and in the shape of the staminate flowers (Fig. 12). The floral morphology of *C. palmata* (Fig. 12A) resembles that of the outgroup taxa – e.g. *A. uncinata* and *E. funifer* – in so far as the tepals are short (i.e. broader than long) and do not project beyond the apices of the elevated stigmata. The apical region of the staminate flowers is broadened, although not distinctly so. Accordingly, once the staminodes are detached from the inflorescence during the pistillate phase of anthesis, the spaces between the apices of the staminate flowers are large. They facilitate the entrance by the pollinating species of *Ganglionus* and *Perelleschus* as well as the oviposition (from the outside) by the species of *Systemotelus*. In *C. rotundifolia* (Fig. 12B) and the two remaining species of *Carludovica*, the tepals are long (i.e. longer than broad) and project above and beyond the apices of the stigmata. The lobes of the four-segmented stigmata are narrow. This reduces the area that can be

accessed from the outside. The stigmata of both *C. drudei* (Fig. 12C) are embedded within the spadix, increasing the distance between them and the surface of the inflorescence. The basal region of the staminate flowers is narrow and the apical region is fairly distinctly broadened. Whereas the latter kind of morphometrical information is difficult to represent cladistically (for discussion see Bookstein, 1994), it is easy to extract from the drawings in Figure 12 and congruent with additional and phylogenetically informative characters (Fig. 3). Finally, in addition to the transformations mentioned above, *C. sulcata* (Fig. 12D) is characterized by basally persistent staminodes: for slightly more than the length of the tepals, the bases of the staminodes are reddish in colour and fibrous in texture (Fig. 13A). They will be detached by derelomines above this section (i.e. in the whitish turgescence region) while the bases remain on the inflorescence throughout the anthesis and for the period of maturation (Fig. 13B). Thus, the staminodes constitute barriers to the inside of the inflorescence of *C. sulcata* by decreasing the space between the apices of the staminate flowers. In order to access the stigmata for oviposition (as well as pollination), the derelomines have to pass the very narrow entrances to the pistillate flowers.

It is possible to quantify the variation in floral morphology among the species of *Carludovica* in various ways, one of which is represented in Figure 14. Here, the length-to-width relations of the tepals of the pistillate flowers are illustrated, ranging from 0.68 in *C. palmata* to 1.44 in *C. sulcata*. Additional variables could be analysed, e.g. the length of the tepals, the length of the stigmata, the relation among the previous two variables, the width of the staminate flowers at the base in relation to the apex, the distance between apices of the stigmata to those of the staminate flowers or the breadth of the entrance between the staminate flowers on the surface of the inflorescence. Because of an apparent correlation among them, such analyses are expected to produce similar results: the pistillate flowers of *C. palmata* are 'easier' to access from the outside than those of *C. sulcata*, with *C. rotundifolia* and *C. drudei* displaying 'intermediate' morphometrical relations.

Coevolutionarily relevant variation is present among the species of derelomines as well. With regard to morphology, there are differences in size and in particular in the shape of the abdomen and corresponding oviposition structures in the females (Fig. 15). With respect to size, the species of *Ganglionus* (1.3–2.3 mm length; Franz & O'Brien, 2001b) are slightly smaller than those of *Perelleschus* (2.0–3.5 mm length; Franz & O'Brien, 2001a) and significantly smaller than the species of *Systemotelus* [4.5–10.5 mm length; Anderson

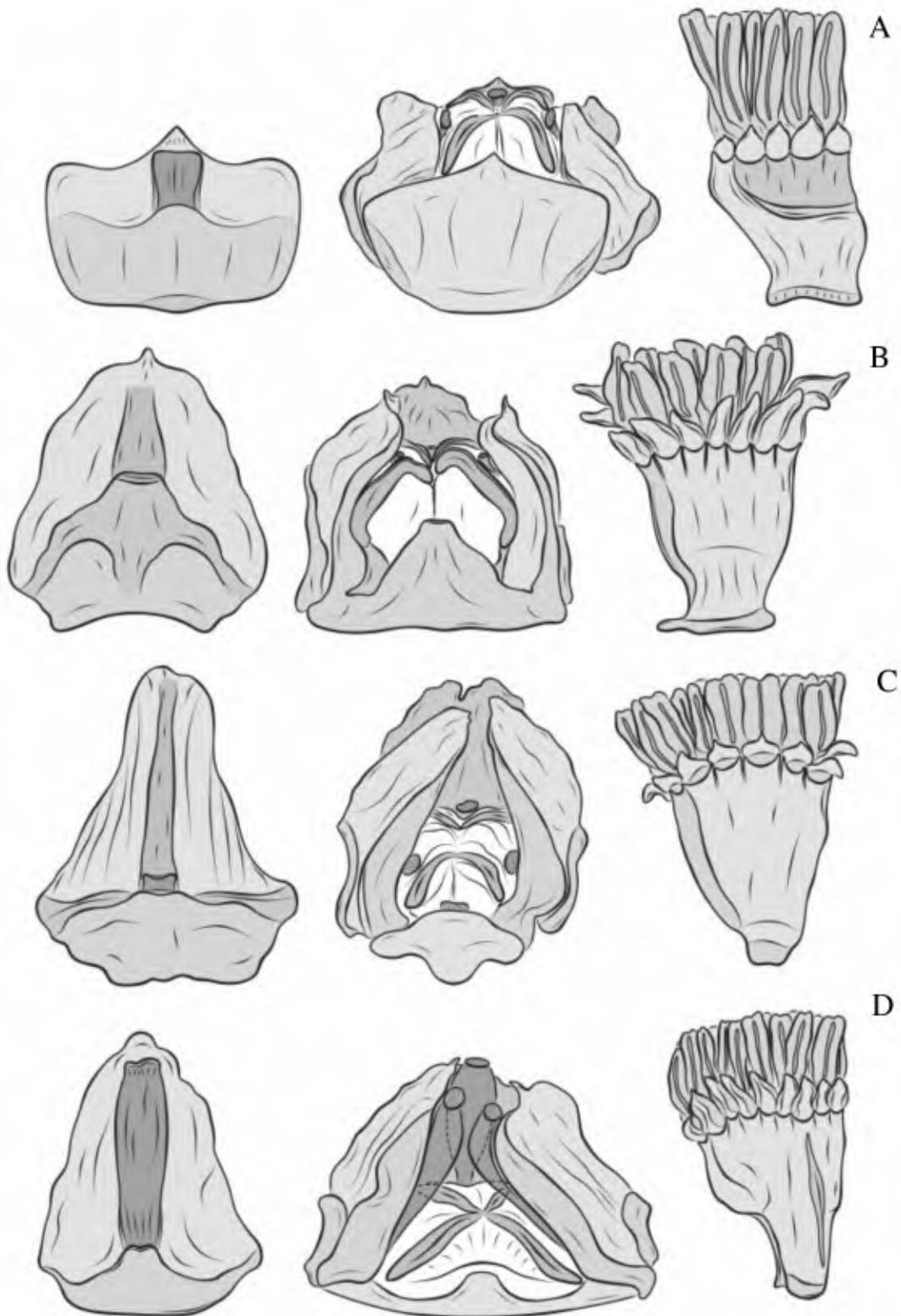


Figure 12. Drawings of pistillate tepals (left; proximad view; with base of staminode), pistillate flowers (centre; viewed at an angle), and staminate flowers (right; lateral view) of the species of *Carludovica*. The stigmata are white whereas the lobes are grey. The anterior pistillate tepal has been removed in (B) to (D). (A) *C. palmata*. (B) *C. rotundifolia*. (C) *C. drudei*. (D) *C. sulcata*, with basally persistent staminodes (see text for details).

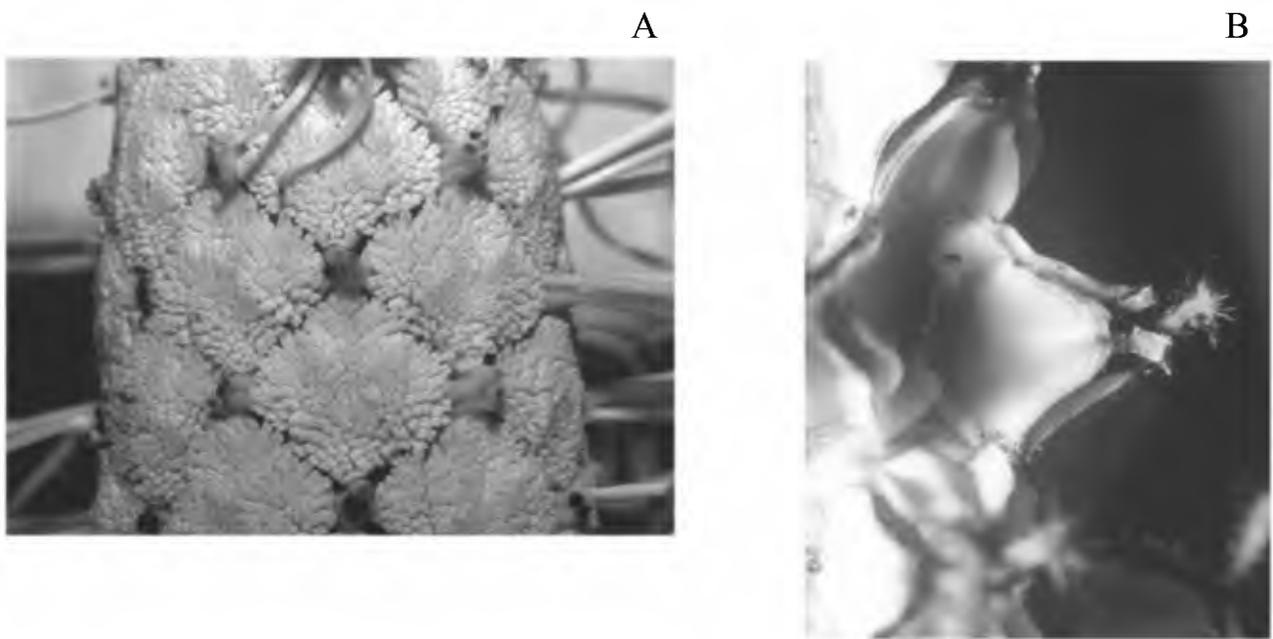


Figure 13. Autapomorphic, basally persistent staminodes in *C. sulcata*. (A) During the pistillate phase, some of the staminodes have been detached above the base, at the end of the fibrous section. (B) Approximately 5 days after anthesis, projecting beyond the apices of the pistillate tepals (staminate flowers have been detached).

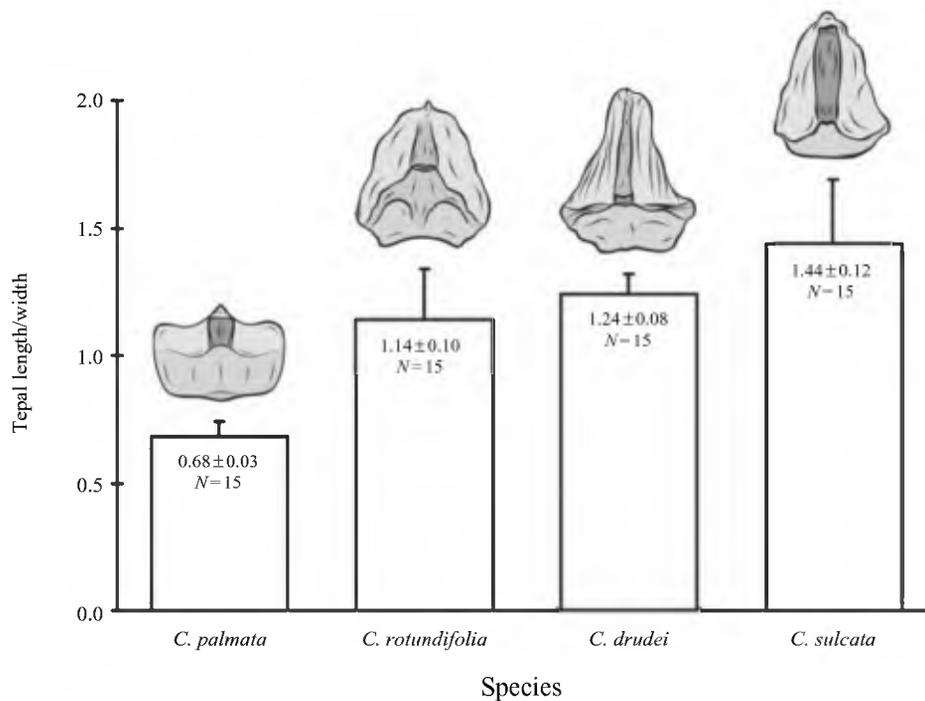


Figure 14. Length-to-width relations of the pistillate tepals of the species of *Carludovica*, arranged in phylogenetic sequence (arithmetic mean ± standard deviation and number of tepals are specified for each column).

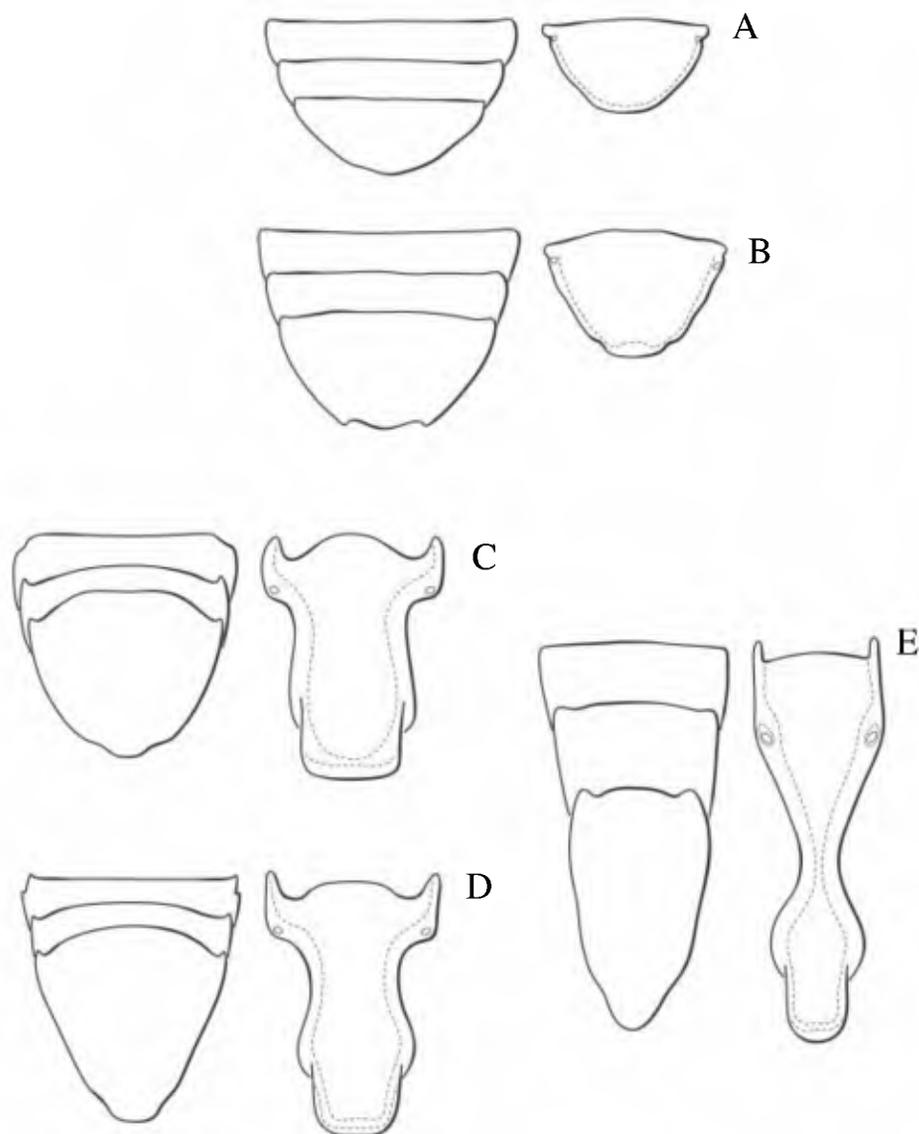


Figure 15. Drawings of ventral segments V to VII (left; ventral view) and pygidium (right; dorsal view) in females of selected species of derelomines. (A) *G. undulatus*. (B) *P. carludovicae*. (C) *S. stockwelli*. (D) *S. costaricensis*. (E) *S. carludovicae*, with centrally narrowed pygidium (see text for details).

& Gómez, 1997 (rostrum not included)]. An extremely large size – at least for derelomines that are associated with Cyclanthaceae – is characteristic for the females of *S. carludovicae* (i.e. 11.0–12.5 mm length, including the rostrum). The differences in the length-to-width relations of the abdomen are just as significant (Fig. 16), ranging from 0.60 in *G. undulatus* to 1.85 in *S. carludovicae*. The drawings in Figure 15 illustrate the extent of transformation in females. In both the species of *Ganglionus* (Fig. 15A) and *Perellesschus* (Fig. 15B), the abdomen, pygidium, venter and associated oviposition structures are equilateral to transverse as would be adequate for oviposition into

plant tissue that can be accessed directly (i.e. with all of the body). However, considerable elongation of these reproductive organs appears to have evolved in the species of *Systemotelus*. In *S. stockwelli* (Fig. 15C), the pygidium is elongate with subparallel lateral margins. The last segment on the venter in *S. costaricensis* (Fig. 15D) is posteriorly triangularly narrowed. Finally, in addition to the increase in size, the pygidium in *S. carludovicae* (Fig. 15E) is significantly more elongate, narrow and constricted near the central region. It facilitates oviposition into plant tissue that cannot be accessed directly. All of the characteristics emphasized in Figure 15 are correlated with

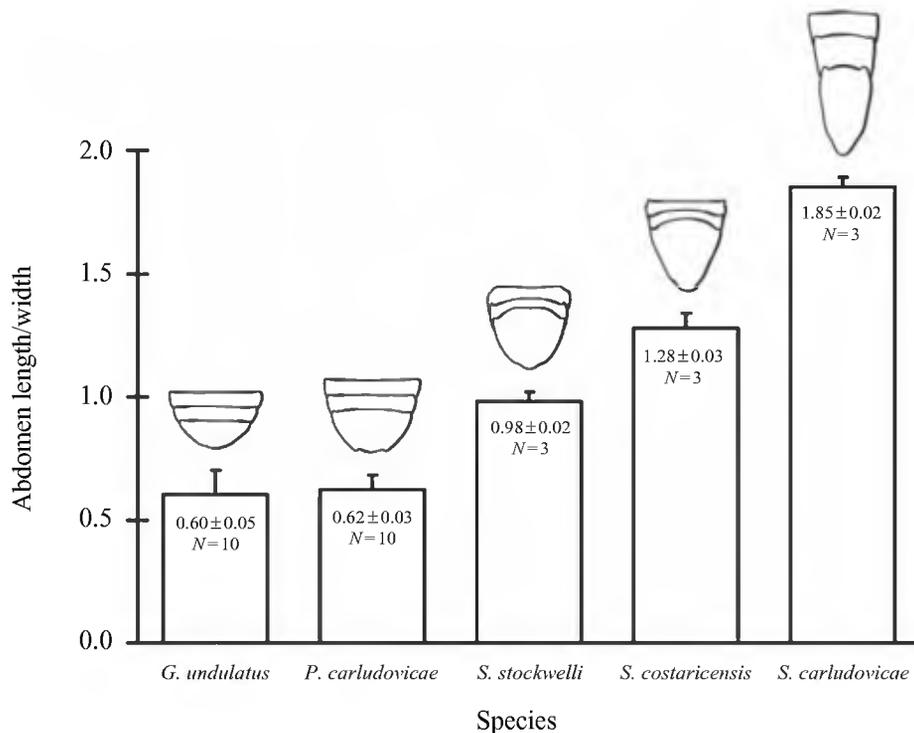


Figure 16. Length-to-width relations of ventral segments V to VII in selected species of derelomines, arranged in phylogenetic sequence (arithmetic mean \pm standard deviation and number of tepals are specified for each column).

additional morphological characters in each of the species. As an example, the abdomen, pygidium and genitalia (e.g. aedeagus, spiculum gastrale and tegmen) of the males are elongate as well. Anderson & Gómez (1997) illustrate the corresponding male structures. In the females, the lengths and widths of the sternum VIII, tergum IX, coxites and bursa copulatrix are similarly increasingly elongate in *S. stockwelli*, *S. costaricensis* and *S. carlundovicae* (Anderson & Gómez, 1997). These specific transformations could be included in the cladistic analysis of derelomines (Fig. 4) without affecting the topology.

The most significant variation in the behaviour of derelomines is displayed in association with the inflorescences of *C. sulcata*. As mentioned above, none of the species of *Systemotelus* can be observed on *C. sulcata* in spite of their occurrence at the same locality. At La Selva, individual plants of *C. rotundifolia* and *C. sulcata* are separated by distances of as little as 100 m yet the locally occurring species *S. costaricensis* visits only the former of the two species. It is plausible to assume that differences in the biochemistry among species – i.e. in the composition of the fragrances – explain this observation (at least in part). Apparently, the adults of *S. costaricensis* are not even attracted to the inflores-

cences of *C. sulcata* whereas they mate and oviposit on those of *C. rotundifolia*. Another interesting situation is reflected in the behaviour of the individuals of *P. carlundovicae* and *P. sulcatae* on *C. sulcata* during the period of arrival. One important difference among the two species of *Perellesschus* is their size. The adults of *P. sulcatae* are slightly smaller than those of *P. carlundovicae* (i.e. 2.0–2.5 mm length and 1.0–1.2 mm width in the former vs. 2.6–3.4 mm length and 1.3–1.6 mm width in the latter; Franz & O'Brien, 2001a). This would be insignificant on the 'easy-to-access' inflorescences of *C. palmata*. In the case of the 'difficult-to-access' inflorescences of *C. sulcata*, however, the larger size does not enable the individuals of *P. carlundovicae* to pass the very narrow entrances between the basally fibrous staminodes and the apically broadened staminate flowers to contact the pistillate flowers. Instead, they drill their way through the apical margins of the staminate flowers, leaving entrance holes in the process. It takes them 15–180 min to access the pistillate flowers in this way ($N \sim 25$). It is conceivable that abundant contacts with non-receptive floral organs reduce the pollen load carried and decrease the efficiency of the adults of *P. carlundovicae* as pollinators of *C. sulcata*.

DISCUSSION

COEVOLUTION AS CONGRUENCE AMONG CHARACTERS

We can now reconcile the information from the phylogenetic hypotheses, field observations and morphological analyses of the derelomine–*Carludovica* association in an attempt to answer the question of coevolution under the character-based approach (Fig. 17). According to the criterion of parsimony, at some time in the past the ancestor of the clade which comprises the species of *Ganglionus*, *Perelleschus* and *Systemotelus* must have come into association with the ancestor of the species of *Carludovica*. Presumably, the behaviour of the ancestor of derelomines resembled that of most outgroup taxa, e.g. *Cyclanthura* or *Phyllotrox*. This signifies that the adults were pollinators ovipositing into caducous floral organs. The larvae were detritivorous during the final stages of their

development. These characteristics appear to have been preserved in, for example, the undescribed pollinating species of *Asplundia*, *Chorigyne*, *Dicranopygium* and *Evodianthus* at La Selva (Franz, 1999) as well as in the species of *Ganglionus*. It can be assumed that the ability to pollinate is plesiomorphic within the derelomine–*Carludovica* association. With the ‘exception’ of *Cyclanthus*, which is pollinated by scarab beetles (Beach, 1982; but see also Franz, 2003b), all extant species of Cyclanthaceae are pollinated by derelomine flower weevils, and exclusively so (Harling, 1958; Gottsberger, 1990; Eriksson, 1994a, b; Seres & Ramírez, 1995; Franz, 2003b). Because the plants of *Carludovica* will typically reproduce sexually (Harling, 1958), the hypothesis of pollination by derelomines as the ancestral condition is supported by ecological and phylogenetic evidence. The same is true for the characteristic of having detritivorous larvae, as

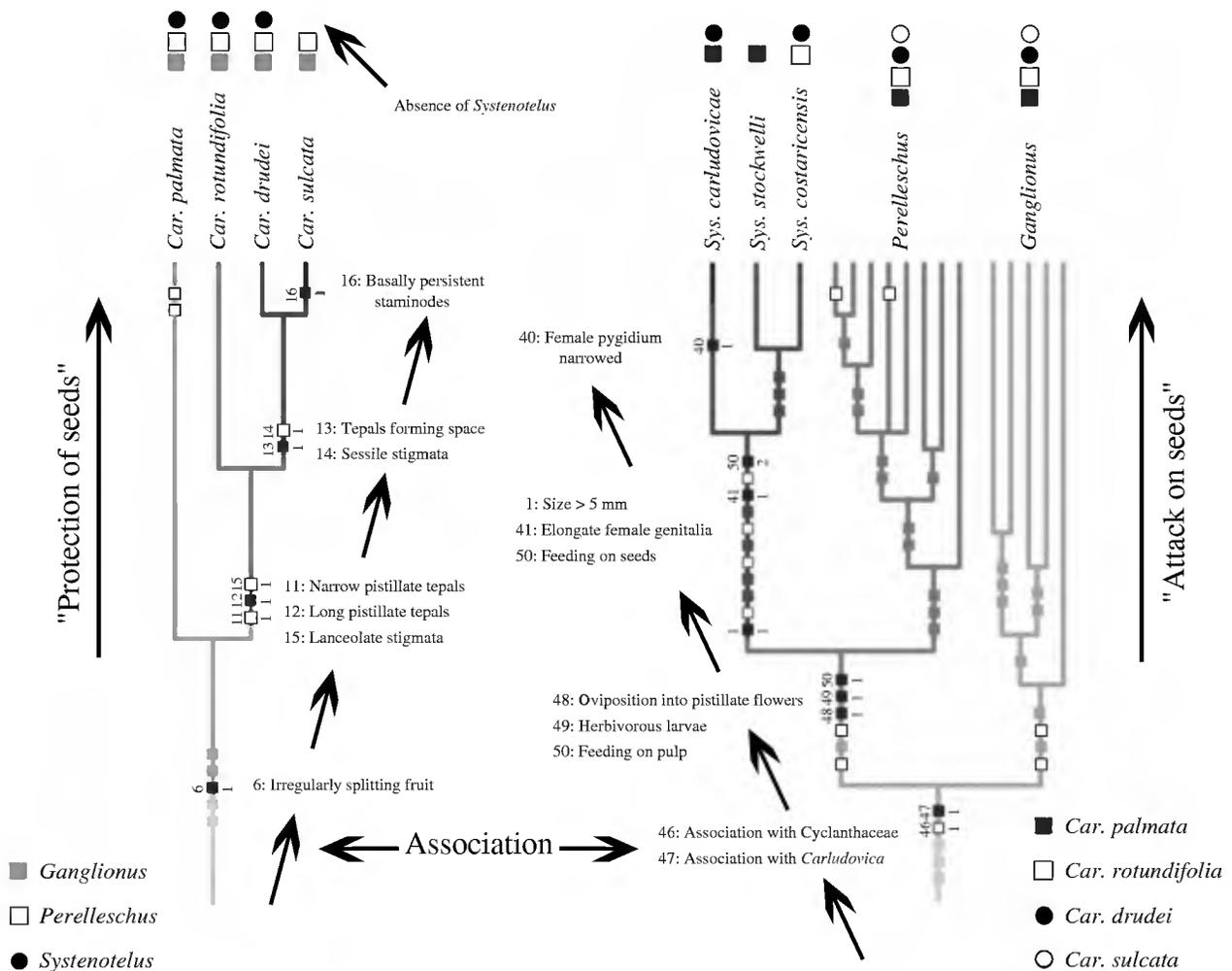


Figure 17. Synthesis of the coevolutionary analysis for the derelomine–*Carludovica* association under the character-based approach (see text for details).

this particular condition is present in the majority of closely related taxa of the *Carludovica*-associated derelomines (e.g. Brown, 1976; Syed, 1979; Henderson, 1986; Eriksson, 1994a; Listabarth, 1996; Anstett, 1999; Franz, 2003b). At an initial stage, then, the interaction was probably largely beneficial for the plants of *Carludovica*.

Analyses under the topology-based approach yield the conclusion that independent events of speciation and colonization have been abundant throughout the history of the association. However, particularly within the clade of *Perelleschus* and *Systemotelus*, there are character state transformations that decrease the benefit and increase the cost of the weevils to the plants in terms of reproductive success. Specifically, the phylogeny indicates the succession from ovipositing into the (caducous) staminate flowers into the (maturing) pistillate flowers of the inflorescences of *Carludovica*, and with it the transition from detritivorous to herbivorous larvae. Within the clade of *Systemotelus* there has been an increase in size that translates into the inability of the adults to function as pollinators. There is thus no benefit for the plants. The oviposition from the outside is facilitated by increasingly elongate abdomens and corresponding genital structures. Finally, the larvae specialize on the predation of seeds. The infestation by them is therefore more costly to the plants, e.g. in comparison with the effect of the larvae of *Ganglionus* or *Perelleschus*. The most extreme case of this succession is represented by *S. carludovicae*. The previously mentioned characters in the derelomines can be interpreted as adaptations to 'attack the seeds' of *Carludovica* (Fig. 17).

The 'attack' by derelomines has occurred on plants evolving transformations as well. In relation to most outgroup taxa the pistillate flowers of the inflorescences of *Carludovica* have become successively more difficult to access from the outside. This has been achieved by the elongation of the pistillate tepals which cover the stigmata, the insertion of the stigmata into the central axis and the expansion of the apical regions of the staminate flowers. Again, *C. sulcata* represents the most extreme case of transformation, with the bases of the staminodes functioning as barriers to the inside of the inflorescences. The adults of *Systemotelus* do not visit *C. sulcata* and those of the larger pollinating species, e.g. *P. carludovicae*, have no immediate access to the pistillate flowers. The evolution of *Carludovica* has been characterized by adaptations to 'protect the seeds' from predation by non-pollinators, apparently in response to selective pressures exerted by the derelomines (Fig. 17).

If one adopts the interpretation of the character state transformations in the species of derelomines (especially within *Systemotelus*) and *Carludovica* as adaptations to attack and protect the seeds, respec-

tively, then the question of coevolution might be answered affirmatively. The association of the ancestors and the congruence of characters within each clade have been established. It is plausible to assume that they function in the ways proposed above. The cladistic analyses indicate that they have evolved gradually and reciprocally, with *C. sulcata* and *S. carludovicae* as the 'most recent transitions' within the longer history of adaptive events. The hypothesis of coevolution as reciprocal (historical) adaptation should be accepted in spite of the absence of congruence among the topologies of insects and plants.

ASSUMPTIONS, LIMITATIONS AND TESTS OF THE CHARACTER-BASED APPROACH

The previous interpretation must be examined critically, for example by assessing how much it depends on the accuracy of the cladistic analyses. The non-monophyly of *Carludovica* would presumably contradict the hypothesis of coevolution by calling into question the exclusiveness (or homology) of the interaction in space and time. To explain the current associations of derelomines, multiple colonizations of *Carludovica* or local extinctions on additional host taxa would be proposed. Some of the adaptations could have evolved independently, e.g. in response to derelomines that are now extinct. Such a scenario implies a reinterpretation of the function of character state transitions within the plants (i.e. as adaptations to different yet unobserved selective pressures). Yet it is also highly unlikely, considering the quality and quantity of characters that support the monophyly of *Carludovica* (Harling, 1958; Hammel, 1986; Hammel & Wilder, 1989; Eriksson, 1994b; Harling *et al.*, 1998). In light of the abundance of incongruence, no possible rearrangement of the relations among the species of *Carludovica* is expected to affect the conclusions from the topology-based analyses. However, if for example the phylogeny were reversed in such a way that the morphology of *C. sulcata* is plesiomorphic whereas that of *C. palmata* is apomorphic, then it would be impossible to relate the character transformations within the plants to those of the insects. To respond to an increasingly costly attack on the seeds by evolving 'easy-to-access' oviposition sites (i.e. pistillate flowers) would be maladaptive. Again, this is unlikely considering the available cladistic evidence. Alternative hypotheses regarding the phylogenetic relationships among *C. rotundifolia*, *C. drudei* and *C. sulcata* have only little effect on the previous conclusions, because the apomorphies of the latter species would remain interpretable as adaptations to protect the seeds.

The situation is significantly more complicated for the derelomines. Each of the genera, and especially *Systemotelus*, is supported by various unreversed syn-

apomorphies. But the monophyly of the clade that comprises *Perellesschus* and *Systemotelus* is based in part on three non-morphological characters (i.e. characters 48, 49 and 50). These are critical to the analysis of coevolution. Even the monophyly of the more inclusive clade that comprises *Ganglionus* (excluding *Cyclanthura* and *Phyllotrox*) is not well supported. As additional new taxa are described from Cyclanthaceae in the Neotropics it could possibly result that neither *Ganglionus* nor *Perellesschus* are most closely related to *Systemotelus*. The actual sister taxon might be associated with another Cyclanthaceae genus, e.g. *Sphaeradenia* (Anderson & Gómez, 1997). There have been multiple colonizations of the inflorescences of *Carludovica* and those species reproducing on the staminodes are related to *Staminodeus* (pers. observ.). Some species such as *Cyclanthura palmata* Franz have been collected on the inflorescences of *C. drudei* and *C. palmata* in Costa Rica, although it is currently not known whether and where they oviposit on them (Franz, 2003b). Regardless, such an interaction appears to be secondary. No other species of *Cyclanthura* have been observed on *Carludovica*. So in conclusion, parsimony indicates that the association of *Ganglionus*, *Perellesschus* and *Perellesschus* with *Carludovica* is homologous (though not 'globally') and precedes any colonizations of other plants. This assumption should be unaffected by additional evidence supporting the monophyly of, for example, (1) *Ganglionus* and *Perellesschus* vs. (2) *Systemotelus* and presently undescribed species of derelomines. The continuity of the interaction is thus not questioned. Within each of the genera, imprecision in phylogeny will be considerably less significant. None of the coevolutionarily critical characters has been transformed among the species of *Ganglionus* and *Perellesschus*, perhaps with the exception of *P. sulcatae*. The characteristics of (the females of) *S. carludovicae* are evidently highly autapomorphic. This interpretation would not differ if future studies indicated that either *S. costaricensis* or *S. stockwelli* are more closely related to the former species.

Another important criticism concerns the inclusion of behavioural and ecological characters (i.e. characters 46–50) in the cladistic analysis of the derelomines. It has been proposed that this kind of character information might be inappropriate for the purpose of reconstructing phylogeny and, in addition, that conclusions from such inclusive analyses are 'circular' or 'biased' in favour of the characters in question. Grandcolas *et al.* (2001; but see also Kluge, 1989) address the majority of these objections, arguing that the primary criterion for using characters is their adequacy for the inference of phylogeny. If one excludes phylogenetically informative characters from an analysis, it precludes them and others from being tested for

congruence. The resulting hypotheses of phylogenetic relationships will be less well supported. As for circularity, it is correct that characters 46–50 affect the topology of the derelomines. When they are excluded the monophyly of the *Ganglionus*–*Systemotelus* clade with respect to *Cyclanthura* and *Phyllotrox* is supported by one out of four most parsimonious cladograms. The polytomy of the consensus neither resolves this clade nor conflicts with the preferred cladogram. The *Perellesschus*–*Systemotelus* clade is monophyletic with or without the information from behavioural and ecological characters. This indicates that their inclusion does not 'bias' the analysis but refines it through additional congruent evidence. Progress in systematics should be considered reciprocal (Hennig, 1966) in the sense that new and old character information is tested against each other for the refinement of both. This process is not viciously circular, so long as the conclusions are capable of differing from the premises. In the present context, this signifies that characters 46–50 had the potential to be optimized as homoplasies if the current evidence from morphology supported this result. Instead, they appear to be congruent homologies and future analyses can be used to test the validity of these (preliminary) conclusions.

With respect to the actual codings of the non-morphological characters there are some critical assumptions as well. The terms used to describe the behavioural and ecological similarities among the species of derelomines are not very precise. 'Association with the inflorescences of *Carludovica*' (character 47) or 'feeding on the pulp of the infructescences of *Carludovica*' are ambiguous homology assessments, even for derelomines. Nevertheless, in either case it is assumed that the descriptions are aligned with discrete, heritable and independent historical events. Additional studies of natural history and expanded cladistic analyses can further increase the congruence and precision of the behavioural and ecological homologies among *Carludovica*-associated derelomines. For now, however, the hypothesis of coevolution among derelomines and *Carludovica* is 'robust' to considerable variation in the associations, numbers of species and topologies of the interactors.

Although parsimony indicates that the ancestral species of the clades of *Ganglionus*–*Systemotelus* and *Carludovica* began to interact in the past, it does not establish how the descendant associations have evolved. Because of abundant colonizations and independent speciations it is impossible to homologize the associations among the 'intermediate' hypothetical ancestors of each clade with more precision. To provide an example, it can be argued that the hypothetical ancestral species of *G. constrictus* and *G. spatulatus* or *P. evelynae* and *P. variabilis* interacted with an

(approximately similar) ancestor of the extant version of *C. palmata* and with no other species of *Carludovica*. Yet such an association cannot be specified for the respective hypothetical ancestor of *S. costaricensis* and *S. stockwelli*. The former species could have evolved many of its extant characteristics before or after having become extinct on (one ancestral representative of) *C. palmata*. The latter species might have interacted with (two historical versions of) *C. rotundifolia* and *C. drudei* with or without evolving specific adaptations to the morphologies of their inflorescences. All analyses under the topology-based approach confirm this same result: there is no unambiguous way to associate the internal nodes of the respective cladograms. It appears that there were multiple historical interactions among the hypothetical ancestors of the extant species of derelomines and *Carludovica*, and the function of each cannot be identified with the information at hand. This is arguably the most significant limitation of the current analysis, and one that might be related to the evolutionary properties of the association.

How can one refine and test the hypothesis of coevolution? First, it is possible to generate additional field observations throughout the range of the included species and to quantify differences in their interactions. Consider the following situation. The association among *S. carludovicae* and *C. palmata* is limited to one particular region where plants of *C. palmata* are interspersed with those of *C. drudei*. The adults of *S. carludovicae* are significantly more abundant on the inflorescences of *C. drudei*, and this is reflected in larger numbers of immature stages in the maturing infructescences. Outside of the region of sympatry, *S. carludovicae* cannot be observed on the former species but only on *C. drudei*. In this particular case it is plausible to assume that the association with *C. palmata* is recent and secondary. One would then propose that some of the adaptations in *S. carludovicae* have evolved in response to an interaction with the clade that includes *C. drudei*. Similar kinds of conclusions could be available for, e.g. *P. carludovicae* and *P. sulcatae*. Second, it is necessary to test the hypothesis of coevolution against biogeographical and palaeontological evidence. The distribution of Cyclanthaceae is Neotropical (Harling, 1958; Eriksson, 1994b; Harling *et al.*, 1998), and although derelomines as a tribe are cosmopolitan (Alonso-Zarazaga & Lyal, 1999) the clade that comprises *Notozonus* to *Systemotelus* is Neotropical as well (with the exception of *Phyllotrox*, which includes North American species). The palaeontological records of each taxon provide only limited information: Harling *et al.* (1998) mention an infructescence that resembles *Cyclanthus* from the Eocene. Considering the age of the presumable sister taxon Pandanaceae (Cox, 1990),

however, Cyclanthaceae might have originated as early as in the Palaeocene (i.e. approximately 60 Mya). Kuschel (1992) assigns *Electrotribus theryi* Hustache from the Oligocene Baltic Amber (i.e. approximately 30 Mya) to the derelomines, noting similarities with the predominantly South American *Celetes* Schoenherr. One can thus posit that the clades of *Ganglionus*–*Systemotelus* and *Carludovica* evolved on the South American continent, probably no earlier than the Middle Miocene (i.e. approximately 15 Mya) because each of them have relatively apical positions within the phylogenies of derelomines and Cyclanthaceae, respectively (Eriksson, 1994b; N. M. Franz, unpubl. data). With this in mind, it appears that the ancestors of the contemporary derelomine–*Carludovica* association have dispersed into Costa Rica and Panama during the formation of the Central American Isthmus, i.e. 3–9 Mya (Stehli & Webb, 1985). The observation that the three ‘recent’ species of *Carludovica* (the *C. rotundifolia*–*C. sulcata* clade) and the species of *Systemotelus* do not occur south of Panama (Harling, 1958; Hammel, 1986; Anderson & Gómez, 1997) is congruent with such a proposition. These species could have coevolved in Central America in as little as 3 million years. Third, molecular studies of the derelomine–*Carludovica* association might be used to infer the age of the clades in question, pending the identification of genes with approximately constant rates of evolution.

Finally, one has to question whether the adaptive functions of the cladistically optimized characters have been preserved from the time of their initial evolution until now. Coddington (1988, 1990, 1994; but see also de Pinna & Salles, 1990) argues that this involves an assessment of the advantage of an apomorphy in terms of reproductive success. First, in the case of *Carludovica* it is proposed that the predation of seeds by the larvae of *Systemotelus* decreases the fitness of the plants. Second, because the adults of *Systemotelus* are unable to access the pistillate flowers of *C. sulcata* and the females of *S. stockwelli* are not sufficiently elongate to oviposit into the inflorescences of *C. rotundifolia* and/or *C. drudei*, the transformations within *Carludovica* are likely to increase the reproductive success by protecting the seeds from predation. But could they have an additional or different function (or none at all)? As an example, stingless meliponine bees have been observed to visit the inflorescences of *Carludovica* for pollen (e.g. Croat, 1978; Schremmer, 1982; Gottsberger, 1990). However, none of the characters that have evolved within *Carludovica* can be related to the predation of pollen, because the anthers of the staminate flowers are equally well exposed on the inflorescences of all species. Furthermore, dissections of hundreds of infructescences of Cyclanthaceae (including those of *Carludovica*) have

not yielded evidence for the presence of herbivores or predators of seeds other than derelomines (Harling, 1958; Schremmer, 1982; Eriksson, 1994a; Anderson & Gómez, 1997; Franz, 1999; pers. observ.). Attine leaf-cutter ants can occasionally come to remove the staminodes before the beginning of anthesis, and rodents or ungulates might even consume entire infructescences. Yet none of the transformations within *Carludovica* can be interpreted as an adaptation in response to these selective pressures. At the same time, the apomorphic morphology of *C. sulcata* indicates that reproductive damage inflicted by the immature stages of *Systemotelus* might be sufficient to render 'difficult-to-pollinate' inflorescences adaptive.

CHARACTERS, COEVOLUTION AND COSPECIATION

In the past, systematists have used a variety of systems of characters and taxa to test the hypothesis of coevolution. There is interest in explaining the diversification of some of the most diverse taxa of herbivorous insects, e.g. Coleoptera (and in particular Polyphaga) or Lepidoptera (e.g. Ehrlich & Raven, 1964; Mitter & Brooks, 1983; Miller, 1987; Farrell & Mitter, 1990; Thompson, 1994). With over 60 000 species presently identified (Kuschel, 1995), weevils qualify as an important clade, although their interactions with plants are not well studied at the level of species (e.g. Anderson, 1993) or at higher taxonomic levels (e.g. Farrell, 1998). Typically, all we have is 'difficult-to-homologize' information on host plant records and larval substrates (Marvaldi *et al.*, 2002). Historical comparative analyses of behaviour, biochemistry, ecology and morphology are exceptional, and do not support the escape-and-radiation hypothesis in all cases (Donaldson, 1992; Schneider *et al.*, 2002).

In this limited context, the present analysis of the derelomine–*Carludovica* association illustrates how the processes of adaptation and speciation occur in response to factors 'inside' and 'outside' of an interaction. In the case of *Systemotelus* the coevolutionarily relevant characters are precisely those that define some of the species of insects and plants. Our best currently available explanation for the causes of the diversification of *Carludovica* in Central America just is constituted by the evolution of *Systemotelus*. As stated by Hammel (1986: 9): '*Carludovica* is the only genus of Cyclanthaceae that is more diverse in Central America than in South America.' At the same time, Harling (1958: 133) comments on the now widely cultivated yet originally South American *C. palmata*: '[b]oth in the vegetation and in the floral characters the variation is greater than in most other species of the family.' Nevertheless, Harling (1958) was unable to separate these different morphologies into species, while confirming the validity of *C. rotundifolia* and *C. drudei* as distinctive Central American species of

Carludovica. The evolution of their particular characters is comprehensible in light of the evolution of the species of *Systemotelus*, and vice versa. Thus it could be argued that *Systemotelus* and *Carludovica* have coadapted and cospeciated – in spite of the incongruence among the topologies of the associated clades. Especially in *C. drudei*, the coevolutionary process appears to continue until the present, because the lengths of the pistillate tepals in this species vary considerably among extant populations (B. E. Hammel, pers. comm.). It would be interesting to correlate this variation with the lengths of the oviposition structures in the females of *S. carludovicae*. In an exclusive (one-to-one) association, such correlation is predicted by the geographical mosaic theory of coevolution (Thompson, 1994). In any event, the *Systemotelus*–*Carludovica* association provides an example in which plausible causes for adaptation and speciation can be identified in the form of character state transformations along the cladograms of each taxon.

The evolutionary homologies within *Ganglionus* and *Perelleschus* are less convincingly explained by the speciation events in *Carludovica*. Particularly in the former genus the differences among species are related to the sculptures of the rostrum and the internal structures of the genitalia. The adults are similar with respect to their reproductive behaviour on the inflorescences of *Carludovica*. At least in the case of *G. constrictus* and *G. spatulatus*, allopatric or sympatric speciation (with dispersal) on (the ancestor of) *C. palmata* is the most parsimonious solution – just as if the host plant species were an area. Reciprocal adaptation cannot be invoked as an alternative. Biogeographical explanations should be preferred for the south-west Costa Rican *G. catenatus* Franz & O'Brien as well (see Franz & O'Brien, 2001b). Although it is possible that the speciation of, for example, *G. mitigatus* Franz & O'Brien has been facilitated by an attraction to the fragrances of *C. rotundifolia*, this hypothesis cannot be tested presently. Morphologically, the species of *Carludovica* do not appear to have evolved adaptations to those of *Ganglionus* in particular (although their respective ancestors evidently must have, at a time when Cyclanthaceae and pollinating derelomine weevils came into association). Similar conclusions apply for most of the species of *Perelleschus*. The northern South American *P. rectirostris* Franz & O'Brien, *P. evelynae*, *P. variabilis* and *P. biventralis* Franz & O'Brien are most significantly differentiated by their reproductive structure and have all 'independently' speciated on *C. palmata* (see Franz & O'Brien, 2001a). The association of the southern Central American *P. splendidus* Franz & O'Brien and *P. pubicoxae* Franz & O'Brien with *C. drudei* has no apparent relation to the morphology of the

host plant species. The most interesting case is *P. sulcatae*, whose small length and width are autapomorphic within the *P. splendidus*–*P. sulcatae* clade. These characteristics facilitate access to the pistillate flowers of the ‘difficult-to-pollinate’ inflorescences of *C. sulcata*. Therefore, the *Systemotelus*-related adaptations in *C. sulcata* might have affected the evolution of *Perelleschus* as well. Although it would be imprecise to refer to this as coadaptation or cospeciation, the example of *P. sulcatae* illustrates that the interaction of the processes of adaptation and speciation can be complex, involving periods of stability and instability among the interactors as well as reciprocal and/or unidirectional selection in response to factors ‘inside’ and ‘outside’ of an association. The evolution of *P. sulcatae* is comprehensible in light of the adaptations by *Systemotelus* to the inflorescences of *Carludovica*; yet it is non-reciprocal and unrelated to the events of speciation in the host plant taxon. The presence of *P. sulcatae* on *C. rotundifolia* could be indicative of an additional incongruent colonization.

IMPLICATIONS FOR HISTORICAL COEVOLUTIONARY ANALYSES

Historical coevolutionary analyses are based on assessing the congruence of the phylogenies of associated taxa (Page, 2003). As the present study indicates, however, tests of the hypothesis of coevolution are incomplete if one is concerned exclusively with the congruence among topologies. Local congruence among character phylogenies might be present in spite of global incongruence among species phylogenies, and even if the phylogenies of characters and species yield similar conclusions, it is important to ask whether the events of speciation in the host (plant) taxon can be related to character state transformations in the parasite (insect) taxon, and vice versa. Biographic and coevolutionary analyses differ in so far as plants – unlike areas of endemism – have the ability to evolve adaptations in response to insects. This is why the approach to develop more significant ways of testing for the congruence among the topologies of hosts and parasites should be combined with phylogenetic tests of the homology and congruence of reciprocal historical adaptations among the interactors.

At a time when molecular phylogenies of insects and plants become increasingly more frequent, behavioural, biochemical, ecological and morphological character analyses are as critical as ever to coevolutionary hypothesis testing. In the case of the derelmine–*Carludovica* association, it will be necessary to assess the validity of the conclusions in light of additional molecular evidence. But such information can

only complement analyses of the homology of adaptations above the molecular level, because it does not constitute the primary kind of evidence for or against the hypothesis of coevolution. Neither molecular observations like ‘ACGT’ nor ecological ones like ‘is associated with’ are adequate for addressing questions regarding the homology of putative adaptations directly. Favouring them over morphological studies would have yielded incorrect conclusions in the present context. Furthermore, by replacing critical analyses of characters with imprecise homology assessments – optimized on an exclusively molecular phylogeny – one abandons (at least in part) the coevolutionary paradigm and corresponding methodology that Darwin (1877; but see also Thompson, 1994) established over 125 years ago.

One final implication concerns the opportunity of reanalysing the evolutionary history of other interactions. As an example, Pellmyr (2002) provides an overview of associations that involve pollinators and plants, discussing the significance of adaptations in the reproductive system, attraction of pollinators (e.g. olfactory or visual), floral recompensation, insect morphology, behavioural specialization, etc. Extreme cases of adaptation and evolutionary stability in interactions among insects and plants have evolved in relation to the phenomenon of active pollination (Pellmyr, 1997). Many associations with some kind of mutual reproductive effect are considerably less stable. Using the approach outlined above, it might be possible to specify the character state transformations within the respective evolutionary interactions with more precision. Locally, the hypothesis by Ehrlich & Raven (1964) could thus receive more support than expected from most of the coevolutionary analyses under the topology-based approach.

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2. Leave blades: (0) with 1–2 segments; (1) with 4 segments (character 22 in Eriksson, 1994b).
 3. Leave blades: (0) acute at apex; (1) dentate at apex (e.g. Harling *et al.*, 1998: 212).
 4. Position of inflorescence: (0) terminal; (1) lateral (character 24 in Eriksson, 1994b).
 5. Insertion of spathes: (0) dispersed along peduncle; (1) clustered along peduncle (character 26 in Eriksson, 1994b).
 6. Splitting of fruiting layer from rachis: (0) regular; (1) irregular (character 30 in Eriksson, 1994b).
 7. Staminate flowers: (0) with perianth lobes absent or present around the entire receptacle; (1) with perianth lobes present on the abaxial side of the receptacle (character 33 in Eriksson, 1994b).
 8. Pollen with aperture: (0) absent or not terminally situated; (1) situated at the end (character 42 in Eriksson, 1994b).
 9. Pistillate flowers: (0) connate; (1) separated (character 44 in Eriksson, 1994b).
 10. Pistillate tepals: (0) separated; (1) connate (e.g. Hammel, 1995).
 11. Pistillate tepals with apex: (0) broad, truncate; (1) narrow, acute (e.g. B. E. Hammel, 1995 unpubl. data).
 12. Pistillate tepals: (0) shorter or as long as stigmata; (1) longer than stigmata (e.g. Harling, 1958: 128).
 13. Pistillate tepals: (0) proximad to stigmata at apex (i.e. forming no internal space in addition to that which is constituted by the staminate flowers); (1) distad from stigmata at apex, forming an internal space above the stigmata (Fig. 12B–12D). Inapplicable in taxa which have the (0) state for character 12.
 14. Shape of stigmata (lateral view): (0) stylate; (1) sessile (e.g. Hammel, 1986: 9).
 15. Shape of stigmata (above view): (0) ovate; (1) lanceolate (e.g. Harling, 1958: 128).
 16. Base of staminodes: (0) filamentous, ephemeral; (1) fibrous, persistent (e.g. Hammel, 1986: 9).
 17. Embryo sac of ovule: (0) with appendage; (1) without appendage (character 47 in Eriksson, 1994b).
 18. Testa: (0) with moderate sculpturing; (1) with minute sculpturing (character 52 in Eriksson, 1994b).
 19. Inner layer of outer integument of ovule: (0) with thick radial cell walls; (1) with thin radial cell walls (character 53 in Eriksson, 1994b).
 20. Inner layer of outer integument of ovule: (0) without papillate cell wall ingrowths; (1) with papillate cell wall ingrowths (character 54 in Eriksson, 1994b).
 21. Inner layer of outer integument of ovule: (0) with thick inner tangential cell walls; (1) with thin inner tangential cell walls (character 55 in Eriksson, 1994b).

APPENDIX 1

Characters and character states used to construct the *Carludovica* data matrix (see Table 1). All characters are binary. Characters 10–16 are inapplicable in *C. bipartitus*.

1. Rhizome: (0) with renewal shoots; (1) without renewal shoots (character 2 in Eriksson, 1994b).

22. Testa: (0) with palisade layer; (1) without palisade layer (character 56 in Eriksson, 1994b).
 23. Seeds: (0) moderately depressed; (1) distinctly depressed (character 59 in Eriksson, 1994b).

APPENDIX 2

Characters and character states used to construct the derelomine data matrix (see Table 2). All characters are binary, with the exception of characters 32 and 50, which were coded as non-additive.

1. Size: (0) (distinctly) smaller than 5.0 mm; (1) (distinctly) greater than 5.0 mm. Variation in size can be difficult to code, and is frequently not informative at more inclusive levels. In this particular case, however, the comparatively large size was considered to be synapomorphic for the species of *Systemotelus* (compare, e.g. with Anderson & Gómez, 1997: 890), and relevant to the interaction with *Carludovica* (for details see text).
2. Maxillary palp: (0) 3-segmented; (1) 2-segmented (character 1 in Franz, 2003b).
3. Labial palp: (0) 3-segmented; (1) 2-segmented (character 2 in Franz, 2003b).
4. Labial palpomere II: (0) indistinct; (1) with distinct apicolateral projection (character 3 in Franz, 2003b).
5. Central region of rostrum in dorsal view: (0) subplane; (1) with shallow elongate impression (e.g. Franz & O'Brien, 2001a).
6. Rostrum in dorsal view in male: (0) glabrate; (1) tuberculate-tumescence (character 1 in Franz & O'Brien, 2001b).
7. Laterodorsal margin of rostrum in male: (0) indistinct; (1) with distinctive tuberculus near basal 2/5 (character 2 in Franz & O'Brien, 2001b).
8. Laterodorsal tuberculus near basal 2/5 of rostrum in male: (0) with dorsal orientation; (1) with lateral orientation (character 3 in Franz & O'Brien, 2001b). Inapplicable in taxa that have the (0) state for character 7.
9. Laterodorsal margin of rostrum in male: (0) indistinct; (1) with row of tuberculi (character 4 in Franz & O'Brien, 2001b). Inapplicable in taxa that have the (0) state for character 7.
10. Rostrum in dorsal view in male: (0) with breadth similar throughout; (1) subbasally distinctly narrowed (character 5 in Franz & O'Brien, 2001b).
11. Pronotum in dorsal view: (0) anteriorly distinctly narrowed, tubulose; (1) anteriorly gradually narrowed. The (0) state is present in many of the South American derelomines.
12. Pronotum (as well as elytron): (0) concolorous; (1) with various black maculations (e.g. Anderson & Gómez, 1997).
13. Prosternum in ventral view: (0) glabrate; (1) with dense short vestiture (character 8 in Franz, 2003b).
14. Procoxal cavities: (0) separated; (1) contiguous (character 9 in Franz, 2003b).
15. Posterior margin of mesosternum: (0) subplane; (1) with distinct, ventrally projected tumescence (e.g. Anderson & Gómez, 1997: 890).
16. Protibia: (0) breadth similar throughout to apically slightly broadened; (1) apically distinctly broadened (character 2 in Franz & O'Brien, 2001a).
17. Apex of protibia: (0) with row of 20–40 narrow setae along both antero- and posteroventral margins; (1) with row of 8–12 broad spines (homologous to setae) along either antero- or posteroventral margin (character 11 in Franz, 2003b).
18. Apex of protibia: (0) with row of spines extending along ventral 2/3 of projected margin; (1) with row of spines extending along entire length of projected margin (character 3 in Franz & O'Brien, 2001a). Inapplicable in taxa that have the (0) state for character 17.
19. Scutellum in dorsal view: (0) pentagonal; (1) triangular (character 6 in Franz & O'Brien, 2001b).
20. Anal lobe of wing: (0) indistinct to small; (1) large.
21. Orientation of pygidium in male: (0) parallel to orientation of tergum; (1) perpendicular to orientation of venter (character 7 in Franz & O'Brien, 2001b).
22. Apices of apical bifurcate region of spiculum gastrale in male: (0) apically gradually narrowed; (1) apically transversely projected, bifurcate (compare, e.g. Figures 8, 21 and 34 in Anderson & Gómez, 1997).
23. Tegmen in male: (0) O-shaped; (1) Y-shaped (character 9 in Franz & O'Brien, 2001b).
24. Anterior tegmental apodeme in male: (0) subrectate; (1) deflexed (character 4 in Franz & O'Brien, 2001a).
25. Male genital complex: (0) not distinctly elongate; (1) very distinctly elongate. This particular character is presumed to represent multiple synapomorphic transformations in the male genital complex of the species of *Systemotelus* (for details see Anderson & Gómez, 1997). More precise specifications are possible, but would not affect the topology of the cladogram.
26. Basal margin of median lobe in male: (0) irregular to subrectate; (1) centrally distinctly emarginate (character 16 in Franz, 2003b).
27. Median lobe in male in dorsal view: (0) laterally (weakly) sclerotized; (1) laterally heavily sclerotized.
28. Lateral margins of median lobe in male in dorsal view: (0) apically gradually narrowed; (1) subbasally (abruptly) narrowed.

29. Lateral margins of median lobe in dorsal view: (0) slightly emarginate to slightly rotundate along apical 1/2; (1) undulate along apical 1/2 (e.g. Anderson & Gómez, 1997: 895).
30. Median lobe in male in lateral view: (0) slightly deflexed; (1) distinctly deflexed (character 5 in Franz & O'Brien, 2001a).
31. Internal sac of median lobe in male: (0) without small, subapical, denticulate, weakly sclerotized sclerite; (1) with small, subapical, denticulate, weakly pigmented sclerite. The (1) state appears to be synapomorphic for the species of *Ganglionus*; however, the internal sclerite is difficult to homologize with structures in other derelomine taxa (including the species of *Perellesschus*).
32. Apex of internal subapical sclerite of median lobe in male: (0) rhomboidal; (1) rectangular; (2) spathulate (character 10 in Franz & O'Brien, 2001b). Coded as non-additive (additive coding does not affect the topology of the cladogram). Inapplicable in taxa that have the (0) state for character 31.
33. Internal sac of median lobe in male: (0) without basicentral, variously structured sclerite(s); (1) with basicentral, variously structured sclerite(s). The (1) state appears to be synapomorphic for the species of *Perellesschus*; however, the internal sclerite is difficult to homologize with structures in other derelomine taxa (including the species of *Ganglionus*).
34. Internal basicentral sclerite(s) of median lobe in male: (0) weakly sclerotized; (1) heavily sclerotized (character 6 in Franz & O'Brien, 2001a). Inapplicable in taxa that have the (0) state for character 33.
35. Internal basicentral sclerite(s) of median lobe in male: (0) nearly 1/2(-2/3) as long as median lobe; (1) distinctly less than 1/2 as long as median lobe. Inapplicable in taxa that have the (0) state for character 33.
36. Internal basicentral sclerite(s) of median lobe in male: (0) positioned near basal region; (1) positioned near central region (character 7 in Franz & O'Brien, 2001a). Inapplicable in taxa that have the (0) state for character 33.
37. Internal central sclerite(s) of median lobe in male: (0) single; (1) paired (character 8 in Franz & O'Brien, 2001a). Inapplicable in taxa that have the (0) states for characters 33 and/or 36.
38. Aedeagal apodemes in male: (0) subbasally slightly broadened; (1) subbasally distinctly broadened (character 9 in Franz & O'Brien, 2001a).
39. Pygidium in female: (0) equilateral to transverse, triangular; (1) elongate, narrow (Fig. 15).
40. Pygidium in female: (0) posteriorly (gradually) narrowed; (1) centrally (distinctly) narrowed (Fig. 15E).
41. Female genital complex: (0) not distinctly elongate; (1) very distinctly elongate (see comments on character 25).
42. Sternum VIII in female: (0) Y-shaped; (1) O-shaped.
43. Basal margin of spermatheca in female: (0) without acute appendix; (1) with acute appendix (character 10 in Franz & O'Brien, 2001a).
44. Orientation of basal acute appendix of spermatheca in female: (0) basal; (1) basilateral. Inapplicable in taxa that have the (0) state for character 43.
45. Apex of spermatheca in female: (0) apically gradually narrowed; (1) apically (abruptly) narrowed, acute (character 11 in Franz & O'Brien, 2001a).
46. Association with the inflorescences of Cyclanthaceae: (0) absent; (1) present (for details see text).
47. Association with the inflorescences of *Carludovica*: (0) absent; (1) present (see details see text). Inapplicable in taxa that have the (0) state for character 46.
48. Oviposition into the inflorescences of *Carludovica*: (0) into staminate flowers; (1) into pistillate flowers (for details see text). Inapplicable in taxa that have the (0) state for character 47.
49. Larval habit: (0) detritivorous; (1) herbivorous (character 31 in Franz, 2003b).
50. Larval developmental substrate on the inflorescences of *Carludovica*: (0) staminate flowers (plant detritus); (1) pulp of the infructescence; (2) seeds of the infructescence (for details see text). Coded as non-additive (additive coding does not affect the topology of the cladogram). Inapplicable in taxa that have the (0) state for character 47.