

Phylogeny of the bee genus *Agapostemon* (Hymenoptera: Halictidae)

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Abstract. A phylogeny for genus *Agapostemon* (Hymenoptera: Halictidae) is reconstructed from morphological characters, using all species, with four representatives of Agapostemonini as outgroup taxa. Parsimony analysis using 150 unordered characters resulted in eighteen equally parsimonious trees, a strict consensus of which is highly resolved for *Agapostemon*. Based on this analysis, *Agapostemonoides* Roberts & Brooks is returned to generic status, and a new subgenus is described: *Notagapostemon*, which includes the *rhopalocerus*, *heterurus*, *atrocaeruleus*, *erebus*, *kohliellus*, *nasutus* and *intermedius* groups of Moure & Hurd. Species groups are proposed for *Notagapostemon* and revised in *A.* (*Agapostemon*). *Agapostemon cockerelli* Crawford is synonymized with *A. obliquus* (Provancher), *A. epichryseus* (Morelos) with *A. leunculus* Vachal, *A. inca* Roberts with *A. heterurus* Cockerell, *A. hispaniolicus* Roberts female with *A. centratus* (Vachal) and *A. hispaniolicus* Roberts male with *A. alayoi* Roberts. Optimization of known behaviours suggests communal ancestry for the genus and infers the prevalence of this behaviour in *Agapostemon*. Optimization of geographical range suggests a Central American or Caribbean origin of *Agapostemon*, with one invasion of North America and multiple invasions of South America and the Caribbean. One invasion of the Caribbean suggests arrival from North America via Florida.

Introduction

Halictidae are often considered an ideal group for studying the evolutionary origin of social behaviour in bees. This family, and in particular subfamily Halictinae, exhibits a wide variety of social behaviours. Solitary, aggregative, communal, parasocial and primitively eusocial (*sensu* Michener, 1974) behaviours all occur among Halictinae (Michener & Lange, 1958; Eickwort & Eickwort, 1969; Roberts, 1969; Michener, 1974, 2000; Eickwort, 1981, 1988; Martins, 1993). Additionally, when considered in the context of phylogeny and classification, the species exhibiting these behaviours are not clustered together. Rather, the distribution is such that several behaviours are frequently found within one group, even within one genus or one population of a species, indicating that in most instances one or more of these behaviours are likely to be relatively recent evolutionary developments (Packer, 1997; Wcislo & Danforth, 1997).

Evolutionary reversals, directly from social to solitary behaviour, have often been inferred from phylogenetic results (reviewed by Packer, 1997; Wcislo & Danforth, 1997; Janjic & Packer, unpublished data). Thus, the assumption of an instinctively logical direction of change (such as from solitary to social) may hinder detection of the phenomenon that has actually occurred. Furthermore, potentially intermediate behaviours, such as communal nesting, are generally not found in the same lineages as eusociality (Packer, 1993). The result is a lack of any clearly evident stepwise pathway from solitary to eusocial behaviour. This is compounded by the suggestion that intermediate series may play no role at all in the evolution of eusociality (Michener, 1985). Thus, the evolutionary positions of potential intermediates, such as communal behaviour, remain uncertain.

As they are distributed among genera within subfamily Halictinae, understanding the fundamental evolutionary patterns of change among the behaviours will require a subfamily level perspective. This approach requires a hypothesis of the behaviour ancestral to each genus, so that evolutionary reversals and innovations within a genus are not mistaken as plesiomorphic. With the ancestral behaviour inferred, the genera can then be viewed as

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terminals in a subfamily phylogeny, onto which behavioural changes can be optimized according to the interrelationships of the genera (Bininda-Emonds *et al.*, 1998).

Just as this perspective requires knowledge of the behaviours at the generic terminals, optimizing these generic terminals themselves requires species-level information and a degree of phylogenetic resolution of the species interrelationships within the genus (Bininda-Emonds *et al.*, 1998). Thus, to draw a general conclusion as to the pattern of behavioural evolution in the subfamily, one needs first to understand the pattern of behavioural evolution within a genus. The necessity of this methodology applies equally to studies of geographical distribution, morphology or any other character for which one wishes to determine a higher-level sequence of change.

The agapostemonine group was first recognized only informally as a group of New World halictine bees distinct from *Halictus*, *Lasioglossum* and *Sphecodes* (Eickwort, 1969a,b). In their discussion of the agapostemonine bees of Mesoamerica, Roberts & Brooks (1987) were unable to find even a single unifying character, and refrained from according the group formal tribal status. The agapostemonines were thus generally recognized as an informal group of New World Halictinae, then consisting of *Agapostemon* Guerin-Méneville, *Agapostemonoides* Roberts & Brooks, *Caenohalictus* Cameron, *Habralictus* Moure, *Paragapostemon* Vachal, *Dinagapostemon* Moure & Hurd (included as a subgenus of *Paragapostemon* by Moure & Hurd, 1987, but assigned generic status by Roberts & Brooks, 1987, a decision followed by Michener, 2000), *Pseudagapostemon* Schrottky, *Rhinotula* Friese and *Ruizantheda* Moure. The two subgenera of the last genus were raised to generic status by Cure (1989), thus adding *Ruizanthedella* Moure to the list. At the same time, Cure also described a new genus, *Oragapostemon*, for *Pseudagapostemon divaricatus* (Vachal). *Oragapostemon* and *Ruizanthedella* have subsequently been synonymized with *Ruizantheda*, which now consists of three species, and *Agapostemonoides* has been reduced to subgeneric status within *Agapostemon* (Michener, 2000).

Despite the unsuccessful attempts of previous authors, M.S. Engel (personal communication) has evidence in favour of, and formally designated (Engel, 2001a), Agapostemonini, consisting of the majority of the above genera. He does not include *Habralictus* in the new tribe, and he places *Caenohalictus* within Caenohalictini Michener. Danforth (2002) has reconstructed a phylogeny for halictid bees based on molecular data, which, although conflicting with Engel (2001a) in tribal resolution, indicates monophyly of Agapostemonini in the sense of Roberts & Brooks (1987). Because Roberts & Brooks (1987) and Michener (2000) both place *Paragapostemon* as sister to *Dinagapostemon*, and Michener even considers synonymizing the genera, these are hypothesized to be the most closely related taxa to *Agapostemon*.

Although Roberts (1972) included forty-three species of *Agapostemon* in his monograph, there have recently been updates to that number, such that there are currently only

forty-one recognized species. R. W. Brooks (personal communication) considers *A. inca* as a junior synonym of *A. heterurus*, whereas A. Pauly (personal communication) considers the female of *A. hispaniolicus* Roberts to belong to *A. centratus*, and indicates that the male described as *A. hispaniolicus* falls within the range of variation of *A. alayoi*. Both putative synonymies were confirmed by the first author and are validated herein.

Most *Agapostemon* species are brilliantly coloured (Fig. 1), making them more commonly collected than many bees of similar size. Nonetheless, few have been studied in the field and behavioural data are generally lacking for the genus, having been studied for only eight of the forty-one species (Table 1). Although the size of this group does not prohibit the eventual study of all species, the application of the phylogenetic approach to the problem will indicate those species for which behavioural data will be most informative, thereby directing future research to the most fruitful path (Packer, 1997). This method, when used with the appropriate selection of outgroups to root the tree, will also permit the optimization of ancestral behavioural traits for *Agapostemon*.

Communal behaviour, the sharing of a nest entrance and tunnels without cooperative provisioning or brood care (*sensu* Michener, 1974), has been reported for *Agapostemon nasutus* (Eickwort & Eickwort, 1969), *A. kohliellus* (Eickwort, 1988), *A. cockerelli* (Eickwort, 1981), *A. virescens* (Abrams & Eickwort, 1980), *A. texanus* (Roberts, 1969; Eickwort, 1981), *A. angelicus* (Eickwort, 1981) and a number of the more distantly and ambiguously related Agapostemonini and Caenohalictini: *Ruizantheda proxima* and *R. mutabilis* (as *Ruizanthedella*) (Michener, 1974), *R. divaricata* (as *P. perzonatus*) (Michener & Lange, 1958) and *Caenohalictus eberhardorum* (Michener *et al.*, 1979). Both *A. sericeus* (as *A. radiatus*, Roberts, 1969; Eickwort, 1981) and *A. splendens* (Roberts, 1969; Eickwort, 1981) are said to be solitary (*sensu* Michener, 1974), with a single adult bee per nest. Either quasisociality or semisociality, has been observed in *P. (Neagapostemon) brasiliensis*, but the data are insufficient to discern a division of labour (Martins, 1993). Thus, the behavioural diversity in this group is relatively broad, with *Agapostemon* containing species exhibiting both communal and solitary behaviour and the tribe as a whole probably presenting new origins of solitary and possibly semi-social behaviour. This makes Agapostemonini valuable for the study of patterns of behavioural evolution, with *Agapostemon* the potential focus for the loss, gain, or both, of the communal habit.

Agapostemon are found only in the New World, ranging coast-to-coast from as far north as British Columbia in Canada to Paraguay, northern Argentina and Chile in the south (Roberts, 1972; personal observation, see Discussion). The other agapostemonine genera are found only in Central and South America, with those most closely related to *Agapostemon* predominantly Central American (Michener, 2000).

In his study of the distribution patterns of West Indian sweat bees, Eickwort (1988), looking only at phenetic relationships,

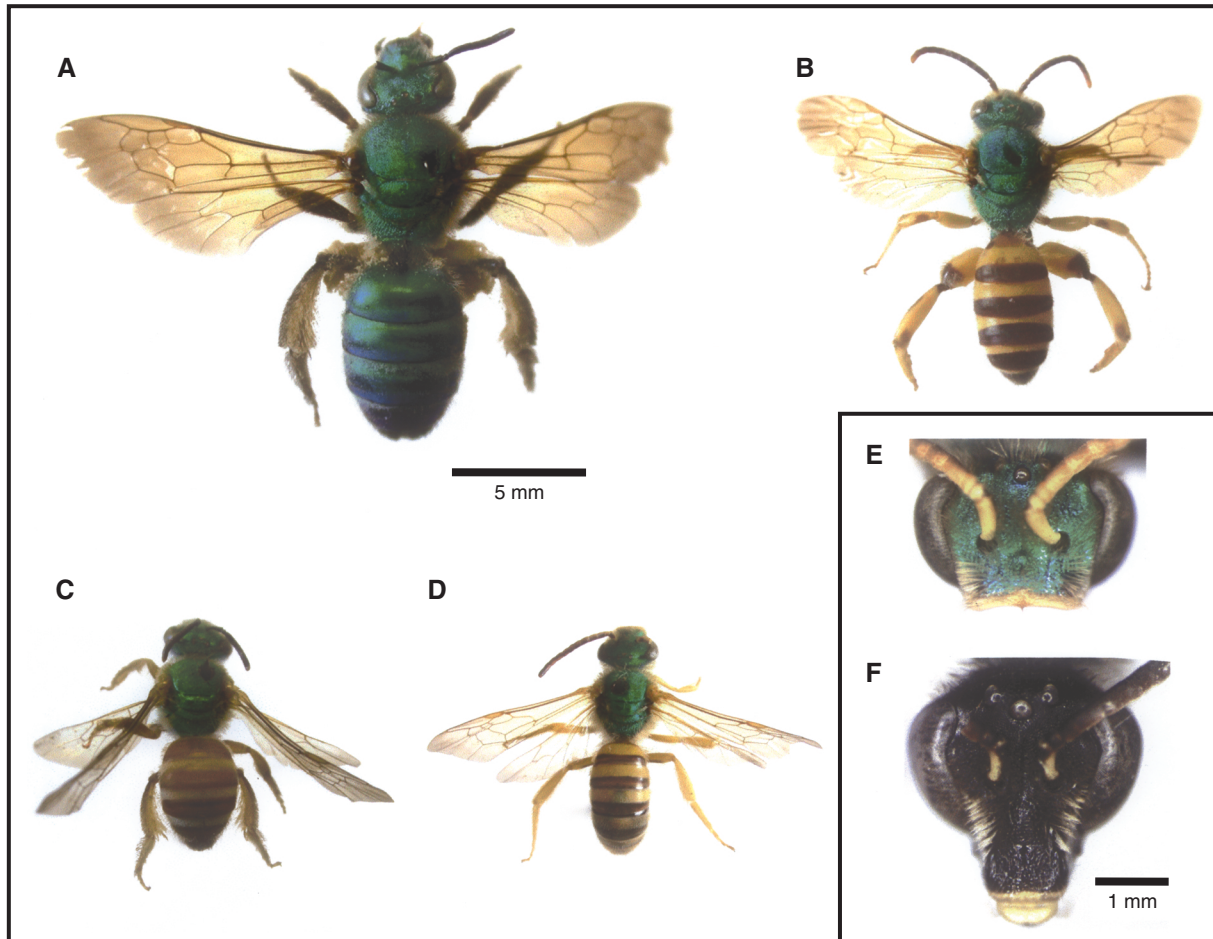


Fig. 1. Whole insect photographs of *Agapostemon*, dorsal views (A–D) and frontal views of heads of males (E,F). A, *Agapostemon splendens* female; B, *A. splendens* male; C, *A. nasutus* female; D, *A. nasutus* male; E, *A. obscuratus*; F, *A. nasutus*. Appendix 1 notes which character states used in the phylogeny are visible in this figure.

Table 1. Agapostemonine taxa and their known behaviour.

Genus	Species studied	Behaviour observed	Reference
<i>Caenohalictus</i> Cameron	<i>C. eberhardorum</i> Michener	Communal	Michener <i>et al.</i> (1979)
<i>Ruizantheda</i> Moure	<i>R. proxima</i> (Spinola)	Communal	L. Packer, personal observation
	<i>R. mutabilis</i> (Spinola)	Communal	Michener (1974)
	<i>R. divaricata</i> (Vachal)	Communal	Michener & Lange (1958); Michener (2000)
<i>Pseudagapostemon</i> Schrottky	<i>P. (N.) brasiliensis</i> Cure	Quasi-/semisociality?	Martins (1993)
<i>Dinagapostemon</i> Moure & Hurd	–	Unknown	N/A
<i>Paragapostemon</i> Vachal	–	Unknown	N/A
<i>Rhinetula</i> Friese	–	Unknown	N/A
<i>Agapostemonoides</i> Roberts & Brooks	–	Unknown	N/A
<i>Agapostemon</i> Guérin-Ménéville	<i>A. nasutus</i> Smith	Communal	Eickwort & Eickwort (1969)
	<i>A. obliquus</i> (Provancher)	Communal	Eickwort (1981)
	<i>A. virescens</i> (Fabricius)	Communal	Abrams & Eickwort (1980)
	<i>A. texanus</i> Cresson	Communal	Roberts (1969); Eickwort (1981)
	<i>A. angelicus</i> Cockerell	Communal	Eickwort (1981)
	<i>A. kohliellus</i> (Vachal)	Communal	Eickwort (1988)
	<i>A. splendens</i> (Lepeletier)	Solitary	Roberts (1969); Eickwort (1981)
	<i>A. sericeus</i> (Forster)	Solitary	Roberts (1969); Eickwort (1981)

proposed a long history for *Agapostemon* species in the Greater Antilles and the Bahamas. He also suggested their origin to have been via Mesoamerica because of the greater phenetic similarity between the Antillean species and those from Central America than between the Antillean species and *A. splendens* in Florida. *Agapostemon splendens* and its immediate relative, *A. texanus*, are the only North American species in Florida, which is the only likely direct bridge between the Caribbean and North America. Eickwort's study, however, did not include a cladistic perspective or inspection of all the species in the genus.

The ranges of the agapostemonine taxa are restricted to the New World and, combined with the large, yet manageable, number of species in *Agapostemon*, this allows for current distributions to be viewed in the light of phylogeny, and the ancestral geographical area for the genus to be inferred, along with likely pathways of dispersal, which do not preclude vicariance events. As more and more 'common-sense' assumptions and hypotheses are being tested and refuted by the application of the phylogenetic method (for examples, see Grandcolas, 1997), it is worthwhile to examine Eickwort's (1988) scenarios in greater detail.

In this paper, the ancestral behaviour and biogeographical history of *Agapostemon* are explored through the construction of a morphology-based phylogeny for species of the genus with the most closely related agapostemonine genera employed as the outgroup.

Materials and methods

Taxon selection

The selection of outgroup taxa was based on a combination of Roberts & Brooks's (1987) listing of genera included in the agapostemonine group, Engel's (2000, 2001a) classification of halictid tribes and Danforth's (2002) generic phylogeny of Halictidae. *Paragapostemon coelestinus* (Westwood), *Dinagapostemon sicheli* (Vachal) and *Rhinotula denticrus* Friese were employed as potential non-*Agapostemon* outgroup taxa. The selection of the first two was based on the aforementioned affinity proposed by Danforth, whereas the latter was included on the basis of characters that link it to *Paragapostemon*, *Dinagapostemon* and *Agapostemon*, particularly modifications of the hind femora and tarsi of males. *Agapostemon (Agapostemonoides) hurdi* (Roberts & Brooks) was included as a potential outgroup taxon because earlier classifications had placed this species in a separate genus (i.e. Roberts & Brooks, 1987), and because its placement in *Agapostemon* had not been based on phylogenetic evidence (Michener, 2000). Our approach was aimed at testing this relationship, without prohibiting or encouraging it.

All species of *Agapostemon*, *sensu* Roberts (1972), and updated to include the aforementioned synonymies of R. W. Brooks and A. Pauly (personal communications, confirmed by the first author), were included in the analysis. Additionally, in an attempt to place the taxa not assigned to species groups by Moure & Hurd (1987) or not dealt with

by Roberts (1972), the type specimens of *A. epichryseus* Cockerell and *A. obliquus* (Provancher) were examined. These are the only unassigned species for which specimens were available.

Agapostemon epichryseus Cockerell keys out to *A. leunculus* Vachal in Roberts's (1972) key. Comparing the morphology of this specimen to other *A. leunculus*, there is nothing to indicate that it is a different species. *Agapostemon epichryseus* is considered here to be a junior synonym of *A. leunculus*, *syn.n.* This specimen, a male, is deposited in the California Academy of Science, San Francisco, California, U.S.A.

Agapostemon obliquus (Provancher), although thought by Moure & Hurd (1987) to be a possible synonym of *A. texanus*, does not have the characteristics of this species, e.g. it does not have punctuation of two sizes on the mesoscutum. Rather, on the basis of geographical locality (mentioned in Moure & Hurd, but not presently labelled on the specimen) and morphology, this species appears in fact to be *A. cockerelli*. However, *Augochlora obliqua* has priority over *A. cockerelli*, and, thus, the latter is considered here to be a junior subjective synonym of *A. obliquus* (Provancher), *syn.n.* The type, a female, is housed in the Collections de l'Université Laval, Laval, Quebec, Canada.

For all species, both males and females were observed, with the exception of *A. ascius*, *A. erebus* and *A. aenigma*, for which males are unknown, and *A. cubensis*, *A. boliviensis*, *A. rhopalocerus* and *A. jamaicensis*, for which females are unknown.

Character selection

Characters were drawn from intense study of all species of *Agapostemon* by the first author, from characters used in ongoing halictine studies (Pesenko & Packer, unpublished data), and from Roberts's (1972) key to *Agapostemon*. One hundred and forty-nine characters were identified from the external morphology of both males and females, and from the hidden internal sterna and genitalia of the male. Missing data in the matrix result most frequently from fragile type specimens for which these parts were broken or obstructed, and where the condition and unique or rare nature of the specimen prohibited relaxation or extraction of particular structures. This is the case for *A. mexicanus*, *A. lanosus*, *A. erebus*, *A. ascius*, *A. inca*, *A. sapphirinus*, *A. ochromops*, *A. aenigma* and *A. cyaneus*. The genitalia and internal sterna are completely unknown for *A. jamaicensis*. The remaining missing data are the result of missing or broken individual parts, either in rare species or in all specimens observed. Characters for which numerous taxa are polymorphic, or for which variation was continuous (such as colour variation on the head and thorax, and the shape of the propodeal carina), were not included in the analysis. The behavioural character (solitary, communal) was included as character 150. The characters are listed in Appendix 1, and the character matrix in Appendix 2.

Of the 150 characters, sixty-four are treated as binary, and eighty-six as multistate. None of the multistate characters were ordered so that no *a priori* transitional restrictions were imposed on the data (Eggleton & Vane-Wright, 1994).

All external characters were observed from dry mounted specimens. To observe labra and genitalia, bees were relaxed for 24–48 h in an airtight container containing a small amount of water. Female labra were removed and cleared briefly in ~5% KOH solution and placed directly into glycerin. Male sterna and genitalia were extracted and placed for up to 18 h in ~5% KOH solution until the non-sclerotized tissue had dissolved and the structures slightly cleared for optimal observation of overlapping and hidden sclerites. These were then rinsed in 5% acetic acid and observed in glycerin.

Phylogenetic analysis

The data were initially entered into WINCLADA (Nixon, 1999a) for ease of import into the ratchet program (Nixon, 1999b) and NONA (Goloboff, 1993), as well as for ease of viewing topologies and character distributions. Because of the number of taxa under analysis, which in this case would yield over 4.5×10^{64} possible unrooted, strictly bifurcating topologies (Swofford & Olsen, 1990), an exhaustive search for the most parsimonious tree could not be performed. We used the *max** command to search for additional trees through branch swapping, and the *unique* and *best* commands to filter out redundant trees, thus retaining only the single (or few) most parsimonious tree (trees). In this method, although character weights are altered to maximize the variation among tree topologies that are sampled, the trees that are retained result from an ultimately unweighted analysis (Nixon, 1999a).

The parsimony ratchet was implemented with 250 iterations and twenty-five characters randomly sampled for re-weighting in each. *Max** in NONA failed to find any more equally parsimonious topologies, and *unique* and *best* filtered out all but the unique most parsimonious unweighted trees. A strict consensus tree was generated from those using WINCLADA. Trees were printed from MACCLADE (Maddison & Maddison, 1992). Decay indices (Bremer, 1994) were calculated for the various nodes in the consensus tree using the commands *bsupport5* and *hold 10000* in NONA.

Tracing behavioural and biogeographical characters

Known behaviours were entered as character states in the matrix. Solitary behaviour is only coded as such for taxa in which it is the only behaviour known, *Agapostemon sericeus* and *A. splendens* (Roberts, 1969; Eickwort, 1981). This removes potential error resulting from the observation of a nest at a non-terminal developmental stage. Taxa exhibiting communal as well as solitary behaviour, are coded as

being communal. The behavioural character is binary, with many unknowns.

Geographic ranges, taken from Roberts (1972), Roberts & Brooks (1987), Michener (2000) and personal observations, were coded and traced as a character in WINCLADA, but were not included as a character in the phylogenetic analysis due to overlapping and extensive ranges in many taxa. After much consideration, the geographical ranges of the taxa were each coded as one of four states and optimized on the consensus tree. The four states are: 'North America', 'Central America', 'South America' and 'Caribbean', the latter including the Bahamas. To avoid any confusion, Central America was taken to extend from southern Mexico to Panama. Taxa that are found in two or more of these areas (e.g. in North and Central America) were coded as the area in which they are most widespread or abundant. Thus, a taxon found widely across North America and only in the northern regions of Central America was coded as being from North America. Likewise, a taxon found in Central America and extending only slightly into North or South America, or both, was coded as Central American. This simplification of the geographical range data allows for a generalized evolutionary perspective, and has been used with this intent in other studies (e.g. Wahlberg & Zimmermann, 2000). Representing the data as more restrictive areas of endemism with a proliferation of states was attempted, but once the states exceeded those used here, autapomorphies and overlap became increasingly common and no biogeographical pattern could be discerned. However, once the general biogeographical trends are shown on the phylogeny, specific ranges can be studied in more detail to infer more precisely the locations of likely dispersal pathways or vicariance events (see Discussion).

Results

The result of *unique* and *best* commands in NONA, operating on the *max** result of the ratchet output file, was eighteen equally most parsimonious trees with a length of 1031 steps, CI = 0.26 and RI = 0.61. The strict consensus of these trees is shown in Fig. 2.

Agapostemon resolves into two major clades: *kohliellus-mourei* and *centratus-ochromops*. These groups are mentioned here to facilitate the presentation of the behavioural and biogeographical results. However, the systematics of the genus are discussed in detail later (see Discussion).

Tracing and optimization of known behaviours (Fig. 3) suggest communal ancestry for *Agapostemon*, but leave much ambiguity within the genus due to the overall lack of behavioural data.

The optimization of geographical range as a four-state character is shown in Fig. 4. With an accelerated transformation, Caribbean ancestry is indicated for both main clades. Delayed transformation indicates Central American ancestry. The delayed transformation optimization is felt to be the more feasible of the two scenarios, for reasons discussed below. This scenario suggests two invasion or

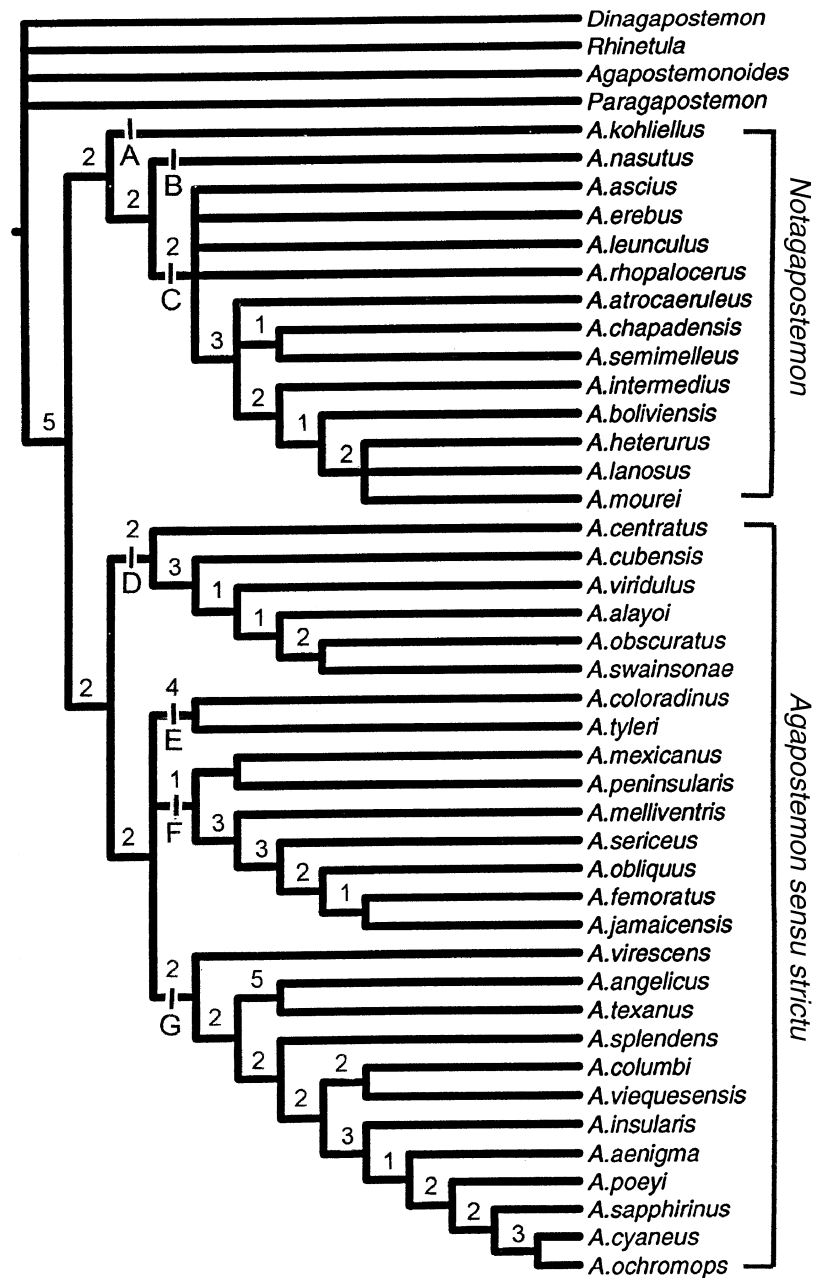


Fig. 2. Consensus of eighteen equally most parsimonious trees for all species of *Agapostemon*. Length of original trees is 1031. Bremer support values are indicated above the nodes. A–C, *Notagapostemon* species groups. A, *kohliellus*; B, *nasutus*; C, *rhopalocerus*. D–G, *Agapostemon sensu strictu* species groups. D, *viridulus*; E, *coloradinus*; F, *sericeus*; G, *splendens*.

vicariant events from Central America to the Caribbean (*A. kohliellus* and the *A. viridulus* group) and one to North America (in the ancestor of the *A. coloradinus-ochromops* clade). It also suggests two dispersal or vicariant events from North America into the Caribbean (*A. jamaicensis* and the *A. columbi-ochromops* clade) and several from Central to South America (in subgenus *Notagapostemon*, the precise number is uncertain because of polytomies in the cladogram).

Discussion

Systematics

The phylogeny generated here (Fig. 2) does not corroborate Michener's (2000) placement of *Agapostemonoides* as a subgenus within *Agapostemon*. Irrespective of which of the possible outgroup genera are used to root the tree, *Agapostemonoides* never resolves as sister taxon to

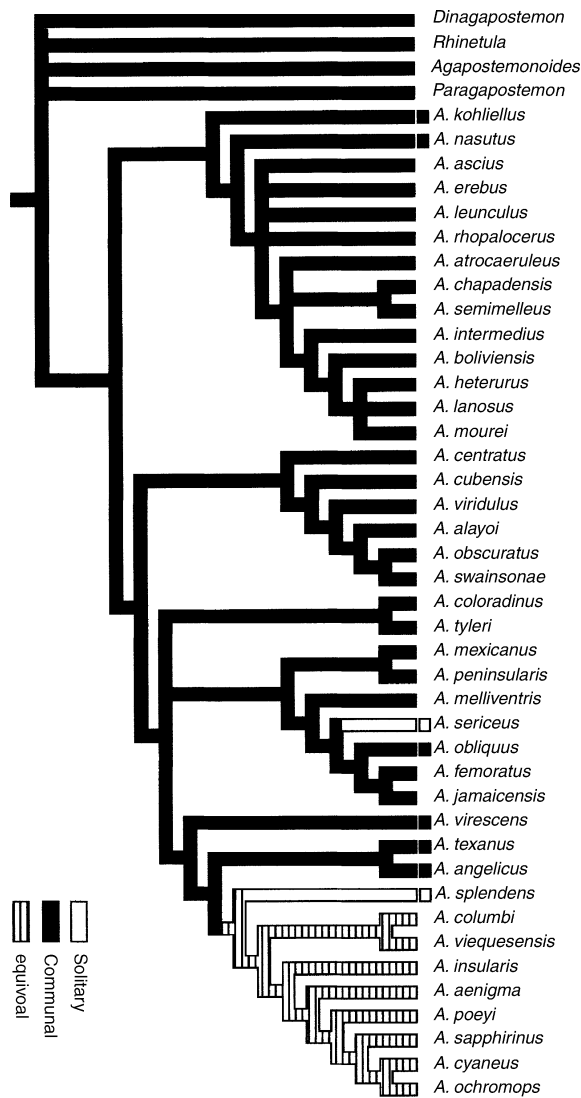


Fig. 3. Known behaviours coded and optimized on the phylogeny presented in Fig. 2.

Agapostemon. It is therefore returned to generic status under the description and diagnosis provided by Roberts & Brooks (1987). As this alters the classification that Michener (2000) used to write his key, the couplet that served to distinguish them as subgenera is now proposed to distinguish *Agapostemonoides* from *Agapostemon* as genera. Thus, his couplet 6 (p. 344) should read:

- 6(5). Posterior surface of propodeum not or only partially enclosed by carina, at least upper transverse part of carina absent 7
 – Posterior surface of propodeum enclosed by strong carina 14

The subgeneric couplet is then moved to a new generic couplet number 14, which distinguishes the two as genera rather than subgenera.

Agapostemon is hereby divided into two subgenera as indicated on the consensus tree by two large and unambiguous sister clades (Fig. 2). The first of these two clades (*centratus-ochromops*) consists of the *splendens*, *sericeus*, *melliventris*, *poeyi*, *viridulus* and *centratus* species groups of Moure & Hurd (1987). This clade is retained as *Agapostemon* (*Agapostemon*). The second consistent *Agapostemon* clade (*kohliellus-mourei*) is composed of the *kohliellus*, *nasutus*, *rhopalocerus*, *heterurus*, *atrocaeruleus*, *erebus* and *intermedius* species groups of Moure & Hurd. This clade is designated below as a new subgenus, *Notagapostemon* subg.n. The species compositions of these clades remain constant throughout the equally most parsimonious topologies. As the species composition of the nominotypical subgenus has changed as a result of this analysis, it is redescribed here.

Subgenus Agapostemon Guérin-Ménéville

Type species. Agapostemon viridulus (Fabricius, 1793) (described as *Apis viridula*), fixed by monotypy.

Diagnosis. There is no single feature that unites the taxa in this subgenus against those in *Notagapostemon*. However, only species of *Agapostemon* have rugose sculpturing on the mesoscutum, yellow markings on the scape of the female and a transverse ridge on S4, long hairs at the apex of the gonocoxite, apical extension of gonostylus without suture, fold or acute angle, and coarse striae laterally on the ventral surface of the gonocoxite in the male. These features are not shared by all members of the subgenus. Both sexes can be distinguished from *Notagapostemon*, as they never have any of the following character states: apically truncate clypeus, a carinate pronotal lateral ridge, anterior upturned scutal flange and woolly hair on the mesoscutum. They also do not have clear striations anteriorly below the pronotal lobe. Each of these characteristics are found in some *Notagapostemon*.

Description. As for the genus (see also Michener, 2000, as subgenus), with the addition of the combination of features mentioned above that is diagnostic. Females always bear a smooth mesothoracic wingbase (*sensu* Engel, 2000), males always have a smooth dorsobasal contour to the gonocoxite and the second stylus originates subapically on the gonostylus. These are consistent throughout but not unique to the subgenus.

Distribution. Species of *A.* (*Agapostemon*) occur from Panama to southern Canada, coast to coast, including the Baja Peninsula of Mexico and Florida. They are also found throughout the Bahamas and Greater Antilles (Roberts, 1972; Michener, 2000).

Based on the relationships indicated by the phylogeny, the species retained in *A.* (*Agapostemon*) are placed in four species groups (Table 2). The *viridulus* group comprises all the species included by Moure & Hurd (1987) in the group of the same name, but now also includes *A. centratus*, which

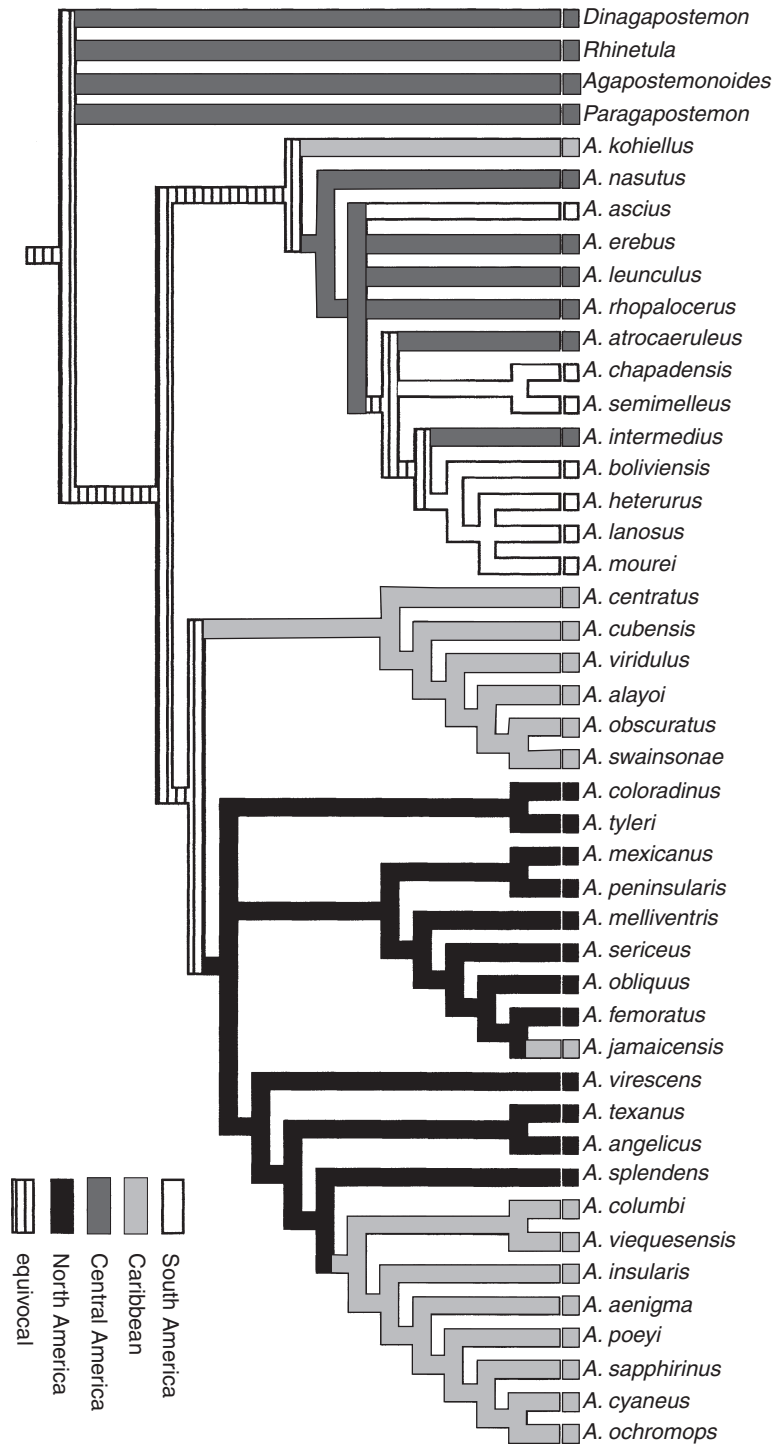


Fig. 4. Four-state geographical range coded and optimized on the phylogeny presented in Fig. 2.

they included in its own group. The *sericeus* group comprises all the species placed by Moure & Hurd in the *sericeus* and *melliventris* species groups. It also includes *A. jamaicensis*, which they had placed in their *poeyi* group. The *splendens* group introduced here is a merging of the

remaining *poeyi* group species of Moure & Hurd with *A. virescens* and the three species they originally assigned to the *splendens* group. Both species of the *tyleri* group introduced here had previously been included in a *virescens* species group, along with *A. virescens*. They now stand apart.

Table 2. Species groups in the two subgenera of *Agapostemon*.

Subgenus <i>Agapostemon</i>	Subgenus <i>Agapostemon</i> (continued)	Subgenus <i>Notagapostemon</i>
<i>viridulus</i> group	<i>splendens</i> group	<i>kohliellus</i> group
<i>A. alayoi</i> Roberts	<i>A. aenigma</i> Roberts	<i>A. kohliellus</i> (Vachal)
<i>A. centratus</i> (Vachal)	<i>A. angelicus</i> Cockerell	<i>nasutus</i> group
<i>A. cubensis</i> Roberts	<i>A. columbi</i> Roberts	<i>A. nasutus</i> Smith
<i>A. obscuratus</i> Cresson	<i>A. cyaneus</i> Roberts	
<i>A. swainsonae</i> Cockerell	<i>A. insularis</i> Roberts	<i>rhopalocerus</i> group
<i>A. viridulus</i> (Fabricius)	<i>A. ochromops</i> Roberts	<i>A. rhopalocerus</i> Smith
	<i>A. poeyi</i> (Lucas)	<i>A. atrocaeruleus</i> Friese
<i>sericeus</i> group	<i>A. sapphirinus</i> Roberts	<i>A. boliviensis</i> Roberts
<i>A. femoratus</i> Crawford	<i>A. splendens</i> (Lepeletier)	<i>A. chapadensis</i> Cockerell
<i>A. jamaicensis</i> Roberts	<i>A. texanus</i> Cresson	<i>A. intermedius</i> Roberts
<i>A. melliventris</i> Cresson	<i>A. viequesensis</i> Cockerell	<i>A. heterurus</i> Cockerell
<i>A. mexicanus</i> Roberts	<i>A. virescens</i> (Fabricius)	<i>A. lanosus</i> Roberts
<i>A. obliquus</i> (Provancher)		<i>A. mourei</i> Roberts
<i>A. peninsularis</i> Roberts	<i>tyleri</i> group	<i>A. semimelleus</i> Cockerell
<i>A. sericeus</i> (Forster)	<i>A. coloradinus</i> (Vachal)	<i>A. ascius</i> Roberts
	<i>A. tyleri</i> Cockerell	<i>A. erebus</i> Roberts
		<i>A. leunculus</i> Vachal

Notagapostemon, *subg.n.*

Type species. *Agapostemon mourei* Roberts, 1972.

Diagnosis. This subgenus is diagnosed by the presence of an acute upturned flange on the anterior edge of the mesoscutum, which is present in both sexes. The exceptions are as follows. *Agapostemon* (*Notagapostemon*) *rhopalocerus* is distinguished in the male (the female is unknown) by the elongate antennae with the apical flagellomere flattened, male *A. (N.) leunculus* are diagnosed by the single carina extending posteroventrally from the lateral angle of the pronotum, female *A. (N.) leunculus* have the process of the labrum acutely pointed and female *A. (N.) ascius* and *A. (N.) erebus* (males are unknown) are distinguished from other species by the combination of punctate anterior region of the mesoscutum and rugose texture on the supra-clypeal and interocular areas. Lastly, *A. (N.) nasutus* and *A. (N.) kohliellus* are distinguished in the males by the abruptly truncate clypeus whereas female *A. (N.) nasutus* are distinguished by the yellow maculation on the lateral pronotal lobe and female *A. (N.) kohliellus* lack the malus beyond the velum of the antennal cleaner. All males of this subgenus, with the exception of *A. (N.) kohliellus*, bear a long protrusion on the medioanterior corner of the volsella, a feature not found in *A. (Agapostemon)*.

Description. As for the genus (see Guérin-Ménéville, 1844; also Michener, 2000), with the following additions. Differing from *A. (Agapostemon)* in having, in females, the apex of the apical process of the labrum triangular and acutely pointed; the mesoscutum obscured by dense plumose, often short, hair; and in males the hind basitarsal ridge sinuate, the punctures on the disc of the first metasomal tergum smaller than those on the anterior edge, metasomal sternum 6 with a large buttonlike process medially towards the posterior third, and the medial edge of the volsella

emarginate anteriorly; and in both sexes the lateral ridge of the pronotum carinate. For all these characteristics, however, there are exceptions. Thus, the absence of one of the aforementioned features can be a trait of either subgenus, but the presence denotes *Notagapostemon*. Species of this subgenus always have the mesothoracic wingbase striate, the parapsidal lines depressed from the plane of the mesoscutum, the texture of the propodeal triangle rugose, the fore coxa and mid trochanter brown in the females and the hind basitarsal ridge of males single. The characters of this latter list are monomorphic in *Notagapostemon*, but are found in these and other states in the other subgenus, and thus are not diagnostic.

Etymology. This name is a combination of *notos* (Gr., southern) and the generic name *Agapostemon*.

Revisions. There are fourteen species in this subgenus, all included in *Agapostemon* by Roberts (1972), with the exception that he described the male of *A. heterurus* as a separate species, *A. inca*. These species include *A. ascius*, *A. atrocaeruleus*, *A. boliviensis*, *A. chapadensis*, *A. erebus*, *A. heterurus*, *A. intermedius*, *A. kohliellus*, *A. lanosus*, *A. leunculus*, *A. mourei*, *A. nasutus*, *A. rhopalocerus* and *A. semimelleus*. Three species groups are proposed (Table 2).

Distribution. *Notagapostemon* occur extensively throughout South America. Their range extends as far north as southern Texas and the Baja Peninsula of Mexico, and species also occur on the islands of Cuba, Hispaniola and Jamaica (Roberts, 1972).

The *kohliellus* and *nasutus* groups are monotypic, as shown here and by Moure & Hurd (1987). The *rhopalocerus* group combines all members of the *atrocaeruleus*, *erebus*, *heterurus*, *intermedius* and *rhopalocerus* groups of Moure & Hurd. Of these, only their *heterurus* group is monophyletic in this analysis, but it renders Moure & Hurd's *atrocaeruleus* group paraphyletic, and is therefore not recognized here.

None of the groups presented by Moure & Hurd (1987) have been split between the subgenera described in this paper. *Agapostemon jamaicensis* is removed from their *poeyi* group, and *A. coloradinus* and *A. tyleri* are removed from their *viridulus* group to form a new species group. Apart from these two changes, if Moure & Hurd's groups have been altered at all, they have simply been merged. With respect to the *rhopalocerus* group (subgenus *Notagapostemon*) and its component species, the groups were joined to reflect the phylogenetic relationships more accurately. Each group described as a result of this phylogenetic analysis is monophyletic. The groups of *A.* (*Agapostemon*) are slightly more complicated in that there was some shuffling of taxa between the Moure & Hurd groups and those supported by the phylogeny. This appears to be a subgenus in which species groups are not easily recognizable by gross morphology.

To update *Agapostemon* systematics, we present a new key for the recognition of the subgenera.

Key to subgenera of *Agapostemon*

1. Male 2
 - Female 3
- 2(1). With one or more of the following: an upturned flange anteriorly on mesoscutum, elongate, apically flattened antennal flagellomeres, a distinct carina extending ventrally from lateral ridge of pronotum, abruptly truncate clypeus and a long protrusion on the medioanterior corner of the volsella (Fig. 7B).
 - *Notagapostemon*
 - With none of the above *Agapostemon*
- 3(1). With one or more of the following: an upturned flange anteriorly on mesoscutum, yellow maculations on lateral lobe of pronotum, process of labrum acutely pointed, both supraclapeal region rugose and anterior third of mesoscutum punctate.
 - *Notagapostemon*
 - With none of the above *Agapostemon*

Behaviour

Even with behaviour known only for eight *Agapostemon* species, optimization of this character suggests that communal behaviour is ancestral for the genus, with two independent reversals to solitary behaviour (Fig. 3). Only the Caribbean group derived from an ancestor shared with *A. splendens*, which is solitary, optimizes as equivocal (Fig. 3). This is clearly a clade for which behavioural data are required. Behavioural information for this group and additional species from the largely unstudied *sericeus* group would provide tests of the pervasiveness of communal behaviour hypothesized by tracing the currently known behaviours.

The two species currently known to be solitary, *A. sericeus* and *A. splendens*, have been studied both through nest excavations (Eickwort, 1981) and field and insectary observations (Roberts, 1969). However, both are relatively wide-ranging species, found from the east coast of North America as far west as Colorado and Utah (*A. sericeus* and *A. splendens*, respectively), and from southern Canada to the very southern limit of the United States; in the case of *A. splendens*, even into coastal central Mexico. Geographic variability in behaviour has been demonstrated in other halictid bees, particularly at the edges of their ranges, e.g. *Halictus (Seladonia) confusus* (R. Tuckerman, personal communication), *H. (Halictus) rubicundus* (Eickwort *et al.*, 1996) and *Augochlorella striata* (Packer, 1990) (reviewed by Packer, 1997 and Wcislo & Danforth, 1997), where otherwise eusocial species have been found exhibiting solitary behaviour. The communal habit does not differ from solitary behaviour to the extent that eusociality does (Michener, 1974), as it involves only the sharing of tunnels and entrances, without any changes to the reproductive behaviour, and this would suggest a greater ease of reversal. Although the behaviour of *A. splendens* and *A. sericeus* has been studied using various methods (field observation, insectary observation and nest excavation), and across much of their ranges (New York, Kansas and Georgia) (Roberts, 1969; Eickwort, 1981), what the methods offer in variety they lack in consistency. No single method has been applied in all three areas, and it is therefore difficult to compare the results because the variables of methods and geographical region have not been held constant. This constancy is particularly important given that solitary behaviour can be observed simply as an incomplete observation of communality (as when only one of the communally nesting bees returns to the nest during the observation period, suggesting solitary behaviour). Not all nests in a given area may in fact demonstrate communal behaviour with the same number of bees sharing a nest, and there might be nests that are not communal at all (Abrams & Eickwort, 1980). It is therefore important that these two species be studied more extensively, especially across and at the extremes of their range, to determine whether they are in fact polymorphic, either within species or within populations.

As the other agapostemonine genera for which behaviour is known are generally communal (see Table 1 for list and references), it is likely that the common ancestor of the outgroups and *Agapostemon* is also communal (as is indicated in Fig. 3). However, given the lack of data for *Dinagapostemon*, *Rhinotula*, *Paragapostemon* and *Agapostemonoides*, this cannot be stated with certainty. These would be important focal taxa for further behavioural studies in this group.

Biogeography

We preface the biogeographical interpretations of this study with a note that parsimonious optimization of the simplified range states and parsimonious interpretation of dispersal and vicariance events in light of geography and geology are not necessarily congruent. The former was performed to

provide a general illustration of the trends, whereas the latter is far more relevant to biogeographical conclusions. Appendix 3 therefore presents geographical ranges in greater detail to permit inference of these vicariance and dispersal patterns.

The geographical ranges of the outgroup taxa are limited to South and Central America. However, because the two basal clades of *Agapostemon* are found in largely disparate geographical zones, and because of the basal positions of *A. kohliellus* in *A. (Notagapostemon)* and of the *viridulus* group in *A. (Agapostemon)*, the ancestral range of the genus optimizes equally parsimoniously as Central American or Caribbean (Fig. 4).

Two scenarios ensue from this equivocal optimization. In the first, *Agapostemon* originated in the Caribbean and subsequently colonized the Central American mainland (or the developing land bridge), South America and North America. In the second scenario, the genus originated on the developing Central American land bridge and subsequently colonized North and South America, as well as the Caribbean islands. The latter scenario is preferred for the following two reasons. First, there are no agapostemonine taxa other than *Agapostemon* on any of the Caribbean islands. Thus, the Caribbean origin scenario is predicated upon one of two ancillary requirements. Either *Agapostemon* and its sister group shared a common ancestor in the Caribbean and the sister group both dispersed from the Caribbean and became extirpated on these islands, or there was a vicariance event in which a proto-Antillean land mass separated from Central America, taking ancestral *Agapostemon* with it. Neither of these events seems plausible in terms of the palaeogeological history of the region (Brown & Lomolino, 1993, and see below). Second, because none of the basal North American *Agapostemon* species are found toward the southeast on this continent (Appendix 3), it would be more parsimonious to view them as having arrived in North America via Central America than through Florida. Once this Central American transition enters the scenario, it becomes more parsimonious, in terms of distance of travel and ease of invasion, for the genus to have had an origin in Central America, with independent invasions of North America, South America and the Caribbean. This also fits with the predominantly western ranges of the most basally derived North American species (*A. coloradinus* to *A. femoratus* in Fig. 4), as well as with the predominantly Greater Antillean range of the earlier derived *viridulus* group as compared to the primarily Bahamian range of the *columbi-ochromops* clade, which our results suggest reached this area via Florida. The Central American origin scenario also fits better in terms of the geological history of Central America and the formation of the Caribbean islands and the Central American land bridge. A brief summary of this history (taken from Pindell *et al.*, 1988; Ross & Scotese, 1988; Pindell & Barrett, 1990; Meschede & Frisch, 1998; Iturralde-Vinent & MacPhee, 1999) follows.

The Caribbean and adjacent areas have the most complex tectonic history of any region of the planet and a large number of models have been suggested to account for the palaeogeographical history of this area. Nonetheless, there is general agreement on the following points. North and South America were connected until about 160 Mya, but

this predates any possible origin of *Agapostemon* because there were no bees present at that time (Engel, 2001b; Michener, 2000). The two continents started separating with the breakup of Pangaea, which eventually resulted in over 3000 km of separation between North and South America, primarily along a NW–SE axis. Since the Cretaceous and the origin of bees, Central America has remained an ever-coalescing archipelago composed of a number of separate geological blocks. These coalesced into a complete land bridge only 3.5 Mya, although one large piece, the Chortis block (comprising southern Guatemala, Honduras, El Salvador, northern Nicaragua and the offshore Nicaraguan rise) moved from west of southwestern Mexico to its present position during the period 80–20 Mya. No Caribbean island has survived as an emergent land mass since before the latest Eocene, 37 Mya.

If agapostemonine taxa were extant in Central America while the land bridge was forming, *Agapostemon* could have arisen from an ancestor on the developing land bridge. Dispersal to the developing Greater Antilles would have been possible, depending on the geological position of those islands at the appropriate time, and would account for the early presence of *Agapostemon* on these larger and older islands. *Agapostemon (A.) kohliellus* and the *A. viridulus* group are likely to have arrived in the Caribbean this way from Central America. The simultaneous extension of *Agapostemon* taxa into North America would have been facilitated by the large and permanent connection between this continent and the developing land bridge. The proximity of the islands of the coalescing land bridge, increasing over time, would have provided increased opportunity for extension of *A. (Notagapostemon)* taxa into South America. That there are several separate origins of this subgenus on that continent implies both reasonable proximity and ease of dispersal. Similarly, the more recent origin of the Caribbean group related to *A. (Notagapostemon) splendens* (the *columbi-ochromops* clade) allows sufficient time for the dispersal of ancestral taxa from Central America to Florida, an extension that is mirrored to some extent in the increasingly eastern ranges of those taxa basal to that Caribbean clade (Appendix 3). Additionally, the primarily Bahamian ranges of species of the *columbi-ochromops* clade support the suggested Floridian origin. Eickwort (1988) based his scenario, in which these taxa arrived in the Caribbean via Central America, on the fact that he saw no apparent basis for a relationship between them and *A. splendens*, to support an origin via Florida. The results of this analysis indicate precisely such a relationship, and thereby undo the arguments supporting his scenario.

The geographical distribution of *A. jamaicensis*, nested deep within a North American clade, would seem difficult to explain. A possible route for this species would have been via Central America and the Nicaraguan rise, which projects towards Jamaica from the Nicaraguan coast. In the late Eocene and early Oligocene, when sea levels were at their lowest, there was a chain of islands on the Nicaraguan rise, providing a possible stepping-stone route to Jamaica (Iturralde-Vinent & MacPhee, 1999).

Caribbean-continental patterns similar to those that we suggest for *Agapostemon* have been found in several other biogeographical studies of Caribbean taxa. Baker & Genoways (1978), Slater (1988) and Brooks (1988) all inferred a Floridian relationship to Caribbean taxa, in bats, lygaeid bugs and anthophorine bees, respectively, corroborating the potential pathway suggested by *A. (Notagapostemon) splendens* and the *columbi-ochromops* clade. Ramos (1988) inferred an origin in Central America and Mexico for Caribbean cicadas and planthoppers, the same pathway suggested by the early divergence of *A. kohliellus* and the *A. viridulus* group. With *Agapostemon* species ranging throughout and restricted to the Americas, this genus forms an ideal focal group for this type of study because it contributes to our understanding of the biogeography of virtually all New World landmasses.

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Appendix 1

Characters used in the phylogenetic analysis. Some characters are presented separately for both males and females. In such cases, the character states assigned to the two sexes differ among the taxa, such that they cannot be merged to form a 'both sexes' character. Where relevant, we refer to figures in Roberts (1972), Roberts & Brooks (1987) and Cure (1989) to illustrate the character states. These papers are denoted by the letters R, RB and C, respectively, followed by the figure numbers from their work. Figure 1 herein is also referred to where relevant. Terminology follows Roberts (1972), Michener (2000) and Engel (2001a).

0. *Male and female, hairs on compound eyes*: (0) absent or minute and inconspicuous (Fig. 1); (1) present, long and conspicuous.
1. *Male and female, marginal cell distal end*: (0) acute or narrowly rounded; (1) truncated or narrowly truncated.
2. *Male and female, longitudinal lateral gradular carinae on metasomal terga*: (0) absent; (1) present on terga 2–5.
3. *Female, anterior edge of mesoscutum*: (0) dorsally directed flange present; (1) flange absent, mesoscutum rounded or weakly angulate in profile.
4. *Female, apex of basal area of labrum laterally in anterolateral view*: (0) emarginate; (1) continuous.
5. *Female, apex of distal process of labrum in ventral view*: (0) rounded, U-shaped; (1) triangular with a blunt apex; (2) triangular with an acute apex; (3) widening subbasally, maximal width at approximate mid-length and tapering to a point at the apex.
6. *Female, length of apical keel of labrum relative to distal process*: (0) same length, not extending beyond distal process; (1) extending beyond the distal process up to 10% of distal process length (2) extending beyond the distal process 10% or more of distal process length.
7. *Female, dorsal surface of keel of labrum, seen in dorsal view*: (0) parallel-sided; (1) narrowing to a point apically, the base one-third width of the distal process; (2) narrowing to a point apically, the base one-half width of the distal process; (3) narrowing to a point apically, the base the full width of the distal process; (4) an inverted triangle, widening apically from a basal point; (5) widening apically to a rounded apex.
8. *Female, distance between attachment point of keel of labrum and base of distal process*: (0) half length of distal process; (1) one-third length of distal process.
9. *Female, shape of basal point of attachment of labral keel to labrum*: (0) widening basally to nearly full width of distal process; (1) narrowing basally from rest of keel.
10. *Female, apex of keel of labrum ventral shape*: (0) as in Fig. 5A, 1 as in Fig. 5B, (2) as in Fig. 5C, (3) as in Fig. 5D, 4 as in Fig. 5E, (5) as in Fig. 5F.
11. *Female, shape of the ventral side of the apical portion of keel of labrum viewed laterally*: (0) weakly concave; (1) flat, but set at an angle from more basal portion; (2) flat, on same plane as more basal portion; (3) weakly convex.
12. *Female, clypeus colour towards apex*: (0) with yellow subapical band; (1) entirely black.
13. *Female, sculpture of the supraclypeal area medially*: (0) clearly and only punctate; (1) rugosostriate, rugae tending to striae or elongated punctures; (2) clearly rugose.
14. *Female, punctures medially on supraclypeal area*: (0) clear and round and distinct in spite of other sculpture; (1) weak or effaced into other sculpture; (2) punctures delimited only by other sculpture.
15. *Female, sculpture of interocular area, between compound eye and subantennal suture, from torulus to base of clypeus*: (0) clearly punctate with round punctures; (1) clearly striate; (2) rugose or without clear punctures or striae.
16. *Female, black band on paraocular area*: (0) expanded anteriorly from notch in eye; (1) narrow throughout.
17. *Female, colour of antennal scape*: (0) brown only; (1) yellow and brown.
18. *Female, sculpture of hypostoma*: (0) weak, widely spaced striae; (1) deeply and coarsely striate; (2) finely striate.
19. *Female, colour of mandibular base*: (0) yellow; (1) bearing a metallic green spot on brown background; (2) brown.
20. *Female, colour of mandible at mid length*: (0) yellow; (1) brown.
21. *Female, sculpture of the vertex behind ocelli*: (0) striate or tending strongly to striate; (1) rugose; (2) punctate.
22. *Female, genae, in dorsal view*: (0) narrowing posteriorly (Fig. 1A,C); (1) expanded and convex before narrowing posteriorly.
23. *Female, occipital carina*: (0) absent; (1) present, weak or strong.
24. *Female, colour of lateral lobe of pronotum*: (0) concolorous with thorax; (1) pale yellow, cream or white.
25. *Female, anterior surface of lateral lobe of pronotum*: (0) flat; (1) weakly convex.
26. *Female, sculpture anteriorly below lateral lobe of pronotum*: (0) smooth; (1) weakly rugose. or striate; (2) clearly striate.
27. *Female, sculpture laterally on pronotal collar*: (0) smooth; (1) chagrined or wrinkled; (2) weakly striate.
28. *Female, shape of lateral ridge of pronotum*: (0) nearly flat or rounded; (1) angulate; (2) carinate.
29. *Female, sculpture of anterior third of mesoscutum*: (0) punctate; (1) rugose.
30. *Female, sculpture of posterior half of mesoscutum, laterally*: (0) punctate, one size; (1) punctate, 2 sizes; (2) rugose, punctures indistinct.
31. *Female, hair type and density on mesoscutum*: (0) sparse, long branched hairs, with the mesoscutum itself clearly visible (Fig. 1A,C); (1) woolly hair (short plumose hairs especially dense) with the mesoscutum itself obscured.
32. *Female, sculpture of mesothoracic wing base*: (0) smooth or widely and weakly rugose; (1) striate.
33. *Female, plane of parapsidal lines, relative to plane of mesoscutum*: (0) depressed; (1) level.

34. *Female, sculpture on disc of scutellum*: (0) punctate, one size only; (1) punctate, 2 sizes interspersed; (2) rugose.
35. *Female, scutellar sculpture*: (0) with markedly more sparsely punctate, often shining, regions lateral of median; (1) uniformly dense.
36. *Female, sculpture of axilla*: (0) punctate entire length; (1) anterior half striate, often only weakly and on close inspection, striae may tend to elongate rugae; (2) striae extending well onto posterior half, striae distinct, striae may tend to elongate rugae.
37. *Female, ventral mesepisternal sculpture, between fore and mid coxae*: (0) punctate; (1) rugose; (2) striate; (3) rugosostriate.
38. *Female, sculpture of hypoepimeron*: (0) striate; (1) rugose.
39. *Female, sculpture of metepisternum*: (0) striate; (1) rugose.
40. *Female, basal area of propodeum*: (0) defined by carina or sculpture; (1) undefined, undifferentiated from lateral areas of dorsal surface of propodeum.
41. *Female, density of sculpture of basal area of propodeum, relative to that of rest of dorsal surface*: (0) sparser; (1) same density; (2) denser.
42. *Female, sculpture of basal area of propodeum*: (0) rugose; (1) striate.
43. *Female, hair type on dorsal surface of propodeum, in addition to usual long, sparse hairs*: (0) short, plumose and appressed hairs around propodeal triangle, visible at low magnification; (1) sparse, plumose and erect hairs around triangle, not visible at low magnifications.
44. *Female, sculpture on lateral surface of propodeum*: (0) smooth; (1) rugosostriate; (2) rugose; (3) striate; (4) punctate.
45. *Female, malus of antennal cleaner extending beyond velum*: (0) short and thick, less than length of velum; (1) long and narrow, equal to or longer than length of velum; (2) absent beyond velum.
46. *Female, length of teeth of malus of antennal cleaner*: (0) extremely short, not much longer than basal width of malus; (1) long; (2) extremely long, several times longer than basal width of malus.
47. *Female, colour of precoxa*: (0) strongly and nearly entirely metallic; (1) brown with a metallic tint; (2) brown; (3) yellow or amber.
48. *Female, colour of mesocoxa*: (0) brown with a metallic tint; (1) brown.
49. *Female, colour of mesotrochanter*: (0) yellow or amber; (1) brown with a metallic tint; (2) brown.
50. *Female, colour of metacoxae*: (0) strongly and nearly entirely metallic; (1) brown with a metallic tint; (2) brown; (3) yellow or amber; (4) brown and yellow or brown and amber.
51. *Female, tegula colour*: (0) brown or amber with an opaque yellow arc anteriorly; (1) brown or amber only; (2) brown or amber with a metallic area, generally towards medial edge; (3) brown or amber with a metallic area and an opaque yellow arc.
52. *Female, band of short, white, appressed hair on basal third of metasomal tergum 1*: (0) present; (1) absent.
53. *Female, size of punctures on disc of metasomal tergum 1 relative to size on anterior surface*: (0) smaller; (1) equal; (2) larger.
54. *Female, basal bands of short, suberect hairs on metasomal terga*: (0) absent; (1) weak, tergum visible through band; (2) strong, tergum not visible except where band is worn (Fig. 1A,C).
55. *Male, apical process of labrum*: (0) small; (1) large/long; (2) absent or extremely small.
56. *Male, clypeus in lateral view*: (0) moderately long, weakly rounded apically, flat dorsally (Fig. 1E); (1) relatively short, rounded to weak medial point dorsally; (2) extremely short, abruptly flattened apically, peaked medially dorsally (Fig. 1F).
57. *Male, anterior edge of mesoscutum*: (0) acute dorsally directed flange present; (1) flange absent, mesoscutum rounded or weakly angulate.
58. *Male, sculpture of the supraclypeal area medially*: (0) clearly and only punctate; (1) rugosostriate, rugae tending to striae or elongated punctures; (2) clearly rugose.
59. *Male, punctures medially on the supraclypeal area*: (0) round, clear and distinct in spite of other sculpture; (1) effaced into other sculpture; (2) delimited only by other sculpture.
60. *Male, colour of antennal scape*: (0) brown only; (1) brown and yellow (Fig. 1E,F).
61. *Male, sculpture of hypostoma*: (0) smooth; (1) weakly and widely striate.
62. *Male, occipital carina*: (0) absent; (1) present, weak or strong.
63. *Male, sculpture of vertex behind ocelli*: (0) striate or tending strongly to striate; (1) rugose; (2) punctate.
64. *Male, shape of head between compound eyes and ocelli*: (0) head, between eye and ocelli, confluent with contour of compound eye; (1) head, between eye and ocelli, depressed from level of compound eye.
65. *Male, lateral lobe of pronotum, anteriorly*: (0) flat; (1) weakly convex.
66. *Male, sculpture below lateral lobe of pronotum, anteriorly*: (0) smooth; (1) weakly rugose or striate; (2) clear striations.
67. *Male, shape lateral ridge of pronotum*: (0) nearly flat or rounded; (1) angled; (2) carinate.
68. *Male, sculpture of pronotal collar, medially*: (0) smooth; (1) chagrined.
69. *Male, sculpture of anterior third of mesoscutum*: (0) punctate; (1) rugose, punctures indistinct.
70. *Male, density of punctures on mesoscutum*: (0) crowded (Fig. 1B,D); (1) sparse.
71. *Male, density of punctures on scutellum*: (0) with markedly more sparsely punctate, often shining, regions lateral of median; (1) uniformly dense.
72. *Male, ventral mesepisternal sculpture, between fore and mid coxae*: (0) punctate; (1) rugose; (2) rugosostriate; (3) striate.
73. *Male, sculpture of mesepisternum, laterally*: (0) punctate; (1) rugose.

74. *Male, sculpture of metepisternum*: (0) smooth or micro-sculptured only; (1) rugose; (2) striate; (3) rugosostriate.
75. *Male, definition of basal area of propodeum*: (0) defined by a difference in sculpture or a carina; (1) undefined.
76. *Male, density of sculpture of basal area of propodeum relative to sculpture on rest of dorsal surface*: (0) sparser; (1) same density; (2) denser.
77. *Male, sculpture of basal area of propodeum*: (0) rugose (Fig. 1B,D); (1) striate.
78. *Male, short plumose hairs on dorsal surface of propodeum*: (0) absent or so fine and sparse as to be imperceptible; (1) present, and sparse surrounding the triangle.
79. *Male, sculpture of posterior surface of propodeum, inside posterior carina*: (0) rugose; (1) striate; (2) weakly rugose, tending to smooth; (3) punctate.
80. *Male, sculpture of lateral surface of propodeum*: (0) punctate; (1) rugosostriate; (2) rugose; (3) striate; (4) weakly striate, tending to smooth.
81. *Male, colour of foreleg coxa*: (0) strongly and nearly entirely metallic; (1) brown with a metallic tint; (2) brown; (3) yellow or amber.
82. *Male, colour of foreleg trochanter*: (0) brown; (1) yellow or amber.
83. *Male, colour of mid leg coxa*: (0) strongly and nearly entirely metallic; (1) brown with a metallic tint; (2) brown; (3) yellow or amber.
84. *Male, colour of midleg trochanter*: (0) brown with a metallic tint; (1) brown; (2) yellow or amber.
85. *Male, colour of hindleg coxa*: (0) strongly and nearly entirely metallic; (1) brown with a metallic tint; (2) brown; (3) yellow or amber; (4) brown and yellow or brown and amber.
86. *Male, colour of hindleg trochanter*: (0) brown with a metallic tint; (1) brown; (2) yellow or amber.
87. *Male, colour of pubescence on the outer surface of hind tibia*: (0) pale, without black or brown (Fig. 1B,D); (1) light coloured with admixture of brown and black or just brown and black pubescence, especially dark toward the base.
88. *Male, ventral edge of femur, towards apex*: (0) edentate (Fig. 1D); (1) with one tooth (Fig. 1B); (2) with 2 teeth.
89. *Male, shape of hind femur*: (0) narrow, width much less than length (Fig. 1D; R 152–154), (1) slightly swollen and rounded, especially from the anterior/posterior view (R 141–145, 151); (2) exceedingly swollen (Fig. 1B; R 146–150).
90. *Male, apical groove on hind basitarsus*: (0) absent (R 143); (1) narrow (R 144–146); (2) very wide, often flattened and as wide as facet of basitarsus (R 168, 170).
91. *Male, carina or angle on the inner posterior edge of hind tibia*: (0) absent, no sharp angle or carina; (1) angle or short carina present; (2) elongate carina present.
92. *Male, apical ridge of hind basitarsus*: (0) absent; (1) narrow; (2) wide.
93. *Male, apical ridge on hind basitarsus*: (0) spatulate or grooved (R 146); (1) angulate or carinate, not grooved or spatulate (R 144).
94. *Male, apical ridge on hind basitarsus*: (0) double, with a narrow ridge inside a wide, spatulate base; (1) single, only one ridge.
95. *Male, apical ridge on hind basitarsus*: (0) straight (R 161–166); (1) sinuate (R 169).
96. *Male, basitibial plate*: (0) present posteriorly only; (1) present only basally or absent.
97. *Male, colour of tegula*: (0) brown or amber with an opaque yellow arc anteriorly; (1) brown or amber only; (2) brown or amber with a metallic area, generally towards medial margin; (3) brown or amber with a metallic area and with an opaque yellow arc.
98. *Male, shape of metasoma*: (0) elongate and cylindrical (Fig. 1B,D); (1) widened and flattened.
99. *Male, size of punctures on disc of metasomal tergum I relative to size on anterior surface*: (0) equal; (1) punctures on the disc are larger than those on anterior surface; (2) punctures on the disc are smaller than those on anterior surface.
100. *Male, colour of metasomal tergum I anteriorly*: (0) amber on yellow; (1) other than amber, concolorous with remainder of abdomen; (2) brown on yellow (Fig. 1D); (3) amber and brown on yellow (Fig. 1B).
101. *Male, bands of colour apically on metasomal terga*: (0) none; (1) black (Fig. 1B,D); (2) weakly metallic, often appearing as if dusty or waxy; (3) brightly metallic.

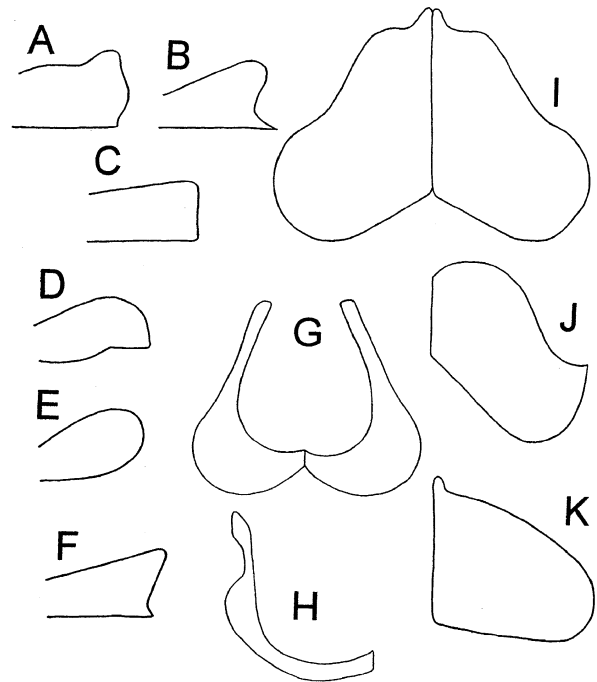


Fig. 5. Representative shapes of the female labra and male genitalia of *Agapostemon*. A–F, Keel of the female labrum, lateral aspect; G, gonobase, ventral aspect; H, left half of the gonobase, ventral aspect; I, gonobase, dorsal aspect; J,K, left half of gonobase, dorsal aspect.

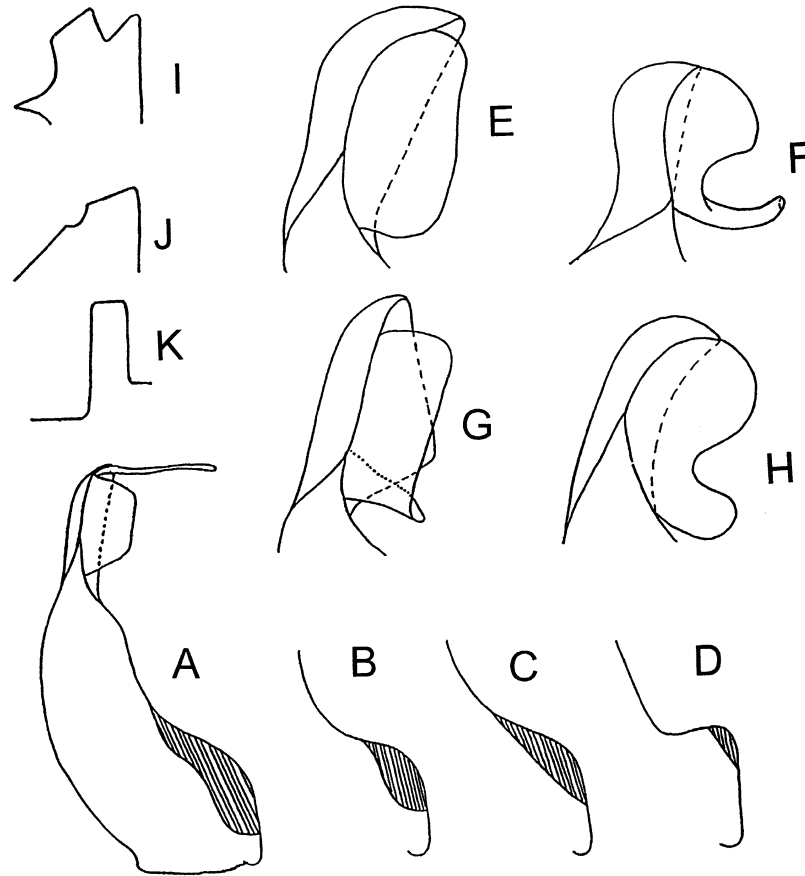


Fig. 6. Representative shapes of the male gonocoxite, gonostylus and penis valve of *Agapostemon*. A, Right gonocoxite, including gonostylus, dorsal aspect (hatched area represents a lamella resulting from the excavation of the opposite side); B–D, Right gonocoxite, dorsal aspect, apical third and gonostylus not illustrated; E–H, lobe of the gonostylus, dorsal aspect, apical stylus not illustrated; I, J, right penis valve, anterodorsal aspect.

102. *Male, transverse ridge on metasomal sternum 4:* (0) absent; (1) subapical, ending before apical margin of sternum; (2) apical, swelling right to apical margin of sternum.
103. *Male, lateral setae on apical margin of metasomal sternum 4:* (0) absent; (1) present.
104. *Male, metasomal sternum 4:* (0) visible, not telescoped between sterna 3 and 5; (1) hidden, telescoped between sterna 3 and 5.
105. *Male, metasomal sternum 6:* (0) flat medially, no longitudinal swelling or ridge, no button; (1) with medial longitudinal ridge or swelling, not flattened into a button; (2) with medial button, flattened ventrally (R 136–140).
106. *Male, apex of metasomal sternum 7:* (0) narrowly rounded (RB 18-b); (1) angulate medially; (2) with a lateral angle either side of the medial pointed protrusion; (3) widely rounded.
107. *Male, shape of subdistal angle of lateral extensions of the base of metasomal sternum 7:* (0) flat; (1) widely rounded; (2) narrowly rounded or widely angulate; (3) sharply angulate.
108. *Male, plane of lateral extensions of metasomal sternum 7:* (0) flat, on same plane as medial part of the sternum; (1) curved dorsad.
109. *Male, shape of anterior edge of metasomal sternum 7:* (0) flat (RB 18-k); (1) arched, concave (RB 18-f); (2) widely angulate, with straight sides (RB 18-h).
110. *Male, apicomedial hairs on metasomal sternum 7:* (0) absent (RB 18-j); (1) present (RB 18-f,b).
111. *Male, apico-medial hairs on metasomal sternum 8:* (0) absent; (1) present.
112. *Male, apex of medial projection of metasomal sternum 8, in dorsal or ventral view:* (0) bearing lateral peaks with a concavity between or flat between; (1) bearing both lateral and medial peaks (a total of 3 or more peaks); (2) broadly convex; (3) bearing lateral peaks and a rounded lobe medially.
113. *Male, short, spiculumlike ridge on metasomal sternum 8:* (0) absent; (1) present.
114. *Male, shape of anterior edge of metasomal sternum 8, medially:* (0) weakly; (1) straight; (2) roundly convex; (3) angularly convex.

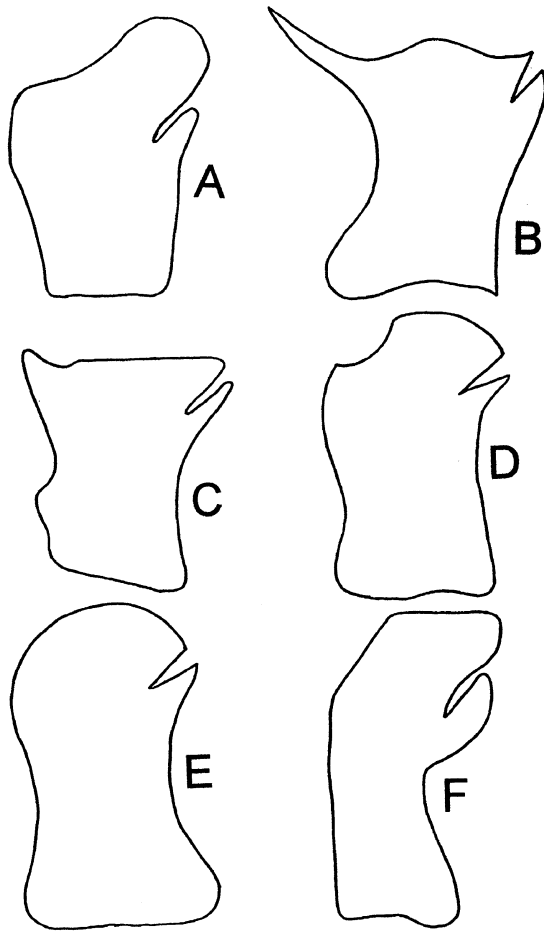


Fig. 7. Left volsella of *Agapostemon*, dorsal aspect, simplified contour shape.

115. *Male, anterior edge of metasomal sternum 8, laterally:* (0) continuously and evenly curved; (1) laterally excavated.
116. *Male, apical edge of metasomal sternum 8, in posterior view, shape:* (0) lobed laterally, lobes tapering towards the midline and meeting at a point medially with no horizontal surface medially; (1) medial horizontal surface thick with weak lobes laterally; (2) thin edged and sinuate; (3) with lateral lobes separated by a thin medial horizontal surface; (4) thick, transversely elongate with lateral edges rounded; (5) transversely elongate with medial lobes extending both dorsally and ventrally; (6) thin edged and transversely linear.
117. *Male, hairs laterally at apex of metasomal sternum 8:* (0) absent; (1) present.
118. *Male, lateral margins of gonobase, in ventral view:* (0) convergent posteriorly; (1) parallel; (2) rounded, nearly circular; (3) open, rounded basally, semicircular.
119. *Male, apex of ventroapical arms of gonobase ventrally:* (0) parallel sided or tapering (Fig. 5G); (1) flared (Fig. 5H).
120. *Male, dorsal margin of gonobase medially:* (0) narrowly bilobed (Fig. 5I,K); (1) broadly convex (Fig. 5J).
121. *Male, posterolateral margin of gonobase dorsally:* (0) strongly concave, nearly right-angled (Fig. 5I); (1) straight (Fig. 5K); (2) sinuate (Fig. 5J).
122. *Male, lateral margin of gonobase dorsally:* (0) angulate (Fig. 5J); (1) obtuse or rounded (Fig. 5I,K).
123. *Male, apical grooves on gonocoxite, near gonostylus base:* (0) absent; (1) present, fine; (2) present, coarse.
124. *Male, width of gonocoxite, dorsally:* (0) much narrowed, long and curving (R 211); (1) neither narrowed nor inflated (R 216); (2) inflated, width nearly two-thirds height in parts (R 221).
125. *Male, inner margin of gonocoxite, dorsally:* (0) gradually curved (Fig. 6A,C); (1) abruptly curved to obtusely angulate (Fig. 6B,D); (2) bearing a triangular tooth.
126. *Male, length of basal straight portion of inner dorsal margin of gonocoxite, in relation to entire length of gonocoxite:* (0) one-sixth; (1) one-third; (2) one-third to one-half; (3) greater than one-half.
127. *Male, excavated area at posterior end of medial margin of gonocoxites dorsally:* (0) concave almost forming a large rectangle when gonocoxites apposed (Fig. 6A); (1) concave almost forming a small rectangle when gonocoxites apposed (Fig. 6B); (2) with large triangular excavation each side, forming a triangle when gonocoxites apposed (Fig. 6C); (3) with small triangular excavation each side, forming a triangle when gonocoxites apposed (Fig. 6D).
128. *Male, sculpture on dorsal surface of gonocoxite, medially:* (0) smooth; (1) fine, narrow, longitudinal striae; (2) coarse, deep longitudinal striae.
129. *Male, sculpture on lateral margins of dorsal surfaces of gonocoxite:* (0) smooth; (1) fine, narrow, longitudinal striae; (2) coarse, deep longitudinal striae.
130. *Male, lateral concavity near base of gonocoxite, in dorsal view:* (0) absent (C 10b); (1) weak (C 11 h, 13b); (2) strong (C 11a,b,d).
131. *Male, lateral concavity at mid-length on gonocoxite, in dorsal view:* (0) absent; (1) weak; (2) strong.
132. *Male, sculpture of ventral surface of gonocoxite:* (0) smooth; (1) fine, narrow, longitudinal striae; (2) coarse, deep longitudinal striae.
133. *Male, gonocoxite shape, at anteromedial juncture, dorsally:* (0) straight or sinuate, without protrusion overhanging gonobase; (1) with a weak but distinct groove basally or so strongly grooved as to be bearing an overhanging lobe on dorsal lip of groove.
134. *Male, point of attachment of gonostylar lobe to gonostylus:* (0) basal; (1) midway to apex.
135. *Male, second stylus of gonostylus:* (0) large (R 184); (1) small or absent (R 190, 218).
136. *Male, origin of second stylus of gonostylus:* (0) sub-apical, distinguished from gonostylus by suture, fold or acute angle; (1) apical, appearing as an extension of gonostylus, without suture, fold or acute angle.
137. *Male, thickened branched hairs on outer apical margin of gonostylus:* (0) absent; (1) short, often

- difficult to see; (2) long, often nearly as long as second stylus.
138. *Male, shape of gonostylar lobe*: (0) single and flat (Fig. 6E); (1) flat and bearing an elongate protrusion on inner anterior margin (Fig. 6F); (2) single, but folded (along a transverse axis) anteriorly (Fig. 6G); (3) flat posteriorly, bearing a short, wide lobe anteriorly (Fig. 6H).
139. *Male, shape of ventrolateral margin of the penis valves, seen in anterodorsal view*: (0) broadly expanded laterally; (1) narrow, not expanded.
140. *Male, apex of penis valve, seen in posterodorsal view*: (0) gradually tapering to a point; (1) narrow and parallel-sided, abruptly pointed at apex; (2) wide and rounded apically.
141. *Male, dorsal margin of penis valve, in anterodorsal view, shape*: (0) as in Fig. 6(I), (1) as in Fig. 6(J), (2) as in Fig. 6(K).
142. *Male, ventral projection at base of penis valve*: (0) absent; (1) short, hidden behind volsella; (2) long, extending past volsella posteriorly.
143. *Male, ventral penis valve projection*: (0) absent; (1) present, widely rounded; (2) present, pointed.
144. *Male, penis valve at apex, seen tip-on*: (0) flat, transverse; (1) nearly flat, weakly convex dorsally; (2) convex; (3) convex, with a groove medially; (4) flat, laterally compressed.
145. *Male, shape of volsella transversely at mid-length*: (0) not angulate or carinate; (1) a smoothed, angled bend in volsella, acarinate; (2) carina present, best seen in anteroventral view, approximately half width of volsella.
146. *Male, posterior margin of volsella, laterally*: (0) bearing a depression between swelling of cuspis and digitus (Fig. 7B); (1) bearing no space between swelling of cuspis and digitus (Fig. 7A,D,E); (2) flat across apical edge of cuspis to digitus (Fig. 7C,F).
147. *Male, posterior margin of volsella, medially*: (0) rounded (Fig. 7E,F); (1) bearing an elongate protrusion (Fig. 7B); (2) emarginate (Fig. 7A,D); (3) bearing a short protrusion (Fig. 7C).
148. *Male, inner edge of volsella, toward apical margin*: (0) rounded (Fig. 7D,E); (1) emarginate (Fig. 7B,C); (2) straight, diagonal (posterolaterally to anteromedially directed) (Fig. 7F); (3) straight, longitudinal (Fig. 7A).
149. *Female, behaviour*: (0) solitary; (1) communal.

Appendix 2. Data matrix of character states for *Agapostemon* and outgroup taxa.

	0000000000	1111111111	2222222222	3333333333	4444444444
	0123456789	0123456789	0123456789	0123456789	0123456789
<i>P. coelestinus</i>	1111101411	3310001002	1110010100	1010001011	1101111102
<i>D. sicheli</i>	1101132511	2012120022	1100011101	0010001211	0000410202
<i>R. denticrus</i>	1111000401	?210000022	1200010000	1001011311	0000010202
<i>A. hurdi</i>	1001021511	3111021022	1001011110	0011010200	0001310202
<i>A. aenigma</i>	0101??????	??10021011	1102002100	1010102110	121030?112
<i>A. alayoi</i>	0101000310	1211021021	1101001201	0011102210	1101111102
<i>A. angelicus</i>	0101001110	3110021010	?101002110	1010112111	0201111112
<i>A. ascius</i>	0101??????	??1222101?	?101002?20	00102??311	11012??202
<i>A. atrocaeruleu</i>	0100021100	2201011020	0002001120	1010002210	1101111202
<i>A. boliviensis</i>	010???????	??????????	??????????	??????????	??????????
<i>A. centratus</i>	0101000310	1211021122	0?01001200	0010102210	1111311112
<i>A. chapadensis</i>	0100011110	5201021020	0002001020	0010002210	1101111212
<i>A. coloradimu</i>	0101000100	3310011022	0101002101	0010002110	1101111112
<i>A. columbi</i>	0101011210	2011221012	0101002111	1010112110	1201102102
<i>A. cubensis</i>	010???????	??????????	??????????	??????????	??????????
<i>A. cyaneus</i>	0101??????	??11121021	1101001100	0010102210	0201311102
<i>A. erebus</i>	0101??????	??1222101?	?101002?20	001010?311	01011??202
<i>A. femoratus</i>	0101001410	3111121012	0101001111	0010102111	1101211112
<i>A. heterurus</i>	0100??????	??10011020	0002002220	0110112210	0201302202
<i>A. insularis</i>	0101011110	2111021012	1102001110	1010102110	0211101202
<i>A. intermedius</i>	0100011100	2202221020	0002001120	1010002210	0101111212
<i>A. jamaicensis</i>	010???????	??????????	??????????	??????????	??????????
<i>A. kohliellus</i>	0101030010	2200021020	0101001100	1010101210	1110322112
<i>A. lanosus</i>	0100??????	??1001101?	?002002?20	011000?210	01001??202
<i>A. leunculus</i>	0101021100	5201221010	0101001010	1010101210	0101111202
<i>A. melliventris</i>	0101000110	3001221110	0101001001	0010002111	0201111010
<i>A. mexicanus</i>	0101??????	??1100102?	?101001?00	001021?211	11013??112
<i>A. mourei</i>	0100020110	220102102?	?002002120	0110002210	1100312202
<i>A. nasutus</i>	0101011200	4301221020	0101101000	0010002210	1101211202
<i>A. obliquus</i>	0101001010	3111011012	0102002111	0010002111	1201111112
<i>A. obscuratus</i>	0101000310	1211021022	1101001201	0010112210	1111311202
<i>A. ochromops</i>	0101??????	??11221011	0101002101	0000112111	0201111102
<i>A. peninsularis</i>	0101010100	0201021010	0101001101	0010202111	1101111102
<i>A. poeyi</i>	0101011110	2012221011	1102002011	0010102110	1111111002
<i>A. rhopalocerus</i>	010???????	??????????	??????????	??????????	??????????
<i>A. sapphirinus</i>	0101??????	??12221011	1102002111	0000102110	0211311102
<i>A. semimelleus</i>	0100011110	5201021020	0002001020	0010002210	1101111212
<i>A. sericeus</i>	0101001010	4111121010	0101001111	0010002111	1101111102
<i>A. splendens</i>	0101011110	2211021012	0101002110	1010101111	0201111112
<i>A. swainsonae</i>	0101000310	1211021020	0001001201	2010202210	1111311102
<i>A. texanus</i>	0101001110	3110021010	?101002110	1010112111	0201111112
<i>A. tyleri</i>	0101000100	1210011022	0101001100	0010001310	1101101111
<i>A. viequesensis</i>	0101010210	2011011020	0101002000	00101?1310	0201202002
<i>A. virescens</i>	0101001010	3111021012	0101002101	0010102311	1101111102
<i>A. viridulus</i>	0101000310	1211021021	1001001200	1010102310	1111311012

	5555555555	6666666666	7777777777	8888888888	9999999999
	0123456789	0123456789	0123456789	0123456789	0123456789
<i>P. coelestinus</i>	1212010122	0100100010	0021311000	2000101002	1221101211
<i>D. sicheli</i>	2110??1120	1?111110?0	01?0101000	0202111022	1220101110
<i>R. denticrus</i>	2112001110	1111110010	0031011010	2102121210	0000100110
<i>A. hurdi</i>	211?011122	0111111100	0021310000	2102100000	0110101200
<i>A. aenigma</i>	02121?????	??????????	??????????	??????????	??????????
<i>A. alayoi</i>	0212210122	11111010?0	0021311012	1001100012	1220001201
<i>A. angelicus</i>	0302110110	1111001000	0011110010	2001000010	001?101001
<i>A. ascius</i>	2112??????	??????????	??????????	??????????	??????????
<i>A. atrocaeruleus</i>	0111101022	11101012?0	0021110010	0212101101	0010100000
<i>A. boliviensis</i>	?????01102	?1??1002?0	0031100010	0313202101	1110100002
<i>A. centratus</i>	0312211110	1011101010	0031311012	3001100000	0000101001
<i>A. chapadensis</i>	2101201022	1110101200	0031310010	0311101002	0110100302
<i>A. coloradinus</i>	0302210122	11110020?0	0011311010	2001100010	0010100300
<i>A. columbi</i>	02121?1122	1011001010	0021302010	2011201111	0111101201
<i>A. cubensis</i>	?????10110	?1??101011	0031311112	4101100011	1211101201
<i>A. cyaneus</i>	0202211112	1111101110	0031302010	2001000111	1221101301
<i>A. erebus</i>	2112??????	??????????	??????????	??????????	??????????
<i>A. femoratus</i>	0302111112	1111001110	0021310010	2011202012	0210101301
<i>A. heterurus</i>	11100?1000	?1??101210	0021300010	0202111002	1210110002
<i>A. insularis</i>	2112101112	1111101010	0021312110	1000100111	1111101301
<i>A. intermedius</i>	0110001022	1110001210	0031300010	0312101100	0000100102
<i>A. jamaicensis</i>	?????11122	1111101110	0021311111	2111200012	1220101301
<i>A. kohliellus</i>	0102012111	1111101010	0101211111	0011202100	000???1001
<i>A. lanosus</i>	20000?1000	1010101210	0021300011	2212100002	?21011?002
<i>A. leunculus</i>	1112201122	1111101010	0011112010	2212201100	0000100001
<i>A. melliventris</i>	0002210120	1111001010	0011111010	2012202000	0000100001
<i>A. mexicanus</i>	1302210112	1110?010?1	0021310010	1001100000	?000100001
<i>A. mourei</i>	2100001000	11101012?0	0021300010	2212111002	1210110000
<i>A. nasutus</i>	2002202122	1111101001	0031211010	2312101000	0000101001
<i>A. obliquus</i>	0302211122	1111001110	0011111010	2011202011	0110101301
<i>A. obscuratus</i>	2111210111	1110101010	0031311111	3202121012	1220001101
<i>A. ochromops</i>	0302111112	1111101110	0031302010	2001100011	1221101301
<i>A. peninsularis</i>	0202210122	11111010?1	0211302010	2001100000	0000100301
<i>A. poeyi</i>	0212111112	1111101000	0011311012	2001100111	1111101301
<i>A. rhopalocerus</i>	?????01122	1111111110	0031111010	2312101100	000???1301
<i>A. sapphirinus</i>	1212111122	1111100110	0011302010	2211201111	1221101301
<i>A. semimelleus</i>	2101201022	1110101210	0021100010	0312202101	0110100000
<i>A. sericeus</i>	0012100122	1111101100	0011311010	2010201011	000?101301
<i>A. splendens</i>	0312100122	1111101010	0011102010	2000100011	0221101301
<i>A. swainsonae</i>	2012210111	11101010?0	1031311111	3012202012	1220001101
<i>A. texanus</i>	03021101?0	1111001010	0011110010	2001100010	011?101301
<i>A. tyleri</i>	0302210110	1011001010	0011311010	2001100010	0000100301
<i>A. viequesensis</i>	2012101122	1111002010	0011312010	2001100111	0111100301
<i>A. virescens</i>	0302210121	1111001011	0011312010	2001101010	0000100301
<i>A. viridulus</i>	1001210111	1111101010	0031311112	4001100012	1220001201

Appendix 2. Continued.

	1111111111 0000000000 0123456789	1111111111 1111111111 0123456789	1111111111 2222222222 0123456789	1111111111 3333333333 0123456789	1111111111 4444444444 0123456789
<i>P. coelestinus</i>	1001100310	000211600?	1110101111	1110000011	102131100?
<i>D. sicheli</i>	1001010312	1000016021	0011202012	001101?030	202221031?
<i>R. denticrus</i>	0100001212	00?1316020	0011201100	201001?0?0	112122202?
<i>A. hurdi</i>	2210001212	0030315020	0001201002	101001?101	112222002?
<i>A. aenigma</i>	??????????	??????????	??????????	??????????	??????????
<i>A. alayoi</i>	0211001211	100121?021	0011111002	2020000020	102221200?
<i>A. angelicus</i>	3221001212	0001304000	0110101200	2010001010	1022210321
<i>A. ascius</i>	??????????	??????????	??????????	??????????	??????????
<i>A. atrocaeruleus</i>	2100011211	1001310000	1201112201	1010000020	010032011?
<i>A. boliviensis</i>	01000213?1	10003???00	1111112200	10?1100000	10??20012?
<i>A. centratus</i>	02110?1311	1000314100	0111212012	2120000020	002231000?
<i>A. chapadensis</i>	2100011111	1001310000	1111112200	0110000020	0100?0211?
<i>A. coloradinus</i>	2200001201	?001210010	0112101011	2010101020	021102000?
<i>A. columbi</i>	33110?????	??????????	1110101001	1010001010	012222130?
<i>A. cubensis</i>	021000?1?1	?000210011	0011111002	0020000020	102221100?
<i>A. cyaneus</i>	2211001112	10?100?001	1111101000	2010001010	102?22120?
<i>A. erebus</i>	??????????	??????????	??????????	??????????	??????????
<i>A. femoratus</i>	22110013?1	?111100000	1002102021	202001?200	122232100?
<i>A. heterurus</i>	010002????	??????????	0112113200	10?1100000	101120012?
<i>A. insularis</i>	2311001311	1111201000	1110100010	2010001010	122122120?
<i>A. intermedia</i>	2100021112	1131300001	1201113000	0011000000	121122011?
<i>A. jamaicensis</i>	231100????	??????????	??????????	??????????	??????????
<i>A. kohliellus</i>	0100001301	0021204000	1001101111	0010000020	1021210001
<i>A. lanosus</i>	010102????	??????????	1200113000	??0?00000	100022011?
<i>A. leunculus</i>	2200001311	0001104000	1001011201	1010000000	010030011?
<i>A. melliventris</i>	0211002311	1131100000	0112101011	202001?220	122132120?
<i>A. mexicanus</i>	2211001112	1131113000	0112101021	102001?220	002230003?
<i>A. mourei</i>	2100021312	1001301000	1111112000	1001000000	120022012?
<i>A. nasutus</i>	2200013212	0010302031	1001213301	0010?1?111	0221400131
<i>A. obliquus</i>	021100????	?031203001	1001101011	202001?220	0222321001
<i>A. obscuratus</i>	201100????	??????????	0011111002	2020000020	102221200?
<i>A. ochromops</i>	2211001212	?010113001	1111101000	2010001010	102222020?
<i>A. peninsularis</i>	2210001312	0131111001	0201101000	102001?200	002231100?
<i>A. poeyi</i>	3311011211	1000016000	0111101000	2010001010	122221120?
<i>A. rhopalocerus</i>	220000????	??????????	1110011200	0000000000	010010200?
<i>A. sapphirinus</i>	3211001112	111110?101	1111101000	2010001010	102222020?
<i>A. semimelleus</i>	01000113?1	1001300000	1111112201	0010000020	010030211?
<i>A. sericeus</i>	?211001311	1111100001	0012101011	202001?200	1221321000
<i>A. splendens</i>	3211001212	1120016100	0?00101000	2010001?10	0121211000
<i>A. swainsonae</i>	0211001012	0101214021	0111111012	2020000020	112221130?
<i>A. texanus</i>	2221001211	0001114000	0110202300	201000	
<i>A. tyleri</i>	2210001311	0001010010	0111111011	2020001020	021102000?
<i>A. viequesensis</i>	0211001112	01111060??	0110101211	1010001010	112222100?
<i>A. virescens</i>	2200001211	1001006000	0011101100	1020000020	0021020001
<i>A. viridulus</i>	2011001010	1001213021	0011111002	2020000020	102221200?

