

## Evolution of the mandibular appendage in fig wasps (Hymenoptera: Agaonidae)

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**Abstract:** The phylogenetic value of the conformation of the mandibular appendages, the number of mandibular glands and other head characters in the Agaonidae are examined. The phylogenetic arrangement suggests that the pre-agaonid had a normal bidentate mandible with two glands, and a undistinct facial groove as in some *Diaziella* (Sycoecinae), *Sycophaga* (Sycophaginae) and in related chalcidoid non-pollinating fig wasps. It also had thirteen-segmented antennae; a long scape, several times longer than wide a long triangular pedicel, two or three anelli and eight flagellomeres with sensilla (as uniquely found in *Tetrapus*). The mandibular appendage apparently co-evolved with the development of the ostiolium of the syconium and the first mandibular appendage was fixed and had ridges or lamellae. A flexible hinge evolved later at its base. The polygamous males were wingless with extendible (solenogastrus) abdomen and mate inside the galls. These characters are also found in most Sycophaginae. The ancestor of Agaonidae was probably a primary sycophilous wasp, with dorsoventral depressed head, thorax and abdomen, that oviposit through the styler channel as still *Sycophaga sycomor* does. *Sycophaga* wasps with its apterous and polygamous males seem to be the sister group of Agaonidae. The Agaonidae females are characterized by their mandibular appendage and the antennal process. They have a prognathous head with gula. The males are wingless polygamous and solenogastrous.

**Key words:** Agaonidae (Hymenoptera), mandibular appendage, evolution, phylogeny.

*Ficus* is pollinated by small chalcidoid wasps of the family Agaonidae. The female agaonids have a flat lamellate or denticulate mandibular appendage that help them to squeeze between the ostiolar bracts and penetrate the syconia to pollinate and oviposit inside of them. The object of this article is to explain the evolution of the mandibular appendage in Agaonidae.

The pre-agaonid female probably had a prognathous subhemispherical or subquadrangular head, almost as long as broad across the eyes (as in Fig. 1, 2, and 3), with the antennal toruli situated close together in the middle of the face, and the facial groove being absent or indistinct as in *Diaziella philippinensis* (Sycoecinae; see Wiebes 1974 a, Fig. 22) and *Sycophaga* (Sycophaginae; Grandi 1916). It also had thirteen segmented antennae with the scape several times longer than wide, and long sensilla on the fourth to eleventh funicular segments, as uniquely found in *Tetrapus* (Agaonidae; see Grandi 1934, Fig. 1, 2),

and two or three antennal anelli. The mandibles were normal bidentate chewing structures with no special modifications as in *Sycophaga sycomor*, a primary cecidogenous wasp which enters the syconia of *Ficus sycomor* L. (Fig. 7) to lay its eggs. It is possible to infer that the mandible of the pre-agaonid probably had two glands in both sexes as it occurs in many Agaonidae as well as in Sycoecinae and *Sycophaga*, which as the Agaonidae are primary sycophilous wasps. *Apocrypta* (Sycophaginae) females also have bidentate mandibles with two glands. The scutellum had lateral grooves (parapsidal furrows) as those found in Sycophaginae (Boucek 1988 a). The male was apterous solenogastrous with extendible abdomen.

Once the inflorescence of the pre-*Ficus* became completely closed (a syconium), those wasps which evolved structures which aided them in squeezing through the ostiolar scales were probably more successful in entering the

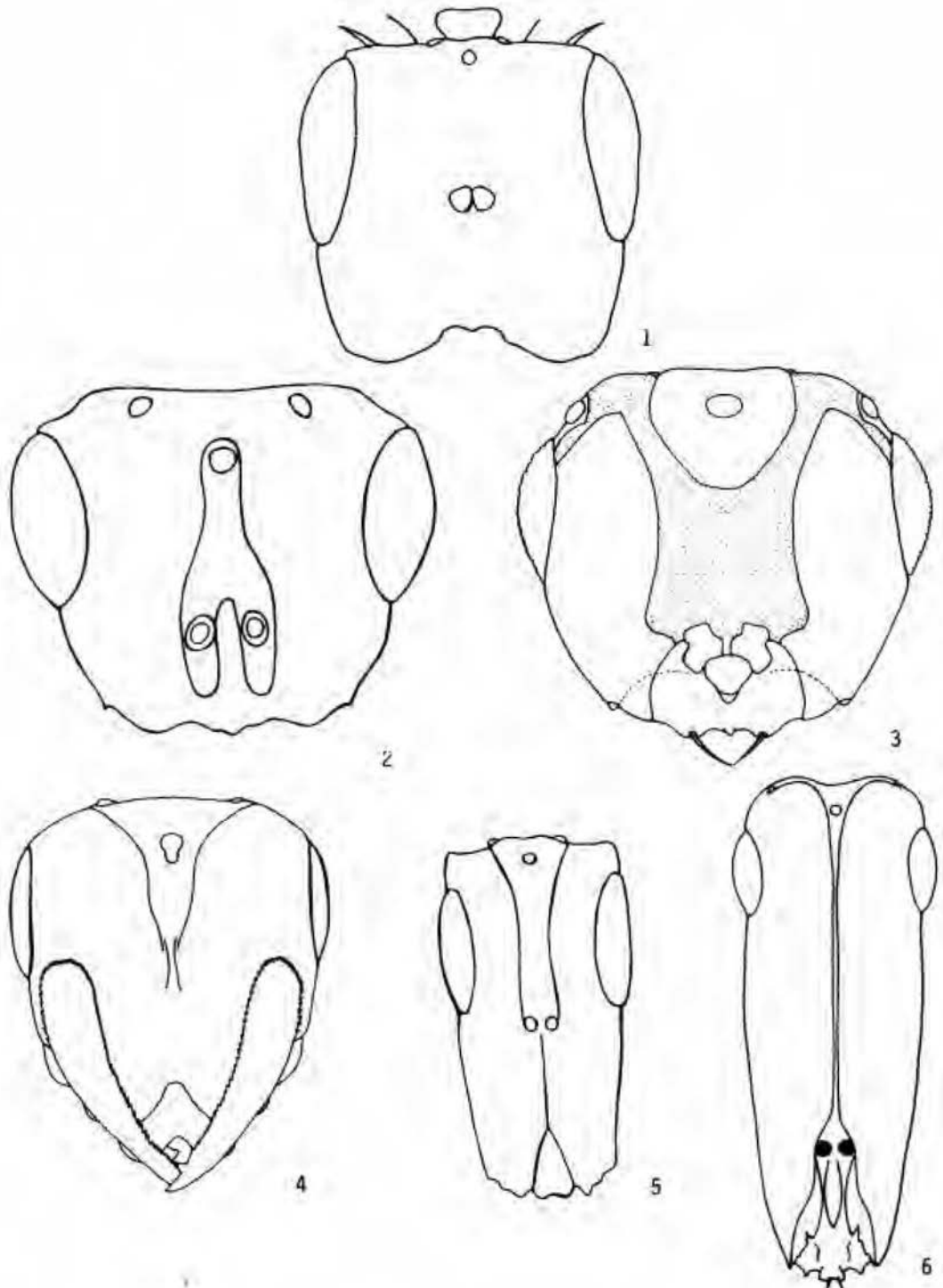


Fig. 1: Facial view of head of *Diaziella philippinensis*, (subfamily Sycocinae), after Wiebes, 1974 a, Fig. 22. Fig. 2: Facial view of head of *Sycophaga valentinae*, (subfamily Sycophaginae), after Grandi, 1952 a, Fig. I, 1. Fig. 3: Facial view of head *Maniella delhiensis*, (subfamily Blastophaginae). Fig. 4: Ventral view of head of *Philocaenus barbarus*, (subfamily Sycocinae), after Grandi, 1955, Fig. VI. Fig. 5: Facial view of head of *Seres armipes*, (subfamily Sycocinae), after Grandi, 1952a, Fig. III, 1. Fig. 6: Facial view of head of *Pleistodontes regalis*, (Agaonidae, subfamily Agaoninae), after Grandi, 1952 b, Fig. IX, 1.

figs. The evolution of Agaonidae seems parallel to the evolution of the syconium of *Ficus*, especially the ostiolum, syconial size, length of styles of the female flower and number, conformation and kind of anthers of the male flowers.

Probably the first mechanisms that the pre-agaonids evolved to facilitate their entry into the figs were the breakage of their antennae and wings and the evolution of structures (e.g. tooth-like or lamellar structures on the front tibiae and mandibles) that eased their movements in the narrow spaces between ostiolar scales.

Wiebes (1973, 1974 b, 1982 a) divided the Agaonidae into two subfamilies: those with lamellate mandibular appendages and short and robust scape (Blastophaginae) and those with crenulate (with denticles) mandibular appendages and elongate scapes (Agaoninae). Wiebes (1973) supposed that the characters of the Agaoninae (e.g., the elongate head, the ventral crenulations of the mandibular appendages, etc.) represent the pleisomorphic (primitive) state. Wiebes (1982 a) also considered that the wide open facial groove (e.g., as in Blastophaginae) is evidently the derived state. Bouček (1988 a) placed the Sycophaginae *s. str.* and Sycoecinae in Agaonidae. While the same author (1988 b) also included in Agaonidae: Epichrysomallinae, Otitesellinae and Sycoryctinae, the Agaoninae including only the fig pollinators. Grandi (1961) suggested that some of the modifications undergone by the agaonid head as inventions seemingly meaningless. The Agaonidae, Sycoecinae and Sycophaginae have a gula and not a postgenal bridge as stated by Bouček (1988a).

**Comparison of the Agaonidae mandible with that of Sycoecinae and Sycophaga:** The mandibles of the female and male *Sycophaga sycomor* (Fig. 7), a wasp which does not have an appendage, may be similar to those in the pre-agaonids. This type of mandible is still found in all agaonid males (Fig. 8). The bidentate mandibles (Figs. 10 and 13) of the Sycoecinae wasps (which as the agaonids also penetrate figs to oviposit) permit some insight into early agaonid mandibular evolution. Bouček (1988 a) also stated that the mandible in some genera of Sycoecinae seems to suggest how the mandible could have developed.

**Cladistic relationships of Agaonidae based on the conformation of the head:** The cladogram (Fig. 18) is especially based on the number of mandibular glands present in the female and male, as well as the conformation of the mandibular appendage, the conformation of the head, the conformation and subdivision of the antennal process (third segment), the conformation of the scape, as well as the presence or absence of maxillary and labial palpus in the female. The loss of one of the mandibular glands does not seem to produce any advantage or disadvantage to the wasps. It is assumed that subhemispherical or subquadrangular dorsoventral depressed heads with wide facial sulcus (as in Blastophaginae) sensilla placoidea in the second flagellomere, the antennal process with divisions, the presence of maxillary and labial palpi, the mandible with fixed appendage, with lamellae and two mandibular glands in both males and females are the pleisomorphic (primitive) states.

**Groups of *Ficus*, their pollinators and relationships:** The pollinators of monoecious subgenus *Pharmacosycea* (*sensu* Corner 1969): The New World section *Pharmacosycea* (Fig. 18-A) is exclusively pollinated by *Tetrapus* wasps. The female *Tetrapus* is primitive because the maxilla has distinct galea and stipes, a bacilliform process (palpus), which in some species is segmented (e.g., *Tetrapus costaricanus*); the labium had a palpus (Wiebes 1982 a). *Tetrapus* is also uniquely characterized among all Agaonidae by having a normal third segment without a prominent scale-like process (Grandi 1925) and sensilla in the first funicular segments, as in the non-agaonid fig wasps. Most female *Tetrapus* (except the pollinator of *F. tonduzii* Stand.) have a head distinctly longer than wide, less than one and a half times as long as broad across the eyes with a narrow facial sulcus, long scape, pedicel without axial spines, reduced unsegmented antennal process and mandibles with only one gland. *Tetrapus* seems to be composed of two well defined groups. In one group the female mandible has two appendages, one large and lamellate (as in Blastophaginae), the other small and with teeth (as in Agaoninae) (Fig. 15). The male of this group of *Tetrapus* has three pairs of functional

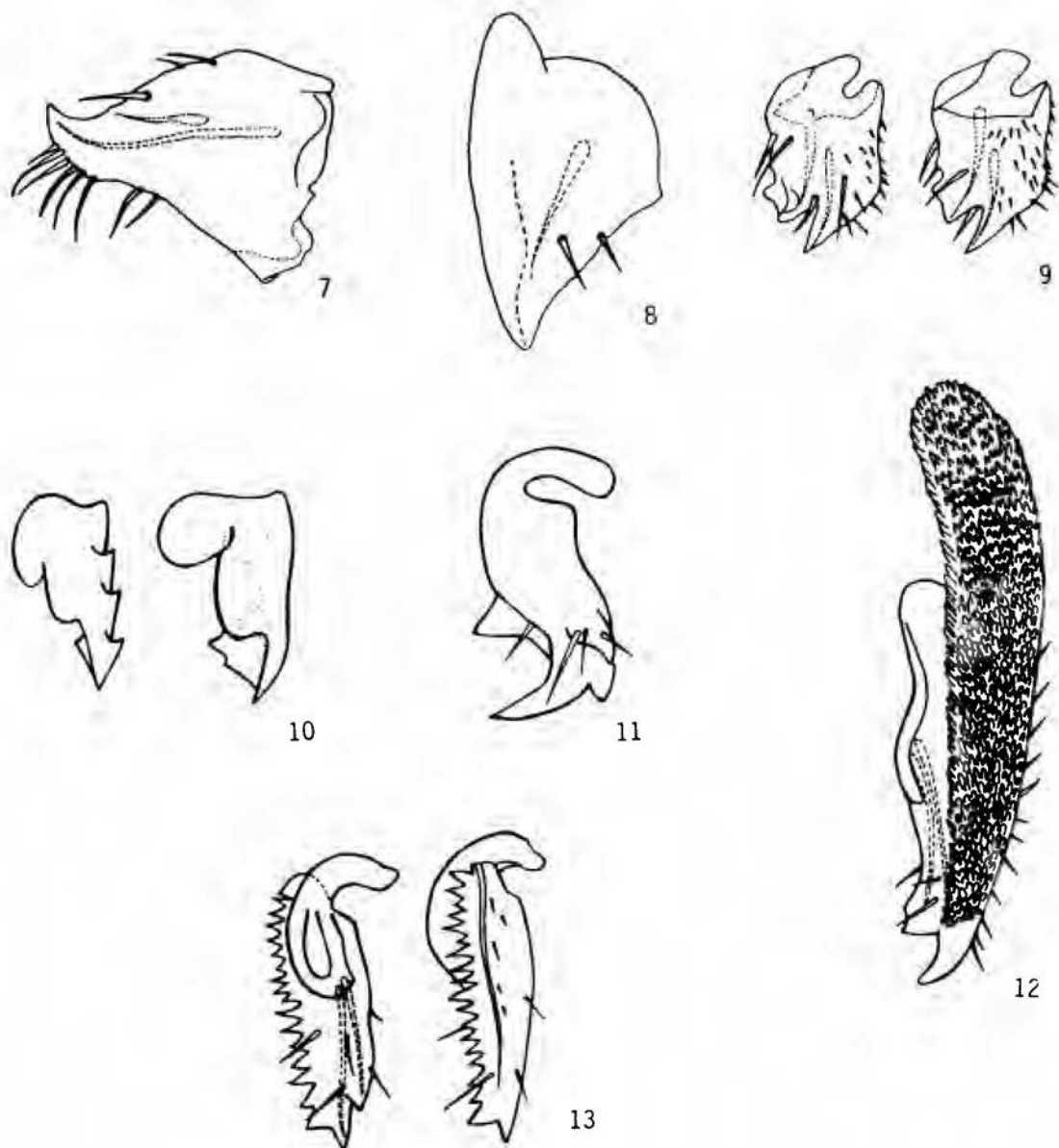


Fig. 7. Mandible of female *Sycophaga sycomori* with two glands (dotted lines) (subfamily Sycophaginae). Fig. 8. Mandible of male *Blastophaga (Pegoscapus) cumanensis*, (subfamily Blastophaginae), Mandibles of *Diaziella bicolor* with two glands (subfamily Sycoecinae) after Grandi, 1928. Fig. 10. Ventral and dorsal view of the mandibles of *Seres armipes*, (subfamily Sycoecinae), after Grandi 1952a; Fig. II, 3. Fig. 11. Mandibles of *Sycoecus thaumastocnema* (subfamily Sycoecinae), after Waterston, 1914, Fig. 3 Fig. 3. Fig. 12. Ventral view of mandible of *Philoceus barbatus* (subfamily Sycoecinae) with a fixed carinated appendage, after Grandi, 1952a, Fig. 5.2. Fig. 13. Ventral and dorsal view, of mandible of *Phagoblastus barbarus*, (subfamily Sycoecinae) after Grandi, 1955, Fig. VII, 3 & 4.

legs (hexapodous). In the second group ("true tetrapodous"), the female has a single long mandibular appendage with two lateral rows of tooth-like serrations (Fig. 16) and the males are tetrapodous.

The pollinators of the Old World section *Oreosycea*: *Oreosycea* figs are monoecious and

pollinated by *Dolichoris* wasps (Fig. 18, Q). The ancestor of the pollinators of section *Oreosycea* and *Urostigma* (Fig. 18, 2-3), as well as those that inhabit subgenus *Ficus* and *Sycomorus* (Fig. 18, 2-18), was probably a *Blastophaga*-like wasp; with two mandibular glands, segmented maxillary bacilliform proces-

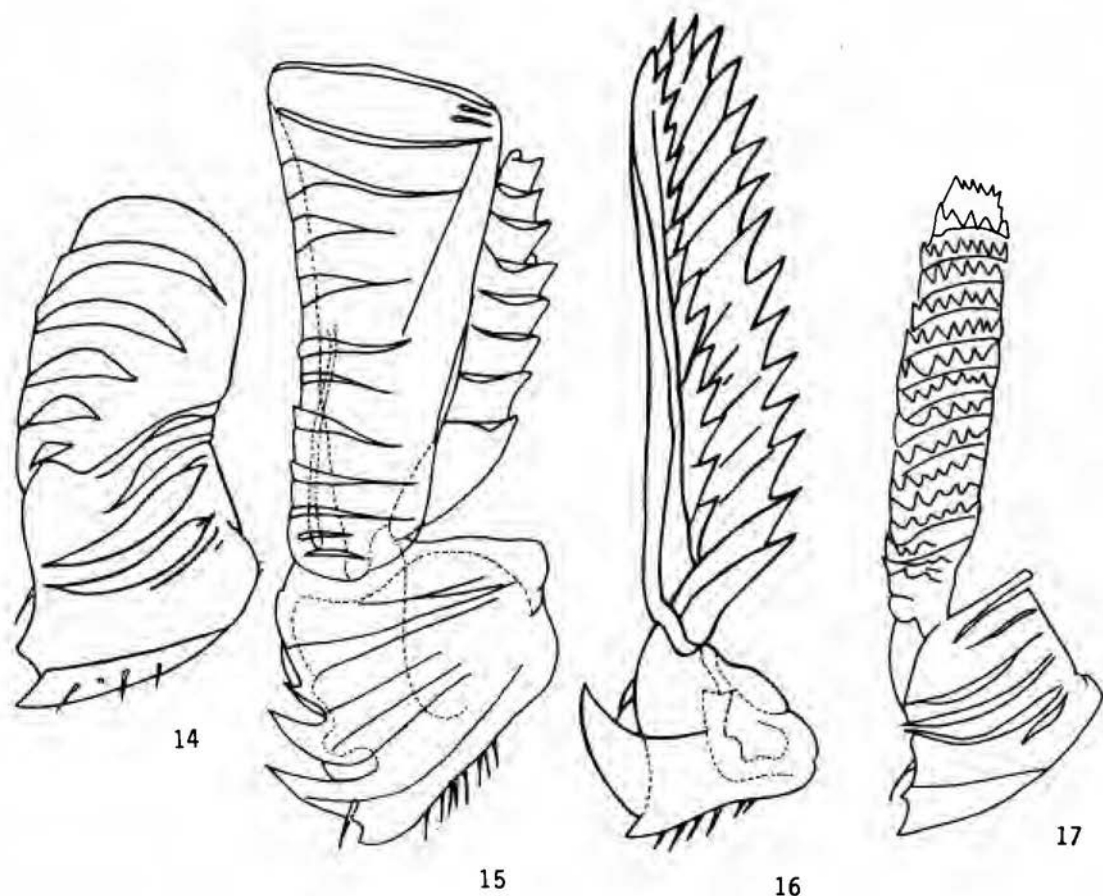


Fig. 14: Mandible of female *Ceratosolen* sp. appendage with lamellae (Agaonidae, Blastophaginae). Fig. 15. Mandible of *Tetrapus* sp., the pollinator of *F. crassiuscula*, subgenus *Pharmacosycea*, with large lamellated and small carinated appendages (subfamily Agaoninae). Fig. 16. Mandible of *Tetrapus costaricanus*, the pollinator of *F. glabrata*, subgenus *Pharmacosycea*, with only one mandibular appendage (subfamily Agaoninae). Fig. 17. Mandible of *Elisabethiella stueckenbergi* (Agaoninae) with a single carinated appendage (subfamily Agaoninae).

ses (as in *Dolichoris flabellata*), pedicel with axial spines, 2-segmented third segment, and the four flagellomere without sensilla placodea. As in *Blastophaga* group F (= *Dolichoris sensu* Wiebes 1979 c; for *Blastophaga* groups, see Ramírez 1977). For example, in *B. nervosae*. However, *Dolichoris vasculosae* has a head distinctly longer than wide, lacks the maxillary bacilliform process, and has the mandibular appendage elongate and loosely attached to the mandible. *Dolichoris* females differ from those of *Tetrapus* because they have pockets and corbiculae to carry pollen and do not have sensilla placodea in the first flagellomere. However, *D. flabellata* female has the first flagellomere with a

whorl of long free free sensilla (Wiebes 1979 c). In the opinion of Wiebes (1982 b), there is an undeniable resemblance between the wasps from *Pharmacosycea* (*Tetrapus*) and those of *Oreosycea* (*Dolichoris*) but this similarity is found in primitive characters and as such is not indicative of phylogenetic relationship.

**The pollinators of subgenera *Ficus* and *Sycomorus*:** The ancestor of the pollinators of *Ficus* and *Sycomorus* (Fig. 18, 2-18) was a *Blastophaga*-like wasp with distinct unsegmented bacilliform process.

Three sections of *Ficus* (*Ficus*, *Kalosycea*, *Rhyzocladus*) are pollinated by *Blastophaga sensu strictu* (= *B.* group A, Ramírez 1978)



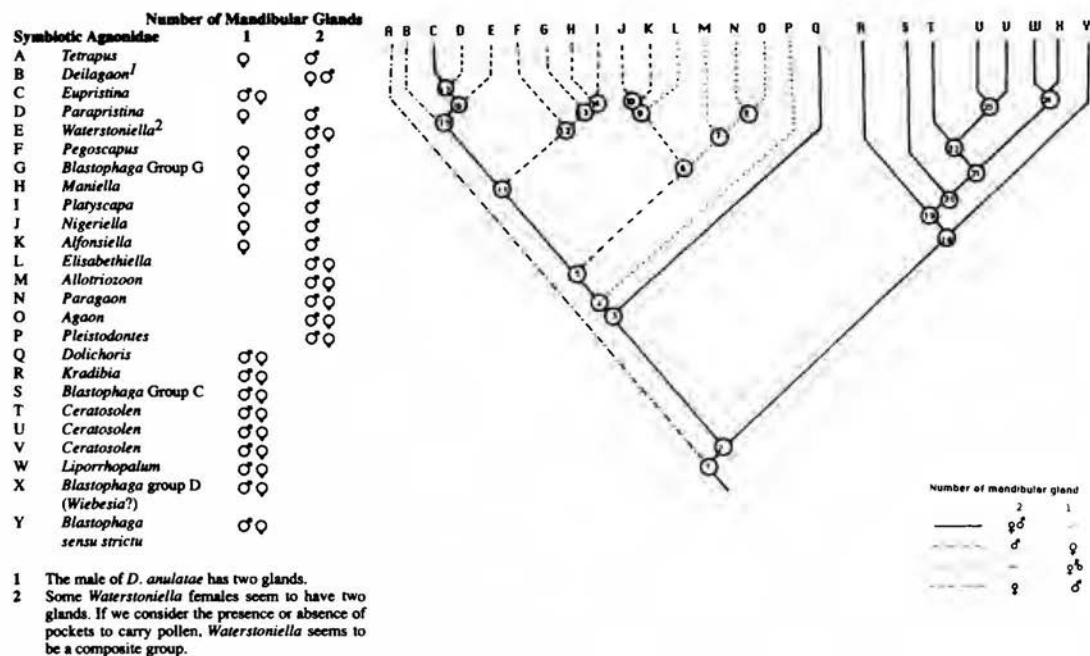


Fig. 18: A cladogram of the different groups of Agaonidae, based on the conformation of the mandible and the number of mandibular glands of both sexes.

which have lost the bacilliform process. The other sections are pollinated by *Blastophaga* group B (= *Kradibia*) *Blastophaga* groups C and D (= *Wiebesia*?), *Ceratosolen* and *Liporrhopalum*. Non-long heads or other special modifications have evolved in the female pollinators of the complex *Ficus-Sycomorus*. The *Sycomorus* (probably natural) is the only fig group comprising both gynodioecious and monoecious species (Berg 1990, Ramírez 1974, 1977).

The pollinators of subgenus *Urostigma* (Fig. 18, B-P): The subgenus *Urostigma* has several sections and is pollinated by several agaonid genera or complexes (Ramírez 1977). The pollinators of section *Malvanthera* (Fig. 18, P), evolved very elongate heads (except *Pleistodontes mandibularis*; Wiebes 1982 a) and long crenulate mandibular appendages. However in *Pleistodontes imperialis* and *P. greenwoodii* the appendage bears lamellae that are scarcely produced into teeth. *Pleistodontes* ♀ and ♂ have onemandibular gland.

The female ancestor (Fig. 18, 5-6) of the pollinators of section *Galoglychia*: *Agaon*, *Alfonsiella*, *Allotriozoon*, *Courtella*, *Elisabethiella*, *Nigeriella*, and *Paragaon* was a *Blastophaga*-like agaonid with one gland in the mandible of the male. Later, long heads and long

mandibular crenulate appendages evolved in most of the females of this group (as in Fig. 17). *Alfonsiella* and *Nigeriella* (Fig. 18, J and K) seem to have the most primitive mandibular appendage among the pollinators of *Galoglychia* as those found in *Blastophaginae*, but having ridges with two teeth or basally without distinct denticulations (see Wiebes 1974 b). In *Alfonsiella* and *Elisabethiella* the head is as long as wide across the eyes or distinctly longer than wide (Wiebes 1974 b, 1982 a). Some females of *Alfonsiella* have two mandibular glands.

*Agaon*, (Fig. 18, O) and *Allotriozoon* (Fig. 18, M) have long heads, usually one and half to two times as long as broad across the eyes and narrow median sulcus. Some *Allotriozoon* (*A. prodigiosum* excepted; Wiebes 1982 a, pers. comm.) have elongate heads although not one and a half times longer than wide. *Paragaon* (Fig. 18, N) has a head a little longer than broad across the eyes. All *Agaon*, *Allotriozoon* and *Paragaon*, (Fig. 18, M-O) have only one gland in the mandible in both sexes and do not have axial spines on the pedicel.

Wiebes (1982 a) noted that in the pollinators of *Malvanthera* and the pollinators of *Galoglychia*, the maxillae do not possess a distinct galea, stipes or palpus as in *Tetrapus*,

which he considers to be primitive states. Unlike *Tetrapus*, they have sensilla placodea in the last seven flagellomeres only. Corner (1985) botanically associates section *Stilpnophyllum* (pollinated by *Blastophaga* group G) with section *Malvanthera* (pollinated by *Pleistodontes*) while Wiebes (1979 a) in his revised cladogram, fits the pollinators of *Stilpnophyllum* in the midst of section *Conosycea* (with several *Blastophaga*-like groups) and according to Corner (1985), this has geographical and botanical support.

The pollinators of sections *Americana*, *Conosycea*, *Leucogyne*, *Stilpnophyllum* and *Urostigma* (Fig. 18 B-I) belong to the subfamily Blastophaginae *sensu* (Wiebes 1973). Their ancestor (Fig. 18, 5-11) was a *Blastophaga*-like wasp with two mandibular glands in both sexes. This type of mandible is still found in *Eupristina* (Fig. 18, C), while in *Parapristina* and *Waterstoniella* (Fig. 18, D and E) the males have only one mandibular gland. In *Deilagaon* the females have one or two glands. The male of *D. annulatae* has two glands (Wiebes 1977 a). *Deilagaon*, *Eupristina*, *Parapristina* and *Waterstoniella* are the pollinators of section *Conosycea*.

In *Pegoscopus* (the pollinator of section *Americana*), *Blastophaga clavigera* (= *Blastophaga* group G), the pollinator of section *Stilpnophyllum* (with one species), *Maniella* (pollinators of sections *Leucogyne*) and *Blastophaga* group E (= *Platyscapa*, the pollinator of section *Urostigma*) the males have one mandibular gland (Fig. 18 F-I). All the pollinators of these sections of *Urostigma* have lamellate mandibular appendages; however, *Waterstoniella williamsii* has small teeth on the appendage (Wiebes 1982 a).

### Mandibular relationships among

**Agaonidae:** The pollinators of subgenera *Ficus* and *Sycomorus*: *Blastophaga sensu strictu*, (= *Blastophaga* group A) group B (= *Kradibia*), *Blastophaga* groups C and D (*Wibesia*), *Ceratosolen* and *Liporrhopalum*, belong to the Old World and form a related group (Fig. 18, R-Y). They belong to subfamily Blastophaginae (*sensu* Wiebes 1973). The pollinators of subgenus *Urostigma* (Fig 18 B-P) form a related group with a common

*Blastophaga*-like ancestor without maxillary bacilliform process.

The pollinators of subgenus *Pharmacosycea*: *Tetrapus* and *Dolichoris* do not seem to be related. *Tetrapus* is the pollinator of the New World section *Pharmacosycea* and belong to the subfamily Agaoninae (*sensu* Wiebes 1973). *Dolichoris* (Fig. 18, Q), the pollinators of *Oreosycea*, belong to the subfamily Blastophaginae (*sensu* Wiebes 1973). In *Dolichoris* (except *D. vasculosae*) and *Tetrapus* there still are maxillary bacilliform processes on the maxillae. Wiebes (1982 a) supposes "all this to be a primitive condition dating from the agaonid ancestor". Wiebes (1973) stated that in his opinion the wasps from *Oreosycea* (*Dolichoris*) share so many apomorphous ("derived") character states with *Blastophaga* from subgenus *Ficus*, that a close relationship seems likely.

Wiebes (1973 and 1982 b) lumped *Tetrapus* (the pollinators of New World section *Pharmacosycea* subgenus *Pharmacosycea*), *Pleistodontes* (the pollinators of *Malvanthera*), and *Agaon*, *Allotriozoon*, *Alfonsiella*, *Elisabethiella* and *Nigeriella* (the pollinators of *Galoglychia*) in subfamily Agaoninae. Unlike *Tetrapus* the pollinators of *Galoglychia* and *Malvanthera* do not possess maxillary palps nor sensilla in the first funicular segment and break the antennae and wings when entering the syconia. The pollinators of the *Urostigma* sections *Americana*, *Conosycea*, *Leucogyne*, *Stilpnophyllum* and *Urostigma* (Fig. 18 B-I) seem to form a holophyletic group that belongs to Blastophaginae (*sensu* Wiebes 1973).

The subfamily Agaoninae (*sensu* Wiebes 1973) does not seem to form an holophyletic group as suggested by Wiebes (1973, 1974 b, and 1982 a). Long heads and crenulate mandibular appendages seem to have evolved independently in three agaonid groups, that is, 1) *Pleistodontes* (Fig. 18, P), the pollinator of the Asian section *Malvanthera*, 2) the pollinators of the African fig section *Galoglychia* (*Agaon*, *Alfonsiella*, *Courtella*, *Allotriozoon*, *Elisabethiella*, *Paragaon* and *Nigeriella* (Fig. 18, J-O), and 3) most species of New World genus *Tetrapus* (Fig. 18, A). Long heads have also evolved in *Ceratosolen inmanis* and *Dolichoris vasculosae*, two Blastophaginae (Wiebes 1982 a), and in *Seres armipes* (Sycoecinae). According to Bouček (1988 b), the presence of denticulate cross laminae on the

mandibular appendages of some *Pleistodontes* seems to raise questions about the subdivision of Agaoninae and Blastophaginae by Wiebes.

The conformation of the mandibular appendage alone and the long head in Agaonidae do not seem to be a good discriminatory subfamily character since *Dolichoris vasculosae* and three species of *Tetrapus* have mandibular appendages intermediate between those of subfamily Blastophaginae (with lamellae) and Agaoninae (with spines or crenulations). Furthermore, *Waterstoniella williamsi*, (Blastophaginae) (*sensu* Wiebes 1973) has a mandibular appendage with ventral lamellae which are shaped so as to form small teeth (as in Agaoninae). This mandibular appendage is quite similar to that of some species of *Elisabethiella* (Agaoninae). Thus, long mandibular appendages with crenulate mandibular appendage seem to have evolved independently in several groups of Agaonidae. These groups develop in unrelated groups of *Ficus* and in different geographical areas and inhabit groups of figs (sections *Galoglychia*, *Malvanthera* and *Pharmacosycea*) with ostiolar bracts bending down to form a tunnel-shaped or crateriform passage. Corner (1985) concluded that the resemblance of sect *Malvanthera* with sect. *Galoglychia* resulted from independent parallel evolution. The same thing could have happened to their pollinators. However, according to Berg (1986), the sections *Galoglychia* and *Malvanthera* may be closely related, but section *Pharmacosycea* is not related to these two *Urostigma* sections. He also states that section *Pharmacosycea* is probably the most primitive of the the subgenus *Pharmacosycea* and probably of the whole *Pharmacosycea-Urostigma* group.

It is also possible that the three groups of Agaoninae represent convergent evolution. It is not difficult to find such a degree of convergence in agaonids that penetrate syconia with very similar ostiola, through which the wasps must enter. Thus, the subfamily Agaoninae (*sensu* Wiebes 1973) does not seem to form a holophyletic group. According to Wiebes (1973) the elongate head does pose the question as to monophyly of the Agoninae. The unique presence of sensilla on the fourth segment of the female *Tetrapus* not only questions the monophyly of Agaoninae but also that of Agaonidae. However, the presence of

mandibular appendage in the agaonid female and solenogastry in the male reinforces their monophylous origin.

## RESUMEN

Se examinaron el valor filogenético de la conformación de los apéndices mandibulares, el número de glándulas mandibulares y otras características de la cabeza de la familia Agaonidae. El arreglo filogenético sugiere que el pre-agaónido tenía una mandíbula normal bidentada, con dos glándulas y una hendidura facial definida como en algunas especies de *Diazella* (Sycocinae), *Sycophaga* (Sycophaginae) y en otros cálidos que habitan los siconios y no son polinizadores. El preagaónido tenía una antena con trece segmentos; escapo largo, varias veces más largo que ancho; un pedicelo largo y triangular; dos o tres anillos ("anelli") y ocho flagelomeros con sensilas (como se encuentra únicamente en *Tetrapus*). El apéndice mandibular aparentemente coevolucionó con el desarrollo del ostiolo del siconio, era fija y contenía rebordes o láminas. Un punto de movimiento (o bisagra) evolucionó más tarde en la base del apéndice. El ancestro de los agaónidos fue probablemente una avispa sicofila primaria con cabeza aplanada, prognata con gula y tórax y abdomen aplastados dorsoventralmente, que ovipositaba a lo largo del canal del estilo. Las avispas sicofilas Sycophaginae con sus machos ápteros y polígamos parecen ser el grupo hermano de los Agaonidae. Los agaónidos están representados, por los polinizadores simbióticos del género *Ficus* y se caracterizan por el apéndice mandibular y el proceso antenal. Los machos son ápteros y solenogastros.

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