

The phylogeny and taxonomic status of the Chlorocystini (sensu stricto) (Homoptera, Tibicinidae)

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Abstract

The “*Baeturia* and related genera complex”, as defined earlier (De Boer, 1990) by shared aedeagal characters, is identified as the tribe Chlorocystini (sensu stricto). The Prasiini (sensu stricto) are identified as the sister group of the Chlorocystini (sensu stricto), while the genus *Muda* is recognized as the nearest outgroup. The phylogeny and biogeography of the sister group and outgroup is briefly discussed. *Baeturia kuroiuae* Matsumura is transferred to the genus *Muda*. A phylogenetic reconstruction of all 147 species of the Chlorocystini (sensu stricto) is presented, based on 154 characters and 409 character states. The computer program PAUP 3.1.1 (Swofford, 1993) was used for analysing the data; the genera *Prasia* and *Muda* were used as outgroups in this analysis. The results obtained from the computer analysis were slightly modified a posteriori, favouring some presumably phylogenetically important characters over strongly fluctuating ones. These final modifications were carried out with the aid of the computer program MacClade 3.0 (Maddison & Maddison, 1992). A complete data matrix and a list of characters and character states are given in an appendix; for descriptions and illustrations of these characters one is referred to previous publications.

Résumé

Le “complexe de *Baeturia* et des genres apparentés”, tel que précédemment défini sur la base de caractères aedégaux partagés (De Boer, 1990), est ici identifié comme tribu Chlorocystini (sensu stricto). La tribu Prasiini (sensu stricto) est considérée comme groupe-frère des Chlorocystini (sensu stricto), tandis que le genre *Muda* est pris en qualité de plus proche “outgroup”. Sont brièvement discutées la phylogénie et la biogéographie du groupe-frère et du “outgroup”. L’espèce *Baeturia kuroiuae* Matsumura est transférée au genre *Muda*. Est proposée une reconstruction phylogénétique de l’ensemble des 147 espèces de Chlorocystini (sensu stricto), reconstruction basée sur 154 caractères et 409 “character states”. Le programme d’ordinateur

PAUP 3.1.1 (Swofford, 1993) a été utilisé pour analyser les données; dans cette analyse les genres *Prasia* et *Muda* ont été choisis comme “outgroups”. Les résultats obtenus lors de cette analyse par ordinateur ont été légèrement modifiés a posteriori, pour favoriser certains caractères supposés phylogénétiquement importants, au dépens de caractères puissamment fluctuants. Ces modifications finales ont été réalisées à l’aide du programme d’ordinateur MacClade 3.0 (Maddison & Maddison, 1992). Une matrice complète des données ainsi qu’une liste des caractères et des “character states” figurent dans un Appendix; on se rapporte à des publications précédentes pour la description et pour l’illustration de ces caractères.

Introduction

This paper presents a cladogram for the “*Baeturia* and related genera complex”, a monophyletic group of tibicinid cicadas from the New Guinean-western Pacific region. This group, here identified as the Chlorocystini (sensu stricto), was selected for area-cladistic study of an area comprising Maluku, New Guinea, and East-Melanesia. A well-solved cladogram is essential for such a study. The phylogenetic and biogeographic data of the genus complex and its presumed sister group, combined with such data of the Cosmopsaltriaria (a similarly distributed monophyletic group of cicadas) are used in an area cladistic analysis of New Guinea and adjacent areas of the Indo-Melanesian region (De Boer, 1995d). In that paper the area cladograms of these groups are related to the palaeogeographical data of the region.

The genus complex under study comprises 147 species, classified into 14 genera. Taxonomic revi-

sions, with descriptions of the species, have been published in separate papers for most of these genera: *Aedeastria* De Boer, 1990 (De Boer, 1990; 1993a), *Guineapsaltria* De Boer, 1993 (De Boer, 1993b), *Gymnotympana* Stål, 1861 (De Boer, 1995a), *Mirabilopsaltria* De Boer, 1995 (De Boer, 1995b), *Papuapsaltria* De Boer, 1995 (De Boer, 1995c), *Scottotympana* De Boer, 1991 (De Boer, 1991), and *Thaumastopsaltria* Kirkaldy, 1900 (De Boer, 1992a). The large genus *Baeturia* Stål, 1866 was subdivided into seven monophyletic species groups that were discussed in separate papers: the *bloetei* group (De Boer, 1989), *conviva* group (De Boer, 1986), *exhausta* group (De Boer, 1994a), *gut-tulinervis* group (De Boer, 1994b), *loriae* group (De Boer, 1994c), *nasuta* group (De Boer, 1982; 1994d), and *viridis* group (De Boer, 1992b); the Australian genera of the complex (*Chlorocysta* Westwood, 1851, *Cystopsaltria* Goding & Froggatt, 1904, *Cystosoma* Westwood, 1842, *Glauropsaltria* Goding & Froggatt, 1904, *Owra* Ashton, 1912, and *Venustria* Goding & Froggatt, 1904) will be treated in a single paper (De Boer, in prep.). For a discussion of the characters used in the present phylogenetic analysis one is referred to these taxonomic revisions.

In order to polarise the characters, two outgroups have been selected. These outgroups are discussed preceding the phylogenetic analysis proper. Some short remarks on their phylogeny and biogeography are made and some of the consequences of the presumed relationships between ingroup and outgroups for the traditional classifications are indicated.

The existing classification of cicadas

The higher classification of cicadas, as presented in the catalogues of Metcalf (1963a, b) and Duffels & Van der Laan (1985) is mainly based on the work of Distant, performed roughly between 1888 and 1920. Many of the "divisions" proposed by Distant survive, virtually unchanged, as tribes in the modern classification. This classification thus pre-dates phylogenetic systematics and the tribes thus formed are phenetic rather than phylogenetic groups. Nevertheless, though most of these tribes

are presumably not monophyletic, most of the genera placed in any single tribe are probably closely related to each other, and the present classification into tribes can certainly form the basis for modern phylogenetic systematic work. The current subdivision of cicadas in six families (Cicadidae, Platypedidae, Plautillidae, Tettigadidae, Tettigarctidae, and Tibicinidae) is even more disputed than the classification in tribes, although the two largest families, the Cicadidae and the Tibicinidae, and the small family Tettigarctidae are generally considered to be sound groups (see Duffels, 1993).

Several tibicinid genera from New Guinea and Eastern Australia were recognized to form one monophyletic group, based on apomorphic aedeagal characters (De Boer, 1990). This group, of which the genera were previously placed in four different tribes (viz., the Chlorocystini, Gymnotympanini, Hemidictyini, and Taphurini), was not given the official status of tribe or subtribe, since its sister-group relationships were not known. Pending the discovery of its sister group, the group was given the preliminary name of "*Baeturia* and related genera complex."

A quest for the sister group of the "*Baeturia* and related genera complex"

The species of the "*Baeturia* and related genera complex" possess, apart from their apomorphic aedeagal shape, one character which separates them from the vast majority of other tibicinid cicadas: they lack a medial uncus lobe. The presence of a distinct and posteriorly directed medial uncus lobe, often larger than either the lateral uncus lobes or the claspers, is found throughout the cicadas, both in the Cicadidae and in the Tibicinidae. This character is very unstable within the Cicadidae since presence and absence often occur among closely related taxa, but it can possibly be regarded plesiomorphous in the Tibicinidae where a total absence occurs less frequently. The mere size of this lobe varies strongly within both families, which makes it questionable whether the lobes as found in these families all have a monophyletic origin.

The "*Baeturia* and related genera complex"

shares the absence of a medial uncus lobe with the Southeast Asian genera *Muda* Distant, 1897 and *Kumanga* Distant, 1905, while this lobe is either absent or strongly reduced in size in the oriental Prasiini (consisting of the genera *Arfaka* Distant, 1905, *Jacatra* Distant, 1905, *Lembeja* Distant, 1892, and *Prasia* Stål, 1863, see De Jong, 1985). Tibicinid species without a distinct medial uncus lobe can also be found in several geographically farther removed genera, for example *Fractuosella* Boulard, 1979, *Abroma* Stål, 1866 (Boulard, 1979), and *Dinarobia* Mamet, 1957 (Oran, 1954) from the Mascarene Isles, *Abrieta* Stål, 1866 (Oran, 1964) from Australia, and the African genera *Trismarcha* Karsch, 1891 (Dlabola, 1960) and *Lamotialna* Boulard, 1975 (Boulard, 1976) all lack a distinct medial uncus lobe. This list does not pretend to be complete; it was based on comparison of genital drawings of a selection of the more recent literature.

Taking into account the above-discussed instability of the character, it is far from certain that the shared absence of a medial uncus lobe forms a synapomorphy for all the genera lacking that lobe and a thorough phylogenetic revision of the higher taxa of cicadas is needed to come to any definite conclusions. However, it is supposed here that the immediate relatives of the “*Baeturia* and related genera complex” must be looked for among the taxa lacking a distinct medial uncus lobe. Based on the absence of a distinct medial uncus lobe (1 in Fig. 1a) the above-listed genera might well form (part of) a monophyletic group.

The oriental Prasiini are the most likely candidate to be the sister group of the “*Baeturia* and related genera complex”. Apart from the reduced or absent medial uncus lobe, the species of that taxon share several characters that also occur in several species of the “*Baeturia* and related genera complex” and represent possible apomorphies: a very narrow hyaline border along the hind margin of the tegmen, a medially furrowed pronotum, a continuous lateral ridge on the pronotum (only in *Prasia*), a very narrow cruciform elevation on the mesonotum, a strongly bent proximal spine on the fore femur (only in *Arfaka* and part of *Lembeja* and *Prasia*), and a ventrally angularly swollen postclypeus. These characters are but rarely encoun-

tered in other groups of cicadas. The first five characters might all be apomorphies for the “*Baeturia* and related genera complex” and the Prasiini together (4–8 in Fig. 1a), but then each of the characters must have reversed several times in these two groups. The angularly swollen postclypeus is also found in *Muda*. One character in particular, viz., the very narrow cruciform elevation on the mesonotum, strongly suggests a close relationship between the oriental Prasiini and the “*Baeturia* and related genera complex”. That remarkable feature is shared by the Prasiini and the genera *Cystopsaltria* and *Cystosoma*. The distributions of the above-discussed characters are regarded to be convincing enough to propose the oriental Prasiini as the sister group of the “*Baeturia* and related genera complex”, provided that complex is monophyletic. Some of these characters could also indicate that the oriental Prasiini are to be included in the “*Baeturia* and related genera complex” and that the latter [exclusively] is not monophyletic. This problem can only be tackled by a phylogenetic analysis that includes the nearest outgroups, and these are at present not known with any certainty. For now the unique aedeagal shape of the “*Baeturia* and related genera complex” is regarded as sufficient evidence for the monophyly of that group (9 in Fig. 1a).

It is supposed that *Muda*, based on its postclypeus shape (2 in Fig. 1a), forms the sister group of the oriental Prasiini and the “*Baeturia* and related genera complex” combined. Several characters of *Muda*, however, indicate a relationship with the oriental Prasiini. The large and inwardly curved lateral lobes of the male pygofer of *Muda* are presumably homologous with similar, but posteriorly directed, lobes in the Prasiini, while the extremely long ovipositor, which is found in *Muda*, *Jacatra*, and *Lembeja*, also might indicate a relationship between *Muda* and the Prasiini. This latter character is not considered a strong synapomorphy, since it occurs in many other cicadas. Based on the pygofer lobe (1 in Fig. 1b), *Muda* and the Prasiini might be sister groups, otherwise this lobe must be synapomorphous for *Muda*, the Prasiini, and the “*Baeturia* and related genera complex” together (3 in Fig. 1a) and must then have reversed in the latter group.

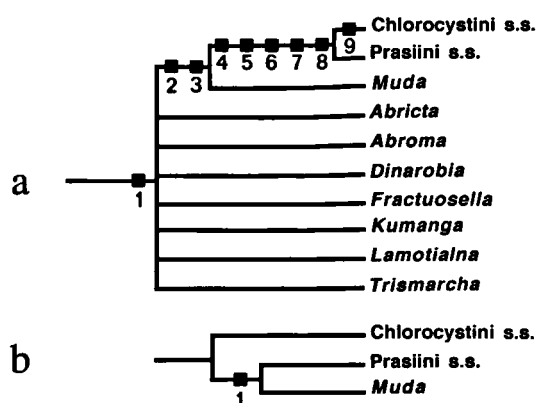


Fig. 1. (a), Cladogram showing the possible relationships of the Chlorocystini (sensu stricto). (b), Alternative cladogram of the possible relationships of the Chlorocystini (sensu stricto) with *Muda* and the Prasiini as sister groups. Numbers refer to characters discussed in the text.

The Southeast Asian genus *Kumanga* and some of the above-listed genera lacking a medial uncus lobe and included in the polytomy of Fig. 1a might possibly have to be included in the sister group of the Prasiini and the “*Baeturia* and related genera complex” combined.

In a tentative cladogram of the Mauritian cicadas, Boulard (1990) does not recognize the relationship between the genera of the “*Baeturia* and related genera complex” (viz., the tribes Chlorocystini and Gymnotympanini, see below) and the oriental Prasiini (the latter do not occur on Mauritius and are not included in the cladogram anyway), but he does indicate the genera *Abricta* and *Abroma* as belonging to the possible sister group. The phylogenetic reasoning behind his cladogram remains obscure.

Tribal allocation of the “*Baeturia* and related genera complex”

The “*Baeturia* and related genera complex” comprises 14 genera: *Aedeastria* De Boer, *Baeturia* Stål, *Chlorocysta* Westwood, *Cystopsaltria* Goding & Froggatt, *Cystosoma* Westwood, *Glaucopsaltria* Goding & Froggatt, *Guineapsaltria* De Boer, *Gymnotympana* Stål, *Mirabilopsaltria* De Boer, *Owra* Ashton, *Papuapsaltria* De Boer, *Scottotympana* De Boer, *Thaumastopsaltria* Kirkaldy, and *Venustria*

Goding & Froggatt. Most of these genera, viz. those of which the descriptions predate that of the “*Baeturia* and related genera complex”, are either included in the tribe Chlorocystini (*Chlorocysta*, *Glaucopsaltria*, *Owra*, *Thaumastopsaltria*, and, recently transferred from the Taphurini by Moulds (1990), *Venustria*), or in the Gymnotympanini (*Baeturia* and *Gymnotympana*). The tribe Gymnotympanini was separated from the Chlorocystini by Boulard (1979), though he regards these tribes as sister groups (Boulard, 1990). *Cystosoma* is included in the Hemidictyini and *Cystopsaltria* was recently transferred from the Chlorocystini to that same tribe (Moulds, 1990).

The presumed monophyletic “*Baeturia* and related genera complex” should be included in the tribe Chlorocystini since the complex contains the type genus, *Chlorocysta*, of that tribe. In this construction the Gymnotympanini must be regarded as a junior synonym of the Chlorocystini, since the type genus of the Gymnotympanini (*Gymnotympana*) also belong to the “*Baeturia* and related genera complex” and therefore to the Chlorocystini in their new concept. This also implies that *Cystosoma* and *Cystopsaltria* must be transferred from the Hemidictyini to the Chlorocystini.

The Chlorocystini

The Chlorocystini (sensu lato) do not form a monophyletic group in the new concept proposed here; the 14 genera of the “*Baeturia* and related genera complex” (the Chlorocystini sensu stricto) are more closely related to the oriental Prasiini than to the remaining genera included in the tribe. These remaining genera of the Chlorocystini, 15 in number, will have to be removed to other tribes. Six of these genera (*Akamba* Distant, 1905, *Bavea* Distant, 1905, *Decebalus* Distant, 1920, *Musoda* Karsch, 1890, *Nablistes* Karsch, 1891, and *Stagira* Stål, 1861) occur in Africa, two (*Fractuosella* and *Dinarobia*) are endemic to Mauritius and Réunion, two (*Muda* and *Kumanga*) come from Southeast Asia, one (*Toxopeusella* Schmidt, 1926) is restricted to Buru Island in Maluku, New Guinea, the Bismarck Archipelago, and the Solomon Islands, and

two (*Conibosa* Distant, 1905 and *Durangona* Distant, 1911) are endemic to Middle and South America, respectively.

As explained above, the genus *Muda* alone might be the sister group of the Chlorocystini (sensu stricto) and the Prasiini (sensu stricto) together (Fig. 1a), but *Dinarobia*, *Fractuosella* and *Kumanga* might be part of that sister group, or be closely related to that sister group.

Several of the African genera have been recently treated in literature. *Bavea*, *Musoda*, and *Stagira* share a large tube-like medial uncus lobe (Boulard, 1979; Villet, 1993). They are supposed to be related to the South African genera *Xosopsaltria* Kirkaldy, 1904 and *Tettigomia* Amyot & Serville, 1843, and should possibly be included in the mainly African tribe Tettigomyiini. *Nablistes* likewise has a very large medial uncus lobe (Dlabola, 1958) and is presumably also more closely related to the Tettigomyiini. No genital drawings have been published for *Akamba*.

Conibosa is reported to share the total absence of opercula with the South American genera *Coata* Distant, 1906 and *Prunasis* Stål, 1862 (Boulard, 1979). *Coata* and *Prunasis* are at present placed in two different families: *Coata* belongs to the Tettigadidae and *Prunasis* to the tribe Parnisini of the Tibicinidae. The correct tribal allocation of *Conibosa* is therefore uncertain. No recent literature is available on *Durangona*, but Distant states in its first description that the genus is allied to *Conibosa*.

Toxopeusella presumably belongs to the tribe Cicadettini (De Boer, 1990). Its species share the typical trifold aedeagus and a reddish costal area of the tegmen with the genera of that tribe (see Boulard, 1981a).

The Prasiini

The Prasiini (sensu lato) are likewise not monophyletic. The four oriental genera (the oriental Prasiini or the Prasiini sensu stricto) are more closely related to the Chlorocystini (sensu stricto) and to the genus *Muda* than to the three other genera of the tribe. Two of these other genera (*Lacetas*

Karsch, 1890 and *Iruana* Distant, 1905) are African, and one (*Sapantanga* Distant, 1905) comes from South America. These non-oriental genera were placed in the Prasiini because of their narrow head and protruding postclypeus. However, closer examination shows that there are large differences between these and the oriental genera. The oriental Prasiini have a much narrower head than either *Lacetas*, *Iruana*, or *Sapantanga*. Furthermore, the postclypeus of these latter three genera is not angularly swollen as is the case in the oriental Prasiini; *Lacetas* and *Sapantanga* have a conically protruding postclypeus, while *Iruana* has a much smaller, hardly swollen, postclypeus. *Iruana* (Dlabola, 1960; Boulard, 1981b, 1990) and *Lacetas* (Boulard, 1975a, 1975b) have a very distinct medial uncus lobe. *Lacetas* is presumably related to *Hovana* Distant, 1905 and *Hemidictya* Burmeister, 1835, sharing a very similar streamlined head and thorax (De Boer, in prep.) and should probably be placed in the tribe Hemidictyini. Only two females of *Sapantanga* were examined. That genus is presumed to be related to the South American genera *Prosotettix* Jacobi, 1907 and *Selymbria* Stål, 1861 of the Taphurini (De Jong, pers. comm.).

Phylogeny and biogeography of the outgroups

The Prasiini (sensu stricto), the supposed sister group of the Chlorocystini (sensu stricto), and the genus *Muda* serve as outgroups in the phylogenetic analysis of the Chlorocystini. In this section some of the most characteristic features and possible apomorphies of the various genera of these outgroups are discussed in relation to a tentative cladogram of the Prasiini. Furthermore, some remarks on the geographical distributions of these genera will be made.

The Prasiini (sensu stricto)

Thanks to the revisionary work of De Jong (1982, 1985, 1986, 1987) and De Jong & Duffels (1981) the oriental Prasiini form a fairly well-known group. Regrettably the revision of this tribe has not been

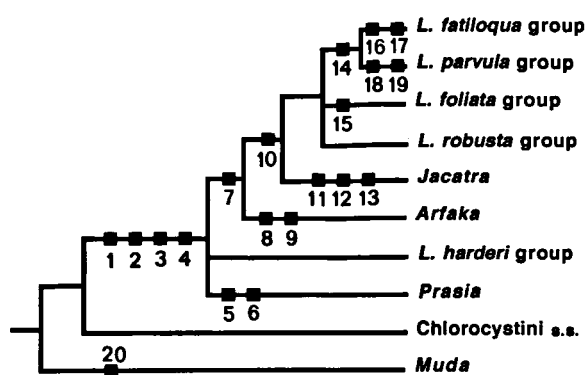


Fig. 2. Tentative cladogram of the Prasiini (*L.* = *Lembeja*). Numbers refer to characters discussed in the text.

completed and a fully solved phylogenetic reconstruction is not available. The following remarks about the phylogeny and the biogeography of the oriental Prasiini are principally based on De Jong's publications and on unpublished observations made by the same author. A tentative cladogram of the Prasiini is presented in Fig. 2.

The oriental Prasiini form a supposedly monophyletic group, containing the genera *Arfaka*, *Jacatra*, *Lembeja*, and *Prasia* (De Jong, 1985), on the basis of the following presumed apomorphies: (1) a very narrow vertex, with the ocelli close together; (2) a large obconical and triangularly protruding postclypeus; (3) a very narrow hyaline border along the hind margin of the wing; and (4) well-developed and posteriorly projecting protuberances on the lateral lobes of the male pygofer (1–4 in Fig. 2). The latter character is presumably homologous with similarly shaped, though incurving, lobes in *Muda*.

Other characters, that either have a very limited distribution outside the oriental Prasiini (a very narrow cruciform elevation on the mesonotum), or are not shared by all members of the group (a fusion of wing veins Cu 2 and A 1, a dorsal aedeagal appendage) also seem to support a close relationship between the species of the oriental Prasiini. The oriental Prasiini are distributed in Sumatra, Java, Borneo, the Lesser Sunda Islands, Philippines, New Guinea, and northern Queensland, but have most species on Sulawesi.

The genus *Prasia* contains seven species, restrict-

ed to Sulawesi and the nearby island of Muna. According to De Jong (1985) the monophyly of *Prasia* is based on a single apomorphy: "the degrading lateral margin of the male pygofer between the lateral lobes and the caudodorsal beak" (5 in Fig. 2). In addition to this, a long and spine-shaped male caudodorsal beak is presumed here to be apomorphic for the genus as well (6 in Fig. 2). Other apomorphies for *Prasia* can possibly be found in the shape of the lateral lobes of the pygofer and in the structure of the base of the aedeagal appendages. *Prasia* is easily separated from the other Prasiini by a sharply edged lateral margin of the pronotum. This character is also found in *Cystosoma*, *Cystopsaltria*, three species of *Mirabilopsaltria*, and three species of *Gymnotympana*. It is assumed that *Prasia* forms the sister group of *Arfaka*, *Jacatra*, and *Lembeja* combined. The latter three genera share a carinated male abdomen as a presumed synapomorphy (7 in Fig. 2).

Arfaka is a small genus with only 3 species, of which one is still undescribed. The genus is presumably endemic to Cendrawasih (the Vogelkop Peninsula of New Guinea) and the adjacent islands of Waigeu and Salawati. *Arfaka* is easily recognized by the long and slender apical areas of the tegmina and wings, a large laminiform protuberance on the lateral lobes of the pygofer, and a peculiar narrow and bilobate aedeagal apex. The first character also occurs in several genera of the Chlorocystini; the latter two characters presumably represent good apomorphies for this genus (8 & 9 in Fig. 2). *Arfaka* presumably forms a monophyletic group with *Jacatra* and *Lembeja*, but its phylogenetic relationships are not unambiguous. *Arfaka* and *Prasia* share a sexual dimorphism in the anal areas of the wings and might be sister groups, together forming the sister group of *Jacatra* and *Lembeja* together. A similar sexual dimorphism was found in *Gymnotympana* (De Boer, 1995a) and the *Baeturia loriae* group (De Boer, 1994c) and therefore the character cannot be regarded a strong synapomorphy. *Jacatra* and *Lembeja* share an elongate first tergite in male individuals as a presumed synapomorphy (10 in Fig. 2).

Jacatra contains only 2 species, occurring in Java and Sumatra. Only one species is described. The

genus can be recognized by three apomorphies: an aberrant vein partly dividing the 4th ulnar area of the tegmen, a proximally weakly tridentate first tergite in males, and a peculiar coalescence of the apical lobes of the aedeagus (characters 11–13 in Fig. 2).

Lembeja, with about 40 species, forms by far the largest genus of the oriental Prasiini. Five monophyletic species groups can be recognized within *Lembeja*, and three such groups have been revised: (1) the *foliata* group, with 13 species endemic to Sulawesi and Sangihe Island, can be recognized by a longitudinal ridge on the first sternite of males (15 in Fig. 2) (De Jong, 1986); (2) the *fatiloqua* group with 10 species, most of which are endemic to Sulawesi, also occurs in Mindanao, northern Borneo, Sumba, southeastern New Guinea and northern Queensland, and has a strongly developed medial dent in the first tergite of males and an inflatable telescoping male abdomen as its presumed apomorphies (16–17 in Fig. 2) (De Jong, 1987); and (3) the small *parvula* group with 2 species endemic to Sulawesi has a hindwards directed distal margin of the male pygofer and five apical areas in the wing as apomorphies (18–19 in Fig. 2) (De Jong, 1987). Two other groups, the *harderi* group from the Lesser Sunda Islands and the *robusta* group from New Guinea, Obi Island, and northern Queensland, can be recognized (De Jong, pers. comm.), but these groups still await description.

The phylogeny of *Lembeja* is not resolved, but the genus is assumed to be non-monophyletic in its present concept. *Lembeja harderi* Schmidt, 1925 and several related, undescribed, species forming the *harderi* group, are probably more closely related to *Prasia* and *Arfaka* than to other species of *Lembeja*. These species lack the carinated male abdomen and elongate first tergite of males, common to the other *Lembeja* species, and share a fairly small tymbal and sexual dimorphism in wings with *Prasia* and *Arfaka*. The four remaining species groups of *Lembeja* together are thought to form a monophyletic group (De Jong, pers. comm.), although no synapomorphous character has as yet been published. The *fatiloqua* and *parvula* groups are supposedly sister groups, with a medial indenta-

tion of the first tergite of the male as presumed synapomorphy (14 in Fig. 2).

The genus *Muda*

Muda presently contains three species, but several new species can presumably be separated from these. *Muda kuroiwae* (Matsumura, 1913) n. comb. from the Ryukyu and Loochoo Islands of southern Japan, is hereby transferred from *Baeturia* to *Muda*. Both other species are distributed over the Greater Sunda Islands (Java, Sumatra, and Borneo), and the Malay Peninsula. *Muda* is easily recognized by its peculiar pygofer, being sharply folded along its dorsal margin and, in consequence, nearly triangular in cross section (20 in Fig. 2). The large and rounded laminiform protuberances on the lateral lobes of the pygofer, which are probably homologous with the large protuberances in the Prasiini (sensu stricto), curve or fold mesiad along the base of the anal valves so that their apices are adjacent. These lobes possibly replace the strongly reduced claspers in function. *Muda* shares a somewhat similarly shaped postclypeus with the oriental Prasiini, and with *Cystopsaltria*, *Cystosoma*, and *Thaumastopsaltria*.

The phylogenetic analysis

Phylogeny and parsimony, the value and restrictions of a computer analysis

The method of phylogenetic reconstruction, as developed by Hennig (1950; 1966), is based on the assumption that if a character state is uniquely shared by two species, that character state did not evolve independently in these two species, but developed only once in the common ancestor of those species. Based on this principle, dichotomous family trees or cladograms can be constructed, in which all the various groupings of species which share a direct common ancestor (monophyletic groups) are supported by one or more shared, but otherwise unique, character states that developed in that common ancestor.

This may sound very simple in theory, but in

practice one immediately runs into trouble when character state distributions conflict. Suppose that a species "A" shares one character uniquely with species "B" and two characters uniquely with species "C". In that case the most parsimonious solution is chosen as the most likely.

The principle of parsimony is nothing but applying Ockham's razor, choosing for the simplest solution in view of all the facts. Translated to phylogenetic analysis, this means that the shortest cladogram is opted for, the cladogram requiring the smallest number of character changes that still is compatible with the data set. In our example, a relationship between "A" and "C" is favoured since in that option only one character need be supposed to have developed twice.

If we accept evolution as being a parsimonious process, a statement that is by no means proven, then it is clear that the "true" cladogram of the evolutionary relationships between species of a group is also the most parsimonious one. Regrettably the reversal of this statement, that the most parsimonious cladogram is also the "true" cladogram, is not necessarily true, perhaps even unlikely. The reason is that any given data set is per definition incomplete. In the present study of cicadas, for example, only morphological characters are used, but song, periodicity, food preference, ecological constraints, and even distribution are all characters of the species. Furthermore, of these morphological characters, only characters of adults were used, as represented by a sometimes very limited number of specimens, and only those characters were used that were recognized as such by the author. In short, the data set contains only a fraction of the total number of characters and that fraction is far from randomly chosen.

Apart from being incomplete, the data set is bound to be inaccurate as well. Many of the homoplasous characters (character states that appear to develop two or more times in the cladogram) that were recognized, and therefore scored, as one and the same character (state) are in fact two or more character(state)s. Often this cannot be recognized a priori, it can only be deduced a posteriori. Consider for example the number of sclerotized ridges on the tymbal of cicadas. If a spe-

cies has six ridges, and provided that this number is not the most plesiomorphous state, it could have acquired that number by gaining a sixth or losing a seventh ridge. If it gained a ridge, this can have happened by the duplication of any of its previous five ridges; if it lost a ridge, this can be due to the loss of any of its previous seven ridges, or to the fusion of any two successive ridges. In short, if any two species share the same number of tymbal ridges, unless these species are closely related, it is unlikely that a shared number of ridges represents a homology. The character "number of tymbal ridges" should therefore only be allowed to play a role within species groups and should be entirely disregarded at a more basal level. Presumably there are many more of these types of characters; they can often be recognized a posteriori by a low consistency index.

Another consideration should be that one character simply does not equal another. While, in genetic terms, the substitution of one base-pair might be sufficient to change one character from a state "A" to a state "B" and back, a much more drastic change in the DNA structure might be required to change another character from state "A" to state "B". One change in the latter character might (in evolutionary sense) be less parsimonious than five changes, gains and losses, in the former. Such character differences cannot be recognized a priori, though an educated guess can be made that the more complex structures and many genital characters and characters responsible for the mutual recognition between the sexes belong to the latter type. Characters of the former, easily changing, type can be recognized a posteriori by a low consistency index, but there is no way of telling how many changes in one character equal a change in another. Even when possible differences in genetic complexity are not made apparent by differences in consistency index, characters with an obvious function in reproduction (as clasper and aedeagal characters) must presumably prevail over characters with an obscure function (as a pointed or truncate caudodorsal beak on the pygofer). However, we must be reluctant in this, since if we do not know the function, this does not mean that there is no function. Still, the former characters are likely to

have been more subjected to natural selection than the latter.

The computer program PAUP 3.1.1 (Swofford, 1993) offers many options to adjust the data set *a priori*, in order to counteract some of the above-discussed problems. Characters can be ordered, or made irreversible, or given a weight (for explanations see the manual of the program), but, since there is, at least in morphological studies as the present one, no objective method to determine what character should be adjusted in what way, it is feared that such manipulations are only performed to bring the computer results closer to the pre-conceived ideas of the scientist. Alternatively, PAUP gives the opportunity to weight characters *a posteriori*, with a character weight relative to the consistency index or retention index of that character (Farris' reweighting method; Farris, 1969). However, then the weights given are dependent on the behaviour of a character in a cladogram that was unsatisfactory to us in the first place. In large data sets as the one presented here, such a successive weighting runs the risk of losing valuable information. When a character supports a sound monophyletic group in one part of the cladogram but is highly inconsistent in other parts, it will have a low consistency index and thus will get a low weight, as a result of which we might lose the support for the monophyletic group. Such a group should then be protected by a constraint before reweighting.

Ockham's razor is used in philosophy to decide between questions where there are no convincing arguments in favour of any one solution. The simplest solution is chosen by lack of good arguments *pro* or *contra*. I plea for a similar use of parsimony in phylogenetic analysis. A monophyletic group is recognized in principle by one or more apomorphous characters, characters that developed in the common ancestor and are inherited by the descendants. Of course, a common ancestor could have developed an apomorphy that changed or reversed in some, or many, of its descendants, as a result of which the monophyletic group cannot easily be recognized as such. The monophyly, though existing in reality, is then apparently not supported by

shared characters and, unless we know exactly how the apomorphous character changed in the descendants, we have no convincing arguments to regard that group as monophyletic. On the other hand, if we do recognize groups of species that share a unique character, we do have a strong argument to regard that group as monophyletic. In that case, unless this group contradicts with other equally well-argued monophyletic groups, there is no need for the parsimony criterion, nor for computer analysis. One should not allow to let the computer compute what is already known. The computer could come up with a more parsimonious solution based on characters, none of which are distinctive for the monophyletic groups they are supposed to support. Only when the scientist does not have any strong arguments in the form of shared apomorphous characters in favour of certain groupings, the most parsimonious solution is the best he can come up with. When a character is regarded as apomorphous for a certain species group by argument of its exclusivity and considered important in view of its supposed genetic complexity, and/or its supposed role in sexual isolation, and that character does not conflict with another equally well-argued possible apomorphy, then the final cladogram should show the species group in question as monophyletic, notwithstanding any conflict with characters of supposed minor importance. When there are such strong arguments in favour of a certain decision, there is no need for parsimony. Only when no clearly apomorphous characters can be found, or when two equally well-supported apomorphies contradict, parsimony offers a last resource and the most parsimonious solution should be chosen as the most likely one.

Although the relative importance of characters can often be made plausible, there is, at least in morphological studies, no way of quantifying that importance and we therefore have to accept that the science of phylogeny will always contain an element of subjectivity.

A computer analysis as discussed below has no other objective than to demonstrate the amount of conflict between the supposed apomorphies and the remaining characters. The amount of consistency between the computer tree and a tree solely based

on the supposed apomorphies can be taken as a kind of measure for the soundness of these apomorphies. Only when the computer tree deviates strongly from the tree based on the recognized apomorphies, the value of these apomorphies must be seriously reconsidered. Since these deviations are not easily quantified, it must be left to the scientist to decide what deviations are acceptable.

The computer analysis

Material. – A cladistic analysis was performed for the 147 species of the *Chlorocystini* (sensu stricto), using 154 characters with a total of 409 character states.

Characters. – All characters are introduced as unordered and no character weights have been applied for reasons discussed above, that is: all characters have an equal weight. A matrix of the data and a list of the characters are included in an Appendix.

Outgroups. – The character states as found in *Prasia* and *Muda* are added to the data matrix, as representing the presumed outgroup states. These two genera were defined as outgroup in the search. *Prasia*, as representing the sister group Prasiini, was chosen for several reasons: (1) *Prasia* is presumably the most basal genus of the oriental Prasiini (see Fig. 2), (2) a taxonomic revision of *Prasia* with genital drawings is available, (3) of all Prasiini, *Prasia* shows the greatest similarity to the species of the *Chlorocystini* (sensu stricto), and has therefore presumably retained more of the plesiomorphous states, but an analysis with a third outgroup is necessary to check this point.

Constraints. – Two topological constraints were built in. The male genitalia (which comprise 47% of the characters used) of the genus *Muda* are so completely different from those of the Prasiini and the *Chlorocystini* that the remaining characters of that genus carry insufficient weight to force *Muda* to an outgroup position within the tree. If a third outgroup were known, this problem would probably not exist. The problem was solved by putting a

topological constraint on the monophyly of the *Chlorocystini*.

A second constraint, on the monophyly of a group containing the genera *Baeturia*, *Chlorocysta*, *Glauropsaltria*, *Guineapsaltria*, *Gymnotympana*, *Owra*, *Papuapsaltria*, *Scottotympana*, and *Venus-tria*, appeared necessary to force some single and deviating species into their correct genus. Although a definite segregation, based on several presumed apomorphies (see Fig. 4), appears to exist between the above nine genera and the remaining five genera of the *Chlorocystini*, some deviations occur in both these subgroups which had a negative effect on the whole tree.

The search. – An heuristic search was made (in view of the size of the data set) with the options random adding sequence by stepwise addition, holding one tree at each step, keeping minimal trees only and collapsing zero length branches, and the option Mulpars off. Swapping was performed on minimal trees only with the swapping algorithm tree bisection – reconnection. The trees found had a length of 875 steps; these were used as starting trees in a new search, now with the option Mulpars on, and a set maximum of 600 equally parsimonious trees was reached.

Results. – The strict consensus tree of these 600 trees is given to a generic or species group level in Fig. 3. The total strict consensus tree has a length of 821 steps; consistency index = 0.29; retention index = 0.82; rescaled consistency index = 0.24. The 50% majority rule consensus tree is one of the 600 trees with a length of 875 steps; consistency index = 0.27; retention index = 0.80; rescaled consistency index = 0.22. This tree shows nearly all previously recognized genera and species groups as monophyletic groups. Parts of this 50% majority rule consensus tree are given in Figs. 5, 6, 7, 9, 12a, and 13. In other parts this tree is identical to the one presented in Fig. 4. Several of the 600 trees found give a most interesting alternative for the phylogeny of the genus *Papuapsaltria* (see Fig. 12b).

Modifications. – The strict, and 50% majority rule consensus trees differ in several instances from

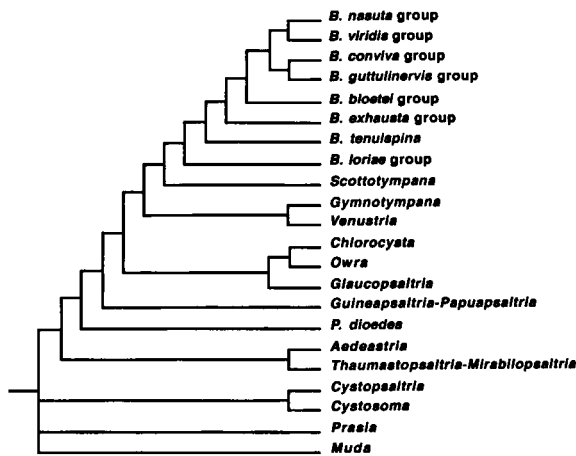


Fig. 3. Simplified version of the Paup reconstruction for the Chlorocvstini s. s. (strict consensus) (B. = *Baeturia*; P. = *Papuapsaltria*).

the tentative cladograms published earlier (De Boer, 1994a, d; 1995a, b, c). These differences are discussed below and some minor modifications are made. The “costs” of each of these modifications and of some proposed alternatives, expressed in the number of extra steps needed to construct the tree, were calculated with the computer program MacClade 3.0 (Maddison & Maddison, 1992). To ensure that the most parsimonious tree that takes the required modifications into account was reached, a new run was made in PAUP, but now using a constraint tree enforcing the proposed changes. The resulting alternative shortest acceptable tree is shown in Fig. 4. This tree has a length of 906 steps. Where several equally parsimonious solutions were possible, the tree of Fig. 4 was made to resemble the 50% majority rule consensus tree as much as possible. Modified in the same way, a tree with the alternative phylogeny for *Papuapsaltria* yields a shortest acceptable tree of 905 steps (cf. Figs. 12c and 14).

The black squares in Fig. 4 indicate one or more characters that are considered phylogenetically meaningful; these are given in Appendix 2. Branches without a black square just represent the most parsimonious way to deal with all characters concerned.

The phylogenies and positions of the various spe-

cies groups and genera will be discussed from left to right (Fig. 4), starting with the genus *Baeturia*.

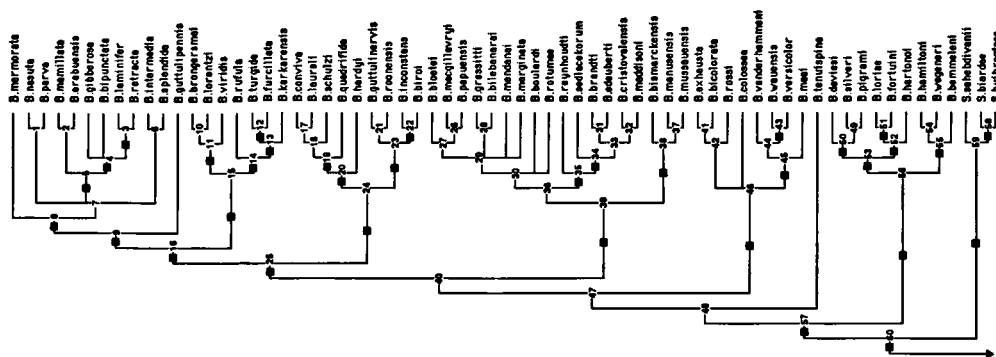
Discussion of modifications

Baeturia

The ingroup phylogeny of the *Baeturia nasuta* group is very uncertain, due to a lack of distinct apomorphies, which is illustrated by the fact that this group appears as a single polytomy in the strict consensus tree. The 50% majority rule tree of this group (Fig. 5) differs from the tentative cladogram published earlier (De Boer, 1994d) in that *B. marmorata* and not *B. guttulipennis* is placed at the base of the group. The *nasuta* group minus *B. guttulipennis* was considered monophyletic based on two apomorphies: a narrowly protruding postclypeus and four tymbal ridges. A transparent abdomen is apomorphous for the *nasuta* group, and the untransparent abdomen of *B. marmorata*, which is responsible for the basal position of that species, was considered a character reversal. The apomorphy of four tymbal ridges was not recognized in the present analysis, caused by the fact that all characters were introduced as unordered (though the number of ridges reduces within *Baeturia* from 7–8 to 4 ridges; the number of ridges can increase in other genera). Removing *B. guttulipennis* to the base of the *nasuta* group, as proposed here, costs 1 extra step (Fig. 4). The phylogeny of the monophyletic subgroup of *arabuensis*, *bipunctata*, *gibberosa*, *laminifer*, *mamillata*, and *retracta* agrees with the cladogram published earlier.

The phylogeny of the *viridis*, *conviva*, and *guttulineris* groups, and their relative positions, agree with the cladograms published earlier (Duffels & De Boer, 1990; De Boer, 1994a, d). Their phylogeny as given in Fig. 4 is identical to that of the 50% majority rule tree and, for the *conviva* and *guttulineris* groups, to the strict consensus tree.

The differences between the species of the *bloetel* group are often very small, which has resulted in an only partly resolved cladogram, with several polytomies. Even this cladogram should be considered as doubtful. Only the monophyly of the Moluccan



and New Guinean species *B. macgillivrayi*, *B. bloetei*, and *B. papuensis* and of the east Melanesian species *B. brandti*, *B. cristovalensis*, *B. edauberti*, *B. maddisoni*, *B. reynhoudti*, and *B. sedlacekorum* are assumed to be sound (Fig. 6). The latter group does not appear in the strict consensus tree, however. The species from the Bismarck Islands (*B. bismarckensis*, *B. manusensis*, *B. mussauensis*), which were presumed to be monophyletic, based on a shared aedeagal shape, and closely related to *B. papuensis* (cf. De Boer, 1989), appears as paraphyletic at the base of the *bloetei* group in the 50% majority rule tree (Fig. 6). Joining these three species to a monophyletic group, as proposed here, costs 1 extra step (Fig. 4). *B. papuensis* should possibly be included in this group. The suggested monophyly of the species of the *bloetei* group excluding these Bismarck species is based on a shared broad aedeagal pore. The aedeagus of the Bismarck species is quite different in aspect from that of other *Baeturia* species. The narrow pore of the Bismarck species might well be a reversal, and the basal position of this subgroup within the *bloetei* group is regarded far from certain.

In an earlier discussion on the phylogeny of the *loriae* group, a subdivision into two monophyletic

The relative positions of the *bloetei*, *exhausta*, and *loriae* groups was considered uncertain in previous publications and a tentative cladogram has been published in which these groups form a

Fig. 6. Section of the 50% majority rule tree dealing with the *Baeturia bloetei* group. Numbers refer to percentages of trees supporting the branch.

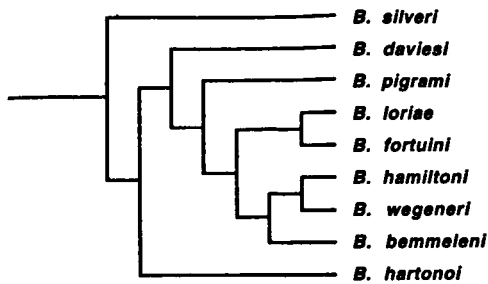


Fig. 7. Section of the strict consensus tree dealing with the *Baeturia loriae* group.

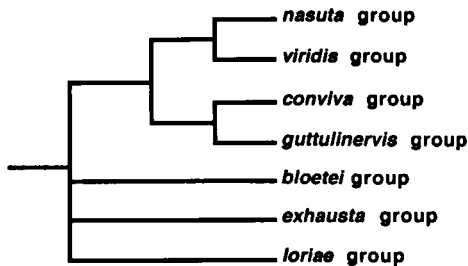


Fig. 8. Alternative cladogram for the species groups of *Baeturia*.

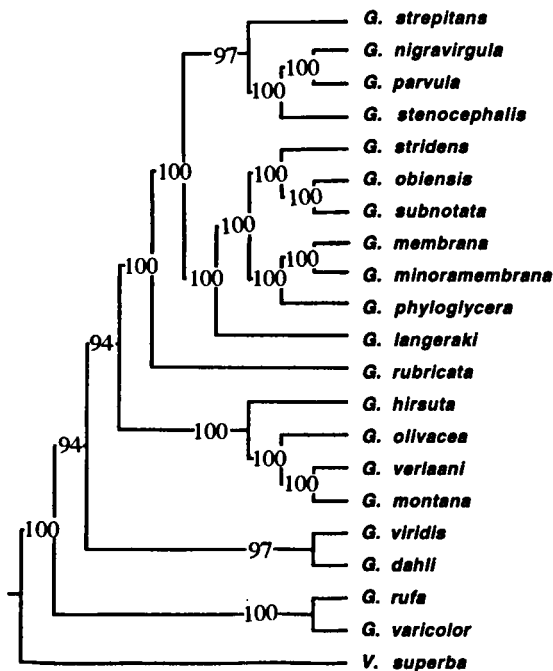


Fig. 9. Section of the 50% majority rule tree dealing with *Gymnotympana*. Numbers refer to percentages of trees supporting the branch.

tions have slightly changed. The tree presented here is, as to these relative positions, regarded as equally acceptable as the one published before. Four species (*G. dahli*, *G. rubricata*, *G. strepitans*, and *G. viridis*) that are supposed to form a monophyletic group based on shared characters of the clasper, and that appeared as paraphyletic in the earlier cladogram (De Boer, 1995a) now appear as being less closely related. Converting these four species into a monophyletic group, in a then most parsimonious reconstruction of *Gymnotympana* as proposed here (Fig. 4) costs 4 extra steps.

Venustria

The position of the monotypic genus *Venustria* as sister taxon of *Gymnotympana*, which also appears in the strict consensus tree (Fig. 3), is in agreement with earlier proposals and here accepted as most likely. Nevertheless, two unique characters contradict this solution and suggest that *Venustria* should be included in *Gymnotympana* as in Fig. 10. *V. superba*, *G. rufa*, and *G. varicolor* share a very similar basal part of the male operculum (1 in Fig. 10), while *V. superba* and *G. rufa* share a distinct ventral thorn on the female genital segment (2 in Fig. 10) (De Boer, 1995a). The inclusion of *Venustria* in *Gymnotympana*, as is considered possible, would cost 5 extra steps.

Chlorocysta, *Glaucopsaltria*, and *Owra*

The phylogenetic reconstruction of *Chlorocysta*, *Glaucopsaltria*, and *Owra*, as presented in Fig. 4, is identical to that in the strict consensus tree and accepted as correct.

In an earlier discussion on the phylogeny of the Chlorocystini (De Boer, 1995a, b, c, d) the relative positions of the Australian genera complex (*Chlorocysta*, *Glaucopsaltria*, and *Owra*) and of the sister genera *Guineapsaltria* and *Papuapsaltria* remained uncertain; either of these groups could be the sister group of the monophyletic group containing *Baeturia*, *Gymnotympana*, *Scottotympana*, and *Venustria*. The most parsimonious solution indicates, also in the strict consensus tree, that the Australian genera form the sister group of the latter group. This solution, however, is not based on convincing synapomorphies. The weakness of this part

of the cladogram is expressed by the fact that swapping the position of the Australian genera with that of *Guineapsaltria* and *Papuapsaltria* would make the total tree only 2 steps longer. In view of the available data, a generic cladogram with a polytomy as in Fig. 11 is a more realistic way of representing these uncertainties.

Guineapsaltria

The most parsimonious reconstruction of *Guineapsaltria* in the 50% majority rule tree (Fig. 12a) is largely in agreement with the earlier discussion on the phylogeny of that genus (De Boer, 1993b). The only problem forms the ambiguous position of *G. chinai*. This species shares a similar clasper with *G. pallida*, *G. pallidula*, and *G. viridula*, but a similar postclypeus with *G. flava*, *G. flaveola*, and *G. stylata*, and has a, presumably plesiomorphous, narrower vertex than other species of *Guineapsaltria*. Consequently, *G. chinai* is placed at the base of the cladogram of *Guineapsaltria*. The striking similarities in the unique clasper shape of *G. chinai*, *G. pallida*, *G. pallidula*, and *G. viridula*, however, are regarded as convincing evidence for the monophyly of that group, though possibly including the deviating *G. pennyi*. Changing the position of *G. chinai* to that group, as proposed here (Fig. 4), costs 2 extra steps.

Papuapsaltria

The monophyly of the genus *Papuapsaltria* was considered doubtful, since its presumed apomorphy, a reduced femoral spine, is not found in all species of the genus (De Boer, 1995c). Several monophyletic groups were recognized within *Papuapsaltria* and it was stated that a subgroup with a mainly northwestern New Guinea distribution showed similarities in tegmen venation with *Guineapsaltria*. Two species, *P. phyllophora* and *P. woodlarkensis*, were tentatively placed at the base of the cladogram since their characters did not give a clue to a possible sister-group relationship with other species (groups) of the genus. In this light, it is remarkable that the computer analysis involving all characters comes up with two equally parsimonious solutions. In Fig. 12b, *Papuapsaltria* is paraphyletic, with the northwestern New Guinea species as sister group of *Guineapsaltria* and the re-

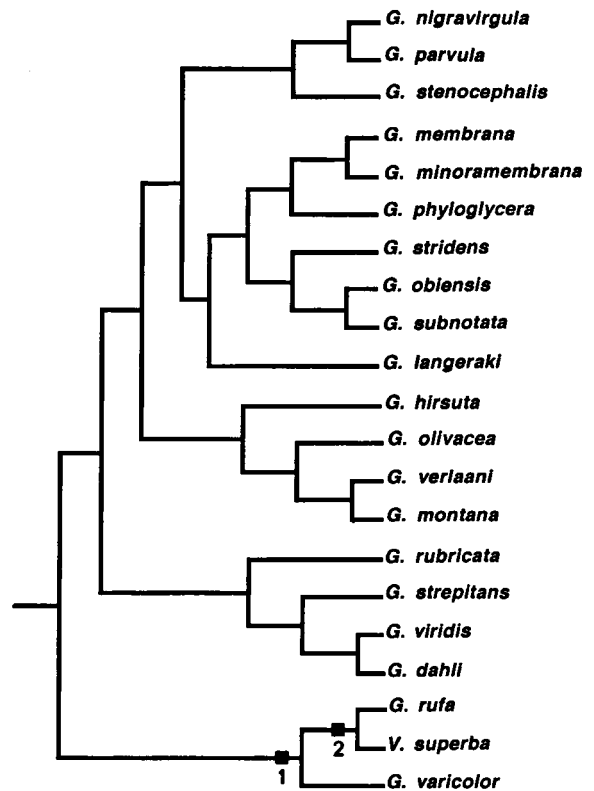


Fig. 10. Cladogram of *Gymnotympana* with *Venustria* included. Numbers refer to characters discussed in the text.

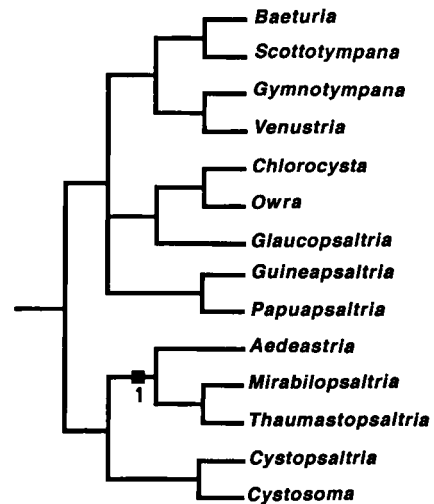


Fig. 11. Generic cladogram of the Chlorocystini with a polytomy for the groups *Baeturia-Venustria*, *Chlorocysta-Glaucopsaltria*, and *Guineapsaltria-Papuapsaltria*. Number refers to character discussed in the text.

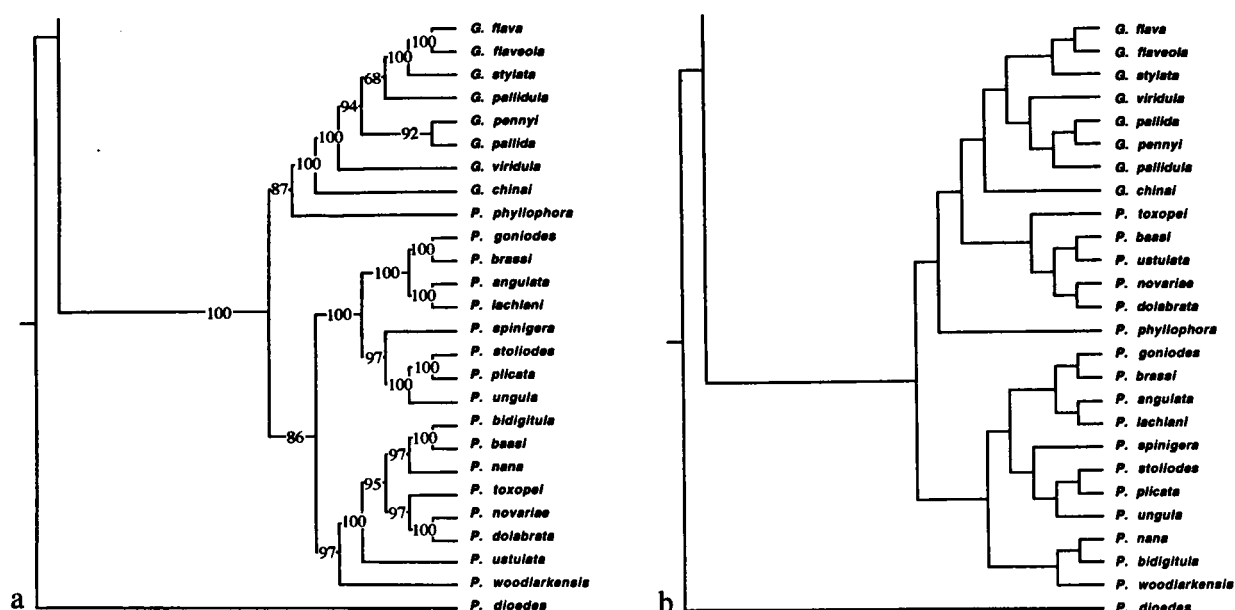


Fig. 12. (a), Section of the 50% majority rule tree dealing with *Guineapsaltria* and *Papuapsaltria*, numbers refer to percentages of trees supporting the branch; (b), alternative phylogenetic reconstruction for the genera *Guineapsaltria* and *Papuapsaltria*, with a paraphyletic genus *Papuapsaltria*.

maining species as sister group of these two groups combined. In Fig. 12a, *Papuapsaltria* is practically monophyletic.

In both these options, which are in principle regarded equally plausible, *P. dioedes* is excluded from *Papuapsaltria* and figures as sister taxon to all the above-discussed genera together (cf. Fig. 3). *P. dioedes* differs strongly from other *Papuapsaltria* species by several presumably autapomorphic male genital characters, but the species does share the presumed apomorphic reduced femoral spine and certainly should be included somewhere within *Papuapsaltria*. Besides, the suggested monophyly of the group including all genera discussed above and excluding *P. dioedes* is based on the presumed apomorphic but strongly fluctuating character of a broadly rounded pygofer opening, which certainly does not characterise that group as a whole and is considered meaningless at this level of the cladogram. Including *P. dioedes* in *Papuapsaltria* in a most parsimonious position costs 3 extra steps in both the monophyletic alternative (Fig. 4) and the paraphyletic solution (Fig. 12c).

The position of *P. dioedes* is very uncertain,

however. This is demonstrated by the fact that its position in the paraphyletic construction as either the sister group of *Guineapsaltria*, or of *toxopei-dolabrata*, or of *phyllophora*, or of *Guineapsaltria-phyllophora*, or of *goniodes-ustulata*, or of *goniodes-woodlarkensis*, is equally parsimonious. The two most parsimonious alternatives (Figs. 12a, b) show several other differences with the earlier cladogram (De Boer, 1995c). In both alternatives, and in the strict consensus tree, *P. goniodes* and *P. brassi* (based on five tymbal ridges and a broader vertex) and *P. angulata* and *P. lachlani* (based on a slender male caudodorsal beak) are sister species, while in the previous cladogram (De Boer, 1995c) *P. goniodes* and *P. angulata* (based on a similar male operculum) and *P. lachlani* and *P. brassi* (based on an extremely long aedeagus) are supposed to be sister species. The latter character is difficult to quantify, and was not included in the matrix. Still, this latter option is preferred here, although it is two steps longer in both alternatives (Figs. 4, 12c).

The northwestern New Guinea subgroup that was recognized before (*P. baasi*, *P. dolabrata*, *P. nova-*

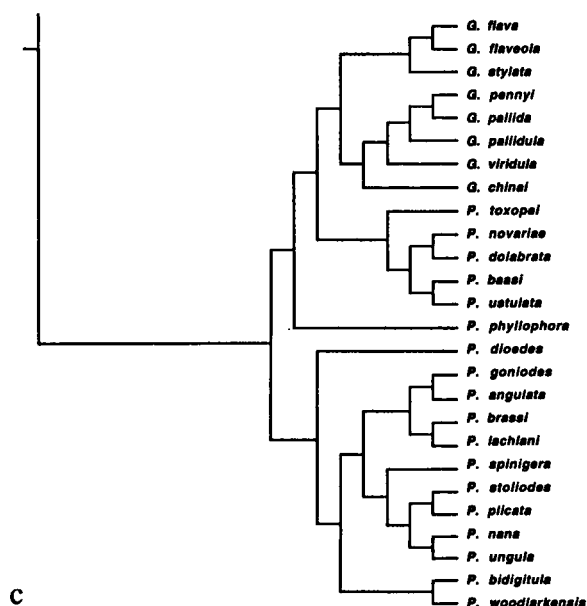


Fig. 12. (c), Most parsimonious McClade reconstruction for the genera *Guineapsaltria* and *Papuapsaltria* in the alternative version with a paraphyletic genus *Papuapsaltria*, and after including the modifications suggested.

riae, *P. ustulata*) is recognized in the paraphyletic option but not in the monophyletic one. In the latter option *P. nana* and *P. bidigitula* are included in that group, based on an in other parts of the tree strongly variable character of the postclypeus. In both these options, the likewise northwestern New Guinea species *P. toxopei* is included in this group. In the cladogram presented earlier (De Boer, 1995c) *P. nana* and *P. bidigitula* were included in a monophyletic group with *P. plicata*, *P. spinigera*, *P. stoliodes*, and *P. ungula*, with *P. nana* as sister species of *P. ungula*, which was based on several convincing apomorphies in the clasper. Removing these species, as proposed here, to their more credible position minimally costs 2 extra steps in both the monophyletic option (Fig. 4) and the paraphyletic one (Fig. 12c).

The phylogenetic position of *P. woodlarkensis* remains dubious; in the paraphyletic option the species is included in the Papuan group, and in the monophyletic option in the northwestern New Guinea group, but after the proposed changes its most parsimonious position is in the Papuan group in the latter option as well. Furthermore, after these

changes, the most parsimonious position of *P. phyllophora* is no longer at the base of *Guineapsaltria*, but at the base of *Papuapsaltria*.

Aedeastria

The most parsimonious reconstruction of *Aedeastria* in the 50% majority rule tree (Fig. 13) is almost identical to that in the strict consensus tree, but completely differs from earlier conclusions on its phylogeny (De Boer, 1993a). The earlier proposed monophyly of a group consisting of *A. digitata*, *A. cobrops*, *A. kaiensis*, *A. latifrons*, *A. sepia*, and *A. waigeuensis* which was recognized on the basis of a unique bicuspidate clasper (De Boer, 1993a), is not recognized in the computer analysis (in that earlier phylogenetic discussion *A. cheesmanae* was abusively exchanged for *A. waigeuensis*). Instead, the remaining species of the genus form a monophyletic group, based on a hook-shaped and apically pointed clasper, a character which frequently occurs in many other genera. Converting the above-listed species into a monophyletic group as proposed here costs 7 extra steps in the then most parsimonious solution (Fig. 4), but only 6 extra steps in the reconstruction with a paraphyletic genus *Papuapsaltria* which gives a slightly different solution (Fig. 14). *A. hastulata* is in a most parsimonious solution part of this group in both cases.

The position of *Aedeastria*, either as sister group of *Mirabilopsaltria* and *Thaumastopsaltria* (based on a shared wrinkled vertex with distinct diverging fissures, 1 in Fig. 11), or as sister group of all above-discussed genera together (based on a shared erect femoral spine, 1 in Fig. 15) was discussed in several previous publications (De Boer, 1995a, b, c, d). The most parsimonious tree unambiguously recognized *Aedeastria* as the sister group of *Mirabilopsaltria* and *Thaumastopsaltria*, but changing *Aedeastria* to a sister-group position of all above-discussed genera (see Fig. 15) will make the total tree only 1 step longer and should still be considered a possibility.

Thaumastopsaltria

The cladogram of *Thaumastopsaltria* in the 50% majority rule tree (Fig. 13) is fully solved and in agreement with previous discussions on the phylogeny of this genus (De Boer, 1992a).

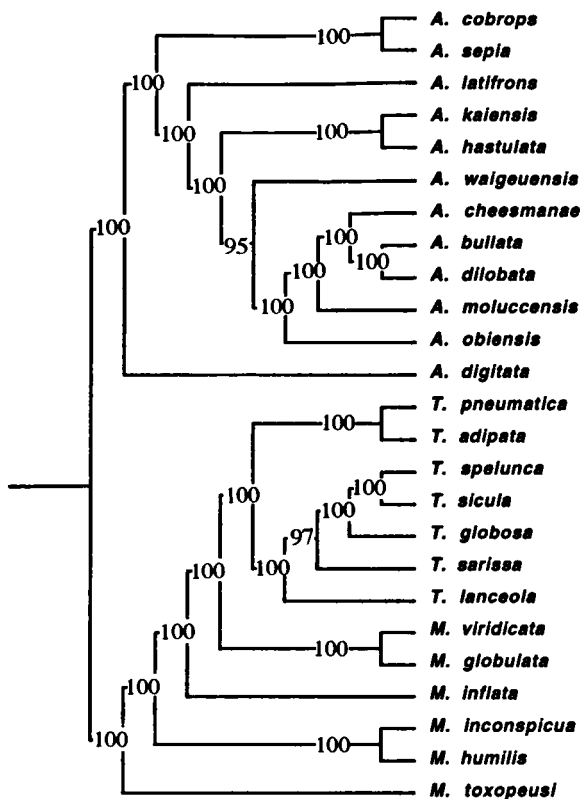


Fig. 13. Section of the 50% majority rule tree dealing with *Aedeastria*, *Thaumastopsaltria*, and *Mirabilopsaltria*. Numbers refer to percentages of trees supporting the branch.

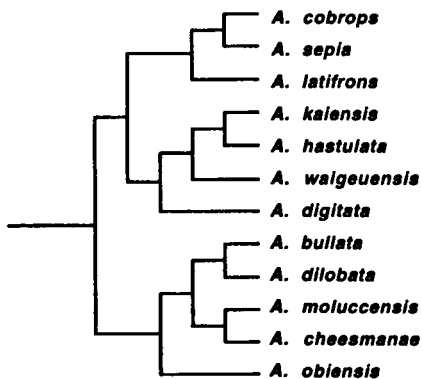


Fig. 14. Most parsimonious McClade reconstruction of *Aedeastria* in the alternative version with a paraphyletic genus *Papuapsaltria*, and after including the modifications suggested.

Mirabilopsaltria

The monophyly of *Mirabilopsaltria* was considered uncertain (De Boer, 1995b). The presumed apo-

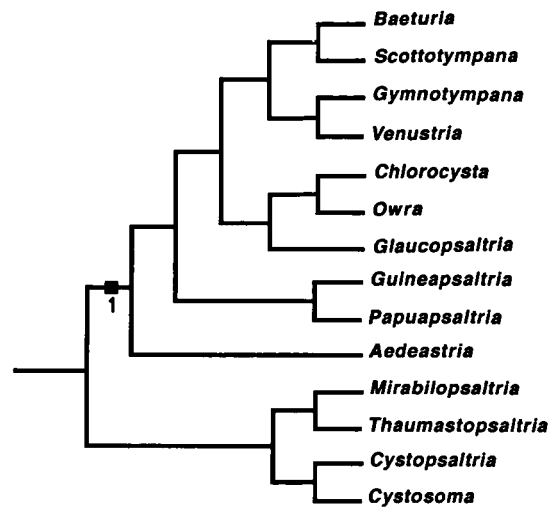


Fig. 15. Generic cladogram of the Chlorocystini with an alternative position for *Aedeastria*. Number refers to character discussed in the text.

morphy in clasper shape is not present in *M. viridicata* and, though possibly changed beyond recognition, in *M. globulata*. This presumed apomorphy is not recognized in the most parsimonious tree, not for *Mirabilopsaltria* as a whole and not for the species that do have that character. In the 50% majority rule tree (Fig. 13) the species of *Mirabilopsaltria* appear as a paraphyletic sister group of *Thaumastopsaltria*. The characters in support of this paraphyletic reconstruction are, with a possible exception of the one determining *M. viridicata* and *M. globulata* as the immediate sister group of *Thaumastopsaltria* (an extremely long 1st apical area in the tegmen), considered less convincing than the clasper character. *M. humilis*, *M. inconspicua*, *M. inflata*, and *M. toxopeusi* are still supposed to form a monophyletic group (Fig. 4). This option is proposed here and makes the tree 2 steps longer. Although the inclusion of *M. viridicata* and *M. globulata* into a monophyletic genus *Mirabilopsaltria* is still a possibility to be considered, depending on the possible homology of the *M. globulata* clasper with that of the other species of *Mirabilopsaltria*, their sister-group relationship to *Thaumastopsaltria* now seems more likely. Including these species in *Mirabilopsaltria* would cost no less than 4 extra steps.

Cystopsaltria and *Cystosoma*

The basal position of *Cystopsaltria* and *Cystosoma* in the most parsimonious reconstruction (Fig. 3) is caused by the several characters these genera share with the outgroup *Prasia*. The there suggested monophyly of the Chlorocystini excluding *Cystopsaltria* and *Cystosoma* is based on two very unconvincing characters that cannot be regarded as representative for that group. In previous discussions on the phylogeny of the Chlorocystini (De Boer, 1995a, b, c, d) it was suggested that *Cystopsaltria* and *Cystosoma* formed the sister group of *Mirabilopsaltria* and *Thaumastopsaltria*, either or not including *Aedeastria* (see above) based on the narrow tymbal cavity shared by *Cystosoma* and most species of *Mirabilopsaltria* and *Thaumastopsaltria*; this solution is still regarded as more credible. Moving *Cystopsaltria* and *Cystosoma* to the base of *Aedeastria*, *Mirabilopsaltria*, and *Thaumastopsaltria* as proposed here costs only 1 step more (Fig. 4). The ingroup phylogeny of *Cystopsaltria* and *Cystosoma* given in Fig. 4 is identical to that of the strict consensus tree.

Conclusions

The final tree which contains all of the presumed synapomorphies and deals with the remaining characters in a most parsimonious way is still considered to have two equally likely solutions for the genus *Papuapsaltria* (Figs. 4, 12c). The option with a monophyletic solution for *Papuapsaltria* has a length of 906 steps, the paraphyletic option has 905 steps in its shortest acceptable solution. Apart from the *Guineapsaltria-Papuapsaltria* part of the cladogram these alternatives only differ slightly in a most parsimonious reconstruction of *Aedeastria* and the *Baeturia nasuta* group.

The results of this phylogenetic analysis, together with the biogeographical data discussed in previous publications (De Boer, 1982 and later works), provide the data for an area cladistic study of the New Guinea-West Pacific region. A comparison of area cladograms with data on the palaeogeology of the area in question suggests that the main speciation events that led to the present-day generic diversity

in the Chlorocystini (sensu stricto) are caused by vicariance following the fragmentation of a historical volcanic island arc (De Boer, 1995d). The phylogenetic reconstruction with a paraphyletic genus *Papuapsaltria* (Fig. 12c) which separates the genus roughly in a western and eastern species group, appears to agree best with the historical explanations provided in that publication. Similarly, a paraphyletic option for the genus *Mirabilopsaltria*, which turns out to be the most parsimonious solution (Fig. 4), better fits the historical explanations. Furthermore, a position of *Guineapsaltria-Papuapsaltria* as sister group to the group *Baeturia-Venustria*, of which the possibility is discussed above (cf. Fig. 11) is in biogeographical sense slightly more parsimonious than the option given in Fig. 4, since the latter requires the extinction of a group in a missing area (De Boer, 1995d).

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Appendix 1. List of characters

Colour

- 1 Body colour: (1) unspeckled, (2) speckled with brown
- 2 Colour of female: (1) uniformly coloured, (2) bicoloured: head and thorax green, abdomen ochraceous

Head

- 3 Postclypeus: (1) anteriorly rounded, (2) with sharp anterior edge
- 4 Anterior margin of postclypeus in dorsal view: (1) continuous with anterior margins of vertex lobes, (2) convexly protruding beyond vertex lobes, (3) strongly curving back laterally and making almost right angle with vertex lobes
- 5 Postclypeus in lateral view: (1) not swollen, (2) angularly swollen, (3) globularly swollen, (4) protruding in obtuse angle, (5) with convex anterior margin
- 6 Lateral sides of postclypeus: (1) without posterior ridge along lorum, (2) with swollen posterior ridge along lorum
- 7 Lateral sides of postclypeus: (1) with distinct rasps of rows of short parallel ridges, (2) with very short and indistinct rows of parallel ridges, (3) without rows of parallel ridges
- 8 Vertex: (1) without dark spots, (2) with dark spots between eyes and lateral ocelli
- 9 Medial part of vertex: (1) distinctly rising from postclypeus, (2) very flat, (3) slightly indented
- 10 Surface of vertex: (1) smooth, (2) with distinct fissures diverging from centre of head to corners of postclypeus
- 11 Distance between lateral ocelli: (1) hardly exceeding width of frontal ocellus, (2) distinctly larger than width of frontal ocellus
- 12 Distance between lateral ocelli: (1) about equalling distance between lateral ocellus and eye, (2) generally slightly larger than distance between lateral ocellus and eye, (3) generally distinctly larger than distance between lateral ocellus and eye

Pronotum

- 13 Pronotal surface: (1) smooth, (2) mottled
- 14 Pronotum: (1) without dark medial spot, (2) with dark medial spot at pronotal collar

- 15 Pronotum: (1) without coloured medial band, (2) with dark streaks along light medial band, (3) with darkened medial band
- 16 Pronotum: (1) without distinct medial furrow, (2) with distinct medial furrow
- 17 Anterolateral side of pronotal collar: (1) rounded, (2) swollen, (3) angularly bent, (4) forming continuous ridge

Mesonotum

- 18 Mesonotal colouring: (1) without spots in front of cruciform elevation, (2) two black spots in front of cruciform elevation
- 19 Cruciform elevation: (1) wider than long, (2) narrower than long

Legs

- 20 Proximal spine of fore femur: (1) erect, (2) bent adjacent to femur
- 21 Proximal spine of fore femur: (1) of normal length, (2) extremely long, (3) reduced
- 22 Proximal spine of fore femur: (1) not shorter than distance to middle spine, (2) distinctly shorter than distance to middle spine, (3) slightly shorter than distance to middle spine
- 23 Middle spine of fore femur: (1) narrow spiny, (2) broad triangular

Tegmina and wings

- 24 Colour of tegmen: (1) hyaline, (2) opaque greenish or reddish, (3) slightly reddish but still hyaline, (4) bronzed
- 25 Colour markings on tegmen: (1) immaculate, (2) brown spots along veins, (3) triangular brown spots at ends of apical areas
- 26 Shape of tegmen: (1) rounded at apex, (2) pointed at apex
- 27 Tegmen venation: (1) not reticulate, (2) reticulate
- 28 Hyaline hind margin of tegmen: (1) very narrow, (2) narrow but distinct, (3) broad
- 29 Costal area of tegmen: (1) narrow to apex, (2) widening to apex
- 30 Number of apical areas in tegmen: (1) eight, (2) eight or nine, (3) nine, (4) nine or ten, (5) variable between nine and fifteen, (6) more than twenty
- 31 Ultimate apical area of tegmen: (1) quadrangular, (2) triangular
- 32 Subapical areas of tegmen: (1) absent, (2) present but not forming a continuous band, (3) forming a continuous band, (?) not clear due to reticulate venation
- 33 Base of first apical area of tegmen: (1) distally of base of third apical area, (2) slightly proximally of base of third apical area, (3) distinctly proximally of base of third apical area
- 34 Veins of tegmen: (1) without or practically without setae, (2) densely set with setae
- 35 Number of apical areas in wing: (1) six, (2) five, (3) six or seven, (4) seven or more
- 36 Sexual dimorphism in anal fields of wing: (1) absent, (2) present

Tymbal organ

- 37 Tymbal: (1) parallel to lateral side of abdomen, (2) strongly curved inwards towards its ventral corner
- 38 Number of tymbal ridges: (1) four ridges or less, (2) five ridges, (3) six ridges, (4) seven ridges, (5) eight ridges, (6) ten ridges, (7) eleven ridges or more
- 39 Tymbal ridges: (1) parallel, (2) aberrant
- 40 Tymbal ridges: (1) not curved around intercalary ridges, (2) curved around intercalary ridges
- 41 Tymbal cavity: (1) broad, (2) narrow

Opercula

- 42 Male opercula: (1) widely separated, (2) juxtaposed medially
- 43 Male operculum: (1) longer than meracanthus, (2) shorter than meracanthus
- 44 Male operculum: (1) not completely covering tymbal cavity, (2) completely covering tymbal cavity
- 45 Male operculum: (1) not elongate at medial margin, (2) elongate at medial margin
- 46 Basal part of male operculum: (1) distinctly vaulted, (2) strongly curved down medially, (3) hardly vaulted
- 47 Basal part of male operculum: (1) almost oblong, (2) laterally longer than medially, (3) laterally shorter than medially and abruptly lengthening, (4) laterally shorter than medially and gradually lengthening
- 48 Lateral crest of operculum base: (1) normally developed, (2) very long and slender
- 49 Shape of distal part of male operculum: (1) angularly oval, (2) squarely rounded, (3) blunt triangular and flat, (4) blunt triangular with straight lateral margin, (5) triangular and domed, (6) small and rounded, (7) small and angular
- 50 Lateral margin of male operculum: (1) not continuous to distolateral corner of operculum base, (2) continuous to distolateral corner of operculum base
- 51 Distomedial margin of male operculum: (1) without recurving rim, (2) with recurving rim
- 52 Medial margin of male operculum: (1) medially of meracanthus, (2) laterally of meracanthus
- 53 Meracanthus in male: (1) normally developed, (2) strongly reduced
- 54 Distal part of female operculum: (1) rectangular oblong, (2) trapezoid, (3) narrow sickle-shaped, (4) broad sickle-shaped, (5) continuous to distolateral corner of basal part, (6) triangular

Abdomen

- 55 Male abdomen: (1) not transparent, (2) transparent
- 56 Male abdomen: (1) rounded lateroventrally, (2) tergites sharply folded lateroventrally
- 57 Abdominal sternites: (1) without medial band, (2) with red medial band
- 58 First sternite of male: (1) short; broader than long, (2) long; longer than broad
- 59 Eighth sternite of male: (1) not sharply incised, (2) sharply incised at distal margin
- 60 Second tergite of male: (1) swollen along tymbal, (2) not

swollen but folded inwards along tymbal, (3) forming a distinct ridge along tymbal

- 61 Second tergite of male: (1) forming a distinct ridge along tymbal cavity, (2) not forming a distinct ridge along tymbal cavity
- 62 Second tergite of male: (1) not membranous, (2) membranous opposite tymbal
- 63 Second tergite of male: (1) not swollen, (2) swollen along tymbal cavity
- 64 Eighth tergite of male: (1) not forming ventral lobe, (2) forming small posteriorly projecting ventral lobe
- 65 Male auditory capsule: (1) swollen and protruding, (2) not swollen and not protruding
- 66 Pygofer and 9th sternite: (1) resting on 8th sternite, (2) elevated relative to 8th sternite
- 67 Connecting bar between tymbal and abdomen: (1) not elongate, (2) strongly elongate
- 68 Connecting bar between tymbal and abdomen: (1) parallel to body axis, (2) directed mesiad

Male pygofer

- 69 Pygofer: (1) not curved to ventral position, (2) curved to ventral position on abdomen
- 70 Pygofer: (1) without lateral fold, (2) with distinct fold at base of caudodorsal beak
- 71 Male caudodorsal beak: (1) erect and not reaching over anal valves, (2) curved and extending over anal valves, (3) absent
- 72 Male caudodorsal beak: (1) not covering anal valves, (2) very strongly curved and covering anal valves
- 73 Male caudodorsal beak: (1) erect, (2) angularly bent and dorsally flattened, (3) bent down towards apices of lateral lobes, (4) strongly rounded; continuously rounded with dorsal margin of pygofer, (5) strongly rounded but not continuous with dorsal margin of pygofer, (6) weakly curved
- 74 Male caudodorsal beak: (1) straight to apex, (2) concave to apex
- 75 Apex of male caudodorsal beak: (1) sharply pointed, (2) rounded, (3) truncate or weakly concave, (4) bicuspidate, (5) broadly rounded, (6) beak missing
- 76 Male caudodorsal beak in lateral view: (1) stout, (2) slender
- 77 Male caudodorsal beak: (1) broad at base, (2) narrow oblong, (3) spine-shaped
- 78 Male caudodorsal beak: (1) hollow, reversed gutter-shaped, (2) massive
- 79 Male caudodorsal beak in dorsal view: (1) oblong with almost parallel lateral margins, (2) triangular with converging margins
- 80 Protuberance on lateral lobe of pygofer: (1) narrow lobate or laminiform, (2) extremely broad and lobate
- 81 Protuberance on lateral lobe of pygofer: (1) not conically elongate beyond pygofer margin, (2) conically elongate beyond pygofer margin
- 82 Protuberance on lateral lobe of pygofer: (1) not triangularly swollen, (2) triangularly swollen
- 83 Protuberance on lateral lobe of pygofer: (1) rounded, (2) with sharp lateral edge
- 84 Protuberance on lateral lobe of pygofer: (1) straightly directed posteriad, (2) upcurving towards apex

- 85 Distal margin of pygofer: (1) curving to base of lateral protuberance, (2) curving to apex of lateral protuberance
- 86 Pygofer: (1) not broadening between lateral protuberances, (2) broadening between lateral protuberances
- 87 Pygofer: (1) not narrowing between lateral protuberances, (2) narrowing between lateral protuberances
- 88 Distal margin of pygofer: (1) weakly convex, (2) strongly convex into a distinct posterior lobe, (3) weakly concave, (4) strongly concave
- 89 Ventral part of pygofer: (1) not or hardly protruding, (2) forming a rectangular corner under lateral protuberance, (3) forming a thorn-shaped protuberance under lateral protuberance
- 90 Pygofer: (1) not swollen at ventral margin, (2) swollen at ventral margin
- 91 Ventral margin of pygofer: (1) straight to base, (2) strongly concave to base
- 92 Pygofer opening: (1) without straight basal margin, (2) with straight basal margin
- 93 Ventral half of pygofer opening: (1) not bordered by a continuous sharp edge, (2) bordered by a continuous sharp edge
- 94 Ventral half of pygofer opening: (1) not horseshoe-shaped, (2) horseshoe-shaped with incurving lateral corners
- 95 Ventral half of pygofer opening: (1) triangular and pointed, (2) broad and rounded, (3) with concave margins and pointed, (4) very long and slender
- 96 Basal margin of pygofer opening: (1) not lowered, (2) lowered
- 97 Anal valves: (1) not swollen, (2) swollen

Clasper

- 98 Claspers: (1) fused or practically fused to a more or less continuous ring around base of anal valves, (2) distinctly separated at base
- 99 Clasper: (1) without lateral plate, (2) with lateral plate
- 100 Clasper: (1) strongly bent and hook-shaped, (2) nearly straight and posteriorly directed
- 101 Clasper: (1) not triangular, (2) triangle-shaped in lateral view
- 102 Clasper: (1) not forming a shaft around aedeagus, (2) forming a shaft around aedeagus
- 103 Claspers: (1) parallel, (2) diverging towards apices
- 104 Clasper: (1) not rectangular laminiform, (2) rectangular laminiform
- 105 Clasper: (1) not transparent ventromedially, (2) ventromedially transparent
- 106 Clasper: (1) without distinct cross fold, (2) with distinct cross fold between basal part and apical part
- 107 Clasper base: (1) without crest protruding beyond pygofer margin, (2) with distinct lateral crest protruding beyond pygofer margin
- 108 Clasper base: (1) not forming clasper heel, (2) forming distinct angular dorsal corner or clasper heel
- 109 Clasper: (1) without dorsally protruding clasper heel, (2) with dorsally protruding clasper heel
- 110 Proximal parts of claspers: (1) not merged between aedeagus and anal valves, (2) merged between aedeagus and anal valves
- 111 Dorsal part of clasper: (1) not forming a shaft around aedeagus, (2) forming a short shaft around aedeagus
- 112 Claspers: (1) without sharp and converging dorsal edges, (2) with sharp and converging dorsal edges
- 113 Dorsal crest of clasper: (1) not angularly protruding, (2) angularly protruding at distal corner
- 114 Dorsal margin of clasper: (1) not rectangularly bent, (2) rectangularly bent at half-length
- 115 Clasper: (1) without dorsal crest, (2) with short dorsal crest on proximal half only, (3) with dorsal crest over almost whole length
- 116 Clasper: (1) with no or straight dorsal crest, (2) with convex dorsal crest
- 117 Dorsal crest of clasper: (1) erect or absent, (2) curving laterad
- 118 Dorsal crest of clasper: (1) absent or not forming dorsal protrusion, (2) forming dorsal protrusion
- 119 Dorsal protrusion of clasper: (1) absent, (2) broad lamiform, (3) narrow finger-shaped, (4) humped
- 120 Dorsal edge of clasper: (1) not curved around aedeagus, (2) forming a rectangular corner around aedeagus, (3) forming a rectangular crest around aedeagus, (4) forming a distinctly swollen protuberance around aedeagus, (5) globularly rounded
- 121 Apical part of clasper: (1) without proximal protrusion, with proximal protrusion
- 122 Clasper apex: (1) not swollen, (2) swollen
- 123 Clasper apex: (1) not globularly swollen, (2) globularly swollen
- 124 Clasper apex: (1) broad in dorsal view, (2) abruptly narrowing in dorsal view
- 125 Clasper apex: (1) pointed or rounded, (2) bicuspidate or dentate
- 126 Apical part of clasper in lateral view: (1) not broader than basal part, (2) broader than basal part
- 127 Clasper: (1) without small triangle-shaped apical part, (2) with very small triangle-shaped apical part
- 128 Clasper hollow: (1) long and strongly bent, (2) long and straight, (3) short and straight, (4) short and strongly bent, (5) short and downcurved, (6) different
- 129 Clasper: (1) without ventromedial protuberance, (2) with broad and laminiform ventromedial protuberance, (3) with narrow and spiny ventromedial protuberance
- 130 Clasper: (1) without distinct rim around ventral hollow, (2) with distinct rim around ventral hollow
- 131 Clasper: (1) without lateral process, (2) with lobate lateral process, (3) with lateral thorn, (4) with lateral crest ending in small thorn

Aedeagus

- 132 Aedeagus: (1) S-curved, (2) C-curved
- 133 Aedeagus: (1) not Z-curved in apical part, (2) Z-curved in apical part

- 134 Surface of aedeagus: (1) smooth, (2) with pattern of concentric ridges
- 135 Orientation of aedeagus: (1) more or less erect between claspers, (2) directed posteriad parallel to and between claspers
- 136 Aedeagus: (1) with lateral crests, (2) with lateral lobes, (3) with elongate lateral lobes
- 137 Lateral lobes of aedeagus: (1) straight or absent, (2) strongly curving laterad
- 138 Lateral crest of aedeagus: (1) gradually tapering towards aedeagal apex, (2) ending in rectangular corner
- 139 Aedeagus: (1) without crest between lateral lobes, (2) with crest between lateral lobes
- 140 Aedeagus: (1) not swollen between lobes, (2) swollen between lobes
- 141 Aedeagus part distally of basal curve: (1) not long and slender, (2) extremely long and slender
- 142 Apical part of aedeagus: (1) not abruptly narrowing, (2) abruptly narrowing and upcurving, (3) abruptly narrowing and downcurving
- 143 Aedeagal apex: (1) not elongated dorsally, (2) distinctly elongated dorsally, (3) slightly elongated dorsally
- 144 Aedeagus: (1) without distinct subapical lobe, (2) with distinct subapical lobe
- 145 Aedeagus: (1) without dorsal crests, (2) with single dorsal crest, (3) with paired dorsal crests, (4) with pair of dorso-lateral protuberances
- 146 Aedeagus: (1) without ventral crest, (2) with ventral crest or keel
- 147 Aedeagus from behind: (1) not bottle-shaped, (2) bottle-shaped; abruptly narrowing towards apex
- 148 Aedeagus: (1) strongly curved and tapering to apex, (2) strongly curved and not tapering to apex, (3) weakly curved
- 149 Aedeagus: (1) not strongly swollen proximally, (2) strongly swollen proximally
- 150 Aedeagal pore: (1) narrow oval, (2) triangular and widening to broadly rounded proximally, (3) apically pointed but not widening proximally, (4) broad oval, (5) round
- 151 Margin of aedeagal pore in lateral view: (1) weakly concave, continuous with curve of aedeagus, (2) strongly concave, not continuous with curve of aedeagus, (3) convex, due to dorsoventral incision, (4) straight
- Female genitalia
- 152 Ovipositor sheaths: (1) reaching to apex of caudodorsal beak, (2) reaching just beyond apex of caudodorsal beak, (3) reaching far beyond apex of caudodorsal beak
- 153 Apex of female caudodorsal beak: (1) sharply pointed, (2) broadly rounded, (3) narrowly rounded, (4) truncate, (5) bicuspidate
- 154 Female pygofer: (1) without ventral thorn, (2) with ventral thorn

Appendix 2. List of presumed apomorphies, the black squares in Fig. 4.

| Internode | Character nr. and state | Homoplasies (H) and reversals (R) |
|-----------|-------------------------|---|
| 4–3 | 119–2 | |
| 5–4 | 119–(2+3+4) | |
| | 153–4 | H in <i>B. edauberti</i> , <i>O. insignis</i> |
| 7–5 | 118–2 | |
| 9–8 | 5–2 | H in <i>B. bemmeleni</i> , <i>B. daviesi</i> , <i>B. guttulinervis</i> , <i>B. hamiltoni</i> , <i>B. pigrami</i> , <i>B. wauensis</i> |
| | 38–1 | H in internode 66–65 |
| 16–9 | 55–2 | R in <i>B. marmorata</i> |
| | | H in internode 67–66 |
| | 73–2 | |
| | 141–2 | H in internode 52–51 |
| 15–11 | 116–2 | H in internode 53–50 |
| 13–12 | 75–4 | H in internode 99–97 |
| 14–13 | 140–2 | |
| 15–14 | 73–3 | H in <i>B. furcillata</i> |
| 16–15 | 83–2 | H in <i>B. inconstans</i> |
| | 107–2 | H in <i>B. inconstans</i> |
| | 79–1 | H in <i>B. guttulipennis</i> |
| 25–16 | | |
| 20–19 | 137–2 | |
| 24–20 | 38–3 | H in many groups |
| 23–22 | 130–2 | |
| 24–23 | 123–2 | |
| 25–24 | 73–4 | H in <i>A. digitata</i> , <i>B. furcillata</i> , <i>B. gressitti</i> & internode 35–34 |
| | 122–2 | |
| | 153–3 | H in <i>B. gibberosa</i> |
| 40–25 | 81–2 | R in node 18–17 |
| 35–34 | 73–4 | H in <i>A. digitata</i> , <i>B. furcillata</i> , <i>B. gressitti</i> & internode 25–24 |
| 36–35 | 124–2 | |
| 39–38 | 150–1 | H in <i>B. papuensis</i> and many groups of <i>Baeturia</i> |
| | | H in <i>B. rossi</i> |
| 40–39 | 49–2 | |
| 44–43 | 113–2 | |
| | 30–4 | |
| 46–45 | 22–3 | H in <i>B. karkarensis</i> , <i>B. rufa</i> , <i>B. turgida</i> |
| 47–46 | 87–2 | |
| | 117–2 | |
| 53–50 | 116–2 | H in internode 15–11 |
| 52–51 | 25–3 | |
| | 144–2 | H in internode 16–9 |
| 53–52 | 126–2 | |
| | 136–3 | |
| 56–53 | 109–2 | H in <i>B. tenuispina</i> |
| 56–55 | 49–3 | H in <i>G. hirsuta</i> , <i>G. olivacea</i> |
| 57–56 | 36–2 | H in internode 80–79 & <i>Prasia</i> |

Appendix 2. Continued.

| Internode | Character nr. and state | Homoplasies (H) and reversals (R) |
|-----------|-------------------------|---|
| 60–57 | 91–2 | H in <i>G. obiensis</i> , <i>G. olivacea</i> , <i>S. huibregtsae</i> , <i>V. superba</i> |
| | 23–2 | H in <i>G. rubricata</i> |
| | 136–(2+3) | |
| | 148–1 | |
| 59–58 | 150–(1–4) | H in <i>A. waigeuensis</i> , <i>A. obiensis</i> , internodes 73–72 & 127–126 |
| | 151–(1+2) | |
| | 88–2 | H in internode 110–109 |
| 60–59 | 99–2 | |
| | 46–2 | |
| | 64–2 | |
| 81–60 | 121–2 | |
| | 138–2 | |
| | 98–1 | H in <i>A. dilobata</i> |
| 69–62 | 120–4 | H in <i>G. varicolor</i> , <i>A. hastulata</i> & internode 99–98 |
| 64–63 | 60–3 | |
| | 62–2 | |
| 67–64 | 89–3 | H in <i>P. woodlarkensis</i> |
| 66–65 | 38–1 | H in internode 8–9 |
| | 40–2 | |
| 67–66 | 48–2 | |
| | 55–2 | H in internode 16–9 |
| 69–68 | 106–2 | |
| | 142–3 | |
| 71–70 | 49–4 | |
| 72–71 | 17–4 | H in <i>M. humilis</i> , <i>Prasia</i> & internodes 131–130 & 139–138 |
| 73–72 | 30–5 | H in <i>B. inconstans</i> , <i>M. inflata</i> , <i>P. goniodes</i> & internodes 86–85 & 131–129 |
| | 31–2 | R in <i>G. olivacea</i> |
| | 32–2 | H in <i>M. inflata</i> , <i>M. globulata</i> & internode 129–128 |
| | 150–4 | H in <i>A. obiensis</i> , <i>A. waigeuensis</i> , <i>G. varicolor</i> |
| 76–75 | 127–2 | |
| 77–76 | 148–2 | |
| 79–77 | 37–2 | R in <i>G. dahli</i> , <i>G. olivacea</i> |
| 79–78 | 47–3 | H in <i>V. superba</i> |
| | 57–2 | |
| 80–79 | 36–2 | H in <i>Prasia</i> & internode 57–56 |
| | 52–1 | H in <i>M. globulata</i> , <i>P. plicata</i> , <i>P. stolidodes</i> |
| 83–82 | 38–7 | |
| 84–83 | 133–2 | |
| 85–84 | 35–2 | H in <i>P. dolabrata</i> |
| 86–85 | 30–5 | H in <i>B. inconstans</i> , <i>M. infla-</i> |

Appendix 2. Continued.

| Internode | Character nr. and state | Homoplasies (H) and reversals (R) |
|-----------|-------------------------|---|
| 93–88 | 32–3 | <i>ta</i> , <i>P. goniodes</i> & internodes 73–72 & 131–129 |
| | 47–4 | |
| | 65–2 | H in <i>C. immaculata</i> |
| | 120–2 | H in internode 131–129 |
| 92–91 | 95–3 | H in internode 104–103 |
| | 110–2 | |
| | 135–2 | H in <i>A. latifrons</i> |
| 93–92 | 6–2 | H in <i>V. superba</i> & internode 138–137 |
| | 101–2 | R in <i>G. pennyi</i> |
| 111–93 | 144–2 | |
| 96–94 | 45–2 | H in <i>G. chinai</i> , <i>P. dioedes</i> |
| 103–96 | 94–2 | |
| | 104–2 | |
| 99–97 | 52–1 | H in <i>M. globulata</i> & internode 86–81 |
| 99–98 | 70–2 | |
| | 75–4 | H in internode 13–12 |
| 100–99 | 120–4 | H in <i>A. hastulata</i> , <i>G. varicolor</i> & internode 69–62 |
| | 105–2 | R in <i>P. plicata</i> |
| 102–101 | 131–3 | H in internode 129–124 |
| 104–103 | 88–2 | H in internode 59–58 |
| | 120–2 | H in internode 86–85 |
| 109–104 | 88–2 | H in internode 59–58 |
| | | R in <i>P. bidigitula</i> , <i>P. nana</i> , <i>P. woodlarkensis</i> |
| 108–107 | 111–2 | |
| 110–109 | 21–3 | R in <i>P. bidigitula</i> , <i>P. nana</i> , <i>P. woodlarkensis</i> |
| | 49–6 | R in several species of <i>Papuapsaltria</i> |
| 140–112 | 16–1 | H in <i>M. toxopeusi</i> |
| | 20–1 | H in <i>Aedeastria</i> , <i>M. viridicata</i> , <i>T. sarissa</i> |
| 114–113 | 28–3 | R in <i>G. stylata</i> , <i>O. insignis</i> , many <i>Papuapsaltria</i> species further evolved? in internode 60–57. H in <i>Muda</i> |
| | 71–3 | H in <i>A. cheesmanae</i> |
| 123–118 | 134–2 | |
| | 149–2 | |
| 136–123 | 125–2 | R in <i>A. hastulata</i> |
| | 17–2 | H in <i>T. sicula</i> |
| 127–126 | 129–2 | |
| 129–128 | 129–(2+3) | H in <i>A. hastulata</i> |
| | 32–2 | H in <i>M. inflata</i> , <i>M. globulata</i> & internode 73–72 |

Appendix 2. Continued.

| Internode | Character nr. and state | Homoplasies (H) and reversals (R) |
|-----------|-------------------------|--|
| 131–129 | 5–4 | R in <i>T. sicula</i> |
| | | H in <i>Prasia</i> & internode 139–138 |
| | 30–5 | H in <i>B. inconstans</i> , <i>M. inflata</i> , <i>P. goniodes</i> & internodes 73–72 & 86–85 |
| | | R in <i>T. adipata</i> , <i>T. lanceola</i> |
| | 90–2 | H in <i>G. rubricata</i> , <i>M. globulata</i> , <i>Muda</i> |
| | 152–3 | |
| 131–130 | 17–4 | H in <i>M. humilis</i> , <i>Prasia</i> , internodes 72–71 & 139–138 |
| 135–131 | 33–3 | |
| 135–134 | 112–2 | |
| 136–135 | 61–2 | R in <i>M. globulata</i> , <i>M. toxopeusi</i> & internode 127–126 |
| 139–136 | 10–2 | R in <i>A. bullata</i> , <i>A. digitata</i> , <i>A. dilobata</i> , <i>M. toxopeusi</i> , <i>M. viridicata</i> . H in <i>G. stenocephalis</i> |
| | | H in <i>Prasia</i> & internode 131–129 |
| 139–138 | 5–4 | |
| | 9–3 | |

Appendix 2. Continued.

| Internode | Character nr. and state | Homoplasies (H) and reversals (R) |
|-----------|-------------------------|---|
| | 17–4 | H in <i>M. humilis</i> , <i>Prasia</i> , internodes 72–71 & 131–130 |
| | 13–2 | H in <i>Prasia</i> |
| | 19–2 | H in <i>Prasia</i> |
| | 26–2 | |
| | 27–2 | |
| 140–139 | 41–2 | R in <i>T. spelunca</i> , <i>T. sicula</i> , <i>M. globulata</i> , <i>C. immaculata</i> & internode 136–123 |

Remarks. – Character 41–2 is H in the PAUP reconstruction; character 43–3 is placed at the base of *Gymnotympana* and *Venustria*; character 73–2 is placed on internode 47–40 by the PAUP reconstruction; character 150–1, regarded apomorphic for the Bismarck species of the *bloetei* group, is regarded plesiomorphic for that group in the PAUP reconstruction; character 153–4 is placed on internode 9–8 by the PAUP reconstruction, presumably due to the interpretation of lacking information.

Appendix 3. Data matrix (? = unknown; – = structure absent; capitals represent the following polymorphies: A = 1, 4; B = 1, 2; C = 5, 6; D = 1, 3; E = 3, 4, 5, 6; F = 1, 4)

[illegible]

[illegible]

Appendix 3. Continued.[illegible]

111

[illegible]

Appendix 3. Continued.[illegible][illegible]