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Supraspecific Classification of Bumblebees based on the Characters of Male Genitalia*

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1. Introduction

The bumblebees are a group of social bees involving about 300 species and prevailing, in contrast to other social insects, in the temperate and cold regions of the northern Hemisphere. In a widely accepted classification, the bumblebees are assigned to the tribe Bombini, which constitutes the family Apidae, together with three sister tribes, Apini, Meliponini and Euglossini (Winston and Michener, 1977). The tribe Bombini is composed of two genera, non-parasitic *Bombus* and parasitic *Psithyrus*. Morphologically, *Bombus* is considerably variable, comprising about thirty subgenera (Richards, 1968), while *Psithyrus* is more compact with seven subgenera (Popov, 1931).

Many taxonomic papers have been accumulated since Linné (1758), but attentions have been paid more to the studies at the specific level than to the supraspecific classification. The natural grouping at supraspecific level was initiated by Radoszkowski (1884), followed by Robertson (1903), Vogt (1911), Franklin (1912, 1913), etc. Interrelation among those supraspecific taxa was first comprehensively studied by Krueger (1917, 1920) and Skorikov (1922, recongizing many subgenera as genera). The system proposed by Krueger, especially distinction of two sections, *Odontobombus* and *Anodontobombus*, was fairly influential, adopted by most subsequent specialists such as Frison (1927), Pittioni (1938), Krusemann (1952), etc. with some modifications. The polyphyletic system recently proposed by Milliron (1961, 1971 - 1973) claimed much disagreement with the conventional recognition, evoking violent controversies (Richards, 1968; Plowright and Stephen, 1973; Tkalců, 1972; 1974b; Sakagami, 1976; etc.). The polygeneric system based on another polyphyletic hypothesis by Tkalců (1972) seems to have brought further dispute rather than resolution. Regrettably, most of these studies have been made on a basis of limited numbers of taxa and characters. The resultant

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lack of a common ground has often hampered fruitful discussion. Keeping this in mind, the present study attempts to give a supraspecific classification of Bombini, covering most so far recognized supraspecific taxa of both *Bombus* and *Psithyrus*. The overall similarity among groups is mainly estimated by a phenetic method on the structures of male genitalia which have been intensively used for the bumblebee taxonomy as in many other insect groups. Classification based on other characters will be dealt with elsewhere.

2. List of supraspecific taxa

All so far proposed nonfossil supraspecific taxa are listed below with synonymous relations (cf. Richards, 1968). The list includes the species groups proposed in some major studies, and those recognized in the present study. The taxa adopted in this study are headed with abbreviations which will be used frequently in tables, figures and enumerations. Parenthetical abbreviations will be used when the taxa are cited with species names. Adoption of these taxa are still tentative. By later comparative studies many taxa will be reduced to lower ranks while some others will be recognized as higher ranked. The subgenera or species groups available in the present paper are specified with a single asterisk. All fossil taxa described by Cockerell (*Chalcobombus*, *Sophrobombus*, *Protobombus*; 1908) are now assigned to some groups of Apidae out of bumblebees (Zeuner and Manning, 1976). The unique fossil taxon, *Bombusoides*, is a nomen nudum (Motschulsky, 1856, ref. Zeuner and Manning, *op*. *cit*.).

AD *Adventoribombus* Skorikov 1922; proposed as a subgenus of *Agrobombus* Vogt; = Thoracobombus Dalla Torre.

Agribombus Skorikov 1938; emend. of *Agrobombus* Vogt; = *Thoracobombus* Dalla Torre.

Agrobombus Vogt 1911; proposed as a subgenus of

Bombus Latreille; = Thoracobombus Dalla Torre.

AO* (Ao.) Allopsithyrus Popov 1931; proposed as a subgenus of Psithyrus Lepeletier.

Alpigenibombus Skorikov 1938; emend. of Alpigenobombus Skorikov; = Alpigenobombus Skorikov.

AG* (Ag.) Alpigenobombus Skorikov 1914; proposed as a subgenus of Bombus Latreille.

Alpinibombus Skorikov 1937; = emend. of Alpinobombus Skorikov; = Alpinobombus Skorikov.

AL* (Al.) Alpinobombus Skorikov 1914; proposed as a subgenus of Bombus Latreille.

Alpinus group Milliron 1961; = Alpinobombus Skorikov.

ADT Anodontobombus Krueger 1917; proposed as a section.

AS* (As.) Ashtonipsithyrus Frison 1927; proposed as a subgenus of Psithyrus Lepeletier.

at* Atratus group. Tentatively recognized in the present study as a unit for comparison; represented by Bombus (Fervidobombus) atratus Franklin 1913.

Atrocinctobombus Skorikov 1933; nomen nudum.

The auricomus group Franklin 1912; = Bombus Robertson.

Auricomus group Milliron 1961; = Bombias Robertson.

Bombellus auctt. 1931; nomen nudum, (cf. Richards 1968).

BI* (Bi.) Bombias Robertson 1903; proposed as a genus.

BO* (Bo.) Bombus Latrielle, 1802; proposed as a genus.

BOP Boopobombus Frison 1927; proposed as a section.

The boreallis group Franklin 1912; = The group of fervidus Robertson = Subterraneobombus Vogt.

Brachycephalus group Milliron 1961; = _Fraternobombus_ Skorikov s. str.

Bremus Jurine 1801; proposed as a genus; invalidated.

_bv_* _Brevivillus_ group. Tentatively recognized in the present study as a unit for comparison; represented by _Bombus_ (_Fervidobombus_) _brevivillus_ Franklin 1913.

Callobombus Dalla Torre 1896; invalid emend. of _Kallobombus_ Dalla Torre.

Chromobombus Dalla Torre 1880; proposed as a subgenus of _Bombus_ Latreille; = _Thoracobombus_ Dalla Torre s. str.

CP* (_Cp_.) _Citrinopsithyrus_ Thorp et al. 1983; renaming for _Laboriopsithyrus_ Frison.

_CC_* (_Cc_.) _Coccineobombus_ Skorikov 1922; proposed as a subgenus of _Alpigenobombus_ Skorikov.

Coccineus group Milliron 1961; = _Coccineobombus_ Skorikov.

_CF_* (_Cf_.) _Confusibombus_ Ball 1914; proposed as a subgenus of _Bombus_ Latreille.

Confusobombus Skorikov 1922; proposed as a subgenus of _Bombus_ Latreille; = _Confusibombus_ Ball.

_CR_* (_Cr_.) _Crotchiibombus_ Franklin 1954; proposed as a subgenus of _Bombus_ Latreille.

Crotchii group Milliron 1961; = _Crotchiibombus_ Franklin.

Cullumanibombus Skorikov 1938; emend. of _Cullumanobombus_ Vogt; = _Cullumanobombus_ Vogt.

_CL_* (_Cl_.) _Cullumanobombus_ Vogt 1911; proposed as a subgenus of _Bombus_ Latreille.

Cullumanus group Milliron 1961; = _Cullumanobombus_ Vogt.

_dl_* _Dahlbomi_ group. Tentatively recognized in the present study as a unit for comparison;

represented by *Bombus* (*Fervidobombus*) *dahlbomi* Guérin 1835.

Dentatus group. Milliron 1961; = *Alpigenobombus* Skorikov, *Crotchiibombus* Franklin (partim).

DV* (Dv.) *Diversobombus* Skorikov 1914; proposed as a subgenus of *Bombus* Latreille.

"The group of *B. dumoucheli*" Radoszkowski 1884; = *Fervidobombus* Skorikov.

The *dumoucheli* group Franklin 1912; = *Fervidobombus* Skorikov.

Dumoucheli group Milliron 1961; = *Fervidobombus* Skorikov.

EP *Eopsithyrus* Popov 1931; proposed as a subgenus of *Psithyrus* Lepeletier.

EV* (Ev.) *Eversmannibombus* Skorikov 1938; proposed as a subgenus of *Agribombus* = *Agrobombus* Vogt.

EX* (Ex.) *Exilobombus* Skorikov 1922; proposed as a subgenus of *Mucidobombus* Skorikov.

FP* (Fp.) *Fernaldaepsithyrus* Frison 1927; proposed as a subgenus of *Psithyrus* Lepeletier.

FV (Fv.) *Fervidobombus* Skorikov 1922; proposed as a genus; tentatively split into six groups in the present study (see at, bv, dl, fv, mr, tv).

"The group of *B. fervidus*" Radoszkowski 1884; = *Subterraneobombus* Vogt.

fv* *Fervidus* group. Tentatively recognized in the present study as a unit for comparison; represented by *Bombus* (*Fervidobombus*) *fervidus* (F.) 1798.

FS (Fs.) *Festivobombus* Tkalců 1972; proposed as a subgenus of *Pyrobombus* Dalla Torre.

fr *Funerarius* group. Tentatively recognized in the present study as a unit for comparison; represented by *Bombus* (*Orientalibombus*) *funerarius* Smith.

FR* (Fr.) *Fraternobombus* Skorikov 1922; proposed as a subgenus of *Alpigenobombus* Skorikov.

The *fraternus* group Franklin 1912; = *Fraternobombus* Skorikov s. str., *Separatobombus* Frison, *Crotchiibombus* Franklin, *Robustobombus* Skorikov, *Rubicundobombus* Skorikov, *Coccineobombus* Skorikov, *Funebribombus* Skorikov.

Fraternus group Milliron 1961; = *Fraternobombus* Skorikov s. str.

FN* (Fn.) *Funebribombus* Skorikov 1922; proposed as a subgenus of *Alpigenobombus* Skorikov.

Funebris group Milliron 1961; = *Funebribombus* Skorikov.

Griseocollis group Milliron 1961; = *Separatobombs* Frison.

Handlirschi group Milliron 1961; = *Rubicundobombus* Skorikov.

Hortibombus Skorikov 1938; emend. of *Hortobombus* Vogt; = *Megabombus* Dalla Torre.

Hortobombus Vogt 1911; proposed as a subgenus of *Bombus* Latreille; = *Megabombus* Dalla Torre.

Hypnorobombus Quilis Pérez 1927; proposed as a subgenus of *Bombus* Latreille; = *Pyrobombus* Dalla Torre.

Hypnorubombus Quilis Pérez 1927 (sic); = *Hypnorobombus* Quilis Pérez = *Pyrobombus* Dalla Torre.

Jonellus group Milliron 1961; = *Pyrobombus* Dalla Torre.

KL* (Kl.) *Kallobombus* Dalla Torre; proposed as a subgenus of *Bombus* Latreille.

The *kirbjellus* group Franklin 1912; = *Alpinobombus* Skorikov.

Kozlovibombus Skorikov 1922; proposed as a genus; = *Melanobombus* Dalla Torre.

Laboriopsithyrus Frison 1927; proposed as a subgenus of *Psithyrus* Lepeletier; =

Citrinopsithyrus Thorp et al.

Laesibombus Skorikov 1938; emend. of *Laesobombus* Skorikov; = *Laesobombus* Skorikov.

LS (*Ls*.) *Laesobombus* Skorikov 1922; proposed as a subgenus of *Agrobombus* Vogt.

Lapidariobombus Vogt 1911; proposed as a subgenus of *Bombus* Latreille; = *Melanobombus* Dalla Torre.

Laponicobombus Neave 1940 (sic); = *Lapponicobombus* = *Pyrobombus* Dalla Torre.

Lapponicobombus Quilis Pérez 1927; proposed as a subgenus of *Bombus* Latreille; = *Pyrobombus* Dalla Torre.

Lapponicus group Milliron 1961; = *Pyrobombus* Dalla Torre.

Leucobombus Dalla Torre 1880; proposed as a subgenus of *Bombus* Latreille; = *Bombus* Latreille s. str.

Mastrucatobombus Krueger 1917; proposed as a subgenus of *Bombus* Latreille; = *Alpigenobombus* Skorikov.

*MG** (*Mg*.) *Megabombus* Dalla Torre 1880; proposed as a subgenus of *Bombus* Latreille.

Megalobombus Schulz 1906; invalid emendation of *Magabombus* Dalla Torre.

*ML** (*Ml*.) *Melanobombus* Dalla Torre 1880; proposed as a subgenus of *Bombus* Latreille.

*MD** (*Md*.) *Mendacibombus* Skorikov 1914; proposed as a subgenus of *Bombus* Latreille.

*MP** (*Mp*.) *Metapsithyrus* Popov 1931; proposed as a subgenus of *Bombus* Latreille.

Mexicanus group Milliron 1961; = *Fervidobombus* Skorikov.

*mr** *Morio* group. Tentatively recognized in the present study as a unit for comparison; represented by *Bombus* (*Fervidobombus*) *morio* (Swedrius) 1787.

MC* Mucidobombus Skorikov 1922; proposed as a genus.

Nevadensibombus Skorikov 1922; proposed as a genus; = Bombias Robertson.

Nigrodorsalis group Milliron 1961 = Fervidobombus Skorikov.

NB* (Nb.) Nobilibombus Skorikov 1933; proposed as a genus.

Obertobombus Reinig 1930; proposed as a subgenus of Bombus Latreille; = Sibiricobombus Vogt.

ODT Odontobombus Krueger 1917; proposed as a section.

OR* (Or.) Orientalibombus Richards 1929; proposed as a subgenus of Bombus Latreille.

Poecilobombus Dalla Torre 1882; proposed as a subgenus of Bombus Latreille; = Pyrobombus Dalla Torre.

Pomibombus Skorikov 1938; emend. of Pomobombus Krueger; = Rhodobombus Dalla Torre.

Pomobombus Krueger 1917; proposed as a subgenus of Bombus Latreille; = Rhodobombus Dalla Torre.

Pratibombus Skorikov 1937; emend. of Pratobombus Vogt; = Pratobombus = Pyrobombus Dalla Torre.

Praticola group Millrion 1961; = Pyrobombus Dalla Torre.

Pratobombus Vogt 1911; proposed as a subgenus of Bombus Latreille; = Pyrobombus Dalla Torre.

"The group of B. pratorum" Radoszkowski 1884; = Pyrobombus Dalla Torre.

Pratorum group Milliron 1961; = Pyrobombus Dalla Torre.

PS* (Ps.) Pressibombus Frison 1935; proposed as a subgenus of Bremus Jurine.

PT* (Pt.) Psithyrus Lepeletier 1832; proposed as a genus.

PR* (Pr.) Pyrobombus Dalla Torre 1880; proposed as a subgenus of Bombus Latreille.

RH* (Rh.) Rhodobombus Dalla Torre 1880; proposed as a subgenus of *Bombus* Latreille.

RB* (Rb.) *Robustobombus* Skorikov 1922; proposed as a subgenus of *Alpigenobombus* Skorikov.

Robustus group Milliron 1961; = *Robustobombus* Skorikov.

RD* (Rd.) *Rubicundobombus* Skorikov 1922; proposed as a subgenus of *Fervidobombus* Skorikov.

Rubicundus group, Milliron 1961, 1971; = *Rubicundobombus* Skorikov.

RF* (Rf.) *Rufipedibombus* Skorikov 1922; proposed as a genus.

Rufipedobombus Milliron 1961 (sic); = *Rufipedibombus* Skorikov.

Rufocinctobombus Frison 1927; proposed as a subgenus of *Bremus* Jurine; = *Cullumanobombus* Vogt.

SX* (Sx.) *Senexibombus* Frison 1930; proposed as a subgenus of *Bremus* Jurine.

SP* (Sp.) *Separatobombus* Frison 1927; proposed as a subgenus of *Bremus* Jurine.

Sibericobombus Krusemann 1952 (sic); = *Sibiricobombus* Skorikov.

Sibiricibombus Skorikov 1938; emend. of *Sibiricobombus* Vogt; = *Sibiricobombus* Vogt 1911.

SB* (Sb.) *Sibiricobombus* Vogt 1911; proposed as a subgenus of *Bombus* Latreille.

Sibiricus group Milliron 1961; = *Sibiricobombus* Vogt.

Soroeensibombus Vogt 1911; proposed as a subgenus of *Bombus* Latreille; = *Kallobombus* Dalla Torre.

Soroensibombus Skorikov 1923 (sic); = *Soroeensibombus* Vogt; = *Kallobombus* Dalla Torre.

Subterraneibombus Skorikov 1938; emend. of *Subterraneobombus* Vogt; = *Subterraneobombus*

Vogt.

_ST*_ (_St_.) _Subterraneobombus_ Vogt 1911; proposed as a subgenus of _Bombus_ Latreille.

Subterraneus group Milliron 1961; = _Subterraneobombus_ Vogt.

SLC _Sulcobombus_ (Vogt) Krueger 1917; proposed as a group name, including _Mendacibombus_ Skorikov and _Confusibombus_ Ball.

Tanguticobombus Pittioni 1939b; proposed as a subgenus of _Bombus_ Latreille; = _Melanobombus_ Dalla Torre (Richards, 1968) or _Pressibombus_ Frison (Tkalců, 1968b)

Terrestribombus Vogt 1911; proposed as a subgenus of _Bombus_ Latreille; = _Bombus_ Latreille s. str.

"The group of _B_. _terrestris_" Radoszkowski 1884; = _Bombus_ Latreille s. str.

The _terrestris_ group Franklin 1912; = _Bombus_ Latreille s. str.

Terrestris group Milliron 1961; = _Bombus_ Latreille s. str.

_TH*_ (_Th_.) _Thoracobombus_ Dalla Torre 1880; proposed as a subgenus of _Bombus_ Latreille.

_tv*_ _Transversalis_ group. Tentatively recognized in the present study as a unit for comparison; represented by _Bombus_ (_Fervidobombus_) _transversalis_ (Oliver) 1789.

_TR*_ (_Tr_.) _Tricornibombus_ Skorikov 1922; proposed as a subgenus of _Agrobombus_ Vogt = _Thoracobombus_ Dalla Torre.

UNC _Uncobombus_ Krueger 1917; proposed as a group name including _Melanobombus_ Dalla Torre, _Pyrobombus_ Dalla Torre, _Cullumanobombus_ Vogt, _Alpigenobombus_ Skorikov s. str.

Volucellobombus Skorikov 1922; proposed as a genus; = _Robustobombus_ Skorikov.

Volucelloides group Milliron 1961; = *Robustobombus* Skorikov.

3. Historical review

The following review deals only with major contributions on the supraspecific classification with emphasis on *Bombus*. Terminology used in the present study basically follows Michener (1944), adopting his later modifications (Michener, 1965). Morphological terms are given in Figs. 1 - 2, together with their abbreviations. References to the species taxonomy will be minimized. Some important classificatory systems so far proposed are schematically shown in Figs. 3 - 11 with that proposed in the present study (Fig. 12). The history of group recognition at the lowest supraspecific level is synoptically summarized in Table 1.

3. 1. The genus *Bombus* Latreille

At the dawn of the animal taxonomy, Linné (1758) placed all bumblebee species in the genus *Apis*. A half century later Latreille (1802) erected the genus *Bombus* for bumblebees known at his time. Separation of *Psithyrus* from *Bombus* was made by Lepeletier (1832). Dalla Torre (1880, 1882) introduced the subgeneric concept in *Bombus*, and erected nine subgenera: *Kallobombus* (=*KL*), *Leucobombus* (=*BO*), *Pyrobombus* (1880, = *PR*), *Melanobombus* (=*ML*), *Poecilobombus* (=*PR*), *Pyrrhobombus* (1882, =*PR*), *Megabombus* (=*MG*), *Chromobombus* (=*TH*), *Thoracobombus* (=*TH*), *Rhodobombus* (=*RH*). Although his grouping based on the hair coat color was entirely unnatural, all his subgeneric names are valid for the nomenclatorial priority (Sandhouse, 1943; Michener, 1944).

Radoszkowski (1884) recognized four supraspecific groups based on structural characters, especially of male genitalia. His five species groups (*terrestris* = *BO*, *pratorum* = *PR*, *fervidus* = *borealis* = *ST*, and *dumoucheli* =

FV) have been accepted by many successors, although considerably amplified by Vogt (1911) who recognized nine subgenera: *Soroeensibombus* (=*KL*), *Terrestribombus* (=*BO*), *Sibiricobombus* (=*SB*), *Cullumanobombus* (=*CL*), *Pratobombus* (=*PR*), *Lapidariobombus* (=*ML*), *Hortobombus* (=*MG*), *Agrobombus* (=*TH*) and *Subterraneobombus* (=*ST*) (cf. Table 1). Some of these names are synonymous to those by Dalla Torre, but the group concepts are still basically accepted.

Several years before Vogt, Robertson (1903), who studied only the Nearctic species, erected the genus *Bombias* (=*BI*) for reception of the species with unusually enlarged eyes in the males and fairly large ocelli in females, which corresponds to *FR*, *BI* and *SP* in the modern sense. Franklin (1912, 1913), in his monograph of the New World bumblebees, reduced *BI* to the subgeneric status and presented the following system of the genus *Bombus* (see also Table 1) with seven species groups.

Subgenus *Bombus*	Subgenus *Bombias*
kirbjellus (=*AL*)	*auricomus* (=*BI*)
terrestris (*BO*)	*fraternus* (=*FR*, *SP*, *CR*, *CL*, *RB* *RD*, *CC* & *FN*
pratorum (=*PR*)	
borealis (=*ST*)	
dumoucheli (=*FV*)	

For the subgenus *Bombus* he followed Radoszkowski except the addition of a new species group, *kirbjellus*-g. For *Bombias* he regarded this as an unnatural group, but retained the classification by Robertson.

As to the European bumblebees, Krueger (1917, 1920; Fig. 3) gave an important contribution to the supraspecific classification of *Bombus*. Based on both structural and metric characters, he divided *Bombus* into two major sections, *Odontobombus* (*ODT*) and *Anodontobombus* (*ADT*). *ODT* was mainly characterized by the apical end of mid basitarsus spinosely produced in females and long malar area in both sexes. The subgenera included in *ODT* were *Hortobombus* (=*MG*), *Agrobombus* (=*TH*), *Pomobombus* (=*RH*) and *ST*. *ADT* was the group having the portion of mid basitarsus round or truncate and having relatively short malar area. It comprised nine subgenera: *Mastrucatobombus* (=*AG*), *Pratobombus* (=*PR*), *Lapidariobombus* (=*ML*), *Soroeensibombus* (=*KL*), *CL*, *BO*, *Alpinobombus* (=*AL*), *Confusibombus* (=*CF*) and *Mendacibombus* (=*MD*). As an evidence for supporting the validity of this division, Krueger indicated a remarkable correspondence between this system and the bionomical grouping independently proposed by Sladen (1912). The group of species which feeds larvae indirectly through a "pocket" situated by brood cells (=pocket makers) was represented by the species of *ST*, *MG* and *TH*, all belonging to *ODT*. The other group feeding larvae through an orifice temporaneously perforated on brood cells (=pollen primers, later renamed non-pocket makers by Sakagami 1976) comprised the species of *CL*, *PR*, *ML* and *BO*, that is, the subgenera of *ADT*. This remarkable correspondence was reconfirmed for the Nearctic species by Plath (1927, 1934). Krueger (1917) subdivided *ADT* into five subgroups: *BO*, *AL*, *Soroensibombus* (=*KL*), *UNC* and *SLC*. The first three were each represented by a single subgenus. *UNC* (mentioned as Vogt's unpublished name) was characterized by the apex of penis valve curved inward and isolated chitinous areas on the membrane between the inner projections of the sting sheath. It contained *PR*, *CL*, *Lapidariobombus* (=*ML*) and *Mastrucatobombus* (=*AG*). *SLC*, involving *MD* and *CF*, corresponded to Franklin's *BI*, as defined by enlarged male eyes. Richards (1927), mainly having focused comparison between *Bombus* and *Psithyrus*, indicated the closest relationship among *PR*, *ML* and *CL* in many morphological characters. He emphasized the alliance of *mastrucatus*-group (=*AG*) to them, supporting the opinion by Krueger, but regarded *ADT* as an artificial group.

The system by Skorikov (1914, 1922; Fig. 4, including his later taxa, 1933, 1938) nomenclatorially greatly differed from the Krueger's one. He raised many taxa originally proposed as subgenera to the generic rank, and erected many new genera and subgenera mostly without descriptions. The peculiarities of his system are summarized as follows: Adoption of many genera and subgenera; splitting of Franklin's *fraternus*-group and Vogt's *Agrobombus* (=*TH*); placing the subgenera related to *fraternus*-group in the genus *Alpigenobombus*. Although most subgenera or genera split by him have been regarded as natural groups, his multigeneric system itself has hardly been accepted except by some Russian students (*e.g.* Panfilov 1956).

The American specialist Frison (1927, 1930, 1935, etc.) used the generic name *Bremus* in place of *Bombus*, having claimed the priority of the former which appeared in "Erlangen List" (Jurine, 1801) later invalidated by the international Committee of Nomenclature (Opinion 135; Hemming, 1939). Frison (1927) basically followed the systems by Radoszkowski, Vogt, Robertson, Franklin and especially Krueger and erected a new section *Boopobombus* (*BOP*, Fig. 5). Actually this taxon is a copy of *Bombias* in the Robertson-Franklin's sense, only differing in the addition of a new element *CL*, which he regarded as transitional to other sections. Franklin's comment suggesting the two distinct lines within *BI* was neglected, and *MD* and *CF* were suggested as the Eurasian representatives of this section.

Working with the Palaearctic groups, Pittioni (1938) basically followed the sectional division by Frison, and proposed to incorporate *SB* and probably also *AG* into the section *BOP* (Fig. 6). After erection of numerous genera and subgenera by Skorikov (1922), several new subgenera, *e*. *g*. *OR*, *SX*, *NB*, *PS*, *EV* and *CR* (excluding those invalidated by or before Richards 1968) had been rather sporadically proposed (see below).

In the ninth International Congress of Entomology, Krusemann (1952, Fig. 7) claimed that the subgenera except *MD*, *CF* and *Nevadensibombus* (=*BI*) should be omitted from the section *BOP*, as they lacked important characters shared by the three subgenera: elongate F_1, main keel ending before the tip of the mandible, labrum having a transverse depression (in *CF* not very clear) in females, and straight sagitta (=Pv)1) in males. For avoiding confusion he gave a new sectional name *Bombias* to the *BOP* *s. str.* He proposed also some changes in the widely accepted Krueger-Frison system, lumping some subgenera together: 1) *SX* and *DV* in *MG*; 2) *MC*, *LS* and *Adventoribombus* (=*TH*) in *Agrobombus* (=*TH*); 3) tentatively, *Kozlovibombus* (=*ML*, synonymized later by Richards 1968) in *Lapidariobombus* (=*ML*); 4) *Tanguticobombus* (=*ML*, *ditto*.) with *PS*; 5) *FR*, *Obertobombus* (=*SB*), *RB* and "probably" (*sic*) *CC* and *FN* in *"Sibericobombus"* (*sic*, =*SB*); 6) *SP* in *PR*.

Franklin (1954), after a long silence since his monumental monograph, published a short evolutionary comment on the bumblebees. Beside an interesting speculation on the *BOP* characters, he gave a tentative classification of the bumblebees as follows (group numbers by the present author): 1) *Pratobombus* (=*PR*) plus "much *BOP*" excluding at least *BI*; 2) subgenera of *ODT*; 3) *BI* *s. str.* (*MD* and *CF* not mentioned but possibly regarded as included here); 4) *BO* *s. str.* His classification was characterized by recognition of *BO* as an isolate group. This view has been later repeated by some authors. For instance, Macfarlane (1976) found that the male proventriculus of *BO* was unique among 15 *Bombus* and 2 *Psithyrus* subgenera by having four semispherical projections.

Against the system gradually developed by Krueger, Richards, Frison, Pittioni and Krusemann, Milliron (1961) proposed an extremely deviated scheme (Fig. 9). He emphasized the importance of venational characters which had not been used much in the bumblebee taxonomy. He raised *Bombus* to a tribal status with three genera, *Bombus*, *Megabombus* and *Pyrobombus*. His *Bombus* was a mere rank elevation of the subgenus *Bombus*, while *MG* and *PR* were largely different from the conventional usage. His *MG*

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1) This and some other abbreviations for structural characters of male genitalia are explained in Chapter 5.

comprised two subgenera *MG* and *BI*, the former more or less corresponding to *ODT*, containing all *ODT* subgenera and three *ADT* subgenera *OR*, *KL* and *AL*. On the other hand, his subgenus *BI* roughly coincided with the section *BI* by Krusemann, but different in exclusion of *CF* and inclusion of *AG*. His genus *PR* consisted of two subgenera, *PR* and *CL*. The subgenus *PR* contained only two old subgenera *PR* and *ML*, while the subgenus *CL* comprised all remaining groups of *ADT*. Although he gave no detailed accounts on the Eurasian groups, *CF* was regarded as representing a distinct line equivalent to his other genera. He adopted the category "species-group" as the lowest supraspecific rank, instead of the subgenus. His recognition of this level was also unique in splitting of old subgenera *PR* and *FV* into four and three species-groups, respectively. Phylogenetically, his view was characterized by hypothesizing an amphiphyletic origin of bumblebees, assuming one line (=*mendax*-line) comprising his genera *BO* and *MG* from the primitive anthophorid stem and another line, his genus *PR* (=*fraternus*-line), from the line of Xylocopini.

Richards (1968) revised all so far described supraspecific groups of non parasitic bumblebees and recognized 35 subgenera under the single genus *Bombus*, from the standpoint to define accurately as many groups as possible. He also gave a useful key to subgenera, redescriptions of both sexes for each subgenus, and brief taxonomical notes. Deliberately avoiding phyletic discussion, he mentioned the morphological uniformity of *ODT* and close relationships among the following groups of subgenera (numbers given by the present author, cf. Fig. 8): 1. *AG*, *NB*; 2. *FR*, *MD*, *CF* and *BI*; 3. *PR*, *CL*, *ML*, *SB* and *PS*; 4. *RB* and *RD*; 5. *MG*, *DV* and *SX*; 6. *LS*, *TH*, *MC* and *AD*; 7. *RH* and *FV*. Richards entirely rejected the Milliron's idea as phantastic because of fundamental reasons, *i.e.* dependence on deceptive characters, and numerous errors in detail.

In 1971 to 1973, Milliron published a monograph of Western Hemisphere bumblebees, slightly modifying his previous system (Fig. 10). *Dentatus*-group (=*AG*) was transferred from the genus *MG* subgenus *BI* into the genus *PR* subgenus *CL*. Besides, *PS* and *RF*, previously not mentioned, were placed in the subgenus *CL*. But there were no fundamental changes in spite of the criticism by Richards. In his revised phyletic dendrogram, the *fraternus*-group is given as branched from Apinae just after cleavage from the xylocopid line . This system also suffered strong objections by some students (Tkalců, 1974b; Michener, 1974; Sakagami, 1976; etc.). Plowright and Stephen (1973) uniquely manifested their agreement with Milliron at one point. Having measured various parts of fore wing, i.e. the venational characters as in Milliron, they applied multivariate analyses. Although their study mainly concerned the origin of *Psithyrus*, comparison between the obtained phenogram and the systems by Frison (1927) and Milliron (1961) revealed the agreement with the latter in separating *BI* *s*. *str*. from "*Fraternobombus-Crotchiibombus-Separatobombus* complex" (sic). However, they opposed Milliron to accommodate *AL* or *KL* in the genus *MG*. They agreed with both Frison and Milliron in associating nearly all *ODT* species-groups together. Concerning the *ODT* subgenera, they uniquely indicated a considerable deviation of *TH*.

Recently the first attempt using biochemical techniques for bumblebee classification was made by Stephen and Cheldelin (1973). Based upon the similarity in *GDH* isozyme patterns, they distinguished three *Bombus* groups and one *Psithyrus* one: *BI*; *BO* *s*. *str*.; the group of all other *Bombus* subgenera examined, *i*. *e*. *PR*, *CL*, *SP*. *FV* and *ST*; and *Psithyrus*. Although they stated that their grouping more corresponded to the system by Burks (1951), which owed much to Frison (1927), than to that of Milliron, curiously it was actually rather closer to the latter. It differed from the Milliron's system mainly in the rejection of placing *BI* *s*. *str*. in *MG*, while disagreed with the Frison's one in recognizing both *BI* and *BO* *s*. *str*. as isolate groups.

Most recently, Tkalců (1972) proposed another multigeneric system for the Old World taxa. He postulated independent derivation of recent bumblebee groups from several ancestral stocks of pre-parasitic *Psithyrus*. Based upon this polyphyletic hypothesis, he split the true bumblebees into eight genera (Fig. 11): *MD*, *CF*, *OR*, *AL*, *BO*, *AG*, *PR* and *MG*. Among them the last two were subdivided into several subgenera (genus *PR*: *PR*, *ML*, *SB*, *CL*, *RF*, *PS*, and *FS* of his own creation; genus *MG*: *TH*, *TR*, *DV*, *ST*, *MG*, *SX*, *RH* and *FV*. In contrast to the subdivision at the generic level, he lumped some subgenera recognized by Richards (1968) together. The old subgenus *KL* was synonymized with *PR*, as he observed that most subgeneric characters previously acknowledged as distinct between the two were actually linked. Furthermore, all subgenera allied to *TH* (=Richards' sixth group, 1968) were incorporated into *TH*.

Baside the studies reviewed above, several related contributions which did not directly focus the supraspecific classification are worth to mention. Medler (1962a, b) measured several parts of mouthparts and radial cell in fore wing of the bumblebees mainly of the Nearctics, and showed that labial index, (*length of prementum/ length of the first segment of labial palpi*)x100, clearly differed among various subgenera. Based upon the great deviation of *B*. (*Pr*.) *pratorum*, he suggested *PR* *s*. *str*. might be an unnatural group. This idea met with both agreement and objection. Richards (1968) disagreed, indicating a great similarity of structures of male genitalia among the *PR* species. On the other hand, Pisani *et al*. (1968) applied a multivariate analysis on the data in Medler (1962b), and demonstrated a great variability among the subgenera of *PR*. Furthermore Pekkarinen (1979) reported that *B*. (*Pr*.) *jonellus* took a particularly isolate position among the *PR* species in the enzyme variability studied by electrophoresis. He also reconfirmed isolation of *BO* having reported by Stephen and Cheldelin (*op*. *cit*.). Besides, he showed the group uniformity in *BO* and *ST*, and isolated position of "*Alpinobombus wurflenii*" (sic = *B*. (*Ag*.) *wurfleini*).

Recent bionomical contributions (Hobbs, 1964a,b etc.; K. Richards, 1975; etc.) were reviewed by Sakagami (1976). *AG* and *AL* had been reported as pocket-makers. He gave a few suggestions possibly useful for bumblebee classification: subgeneric uniformity within *BO* and, to less extent, *ST*; isolated position of *BI*, and to less extent, of *BO* and *AL*, etc. From the evolutionary viewpoint Sakagami and Ito (1980) surveyed specific and subgeneric variations in tibial corbiculation of male bumblebees of more than 100 species, representing nearly all subgenera. They showed more cobiculated conditions in the section *ADT*, particularly in *BO*, than in the section *ODT*, although in the latter *MG*, *DV* and a group in *FV* exhibited the most corbiculated state. Giving discussion on the evolution of this apparently functionless character, they concluded that corbiculated state of the male was probably ancestral.

Since Stephen and Cheldelin (1973) many biochemical contributions more or less related to the classification of bumblebees have been published. At the species level some of them gave excellent results (e.g. Bergstroem and Svensson 1973; Svensson, 1979, 1980; etc.). But few attempts have been made at the supraspecific classification. Very recently, Obrecht and Scholl (1981) studied the phylogenetic relationship of the genera *Bombus* and *Psithyrus* using enzyme electrophoretic techniques. The results were much different from those reported by Stephen and Cheldelin who used similar techniques:

Group (Numbered by me)	Stephen and Cheldelin	Obrecht and Scholl
1	*BO*	BO, *AS*, *FP*, *MP*, *AO* (compact except for *BO*
2	*BI*	*PR* with fairly isolate species *B*. (*Pr*.) *lapponicus*
3	*PR*, *CL*, *SP*, *FV* and *ST*	*TH*
4	*AS*, *LP*, *EP*	*PT*

The grouping by Obrecht and Scholl was unique in indicating the affinity between BO and most Psithyrus subgenera except PT.

In contrast to accumulation of the comparative studies based on adult characters, little effort has been paid for larvae, with a few exceptions such as Ritcher (1933) and Stephen and Koontz (1973). Ritcher mentioned the importance of spiracular structures to characterize species. Stephen and Koontz (op. cit.) enumerated numerous diagnostic characters, and suggested a great differentiation of BI, especially in the antennal structures, from other subgenera. But no subgeneric differences in the larval characters have been established yet.

The systems or opinions reviewed above reveal great disagreements in both rank assignment and recognition of groups. Nomenclatorially, some authors adopted multigeneric systems (Robertson 1903; Skorikov 1914, 1922; Milliron, 1961, 1971-1973; Tkalců, 1972; etc.), while others retained a single genus Bombus. The latter usually adopted two or three sections each covering many subgenera (ODT and ADT: Krueger, 1917, 1920. ODT, ADT and BOP: Frison 1927, Pittioni 1938. ODT, ADT and BI (=BOP s. str.): Krusemann, 1952. ODT: Richards, 1968). A few authors synonymized numerous described subgenera to a few large ones (typically, Milliron, op, cit.). As these rank assignments or recognitions of groups were mostly either empirically or intuitively performed, it is difficult to compare the ranking criteria held in different systems. Anyhow, it is evident that positions of many subgenera (e.g. AG, KL, BI, OR, AL, FR, etc.) are unstable among various systems (Figs. 3-11), whereas the recognition of the lowest supraspecific groups is more or less stable (Table 1).

3. 2. The genus Psithyrus Lepeletier

The morphological distinction of parasitic bumblebees was first recognized by Kirby (1802), followed by Illiger (1806) and Dahlbom (1932) (from Franklin, 1912). Lepeletier

(1832) confirmed its parasitic habit, and erected a separate genus *Psithyrus*. Gaschott (1922) compared the male genitalia of *Psithyrus* with their hosts. He revealed all the parasites shared some common features while none of them resembled their respective host species. As to the derivation of *Psithyrus* he concluded a monophyletic origin, assigning the probable ancestor on *B*. (*Md*.) *mendax* because of the resemblance of male genitalia, especially in the simple form of sagittae (=Pv), squama and 'volsella' (=Gs) (cf. Skorikov, 1922).

Working on British species Richards (1927) carefully examined the differences between *Bombus* and *Psithyrus*, and enumerated 30 alternatives. he recognized the structural resemblance between *Psithyrus* and *ODT*, especially *Agrobombus* (=*TH*). Nevertheless, he held the view of polyphyletic origin of *Psithyrus*, mentioning the host fidelity in *Psithyrus* and frequent interspecific nest usurpation by *Bombus* queens which was regarded as an indication of independent appearance of parasitism. He explained the morphological resemblance among various *Psithyrus* species by the convergence due to the parasitic habit.

Frison (1927) who described three subgenera *AS*, *FP* and *Laboriopsithyrus* (=CP; Thorp *et al*. 1983), briefly mentioned the alliance between *Psithyrus* and *TH*.

The Palaearctic *Psithyrus* was revised by Popov (1931). He recognized seven subgenera *PT*, *AS*, *FP*, *Laboriopsithyrus* (=*CP*), *MP*, *AO* and *EP*, the last three erected by himself. From morphological consideration he followed the monophyletic view by Gaschott (*op*. *cit*.). His systematic dendrogram indicated a close affinity among *PT*, *CP*, *MP* and *EP*, a relatively remote relation between *FP* and *AO*, and an isolated position of *AS* as the most primitive group. Milliron (1961, 1971) also considered *Psithyrus* as a monophyletic group, and suggested its derivation from *mendax*-line at the differentiation of either his genus *BO* or *confusus*-group. The close affinity among the subgenera of *Psithyrus* was repeatedly reported in recent biometrical and enzymological studies (Medler, 1962a,b; Plowright and Stephen, 1973) except in Obrecht and Scholl (1981).

Among recent contributions Taklců (1972) was unique in postulating a polyphyletic origin of *Psithyrus*. Contrary to Richards (1927) he asserted the resemblance among the non-parasitic bumblebee groups as convergence caused by social habits. The morphological similarities shared by the subgenera of *Psithyrus* were explained by the preservation of primitive characters. The host fidelity was, as Richards, regarded as an outcome of monophyletic origin of each couple of parasites and hosts. The long discussed question of the mono- or polyphyly of *Psithyrus* still remains unsolved.

4. Taxa studied

Taxa studied In spite of the diversity among the supraspecific systems both in interpretation and nomenclature, there is a relatively good agreement in recognition of the lowest supraspecific groups (e.g. *AL* in Table 1). This owes to the morphological compactness within each group and distinct segregation among the groups. The recent numerical or enzymological studies also confirmed this agreement for most subgenera (Plowright and Stephen, 1973; Stephen and Cheldelin, 1973; Pekkarinen, 1979; Obrecht and Scholl, 1981). Taxa compared in this study are the groups at this lowest level, that is, subgenera in the sense of Krueger (1917, 1920) or Richards (1968) though several lower groups could be recognized in some of these subgenera, particularly in larger ones such as *Pyrobombus* and *Thoracobombus*.

The specimens used were mainly from the collections accumulated by Sakagami and myself, and deposited for the time being in the Institute of Low Temperature Science, Hokkaido University (*LTH*). Some specimens deposited in the following institutions were also used for the study: Entomological Institute, Faculty of Agriculture, Hokkaido University, Sapporo (EAH); Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka (EAK); Zoological Institute, Academy of Sciences, Leningrad (ZASL); Department of Entomology, British Museum (Natural History), London (BM); and Department of Entomology, University of Kansas, Lawrence (EK). Some additional specimens were also placed at my disposal through courtesy of colleagues as acknowledged at the end of the study.

The species used are listed in Table 2. The recognition of subgenera in the present study basically follows Richards (1968) on *Bombus*, and Popov (1931) on *Psithyrus*. The taxa covers 33 of 35 Richards' subgenera (except *Exilobombus* and *Laesobombus*). Tkalců (1972) proposed considerable modifications to Richards' recognition. Among his synonymizations incorporation of *AD* in *TH* was here adopted. *Festivobombus* established by him, probably a good subgenus, was not accessible. His other synonymizations were not accepted because of insufficient reasoning. Propositions of splitting *PR* into a few subgenera by Medler (1962a, b) or Milliron (1971) were also not followed on account of the structural stability in this subgenus (cf. Richards, *op. cit.*). The morphological diversification of genitalia among *FV* species is noteworthy, but the division of *FV* by Milliron was not adopted. Judging from his illustrations of genitalia, segregation among the three Milliron's species-groups (=subgenera in the present sense) seems not evident. In the present study, each available species of *FV* was treated as representing its own group. Besides, *B. funerarius* Smith was treated as representing an isolate group *fr*. Frison (1935) considered this species (=*B. priscus* Frison) as closest to *TH* or *MC*. Later, Richards (*op. cit.*) placed it in *OR*. All these subtle groups are subsequently cited as if each representing a subgenus. Concerning *Psithyrus*, all seven Popov's subgenera were recognized as valid although later renaming (*Laboriopsithyrus* to *CP*, Thorp *et al.*, 1983) was adopted. However, *EO* was not available.

Consequently, a total of 44 taxa were studied. Beside four unavailable subgenera, *EX*, *FS*. *LS* and *EO*, some distinct groups might be overlooked. Judging from the illustrations of genitalia given by Milliron (1971-1973), *B*. (*Fr*.) *handlirschi*, *B*. (*Cr*.) *haueri* and other *FV* species might represent such groups. Nevertheless, this study may cover most if not all important groups of the tribe Bombini.

Selection of studied species It is the best to examine all the described species, and to compare them either directly among species, or among subgenera after clarifying the intrasubgeneric variation. In the present study the examination was carried out for only one species for each subgenus. Minor structural differences of genitalia within many subgenera so far empirically known by numerous taxonomic studies may support this treatment. But, it should mask the intrasubgeneric variation in some subgenera, particularly *TH*, *PR*, *ST* and *MG*, and consequently bring considerable errors in estimation of similarity among subgenera.

5. Structure of male genitalia

The structures of male genitalia of bumblebees are here briefly sketched (cf. Franklin, 1912, 1913). Detailed structures of each sclerite described below are abbreviated as follows:

(Gonobase) Gb Gb_1: mediolongitudinal suture (Fig. 13)
Gb_2: median incision (Fig. 13)
Gb_3: genital foramen (Fig. 14)
Gb_4: median tubercle (Fig. 14)
(Gonocoxite) Gc Gc_1: basidorsal protuberance (Fig. 13)
Gc_2: basal bridge (Figs. 13, 14, 16)
Gc_3: innerbasal angulation (Fig. 13)
Gc_4: innerdorsal depression (Fig. 13)
Gc_5: laterosubapical depression (Fig. 15)
Gc_6: innerbasal petiole (Fig. 16)

(Squama) Sq Sq_1: main body (Figs. 13, 15, 16)
Sq_2: inner process (Figs. 13, 14, 16)
Sq_3: median ridge (Fig. 13)
(Gonostylus) Gs Gs_1: apical angulation (Figs. 13 - 15)
Gs_2: innerapical process (Figs. 13 - 15)
Gs_3: inner subapical angulation (Figs. 13, 14)
Gs_4: apical tubercle (Fig. 14)
Gs_5: innerbasal elevation (Fig. 13)
(Spatha) Sp Sp_1: apical area (Fig. 13)
Sp_2: basal area (Fig. 13)
Sp_3: lateral ridge (Fig. 13)
Sp_4: laterobasal angulation (Fig. 13)
Sp_5: basal projection (Fig. 13)
Sp_6: sublateral flexion (Fig. 14)
(Penis valve) Pv Pv_1: apical part (Fig. 13)
Pv_2: basal part (Fig. 17)
Pv_3: median part (Fig. 16)
Pv_4: ventrobasal angulation of Pv_2 (Fig. 16)
Pv_5: apex (Figs. 16, 17)
Pv_6: lateral flange of Pv_5 (Fig. 17)
Pv_7: median process (Figs. 14, 17)
Pv_8: subbasal widening (Fig. 17)
Pv_9: lateral projection of Pv_3 (Fig. 17)
(Metasomal sternum VIII) S_8 (Fig. 2, bottom-middle)
S_{8-1}: spiculum
S_{8-2}: apical area
S_{8-3}: apodeme
S_{8-4}: median fenestra

Gonobase (Gb, Figs. 13, 14 = Cardo: Franklin, 1912; Richards, 1927, 1968; Basal ring: Milliron 1971): Basal, robust sclerite; dorsally wide and weakly protuberant, occupying one third to one fifth of total length of genitalia, medially with subtle to distinct longitudinal suture as a trace of fusion (Gb_1); dorsapical contour weakly or moderately incurved, sometimes with median incision (Gb_2) at the apical end of the medio-longitudinal suture; ventrally with a large genital foramen (Gb_3) fringed with narrow marginal area, which is mediobasally strongly tapering to the middle, forming a small tubercle (Gb_4) weakly protruding below.

Gonocoxite(s) (Gc, Figs, 13-16; = Stipes (Stipites): Skorikov, 1922; Richards, 1927, 1968; Tkalců, 1972, 1974a; Clasper: Franklin, 1912; Outer clasper: Milliron, 1971): A pair of lateral sclerites, fused each other at inner mediobasal part and shallowly inserted basally in gonobase; each robust, conical, elongate and apically tapering; inner contour strongly incurved; dorsal surface basomedially forming a thin, deeply concaved plate which is medially connected with each other (Gc_2); dorsal subbasal angle tuberculate (Gc_1); mediobasal contour seen dorsally more or less angulate (Gc_3); dorsal surface usually with depression along inner contour (Gc_4), delimited by subtle or distinct flexion; laterapically often with a weak depression (Gc_5); laterapical contour truncate or weakly outcurved but in the ventral half incurved in variable extent; ventral surface strongly narrowed medioventrad and fused with Gb_4; basoventral end curved inward, ending in a more or less convex petiole (Gc_6).

Squama (Sq, Figs. 13 - 16): A small dorsapical plate, inserted shallowly in the apical end of gonocoxite with which either fused or connected by means of membraneous structure (Fig. 178); with gonostylus connected by means of a membraneous structure; laterodorsally widest, forming main body (Sq_1) usually with mediolongitudinal or semitransverse keel or flexion (Sq_3); innerbasally with projection of variable extention and shape, or swelling (Sq_2). Probably this sclerite forms a part of Gs. Here the tranditional term squama, which is homologically noncommittal, is tentatively used.

Gonostylus (Gs, Figs. 13 - 15); = Lacinia: Skorikov, 1922; Pittioni, 1938; Richards, 1968; Tkalců, 1972, 1974a; Volsella: Richards, 1927; Milliron, 1971): A relatively large sclerite basally contiguous to Gc; apically narrowed; ventrobasally fused with the periphery of Gc; basally weakly convex (Gs_5); sometimes with longitudinal elevation with or without flexion at the top; apically or subapically, usually tuberculate subtransversely (Gs_4); median surface between these two elevations usually concave weakly; the top of the tubercle usually ridged; normally hairy, especially above; the haired area sometimes well delimited; basoventral margin often subtly ridged; inner contour subapically weakly or strongly angulate, sometimes with acute or flaring projection (Gs_3); the apical area variable in shape and width, with the apex (Gs_1) spinosely protruding, rounded, angulate, shortly truncate with dull or pointed angle, or broadly truncate with the contour more or less incurved; when truncate the inner angle usually protruding inward in various extent with apex variously modified (Gs_2); inner gap between Gc membraneous; outer gap between apical Gc intervened with rather stout membrane, usually with dense, short bristles.

Spatha (Sp, Fig. 13; = Uncus: Franklin, 1912): A thin, small, mediodorsal sclerite basally fused with basodorsal part of penis valve; narrow to relatively broad, but always longer than width; apical part (Sp_1) gradually narrowed above and curved ventrad; mediapical end often with longitudinal depression; laterapical contour more or less incurved, especially below; the widest part with lateral margin strongly ridged or folded (Sp_3), protruding over the area connected with penis valve; dorsal surface submedially with subtle to distinct flexion (Sp_2); basolateral contour usually more or less angulate or produced (Sp_4); basal margin below Sp_4 sharply ridged or folded, covering inner areas; mediobasally protruding with round or sharp apex (Sp_5) from which median ridge is formed ventrad; the ridge reaching the inner end of spatha or ending slightly before; the inner end facing to the innerdorsal margin of Gc_2 with a narrow gap.

Penis valve(s) (Pv, Figs. 13, 14, 16, 17; = Sagitta(e): Franklin, 1912; Skorikov, 1922; Pittioni, 1938; Richards, 1927, 1968; Tkalců, 1972, 1974a): A pair of elongate sclerites between Gc; rod-like and crank-shaped; each composed of apical and basal parts (Pv_1 and Pv_2, respectively), both longitudinal and subequal in length, connected with each other via short undulate structure (Pv_3) running dorsoventrad; basal part (Pv_2) protruding deeply in Gb, apically slightly curved outward with the base tuberculate or slightly produced upward (Pv_4); apical exposed part clavate or plate-like with fairly flat lateral plane; apex (Pv_5) subtly to rectangularly bent ventrad, often weakly or strongly curved inward, or subtly curved outward, rarely straight; lateral margin of Pv_5 usually narrowly and membraneously flanged (Pv_6); the flange often serrate, rarely with basal end dully or acutely angulate; lateral contour seen dorsally substraight throughout or mediobasally swollen laterad in variable extent; ventral contour in the lateral view variable, nearly straight or having a median process (Pv_7) of variable size; often subbasally widened in variable extent (Pv_8); Pv_3, the structure connecting apical (Pv_1) and basal parts (Pv_2), subvenrally produced laterad (Pv_9); the tip or the projection tuberculate or slightly hooked upward, connected with inner base of Gc.

Metasomal sterna VII and VIII (S;= Couvercles genitalux: Radoszkowski 1884; Spathae: Franklin 1912; Gastral sternites: Richards, 1968). Metasomal sternum VII (S_7: Fig. 2, bottom left; = Outer spatha: Franklin, 1912): Weakly chitinized; basal margin incurved and apical margin outcurved; wide and more or less crescent; apex truncate, protruding or weakly bilobed; apically provided with bristles variable in length, number, density, and distribution. Metasomal sternum VIII (S_8: Fig. 2, bottom-middle; = Inner spatha: Franklin, 1912): Weakly chitinized, basal margin with distinct, usually truncate spiculum (S_{8-1}); apical lobe variable in length and width; with apex subtly incurved, truncate or mildly produced; the apical area (S_{8-2}) with bristles variable in density and coverage, mediolongitudinally more or less sparser; apodeme gradually tapering laterad, variable in length and width (S_{8-3}); usually with a pair of streaks (= deformed gradulus) mediolongitudinally, apically gradually closer and fused with each other, medially thinned and usually embracing a small mal-chitinized fenestra (S_{8-4}); or rarely a pair of narrow fenestrae subapically.

6. Characters employed

6. 1. Characters of male genitalia

Selection of characters   Characters were first screened out from sclerotized parts visible without dissection. All characters having been proved to exhibit distinct intersubgeneric differences and no conspicuous intra-subgeneric variations were listed up. Characters excluded were as follows: Gonobase: dorsal convexity of Gb; gonocoxite: degree of insertion of Gb, inward curvature of inner median contour seen dorsally, dorsal inclination of dorsosubbasal projection (Sq_2), curvature of apical contour; gonostylus: density and length of bristles along lateral margins seen dorsally; exposure of the apical area above Sq seen dorsally; minute modifications on the apical margin between Gs_1 and Gs_2; spatha: length and depth of mediapical depression; length of inner mediobasal ridge; penis valve: width seen dorsally; distance between the pair.

For detecting individual variation, five individuals were examined for the species except those for which only one or a few specimens were available (asterisked in Table 2). The resulting observational errors might have been compensated in part by exclusion of characters which are empirically known to be individually variable, e.g. coloration of each sclerite, number of teeth on the apical flange of penis valve, small processes sometimes appearing on the apical margin of gonostylus.

The features which characterize only one subgenus were also omitted despite their high diagnostic value, because their inclusion would lower the level of similarity values calculated among subgenera, and consequently make elucidation of interrelationship difficult. This treatment might cause some distortions and overestimations of the similarities among taxa. These errors would be serious for the subgenera having many such "diagnostically valuable" features. Fortunately, characters excluded by this reason were relatively few and rather evenly distributed among subgenera:

CF: Enormously extended inner plate of Sq.
MD: Occurrence of dense bristles on innersubapical surface of Pv.
CL: Innermedian process of Sq.
AL: Inner subbasal angulation of Sq.
RD: Dorso-subapical spike of Pv.
PS: Extreme inward inclination of Sq_1; extreme thickening of Pv_5.
DV: Minute modifications of the apex of Gs_2.
ST: Innerapical plate-like projection at dorsoinnerapical corner of Gc.
mr: Membraneous extension at dorsoinnerapical corner of Gc.
MP: Membraneous fringe on dorsal margin of Gb.

Homologies adopted As aforementioned each genital sclerite excluding Gb is morphologically very variable among subgenera. In some structures confirmation of homology is necessary prior to distinction of character states.

(Squama) This sclerite is considered as composed basically of two parts, main body (Sq_1) and innerbasal projection (Sq_2). The shape of the innerbasal area of Sq is particularly variable. Although in most taxa Sq_2 is conspicuous, it is absent or indistinct in *MD*, *BI*, *OR*, *fr* and *PS*, indicated but ill-defined from Sq_1 in *PR*, *KL*, *MG*, *ST*, *tv* and *bv*, and distinctly bifurcated in *AL*, *CL* and *TR*. For these subgenera the following structures were considered homologous with Sq_2:

MD, *BI*, *OR*: Innersubbasal swelling
PR, *PS*: Innerbasal angulation
KL: Inner angulation
MG, *SX*, *TR* (including both ventral and dorsal projections): innerbasal upturned area
ST: Inner curved area
tv: Innerbasal concave plate
bv: Innersubbasal angulation
AL, *CL*: Basalmost process
TR: A couple of basal projection

Squama usually has two ridges. Apical one usually represents apical contour of squama seen dorsally. The other one is highly variable in position, direction and distinctiveness. This second ridge is regarded as homologous to Sq_3 in other subgenera. Possibly this ridge was derived from dorsobasal flexion of Sq_2, because it is sometimes connected with this flexion and absent in the subgenera lacking distinct Sq_2. Consequently, the following structures were homologized with Sq_3:

CF: Dorsal prominent ridge
BO: Apical transverse ridge
PR: Subinner longitudinal ridge.

Apical transverse ridge of *ST* is considered a marginal structure independent of Sq_3.

(Gonostylus) Gonostylus of bumblebees is classified into tri- and biangulate types. The former has three angulations or processes, apical (Gs_1), innerapical (Gs_2) and innersubapical (Gs_3), while the latter has only two, apical and innersubapical or innermedial. Between these two types the homology of the apical angulation is self-evident, whereas it is difficult to homologize the second process of the biangulate type with either second (= Gs_2) or third angulation (= Gs_3) of the tri-angulate type. In this study the homology with the third angulation was postulated and is subsequently mentioned as Gs_3. In triangulate type Gs_2 nearly always (excl. *TH*) occupies positions closer to Gs_1 than to Gs_3, and either fairly remote from or relatively closer to Gs_1. The last case represented by *OR*, *PS*, and *FP* is virtually undistinguishable from the biangulate type represented by *RF*, *fr*, *MD*, *CF* and the subgenera of *Psithyrus* excluding *FP*. These facts suggest that Gs_2 is actually an inner angulation of Gs_1, that is, a derivative of secondary widening of the originally single-angled apex of Gs_1.

In *OR* the apex of gonostylus is strongly twisted innerdorsad. Owing to the above context, the most apical angle seen dorsally is assigned to Gs_2, not Gs_1. Similar transformation might be suggested for *CC*. But its first and second apical angles seen dosally are tentatively regarded as Gs_1 and Gs_2 respectively, because detailed structures are degenerated there, making homologization difficult. Apical ramified structures of *DV* were regarded as modifications of Gs_2 except for the outermost process (= Gs_1).

Many subgenera possess ventrosubapical tubercle or elevation (= Gs_4), sometimes accompanied by a distinct transverse flexion or ridge, e.g. in *TH*, *bv*, etc. In others, this structure is indistinct or weak, but some of them exhibit a distinct elevation on the submedian or subapical surface, e.g. *RB*, *RD*. As these two structures are nearly alternative, their homology was postulated. A few subgenera (e.g. *ML*, *PR*) hardly exhibit either state. For them the apicalmost transverse flexion was tentatively regarded as homologous to those states.

(Spatha) Spatha of *OR* has a long lateral bridge connected with the base of penis valve and the bridge is entirely exposed dorsally (Fig. 127). Its submedian ridge is very distinct and similar to the lateral ridge (= Sp_3) in other subgenera. But this structure is possibly homologous to sublateral flexion (= Sp_6), because the latter appears in all subgenera but *OR*.

(Penis valve) Penis valve of *BO* is peculiar, forming a laterally undulated plate-like structure, laterally wide, apically wider, with the apex having dorsal and apical angulations. Although its homology to the structures held by other subgenera is not resolved, the following interpretation was adopted: Dorso-ventrad widening was caused by chitinous connection between apical bending part (= Pv_5) and subbasal widening (= Pv_8, not Pv_7) caused by excessive chitinization; the dorsapical angulation was derived by the modification of the dorsapical corner of Pv_5.

The homologizations given above are mostly no more than preliminary tentatives. However, most interpretations may not be seriously distant from the reality as these were derived from comparison of as many as taxa available.

Number of characters   A total of 121 characters were recognized, covering most if not all subgeneric characters so far used for male genitalia, together with numerous newly adopted ones. Use of further characters may not radically change the results.

Although not purposively attempted, distribution of the characters on various sclerites was relatively uniform, except for gonostylus.

	no. of characters	newly adopted ones
General size and propotion	 3	(0)
Gonobase (Gb)	 8	(7)
Gonocoxite (Gc)	 23	(21)
Squama (Sq)	 13	(2)
Gonostylus (Gs)	 28	(12)
Spatha (Sp)	 11	(0)
Penis valve (Pv)	 18	(7)
Metasomal sternum VII (S_7)	 6	(0)
Metasomal sternum VIII (S_8)	 11	(1)
	121	(50)

Distinction of states and coding   The genitalia, S_7 and S_8 of the examined species are depicted in Figs. 18 - 147 (S_7: Figs. 18 - 60; S_8: Figs. 61 - 103; Genitalia: Figs. 104 - 147). S_7 and S_8 of EV were not available, but the features were referred to the illustrations and description given by Richards (1968, p. 225). The arrangement of subgenera follows the final grouping established by the present study, although the *Psithyrus* subgenera are cited later.

Of each character the species are described with codes 1 to 5 corresponding to respective states. At the present step of the study, the cladistic polarity is not established, i.e. state 1 means neither the most apomorphic nor the most pleisiomorphic end. Differences between states are usually continuous, not distinctly disruptive. If a character is measurable, standards for the five arbitrarily distinguished states are given by dividing equidistantly the total variation range (cf. Fig. 148 - 165). Concerning unmeasurable characters, standards are determined for each character by comparing variation range of all taxa examined (cf. Figs. 166 - 232).

In the actual process of codification the total variation range was first fixed for each character by surveying all subgenera of *Bombus*. Some subgenera of *Psithyrus* exhibited high differentiations beyond this range. In such case, the extreme code, either 1 or 5, was applied to, irrespective of the actual degree of excess. This treatment might cause considerable underestimations of the difference between each *Psithyrus* subgenus and all other taxa.

List of the characters and standards for coding   For each character the following items are listed below: Code number; sclerite concerned; character; orientation for observation if necessary; definition of character and/or figure no. referred to; five states distinguished, together with value ranges for measurable characters. "Remarks" mainly deal with the views adopted to codify some peculiar structures exhibited by certain subgenera. The codes given for such instances are parenthetically mentioned.

The following abbreviations are valid for this section alone (the terms length and width represent the maximum values, and distance the minimum value, unless otherwise specified): L longitudinal length of genitalia (Fig. 148); W transverse width of genitalia (Fig. 148); T dorsoventral thickness of genitalia, measured along laterapical contour of Gb (Fig. 149); / divided by; ° newly adopted characters; * characters not having been observed for PS; ** characters difficult to define and, therefore, probably including considerable errors in coding, cf. 6.2.

1. (General) width of genitalia, dorsal view; W/p (Fig. 1, bottom-left): 1 narrow (- 0.79), 2 relatively narrow (0.80 - 0.92), 3 medium (0.93 - 1.05), 4 relatively wide (1.06 - 1.18), 5 wide (1.19 -).

2. (General) Length of genitalia, dorsal v.; L/W: 1 short (- 1.25), 2 relatively short (1.26 - 1.31), 3 medium (1.32 - 1.37), 4 relatively long (1.38 - 1.43), 5 long (1.44 -).

3. (General) thickness of genitalia, lateral v.; T/W: 1 thin (- 0.44), 2 relatively thin (0.45 - 0.48), 3 medium(0.49 - 0.52), 4 relatively thick (0.53 - 0.56), 5 thick (0.57 -).

4. (Gonobase) length of gonobase, dorsal v.; length (4 in Fig. 151)/L: 1 short (- 0.32), 2 relatively short (0.33 - 0.36), 3 medium (0.37 - 0.40), 4 relatively long (0.41 - 0.44), 5 long (0.45 -).

5.° (Gonobase) curvature of dorsapical contour, dorsal v.; mediolongitudinal length (5 in Fig. 151)/(4 in Fig. 151): 1 weak (- 0.63), 2 relatively weak (0.64 - 0.71), 3 medium (0.72 - 0.79), 4 relatively strong (0.80 - 0.87), 5 strong (0.88 -).

6.°** (Gonobase) distinctiveness of Gb_1, dorsal v.; Fig.

166: 1 virtually absent, 2 subtle, 3 weak, 4 distinct, 5 very distinct.

7.°** (Gonobase) incision of Gb_2, dorsal v., Fig. 167: 1 absent, 2 subtle, 3 weak, 4 relatively strong, 5 strong.

Remarks MP(5) possesses a peculiar fringe along dorsapical margin, medially with a distinct emargination which was tentatively judged as homologous to Gb_2 (Fig. 147).

8.°** (Gonobase) curvature of ventral contour, lateral v.; depth (8a in Fig. 149)/length of gonobase seen laterally (8b in Fig. 149): 1 straight or rather outcurved (- 0.03), 2 weakly incurved (0.04 - 0.07), 3 moderately incurved (0.08 - 0.11), 4 rather strongly incurved (0.12 - 0.15), 5 strongly incurved (0.16 -).

9.°* ** (Gonobase) length of Gb_3, ventral v.; length of Gb_3 (9a in Fig. 156)/width of Gb_3 (9b in Fig. 156): 1 short (- 0.73), 2 relatively short (0.74 - 0.80), 3 medium (0.81 - 0.87), 4 relatively long (0.88 - 0.94), 5 long (0.95 -).

10.°* ** (Gonobase) downward projection of Gb_4, ventral v.; length of Gb_4 measured from apical tangent of Gb_3 (10 in Fig. 156)/length of Gb_3 (9a in Fig. 156): 1 virtually not projecting (- 0.04), 2 subtle (0.05 - 0.08) 3 weak (0.09 - 0.12), 4 moderate (0.13 - 0.16), 5 strong (0.17 -).

11. (Gonocoxite) angulation of innerapical contour, dorsal v.; Fig. 168: 1 absent, 2 dull, 3 subrectangular, but not projecting inward, 4 angulate and weakly projecting inward, 5 strongly projecting inward.

Remarks Code (4) was tentatively given for the peculiar state in mr (Fig. 135) having membraneous angulate plate at the corner.

12.° (Gonocoxite) inclination of outerapical contour of Gc_1, dorsal v.; angle of outerapical contour against transverse line (12 in Fig. 151): 1 anterad (- -5°), 2 transverse or slightly posterad (-4° - +19°), 3 moderately posterad (+20° - +44°), 4 fairly posterad (+45° - +69°), 5 distinctly posterad (+70° -).

Remarks Angle of the line connecting apical tip of Gc$_1$ with the bottom of the inner contour of gonocoxite. In a few subgenera, the inner contour gradually lowered anterad without forming bottom. This state was coded as 1: AG (Fig. 104), NB (Fig. 105), bv (Fig. 141).

13.° (Gonocoxite) length of Gc$_1$, dorsal v.; relative length compared with transverse width at the base which is defined as the bottom of contour (Fig. 169): 1 very short or virtually absent, 2 short, 3 more or less quadrate, 4 rather long, 5 long.

Remarks The base line of Gc$_1$ is ill-defined in bv (1, Fig. 141). In this and the next character, coding is somewhat subjective.

14.° (Gonocoxite) width of Gc$_1$, dorsal v.; transverse width (13 in Fig. 153)/W: 1 narrow (- 0.10), 2 relatively narrow (0.11 - 0.12), 3 medium (0.13 - 0.14), 4 relatively wide (0.15 - 0.16), 5 wide (0.17 -).

Remarks bv(5): cf. 11.

15.° (Gonocoxite) length of gonocoxite at innerbasal part, dorsal v.; length measured from transverse line on the bottom of innerapical contour to Gc$_3$ (15 in Fig. 151)/length of gonocoxite (16 in Fig. 151): 1 short (- 0.19), 2 relatively short (0.20 - 0.25), 3 medium (0.26 - 0.31), 4 relatively long (0.32 - 0.37), 5 long (0.38 -).

Remarks Coding for the subgenera not exhibiting a sharply defined contour of Gc$_3$ might include considerable errors: CF(5, Fig. 122), BI(4, Fig. 121), CL(3, Fig. 106), dl(4, Fig. 136), tv(3, Fig. 134), mr(4, Fig. 135), bv(5, Fig. 141).

16.° (Gonocoxite) length of gonocoxite, dorsal v.; length (16 in Fig. 151)/W: 1 short (- 0.47), 2 relatively short (0.48 - 0.54), 3 medium (0.55 - 0.61),4 relatively long (0.61 - 0.67), 5 long (0.68 -).

17.°* ** (Gonocoxite) relative position of Gc_3, dorsal v.; length between Gc_3 and the basal tangent of gonocoxite (17a in Fig. 151)/distance between the bottom of posterior contour of gonocoxite and the basal tangent of gonocoxite (17b in Fig. 151): 1 high (- 0.59), 2 relatively high (0.60 - 0.69), 3 medium (0.70 - 0.79), 4 relatively low (0.80 - 0.89), 5 low (0.90 -).

Remarks Coding for the subgenera cited in 15 and 16 might involve some errors in measurements.

18. (Gonocoxite) development of the ridge of Gc_4, dorsal v.; Fig. 170: 1 absent, 2 subtle or weak, 3 moderately indicated, 4 distinct but not carinate, 5 distinctly carinate.

19.° (Gonocoxite) curvature of ventrolaterapical contour seen laterally; Fig. 171: 1 subtle or virtually absent, 2 weak, 3 moderate, 4 strong, 5 very strong.

20.° (Gonocoxite) distinctiveness of latero-subapical depression (Gc_5), lateral v.; Fig. 172: 1 absent, 2 subtle, 3 weak, 4 relatively distinct, 5 distinct.

21.°** (Gonocoxite) distinctiveness of laterodorsal line, lateral v.; Fig. 173: 1 absent, 2 subtle, 3 weak, 4 relatively distinct, 5 distinct.

22.° (Gonocoxite) angulation of lateral dorsapical contour, lateral v.; Fig. 174: 1 weakly curved without forming distinct angulation, 2 rather strongly curved with rounded angle, 3 distinctly angulate but not projecting, 4 weakly projecting dorsad, 5 strongly prodjecting dorsad.

Remarks ST(3, Fig. 125) has a peculiar inner projection scarcely seen laterally.

23. (Squama) length of Sq_1, maximal v.; length (23 in Fig. 154)/W: 1 very short (- 0.20), 2 short (0.21 - 0.25), 3 medium (0.26 - 0.30), 4 relatively long (0.31 - 0.35), 5 long (0.36 -).

Remarks Length was measured from apical tip of squama to the nearest contour of gonocoxite. In RF(3, Fig. 117) replaced by the distance between apical tip of squama and the bottom of posterior contour of squama seen dorsally.

24. (Squama) length of squama, maximal v.; length (23 Fig. 154)/width (24 in Fig. 154): 1 very short (- 0.59), 2 short (0.60 - 0.88), 3 medium (0.89 - 1.17), 4 relatively long (1.18 - 1.46), 5 long (1.47 -).

Remraks Width was measured between the basal end and the ventral contour, both viewed at the maximum width, but in RF(1) alone, between apical and basal tip (Fig. 117).

25.°** (Squama) sharpness of the apical marginal ridge, dorso-laterapical v.; Fig. 175: 1 not ridged, 2 angulate but not distinctly ridged, 3 more or less ridged, 4 sharply ridged, 5 thinly folded.

26. (Squama) inward inclination of Sq_1, dorsal v.; angle between the line used for measuring the length of squama in 23 and the longitudinal line (26 in Fig. 152): 1 very strong (- 60°), 2 strong (61° - 90°), 3 moderate (91° - 120°), 4 weak (121° - 150°), 5 very weak (151° -).

27. (Squama) distinctiveness of mediolongitudinal ridge (Sq_3), dorsolaterapical v.; Fig. 176: 1 absent, 2 weak, 3 rather distinct, 4 distinct, 5 extremely developed.

28. (Squama) maximum concavity of Sq_1, innerdorsal v.; Fig. 177: 1 strongly concave, 2 concave, 3 subtly concave or virtually flat, 4 rather convex, 5 convex.

29.** (Squama) degree of separation from gonocoxite, dorsal laterapical v. (maximal v.); Fig. 178: 1 distinctly separated, 2 moderately separated, 3 weakly separated, 4 touched or weakly fused with gonocoxite, 5 strongly fused with gonocoxite.

30. (Squama) length of Sq_2, dorsal v.; Fig. 179: 1 Sq_2 virtually absent, 2 short, 3 medium, 4 long, 5 very long.

Remarks Coding was difficult for the subgenera having Sq_2 ill-defined from Sq_1. They were coded on the basis of the distance between gonocoxite and the apicalmost tip of the inner projection: MG(4, Fig. 137), ST(4, Fig. 125), bv(3, Fig. 141).

31. (Squama) curvature of Sq$_2$, apical v. (max. v.); the curvature of posterior contour of Sq$_2$, Fig. 180: 1 Sq$_2$ virtually absent or very short, 2 weak, 3 moderate, 4 relatively strong, 5 strong.

32. (Squama) thickness of Sq$_2$, apical v.; transverse width at the base, Fig. 181: 1 very thin, 2 thin, 3 moderate, 4 thick, 5 very thick.

33. (Squama) apical modification of Sq$_2$, apical v.; Fig. 182: 1 pointed, 2 rounded, 3 truncate, 4 weakly bicorned, 5 bicorned.

34.°** (Squama) concavity of the widest surface of Sq$_2$, innerapical v.; Fig. 183: 1 rather convex, 2 nearly flat, 3 weakly concave, 4 moderately concave, 5 strongly concave.

35. (Squama) direction of Sq$_2$, dorsal v.; angle between the basal tangent squama and the line connecting the basalmost point of squama with the tip of Sq$_2$ (35 in Fig. 152): 1 rather anteriad (- 9°), 2 inward (10° - 14°), 3 weakly posterad (15° - 39°), 4 moderately posterad (40° - 64°), 5 strongly posterad (65° -).

Remarks The subgenera having indistinct Sq$_2$ were arbitrarily coded: OR(2, Fig. 127), MD(3, Fig. 120), BI(3, Fig. 121), ST(5, Fig. 125), tv(3, Fig. 134), bv(2, Fig. 141).

36.°* (Gonocoxite) size of Gc$_6$, innerventral v.; Fig. 184: 1 very small, 2 small, 3 medium, 4 relatively large, 5 large.

37.°* ** (Gonocoxite) convexity of the inner surface of Gc$_6$, innerventral v.; Fig. 185: 1 subflat, 2 subtly convex, 3 weakly convex, 4 moderately convex, 5 strongly convex.

38.°* ** (Gonocoxite) development of the gap isolating Gc$_6$ from innerbasal part of gonocoxite, innerdorsal v.; Fig. 186: 1 subtle, 2 shallow, 3 moderate, 4 relatively deep, 5 very deep.

39. (Gonostylus) length above gonocoxite, dorsal v.;

length (39 in Fig. 151)/L: 1 short (- 0.09), 2 relatively short (0.10 - 0.14), 3 medium (0.15 - 0.19), 4 relatively long (0.20 - 0.24), 5 long (0.25 -).

40.° (Gonostylus) distinctiveness of Gs_5, dorsal v.; height from Gc_6, Fig. 187: 1 very low, 2 low, 3 moderate, 4 high, 5 very high.

41.°* ** (Gonostylus) size of inner-basalmost projection, innerdosal v.; Fig. 188: 1 hardly developed, 2 very small, 3 rather small, 4 rather large (represented by no subgenera), 5 large.

42.°** (Gonostylus) degree of isolation at the middle of gonostylus from squama, apical v.; Fig. 189: 1 weakly fused, 2 scarcely isolated, 3 narrowly isolated, 4 moderately isolated, 5 distinctly isolated.

43. (Gonostylus) shape of the tip of Gs_1, dorsal v. (max. v.); Fig. 190: 1 rounded, 2 obscurely angulate, 3 more or less angulate, 4 pointed, 5 projecting and pointed.

44. (Gonostylus) development of Gs_2, dorsal v.; Fig. 191: 1 Gs_2 absent, 2 subtly projecting, 3 weakly projecting, 4 moderately projecting 5 distinctly projecting.

45. (Gonostylus) shape of the tip of Gs_2, dorsal v.; Fig. 192: 1 Gs_2, absent or pointed, 2 truncate, 3 subtly bifurcated, 4 distinctly bifurcated or trifurcated, 5 strongly ramified.

46. (Gonostylus) distance between Gs_1 and Gs_2, max. v.; Fig. 193: 1 Gs_2 absent, 2 short, 3 medium, 4 long, 5 very long.

47.** (Gonostylus) curvature of the contour between Gs_1 and Gs_2, max. v.; Fig. 194: 1 Gs_1 absent, 2 substraight, 3 weakly concave, 4 moderately concave, 5 strongly concave.

48.** (Gonostylus) direction of apical twisting, dorsal v.; Fig. 195: 1 twisted rather ventrad, 2 not twisted, 3 subtly twisted dorsad, 4 moderately twisted dorsad (represented by no subgenera), 5 strongly twisted dorsad.

Remarks The apex of gonostylus of PT(1) inclining dorsad and rather twisted outward (Fig. 142).

49.° (Gonostylus) inter-Gs_1 distance, dorsal v.; distance (49 in Fig. 156)/W: 1 short (- 0.26),, 2 relatively short (0.27 - 0.39), 3 moderate (0.40 - 0.52), 4 relatively long (0.53 - 0.63), 5 long (0.64 -).

50.°** (Gonostylus) inter-Gs_2 distance, dorsal v.; distance (50 in Fig. 156)/W: 1 short (- 0.25), 2 relatively short (0.26 - 0.33), 3 moderate (0.34 - 0.41), 4 relatively long (0.42 - 0.49), 5 long (0.50 -).

51. (Gonostylus) distinctiveness of Gs_3, ventral v.; Fig. 196: 1 hardly angulate, 2 weakly angulate, 3 moderately angulate, 4 distinctly angulate, 5 projecting.

52.** (Gonostylus) density of the bristles on apical margin, dorsal v.; if Gs_2 present, of those between Gs_1 and Gs_2, otherwise of those on apical half of the inner contour of gonostylus between Gs_1 and Gs_3; Fig. 197: 1 virtually absent, 2 very sparse, 3 relatively sparse, 4 relatively dense, 5 dense.

53.** (Gonostylus) length of the bristles on apical margin, dorsal v.; length of the longest bristle (53 in Fig. 152)/W; definition of the area, see 52: 1 absent, 2 short (0.01 - 0.03), 3 medium (0.04 - 0.07), 4 relatively long (0.08 - 0.11), 5 long (0.12 -).

54.** (Gonostylus) density of the bristles on median part of inner surface seen dorsally; Fig. 198: 1 virtually absent, 2 sparse, 3 medium, 4 relatively dense, 5 dense.

55.** (Gonostylus) length of the bristles on inner surface seen dorsally; length of the longest bristle (55 in Fig. 152)/W, measured for those between Sq_2, or if Sq_2 absent, those between Gs_3 and base of gonostylus seen dorsally: 1 absent, 2 short (- 0.03), 3 medium (0.04 - 0.07), 4 relatively long (0.08 - 0.11), 5 long (0.12 -).

56.°* ** (Gonostylus) width of gonostylus, innerapical v.

(max. v.); maximum transverse width (56 in Fig. 157 or 161)/T: 1 very narrow (- 0.14), 2 narrow (0.15 - 0.18), 3 medium (0.19 - 0.22), 4 wide (0.23 - 0.26), 5 very wide (0.27 -).

57.°** (Gonostylus) thickness of Gs_1, apical v.; Fig. 199: 1 very thin, 2 thin, 3 medium, 4 relatively thick, 5 thick.

Remarks This character exhibits a remarkable difference among subgenera, but difficult to be measured accurately. Coding might be not free from subjectivity.

58. (Gonostylus) position of the top of Gs_4, innerventral v.; Fig. 200: 1 very apical 2 apical, 3 relatively apical, 4 rather medial, 5 rather basal.

59.° (Gonostylus) distinctiveness of the flexion of Gs_4, innerventral v.; Fig. 201: 1 absent, 2 subtle, 3 weakly indicated, 4 relatively distinct, 5 distinct.

60.°** (Gonostylus) curvature of inner contour of gonostylus seen ventrally; average curvature between base and Gs_2, or in the subgenera devoid of Gs_2, Gs_1; Fig. 202: 1 very weak, 2 weak, 3 moderate, 4 relatively strong, 5 strong.

61. (Gonostylus) relative height of the innerbasal contour seen ventrally; height from posterior tangent of genital foramen (Gb_5) (61 in Fig. 156)/L: 1 low (- 0.11), 2 relatively low (0.12 - 0.17), 3 medium (0.18 - 0.23), 4 relatively high (0.24 - 0.29), 5 high (0.30 -).

62.°* ** (Gonostylus) distinctiveness of subapical longitudinal flexion, innerventral v.; Fig. 203: 1 absent, 2 subtle, 3 weak, 4 distinct, 5 very distinct.

Remarks Inner-subbasal longitudinal flexion of MD(3) and mediosubbasal flexion of SP(2) are considered homologous to the flexion mentioned.

63.** (Gonostylus) convexity of basal surface, innerventral v.; Fig. 204: 1 rather concave, 2 nearly flat, 3 weakly convex, 4 moderately convex, 5 strongly convex.

64.°** (Gonostylus) curvature of lateral contour, ventral v.; Fig. 205: 1 weak, 2 relatively weak, 3 moderate, 4 relatively strong, 5 strong.

65.° (Gonostylus) thickness of Gs_4, innerapical v.; magnitude of innerventrad elevation of Gs_4 from Gs_1, Fig. 206: 1 very thin, 2 thin, 3 moderate, 4 thick, 5 very thick.

66. (Spatha) width of spatha, dorsal v.; maximum width (66 in Fig. 158): 1 very narrow (- 0.18), 2 narrow (0.19 - 0.25), 3 medium (0.26 - 0.32), 4 wide (0.33 - 0.39), 5 very wide (0.40 -).

67.** (Spatha) length of spatha, dorsal v.; length seen dorsally (67 in Fig. 158)/L (Fig. 148): 1 very short (- 0.25), 2 short (0.26 - 0.32), 3 medium (0.33 - 0.39), 4 long (0.40 - 0.46), 5 very long (0.47 -).

Remarks The apical part of spatha usually curves ventrad. The degree of curvature is remarkably different among subgenera. But artificial distortion at pulling out the genitalia from metasoma might bring some errors in coding.

68. (Spatha) length of Sp_2, dorsal v.; length (68 in Fig. 158)/W: 1 very short (- 0.08), 2 short (0.09 - 0.11), 3 medium (0.12 - 0.14), 4 long (0.15 - 0.17), 5 very long (0.18 -).

69. (Spatha) curvature of lateral contour of Sp_1, dorsal v.; Fig. 207: 1 very strongly incurved, 2 strongly incurved, 3 moderately incurved, 4 subtly incurved, 5 rather outcurved.

70. (Spatha) curvature of lateral contour of Sp_2, dorsal v.; Fig. 208: 1 strongly incurved, 2 moderately incurved, 3 weakly incurved, 4 semistraight, 5 rather outcurved.

71. (Spatha) shape of the tip of Sp_5, dorsal v.; Fig. 209: 1 emarginate, 2 rounded or truncate, 3 angulate and weakly projecting, 4 sharp and moderately projecting, 5 sharp and conspicuously projecting.

72.** (Spatha) shape of laterobasal angulation, dorsal v.; Fig. 210: 1 rounded, 2 subtly angulate, 3 dully angulate, 4 rectangular, 5 acutely angulate.

73. (Spatha) distinctiveness of sublateral flexion, laterodorsal v.; Fig. 211: 1 virtually absent, 2 subtle, 3 weak, 4 distinct, 5 very distinct and sharply ridged.

74. (Spatha) degree of lateral extension of Sp$_3$, dorsal v.; Fig. 212: 1 recognized as a flexion, and the suture with penis valve entirely exposed, 2 weakly extending laterad, 3 moderately extending laterad, just covering the suture, 4 rather strongly extending laterad, covering the suture, 5 strongly extending laterad, excessively covering the suture.

75.* (Spatha) curvature of median ridge just below Sp$_5$, laterodorsal v.; Fig. 213: 1 strongly incurved, 2 weakly incurved, 3 semistraight, 4 weakly outcurved, 5 distinctly outcurved.

76.** (Spatha) transverse convexity of median surface, dorsobasal v.; Fig. 214: 1 virtually flat, 2 weak, 3 moderate, 4 relatively strong, 5 strong.

77. (Penis valve) ventrad curvatue of apex (Pv$_5$), laterodorsal v.; Fig. 215: 1 subtle, 2 weak, 3 moderate, 4 strong, 5 subrectangular.

Remarks Pv$_5$ of bv(4) is gradually bent and ill-defined from the basal part of penis valve, but the curvature as a whole is strong (Fig. 141).

78. (Penis valve) length of Pv$_5$, laterodorsal v. (maximum v.); length (78 in Fig. 159)/length of Pv$_1$ measured from the basal tangent of the inner contour of gonocoxite (78 in Fig. 152): 1 short (- 0.10), 2 relatively short (0.11 - 0.20), 3 medium (0.21 - 0.30), 4 relatively long (0.31 - 0.40), 5 long (0.41 -).

Remarks In the subgenera having indistinct basal angulation of Pv$_5$ (e.g. MD, Fig. 120; BI, Fig. 121; CF, Fig. 122; bv, Fig. 141; etc.), the length of Pv$_5$ was measured from the basal end of Pv$_6$. As to bv(5), cf. 77.

79. (Penis valve) curvature of Pv$_5$, apical v.; Fig. 216: 1 rather outcurved, 2 virtually straight, 3 weakly

incurved, 4 subrectangularly incurved, 5 strongly incurved.

Remarks In tv(3) Pv$_5$ as a whole straightly directed suboutward (Fig. 134); bv(2), cf. 77 (Fig. 141).

80. (Penis valve) development of laterapical flange of Pv$_5$, laterapicodorsal v.; Fig. 217: 1 virtually absent, 2 weak, 3 moderate, 4 relatively strong, 5 strong.

Remarks In BO(4) the flange is ill-defined, and the coding is subjective.

81.° (Penis valve) angulation of basal corner of Pv$_6$, laterapicodorsal v.; Fig. 218: 1 not angulate, semistraight or mildly curved, 2 dully angulate, or moderately curved, 3 subrectangular or strongly curved, 4 acutely curved, 5 spinosely projecting.

82. (Penis valve) serration of Pv$_6$, laterapicodorsal v.; Fig. 219: 1 absent, 2 very fine, 3 weak, 4 relatively strong, 5 strong.

83. (Penis valve) development of Pv$_7$, laterodorsal v.; Fig. 220: 1 absent, 2 subtle, 3 weak, 4 strong, 5 very strong, thinned, and widened apically.

84. (Penis valve) angulation of Pv$_7$, laterodorsal v.; Fig. 221: 1 very mild or Pv$_7$ absent, 2 rounded, 3 dull, 4 subacute, 5 acute.

85.* (Penis valve) width of penis valve, inner-subapical v.; width measured just above Pv$_7$, if Pv$_7$ absent, approximately at the middle (85 in Fig. 159)/T: 1 very narrow (- 0.16), 2 narrow (0.17 - 0.21), 3 medium (0.22 - 0.26), 4 wide (0.27 - 0.31), 5 very wide (0.32 -).

Remarks Precise measurement was often hampered by the inadequate condition of penis valve. Considerable errors might be included in the results.

86. (Penis valve) development of Pv$_8$, laterodorsal v.; Fig. 222: 1 absent, 2 subtle, 3 moderate, 4 relatively strong, subapically more or less angulate, 5 strong, subapically distinctly angulate.

Remarks Concerning BO(5), see the homology given previously.

87.* ** (Penis valve) development of inner plate of Pv_1, dorsal v.; degree of coverage over the longitudinal membraneous part, Fig. 223: 1 poor, the plate hardly or only partly observable, 2 rather poor, the plate narrowly but nearly throughout observable, 3 moderate, rather widely observable throughout, 4 well developed, partly covering the membraneous part, 5 very well developed, covering distinctly the membraneous part.

88. (Penis valve) exposure of laterobasal plate of Pv_1, dorsal v.; Fig. 224: 1 widely exposed, 2 moderately exposed, 3 hardly exposed, 4 weakly hidden, 5 strongly hidden.

<u>Remarks</u> Exposure from the basodorsal surface of Pv_1, not from spatha, was inspected. The degree of hiding was examined laterodorsally.

89.°** (Penis valve) dorsad inclination of Pv_1, lateral v.; judged from the degree of exposure from gonocoxite seen laterally, Fig. 225: 1 subtle, hardly exposed, 2 weak, slightly exposed, 3 moderate, basal half exposed, 4 relatively strong, exposed except apex, 5 strong, nearly entirely exposed.

90.° (Gonobase) dorsad inclination of ventral contour of gonobase seen laterally; angle between the tangent of ventral contour of gonocoxite and the tangent of ventral contour of gonobase lined from the basoventral end of gonocoxite, 90 in Fig. 163): 1 subtle (- 9°), 2 weak (10° - 19°), 3 medium (20° - 29°), 4 rather strong (30° - 39°), 5 strong (40° -).

91.°* (Penis valve) length of Pv_2, ventral v.; length of Pv_2 (91 in Fig. 156)/L: 1 short (- 0.27), 2 relatively short (0.28 - 0.30), 3 medium (0.31 - 0.33), 4 relatively long (0.34 - 0.36), 5 long (0.37 -).

92.°* (Penis valve) inter-Pv_2 distance, ventral v.; distance between tips (92 in Fig. 156)/W: 1 short (- 0.35), 2 relatively short (0.36 - 0.42), 3 medium

(0.43 - 0.49), 4 relatively long (0.50 - 0.56), 5 long (0.57 -).

93.°* (Gonocoxite) inclination of lateral contour of Gc_2 seen ventrally; angle to the horizontal line at the most concave point of lateral contour (93 in Fig. 162): 1 weak (- 24°), 2 relatively weak (25° - 34°), 3 medium (35° - 44°), 4 relatively strong (45° - 54°), 5 strong (55° -).

Remarks On account of the variable curvature of lateral contour, coding was not free from subjectivity.

94.°* (Gonocoxite) relative length of Gc_2, ventral v.; length along median line (94a in Fig. 162)/transverse width at the most concave point on lateral contour (94b in Fig. 162): 1 very short (- 0.48), 2 short (0.49 - 0.79), 3 medium (0.80 - 1.10), 4 long (1.11 - 1.41), 5 very long (1.42 -).

Remarks Extremely elongate in MP(5, Fig. 147) and to less extent, PT(5, Fig. 142).

95. (Gonostylus) level of the surface along basal margin, inner ventral v.; level of the innerbasal surface of gonostylus, compared with the basal suture, Fig. 226: 1 rather depressed, 2 semiflat, 3 mildly elevated, 4 moderately elevated, 5 strongly elevated, accompanied by a relatively distinct ridge above the suture.

Remarks In RD(2, Fig. 116) gonostylus and gonocoxite are strongly fused at the area concerned, with wide poorly-chitinized depression or fenestra.

96.°* ** (Gonocoxite) curvature of ventrobasal contour seen apically; length from the ventrobasal tangent of gonostylus to ventrobasal extremity of gonocoxite (96 in Fig. 160)/T: 1 subtle (- 0.08), 2 weak (0.09 - 0.13), 3 moderate (0.14 - 0.18), 4 relatively strong (0.19 - 0.23), 5 strong (0.24 -).

97.°* ** (Gonocoxite) outward curvature of innerbasal contour seen apically; depth from the line between the tip of Gc_6 and Gb_4 (97a in Fig. 160)/length of the line mentioned (97b in Fig. 160): 1 virtually straight (- 0.04), 2 subtle (0.05 - 0.09), 3 weak (0.10 - 0.14), 4 moderate (0.15 - 0.19), 5 strong (0.20 -).

Remarks in CP(5, Fig. 146) and bv(1, Fig. 141) the contour is fairly undulate, not uniformly concave.

98.°* (Gonocoxite) inter-Gc_6 distance, apical v.; distance between tips (98 in Fig. 161)/W: 1 short (- 0.19), 2 relatively short (0.20 - 0.24), 3 medium (0.25 - 0.29), 4 relatively long (0.30 - 0.34), 5 long (0.35-).

99.°* (Penis valve) inter-Pv_4 distance, apical v.; inter-Gc_6 distance (98 in Fig. 161)/distance between tips (99 in Fig. 161): 1 short (- 1.16), 2 relatively short (1.17 - 1.51), 3 medium (1.52 - 1.86), 4 relatively long (1.87 - 2.21), 5 long (2.22 -).

100.°* ** (Gonocoxite) distance between basoventral tip of spatha and mediodorsal tip of Gc_2, apical v.; distance (100 in Fig. 161)/T: 1 short (- 0.24), 2 relatively short (0.25 - 0.29), 3 medium (0.30 - 0.34), 4 relatively long (0.35 - 0.39), 5 long (0.40 -).

101.°* ** (Penis valve) outward curvature of Pv_3, apical v.; depth from the line connecting the tips of inner contour of Pv_4 and dorsal angulation of Pv_3 (101a in Fig. 160)/length of the line mentioned (101b in Fig. 160): 1 virtually straight (- 0.07), 2 subtle (0.08 - 0.14), 3 weak (0.15 - 0.21), 4 moderate (0.22 - 0.28), 5 strong (0.29 -).

102.°* ** (Penis valve) length of Pv_3, apical v.; length defined in 101 (101b in Fig. 160)/T: 1 short (- 0.19), 2 relatively short (0.20 - 0.26), 3 moderate (0.27 - 0.33), 4 relatively long (0.34 - 0.40), 5 long (0.41-).

Remarks Dorsal angulation of inner contour is usually dull and obscure, Therefore coding might include considerable errors.

103.° (Gonocoxite) position of ventrapical corner seen laterally; length of gonostylus measured from the ventrapical corner of gonocoxite seen laterally (103a in Fig. 149)/length between apex of gonostylus and ventrobasal end of gonocoxite (103b in Fig. 149): 1 high (- 0.26), 2 relatively high (0.27 - 0.35), 3 moderate (0.36 - 0.44), 4 relatively low (0.45 - 0.53), 5 low (0.54 -).

Remarks As basal tip of venral corner of gonocoxite is affected by slight change of orientation of genitalia, coding of this character might include considerable errors.

104.° (Gonocoxite) concavity of ventral contour of gonocoxite, lateral v.; distance between the tangent of gonostylus lined from the basoventral end of gonocoxite and the most concave point of ventral contour of gonocoxite seen laterally (104a in Fig. 163)/length between the two points of contact of the tangent mentioned (104b in Fig. 163): 1 not or hardly inclined (- 0.02), 2 weak (0.03 - 0.05), 3 moderate (0.06 - 0.08), 4 relatively strong (0.09 - 0.11), 5 strong (0.12 -).

105. (S_7) curvature of basal contour; depth from the basal tangent (105a in Fig. 164)/length of the basal tangent (105b in Fig. 164): 1 subtle (- 0.11), 2 weak (0.12 - 0.19), 3 moderate (0.20 - 0.27), 4 relatively strong (0.28 - 0.35), 5 strong (0.36 -).

106. (S_7) length of S_7; mediolongitudinal length (106 in Fig. 164)/width (105b in Fig. 164): 1 short (- 0.23), 2 relatively short (0.24 - 0.33), 3 medium (0.34 - 0.43), 4 relatively long (0.44 - 0.53), 5 long (0.54 -).

107. (S_7) shape of midiapical contour; Fig. 227: 1 angulate, 2 rounded, 3 subtruncate, or very subtly curved either in- or outward, 4 rather strongly incurved, 5 strongly incurved.

108. (S_7) number of bristles: 1 few (- 10), 2 relatively few (11 - 50), 3 medium (51 - 100), 4 relatively

numerous (101 - 200), 5 numerous (201 -).

109. (S_7) curvature of laterosubapical contour; Fig. 228: 1 incurved or substraight or subtly outcurved, 2 weakly outcurved, 3 moderately and roundly outcurved, 4 more or less angulate, 5 distinctly angulate.

110. (S_8) length above inter-S_{8-4} line; length (110a in Fig. 165)/width of S_8 (110b in Fig. 165): 1 short (- 0.20), 2 relatively short (0.21 - 0.26), 3 medium (0.27 - 0.32), 4 relatively long (0.33 - 0.38), 5 long (0.39 -).

111. (S_8) shape of spiculum (S_{8-1}); length of spiculum (111 in Fig. 165)/width of spiculum (112 in Fig. 165): 1 very transverse (- 0.43), 2 transverse (0.44 - 0.67), 3 slightly transverse (0.68 - 0.91), 4 nearly quadrate (0.92 - 1.15), 5 elongate (1.16 -).

Remarks Due to the difficulty in defining the reference points the results might include some errors.

112. (S_8) width of spiculum; width (cf. 112 in Fig. 165)/width of S_8 (110b in Fig. 165): 1 narrow (- 0.14), 2 relatively narrow (0.15 - 0.20), 3 medium (0.21 - 0.26), 4 relatively wide (0.27 - 0.32), 5 wide (0.33 -).

113. (S_8) width of S_{8-2}; width between laterapical angulation (113 in Fig. 165)/width of S_8 (110b in Fig. 165): 1 narrow (- 0.14), 2 relatively narrow (0.15 - 0.20), 3 medium (0.21 - 0.26), 4 relatively wide (0.27 - 0.32), 5 wide (0.33 -).

Remarks For the subgenera having indistinct angulation, e.g. CL(2, Fig. 63), BO(4, Fig. 75), OR(3, Fig. 80), coding might be somewhat arbitrary.

114. (S_8) length of S_{8-2}; length from the transverse line on the most incurved points of lateral contour (114 in Fig. 165)/width of S_8 (110b in Fig. 165): 1 short (- 0.26), 2 relatively narrow (0.27 - 0.34), 3 medium (0.35 - 0.42), 4 relatively wide (0.43 - 0.50), 5 wide (0.51 -).

Remraks The difficulty to determine the base line in some subgenera might bring some errors in coding: ML(1, Fig. 64), RB(2, Fig. 72), BO(1, Fig. 76), CF(1, Fig. 79), SX(3, Fig. 94).

115. (S_8) inward curvature of lateral contour; depth from the tangent for laterapical angulation and S_{8-3}(115a in Fig. 165)/length between the two points of contact (115b in Fig. 165): 1 subtle (- 0.12), 2 weak (0.13 - 0.24), 3 medium (0.25 - 0.36), 4 relatively strong (0.37 - 0.48), 5 strong (0.49 -).

116. (S_8) distinctiveness of mediosubbasal fenestra (S_{8-4}); Fig. 229: 1 absent, 3 marked, but not opened, 5 distinctly opened.

Remarks Codes 2 and 4 were excluded on the absence of corresponding states.

117. (S_8) distinctiveness of subapical fenestrae; Fig. 230: 1 absent, 3 marked, but not opened, 5 distinctly opened.

Remarks See 116.

118. (S_8) apical bristled area; Fig. 231: 1 bristles absent, or only marginal, 2 narrow, covering about apical one-fifth, 3 medium, covering about apical one-fourth, 4 relatively wide, covering apical one-third, 5 wide, nearly covering apical half.

Remraks Due to the variation of the distribution of bristles, coding might not be free from subjectivity.

119. (S_8) degree of chitinization: 1 weak, 2 relatively weak, 3 medium, 4 relatively strong, 5 strong.

Remarks This character cannot be measured and illustrated. In spite of distinct differences found among the subgenera, subjectivity in coding is inevitable.

120.° (S_8) maximal distance between a pair of mediolongitudinal streaks (= deformed gradulus)(120 in Fig. 165)/width of S_8 (110b in Fig. 165): 1 short (- 0.09), 2 relatively short (0.10 - 0.16), 3 medium (0.17 - 0.23), 4 relatively long (0.24 - 0.30), 5 long (0.31 -).

Remarks For the subgenera having indistinct streaks the width of the median fenestra, if any, was measured: *OR*(1, Fig. 84), *DV*(1, Fig. 95), *PT* (1, Fig. 98), *CP*(1, Fig. 102); cf. 116. For the subgenera without both the streaks and the fenestra, coding was tentatively given on the basis of the width of S_{8-2}, as follows: *MD*(5, Fig. 77), *BI*(5, Fig. 78), *FP*(1, Fig. 101).

121. (S_8) curvature of apical contour of S_{8-2}; Fig. 232: 1 strongly incurved, 2 moderately incurved, 3 substraight, or subtly in- or outcurved medially, 4 weakly outcurved, or more or less produced medially; 5 distinctly produced.

6. 2. Numerical techniques applied

Based upon the original data matrices of subgenus × character (Appendix), intersubgeneric affinity was measured with Pearson's product-moment correlation coefficient for every pair of subgenera. The coefficient between subgenus j and k is calculated as

$$r_{j,k} = \frac{\sum_{i=1}^{n} (x_{i,j} - \bar{x}_j)(x_{j,k} - \bar{x}_k)}{\sqrt{\sum_{i=1}^{n} (x_{i,j} - \bar{x}_j)^2 \sum_{i=1}^{n} (x_{i,k} - \bar{x}_k)^2}}$$

where $x_{i,j}$ or $x_{i,k}$ stands for state code of character i in species j or k, $\bar{x}_j$ or $\bar{x}_k$ is the mean of all state codes for species j or k, and n is the number of characters.

The correlation matrices were summarized by the cluster analysis, using arithmetic average: UPGMA (unweighted pairgroup method using arithmetic average; Sneath and Sokal, 1973). In this method the distance, D, between a given pair of the cluster, C_f and C_g, is defined as follows:

$$D = \frac{1}{n_f \cdot n_g} \sum_{\alpha=1}^{n_f} \sum_{\beta=1}^{n_g} D_{\alpha,\beta}$$

where n_f and n_g stand for the number of OTU (operational taxonomical unit; Sneath and Sokal, *op. cit.*) included in C_f and C_g, respectively. The $D_{\alpha,\beta}$ represents the similarity (the correlation coefficient here) or distance between the OTUs (subgenera here) α in C_f and β in C_g.

UPGMA was applied for the following five combinations of subgenera and characters:

combination code	sclerites	no. of subgenera	no. of characters	phenogram
I	Genitalia	37 excl. *PS* and *Psithyrus* subgenera	67	I (Fig. 285)
II	"	37 (")	104	II (Fig. 286)
III	"	44 (all)	58	III(Fig. 287)
IV	"	44 (")	81	IV (Fig. 288)
V	S_7, S_8	44 (")	17	———

Combination II and IV include all examined characters of genitalia while combinations I and III do only the well-defined characters (excluding those specified with double asterisks in the list above).

Among many algorithms of cluster analysis, UPGMA is known by a relatively faithful representation of the original similarity (or distance) matrix (Rohlf, 1965; Sneath and Sokal, 1973; Tadauchi, 1975, 1978a, b). However, like in other algorithms, later associations represent poorer reliability owing to the distorsion accumulated in the sequence of amargamation (Sneath and Sokal, *op, cit.*).

This defect may be compensated partly by PCA (principal component analysis) which gives a faithful summary for the interrelations between remote OTUs while it poorly represents interrelations between close ones (Rohlf, 1968). PCA was carried out for the correlation matrix of combination II. The results are given in the component pattern diagrams (Tadauchi, 1975) showing the component scores of each OTU for the first twelve principal components. This technique displaying the phenetic relationships among OTUs is useful when an appreciable proportion of the variability is not explained by the first three dimensions (cf. Tadauchi *op. cit.*). The component scores were calculated as

$$Z_{j,k} = \sum_{i=1}^{n} (W_{j,i} \cdot l_{k,i}),$$

where $Z_{j,k}$ means the component score of OTU *j* in component *k*, $w_{i,j}$ is the standardized character state value of character *i* in OTU *j*, $l_{k,i}$ is the element of eigenvector in component *k*, and *n* the number of characters.

All computations were undertaken by the Hitac-3 Computer in the Computer Center of Hokkaido University. An application program BMDP (Biomedical Computer Programs-P, developed by the University of California) was utilized, BMDP1M for cluster analysis, and BMDP6M for PCA.

7. Grouping based on the characters of male genitalia

Table 3 describes each OTU by the code values for 121 characters. States of unexamined characters are coded zero. Figs. 233-276 depict the closest ten subgenera for each subgenus, exhibiting high correlations as to the structures of genitalia (G: right) and apical sterna (S: left). Correlation values of *Pressibombus* (*PS*) and the subgenera of *Psithyrus* are cited from the matrices of combination IV for genitalia and -V for apical sterna. Those values of other taxa are taken from the matrices of combinations II (Appendix) and V. The trends of similarity in these figures are commented below for each subgenus in the order arranged in phenogram II (Fig. 287) with special reference to ODT and ADT in Krueger's sense. The ODT subgenera are specified with a single asterisk.

Bombus

Alpigenobombus (Fig. 233). Genitalia: The higher ranks of correlations are occupied by the Holarctic subgenera of ADT in Krusemann's sence (op. cit.). Correlations with the subgenera of ODT are very low except for fv (r=0.30), ST (r=0.26) and EV (r=0.26). The highest correlation is occupied by NB (r=0.82), followed by CL, ML and PR, the members of UNC in Krueger's sense (1917). Sterna: The high correlation with NB is retained, but a half of the top ranks are occupied by the subgenera of ODT. The highest correlation is shown by DV.

Nobilibombus (Fig. 234). Genitalia: Very similar to those of AG, with which it shares the highest correlation. Sterna: Trend is similar to that of AG, with DV at the top. But correlations to the ODT subgenera are generally much lower.

Cullumanobombus (Fig. 235). Genitalia: Similarity to ADT is distinct, showing high correlations to AG, ML, CR, PR, NB, etc., all Old World or Holarctic representatives. Among the ODT subgenera, the highest correlation is represented by fv (r=0.25). Sterna: Highly correlated elements and their order markedly differ from those in genitalia. The similarity to ADT is weaker, and rather closer to some ODT subgenera (EV, TH, etc.).

Melanobombus (Fig. 236): Highly correlated elements are very similar to CL although their order is slightly different. As in CL, no subgenera of ODT exhibit high correlation. Sterna: No subgenera of ODT are included in the higher ranks. The highly correlated elements differ distinctly from those of genitalia. The highest similarity is observed with BI, then, with AL, RF, etc.

Pyrobombus (Fig. 237). Genitalia: The correlation values of the highly ranked subgenera are relatively even. The basic pattern is similar to *CL* and *ML*, but a relatively high correlation to *FN* is noteworthy. Sterna: The highly ranked elements are greatly different from both *CL* and *ML*. No subgenera exhibit high correlation.

Bombus s. str. (Fig. 238). Genitalia: Most correlation values are low. The highest correlation is observed with *AL* but only of 0.40. Among *ADT*, the W. Hemisphere subgenera exhibit slightly higher similarities than those of E. Hemisphere. Correlation to the *ODT* subgenera is generally low except for *dl* and *mr*. Sterna: The higher ranks are occupied by the *ADT* subgenera, with *RF* at the top.

Fraternobombus (Fig. 239). Genitalia: Correlation to the *ODT* subgenera are very low as in *CL*, *ML* and *PR*. But, with a marked contrast to these subgenera, the first four ranks are occupied by the W. Hemisphere representatives. Sterna: The similarity to the W. Hemisphere *ADT* is more or less observed, but the highest rank is occupied by *AL*. Further, a few *ODT* subgenera exhibit relatively high correlations.

Coccineobombus (Fig. 240). Genitalia: Trend is similar to that of *FR*. The highest correlation is held with *RD*. Sterna: *RD* exhibits again the highest correlation, but affinity to *ADT* is generally indistinct.

Separatobombus (Fig. 241). Genitalia: The pattern is similar to those of *FR* and *CC*, but the first three ranks are occupied by *RB*, *CR* and *FN*. Sterna: The similarity to *ADT* is less distinct. A high similarity is observed with *FV* and *CL*.

Crotchiibombus (Fig. 242). Genitalia: Ten top ranks are exclusively occupied by the *ADT* subgenera, with *SP* at the top. Level of correlation values is generally high. Sterna: The highest correlation is seen with *CL*. The subsequent ranks are occupied by the subgenera of diverse lines.

Funebribombus (Fig. 243). Genitalia: The affinity to *ADT* is distinct as in *CR*. The highest correlation is seen with *SP* and *CR*. Sterna: Trend is similar to that of genitalia, although the order and components do not exhibit exact correspondences.

Robustobombus (Fig. 244). Genitalia: Affinity to the *ADT* subgenera, especially of the W. Hemisphere, is distinct. *RD* and *SP* nearly share the top rank. Sterna: Most elements in the higher ranks for genitalia are replaced, but a marked similarity to *ADT* is retained.

Rubicundobombus (Fig. 245). Genitalia: Trend is similar to that of *RB*, though different in the order of subgenera. Sterna: Affinity to *ADT* is indistinct. *CC* occupies the top, while the similarity to *RB* is rather low.

Sibiricobombus (Fig. 246). Genitalia: Affinity to *ADT* is evident. Higher ranks are mostly occupied by the W. Hemisphere representatives, e.g. *CR*, *SP*, *RB*, *RD*. Sterna: The pattern is characterized by the precedence of the *ODT* subgenera.

Rufipedibombus (Fig. 247). Genitalia: The level of correlation values is generally low. The higher ranks are occupied by the subgenera possibly of diverse lines: *MC*, *ST*, *mr* and *BO*. Affinity to *ADT* is ambiguous. Sterna: Affinity to *ADT* is more or less evident. The top rank is nearly shared by *CC* and *BO*.

Kallobombus (Fig. 248). Genitalia: *ST* exhibits the highest correlation, closely followed by *AL*, *fv* and *SB*. The subgenera of both *ADT* and *ODT* are included in the higher ranks. Sterna: Elements in the higher ranks in genitalia are mostly replaced. Affinity to *ADT* is subtly demonstrated.

Bombias (Fig. 249). Genitalia: The level of correlation values to other subgenera is relatively low. The highest correlation is observed with *KL*, closely followed by *CF*. Affinity to *ADT* is subtly observed. Sterna: *MD* occupies the top rank. Affinity to *ADT* is distinct.

Confusibombus (Fig. 250). Genitalia: The highest correlation is attained by *BI* although the level is rather low ($r=0.43$). Affinity to *ADT* is evident. Sterna: Trend is more or less similar to that in genitalia. _RB_ as well as _BI_ exhibits high correlations.

Orientalibombus (Fig. 251). Genitalia: The highest correlation is occupied by _fr_ (_r_=0.71). Except for _fr_ and _AL_, the affinity to _ODT_ is evident. Among the _ODT_ subgenera, _fv_, _TH_ and _MC_ are highly correlated, whereas the groups of _Fervidobombus_ (_mr_, _dl_ and especially _bv_) are poorly correlated. Sterna: Trend is basically similar to that in genitalia, but the highly ranked elements are largely replaced.

funerarius-group (Fig. 252). Genitalia: The pattern is very similar to that in _OR_, demonstrating high affinity to _ODT_. As in _OR_, _AL_ is the highest correlated among the _ADT_ subgenera excluding _OR_. Sterna: As in genitalia, similarity to _ODT_ is remarkable. General trend is very similar to that of sterna in _OR_.

_Eversmannibombus_* (Fig. 253). Genitalia: The highest correlation is found with _MC_, and general trend confirms affinity to _ODT_. But, some _ADT_ subgenera, _fr_, _OR_, _SB_ and _AG_ also exhibit relatively high correlations. Sterna: The top rank elements are largely replaced from those in genitalia. Affinity to _ODT_ is more or less retained although a few _ADT_ subgenera are included in higher ranks.

_Mucidobombus_* (Fig. 254). Genitalia: Trend is similar to _EV_, confirming affinity to the _ODT_ subgenera, especially _EV_, _TH_ and _fv_. Sterna: The pattern is more or less parallel to that of genitalia. However, the highest correlation is observed with _TH_, while similarity to _EV_ is low.

_Thoracobombus_* (Fig. 255). Genitalia: Trend is similar to _MC_. The highest rank is nearly shared by _fv_ and _MC_, although the order of subgenera is considerably different. Sterna: _ODT_ affinity is again evident. The species groups related to _FV_ generally exhibit high correlations.

fervidus-group* (Fig. 256). Genitalia: Affinity to _ODT_ is slightly less evident than in _TH_ or _MC_. The second highest correlation to _RH_, and a relatively high affinity to

_KL_ and _AL_ might characterize this subgenus. Sterna: Affinity to _ODT_ is remrakable. Among the _ADT_ subgenera, _fr_ exhibits the highest correlation.

morio-group* (Fig. 257). Genitalia: The highest similarity is observed with _dl_ (r=0.51). High correlations are also achieved by _ST_, _at_ and _RH_. Affinity to _ODT_ is more or less distinct although _CC_ and _BO_ occupy relatively high ranks. Sterna: Most of the top ranks are occupied by the _ODT_ subgenera, but _ODT_ affinity is rather ambiguous.

dahlbomi-group* (Fig. 258). Genitalia: Trend is similar to those observed in other _ODT_ subgenera. The highest correlation is held by _mr_, followed by the species groups of _Fervidobombus_ and _ST_. Affinity to _ODT_ is distinct although the _ADT_ subgenera, and _fr_ and _BO_ exhibit relatively high similarities. Sterna: The _ODT_ subgenera occupy most of higher ranks excluding the second and third, which are represented by _fr_ and _OR_.

transversalis-group* (Fig. 259). Genitalia: Ten top ranks are exclusively occupied by the _ODT_ subgenera, with the top by _at_. Sterna: The highest correlation is observed with _bv_. Similarity to _ODT_ is indistinct.

atratus-group* (Fig. 260). Genitalia: The pattern is very similar to that in _tv_. Among the _ADT_ subgenera _SB_ exhibits a relatively high correlation. Sterna: As in the subgenera above, great affinity to _ODT_ is observed, _SX_ occupying the top, closely followed by _dl_ and _TH_.

Alpinobombus (Fig. 261). Genitalia: The top ranks comprise the subgenera of both _ODT_ and _ADT_, each possibly belonging to variable lines. The highest correlation is held with _ST_ (r=0.47), followed by _KL_ (r=0.43), _fv_ and _BO_ (r=0.40). Sterna: Top rank elements are mostly replaced. Affinity to either _ADT_ or _ODT_ subgenera is indistict. _FN_ exhibits the highest correlation. Among the _ODT_ subgenera, _RH_ exhibits the highest correlation (r=0.50).

_Subterraneobombus_* (Fig. 262). Genitalia: The top and the second ranks are represented by the _ADT_ subgenera _AL_ and _KL_. In contrast to the pattern of _AL_, most subsequent ranks are filled with the _ODT_ subgenera. Sterna: The top rank elements differ greatly from those in genitalia, including rather evenly the subgenera of both _ODT_ and _ADT_. The highest correlation is attained by _MG_.

_Rhodobombus_* (Fig. 263). Genitalia: Affinity to _ODT_ is evident. The top rank is represented by _fv_ (_r_=0.49), closely followed by _ST_ (_r_=0.45). Sterna: Similarity to _ODT_ is less distinct, but the order is characterized by the precedence of the species groups of _FV_.

_Megabombus_* (Fig. 264). Genitalia: The affinity to _ODT_ is distinct. _SX_ and _DV_ exhibit very high correlations (0.65 and 0.59, respectively). The third rank is represented by _TR_ (_r_=0.44). Sterna: Affinity to _ODT_ is indistinct. Top similarity is attained by _ST_ (_r_=0.56).

_Senexibombus_* (Fig. 265). Genitalia: The pattern is very similar to that in _MG_, the top ranks comprising virtually the same components. Sterna: Affinity to _ODT_ is retained. The top ranks are occupied by _at_, _EV_, _dl_, _TH_, etc.

_Diversobombus_* (Fig. 266). Genitalia: The pattern is quite similar to those of above two subgenera. Sterna: _NB_ represents the highest correlation, closely followed by _AG_. Affinity to _ODT_ is indistinct.

_Tricornibombus_* (Fig. 267). Genitalia: Affinity to _ODT_ is remarkable. The correlation values of top ranks are relatively even. _DV_ and _SX_ nearly share the top rank (_r_=0.51). Sterna: _ODT_ affinity is reconfirmed although the order of subgenera is considerably different.

brevivillus-group* (Fig. 268). Genitalia: The pattern is characterized by the low level of correlation values. Affinity to _ODT_ is more or less observed. The four top ranks are occupied by the species-groups of _FV_. Sterna: Affinity to _ODT_ is more distinct. The two top ranks are occupied by _tv_ and _at_ in genitalia.

Mendacibombus (Fig. 269). Genitalia: Characterized by an extremely low level of correlation values. The highest correlation held with _BI_ is only 0.21. Most of the ten top ranks are occupied by the subgenera of ADT. Sterna: The top rank is occupied by BI. Like in genitalia, affinity to ADT is confirmed.

Pressibombus (Fig. 270). Genitalia: Affinity to the ADT subgenera, especially RF (r=0.55) is demonstrated. Among ODT subgenera, ST (r=0.28) exhibits a relatively high correlation. Sterna: With marked contrast to the pattern of genitalia, similarity to ODT is observed. The top and the third ranks are occupied by OR and fr of ADT which exhibit aforementioned similarity to ODT.

Psithyrus

Correlation between the pairs of the Psithyrus subgenera are all quite high although it owes partly to the adopted procedure as mentioned in Chapter 6. Interpretation on the relationships among the subgenera is beyond the scope of the present study. Subsequent remarks concern only with the similarity of each Psithyrus subgenus to Bombus subgenera. The similarity might be overestimated, again due to the procedure mentioned. Beside the affinity to ODT or ADT, the correlation to the host subgenera will be pursued.

The patterns in genitalia in all Psithyrus subgenera are characterized by high correlations to fv, TH, MC and EV (Figs. 271 - 276). The first three subgenera are always included within the ten top ranks, in particular in AS, FP and CP within the first four or five ranks. RH (excluding in AS and FP), TR(in PT and AS) and at (in PT and CP) also exhibit relatively high correlations but no other ODT subgenera appear in the higher ranks. Among the subgenera of ADT, OR and fr are relatively high ranked except PT. Sometimes relatively high correlations are held with some other ADT subgenera, e.g. SP in PT, AO and MP, AL in PT and AO, and SB in AS and FP. Correlation values at higher ranks are relatively even, with levels rather high in AS, CP, moderate in PT, AO and MP, and low in AO. In sterna, ODT affinity is more distinct. Only a few representatives of ADT are included in the ten top ranks: fr in PT and CP; MD, *SB* and *CF* in *AO*; *PR* and *SB* in *AS* and *MP*; *fr* and *PR* in *FP*. The top rank elements are far less constant than in the patterns in genitalia. Beside the aforementioned subgenera *RH*, *ST*, *MG*, *at*, *dl* and *tv* often appear within ten elements. The correlations to the host subgenus (Popov, 1931) are usually very low in both genitalia and sterna. Only in *CP* and *MP*, their respective hosts, *fv* and *TH*, exhibit relatively high correlations (Figs. 275, 276). Figs. 277 - 284 show the order and correlation values of each host subgenus to all *Psithyrus* subgenera. The parasite subgenera do not occupy the top rank except for *fv* in genitalia (Fig. 281). Furtheremore, no pairs of host and its parasite achieve reciprocally the highest correlations.

The results on sterna greatly differ from those on genitalia for both *Bombus* and *Psithyrus*. Richards (1927) indicated that a slight change in the chitin supply might cause a great structural modification in apical sterna. The apical elongated area in S_7 of *FR* (Fig. 24) or *BI* (Fig. 35) may be derived from such an excessive chitinous accumulation. In the course of screening characters, it has been noticed that the characters of $S_{7, 8}$ exhibit much more variation within both species and subgenus than those of genitalial sclerites. This implies that use of the characters of S, either solely or in combination with those of genitalia, is unsuitable for tracing the intersubgeneric relationships. Actually the results on S exhibited very poor supraspecific constancy (cf. Figs. 233 - 276, left). Furthermore, the number of characters detected in S was apparently insufficient to give reliable groupings in the phenetics. By these reasons, characters of S will be omitted from the subsequent discussion.

Reviewing the contents of correlation ranks described above, the subgenera may be preliminarily classified as follows:

1. The group of *ADT* affinity: *CL*, *ML*, *PR*, *FN*, *SP*, *CC*, *FR*, *CR*, *RB*, *RD* and *SB* (the subgenera having no *ODT* subgenera

in the ten top ranks); *AG*, *NB*, *PS*, *CF*, *BI* and *MD* (the subgenera exhibiting considerable affinity to *ADT*).

2. The group of *ODT* affinity: *TR*, *tv*, *at*, *SX*, *DV*, *OR*, *fr*, *bv*, *dl*, *fv*, *RH*, *mr*, *MC*, *TH*, *MG* and *EV*.

3. The intermediate groups: *ST*, *RF*, *AL*, *KL* and *BO* (the subgenera exhibiting no clear affinity to either *ODT* or *ADT*).

On the other hand, grouping may be possible on the basis of the level of correlation values. Subgenera exhibiting generally low correlation values to all other taxa should be considered as isolated lines of old origins, e.g. *bv*, *MD*, *CF*, *FR*, *PR* and *AL*. While, the closest relative should be indicated reciprocally by the highest correlations, as follows: *AG*/*NB*; *MG*/*SX*; *OR*/*fr*; *RD*/*RB*; *TH*/*fv*; *dl*/*mr*; *at*/*tv*; *PS*/*RF*.

A more comprehensive summary of the correlation matrices is given by the cluster analysis. Four phenograms of genitalia derived from variable number of characters (58, 67, 81 and 104 characters; Figs. 285 - 288) remarkably agreed with each other. It has been repeatedly confirmed that phenograms were appreciably altered according to the addition of used characters (Sneath and Sokal, 1973; Tadauchi 1978b). To argue this unstability of phenograms the pheneticists apply the matches asymptote hypothesis "which assumes that as the number of characters sampled increases, the value of the similarity coefficient becomes more stable" (Sneath and Sokal, *op. cit.*; p. 106 - 107). Tadauchi (*op. cit.*) gave a support for this hypothesis in the phenetic study of Japanese andrenid bees. He found the relationships among OTUs of the first major group in phenograms were not much altered when 70 or more characters were used. In this study the combination of characters were intentionally altered according to the ease of definition or description (see 6. 2.). Nevertheless, the stability observed among the four phenograms should not be ignored. The agreements of clustering in the four phenograms as well as the level of values of amargamation are used for determining groups of taxa.

In all phenograms two major groups are obtained, each including nearly constant elements. The one, tentatively named group A, includes constantly the following subgenera: *AG*, *NB*, *CL*, *ML*, *PR*, *FR*, *CC*, *SP*, *CR*, *FN*, *RB*, *RD*, *SB*, *RF* and *PS*. In the phenogram II (Fig. 286) *BO*, *KL*, *BI* and *CF* are also accomodated here. The other one named group B, invariably comprises the following subgenera: *OR*, *fr*, *EV*, *MC*, *TH*, all the species groups of *FV* excluding *bv*, *AL*, *ST*, *RH*, *MG*, *SX*, *DV* and *TR*, and also all *Psithyrus* subgenera. Three more subgenera are included here only in one or a few phenograms: *KL* in phenogram I, III and IV; *BO* in phenogram I and III; *BI* in phenogram III. In every phenogram the subgenera outside these two major groups are quite few, either forming a very loose cluster as in phenograms I, III and IV, or each representing independent lines as in phenogram II. *MD* and *bv* always stay here, accompanied by *CF* (in I, III and IV) or *BI* (in III and IV). Subsequently the subgroups within each of two major groups are expressed by enumeration of all elements in parentheses, which are given at every clustering step. The included elements are shown as (e_1-e_2-e_3 ......) if subgroups are not otherwise specified, whereas as (e_1-e_2, e_3 .....), (e_1-e_2, e_3; e_4-e_5, e_6) or (e_1-e_2, e_3; e_4/e_5-e_6, e_7 .....) when lower subgroups are mentioned.

Within the group A two major subgroups are distinguished. The first one, A_1, comprises *AG*, *NB*, *ML*, *CL*, *PR*, and occasionally, *RF* and *PS*. Within A_1, (*AG*-*NB*) is always formed, and (*CL*-*ML*) in three phenograms. A regular element *PR* never enters in any primary clusters, forming an isolate unit. The other subgroup, A_2, involves remarkably constant subgenera: *FR*, *CC*, *SP*, *CR*, *FN*, *RB*, *RD* and *SB*, and only in two phenograms, *BO*. In contrast to this stability, subclusters within A_2 are rather unstable. The relatively stable association is observed between *FR* and *CC*. Besides, tight connections are represented by (*SP*-*RB*) in phenograms I, III and IV, and by (*RB*-*RD*) in phenogram II. Like in *PR* within the group A_1, *SB* represents an independent line loosely connected to others. *RF*, the occassional element of A_1, is tied with *PS* when the concerned characters in *PS* were studied, forming the third, loose subcluster, A_3. In the absence of *PS*, it stays outside both A_1 and A_2.

The group B comprises more numerous subgroups, with the following five stable ones: B_1 (*OR*-*fr*), B_2 (*EV*, *MC*), B_3 (*mr*-*dl*), B_4 (*MG*-*SX*-*DV*) and the *Psithyrus* subgenera B_p (*PT*-*CP*-*MP*-*AO*-*FP*-*AS*). The elements of other subgroups are variable, with three loose groups B_5 (*AL*-*ST*-*RH*-*KL*), B_6, (*TH*-*fv*), B_7, (*at*, *tv*). *BI* is included in B_5 in phenogram I and *KL* is translocated into a different cluster comprising *BI* and *CF* in phenogram II. B_6 in phenogram III and B_7 in phenograms I and III, are transformed to (*at*-*fv*, *TH*) and (*TH*, *at*-*fv*; *tv*), respectively. The remaining element of group B, *TR*, is usually clumped with B_4, rarely with B_6. Among these subgroups only a few stable associations are obtained. When the *Psithyrus* subgenera are included, they are always clumped with B_2, and then with B_1, as (B_1, B_2-B_p). In the absence of B_p, B_2 is united either with B_1 (in phenograms I and III) or with B_6 (in phenogram II). Besides, B_6 and B_7 are apt to fuse with each other as aforementioned. In phenogram II two subgroups (B_2-B_6) and (B_3-B_7) are constructed at a relatively distinct similarity. The positions of *BI*, *CF*, *KL* and *BO* vary among four phenograms, and *BO* is always rather isolated.

Most if not all these groups agree with those preliminarily recognized on the basis of the trends in correlation ranks. The groups A and B correspond to the two major groups aforementioned, each having *ADT* and *ODT* affinity. The isolate subgenera exhibiting generally low correlation values to other subgenera are isolatedly placed, or only loosely tied with the major groups.

PCA for the correlation matrix of combination II gave the first three principal components accounting for only a fraction of the total variance (31 %). The component pattern diagrams given for the first twelve principal components accounted for about 70 % of the total variance (Table 4). Interrelations among groups are evaluated on the basis of the similarity in these patterns. The obtained grouping agreed remarkably with that by the cluster analysis (Fig. 286, left) with distinction of two major groups (Fig. 286, right).

The first group is characterized by a high positive value of the first principal component, negative value of the second one, and positive value of the third one. It contains most elements of group A. *CL*, *ML*, *PR*, *FR*, *SP*, *CR*, *FN*, *RB*, *RD* and *SB*. *AG* and *NB* take nagative values in the third principal component, and *CC* and *RF* show the positive values in the second one. However, these four subgenera basically follow the overall trend of the obtained group. The second group is represented by the nearly symmetrical pattern, that is, negative and positive values of the first two principal components. This group comprises most elements of group B: *MC*, *TH*, *fv*, *dl*, *at*, *tv*, *RH*, *MG*, *SX*, *DV* and *TR*. From the resemblance in the overall pattern, *mr* is included here. Compared to these two groups, the third group is less distinct, characterized by positive, nagative, negative and negative values of the first four principal components. *KL*, *BI*, *CF*, *MD* and *bv* are included here. Among these five subgenera, the first three forming a loose cluster in phenogram II exhibit a slight resemblance one another. *MD* and *bv* are most distinctive, but *MD* might be less deviated from others than *bv*. This third group as a whole might be closer to the first than to the second group in having positive and negative values of the first two principal components. In the subgenera of the group A, a remarkable resemblance of the pattern is observed in the pairs *AG*-*NB*, and, to lesser extent, in *CL*-*ML*, *RB*-*RD*, and *SP*-*RB*. The pairs *CR*-*FN*, and *SP*-*RD* also exhibit a considerable resemblance from each other. The patterns of *PR* and *SB* are relatively distinct in A_1 and A_2, respectively, although the pattern of *SB* might be closest to that of *CR*. The aforementioned division of subgroup A_1 and

A_2 is confirmed by these patterns. A_1 is distinguished from A_2 by a negative or low positive value of the third principal component and a high positive value of the fourth principal component. Each BO and RF, clumped loosely in the group A in phenogram II, exhibits a pattern distinct from all others. Among the elements of group B, the subgenera of B_4 exhibit a great intragroup resemblance, especially between MG and SX. The subgenera of each subgroup of B (except B_5) also share similar patterns. As to the subgenera of B_5, KL exhibits a similarity to BI, and belongs to the third group in PCA. The pattern of AL is relatively distinctive in taking low absolute values of the first six principal components, but the overall trend shows an obvious similarity to KL. The pattern of RH is relatively distinctive from both KL and AL, and apparently involved in the second group corresponding to the group B. The last element ST exhibits a weak similarity to AL, but much closer to RH. The similarity between AL and ST or RH is suggested by the patterns in the several principal components; especially of the fifth to ninth principal components with ST and the third to seventh ones with RH. The patterns of the six subgenera of B_1, B_2 and B_6 more or less exhibit a spectral variation. Each subgenus is similar in the pattern to the subgenera contiguously arranged in phenogram II. For example, the pattern of fr is approximately intermediate between those of OR and EV. Summarizing, the results of PCA as a whole remarkably agree with those of the cluster analysis in the recognition of both major and minor groups, with only subtle differences: e.g. the positions of BO, RH, etc.

From all the results cited above, the bumblebees including both *Bombus* and *Psithyrus* may be classified as follows:

Group	Subgroup	Subgenera included	
Pyrobombus group	Pyrobombus subgroup	PR-I	AG, NB, CL ML
		PR-II	PR
	Fraternobombus subgroup	FR-I	SB
		FR-II	FR, CC, SP, CR FN, RB, RD
	Rufipedibombus subgroup	RF-I	RF
		RF-II	PS
Bombus group			BO
Mendacibombus group			MD
Bombias group	Bombias subgroup		BI
	confusibombus subgroup		CF
Alpinobombus group	Alpinobombus subgroup		AL, KL
	Subterraneobombus subgroup		ST, RH
Megabombus group	Orientalibombus subgroup		OR, fr
	Thoracobombus subgroup	TH-I	EV, MC,
		TH-II	TH, fv
	Atratus subgroup	at-I	at, tv
		at-II	mr, dI
	Megabombus subgroup	MG-I	MG, SX, DV
		MG-II	TR
	Psithyrus subgroup		PT, AO, AS, FP CP, MP
brevivillus group			bv

In this system neither equivalency of gaps between each group nor hierarchial correspondence among groups are warranted, just as in the traditional classification. However, the classification is based exclusively on the similarity values concerning as many characters of male genitalia as possible. Therefore, subjectivity in grouping would be considerably reduced.

Among the seven primary divisions the two major groups *Pyrobombus*- and *Megabombus* groups are both relatively compact, and relatively well correspond, respectively, to the sections *ADT* and *ODT* in Krueger's sense. *Pyrobombus* group is further divided into three subgroups. *Pyrobombus* subgroup exactly corresponds to *UNC* of Krueger (1917, Fig. 3) and Richards (1927). A great similarity between *AG* and *NB* may favor the synonymization of the latter with the former by Tkalců (1972, Fig. 12). Richards (1968, Fig. 8) has also mentioned their alliance. Skorikov (1922, Fig. 4) placed the representative species of *SP* and *CR* in his subgenus *AG*. Furthermore, he subordinated *FR*, *RB*, *CC* and *FN* to his genus *AG*. The present study also confirms the similarity between *AG* and these Western subgenera. But, *AG* is evidently more similar to *ML*, *CL* and *PR*. No support is obtained as to Milliron's view admitting the alliance between *AG* and *MD* or *BI* (Figs. 9, 10). Among the other three subgenera in *Pyrobombus* subgroup, *ML* and *CL* may also represent a lowest group. This view again disagrees with Milliron who regarded *ML* as closer to *PR* than to *CL*. *PR* seems to take a somewhat isolate position in *Pyrobombus* subgroup (*PR*-II), having a fair similarity to the elements of *Fraternobombus* subgroup.

Fraternobombus subgroup is also considerably compact. Franklin (1954) already mentioned the male genitalia of the Western *ADT* subgenera excluding *BI* bear a basically common plan. Many conflicting views have been proposed on the interrelationship among the subgenera of this group. Skorikov (Fig. 4) placed *RD* in the genus *FV*, and all others in the genus *AG*. Frison (Fig. 5) accommodated *CL* and all the New World subgenera of *ADT* in *BOP*. Pittioni (Fig. 6) placed *SB* there, suggesting inclusion of *AG*. Krusemann (Fig. 7) proposed incorporation of five subgenera *SB*, *CC*, *FN*, *FR* and *RB* in a single subgenus. He also mentioned a close alliance between *PR* and *SP*. Richards (Fig. 8) acknowledged the affinity between *RD* and *RB*, and between *FR* and the subgenera of section *BI* in Krusemann's sense. The present grouping is closest to Krusemann, placing *SB* in this group, though special alliance between *SP* and *PR* is not supported. *SB* is possibly closest to *CR* and *SP*, but, on account of its fair deviation, it is distinguished as representing itself a subgroup *FR*-I separated from all other members of *FR*-II. Further division of *FR*-II is difficult although three groups, (*RB*-*RD*-*SP*), (*FR*-*CC*) and (*CR*-*FN*) are suggested.

Rufipedibombus subgroup is represented by *RF* (*RF*-I) and *PS* (*RF*-II). Many authors suggested the affinity of *RF* to *Pyrobombus* in the wider sense (or *ADT* of Krueger's sense, Fig. 3). However, the level of similarity of *RF* to all subgenera excluding *PS* is generally low. Therefore this taxon may represent a distinct line though tentatively placed in *Pyrobombus* group on account of a close relation to *PS* which exhibits appreciably a *Pyrobombus* affinity.

The second primary group, *Bombus* group, is monobasic including *BO* alone which is characterized by overall low affinity to any other subgenera. The orthodox line of bumblebee classification considered *BO* a distinct subgenus subordinated to *ADT*. However, its deviation from other subgenera has been repeatedly insisted on biochemical (Stephen and Cheldelin, 1973), anatomical (Macfarlane, 1976), bionomical (Sakagami, 1976) and morphological basis (Sakagami and Ito, 1981), as in the present result. Skorikov uniquely considered its close phylogenetic relationship with *ST*, which was not supported in the present study. *BO* has a very specialized penis valve. In this study detail structures of penis valve of *BO* was rather intuitively homologized with those of other subgenera.

Different elucidation on their homology would largely alter the result. Therefore, the final determination of the position of *BO* must be suspended here.

Mendacibombus group is also monobasic, represented by *MD* alone. It has been known that *MD*, *BI* and *CF* share several common character states in both males and females. Simultaneously, a distinct morphological segregation among them has also been reported. Weighing those characters variously, some students acknowledged a loose group *BOP*, while others treated them as representing each a distinct group. Isolation of *MD* from all other groups has been proposed by Skorikov (Fig. 4) and Tkalců (Fig. 11). Their handling is followed here on account of the remarkably low similarity to all other subgenera.

The fourth group, *Bombias* group, is represented by *BI* and *CF*. These two subgenera exhibit a considerable affinity to the *ADT* subgenera. Particularly *BI* is closest to *KL*, followed by *RH* or *AL*. Simultaneously, they are the closest relatives of *MD* as aforementioned. Therefore, this group seems to take an position intermediate among those subgenera or groups. Skorikov indicated a close phyletic relationship of *CF* to *FV* and *RH*. Milliron considered *CF* representing a distinct genus. Tkalcu assigned each of them to a generic rank. The overall low level of the correlation values to other subgenera may support their opinions. But, on the basis of the relatively distinct affinity to *BI*, *CF* is placed here as a unique element of *Confusibombus* subgroup, considerably isolated from *Bombias* subgroup (= *BI*).

The fifth group, *Alpinobombus* group is a very loose group, corresponding to B_5 in phenograms. It involves four subgenera *AL*, *KL*, *ST* and *RH*. This group is characterized by comprising the elements of both *ADT* and *ODT*. The classificatory position of *KL* has been controversial, including synonymization with *PR* (Tkalců, 1972), although most students considered it a subgenus in *ADT* in Krueger's (1917,1920) or Krusemann's sense (1952). In this study *KL* exhibited a fair deviation from any other subgenera, and a relatively high similarity to *AL*, *BI*, *ST* and *fv*. Although it is tentatively placed in this group, information obtained seems to be still insufficient to determine its position. *AL* is also a controversial subgenus. Morphologically, it belongs to *ADT*, but bionomically it is a pocket-marker, suggesting an *ODT* affinity. Plowright and Stephen (1973) reported the isolated position of *AL* among all subgenera including *Psithyrus* in metric characters of venation. The present study confirms its morphological position intermediate between *ODT* and *ADT*. Among the *ODT* subgenera it is closest to *ST*, then to *fv* and *RH*. The comprehensive comparison of the trends in the correlation matrices indicates *ST* or *KL* as phenetically closest. Its alliance to other subgenera has so far been hardly mentioned except by Skorikov (1922, P.129) and Milliron (1961,1971). Skorikov indicated that *AL* is close to five subgenera in the structures of male genitalia: *KL*, *MG*, *ST*, *FV* and *RH*. His view is supported here except for *MG*. Milliron subordinated *AL* and *KL* to his genus *MG* without stating reasons. Tkalců (1974b) opposed to this idea. But the present grouping is consistent with Milliron's idea at this point. *ST*, the third element of this group, shows a distinct similarity to two *ADT* subgenera, *AL* and *KL*. But, except for them, an affinity to *ODT* is evident, as exemplified by the greatest similarity to *RH* in PCA. With a marked contrast to the other elements of *Alpinobombus* group, *RH* exhibits a relatively distinct similarity to *fv*, *at*, *mr*, *TR* and *MG* than to *AL* or *KL* (Fig. 263). This fact is more or less consistent with the traditional views regarding *RH* as morphologically closest to *FV* (e.g. Skorikov, *op*. *cit*.; Richards, 1968; etc.). Owing to a great similarity to *ST*, it is tentatively grouped here. This taxon might be better placed at a position linking *ST* and *Megabombus* group. Based on the consideration given above, two subgroups are distinguished within *Alpinobombus* group: *Alpinobombus* subgroup (*AL* and *KL*) of *ADT* affinity and *Subterraneobombus* subgroup (*ST* and *RH*) of *ODT* affinity. The results of PCA showed much variation within this group. Further studies might alter this treatment. Nevertheless, recognition of *Alpinobombus* group may be important as this group is characterized by the position linking most if not all distinct groups.

The sixth group named *Megabombus* group corresponds to group B excluding B_5 in the phenograms. This group comprises many subgenera of *ODT*, excluding *ST*, *RH* and *bv*, two of *ADT* and all *Psithyrus* subgenera. All the results strongly demonstrated close relationships among these subgenera. Five subgroups are distinguished: *Orientalibombus* subgroup, *Thoracobombus* subgroup, *atratus* subgroup, *Megabombus* subgroup and *Psithyrus* subgroup. *Orientalibombus* subgroup is represented by *OR* and *fr*. *OR* has been considered a distinct subgenus in *ADT* (Figs. 7, 8) or an independent genus (Fig. 11). The present result indicates its obvious affinity to the *ODT* subgenera, especially *MC*, *EV*, *fv* and *TH*, not to those of *ADT*. Frison (1935) described *fr* as a species of *TH*, suggesting an affinity to *MC*. This study confirmed his suggestion, but *fr* is apparently closer to *OR* than to *MC* or *TH* as treated by Richards (*op*. *cit*.). In the Milliron's system, *OR* was included in his subgenus *MG* together with *AL* and *KL* (Fig. 9). His recognition is close to the present result.

Thoracobombus subgroup nearly corresponds to *TH* in Tkalců's sense (1972) except inclusion of *fv* which is a taxon of *FV* in the current usage. This subgroup is divided into TH-I (*EV*, *MC*) and TH-II (*TH*, *fv*). Among the four elements, *EV* may be closest to *Orientalibombus* subgroup, especially *fr*. *MC* takes a position somewhat intermediate between *EV* and *TH*, although closer to the former. Likewise, *TH* may link *fv* and *MC*. Skorikov (*op*. *cit*.) assigned the generic status for *MC* which accomodated *EV* (=TH-I). Many authors have acknowledged an affinity among *TH*, *MC* and *EV*. But, recognition of a close relationship between *TH* and *fv* has not hitherto been mentioned.

Atratus subgroup is composed of four species groups of

FV: *at*, *tv*, *mr* and *dl*. It is subdivided into two groups: *at*-I (*at*, *tv*) *at*-II (*mr*, *dl*). The former is less compact, and relatively close to *Thoracobombus* subgroup, especially *TH* and *fv*. A remarkable diversification of the structure of male genitalia in the subgenus *FV* in the sense of Richards (1968) has been indicated (cf. also Moure and Sakagami, 1962; Franklin, 1954). But no subdivision of this group has been attempted except by Milliron (1972). His recognition of three species-groups does not well correspond to the present result.

Milliron	Ito
dumoucheli group	*Thoracobombus* subgroup (*fv*), *atratus* subgroup (At-I: *mr*, *dl*; At-II: *at*)
mexicanus group	*Atratus* subgroup (AT-II: *tv*), *brevivillus* group (*bv*)
nigrodorsalis group	unaccessible

Megabombus subgroup comprises four subgenera, *MG*, *SX*, *DV* and *TR*, corresponding to the subgroup B_4 in the phenograms. The first three subgenera are highly allied one another (*MG*-I) and separated from *TR* (*MG*-II). The recognition of *MG*-I is consistent with the view held by Krusemann (1952) or Richards (1968). Among the three subgenera *MG* and *SX* are closest to each other, suggesting their synonymization. *TR* takes a position linking *Thoracobombus* subgroup and *MG*-I.

Psithyrus subgroup is purely composed of the *Psithyrus* subgenera. The morphological similarity in male genitalia between *Psithyrus* subgroup and *ODT* or *TH* in the wider sense has been mentioned by a few authors (Frison, 1927; Richards 1927). But, the *Psithyrus* has been assigned to an independent genus or even tribe by all predecessors. In spite of great bionomic specialization of *Psithyrus*, the remarkable affinity to *ODT* in the structure of male genitalia necessitates its subordination under *Megabombus* group. The *Bombus* subgenera close to *Psithyrus* are *EV*, *MC*, *fr*, *OR* etc. Distinct similarity between each pair of host and parasite is not observed. That is apparently disadvantageous for the polyphyletic hypothesis on the origin of *Psithyrus* (Taklců, 1972, 1974a). Recently, Obrecht and Scholl (1981) detected a similarity between *Psithyrus*, especially *PT*, and *BO* on the basis of isozyme patterns. The present result gives no additive support for their alliance.

The last group named *brevivillus* group is represented by *Bombus* *brevivillus* (=*bv*) alone, which belongs to the subgenus *FV* in the current taxonomy. This taxon exhibits an evident affinity to *ODT*, especially to *atratus* subgroup, suggesting the validity of current recognition. But, the extremely low level of the correlation values to all other subgenera characterizes this taxon. At any rate, the degree of diversification within *FV* possibly deserves to split this subgenus into a few subgenera, although nomenclatorial propositions are postponed until more species have been examined.

Three subgenera of *Bombus* and one of *Psithyrus* were not available. Judging from the description or illustrations of male genitalia (Tkalců 1972, 1974b, of *FS* and *EX*; Pittioni 1938, of *LS*; Popov 1931, of *EO*), they may belong to the following groups. *FS*: *Pyrobombus* subgroup. *LS* and *EX*: *Thoracobombus* subgroup. *EO*: *Psithyrus* subgroup.

Summarizing, the present grouping more or less agrees with so far proposed systems in the following recognitions; Close alliance of *AG* and *NB*; *AG*, *NB*, *PR*, *ML* and *CL*; *EV*, *MC* and *TH*; and *MG*, *SX* and *DV*; as well each of two major groups *ODT* and *ADT* in a weaker sense. Where there were any controversies among previous authors, most of our results more or less favor one of those opinions. The following items show the present opinions consitent with those by the authors parenthetically cited: close alliance between *OR* and *fr* (Richards 1968), *ODT* affinity of *OR*, *AL* and probably *KL* (Milliron, 1971 - 1973; Skorikov, 1922); *UNC* affinity of *AG* (Krueger, 1917; Richards, 1927); alliance among *SB*, *FR* and American *ADT* subgenera excluding *BI* (Krusemann, 1952); alliance among *AL*, *KL*, *ST* and *RH* (Skorikov, *op*. *cit*.); association of *Psithyrus* with *Thoracobombus* subgroup (Frison, 1927, partly); rejection of *BOP* in the wider sense (Franklin, 1954; Stephen, 1973; etc.); isolate positioning of *MD* and *BO* (Tkalců, 1972). The following points are new proposition in the present study: preliminary establishment of *Alpinobombus* group which includes *AL*, *KL*, *ST* and *RH*; splitting of *FV* into four groups with recognition of one very isolated group (*brevivillus* group); alliance between *fv* and *TH*; alliance between *RF* and *PS*.

Summary

A supraspecific classification of the bumblebees (Hymenoptera; Apidae; Bombini) was attempted on the basis of the structures of male genitalia including metasomal sterna VII and VIII, using a total of 44 species each representing supraspecific taxon. The materials covered 32 out of 35 subgenera of the genus Bombus Latreille and 6 out of 7 of the genus Psithyrus Lepeletier so far proposed, together with 6 other species groups of Bombus tentatively recognized in the present study. Affinity among the groups was evaluated on the basis of the values of similarity index. Determination of the higher groups and their interrelationships were performed through the following steps:

1) Survey of subgeneric characters.
2) Selection or exclusion of suitable and unsuitable characters.
3) Determination of total variation range for each character.
4) Distinction of five stages for each character.
5) Attribution of state values 1 - 5 to each stage.
6) Description of each unit taxon with state values.
7) Calculation of similarity by Pearson's product-moment correlation coefficient for all pairs of the unit taxon in five combinations of the characters of genitalia, each using 104, 81, 67 and 58 of genitalia; and 17 characters of metasomal sterna VII and VIII.
8) Summarization of the correlation matrices by the cluster analysis (UPGMA) for all combinations, and the principal component analysis (PCA) for one combination.
9) Recognition of the higher groups and interrelationships between them on the basis of the stability in the grouping in four phenograms for characters of genitalia, the resemblance in the

patterns of component pattern diagrams, and the correlation values themselves of each subgenus.

As the result a new hierarchical classification scheme of all bumblebees including parasitic groups is proposed. Seven primary groups are distinguished: *Pyrobombus*, *Bombus*, *Mendacibombus*, *Bombias*, *Alpinobombus*, *Megabombus* and *B*. *brevivillus*.

Pyrobombus group comprising fifteen subgenera, is further divided into three subgroups, *Pyrobombus* s. str., *Fraternobombus* and *Rufipedibombus*. The elements of each subgroup are: *Pyrobombus*: *Alpigenobombus*, *Nobilibombus*, *Cullumanobombus*, *Melanobombus* and *Pyrobombus* s. str. *Fraternobombus*: *Fraternobombus* s. str., *Crotchiibombus*, *Funebribombus*, *Separatobombus*, *Rubicundobombus*, *Coccineobombus*, *Robustobombus* and *Sibiricobombus*; *Rufipedibombus*: *Rufipedibombus* s. str. and *Pressibombus*. *Pyrobombus* g. and *Fraternobombus* g. are each fairly compact. The subgroup *Pyrobombus* may be subdivided into two lowest groups, *PR*-I *Alpigenobombus*, *Nobilibombus*, *Cullumanobombus* and *Melanobombus*, -II *Pyrobombus*. In *PR*-I *Alpigenobombus* and *Nobilibombus* are very similar to each other. *Pyrobombus* seems to lie relatively isolate between the subgroups *Pyrobombus* and *Fraternobombus*. Among the elements of the subgroup *Fraternobombus* *Sibiricobombus* is relatively close to the subgroup *Pyrobombus*, and possibly constitutes the sole lowest group, *FR*-I. All others, *FR*-II, are closely allied one another, making further division difficult. The subgroup *Rufipedibombus* is a loose group, and fairly remote from both other two subgroups. *Pressibombus* is relatively close to the subgroup *Pyrobombus*, while *Rufipedibombus* s. str. is very distinctive.

Another large group *Megabombus* is also relatively compact, comprising fourteen *Bombus* and all six *Psithyrus* taxa studied. Five subgroups are distinguished: *Orientalibombus*, *Thoracobombus*, *B*. *atratus*, *Megabombus* and *Psithyrus*. The elements of each subgroup are: *Orientalibombus*: *Orientalibombus* and *B*. *funerarius*;

Thoracobombus: *Eversmannibombus*, *Mucidobombus*, *Thoracobombus* s. str., and *B. fervidus*; *B. atratus*: *B. atratus*, *B. transversalis*, *B. morio* and *B. dahlbomi*; *Megabombus*: *Megabombus*. *Senexibombus*, *Diversobombus* and *Tricornibombus*; *Psithyrus*: *Psithyrus* s. str., *Allopsithyrus*, *Ashtonipsithyrus*, *Fernaldaepsithyrus*, *Citrinopsithyrus* and *Metapsithyrus*. The subgroup *Orientalibombus* is most compact, while the subgroup *Thoracobombus* is less. *Thoracobombus* is further divided into *TH*-I (*Eversmannibombus* and *Mucidobombus*)and *TH*-II (*Thoracobombus* s. str. and *B. fervidus*). *TH*-I is close to *Orientalibombus* subgroup, especially to *B. funerarius*, while *TH*-II, especially *B. fervidus*, is evidently allied to the subgroup *B. atratus*. The elements in the *B. atratus* subgroup are all the taxa assigned to the subgenus *Fervidobombus* in the current taxonomy. They are subdivided into *AT*-I (*B. atratus* and *B. transversalis*) and -II (*B. morio* and *B. dahlbomi*), the latter being more compact. In the subgroup *Megabombus* the first three subgenera are closely allied, forming *MG*-I. *Megabombus* and *Senexibombus* are particularly close to each other. *Tricornibombus*, assigned to *MG*-II, lies between the subgroup *Thoracobombus* and *MG*-I. The subgroup *Psithyrus* is represented by the subgenera of the genus *Psithyrus* in the current taxonomy. They are closely allied one another, and exhibit a fair affinity to the subgroup *Thoracobombus*, especially to *Eversmannibombus* and *Mucidobombus*.

Three primary groups, *Bombus*, *Mendacibombus* and *B. brevivillus* are monobasic, represented by the subgenera *Bombus* s. str., *Mendacibombus* and *B. brevivillus*, respectively. They are each distinct from all other subgenera.

Bombias group comprises two subgenera, *Bombias* and *Confusibombus*, each representing a monobasic subgroup of its own. This group may link *Mendacibombus* group with *Alpinobombus* group, especially the subgenus *Kallobombus* (cf. below).

Alpinobombus group is loose, comprising two subgroups, *Alpinobombus* (*Alpinobombus* and *Kallobombus*) and *Subterraneobombus* (*Subterraneobombus* and *Rhodobombus*), characterized by the position linking most primary groups, especially *Megabombus*, *Pyrobombus* and *Bombias*. *Alpinobombus* subgroup exhibits a good affinity with *Pyrobombus*, *Bombias* and *Bombus* groups, while *Subterraneobombus* subgroup, especially *Rhodobombus*, is allied to *Megabombus*.

Compared to various previous systems the proposed system is characterized by the following points: Recognition of *Alpinobombus* group containing the elements of both *Anodontobombus* and *Odontobombus*; less compact preservation of *Anodontobombus* (=*Pyrobombus* group) and *Odontobombus* (= *Megabombus* group); definitive rejection of *Boopobombus* in Frison's sense (1927); association of the taxa of *Anodontobombus* (*Orientalibombus* and *B. funerarius*) and the parasitic bumblebees (*Psithyrus* s. lat.) with *Megabombus* group; subdivision of the subgenus *Fervidobombus*, exemplified by the recognition of very isolate position of *B. brevivillus*.

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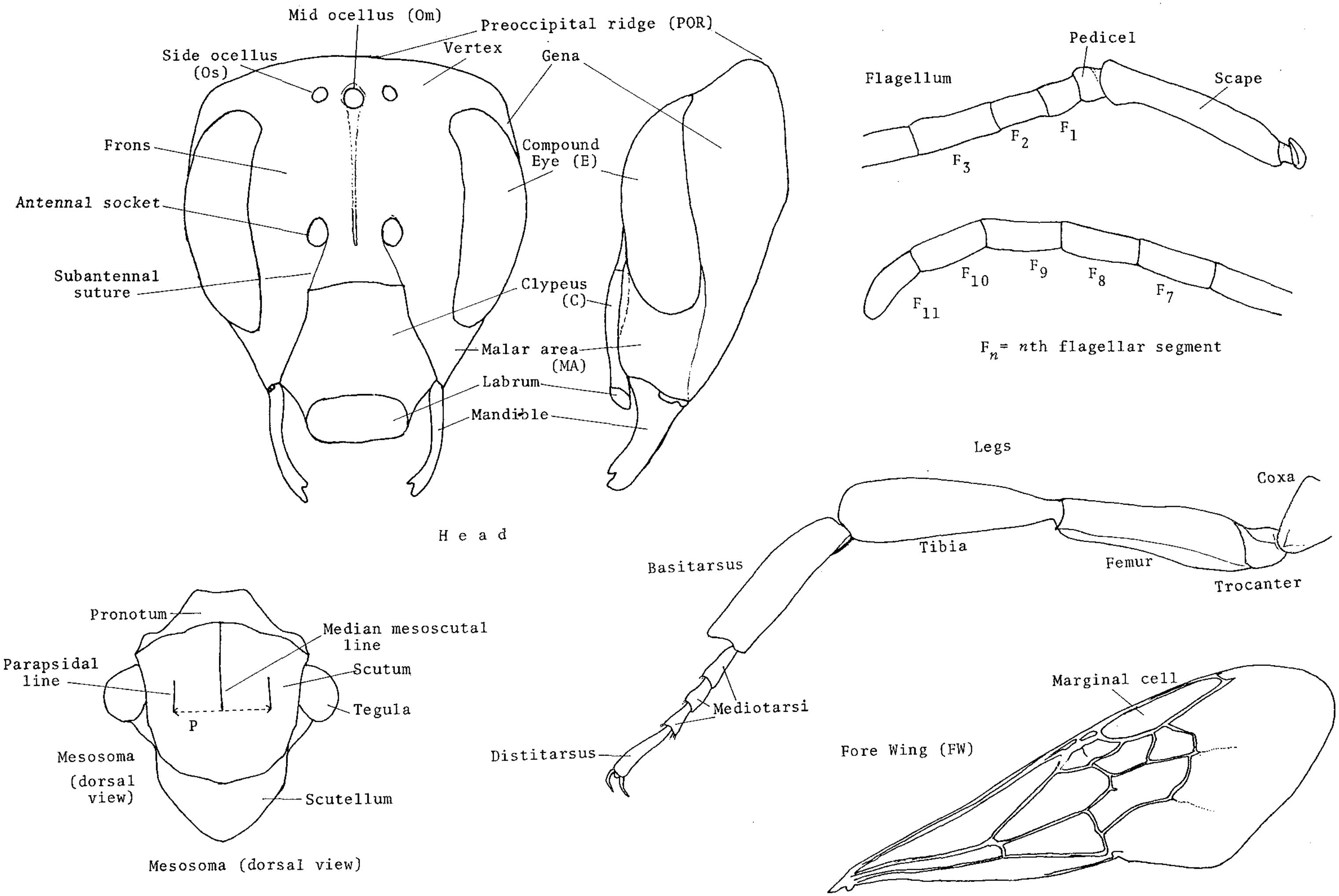
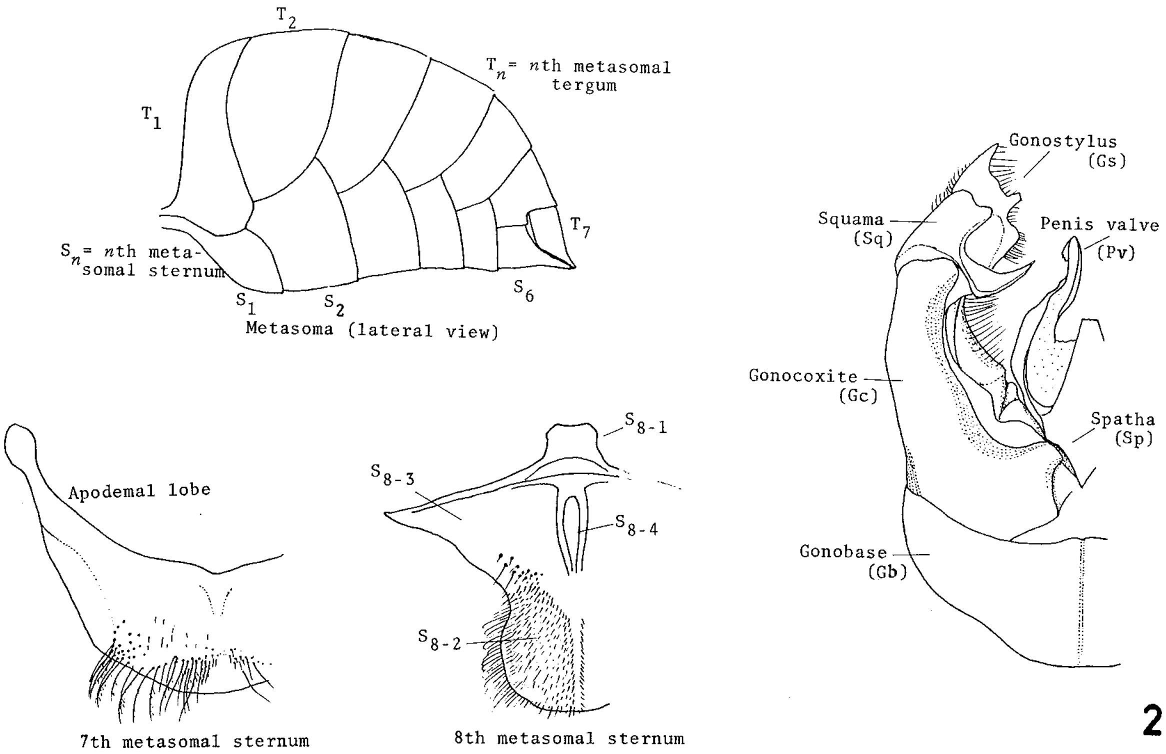
* Papers not directly accessible.



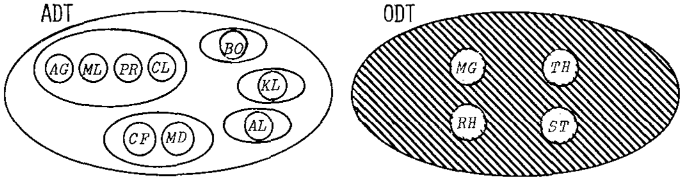
1

Fig. 1. Morphological terms used: Head and mesosoma.



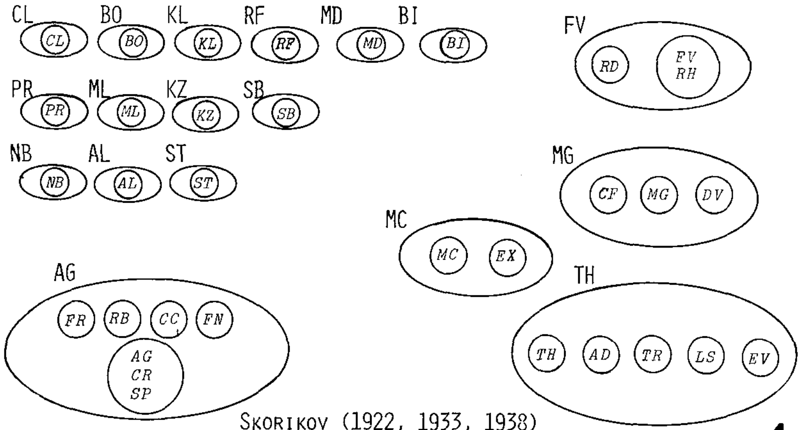
2

Fig. 2. Morphological terms used: Metasoma and male genitalia. Explanations of the abbreviations in text, chapter 5.



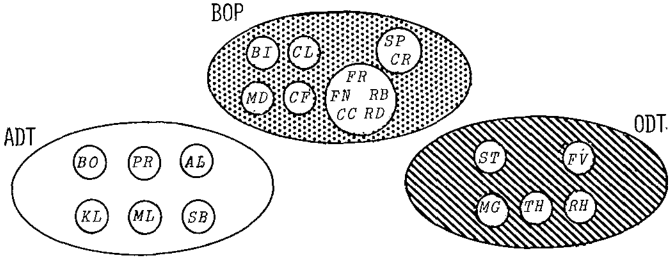
KRÜGER (1917, 1920)

3



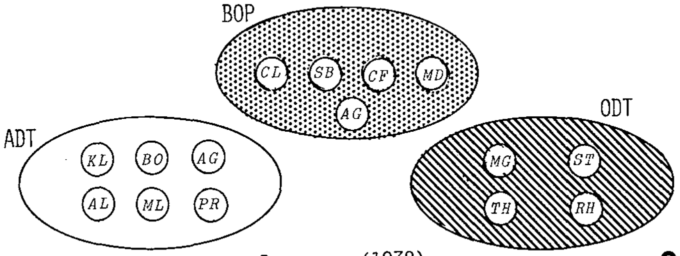
SKORIKOV (1922, 1933, 1938)

4



FRISON (1927)

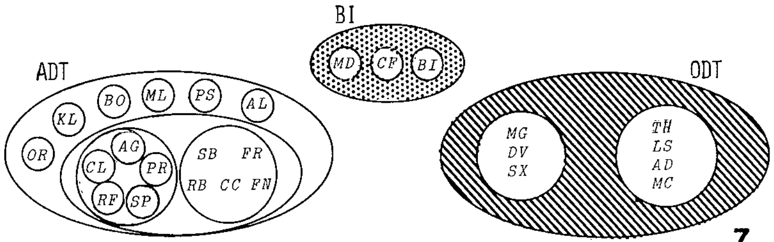
5



PITTIONI (1938)

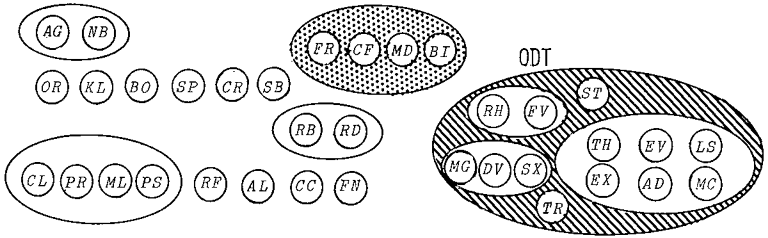
6

Figs. 3 - 6 . Supraspecific classificatory systems so far proposed. Taxa are cited with abbreviation given in text, chapter 2, not with the names adopted by each author. Circle: Taxon at the lowest category. Ellipse: Higher groups. Broken circle or ellipse: Groups suggested but not clearly proposed. Hatched: Odontobombus or its correspondents. Dotted: Boopobombus or its correspondents. Plain: Anodontobombus and other groups. Fig. 3. Krueger (1917, 1920): Western Hemisphere groups not mentioned. Fig. 4. Skorikov (1922, 1933, 1938). Kz: Kozlovibombus (= ML). Fig. 5. Frison (1927). Mainly on Western Hemisphere groups. Fig. 6. Pittioni (1938).



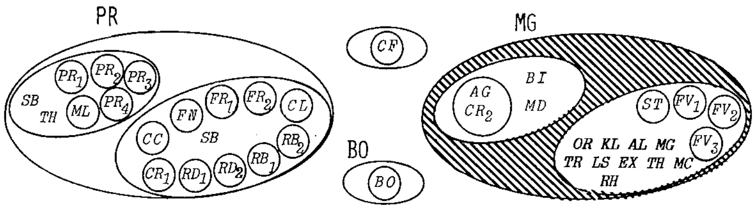
Krusemann (1952)

7



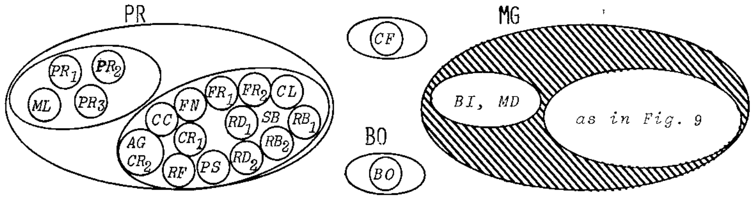
Richards (1968)

8



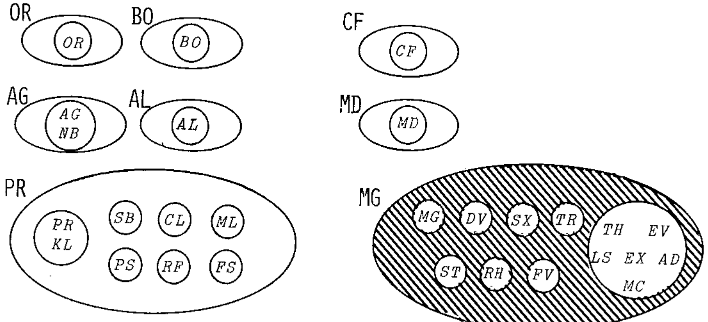
Milliron (1961)

9



Milliron (1972, 1973)

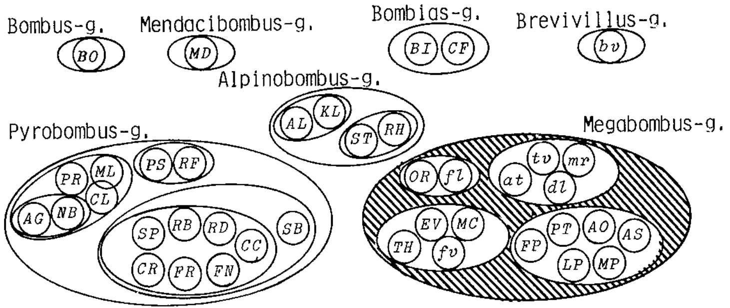
10



Tkalců (1972)

11

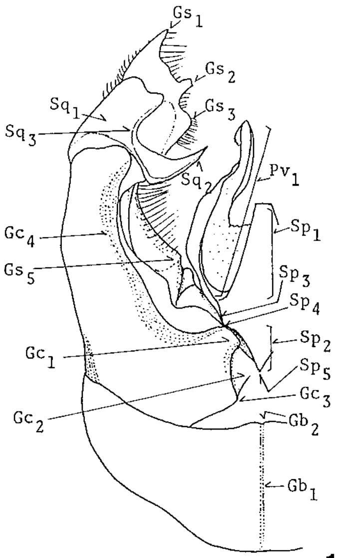
Figs. 7 - 11. Supraspecific classificatory systems so far proposed. (Continued) Fig. 7. Krusemann (1952). Obertibombus (= SB) and Kozlovibombus (= ML) not illustrated. Fig. 8. Richards (1968). Fig. 9. Milliron (1961). FR_1: fraternus group. FR_2: brachicephalus g. SB_1: Obertobombus g. SB_2: Sibiricobombus g. PR_1: pratorum g. PR_2: jonellus g. PR_3: praticola g. PR_4: lapponicus g. RB_1: robustus g. RB_2: volucelloides g. CR_1: crotchii g. CR_2: B. haueri. FV_1: dumoucheli g. FV_2: nigrodorsalis g. FV_3: mexicanus g. Eurasian subgenera excluding CF were mentioned only in the synonymic tables. Fig. 10. Milliron (1971 - 1973). See the legends of Fig. 9. Fig. 11. Tkalců (1972). Eastern Hemisphere groups including FV were dealt with.



Ito (1985)

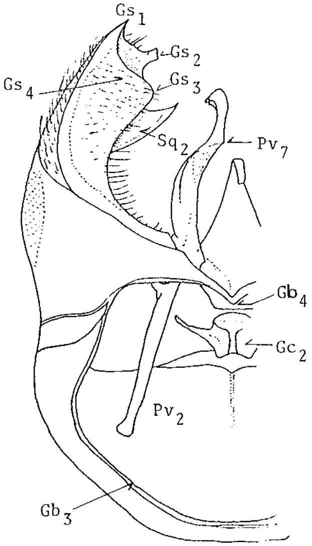
12

Fig. 12. System established in the present study. Cf. the legends of Figs. 3 - 11.



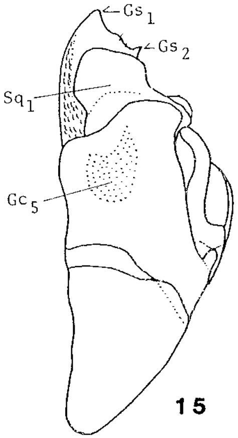
13

Male genitalia
(dorsal view)



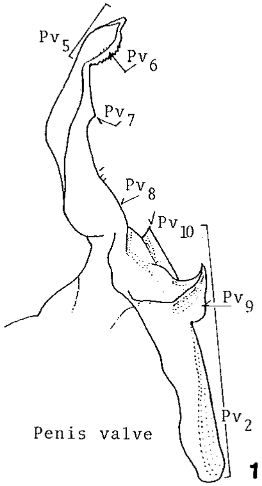
14

Male genitalia
(ventral view)



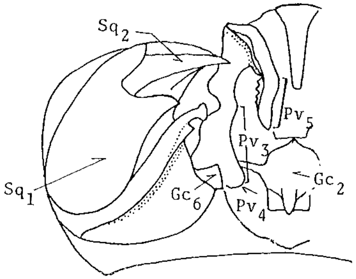
15

Male genitalia
(lateral view)



Penis valve

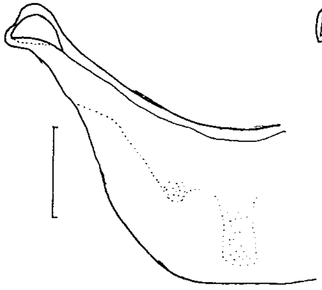
17



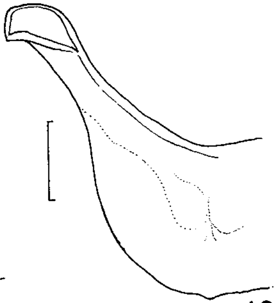
16

Male genitalia
(apical view)

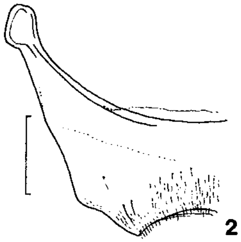
Figs. 13 - 17. Detailed structures of male genitalia of Bombus (Thoracobombus) schrencki albidopleuralis Skorikov. Explanation on the abbreviations in text, chapter 5.



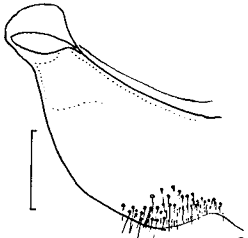
Ag. wurfleini **18**



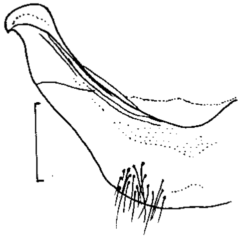
Nb. sikkimi **19**



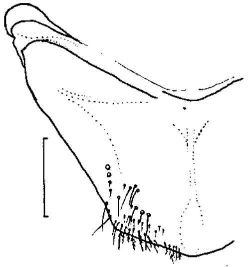
20 *Cl. rufocinctus*



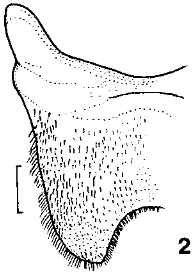
Ml. lapidarius **21**



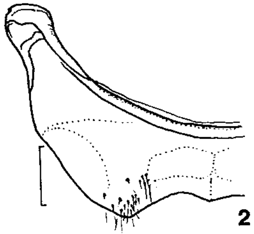
22 *Pr. ardens*



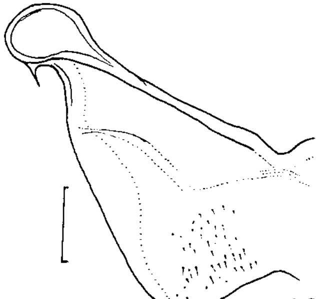
23 *Sb. callophenax*



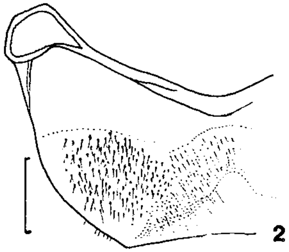
24 *Fr. fraternus*



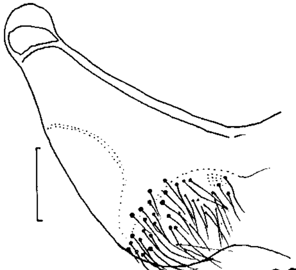
25 *Cc. coccineus*



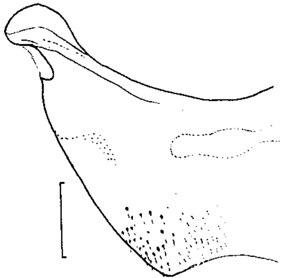
26 *Sp. griseocollis*



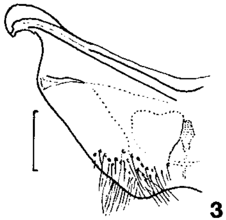
27 *Cr. crotchii*



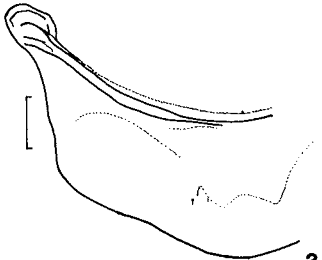
28 *Fn. funebris*



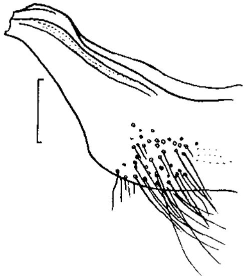
Rb. robustus **29**



30 *Rd. rubicundus*

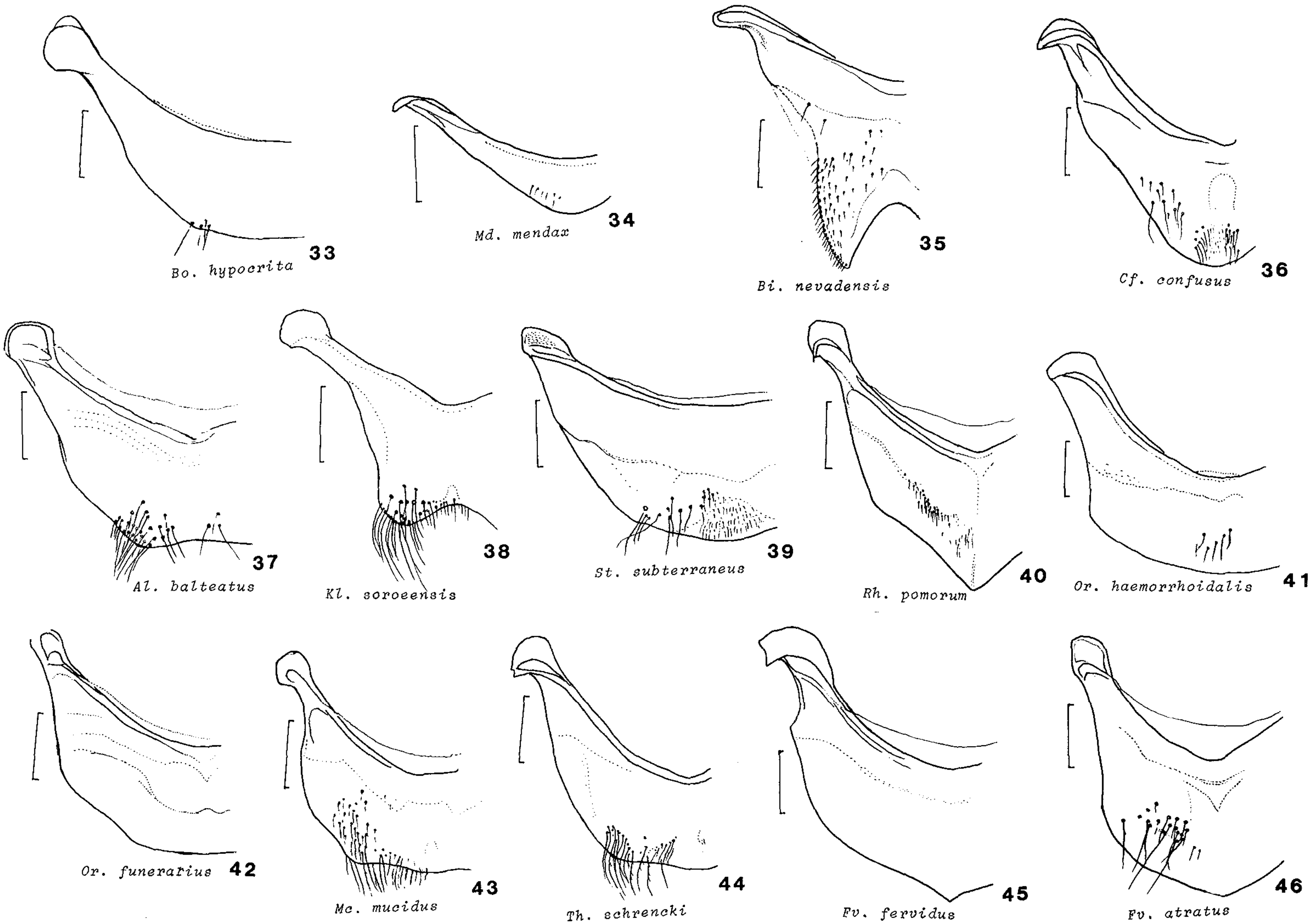


Rf. eximius **31**



32 *Ps. pressus*

Figs. 18 - 32. Metasomal sternum VII.
(Unit = 0.40 mm in Figs. 18 - 147.)


33 *Bo. hypocrita*

34 *Md. mendax*

35 *Bi. nevadensis*

36 *Cf. confusus*

37 *Al. balteatus*

38 *Kl. soroeensis*

39 *St. subterraneus*

40 *Rh. pomorum*

41 *Or. haemorrhoidalis*

42 *Or. funerarius*

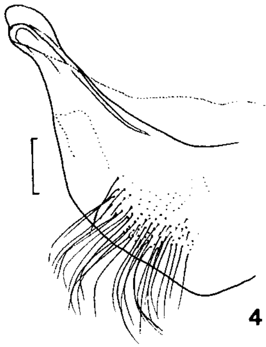
43 *Mc. mucidus*

44 *Th. schrencki*

45 *Fv. fervidus*

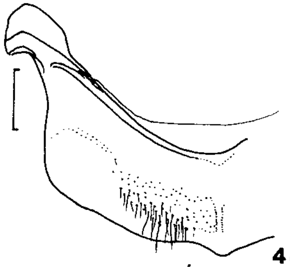
46 *Fv. atratus*

Figs. 33 - 46. Metasomal sternum VII. (Continued)



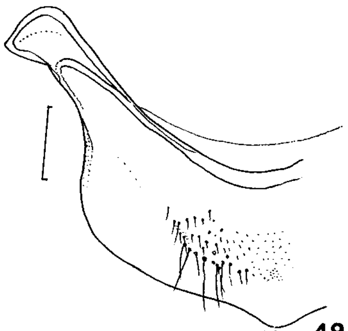
47

Fv. transversalis



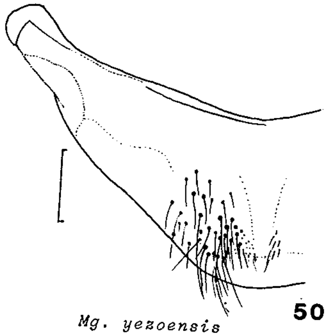
48

Fv. morio



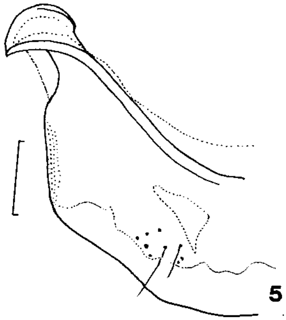
49

Fv. dahlbomii



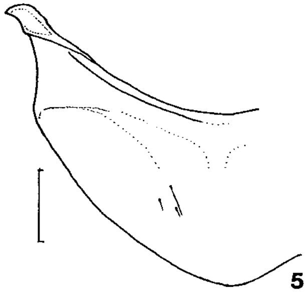
50

Mg. yezoensis



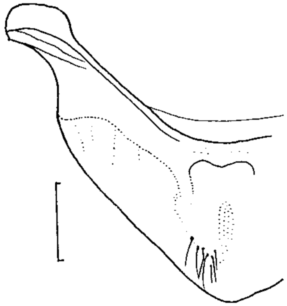
51

Sx. irisanensis



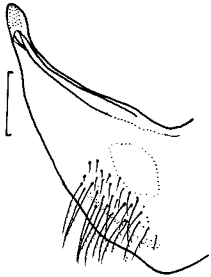
52

Dv. diversus



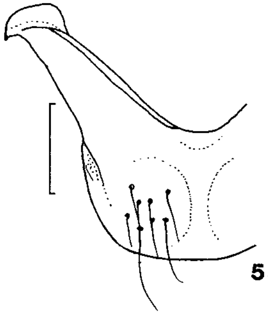
53

Tr. tricornis



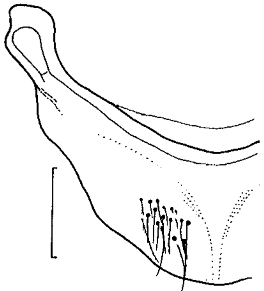
54

Fv. brevivillus



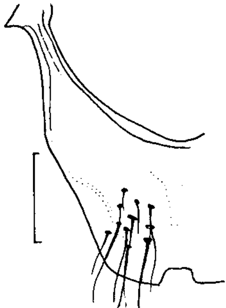
55

Pt. rupestris



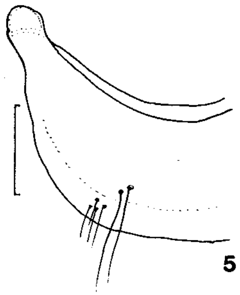
56

Ao. maxillosus



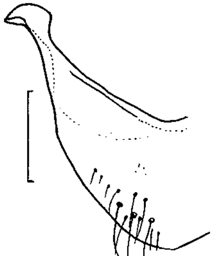
57

As. vestalis



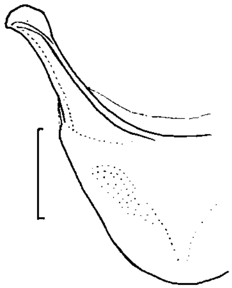
58

Fp. norvegicus



59

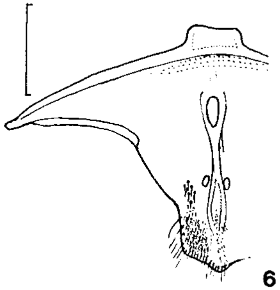
Cp. insularis



60

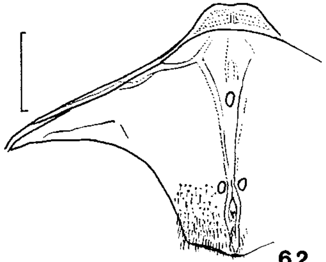
Mp. campestris

Figs. 47 - 60. Metasomal sternum VII. (Continued)



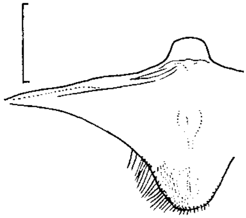
61

Ag. wurfleini



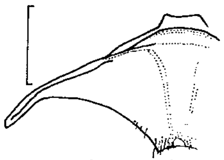
62

Nb. sikkimi



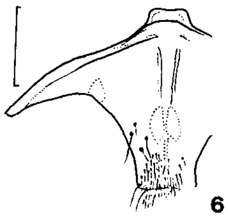
63

Cl. rufocinctus



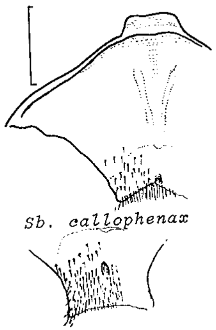
64

Ml. lapidarius



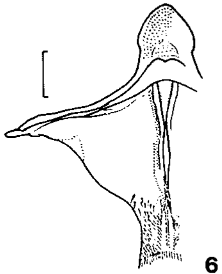
65

Pr. ardens



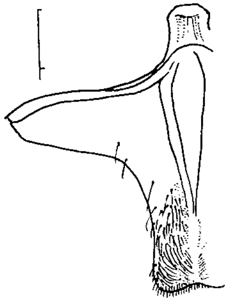
Sb. callophenax

66



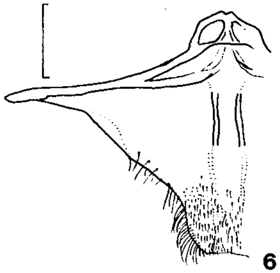
67

Fr. fraternus



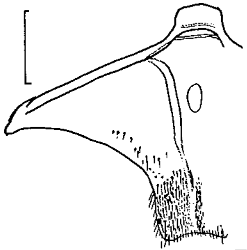
68

Cc. coccineus



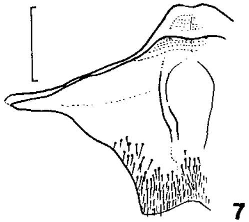
69

Sp. griseocollis



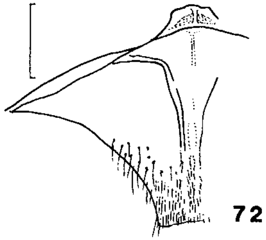
Cr. crotchii

70



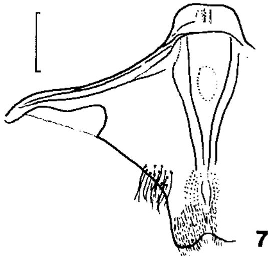
71

Fn. funebris



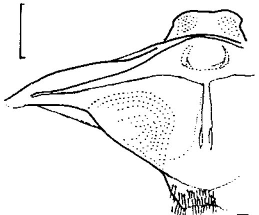
72

Rb. robustus



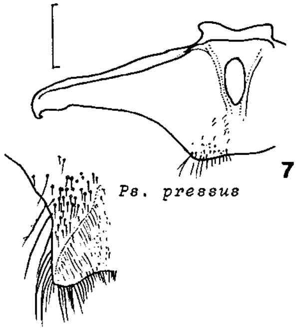
73

Rd. rubicundus



74

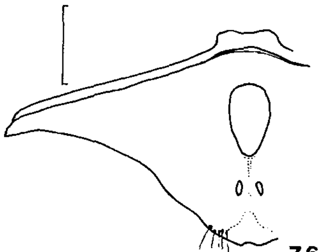
Rf. eximius



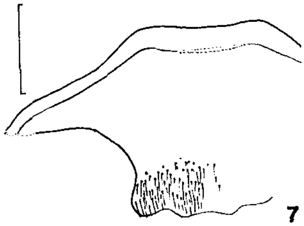
Ps. pressus

75

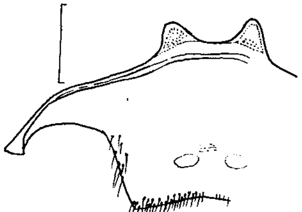
Figs. 61 - 75. Metasomal sternum VIII.



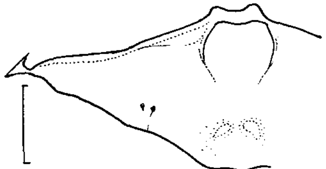
Bo. hypocrita **76**



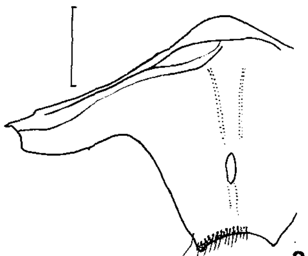
Md. mendax **77**



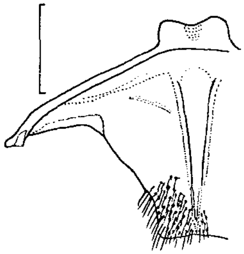
Bi. nevadensis **78**



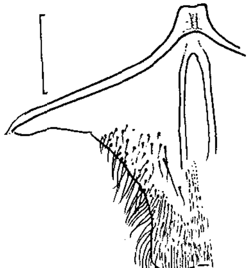
Cf. confusus **79**



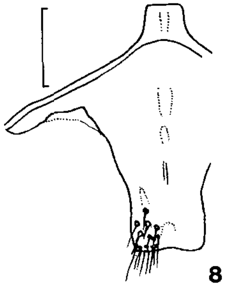
Al. balteatus **80**



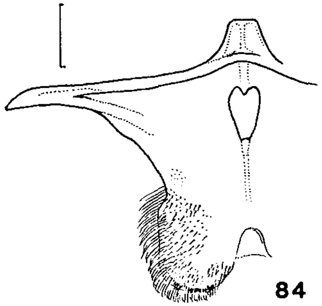
Kl. soroeensis **81**



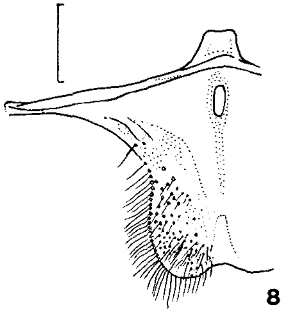
St. subterraneus **82**



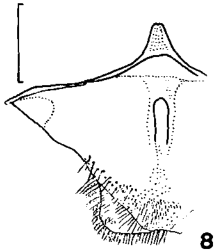
Rh. pomorum **83**



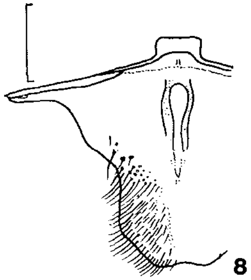
Or. haemorrhoidalis **84**



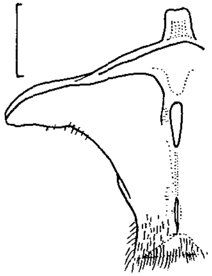
Or. funerarius **85**



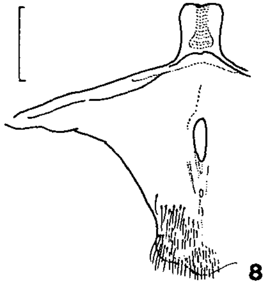
Mc. mucidus **86**



Th. schrencki **87**

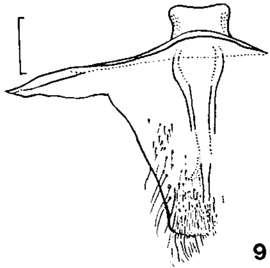


Fv. fervidus **88**



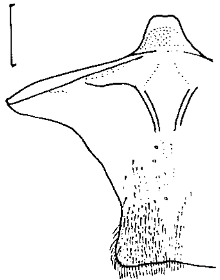
Fv. atratus **89**

Figs. 76 - 89. Metasomal sternum VIII. (Continued)

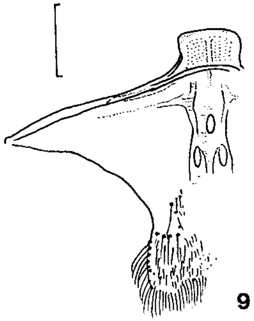


90

Fv. transversalis

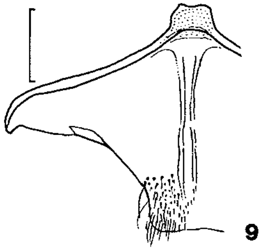


Fv. morio **91**



92

Fv. dahlbomii



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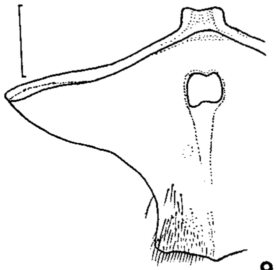
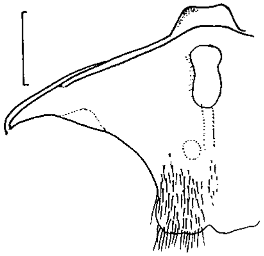
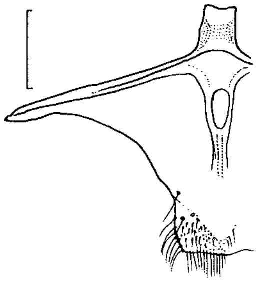
Mg. yezoensis



Sx. irisanensis **94**

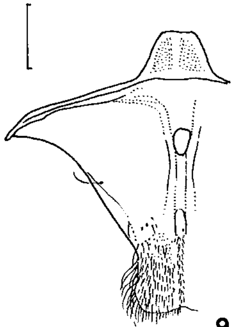


Dv. diversus **95**

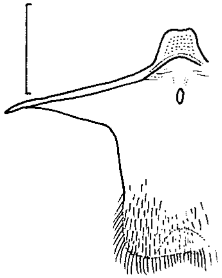


96

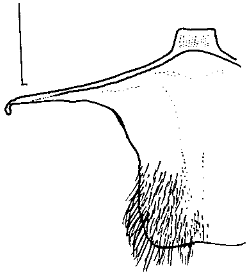
Tr. tricornis



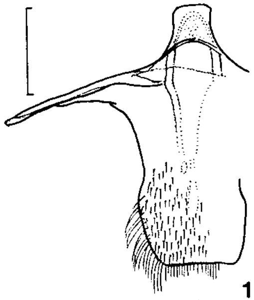
Fv. brevivillus **97**



Pt. rupestris **98**

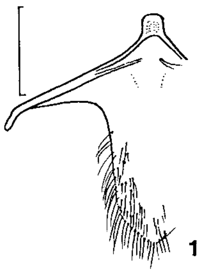


Ao. maxillosus **99**



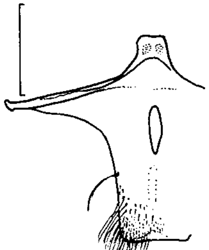
100

As. vestalis

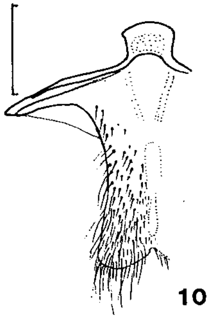


101

Fp. norvegicus



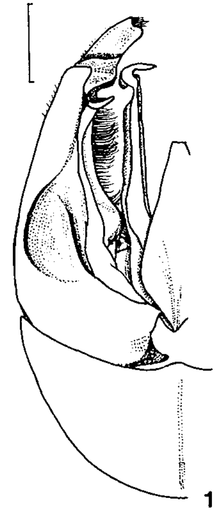
Cp. insularis **102**



103

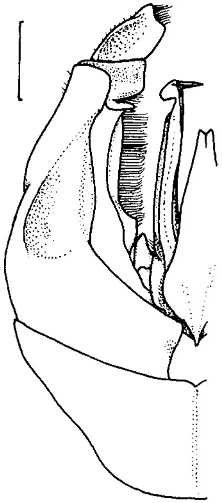
Mp. campestris

Figs. 90 - 103. Metasomal sternum VIII. (Continued)



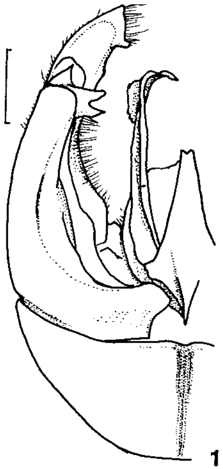
104

Ag. wurfleini



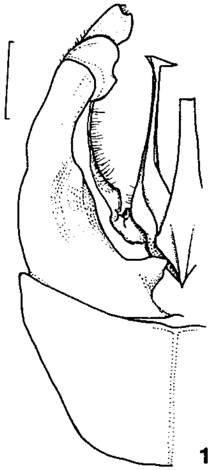
105

Nb. sikkimi



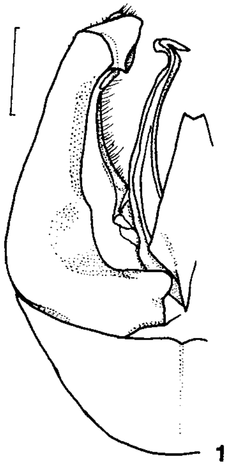
106

Cl. rufocinctus



107

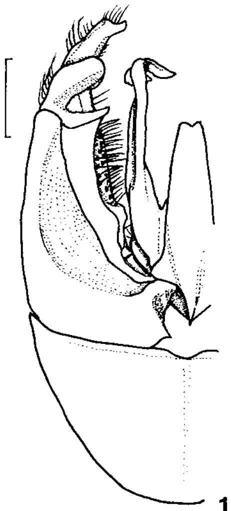
Ml. lapidarius



108

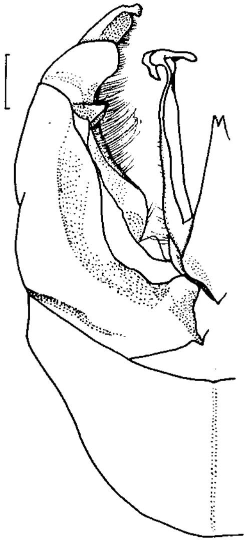
Pr. ardens

Figs. 104 - 108. Male genitalia.



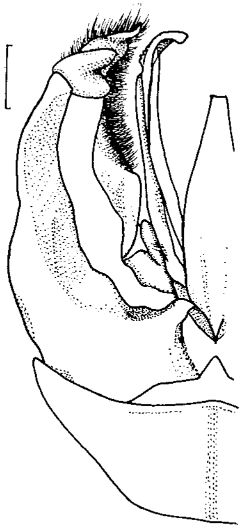
109

Sb. callophenax



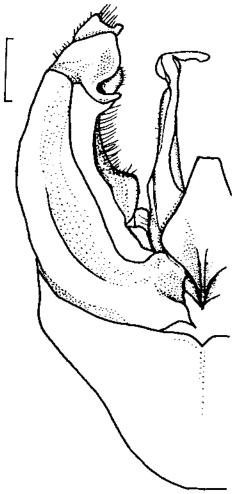
110

Fr. fraternus



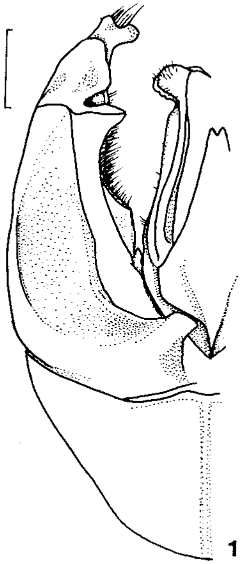
111

Cc. coccineus



112

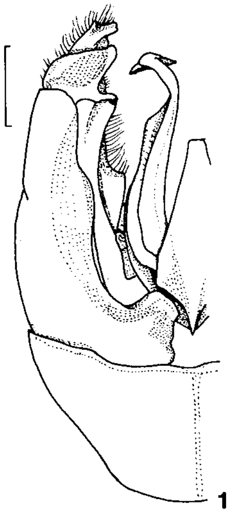
Sp. griseocollis



113

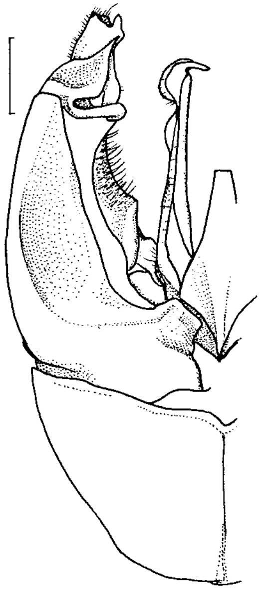
Cr. crotchii

Figs. 109 - 113. Male genitalia. (Continued)



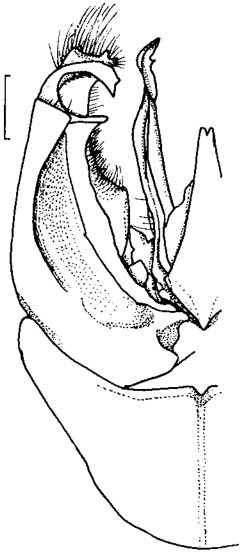
114

Fn. funebris



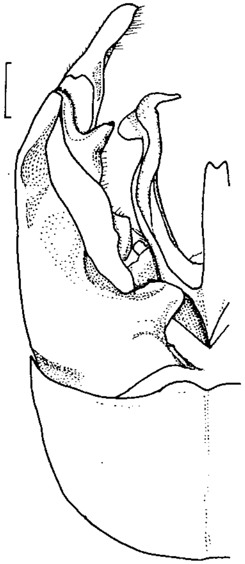
115

Rb. robustus



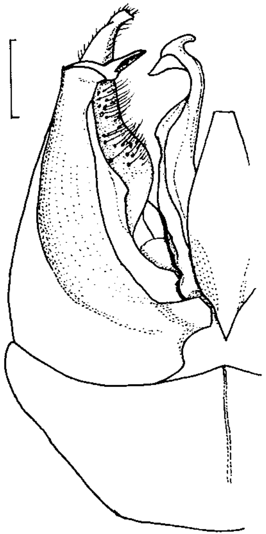
116

Rd. rubicundus



117

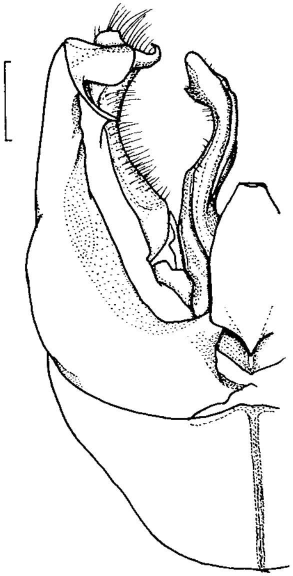
Rf. eximius



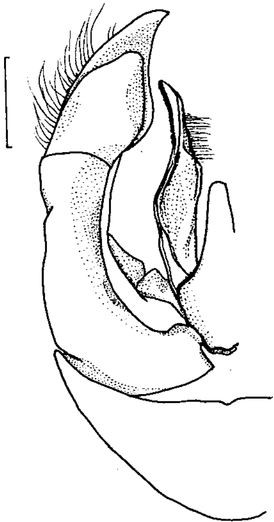
118

Ps. pressus

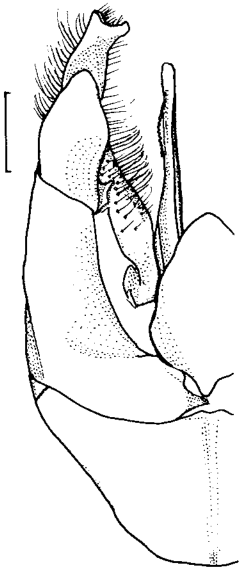
Figs. 114 - 118. Male genitalia. (Continued)



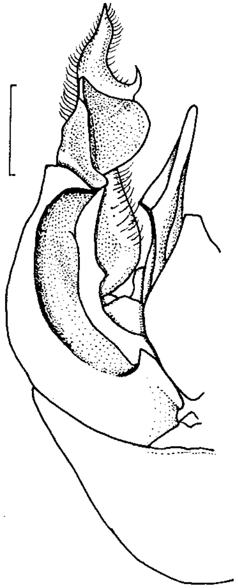
Bo. hypocrita **119**



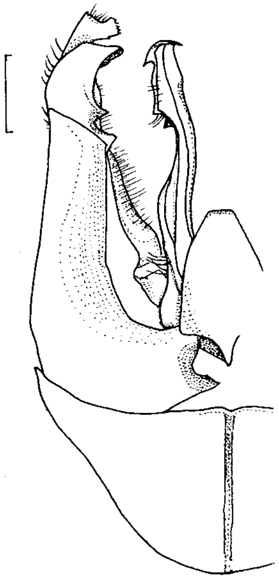
Md. mendax **120**



Bi. nevadensis **121**

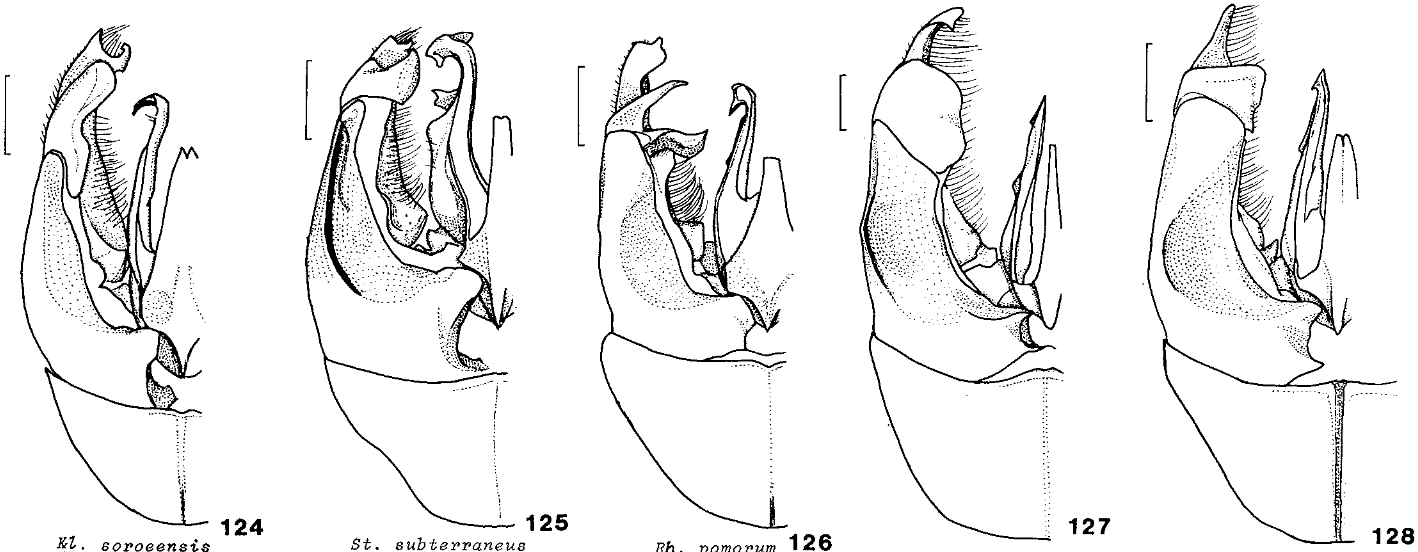


Cf. confusus **122**



Al. balteatus **123**

Figs. 119 - 123. Male genitalia. (Continued)



124 *Kl. soroeensis*

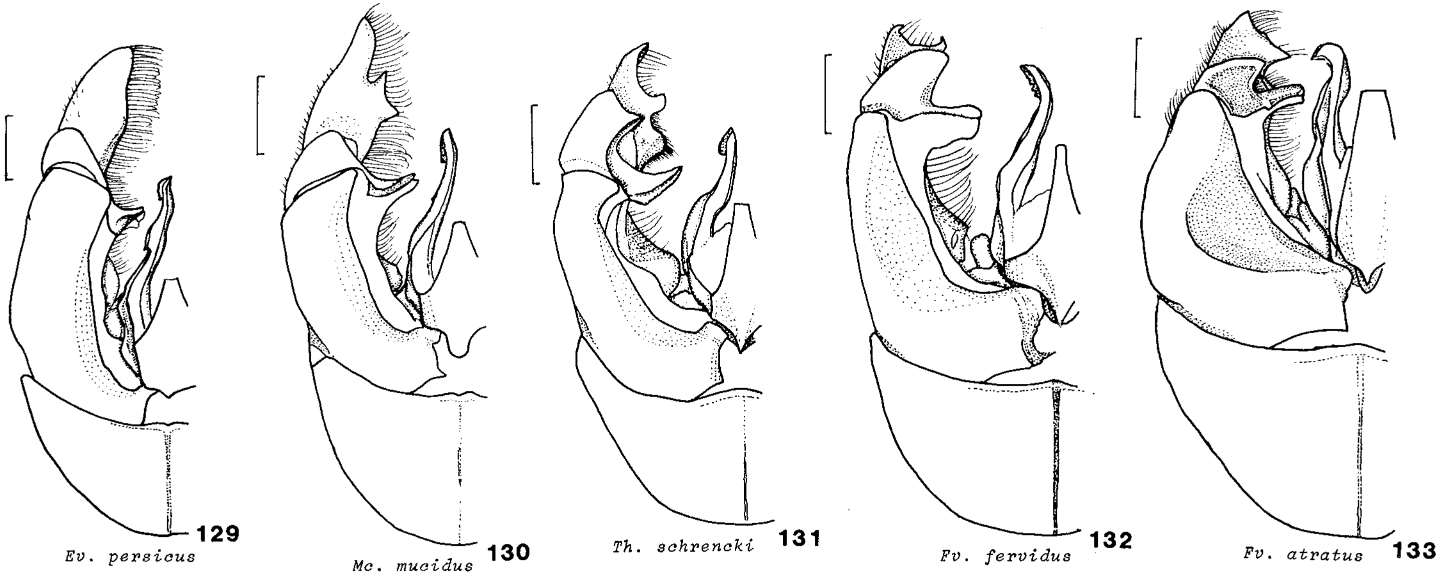
125 *St. subterraneus*

126 *Rh. pomorum*

127 *Or. haemorrhoidalis*

128 *Or. funerarius*

Figs. 124 - 128. Male genitalia. (Continued)


129 *Ev. persicus*

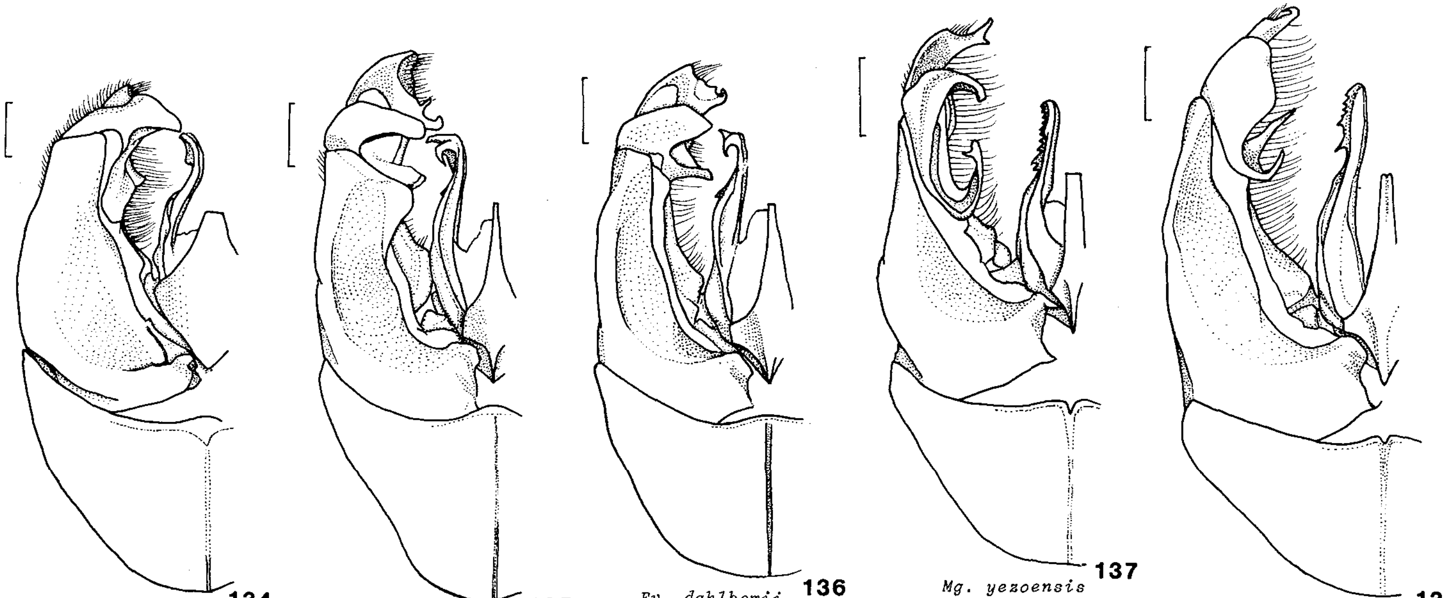
130 *Mc. mucidus*

131 *Th. schrencki*

132 *Fv. fervidus*

133 *Fv. atratus*

Figs. 129 - 133. Male genitalia. (Continued)



Fv. transversalis **134**

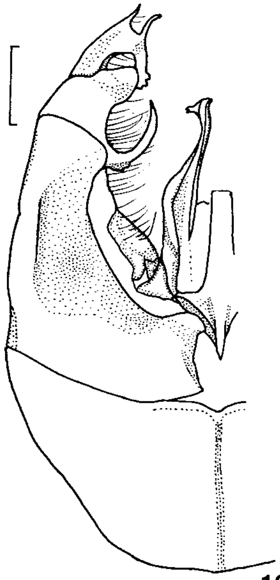
Fv. morio **135**

Fv. dahlbomii **136**

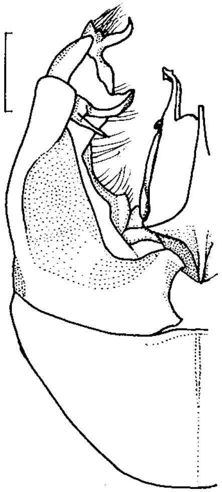
Mg. yezoensis **137**

Sx. irisanensis **138**

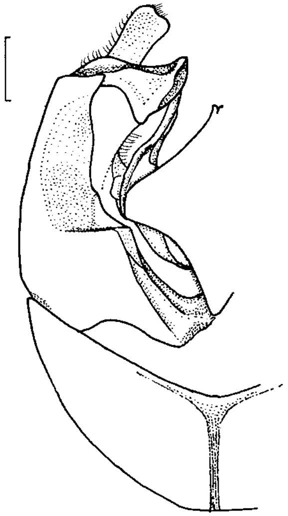
Figs. 134 - 138. Male genitalia. (Continued)



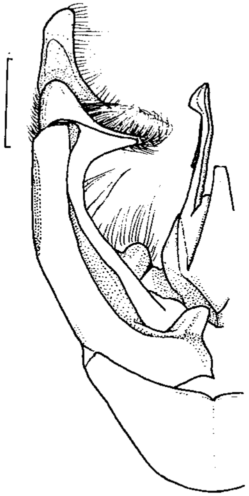
Dv. diversus **139**



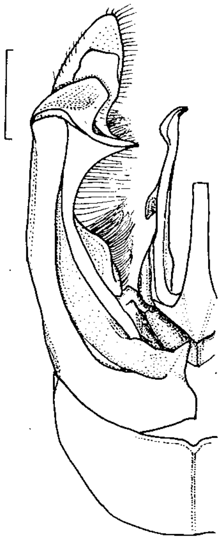
Tr. tricornis **140**



Fv. brevivillus **141**

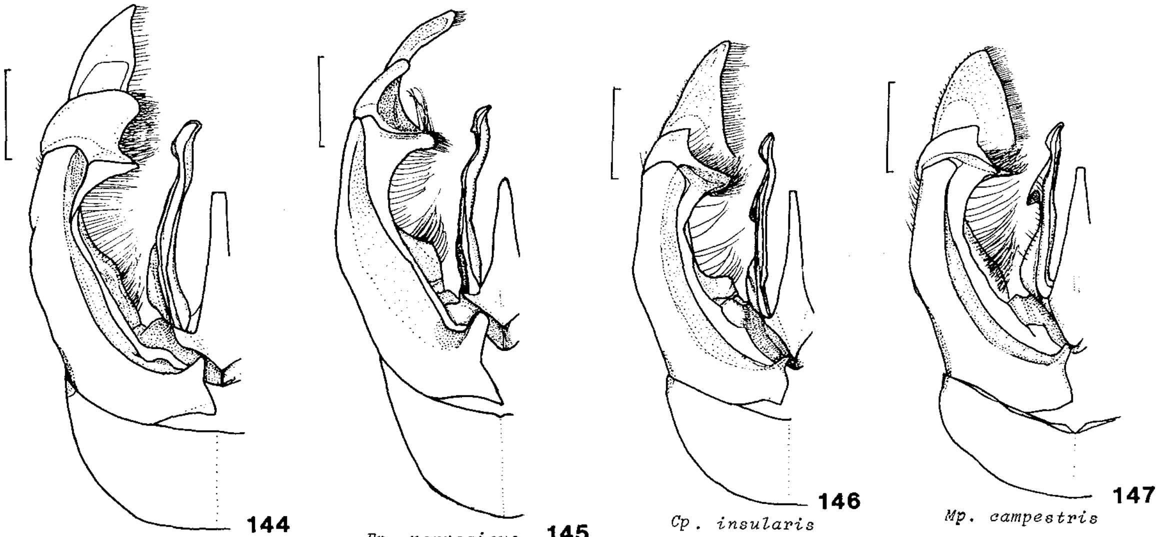


Pt. rupestris **142**



Ao. maxillosus **143**

Figs. 139 - 143. Male genitalia. (Continued)



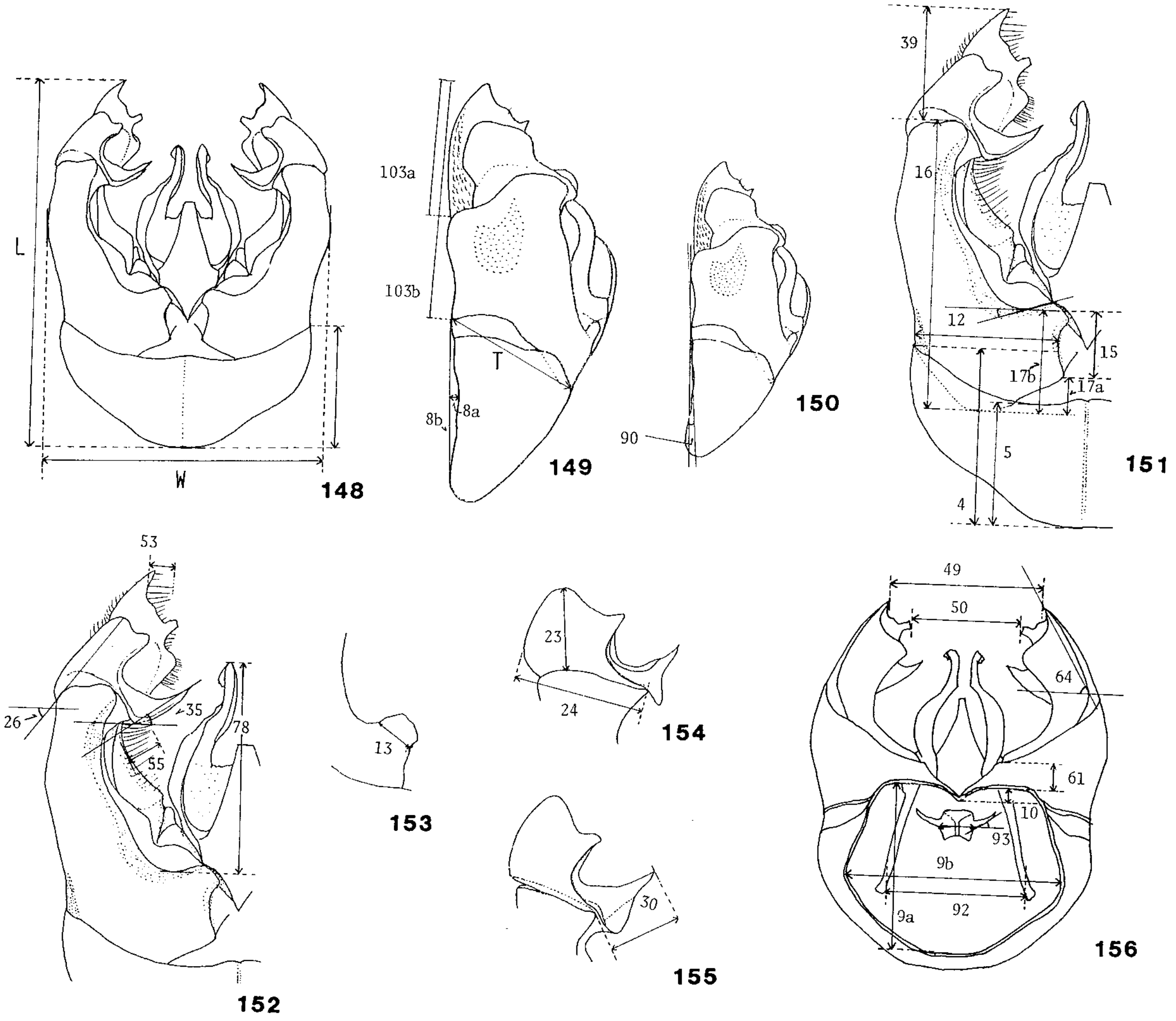
144 *As. vestalis*

145 *Fp. norvegicus*

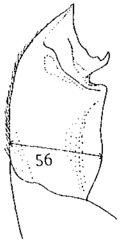
146 *Cp. insularis*

147 *Mp. campestris*

Figs. 144 - 147. Male genitalia. (Continued)



Figs. 148 - 156. Measured parts of male genitalia. Explanations in text, chapter 6.



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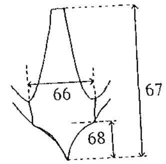
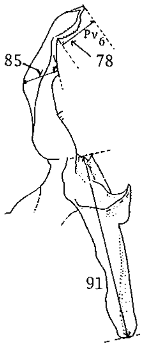


158



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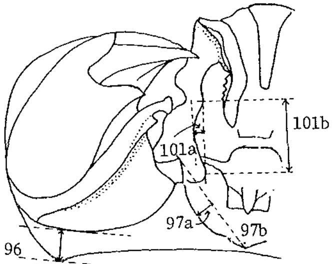

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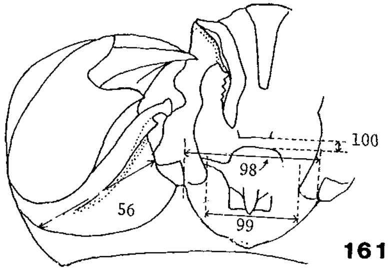

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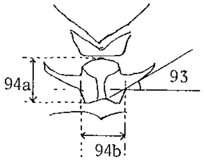

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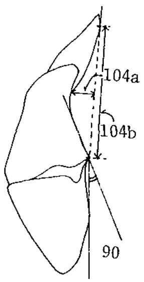

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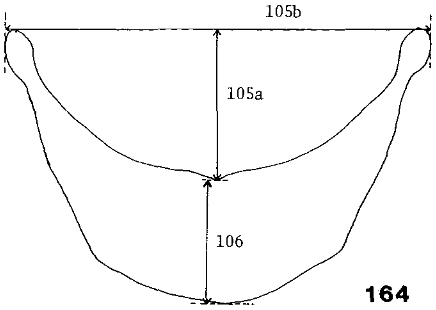

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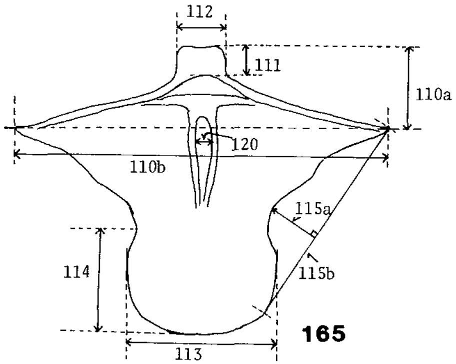

165

Figs. 157 - 165. Measured parts of male genitalia. (Continued)

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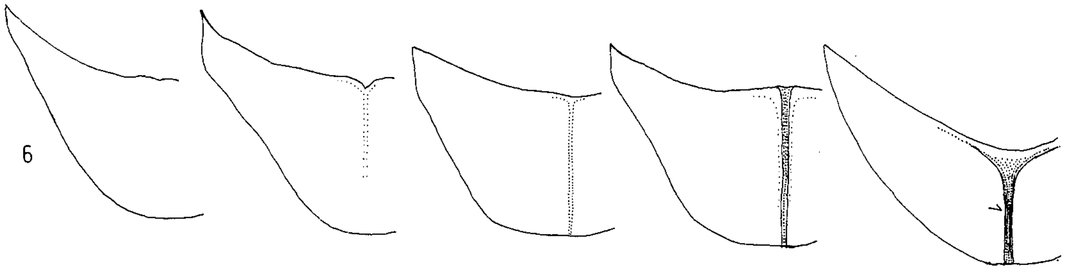

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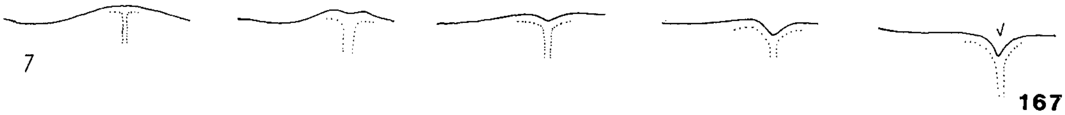

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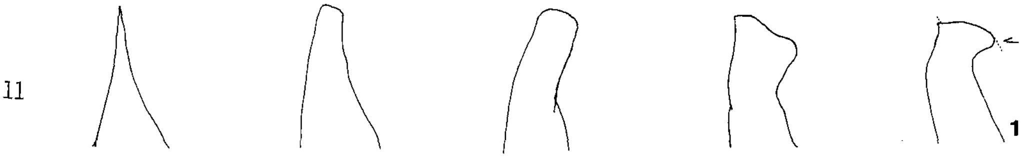

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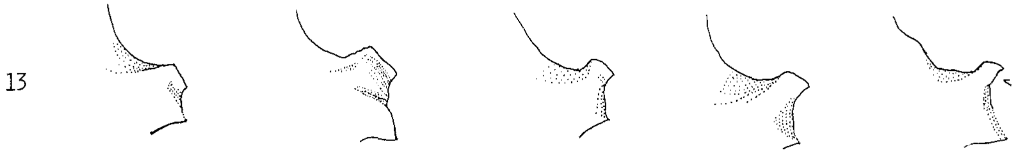

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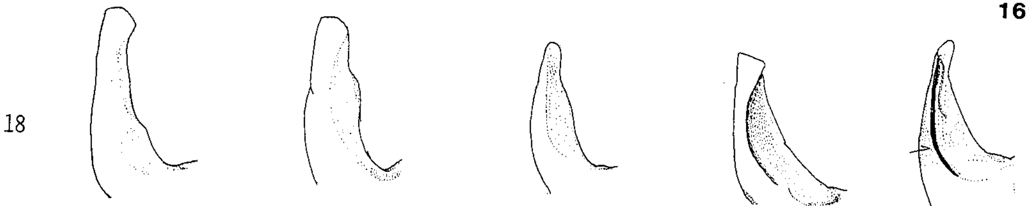
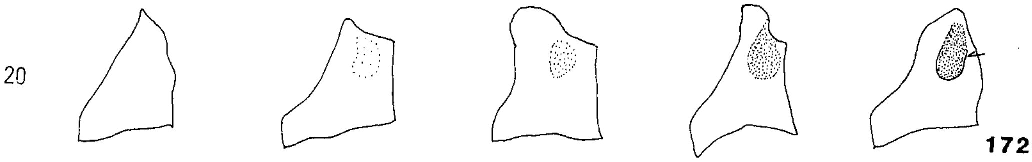


170

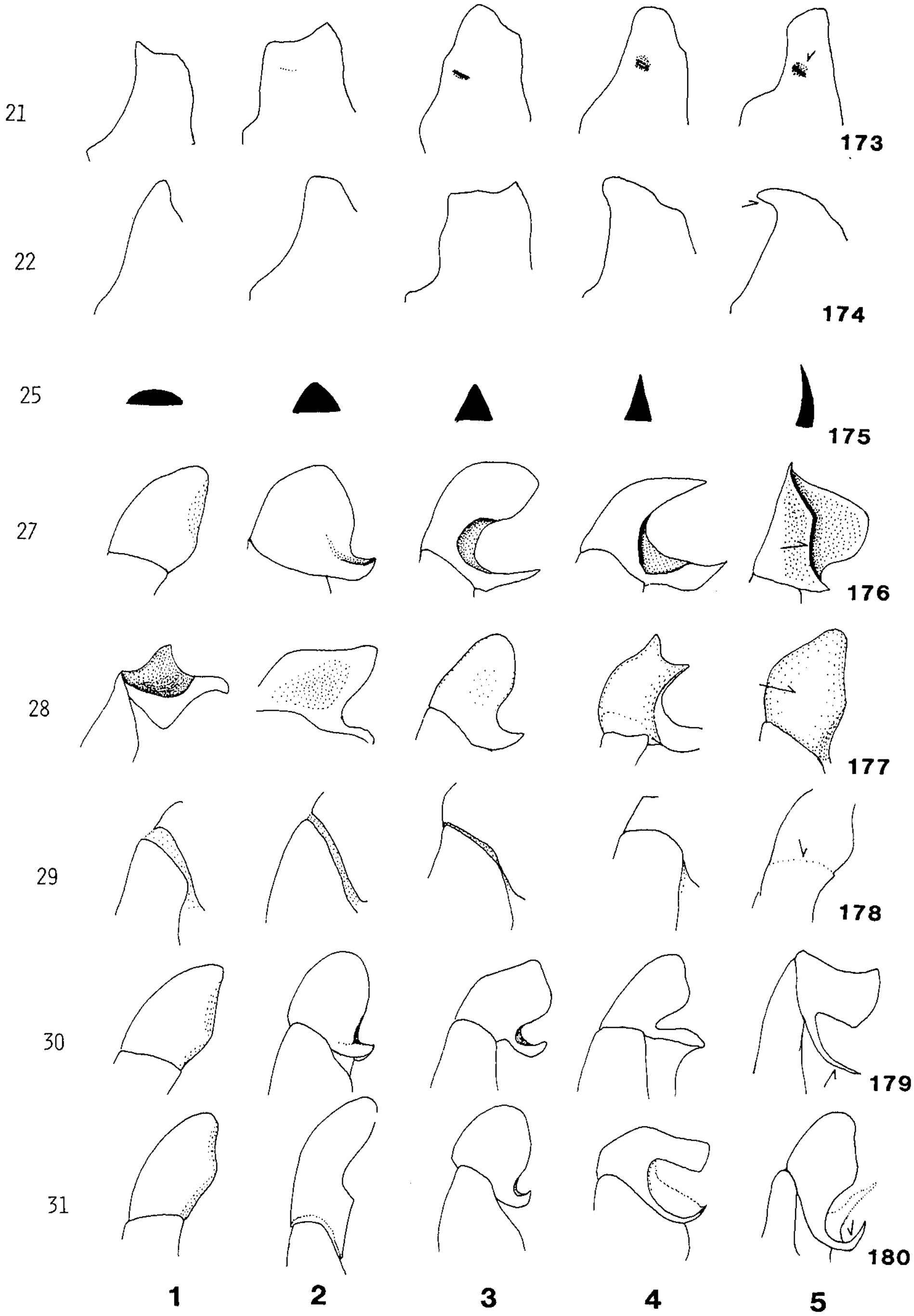
171



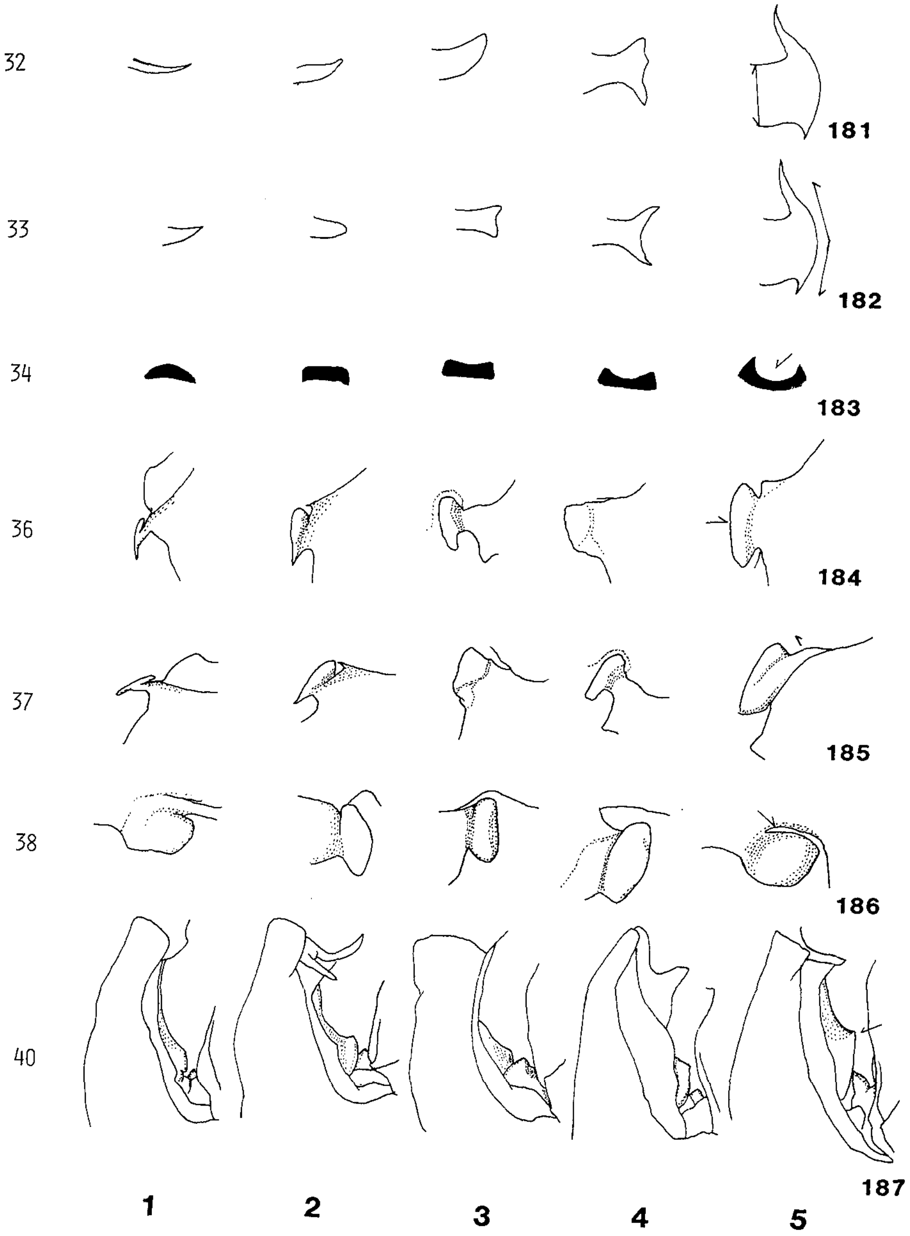
172

Code 1 2 3 4 5

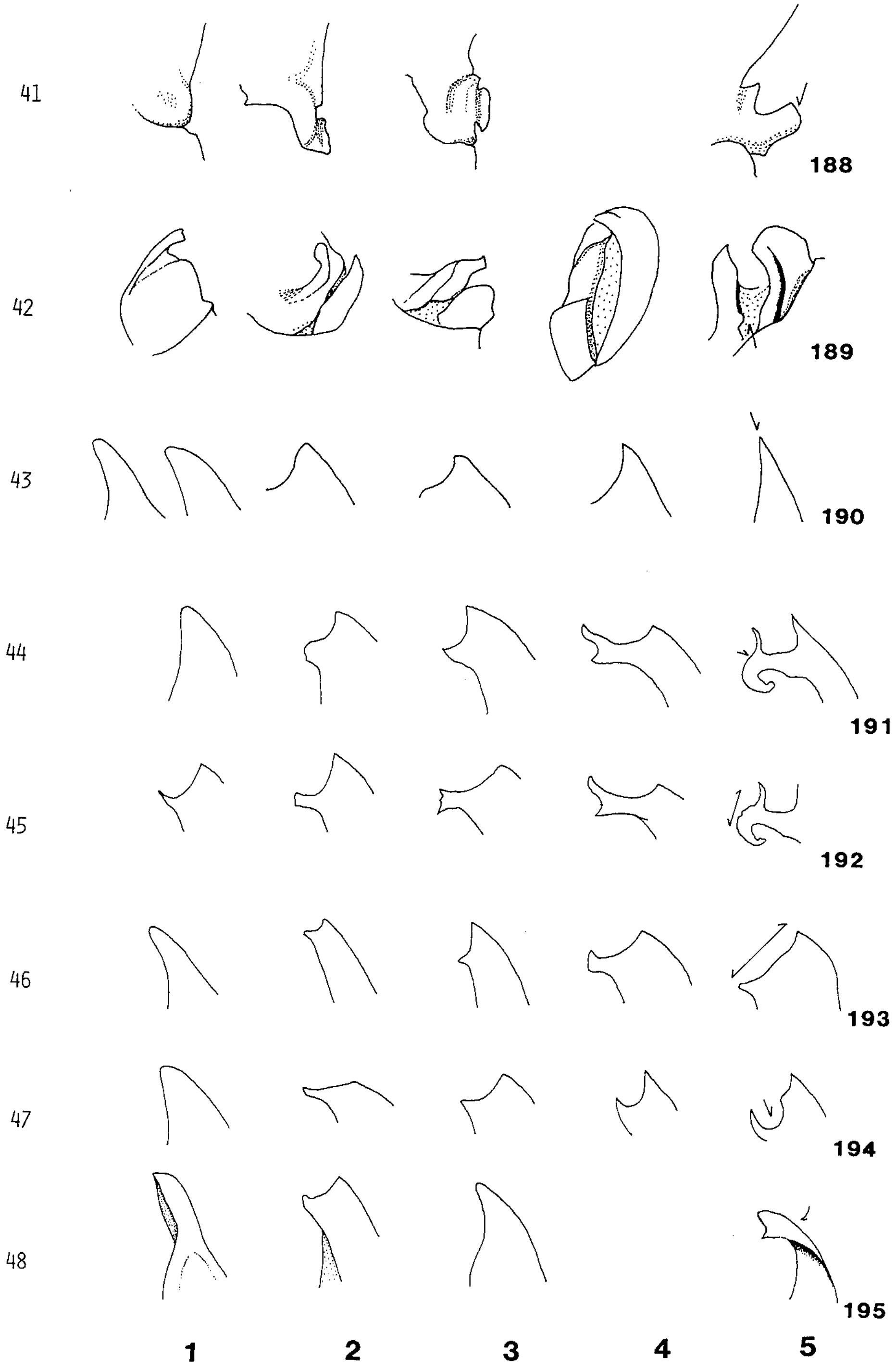
Figs. 166 - 172. Standard for coding of non-metric characters.



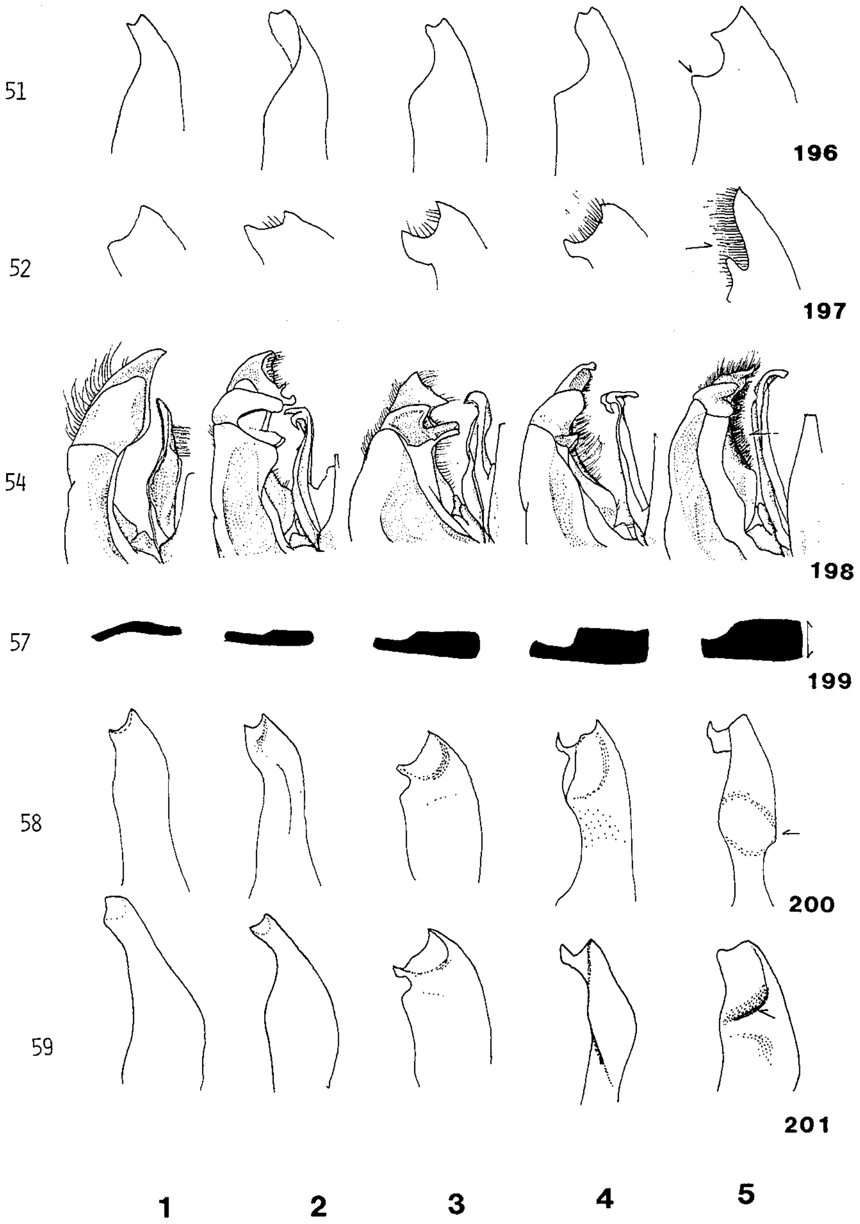
Figs. 173 - 180. Standard for coding of non-metric characters. (Continued)



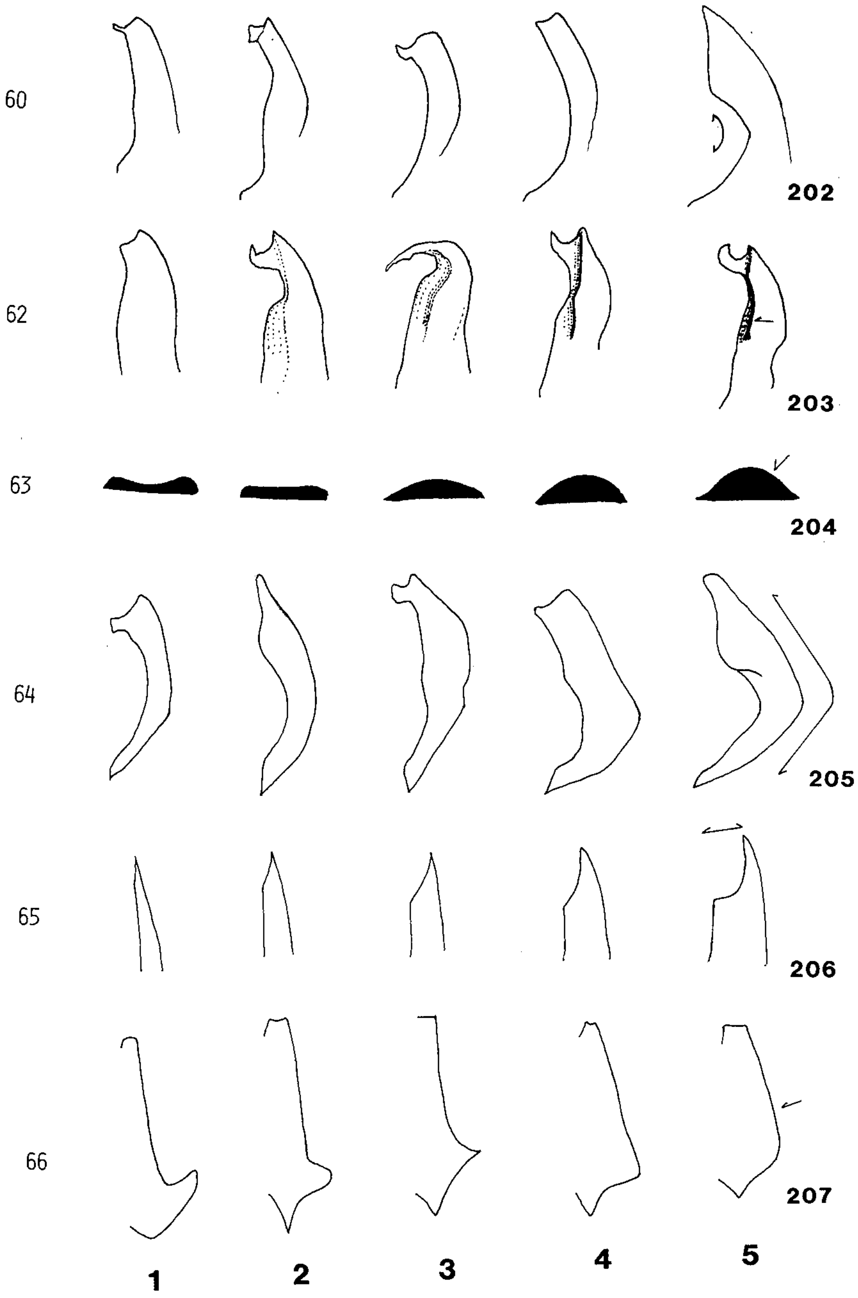
Figs. 181 - 187. Standard for coding of non-metric characters. (Continued)



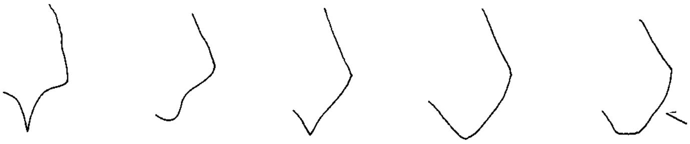
Figs. 188 - 195. Standard for coding of non-metric characters. (Continued)



Figs. 196 - 201. Standard for coding of non-metric characters. (Continued)



Figs. 202 - 207. Standard for coding of non-metric characters. (Continued)



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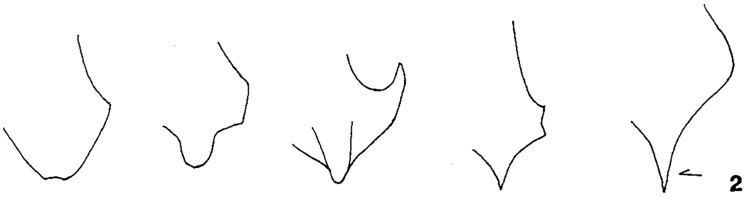

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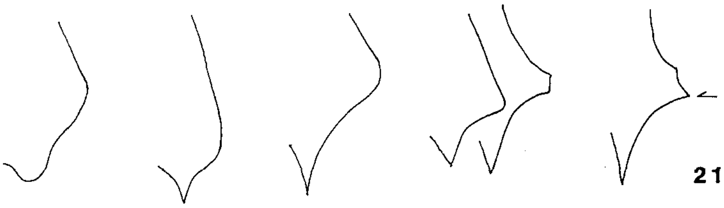

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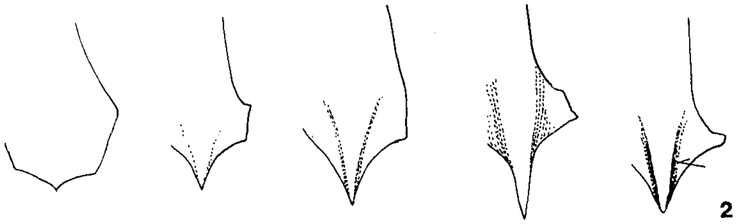

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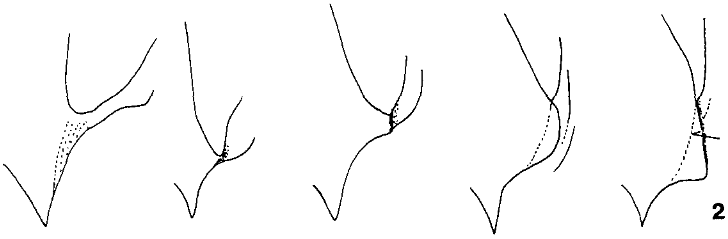

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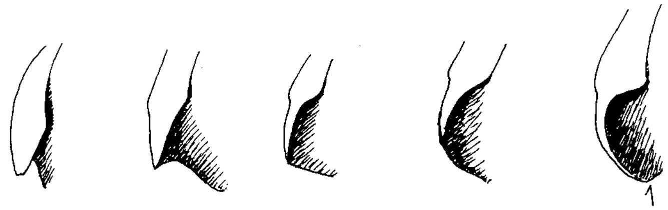
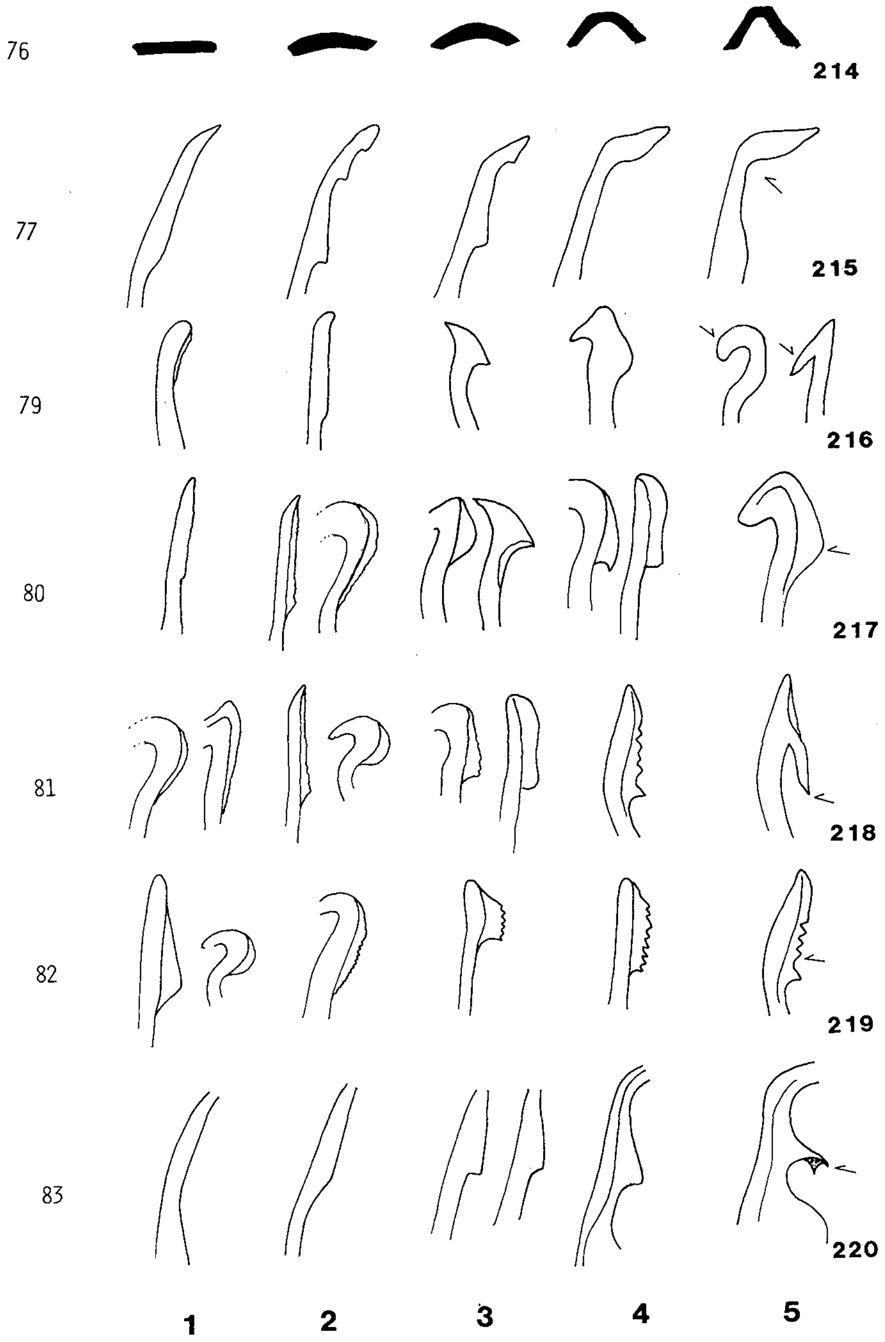


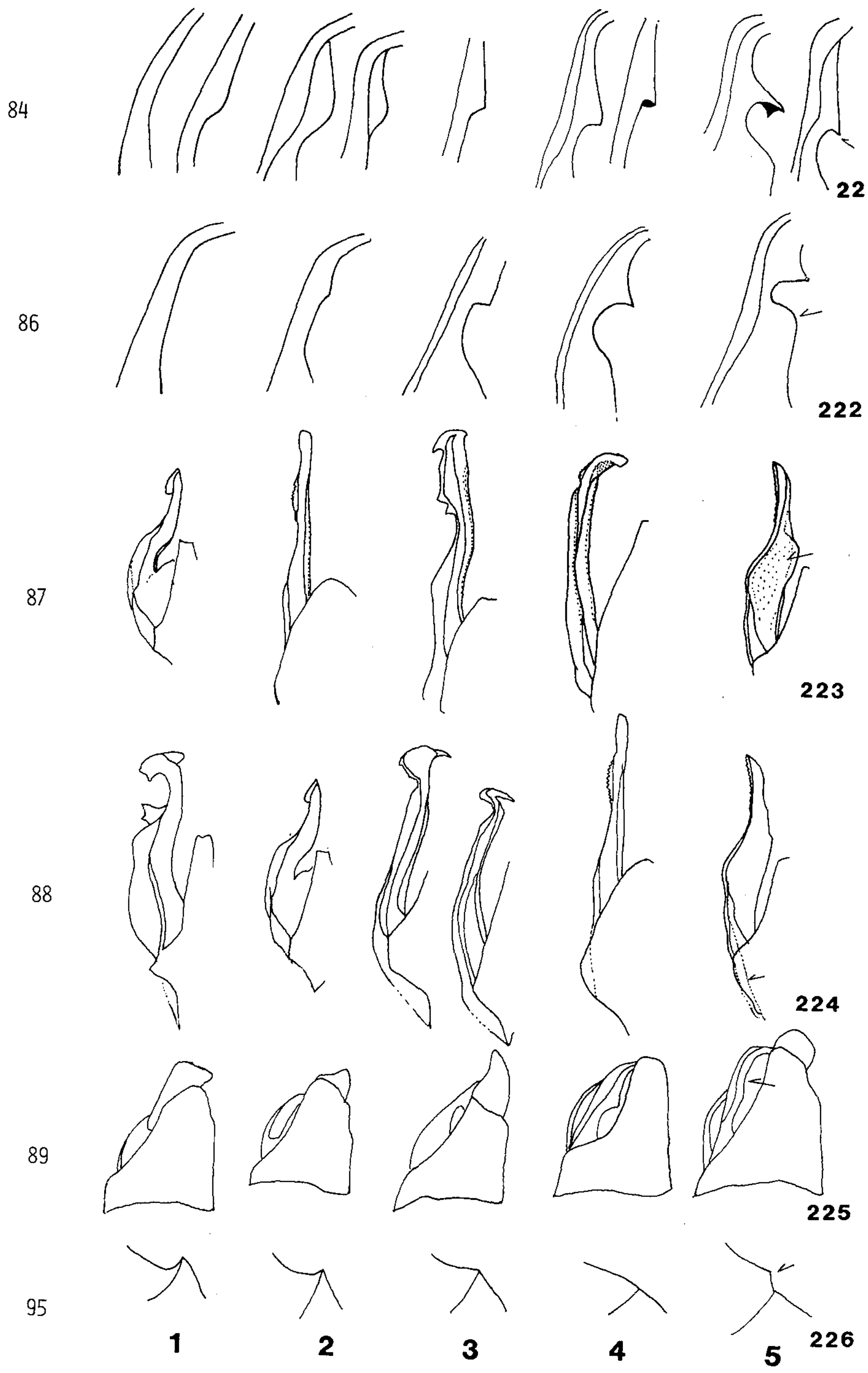
213

1 2 3 4 5

Figs. 208 - 213. Standard for coding of non-metric characters. (Continued)



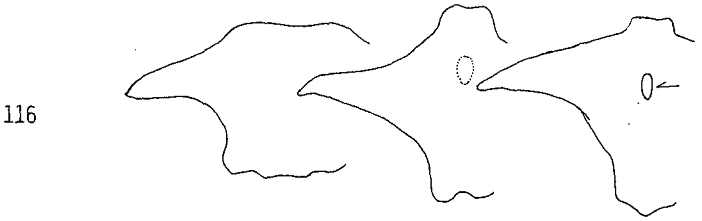
Figs. 214 - 220. Standard for coding of non-metric characters. (Continued)



Figs. 221 - 226. Standard for coding of non-metric characters. (Continued)

227

228



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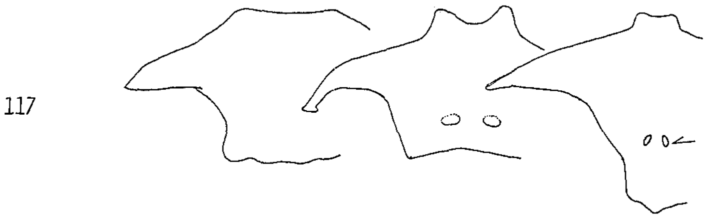

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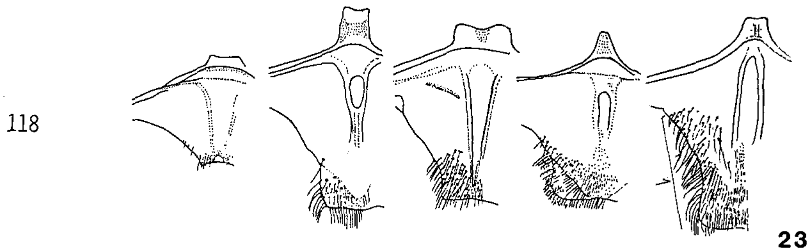

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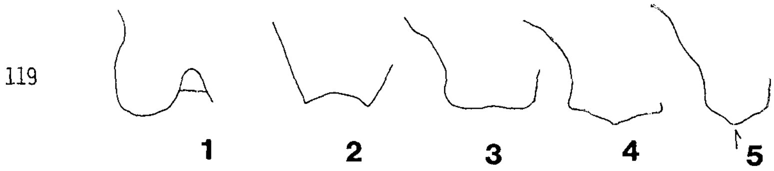
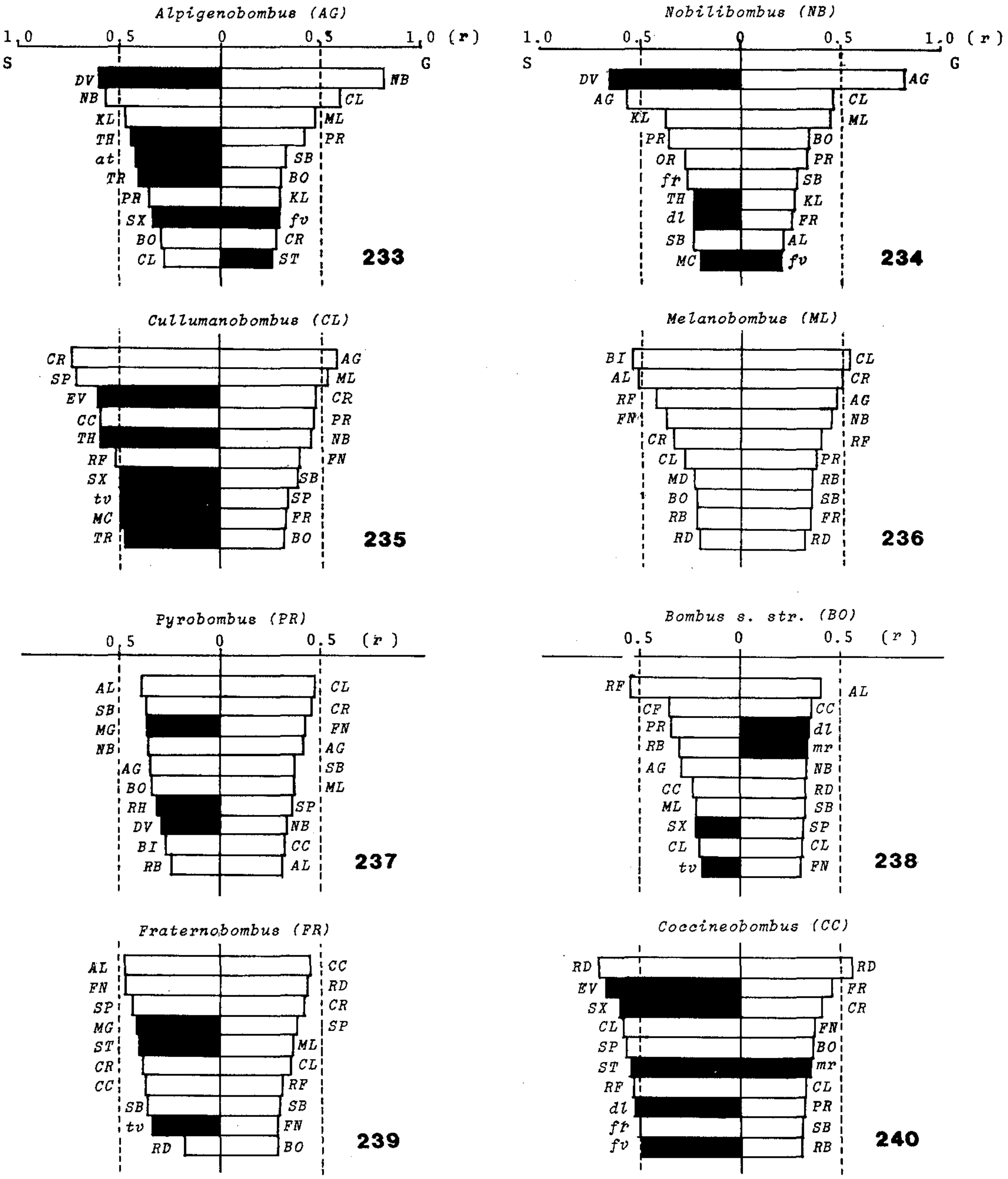
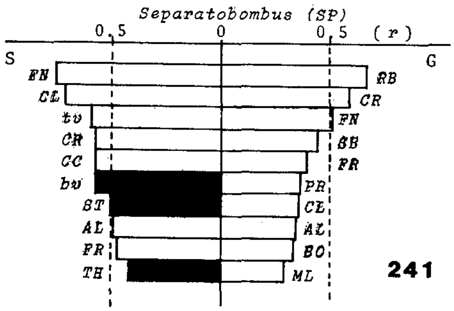


232

Figs. 227 - 232. Standard for coding of non-metric characters. (Continued)



Figs. 233 - 240. Ten taxa exhibiting distinct similarity to each subgenus of Bombus, based upon the correlation matrices. Right: Genitalia. Left: Apical sterna. Open bars: The subgenera of Anodontobombus including Boopobombus. Filled bars: The subgenera of Odontobombus.



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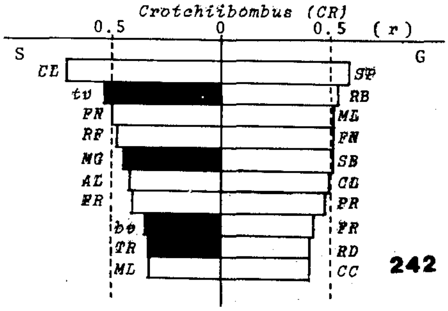

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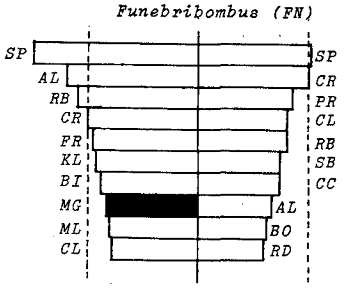

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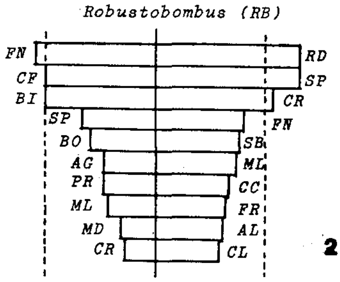

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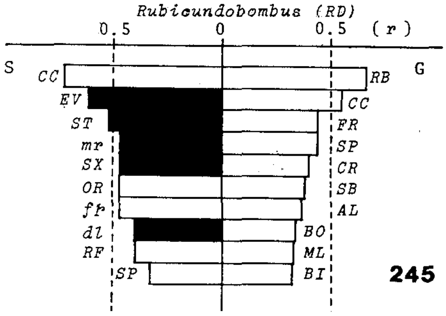

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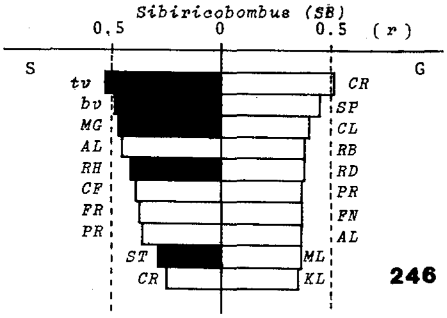

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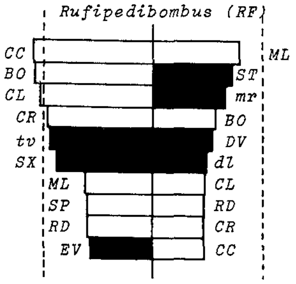

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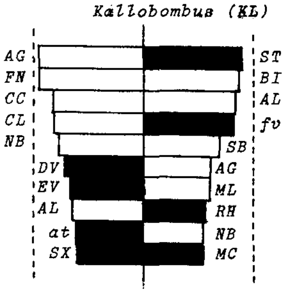
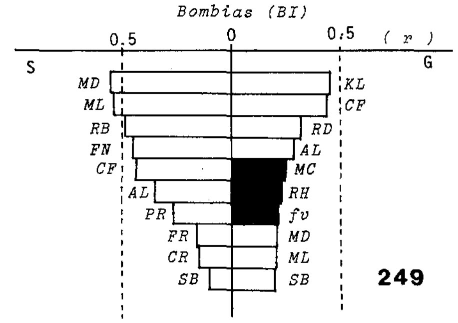


248

Figs. 241 - 248. Ten taxa exhibiting distinct similarity to each subgenus of Bombus. (Continued)



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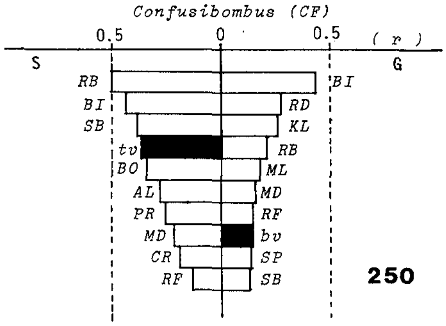

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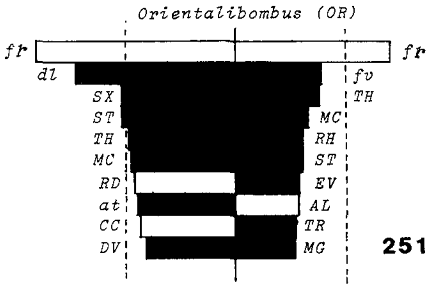

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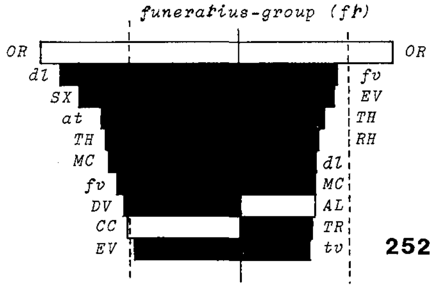

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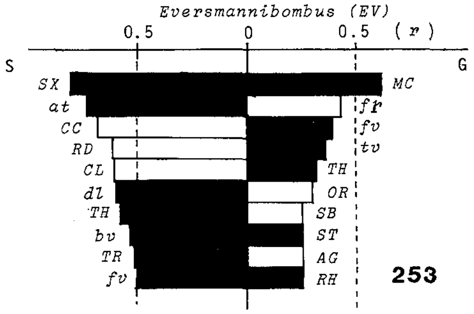

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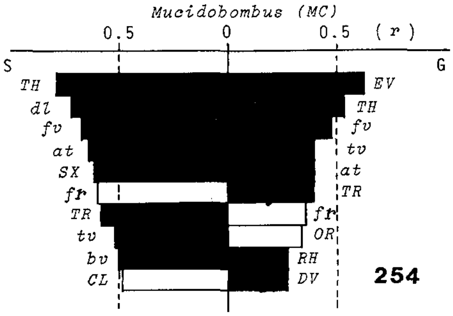

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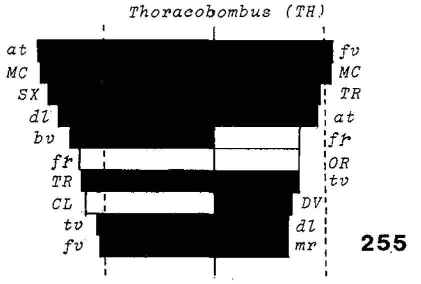

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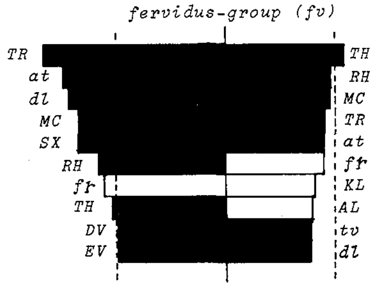
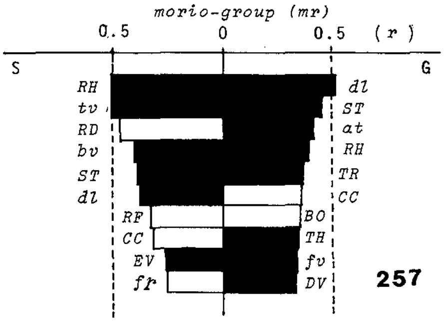


256

Figs. 249 - 256. Ten taxa exhibiting distinct similarity to each subgenus of Bombus. (Continued)



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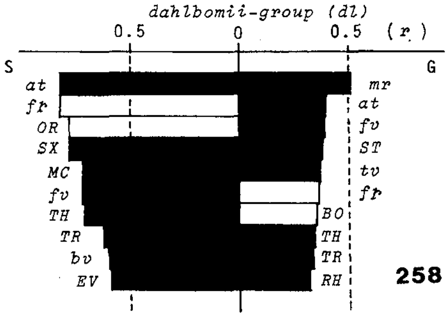

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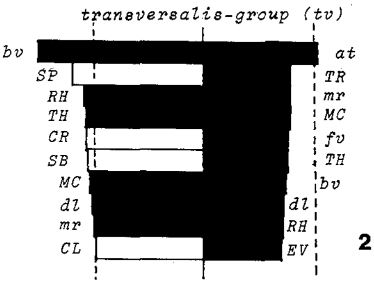

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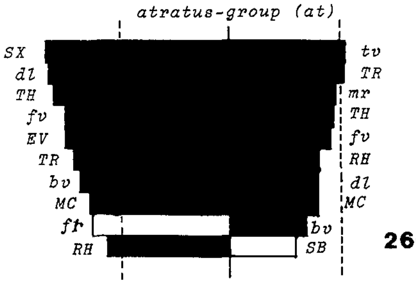

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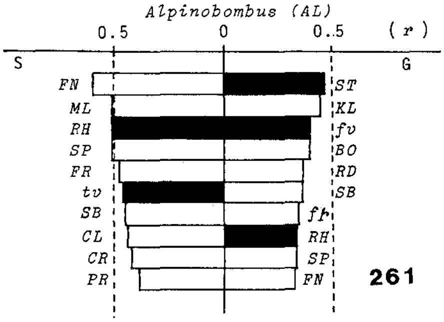

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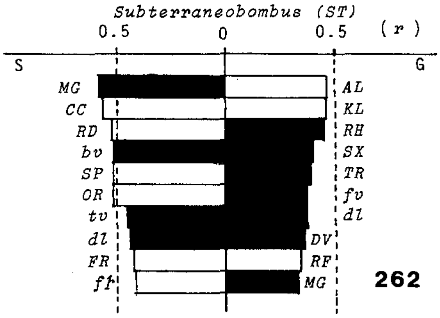

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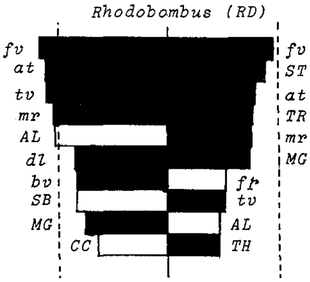

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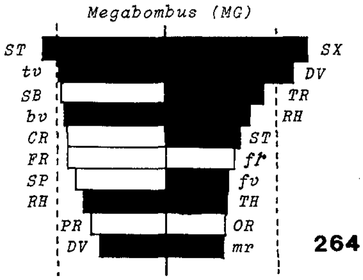
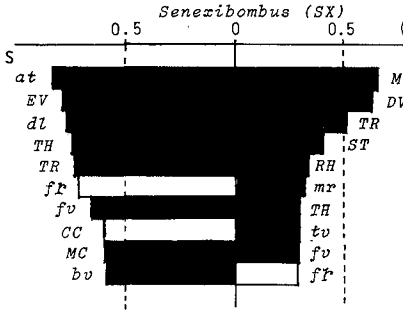


264

Figs. 257 - 264. Ten taxa exhibiting distinct similarity to each subgenus of Bombus. (Continued)



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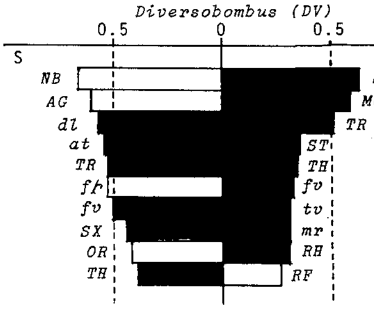

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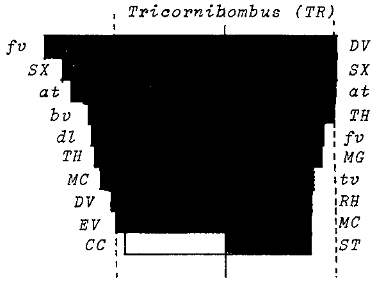

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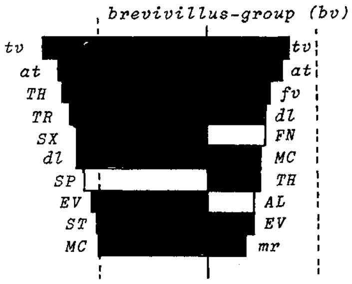

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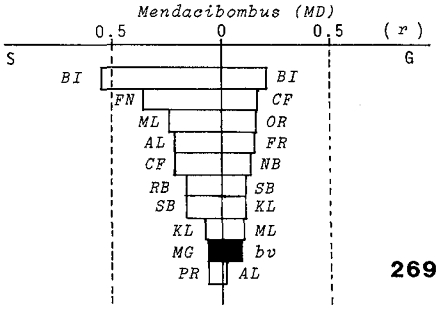

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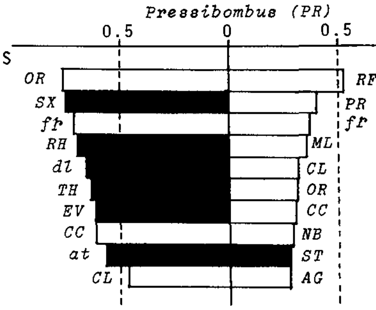
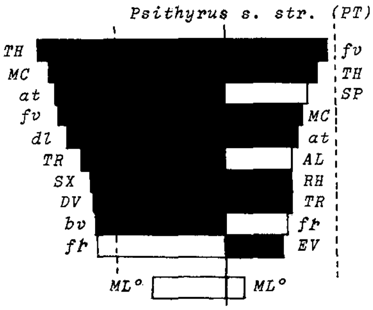


270

Figs. 265 - 270. Ten taxa exhibiting distinct similarity to each subgenus of Bombus. (Continued)



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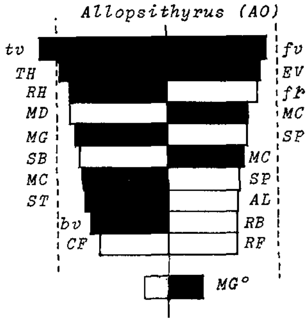

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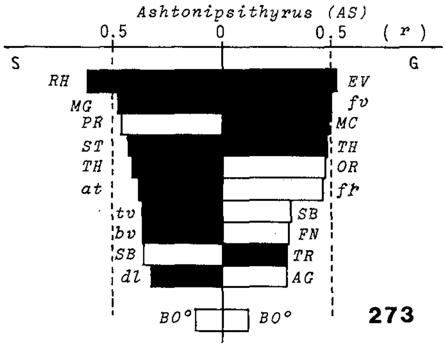

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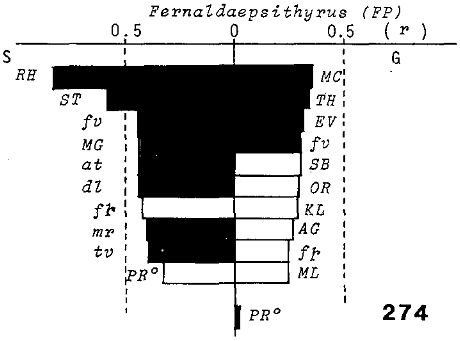

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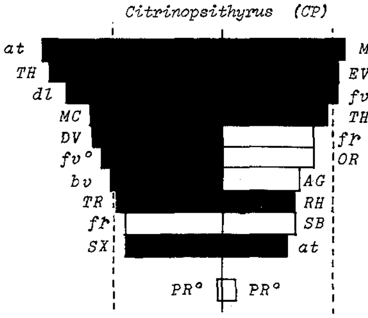

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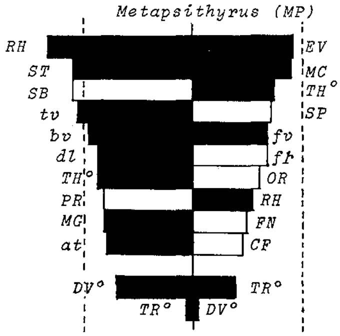
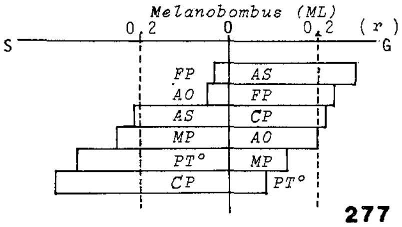


276

Figs. 271 - 276. Ten taxa exhibiting distinct similarity to each subgenus of Psithyrus. Cf. the legends of Figs. 233 - 240. Circle is given for host subgenera.



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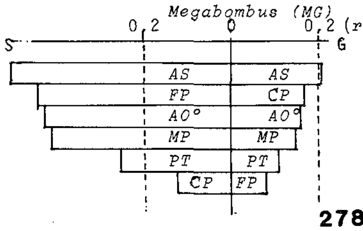

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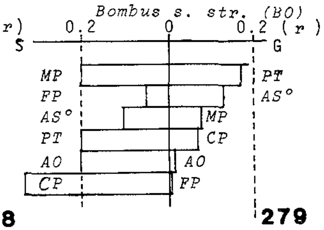

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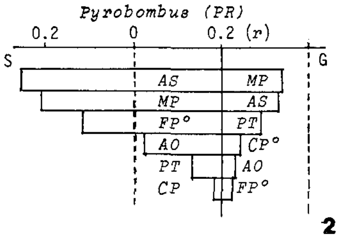

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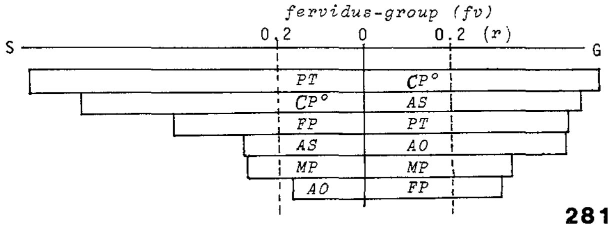

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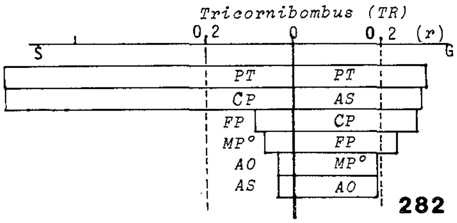

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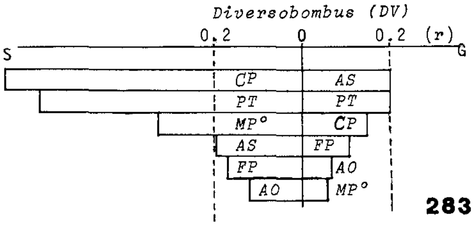

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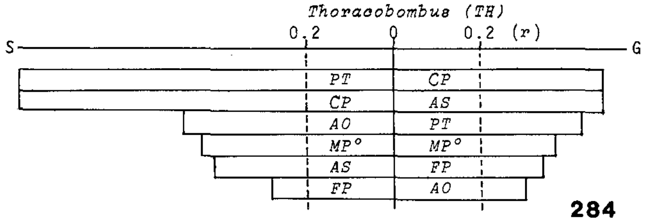
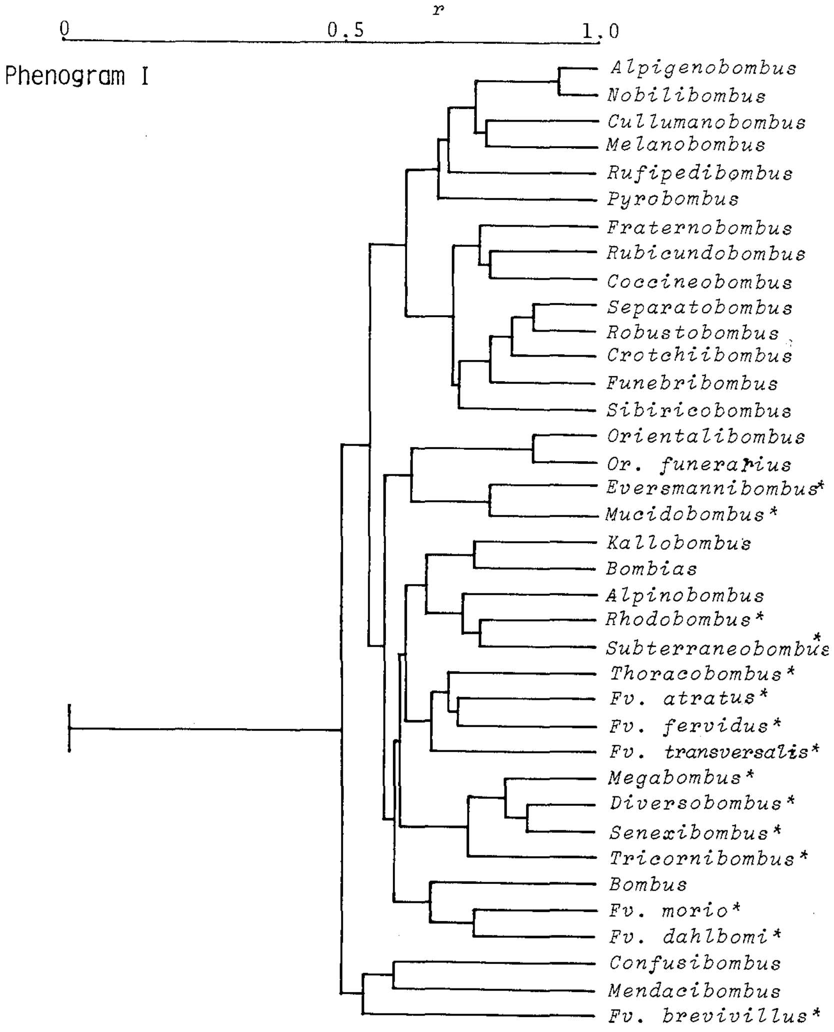


284

Figs. 277 - 284. The order of similarity and correlation values of each host subgenus to six Psithyrus subgenera. Circle is given for its own parasite. Cf. the legends of Figs. 233 - 240.



Figs. 285 - 288. Correlation phenograms on the basis of UPGMA.
A single asterisk specifies the subgenera of Odontobombus.
Fig. 285. Phenogram for combination I, cf. text 6. 2.

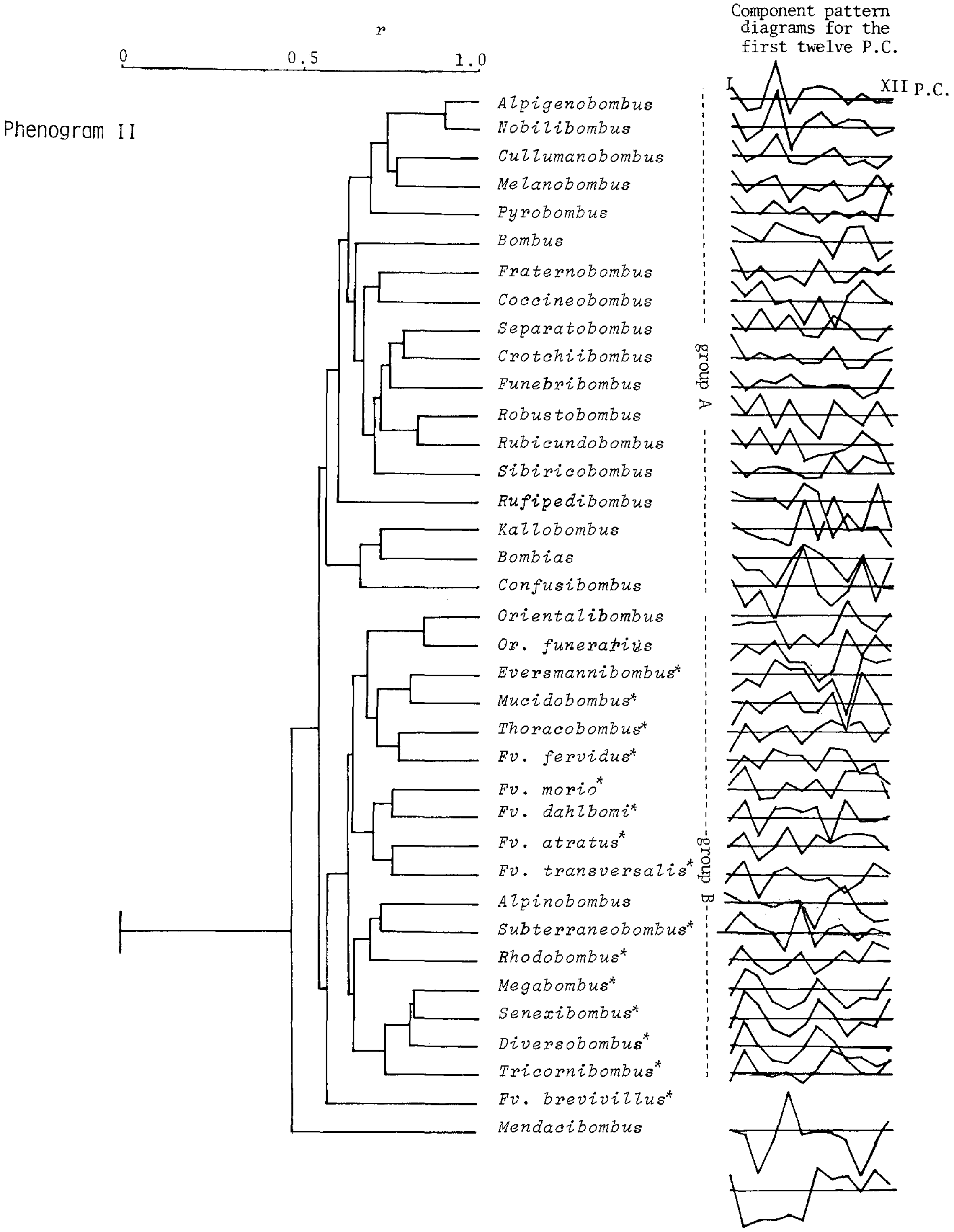


Fig. 286. Phenogram for combination II, together with component pattern diagrams for the first twelve principal components. Cf. text 6. 2.

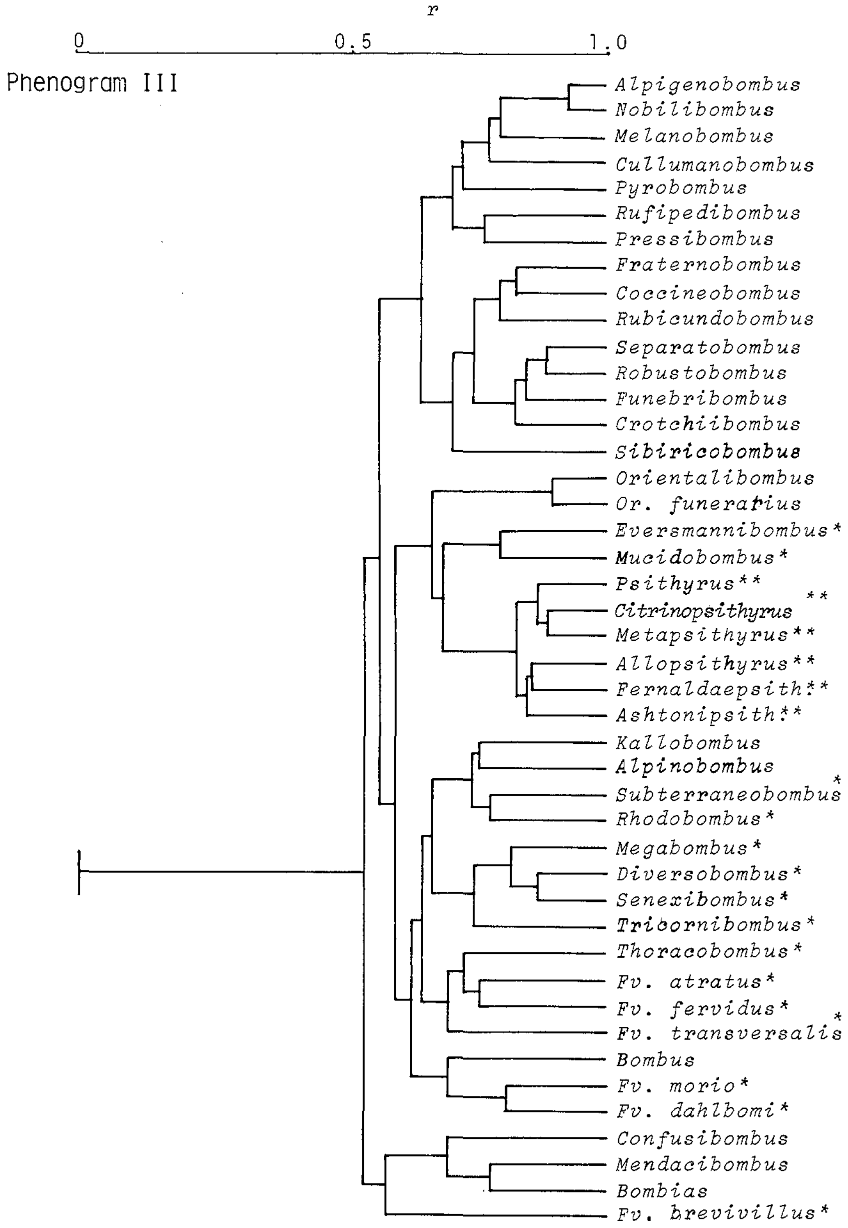


Fig. 287. Phenogram for combination III, cf. text 6. 2.
The subgenera of Psithyrus are specified with double asterisks.

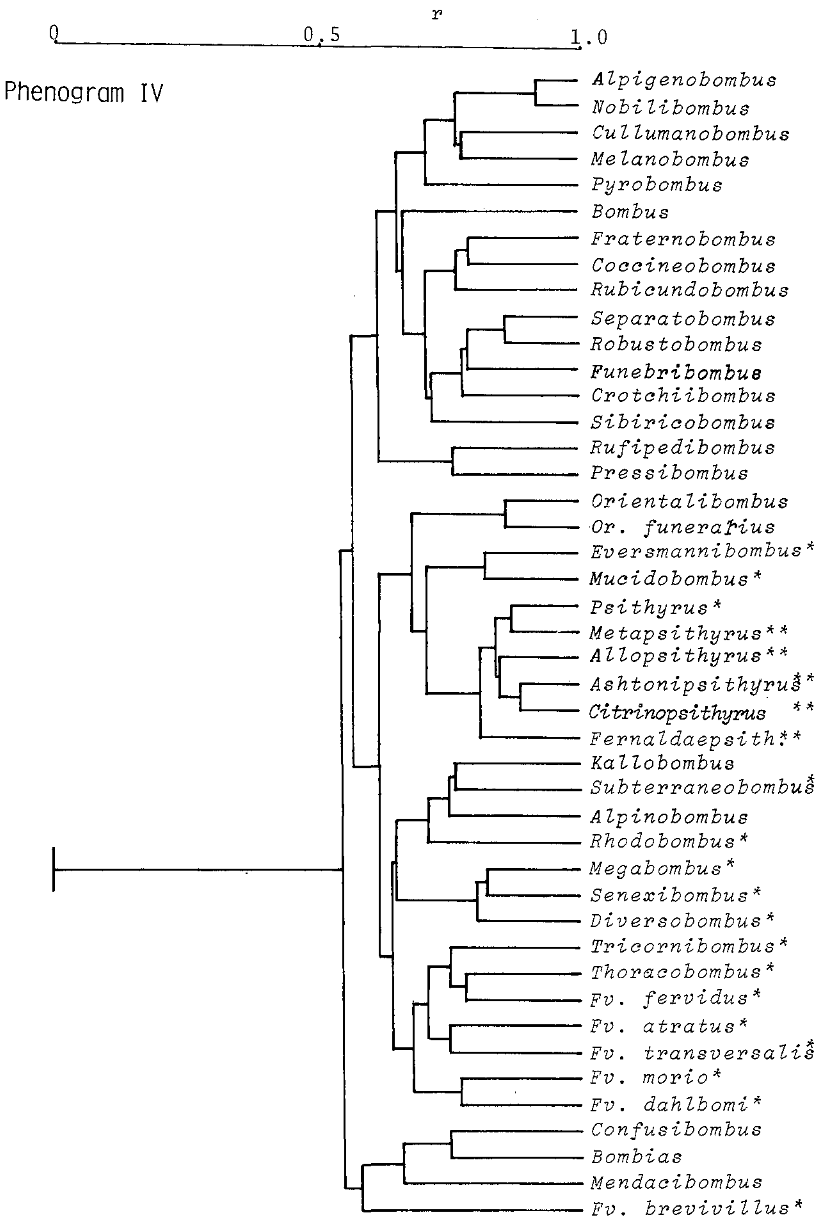


Fig. 288. Phenogram for combination IV, cf. text 6. 2. The subgenera of Psithyrus are specified with double asterisks.

Table 1. Synopsis of the lowest supraspecific taxa of bumblebees (cf. Figs. 3 - 11). Taxa adopted in the present study are given with abbreviations mentioned in chapter 2. A single asterisk: Eastern Hemisphere taxa. Double asterisks: Western Hemisphere taxa. Unmarked: Holarctic taxa.

Vogt(1911)	Franklin(1912, 1913)	Krueger(1917, 1920)	Skorikov(1914, 1922, 1933)	Frison(1927)	Milliron(1971-1973)	Richards (1968)	Tkalcu (1972)
		Mastrucatobombus	AG		Dentatus-group	AG*	AG
			NB			NB*	AG
						OR*	OR
Soroeensibombus		Sorroeensib.	Soroensib.			KL*	PR
Terrestrib.	Terrestris-g.	Terrestrib.	Terrestrib.	Terrestrib.	Terrestris-g.	BO	BO
	Fraternus-g.		FR	FR	Fraternus-g	FR**	
					Brachicephalus-g.		
		CF	CF		Confusus-g.	CF*	CF
		MD	MD			MD*	MD
	Auricomus-g.		Nevadensib.	Nevadensib.	Auricomus-g.	BI**	
	Fraternus-g.		AG	SP	Griseocollis-g.	SP**	
	Fraternus-g.		AG	SP	Dentatus-g.	CR**	
					Crotchii-g.		
SB			SB		Sibiricus-g.	SB*	SB
CL	Fraternus-g.	CL	CL	CL	Cullumanus-g.	CL	CL
Pratob.	Pratorum-g.	Pratob.	Pratob.	Pratob.	Pratorum-g.	PR	PR
					Jonellus-g.		
					Praticola-g.		
					Lapponicus-g.		
Lapidariob.		Lapidariob.	Lapidariob.		Lapidarius-g.	ML*	ML
			Koziovib.				
						PS*	PS
			RF			RF*	RF
	Kirbjellus-g.	AL	AL	AL	Alpinius-g.	AL	AL
	Fraternus-g.		RB	FR	Robustus-g.	RB**	
			Volucellob.				
	Fraternus-g.		RD	FR	Rubicundus-g.	RD**	
					Handlirschi-g.		
	Fraternus-g.		CC	FR	Coccineus-g.	CC**	
	Fraternus-g.		FN	FR	Funebris-g.	FN**	
Hortob.		Hortob.	Hortob.			MG*	MG
			DV			DV*	DV
						SX*	SX
			TR			TR*	TR
			EV			EV*	TH
Agrob.		Agrob.	LS			LS*	TH
			EX			EX*	TH
Agrob.		Agrob.	Agrob.			TH*	TH
			Adventorib.			Adventorib.*	TH
		Agrob.	MC			MC*	TH
ST	Borealis-g.	ST	ST	ST	Subterraneus-g.	ST	ST
		Pomob.	FV			RH*	RH
	Dumoucheli-g.		FV	FV	Dumoucheli-g.	FV**	FV
					Nigrodorsalis-g.		
					Mexicanus-g.		
						PR	FS

Table 2. Subgenera recognized and species studied in the present study.
Explanation of abbreviations in text, chapter 2.

Genus Bombus	Abbrev.	Approximate no of species	Species studied	Provenance of specimen
Alpigenobombus	AG	± 8	wurfleini mastrucatus Gerst.	Czechoslovakia
Nobilibombus	NB	± 3	sikkimi Friese*	Sikkim
Orientalibombus	OR	± 6	haemorrhoidalis pectoralis Friese	Nepal
	fr		funerarius Frison	Sikkim
Kallobombus	KL	1	soroeensis proteus Gerst.	Czechoslovakia
Bombus	BO	± 15	hypocrita sapporoensis CKll.	Hokkaido
Fraternobombus	FR	± 3	fraternus Smith*	Ohio
Confusibombus	CF	2	confusus Schenk	Czechoslovakia
Mendacibombus	MD	± 10	mendax Gerst.	Austria
Bombias	BI	1	nevadensis auricomus (Robertson)	Minesota
Separatobombus	SP	2	griseocollis (Degeer)*	Oregon
Crotchiibombus	CR	2	crotchii Cresson	California
Sibiricobombus	SB	± 15	callophenax Ckll.*	N. India
Cullumanobombus	CL	4	rufocinctus Cresson	Wyoming
Pyrobombus	PR	± 60	ardens sakagamii (Tkalců)	Hokkaido
Festivobombus	FS	1		
Melanobombus	ML	± 17	lapidarius (L.)	Czechoslovakia
Pressibombus	PS	2	pressus Frison*	Sikkim, Nepal
Rufipedibombus	RF	2	eximius eximius Smith	Nepal
Alpinobombus	AL	± 7	balteatus Dahlbom	Alberta
Robustobombus	RB	± 8	robustus Smith	Ecuador
Rubicundobombus	RD	± 2	rubicundus Smith	Bolivia
Coccineobombus	CC	3	coccineus Friese*	Peru
Funebribombus	FN	1	funebris Smith	Ecuador
Megabombus	MG	± 17	yezoensis Matsumura	Hokkaido
Diversobombus	DV	9	diversus tersatus Smith	Hokkaido
Senexibombus	SX	4	irisanensis Ckll.*	Luzon
Tricornibombus	TR	3	tricornis Radoszkowski*	N.E. China
Eversmannibombus	EV	1	persicus Radoxzkowski*	USSR
Laesobombus	LS	± 3		
Exilobombus	EX	1		
Thoracobombus	TH	± 18	schrencki albidopleuralis SK.	Hokkaido
Mucidobombus	MC	1	mucidus Gerstaecker*	France
Subterraneobombus	ST	± 14	subterraneus (L.)	Czechoslovakia
Rhodobombus	RH	± 5	pomorum (Panzer)	Czechoslovakia
Fervidobombus	FV	± 25		
	at		atratus Franklin	Brazil
	bv		brevivillus Franklin*	Brazil
	dl		dahlbomi Guérin	Patagonia
	fv		fervidus (F.)	California
	mr		morio (Swedrius)	Brazil
	tv		transversalis (Oliver)	Brazil
	T =	± 276		
Genus Psithyrus				
Psithyrus	PT	4	rupestris (F.)*	Czechoslovakia
Allopsithyrus	AO	2	maxillosus (Klug.)*	Czechoslovakia
Ashtonipsithyrus	AS	5	vestalis (Fourcr.)*	Czechoslovakia
Fernaldaepsithyrus	FP	9	norvegicus japonicus Yasumatsu	Honshu
Citrinopsithyrus	CP	7	insularis (F.)	Alberta
Metapsithyrus	MP	4	campestris (Panzer)*	Czechoslovakia
Eopsithyrus	EP	5		
		T = 36		

Table 3. Character states in terms of code values, held by the taxa examined.
Zero is given for the characters not examined.

Subgenera	A	N	O	f	K	B	F	C	M	B	S	C	S	C	P	M	P	R	A	R	R	C	F	M	D	S	T	E	T	M	S	R	m	a	f	d	t	b	P	A	A	F	C	M
	G	B	R	r	L	O	R	F	D	I	P	R	B	L	R	L	S	F	L	B	D	C	N	G	V	X	R	V	H	C	T	H	r	t	v	l	v	v	T	O	S	P	P	P
Character No.																																												
1	2	3	4	4	4	4	3	1	1	1	2	2	4	2	3	3	5	4	3	2	3	2	2	4	5	4	4	4	4	3	3	3	4	5	4	4	5	5	3	2	3	2	2	2
2	4	4	4	4	5	1	3	4	4	4	1	2	4	2	1	5	1	4	4	3	3	1	1	3	3	3	1	5	2	5	3	4	4	1	5	2	2	3	2	5	3	5	5	3
3	3	5	2	3	5	4	3	5	4	5	2	4	5	2	3	5	5	5	4	3	5	5	2	3	3	2	3	1	1	1	5	4	5	3	1	5	1	1	2	3	1	4	1	2
4	2	3	3	3	2	3	5	3	4	4	4	4	4	3	3	3	3	3	3	4	4	2	3	4	4	3	5	3	3	2	3	4	4	4	1	5	5	4	1	2	1	2	1	1
5	3	3	4	4	4	3	3	3	3	2	4	4	4	4	3	4	4	3	5	4	4	4	4	3	4	3	3	3	3	5	4	4	4	4	4	3	3	1	3	3	3	3	3	1
6	3	4	2	4	3	4	3	1	2	3	2	4	2	5	2	4	4	3	4	4	3	3	3	3	5	3	3	4	3	2	2	3	3	3	4	5	2	5	2	3	2	2	2	2
7	1	1	1	2	3	3	3	3	2	2	5	3	2	3	3	3	3	4	3	5	4	1	4	5	4	3	1	1	1	2	1	2	2	1	1	1	1	1	3	5	1	3	1	5
8	1	3	1	2	3	3	3	1	5	2	2	3	4	2	2	2	1	1	4	2	2	2	2	2	2	2	2	1	2	1	1	3	2	2	2	1	2	2	3	3	1	1	3	3
9	2	1	3	5	5	4	4	5	1	3	4	4	4	3	2	3	0	5	5	5	5	2	3	2	4	3	3	4	3	5	5	3	5	5	3	5	5	5	4	3	2	5	5	2
10	4	5	2	1	4	4	4	3	3	2	5	3	2	3	3	3	0	3	4	3	2	2	3	2	3	3	3	2	2	2	4	1	3	2	1	2	2	1	1	1	1	1	1	1
11	3	3	3	3	2	2	2	3	4	3	2	2	2	3	3	3	3	2	3	2	2	2	3	1	3	2	3	4	5	4	2	3	4	3	3	3	3	3	3	3	3	1	3	3
12	1	1	2	2	2	3	2	5	2	3	3	2	2	2	2	2	2	2	2	2	1	3	2	2	2	2	2	3	3	2	2	2	2	2	2	2	1	1	3	3	3	4	2	3
13	2	2	3	3	3	4	3	2	1	1	2	4	4	4	3	3	4	4	3	2	3	5	3	4	3	3	4	4	3	3	4	1	2	1	3	1	1	1	4	4	4	5	3	4
14	2	3	1	1	4	2	2	1	2	3	3	3	2	3	4	3	2	3	5	3	2	1	4	2	2	3	3	1	2	1	4	4	3	3	4	3	2	5	2	2	1	2	1	1
15	2	2	3	4	4	3	3	5	4	4	3	2	3	3	3	1	2	3	4	4	4	3	3	3	4	3	4	2	4	3	4	4	4	5	4	3	2	5	2	3	2	3	2	2
16	4	4	2	4	1	5	5	3	1	2	3	3	2	3	5	3	3	3	3	2	3	4	3	3	2	3	3	3	2	1	3	2	3	2	1	5	3	2	2	2	2	2	2	3
17	5	3	1	1	5	2	4	1	2	2	3	3	1	3	3	4	0	3	2	3	1	2	4	1	3	2	2	3	2	2	4	2	1	1	3	2	2	5	2	4	4	5	4	4
18	4	4	3	3	3	2	3	5	1	1	3	3	3	3	1	2	4	3	1	4	4	4	2	2	3	3	3	2	2	1	5	3	3	3	3	2	1	2	4	5	4	4	4	4
19	2	2	2	2	1	2	2	1	1	1	2	2	2	3	3	2	2	2	1	2	2	2	2	1	2	1	2	1	3	2	1	2	4	5	4	4	5	3	1	2	2	2	1	1

Table 3 (Continued)

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21	2	5	1	1	1	3	4	2	2	2	1	1	1	1	1	1	1	2	1	1	2	3	3	3	3	1	3	1	1	1	1	3	1	3	1	3	2	1	3	1	1	1	1	1
22	2	2	5	5	3	2	2	4	3	3	2	2	2	2	3	1	5	3	2	3	3	4	2	1	4	3	3	1	4	3	3	3	4	2	3	4	4	4	2	2	2	2	2	2
23	1	2	5	4	2	3	3	3	3	3	2	2	1	2	1	2	1	3	2	1	2	3	3	5	4	3	1	3	4	4	3	4	3	1	2	4	2	4	2	2	3	1	3	3
24	2	1	2	1	5	1	2	3	5	3	2	2	3	1	2	2	3	1	2	3	3	1	2	2	1	1	3	2	2	2	2	2	3	2	2	2	3	1	1	2	2	5	1	1
25	5	5	5	5	5	4	4	4	3	2	4	4	5	4	5	5	1	1	4	4	4	4	4	4	4	5	5	5	5	5	4	4	4	4	5	4	4	4	5	5	5	5	5	5
26	3	3	5	5	5	3	4	5	4	5	4	4	4	4	4	4	4	1	5	4	4	4	4	3	4	3	5	5	4	4	5	4	3	4	4	3	3	3	5	4	4	4	5	5
27	1	1	1	1	1	1	2	5	1	1	2	2	3	1	3	1	2	1	1	3	1	1	2	1	1	1	1	3	2	2	1	4	1	2	1	1	1	1	1	1	1	1	1	1
28	3	2	4	3	4	3	3	3	3	5	3	3	4	3	4	4	3	3	3	2	4	4	2	4	4	5	4	4	4	4	4	2	4	4	3	3	5	1	2	2	3	3	3	4
29	4	5	5	2	2	4	3	3	5	2	3	3	4	4	3	4	5	3	5	3	3	4	3	2	4	1	3	2	3	2	3	3	1	3	3	3	2	5	3	3	3	4	3	3
30	3	3	1	1	1	5	2	2	1	2	3	3	3	2	1	2	2	3	2	3	3	3	3	4	5	4	5	3	5	4	4	4	3	4	4	4	2	3	4	4	3	4	4	4
31	2	2	1	1	2	3	3	2	1	1	3	3	2	2	2	2	1	3	3	2	3	3	2	5	5	5	4	3	3	3	5	3	4	3	2	3	3	2	2	3	3	2	2	2
32	2	3	3	3	5	1	3	3	3	3	2	2	3	3	3	2	4	2	2	3	2	3	3	5	4	5	5	4	4	4	5	5	4	4	2	2	5	4	1	1	2	3	3	2
33	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	2	1	3	1	1	1	1	1	5	5	5	1	1	2	1	2	1	1	1	1	1	2	1	1	1	1	1	1
34	2	2	1	1	1	2	2	2	1	1	2	3	3	2	3	2	1	1	1	2	1	1	2	2	2	4	3	3	3	3	3	4	3	4	1	2	2	1	2	3	2	4	2	2
35	3	3	2	1	4	1	4	3	3	3	4	3	3	3	3	4	1	4	3	3	3	3	3	5	5	5	4	3	3	3	5	4	3	3	3	2	3	2	3	3	3	3	3	3
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37	5	4	3	5	2	3	2	1	2	1	2	3	4	4	3	3	0	2	2	2	2	2	4	3	3	2	5	5	4	3	4	4	3	4	4	5	3	3	1	2	4	1	1	2
38	3	2	1	2	2	2	4	2	2	2	5	4	3	4	3	2	0	2	2	3	3	2	3	3	2	2	1	2	1	1	2	2	1	1	1	1	2	1	2	1	2	2	1	2
39	2	2	4	3	5	1	2	5	5	5	2	3	3	3	1	2	2	2	3	2	1	2	2	3	3	2	3	5	5	5	3	3	3	3	3	3	2	2	4	4	5	5	5	4
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41	2	2	2	2	1	2	3	3	1	5	2	2	2	2	2	2	0	3	2	1	1	2	2	3	3	3	2	3	3	3	3	3	3	3	2	3	3	3	3	2	3	2	2	2
42	3	3	4	3	2	5	2	2	1	1	3	3	3	4	3	2	5	4	3	2	1	3	3	2	3	4	4	2	3	3	2	3	4	4	3	2	4	2	2	2	1	1	1	2
43	2	2	3	1	4	2	2	5	1	2	2	2	2	2	2	3	2	2	2	2	2	1	3	2	5	2	2	1	3	2	2	1	2	2	2	2	2	2	3	1	2	3	2	2

Table 3 (Continued)

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45	2	2	1	1	2	3	3	2	1	2	3	2	2	2	2	2	1	1	2	2	3	5	3	4	4	2	2	1	3	1	2	2	4	1	2	4	1	1	1	1	1	1	1	1
46	3	3	2	1	3	4	2	1	1	3	3	3	2	3	2	3	1	1	3	3	4	3	2	3	3	3	5	1	5	5	3	3	5	4	5	5	4	4	1	1	1	1	1	1
47	3	3	2	1	4	3	3	1	1	3	3	3	3	2	3	3	2	1	3	4	2	2	3	3	4	3	5	1	3	4	3	2	4	3	4	3	3	2	4	2	2	2	3	2
48	2	3	5	3	2	2	4	3	3	2	2	2	3	2	2	2	2	1	2	2	2	3	3	3	1	4	1	1	1	1	1	2	2	2	1	2	2	2	1	2	2	2	2	2
49	2	1	4	4	4	4	4	3	1	3	5	4	4	3	4	3	3	3	5	5	5	5	4	5	3	3	4	4	3	4	4	5	3	4	5	3	3	3	3	4	3	1	4	4
50	1	1	4	5	3	4	3	4	3	3	5	4	4	3	4	3	4	4	5	5	4	3	3	4	2	3	5	4	3	4	3	5	2	3	5	2	2	2	5	5	5	1	4	5
51	1	1	4	4	3	2	3	4	5	3	3	2	3	2	1	1	1	1	3	3	3	3	3	3	2	3	5	2	5	5	2	4	2	5	4	2	2	4	5	3	3	5	4	5
52	4	3	1	3	3	4	2	3	1	3	3	3	4	4	3	2	2	3	3	3	3	3	4	2	2	3	2	5	3	5	3	2	3	3	3	5	4	4	3	3	4	4	5	5
53	3	3	1	4	3	4	3	3	1	3	3	3	3	4	3	2	2	3	3	3	5	3	3	4	4	5	4	4	4	5	3	2	4	3	4	4	3	3	5	3	3	3	4	3
54	4	4	4	3	3	3	4	3	1	4	3	3	4	4	4	3	3	2	4	4	5	5	4	3	3	3	3	5	3	5	3	3	2	3	3	3	4	2	3	4	5	3	3	5
55	4	3	4	5	3	3	3	3	1	3	3	2	3	3	3	2	3	2	3	3	2	2	3	4	5	5	4	4	5	4	3	5	2	3	4	4	5	3	5	5	5	5	5	5
56	2	3	5	4	3	2	1	2	4	3	1	1	3	1	1	1	0	1	4	1	2	1	4	2	1	3	2	4	4	4	3	2	3	3	3	3	2	3	5	4	3	3	4	5
57	1	1	1	2	2	3	3	2	1	2	1	2	3	2	3	1	3	3	3	4	5	5	3	3	2	3	3	1	1	3	3	2	4	3	1	3	3	3	1	1	1	2	1	1
58	1	1	1	1	2	3	2	3	4	2	5	2	5	1	1	2	1	2	2	5	2	1	4	2	2	2	4	5	3	5	1	2	2	3	3	2	4	4	3	5	3	5	5	5
59	1	1	1	1	1	3	3	4	1	2	5	4	2	1	4	1	1	1	3	4	4	5	3	1	2	2	2	1	3	2	1	3	4	3	1	1	3	5	5	2	1	3	2	5
60	4	4	2	2	2	3	5	3	5	2	4	2	4	4	3	3	2	3	2	2	3	3	3	2	3	3	4	2	4	4	1	2	4	4	3	4	2	4	5	3	4	5	5	5
61	2	2	1	1	3	3	4	5	2	2	3	3	3	2	3	3	5	2	3	3	3	3	3	2	2	1	2	1	2	1	3	2	2	2	1	2	2	2	1	1	1	1	1	1
62	1	1	1	1	2	1	2	2	3	2	2	4	2	2	2	4	0	2	2	5	2	2	3	2	3	3	2	1	1	2	2	4	3	2	1	2	1	1	1	1	1	1	1	1
63	2	2	1	1	4	3	3	2	2	2	1	5	2	3	2	2	2	2	3	2	2	3	5	2	2	2	2	2	2	2	3	1	2	3	2	2	3	5	2	2	2	1	1	1
64	2	1	2	2	2	1	3	1	4	1	2	3	2	2	3	2	4	2	2	1	1	4	2	2	3	3	3	3	4	2	2	2	4	5	2	3	4	4	2	2	2	2	2	3
65	2	2	3	1	2	2	4	2	5	3	5	4	3	1	1	1	1	1	2	4	4	4	4	2	2	2	3	1	3	2	1	4	4	5	2	2	3	5	5	5	5	5	5	5
66	2	2	2	2	4	2	2	4	3	3	2	3	2	2	3	2	2	1	3	2	2	1	2	2	2	2	2	3	2	2	2	2	1	1	2	3	3	5	1	2	2	2	1	3
67	3	3	2	1	3	2	2	1	1	2	1	3	4	4	5	2	2	2	1	3	3	4	3	3	1	3	2	1	2	1	2	2	2	2	1	3	1	1	1	2	2	2	2	2

Table 3 (Continued)

68	1	1	1	2	2	1	1	3	3	1	2	4	2	2	4	2	2	1	1	3	1	1	3	3	2	2	4	2	1	1	2	1	1	1	1	1	3	5	1	1	1	1	1	2
69	5	5	1	1	4	5	4	5	3	5	4	4	3	4	4	3	4	3	4	4	4	4	4	3	2	2	2	3	2	2	2	3	3	4	3	1	3	2	4	2	1	1	4	3
70	3	3	5	3	1	1	3	5	5	2	2	3	1	3	3	5	4	5	1	3	3	2	3	3	3	2	3	3	2	3	2	1	2	2	1	1	2	1	3	3	3	3	4	4
71	3	4	3	3	4	5	5	2	1	2	5	5	5	4	5	5	4	4	5	5	3	5	5	5	5	5	5	2	4	2	5	5	5	5	5	4	4	2	4	3	5	5	4	2
72	1	1	4	4	3	4	2	1	2	1	3	3	4	1	2	2	2	4	4	1	1	3	4	4	4	4	4	4	3	3	5	3	4	2	3	4	3	3	2	4	4	3	4	3
73	4	4	5	5	1	2	2	1	2	2	5	3	2	4	3	3	3	2	2	3	1	3	3	5	5	5	4	1	2	1	4	2	3	2	3	2	2	1	2	1	2	2	2	1
74	4	3	3	2	3	4	4	5	4	3	3	4	4	3	3	3	3	1	5	3	3	3	3	2	2	3	2	5	2	2	5	3	3	2	2	2	3	4	1	1	1	1	1	1
75	3	2	3	3	5	2	1	1	1	5	5	5	4	3	3	3	0	3	3	4	3	5	4	4	5	3	4	1	5	1	5	4	5	3	3	2	3	1	3	2	5	4	3	2
76	1	1	5	4	1	1	2	1	4	2	1	2	1	3	1	4	3	4	1	2	2	4	2	5	4	4	4	2	2	3	2	4	4	3	3	3	5	1	2	3	3	3	2	3
77	4	4	2	3	5	5	4	3	3	1	4	4	4	4	4	3	3	3	2	4	3	4	4	3	3	3	4	3	2	3	3	3	5	4	3	3	3	4	1	3	2	2	2	2
78	2	3	2	1	2	4	2	5	3	3	3	2	2	3	2	2	2	3	3	3	2	1	3	1	1	1	3	2	1	2	2	2	3	3	3	3	2	5	2	2	2	2	2	2
79	5	4	2	1	3	3	5	2	2	2	4	4	5	4	5	4	4	4	3	4	4	4	3	1	3	2	2	2	2	2	3	1	1	1	1	1	3	2	2	3	3	3	2	2
80	2	2	2	2	4	4	3	4	1	2	2	3	3	2	3	2	5	5	2	3	2	4	3	3	3	4	3	3	2	2	5	5	5	3	2	3	3	1	2	2	2	2	2	2
81	2	2	2	4	4	5	4	3	2	2	1	1	1	1	2	1	2	3	4	1	1	4	1	2	4	4	3	1	2	2	4	4	5	2	3	4	3	1	3	2	2	2	2	2
82	1	1	1	2	1	2	3	1	3	2	1	2	3	2	1	2	2	1	1	2	1	3	3	5	3	5	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
83	3	4	5	4	4	1	1	1	2	2	1	1	2	1	3	1	4	3	4	1	1	1	2	3	4	5	4	5	2	4	5	4	1	3	3	4	4	2	3	4	2	3	3	3
84	3	3	4	4	5	1	1	1	1	2	2	1	1	1	3	1	3	2	4	1	1	1	2	4	4	5	5	4	4	3	5	5	1	3	5	3	4	1	5	5	3	5	5	5
85	4	3	3	2	3	5	2	3	2	2	2	2	2	3	2	3	0	3	4	2	1	2	3	2	2	1	3	1	1	1	5	4	3	2	2	3	3	1	3	3	2	4	2	3
86	1	1	3	3	3	5	1	1	1	1	2	1	2	2	2	2	3	2	3	2	3	1	2	3	3	4	5	4	4	4	5	3	4	3	2	4	3	1	3	3	4	4	3	3
87	1	1	1	1	2	1	4	1	5	2	1	2	2	2	1	2	0	2	2	2	2	4	1	1	2	2	1	2	1	2	1	2	2	1	1	1	1	1	1	1	2	2	2	1
88	2	2	2	2	3	3	3	3	5	4	3	3	3	2	2	2	4	2	2	2	3	3	2	1	2	1	1	2	2	1	2	2	1	3	2	1	3	2	3	2	2	1	2	2
89	4	4	3	2	3	2	4	3	3	2	5	3	5	5	3	3	2	4	4	5	4	5	5	1	1	2	2	1	2	1	4	2	2	2	3	3	1	1	3	4	3	4	4	3
90	4	5	2	2	5	5	4	5	4	5	4	5	5	4	5	5	5	5	4	4	4	5	5	4	5	4	3	4	1	4	4	5	5	4	4	4	4	4	4	2	4	4	3	5
91	2	2	2	3	1	3	2	4	3	2	2	2	2	3	5	2	0	1	4	1	2	4	5	2	1	2	3	2	3	1	4	2	2	3	1	5	1	2	4	2	2	5	2	3

Table 3 (Continued)

92	4	4	2	3	4	3	2	4	2	3	2	3	2	3	3	4	0	4	1	2	1	2	3	2	2	2	2	4	3	3	3	4	2	2	3	2	5	3	1	3	2	4	2	1
93	3	4	2	4	3	3	2	2	5	2	2	3	3	2	2	3	0	2	4	4	4	4	3	3	3	2	4	3	3	4	1	3	4	3	1	3	4	4	1	3	3	4	1	2
94	1	1	3	4	2	2	2	5	1	2	2	2	1	2	1	3	0	2	2	3	3	2	2	4	4	5	5	2	2	2	1	2	3	3	2	2	2	2	5	4	3	5	4	5
95	4	5	5	5	5	3	1	5	1	4	1	2	4	3	4	4	4	3	3	1	1	3	2	4	4	4	4	4	4	5	4	5	4	4	4	4	4	4	3	4	3	4	4	4
96	3	3	1	1	2	3	2	2	2	3	2	3	3	2	3	1	0	5	2	1	2	2	3	2	3	3	2	3	1	1	3	1	3	4	3	5	3	3	3	1	2	2	3	2
97	4	5	4	4	2	5	1	1	1	2	5	3	4	4	3	4	0	2	3	5	4	4	3	3	4	2	4	2	4	4	3	2	3	4	2	2	3	1	2	3	3	1	5	3
98	4	4	2	2	2	2	2	2	5	1	1	2	2	2	2	2	0	2	1	2	1	1	1	2	1	1	2	2	2	2	2	2	1	2	2	2	1	1	4	2	2	3	2	1
99	3	4	3	4	4	3	2	4	5	2	3	3	3	2	4	2	0	2	2	2	2	2	3	3	2	3	3	3	3	2	2	3	4	2	4	4	2	1	5	2	3	4	3	2
100	3	5	3	4	4	2	4	2	5	2	2	3	2	4	2	3	0	1	3	2	3	2	1	1	1	2	2	1	2	2	3	1	2	1	1	1	1	1	1	3	2	2	2	2
101	2	2	3	2	3	3	1	2	1	4	2	1	1	1	2	1	0	2	2	5	3	2	1	4	4	4	3	2	4	3	5	3	2	3	4	2	3	2	3	2	4	4	2	2
102	5	5	2	2	5	3	2	3	4	3	3	3	4	4	3	2	0	2	2	1	1	1	3	2	2	2	2	2	4	3	1	1	3	2	3	2	2	3	3	2	2	2	3	3
103	4	4	2	4	2	4	3	3	1	1	3	3	3	4	3	3	5	3	3	3	3	4	4	3	3	3	4	4	4	4	3	4	5	3	4	3	4	3	2	4	5	4	4	5
104	3	3	1	1	1	3	2	1	3	1	1	2	2	1	1	2	1	1	1	1	2	2	1	1	1	1	2	5	1	5	1	1	2	3	1	2	1	1	2	1	1	1	2	2
105	3	3	1	3	2	4	4	4	3	3	4	4	4	4	4	3	2	3	4	3	3	3	3	2	3	4	4	5	4	5	2	5	4	4	5	4	5	4	5	4	4	4	4	5
106	2	3	2	2	2	2	5	3	1	4	2	3	4	2	2	2	1	2	2	3	2	2	2	3	3	2	3	1	2	2	3	2	2	2	3	2	3	4	3	3	3	3	3	3
107	2	3	3	3	5	3	5	1	2	5	4	3	1	4	2	4	3	2	3	4	4	4	4	1	1	2	1	3	2	3	3	1	2	1	2	1	1	1	2	1	2	2	1	1
108	1	1	2	1	1	1	5	2	2	4	2	5	4	3	2	3	2	2	2	2	3	2	2	2	1	1	1	2	2	3	2	2	3	2	1	2	3	2	1	2	2	1	2	1
109	1	1	5	5	1	5	1	1	1	1	1	2	1	2	1	3	4	4	1	1	5	4	1	1	2	4	2	4	2	2	3	3	5	3	3	4	2	2	1	1	2	4	1	3
110	2	3	1	1	3	1	5	1	2	1	2	2	4	1	3	2	2	1	2	2	4	3	2	2	2	2	2	3	1	2	3	4	3	3	3	2	1	3	2	1	3	4	2	3
111	1	1	2	2	1	1	4	1	1	1	2	2	1	2	2	1	1	2	1	1	1	3	1	2	2	2	4	1	2	4	2	3	3	2	5	3	2	2	3	2	3	3	2	2
112	2	3	1	1	2	1	2	2	5	3	2	2	3	1	1	2	2	1	2	3	2	1	3	1	2	1	1	1	1	1	1	1	4	1	1	1	1	2	1	1	2	1	2	2
113	2	4	5	5	2	2	2	2	5	4	2	2	4	1	2	1	3	1	2	1	3	2	2	2	4	3	2	1	4	5	4	3	4	3	3	4	3	3	4	4	3	4	4	5
114	2	3	4	4	2	1	3	1	1	1	2	1	3	2	1	1	2	1	2	1	3	3	1	1	2	3	2	5	4	4	3	4	5	4	4	4	3	4	4	3	5	4	4	4
115	4	3	3	3	5	2	3	1	4	4	2	3	3	2	5	3	2	2	3	3	2	3	3	4	4	2	2	2	2	1	3	4	2	3	3	3	2	2	3	3	5	5	3	4

Table 3 (Continued)

116	5	5	5	5	5	1	1	1	1	1	1	3	1	3	1	1	5	1	1	1	3	3	1	1	5	5	5	5	5	5	1	1	1	5	5	5	1	3	5	1	2	1	5	1
117	5	5	1	1	1	5	1	3	1	3	1	1	3	1	5	1	1	1	1	5	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	3
118	3	4	4	3	3	1	3	1	3	2	4	3	3	3	2	1	4	2	1	3	3	3	3	3	2	3	2	3	5	4	5	2	3	3	2	4	3	4	4	4	5	4	3	5
119	3	3	3	3	3	3	5	2	1	2	5	4	3	3	1	1	4	3	2	5	5	5	4	3	3	4	4	5	3	3	4	2	4	3	3	4	4	5	2	1	2	1	2	2
120	1	1	1	1	2	1	1	3	5	5	1	2	1	1	1	3	1	2	1	5	2	1	2	1	1	2	1	2	1	1	1	1	2	1	1	1	1	1	1	0	2	1	1	1
121	5	4	1	2	3	3	1	2	2	1	4	4	3	4	1	2	1	3	2	3	2	3	2	2	2	4	4	4	5	3	2	3	3	4	3	2	3	4	3	3	3	5	3	5

Table 4. Variance explained by each principal component and cumulative proportion of total variance in the PCA for the data of genitalial characters.

Principal component	Variance explained	Cumulative proportion of total variance
1	13.7	0.13
2	10.6	0.23
3	7.8	0.31
4	6.8	0.37
5	5.4	0.43
6	5.4	0.48
7	4.8	0.52
8	4.4	0.57
9	4.1	0.60
10	3.5	0.64
11	3.5	0.67
12	3.2	0.70
13	2.8	0.73
14	2.6	0.75
15	2.3	0.78

Appendix. Correlation matrix for combination II, cf. text 6. 2.

1 AG, 2 NB, 3 OR, 4 fr, 5 KL, 6 BO, 7 FR, 8 CF, 9 MD, 10 BI, 11 SP, 12 CR, 13 SB, 14 CL, 15 PR, 16 ML, 17 RF, 18 AL, 19 RB, 20 RD, 21 CC, 22 FN, 23 MG, 24 DV, 25 SX, 26 TR, 27 EV, 28 TH, 29 MC, 30 ST, 31 RH, 32 mr, 33 at, 34 fv, 35 dl, 36 tv, 37 bv.

	1	2	3	4	5	6	7	8	9	10
1	1.0000									
2	0.8204	1.0000								
3	0.1509	0.1861	1.0000							
4	0.1590	0.1713	0.7071	1.0000						
5	0.3123	0.2745	0.2125	0.2182	1.0000					
6	0.3129	0.3360	-0.0430	0.1497	0.1198	1.0000				
7	0.2556	0.2463	-0.0801	-0.0209	0.1113	-0.2815	1.0000			
8	0.0519	0.0617	0.1241	0.1146	0.2593	0.1101	0.2133	1.0000		
9	0.0007	0.1344	0.1600	0.0236	0.1086	-0.2598	0.1528	0.1603	1.0000	
10	0.1270	0.1284	0.1698	0.0829	0.4539	0.0444	0.1205	0.4275	0.2087	1.0000
11	0.2241	0.0873	0.0324	0.0465	0.1069	0.3235	0.3861	0.1366	-0.0668	0.1234
12	0.2772	0.1767	-0.1042	0.0085	0.2588	0.3014	0.4164	0.1109	0.0128	0.1591
13	0.3288	0.2849	0.1303	0.1600	0.3477	0.3266	0.2911	0.1340	0.1088	0.2037
14	0.5938	0.4609	0.1150	0.2133	0.1921	0.3229	0.3267	0.0557	-0.0346	0.1148
15	0.4165	0.3307	0.0679	0.1675	0.2376	0.2887	0.2591	0.1326	-0.1709	0.0819
16	0.4786	0.4473	0.2399	0.2161	0.3086	0.2314	0.3459	0.1666	0.1008	0.2075
17	0.1887	0.1854	0.1432	0.1942	0.1958	0.2889	0.2030	0.1423	-0.1271	0.1138
18	0.1564	0.2170	0.2876	0.3485	0.4312	0.3995	0.2283	0.1186	0.0318	0.2768
19	0.0863	0.0100	-0.0083	0.0468	0.1751	0.1979	0.2993	0.2046	-0.0826	0.1757
20	0.1222	0.1276	0.0586	0.1400	0.1863	0.3278	0.4434	0.2733	-0.0304	0.3089
21	0.1601	0.1411	0.1021	0.1245	0.0469	0.3590	0.4507	0.1066	-0.0892	0.1738
22	0.2369	0.1736	0.0215	0.0501	0.1361	0.3137	0.2820	0.1126	-0.0718	0.0840
23	-0.0808	-0.0595	0.2713	0.3195	0.1464	0.1185	0.0372	-0.0727	-0.2095	0.1683
24	0.0625	0.0216	0.2354	0.2273	0.2289	0.1495	0.0193	-0.0652	-0.2837	0.1832
25	-0.0653	-0.1051	0.2355	0.2771	0.1592	0.0136	-0.0413	-0.1289	-0.3272	0.0433
26	0.0447	0.0197	0.2767	0.3348	0.1568	0.2184	-0.1105	-0.0898	-0.1748	-0.0094
27	0.2626	0.1743	0.2938	0.4320	0.2119	0.1389	-0.0028	0.1325	0.0210	0.1315
28	0.1169	0.0265	0.3880	0.3928	0.1932	0.1036	-0.1654	-0.0293	-0.0806	0.1882
29	0.1386	0.0662	0.3317	0.3548	0.2652	0.1592	-0.0775	0.1264	-0.0040	0.2352
30	0.2639	0.1696	0.3067	0.3091	0.4586	0.2478	0.0179	0.0347	-0.2727	0.1695
31	0.0204	0.0727	0.3108	0.3738	0.2753	0.1209	0.0210	0.1238	-0.0969	0.2292
32	0.0503	0.0581	0.1059	0.2361	0.2449	0.3463	0.0925	0.0819	-0.1151	0.1612
33	0.0978	0.1110	0.1986	0.2040	0.1207	0.2917	0.0672	0.0449	-0.0497	0.1854
34	0.3049	0.2033	0.3891	0.4461	0.4131	0.2524	-0.0447	-0.0115	-0.1227	0.2152
35	0.1666	0.1981	0.1664	0.3589	0.0870	0.3517	-0.0062	-0.0511	-0.1933	0.1005
36	0.1662	0.0699	0.2701	0.3219	0.2347	0.1944	0.0320	-0.0653	-0.1646	0.1659
37	0.0482	0.0509	0.0239	0.0864	0.1471	0.1210	0.1020	0.1378	0.0883	0.1486

	11	12	13	14	15	16	17	18	19	20
11	1.0000									
12	0.5845	1.0000								
13	0.4363	0.5051	1.0000							
14	0.3448	0.4747	0.3959	1.0000						
15	0.3643	0.4584	0.3725	0.4653	1.0000					
16	0.2799	0.5133	0.3607	0.5380	0.3677	1.0000				
17	0.1591	0.2261	0.1832	0.2390	0.2147	0.3998	1.0000			
18	0.3378	0.7888	0.3656	0.2682	0.3142	0.2977	0.2134	1.0000		
19	0.6554	0.5265	0.3816	0.2842	0.2525	0.3629	0.1807	0.2903	1.0000	
20	0.4424	0.4048	0.3812	0.2918	0.2390	0.3156	0.2306	0.3673	0.6623	1.0000
21	0.2728	0.3995	0.3149	0.3211	0.3175	0.2534	0.2250	0.2157	0.3052	0.5467
22	0.5087	0.5065	0.3682	0.4037	0.4343	0.2711	0.1872	0.3287	0.4029	0.2924
23	0.1579	0.1086	0.1382	0.0636	0.0779	0.2036	0.1970	0.0922	0.1350	0.1633
24	0.1314	0.0541	0.0481	0.1536	-0.0115	0.2501	0.2698	0.1716	0.0965	0.1144
25	0.0226	-0.0737	0.0656	0.0424	0.0587	0.0008	0.1155	0.1248	-0.0208	-0.0037
26	0.1984	0.0563	0.1764	0.1551	0.1300	0.1115	0.0195	0.2405	0.1604	0.1374
27	-0.0139	0.0631	0.2640	0.1021	0.1387	0.2093	0.1640	0.2352	-0.0401	0.0253
28	0.1830	-0.0217	0.2053	0.1042	0.0569	-0.0039	-0.1319	0.1561	0.0156	0.0601
29	0.0229	-0.0784	0.2350	0.0980	-0.0636	0.1562	0.0453	0.2082	0.1114	0.2298
30	0.1688	0.1845	0.2417	0.1491	0.2668	0.2178	0.3582	0.4676	0.1196	0.1119
31	0.1452	0.1043	0.1993	-0.0461	0.1369	0.1494	0.2082	0.3445	0.2222	0.0763
32	0.2141	0.2378	0.2520	0.0714	0.1129	0.2026	0.2965	0.2189	0.1936	0.3034
33	0.2107	0.1521	0.3023	0.1386	0.1584	0.0525	0.1159	0.2057	0.1873	0.2781
34	0.2455	0.1208	0.2918	0.2526	0.1663	0.2260	0.2096	0.4035	0.1933	0.1118
35	-0.0117	-0.0063	0.1657	0.0674	0.1846	0.0637	0.2414	0.2692	-0.0865	0.1241
36	0.1275	0.1158	0.1843	0.0737	0.2522	0.1335	0.1993	0.1633	0.0855	0.0955
37	0.0980	0.1921	0.1049	0.0692	0.0837	-0.0039	0.0083	0.2117	0.1366	0.1312

	21	22	23	24	25	26	27	28	29	30
21	1.0000									
22	0.3591	1.0000								
23	0.2064	0.1526	1.0000							
24	0.1730	0.0064	0.5922	1.0000						
25	0.0807	-0.0317	0.6496	0.6321	1.0000					
26	0.0952	0.0876	0.4424	0.5106	0.5101	1.0000				
27	-0.1005	0.1049	0.1610	0.0667	0.1518	0.1861	1.0000			
28	0.0742	0.0818	0.2827	0.3607	0.2927	0.4935	0.3190	1.0000		
29	-0.0101	0.0127	0.2096	0.2678	0.2666	0.3946	0.6187	0.5385	1.0000	
30	0.1773	0.1515	0.3415	0.3662	0.3975	0.3928	0.2633	0.2638	0.1251	1.0000
31	0.1522	0.1020	0.3822	0.3189	0.3304	0.3973	0.2614	0.3353	0.2714	0.4525
32	0.3545	0.1265	0.2607	0.3215	0.3101	0.3597	0.0198	0.3411	0.2633	0.3156
33	0.2122	0.2076	0.1517	0.2389	0.1839	0.5063	0.2185	0.4652	0.3950	0.2013
34	0.0419	0.1767	0.2848	0.3286	0.2862	0.4526	0.3906	0.5526	0.4780	0.3810
35	0.1211	0.1594	0.1962	0.2487	0.2109	0.3366	0.2332	0.3421	0.2143	0.3767
36	0.0617	0.1021	0.2237	0.3227	0.2877	0.4030	0.3612	0.3866	0.3986	0.2608
37	-0.0294	0.2679	-0.1048	0.0749	-0.0460	0.1405	0.2114	0.2414	0.2459	-0.0257

	31	32	33	34	35	36	37
31	1.0000						
32	0.3861	1.0000					
33	0.4104	0.4815	1.0000				
34	0.4908	0.3260	0.4513	1.0000			
35	0.3195	0.5147	0.4034	0.3938	1.0000		
36	0.3713	0.4001	0.5214	0.3944	0.3745	1.0000	
37	0.1212	0.1696	0.3505	0.2903	0.2739	0.3756	1.0000