

Male genitalia in Miridae (Heteroptera) and their significance for suprageneric classification of the family. Part I: general review, Isometopinae and Psallopinae

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Abstract

The paper starts a series of works on the structure of the ectodermal part of the male genital apparatus in Miridae and is based on the investigation of nearly two hundred species of Miridae, belonging to 31 tribes from all subfamilies. A general review of the structure and functioning of the main genitalia elements in various groups of Miridae is given. A list of terms used by previous researchers for different homologous structures is presented and an attempt to stabilize this terminology is made. Detailed description of genitalia structure in subfamilies Isometopinae and Psallopinae is given. Characters, valuable for the recognition of monophyletic taxonomical groupings are discussed.

Keywords: Miridae, Isometopinae, Psallopinae, genitalia, morphology, systematics.

Introduction

The structure of external genitalia is widely used in the taxonomy of Miridae. A number of high ranked groups, e. g. subfamily Phylinae or tribe Halticini, can be clearly defined only on the base of genitalia structure (SCHUH, 1974, 1984, 1995). Phylogenetic relationships of Dicyphini and Pilophorini were revealed only after this set of data was taken into consideration (WAGNER, 1955; SCHUH, 1974, 1976, 1995). Nevertheless, the structure of genitalia is still used mainly for differentiation of closely related species. Morphological works on genitalia of Miridae are scarce and usually based on taxa common in the Northern Hemisphere. Besides, there is no universal nomenclature for different parts of external genitalia, because different authors use various terms for the same structures and the same terms for different structures. This paper is an

attempt to trace the homologies for all genitalia elements, estimate their variability and their potential value for reconstruction of natural taxonomic groups in the largest heteropteran family.

The terms already adopted in the current literature are predominantly used in order to make nomenclature of genitalia workable. In complicated cases, preference is given to the earliest term for the corresponding structure. As the homologies between the main parts of genitalia are generally clear for all Heteroptera, the terms not previously used within Miridae, but already adopted in other groups are involved for designation of several structures. An attempt was made to analyze the main publications on the genitalia structure not only within Miridae, but also within the whole order. The list of terms used in this paper with the names applied by other authors for corresponding structures is given in Table 1.

The methods used to study male genitalia have been described by Kerzhner & Konstantinov (1999). All scale bars in figures are equal to 0.05 mm.

Table 1. Synonymy of terms used for homologous structures of male genitalia in Miridae

Term accepted in this paper	Terms used by other authors	References ¹
Aedeagus	Aedeagus	SINGH-PRUTHI, 1925; BAKER, 1931; LESTON, 1953, 1954a, 1954b, 1955, etc.; KUMAR, 1962; McDONALD, 1966; SCHAEFER & WILCOX, 1966; SCHAEFER, 1969, 1977 etc.; KERZHNER & KONSTANTINOV, 1999
	Phallus	SNODGRASS, 1935, 1936, 1957; BONHAG & WICK, 1953; DUPUIS, 1955, 1963; 1970; DUPUIS & CARVALHO, 1956; ASHLOCK, 1957; KAHLOW, 1962; KELTON, 1959; KUMAR, 1962; SCHMITZ, 1968; LEE, 1969; COBBEN, 1978; DECKERT, 1990
	Penis	KULLENBERG, 1947; WAGNER, 1955, 1970; WAGNER & WEBER, 1964; CHÉROT, 1997; MATSUDA, 1976
Phallobase	Phallobase	SNODGRASS, 1935, 1936, 1957; KELTON, 1959; SCHMITZ, 1968; MATSUDA, 1976; COBBEN, 1978; DECKERT, 1990 (Phallobasis); KERZHNER & KONSTANTINOV, 1999
	Basal plates	SINGH-PRUTHI, 1925; BAKER, 1931; KUMAR, 1962; McDONALD, 1966 (basal plate); LESTON, 1954a, 1955 (basal plate); DUPUIS & CARVALHO, 1956; SCHAEFER, 1966 (basal plates apparatus); LEE, 1969
	Stapes	BONHAG & WICK, 1953; ASHLOCK, 1957; DUPUIS, 1970; MATSUDA, 1976
	Basis	KULLENBERG, 1947; WAGNER, 1955, 1970; WAGNER & WEBER, 1964 (base); CHÉROT, 1997 (base)
Basal plates bridge	Basal plates bridge	SINGH-PRUTHI, 1925; DUPUIS & CARVALHO, 1956; KAHLOW, 1962; KUMAR, 1962
	Ponticulus basilaris	DUPUIS, 1955; ASHLOCK, 1957; COBBEN, 1978
	Ponticulus transversalis	DUPUIS, 1970

¹ Repeated citation of the same work opposite the same accepted term means that several terms were used for the corresponding structure in one paper.

Basal foramen	Basal foramen	SINGH-PRUTHI, 1925; KULLENBERG, 1947; LESTON, 1954a; DUPUIS, 1955 (foramen basilare), 1970; DUPUIS & CARVALHO, 1956; LEE, 1969; COBBEN, 1978; SCHAEFER, 1977
Septum	Septum	KULLENBERG, 1947; BONHAG & WICK, 1953; DUPUIS, 1970; COBBEN, 1978
Dorsal connectives	Dorsal connectives	BAKER, 1931; LESTON, 1953, 1954a; DUPUIS, 1955 (connectifis dorsaux), 1970; DUPUIS & CARVALHO, 1956; KAHLOW, 1962; KUMAR, 1962
	Promotor apodeme	BONHAG & WICK, 1953; MATSUDA, 1976
	Capitate processes	ASHLOCK, 1957 (processus capitati); COBBEN, 1978
Capitate processes	Capitate processes	DUPUIS, 1955 (processus capitati), 1970; KAHLOW, 1962 (Processus capitatus); KUMAR, 1962; KERZHNER & KONSTANTINOV, 1999
	Muschelförmige Platte	KULLENBERG, 1947
	Ansatzplatten	WAGNER, 1955, 1970
	Capitate disk of apodeme	LEE, 1969
	Plaques arrondies	WAGNER & WEBER, 1964; CHÉROT, 1997
Ventral connectives	Ventral connectives	LESTON, 1953, 1954a; DUPUIS, 1955 (connectifis ventraux), 1970
Theca	Theca	SHARP, 1890; BAKER, 1931; SNODGRASS, 1935; KULLENBERG, 1947; LESTON, 1953, 1954a, 1954b, 1955 etc.; WAGNER, 1955; WAGNER & WEBER, 1964 (thèque); McDONALD, 1961, 1966; SCHMITZ, 1968 (thèque); LEE, 1969; WAGNER, 1970 (Theka); DECKERT, 1990; CHÉROT, 1997 (thèque); KERZHNER & KONSTANTINOV, 1999
	Phallosoma	SINGH-PRUTHI, 1925; DUPUIS, 1955, 1963; 1970; DUPUIS & CARVALHO, 1956; SCHAEFER, 1966
	Phallotheca	SNODGRASS, 1936; DUPUIS, 1955, 1963; 1970; DUPUIS & CARVALHO, 1956; ASHLOCK, 1957; KELTON, 1959; KAHLOW, 1962; KUMAR, 1962; LEE, 1969; MATSUDA, 1976; COBBEN, 1978; DECKERT, 1990
	Phallobase	BONHAG & WICK, 1953
	Aedeagus	MATSUDA, 1976
	Endosoma	SINGH-PRUTHI, 1925; DUPUIS, 1955, 1963; 1970; DUPUIS & CARVALHO, 1956; KUMAR, 1962; LEE, 1969; COBBEN, 1978; DECKERT, 1990; KERZHNER & KONSTANTINOV, 1999
Endosoma	Aedeagus	SHARP, 1890 (oedeagus); KULLENBERG, 1947; BONHAG & WICK, 1953;
	Endophallus	SNODGRASS, 1935, 1936; SCHMITZ, 1968; MATSUDA, 1976
	Vestea	KELTON, 1959; SCHMITZ, 1968
Conjunctiva	Conjunctiva	SINGH-PRUTHI, 1925; KULLENBERG, 1947; BONHAG & WICK, 1953 (disti- + basicconjunctiva); LESTON, 1953, 1954a, 1954b, 1955 etc.; WAGNER, 1955, 1970; WAGNER & WEBER, 1964 (connexiva); DUPUIS, 1955, 1963; 1970; DUPUIS & CARVALHO, 1956; ASHLOCK, 1957; McDONALD, 1961, 1966; SCHAEFER, 1966; MATSUDA, 1976; COBBEN, 1978 (conjunctivum); DECKERT, 1990; KERZHNER & KONSTANTINOV, 1999

Vesica	Vesica	SINGH-PRUTHI, 1925; KULLENBERG, 1947; BONHAG & WICK, 1953; LESTON, 1953, 1954a, 1954b, 1955 etc.; WAGNER, 1955; WAGNER & WEBER, 1964; DUPUIS, 1955, 1963; 1970; DUPUIS & CARVALHO, 1956; ASHLOCK, 1957; McDONALD, 1961, 1966; KUMAR, 1962; WAGNER, 1970 (Vesika); MATSUDA, 1976; COBBEN, 1978; SCHWARTZ, 1987; STONEDAHL, 1988; DECKERT, 1990; KERZHNER & KONSTANTINOV, 1999
Ductus seminis	Ductus seminis	KULLENBERG, 1947; LESTON, 1954b; WAGNER, 1955, 1970; DUPUIS, 1955, 1963; 1970; KELTON, 1959; KAHLOW, 1962; KUMAR, 1962; WAGNER & WEBER, 1964; SCHAEFER, 1966 (seminal duct); SCHMITZ, 1968 (canal séminal); COBBEN, 1978; SCHWARTZ, 1987; STONEDAHL, 1988; DECKERT, 1990; CHÉROT, 1997; KERZHNER & KONSTANTINOV, 1999
	Ejaculatory duct	BAKER, 1931; LEE, 1969; MATSUDA, 1976
	Endophallus	BONHAG & WICK, 1953
Ductus ejaculatorius	Ductus ejaculatorius	KULLENBERG, 1947; BONHAG & WICK, 1953 (ejaculatory duct); DUPUIS, 1955, 1963; 1970; KAHLOW, 1962; KUMAR, 1962; SCHMITZ, 1968 (canal éjaculateur); COBBEN, 1978; KERZHNER & KONSTANTINOV, 1999
Primary gonopore	Primary gonopore	WAGNER, 1955, 1970 (primäre Gonopore); DUPUIS, 1955 (gonopore primaire), 1970; WAGNER & WEBER, 1964 (gonopore primaire); SCHMITZ, 1968 (gonopore primaire); KERZHNER & KONSTANTINOV, 1999
Secondary gonopore	Secondary gonopore	KULLENBERG, 1947 (sekundäre Gonopore); WAGNER, 1955, 1970 (sekundäre Gonopore); DUPUIS, 1955 (gonopore secondaire), 1970; ASHLOCK, 1957; KAHLOW, 1962; WAGNER & WEBER, 1964 (gonopore secondaire); McDONALD, 1966; SCHMITZ, 1968 (gonopore secondaire); COBBEN, 1978; SCHWARTZ, 1987; STONEDAHL, 1988; CHÉROT, 1997 (gonopore secondaire); KERZHNER & KONSTANTINOV, 1999
	Gonopore	SINGH-PRUTHI, 1925; KELTON, 1959; LESTON, 1954b
	Phallosome	MATSUDA, 1976
Genital capsule	Genital capsule	KULLENBERG, 1947 (Genitalkapsel); BONHAG & WICK, 1953; SCHAEFER, 1966, 1977 etc.; SCHAEFER & WILCOX, 1969
	Pygophore	LESTON, 1953; DUPUIS, 1955, 1963; 1970; DUPUIS & CARVALHO, 1956; ASHLOCK, 1957; McDONALD, 1961, 1966; KAHLOW, 1962; SCHMITZ, 1968; LEE, 1969; MATSUDA, 1976; COBBEN, 1978; DECKERT, 1990
	Genital segment	SHARP, 1890; SNODGRASS, 1935, 1936
	IX segment	SINGH-PRUTHI, 1925
Genital chamber	Genital chamber	SINGH-PRUTHI, 1925; SNODGRASS, 1935, 1936; KULLENBERG, 1947 (Genitalkammer); DUPUIS, 1955 (chambre génitale), 1970
	Genital cup	BAKER, 1931
	Terminal chamber	SHARP, 1890
Intersegmental membrane	Intersegmental membrane	KULLENBERG, 1947
	Segmental membrane	SINGH-PRUTHI, 1925
	Diaphragm	DUPUIS, 1955, 1963; 1970; KAHLOW, 1962; COBBEN, 1978

• Proctiger	Proctiger	BAKER, 1931; BONHAG & WICK, 1953; LESTON, 1955; ASHLOCK, 1957; McDONALD, 1966; DUPUIS, 1970; SCHAEFER, 1977
	Anal tube	DUPUIS, 1970; DUPUIS & CARVALHO, 1956; SCHMITZ, 1968 (tube anal)
	Analkonus	KULLENBERG, 1947; WAGNER, 1970
	Rectal-cauda	SHARP, 1890
Paramere sockets	Paramere sockets	SCHAEFER, 1966, 1977 etc.; SCHAEFER & WILCOX, 1969
	Paramerenhöhlen	KULLENBERG, 1947; DECKERT, 1990
Cuplike sclerite	Cuplike sclerite	SCHAEFER, 1966, 1977 etc.; SCHAEFER & WILCOX, 1969
	Subgenitalplatte	KULLENBERG, 1947
	Aedeagal strut	LESTON, 1954a, 1955
	Sklerotisiertes Diaphragma	KAHLOW, 1962
	Phallic pivot	COBBEN, 1978
	Innerer Sklerite	DECKERT, 1990
Suspensory apodemes	Suspensory apodemes	DUPUIS, 1955 (apodèmes suspenseurs), 1970; DUPUIS & CARVALHO, 1956; ASHLOCK, 1957; KAHLOW, 1962 (apodèmes suspenseurs); SCHMITZ, 1968 (apodème de suspension du phallus); SCHAEFER, 1977
	Zipfel	KULLENBERG, 1947
	Arms of phallic pivot	BONHAG & WICK, 1953
	Lateral connectives	LESTON, 1954a
	Dorsal attachments	KELTON, 1959
	Phallic pivot	DUPUIS, 1970
	Apodeme	DECKERT, 1990
	Ventral connectives	BAKER, 1931
Parameres	Parameres	SINGH-PRUTHI, 1925; SNODGRASS, 1935, 1936; KULLENBERG, 1947 (Parameren); WAGNER, 1955, 1970 (Parameren); DUPUIS, 1955 (paramères), 1970; LESTON, 1953, 1954b; DUPUIS & CARVALHO, 1956; ASHLOCK, 1957; KAHLOW, 1962; KUMAR, 1962; WAGNER & WEBER, 1964 (paramères); SCHAEFER, 1966, 1977 etc.; SCHMITZ, 1968 (paramères); LEE, 1969; SCHAEFER & WILCOX, 1969; SCHWARTZ, 1987; STONEDAHL, 1988; SCHWARTZ & FOOTIT, 1998; DECKERT, 1990; CHÉROT, 1997 (paramères)
	Claspers	BAKER, 1931; KELTON, 1959; McDONALD, 1961, 1966; MATSUDA, 1976
	Lateral appendages	SHARP, 1890
	Harpagones	LESTON, 1954a, 1955
	Gonostyli	BONHAG & WICK, 1953
Paramere body	Paramerencörper	KULLENBERG, 1947; WAGNER, 1955, 1970; WAGNER & WEBER, 1964 (corps du paramère); CHÉROT, 1997 (corps)
	Arm	STONEDAHL, 1988
	Schaft	DECKERT, 1990
Apical process of paramere	Shaft + angle + apex (left paramere); apex (right paramere)	STONEDAHL, 1988; SCHWARTZ & FOOTIT, 1998
	Hakenfortsatz	KULLENBERG, 1947; KAHLOW, 1962; DECKERT, 1990
	Hypophysis	WAGNER, 1955, 1970; WAGNER, 1970
	Apophyse	WAGNER & WEBER, 1964; CHÉROT, 1997

Sensory lobe of paramere	Sensory lobe (left paramere)	KELTON, 1959; WAGNER & WEBER, 1964 (lobe sensoriel, the term applied to both parameres); STONEDAHL, 1988; SCHWARTZ & FOOTITT, 1998; CHÉROT, 1997 (lobe sensoriel)
	Sinnesfortsatz	KULLENBERG, 1947; KAHLOW, 1962; DECKERT, 1990
	Sinneshöcker	WAGNER, 1955, 1970
Basal process of paramere	Basalfortsatz	KULLENBERG, 1947; WAGNER, 1955
	Basis	KAHLOW, 1962 (basis parameri); WAGNER, 1970; DECKERT, 1990; WAGNER & WEBER, 1964 (base); CHÉROT, 1997 (base)

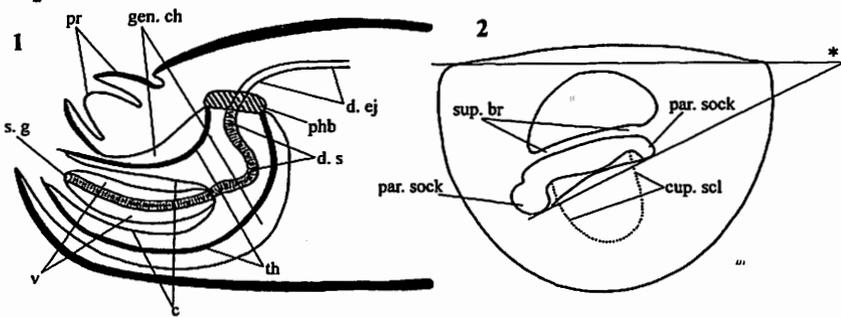
List of terms and their abbreviations:

aed	aedeagus	par	paramere
ap. pr	apical process	par. b	paramere body
app	sclerotized appendage	par. sock	paramere socket
b. for	basal foramen	phb	phallobase
bas. pr	basal process	pr	proctiger
c	conjunctiva	r. par	right paramere
c. p	capitate processes	s. g	secondary gonopore
cup. s	cuplike sclerite	sen. l	sensory lobe
d. con	dorsal connectives	sup. br	supragenital bridge
d. ej	ductus ejaculatorius	susp. ap	suspensory apodeme
d. s	ductus seminis	th	theca
duc	ductifer	th. m	theca mouth
es	endosoma	v	vesica
gen. cap	genital capsule	v. con	ventral connectives
gen. ch	genital chamber	X	X th segment
l. par	left paramere	XI	XI th segment
p. g	primary gonopore		

The Structure of male genitalia in Miridae

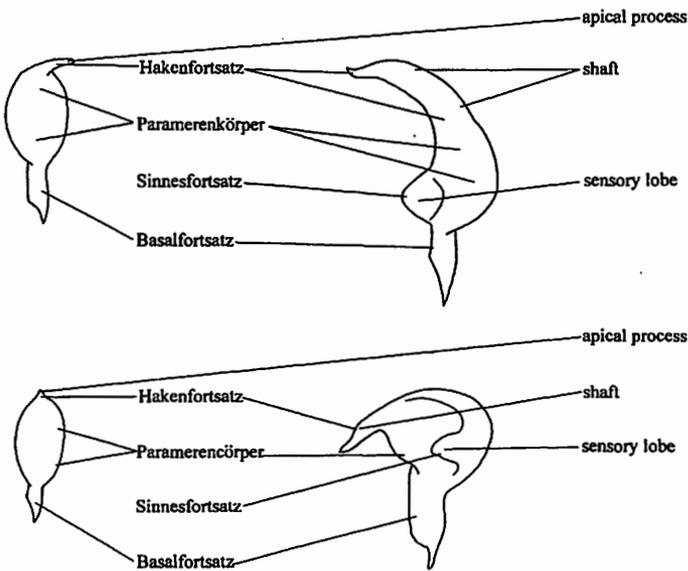
In all Hemiptera the abdomen consists of ten segments, the first segment is reduced to a small tergal plate; the 9th bears the genital opening and appendages, while the *proctiger* is composed of the 10th segment, probably with the vestiges of the 11th. The following three main elements can be recognized in the ectodermal part of the genital apparatus: the *genital capsule*, the *aedeagus* and a pair of *parameres*.

Unlike most other families of Heteroptera, in Miridae the genital capsule is not drawn into pregenital segments. Only the basal half of the genital capsule is occasionally covered with the eighth segment. In nearly all Miridae, the genital capsule (pygophore) is a solid segment without any sutures. Lateral sutures delimiting dorsal and ventral walls of the genital capsule in Isometopinae (Fig. 15-21), Bothriomirini and *Rhynocylapidius* (Fulviini) are apparently of secondary origin, as the genital capsule is undivided in other Hemiptera (with a few exceptions, also of secondary origin). The genital capsule is usually



3 Terminology by KULLENBERG, 1947:

Terminology by KELTON, 1959:



Figs 1-3. 1: scheme of the male genital segment with aedeagus in repose, sagittal section. 2: scheme of the male genital capsule, caudal view, an angle is shown between the dorso-ventral body plane and the plane of phallic structures (*). 3: comparison of the terms of paramere parts by KULLENBERG (1947) AND BY KELTON (1959).

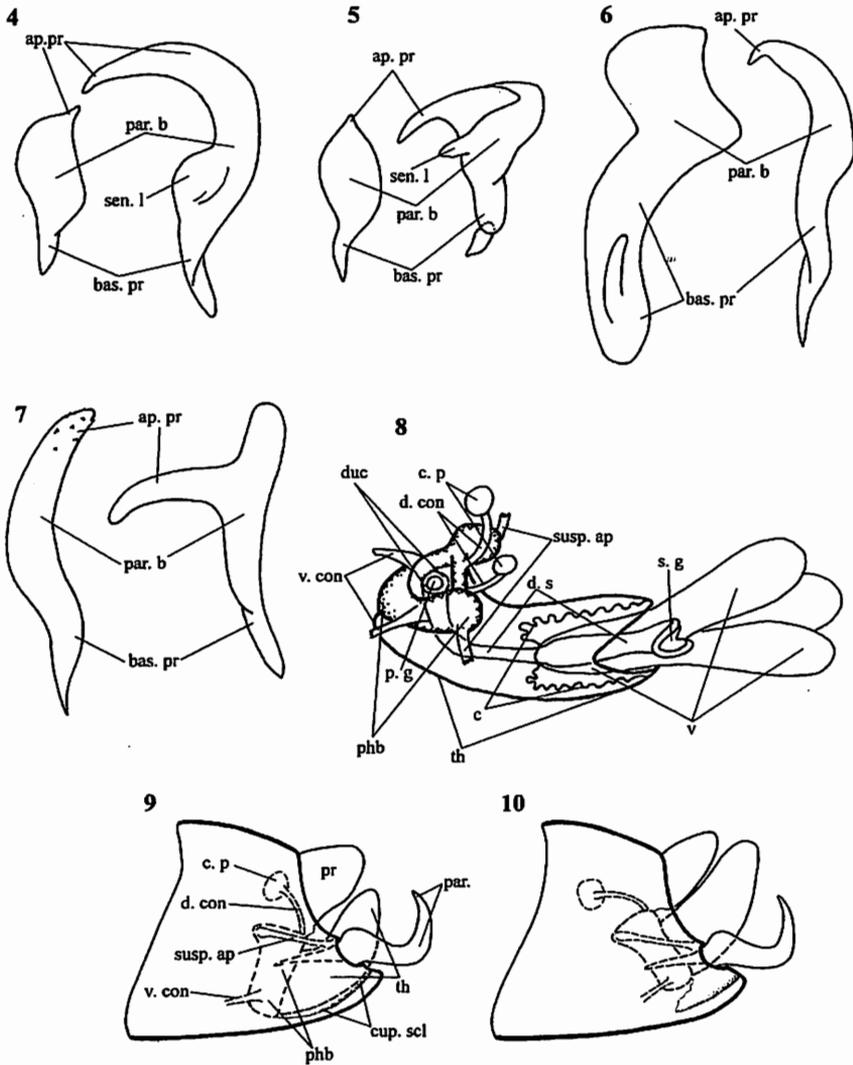
considered to be a result of fusion of 9th tergum and 9th sternum (SNODGRASS, 1935; DUPUIS, 1955, 1970) but BONHAG & WICK (1953) doubted this point of view. According to them, the 9th tergum and sternum were reduced greatly and involved in the formation of the proctiger, while the genital capsule is formed of the gonocoxites of the 9th segment, fused along midline; consequently,

parameres are treated as gonostyles. The latter view remains generally unaccepted by hemipterists except MATSUDA (1976). The problem of origin of the genital capsule is far beyond the scope of this paper. Detailed critique of the gonocoxal theory can be found in the works of DUPUIS (1955, 1963) and SCHAEFER (1977). The latter author (1977, 1980) believes that the genital segment is formed by the 9th sternum alone, expanded laterally and fused dorsally along midline.

The genital capsule is rounded or more or less flattened in dorso-ventral direction, usually gradually narrowed towards the apex. As a rule, it is well sclerotized and boat-shaped, as its dorsal wall is less developed than the ventral one. Consequently, the posterior opening of the genital capsule is directed upwards (Fig. 1, 9, 10). A tube-shaped genital capsule with equally developed dorsal and ventral walls is found only in Bryocorini. The ventral margin of the posterior opening is usually sclerotized, forming the so-called antecosta (KULLENBERG, 1947; transverse ridge, SCHAEFER, 1977). The anterior margin of the ventral wall of genital capsule has two semicircular incisions, or *paramere sockets*, in which parameres are attached (Fig. 2). The posterior opening of the genital capsule is partly covered by the proctiger. An assumption can be made, that the two sections of the proctiger represent the 10th and 11th segments respectively. Both sections are small, weakly sclerotized and usually almost completely membranous. The 11th segment is telescopically drawn into 10th in repose and completely exposed during defecation. In nearly all studied representatives of Deraeocorinae, Mirinae and Orthotylinae, the apex of aedeagus in repose is placed in a fold (pileus, KULLENBERG, 1947) of the ventral wall of the 10th segment and thus the posterior opening of the genital capsule is completely covered by the proctiger. In other subfamilies, the apex of aedeagus in repose is free and can be seen from above.

The *intersegmental membrane* between the 9th and 10th segments, i.e. between the ventral walls of genital capsule and proctiger, is enlarged and deeply plunged into the genital capsule, forming the so-called *genital chamber* (Fig. 1, 9, 10, 23). Aedeagus is located dorsally on the bottom of the chamber and parameres are placed laterally on each side of the chamber's opening. The ventral wall of the genital chamber is more or less sclerotized apically, spoon-like and tightly adjoined to the aedeagus in repose (Fig. 9). KULLENBERG (1947) used for this sclerotized part the term "Subgenitalplatte", but as the same term is traditionally applied to the sternal part of the genital capsule in Homoptera, the term "*cuplike sclerite*" (SCHAEFER, 1966) seems more preferable. The apex and lateral margins of the cuplike sclerite are especially strongly sclerotized, and the apex is tightly attached to the anterior margin of the ventral wall of the genital capsule. Lateral portions of the cuplike sclerite partially form the paramere sockets from the inner side (Fig. 22-25).

The membranous dorsal wall of the genital chamber is attached to the weakly sclerotized sternum of the 10th segment. In most Bryocorinae and Cylapinae, the border between the genital chamber and the proctiger is strengthened by a sclerotized transverse bridge (pont scléreux transverse du pygophore, SCHMITZ, 1968). This bridge (Fig. 2) subdivides the posterior



Figs 4-10. 4-7: main types of paramere structure. 4: *Lygus*-type. 5: *Plagiognathus*-type. 6: *Halticus*-type. 7: *Cyllocoris*-type. 8: scheme of the everted aedeagus. 9-10: scheme of the male genital segment, lateral view: 9: with aedeagus in repose. 10: with everted aedeagus.

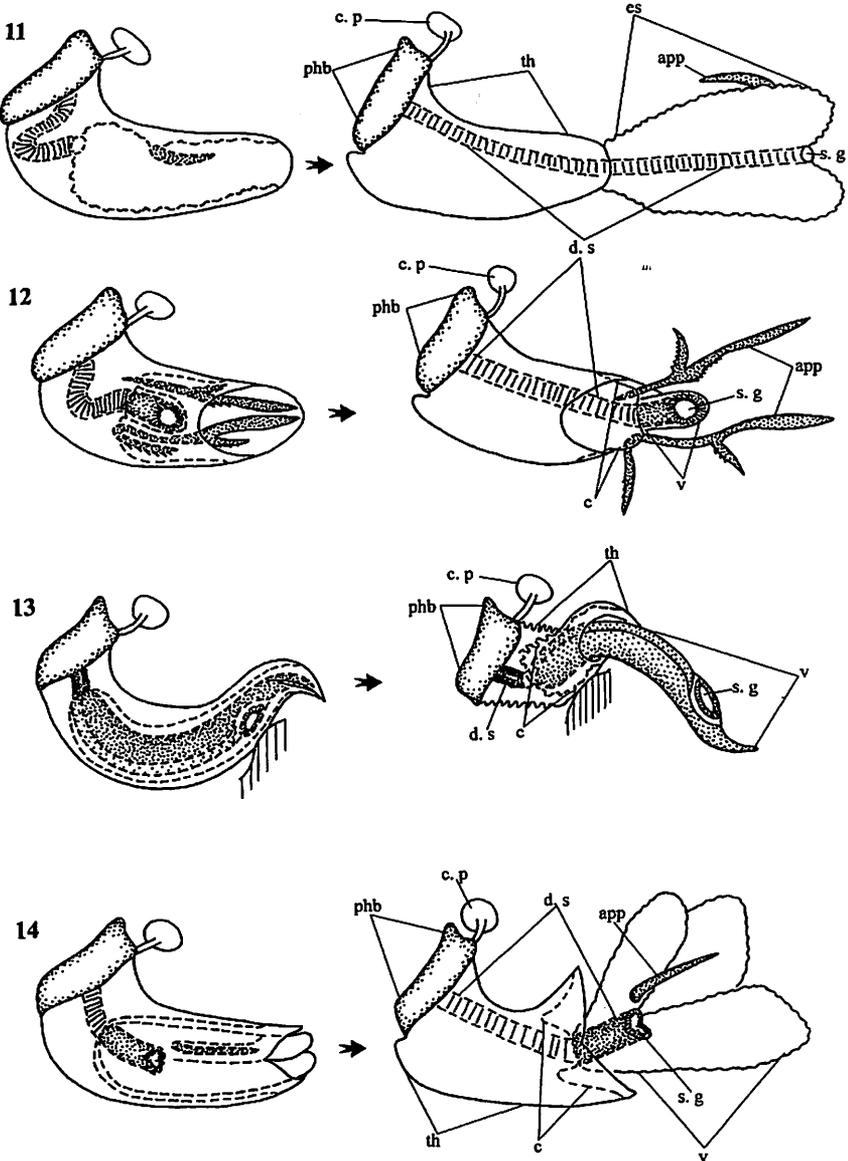
opening of the genital capsule into the upper part bearing the proctiger and the lower part, containing the genital chamber. It is designated here as the *supragenital bridge*.

The male copulatory apparatus and the genital capsule in particular are more or less asymmetrical in all Miridae. Apart from the difference in the structure of

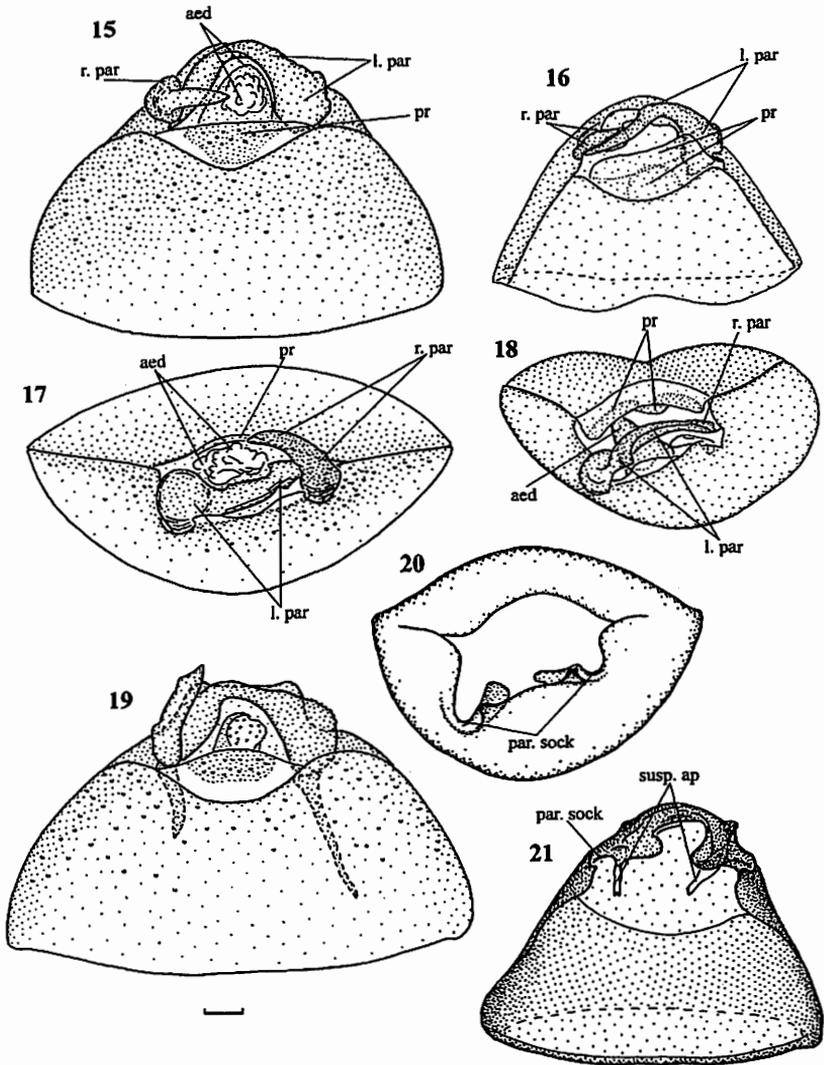
the left and right parameres, this asymmetry is revealed in partial rotation and modification of the apical part of the genital segment with its appendages in relation to the symmetrical basal part of the segment. According to my observations, the level of asymmetry of the genital capsule seems to be a valuable taxonomical character. It can be described as an angle between the plane of phallic structures and the dorso-ventral body plane. The plane of phallic structures is designated here as a plane running through the bases of parameres when the genital segment is viewed from behind (Fig. 2). The aedeagus is directed strictly perpendicularly to the mentioned plane in all examined Miridae, except two genera (*Sixeonotus* and *Coridromius*) which will be specially discussed in subsequent papers. The plane of phallic structures is always turned contraclockwise and the angle of the turn varies from 10 to 80° in different groups. The angle between the dorso-ventral body plane and the plane of phallic structures is given in descriptions below. Apart from asymmetry of the apex of the genital capsule, rotation of the whole genital segment in relation to the insect body takes place in some mirids (Termtophylini, Hyaliodini). The genital capsule is rotated 90° and the opening is directed contraclockwise in these groups.

The parameres (claspers, lateral appendages) are a pair of integral appendages lying on either side of the aedeagus. Parameres are apparently of phallic nature (SNODGRASS, 1936, 1957; DUPUIS, 1955, 1963, 1970; SCHMITZ, 1968) and originally developed as a heavily sclerotized outgrowth of the intersegmental membrane. Parameres have an inner cavity which is connected with the body cavity. They are attached to the genital capsule and lie in the paramere sockets. Muscles of each paramere are attached to its basal process, which is usually well developed and deeply prolonged into the body cavity. Parameres are asymmetrical in all mirids, and the extent of their asymmetry is an important diagnostic character. In all known species the parameres differ in structure and size from the each other, and in most cases the left one is larger (usually significantly). In several groups the right paramere is greatly reduced, sometimes (Termtophylini, *Cyrtopeltis*, some species of *Fulvius*) to a hardly recognizable rudiment. However in Halticini, most of Ecritotarsini and some Orthotylini the reverse is true: the right paramere is larger than the left.

In comparative works on the genitalia of Miridae most authors pay little attention to parameres probably because their structure is simple and variable. Two ideas seem apparent, however. First, because even in closely related species the parameres can be very different the terms applied to their parts are usually descriptive and topographical. Therefore it is hard to establish direct homologies of paramere elements between different subfamilies. Second, because in mirid ancestors the parameres were symmetrical it seems possible to reveal their common ground plan and, consequently, the same terms can be applied to the elements of both parameres.



Figs 11-14. Main types of aedeagi in repose (left) and everted (right) conditions, schematically.
 11: with undifferentiated endosoma. 12: with vesica of Orthotylini-type. 13: with vesica of Phyllinae-type. 14: with vesica of Mirinae-type.



Figs 15-21. Genital segments of Isometopinae. 15: dorsal view, *Isometopus rugiceps* KERZHNER, 1988. 16: dorsal view, *Myiomma* sp. No 1. 17: caudal view, *Isometopus rugiceps* KERZHNER, 1988. 18: caudal view, *Myiomma* sp. No 1. 19: dorsal view, *Isometopus intrusus* (HERRICH-SCHAEFFER, 1835). 20: genital capsule in caudal view, *Corticoris signatus* (HEIDEMANN, 1908). 21: genital capsule in dorsal view, *Corticoris signatus* (HEIDEMANN, 1908).

According to KULLENBERG (1947), who proposed the first comprehensive nomenclature for the parts of parameres of Miridae, both parameres have the following indistinctly delimited parts: "Paramerenkörper", "Hakenfortsatz",

“Sinnesfortsatz” and “Basalfortsatz” (Fig. 3). My examination of available material confirms that in both parameres the four main parts proposed by KULLENBERG can be recognized, but his approach was not accepted in English literature. Nowadays, the nomenclature proposed by KELTON (1959) or its subsequent modifications (for example, STONEDAHL, 1988) is most often used. Accordingly, the terminology accepted in this paper is a result of compromise between those of KELTON and KULLENBERG. The central part of each paramere is named *paramere body*, while its apical, basal and lateral outgrowths are termed *apical process*, *basal process* and *sensory lobe* correspondingly (Fig. 4-7). The latter is usually absent in the right paramere and often poorly developed or completely absent in the left.

The following three types of parameres were distinguished in Miridae by KULLENBERG: Lygus-type (Fig. 4, Mirinae, Bryocorinae (Bryocorini and Dicyphini) and *Bothynotus* (Deraeocorinae)), Cylocoris-type (Fig. 7, Orthotylini) and Plagiognathus-type (Fig. 5, Phylinae). As KULLENBERG had described genitalia in only a few common European species, the structure of external genitalia in several tribes and subfamilies remained undescribed. Therefore, the types of parameres recognized by KULLENBERG do not exactly correspond to those described in this paper.

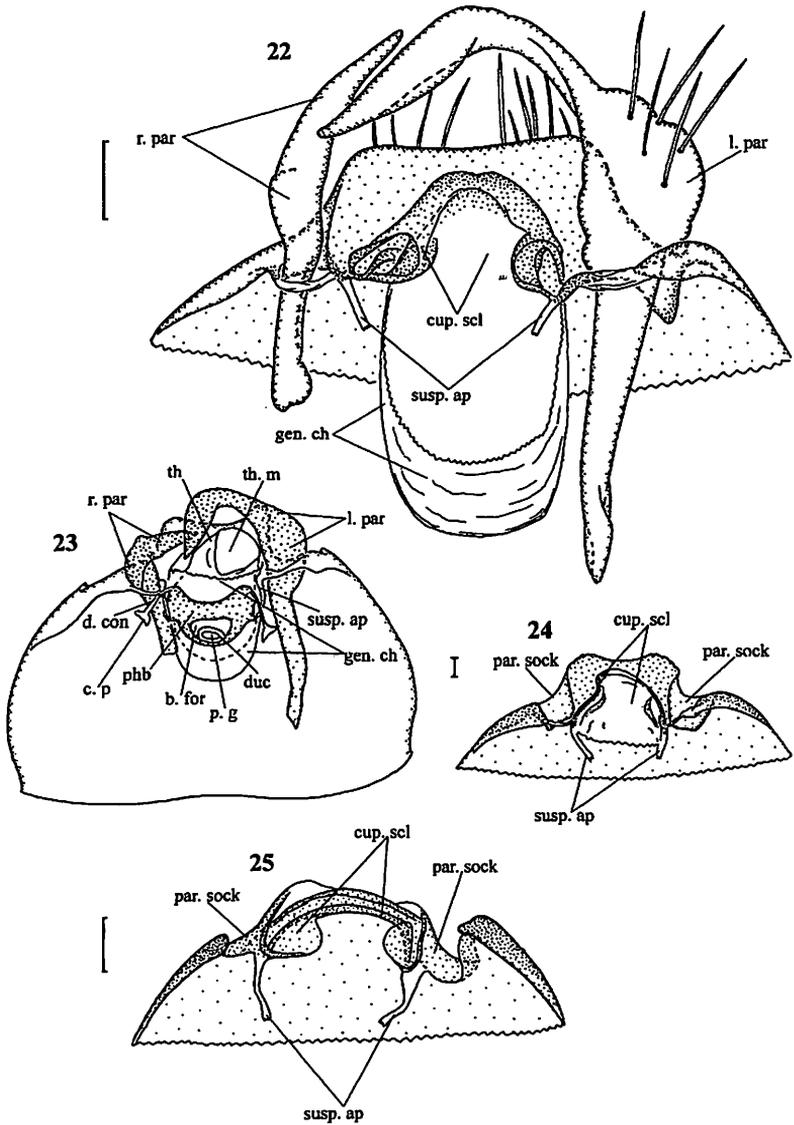
Parameres of Lygus-type (Fig. 4) are common in mirids, namely in the Isometopinae, most Cylapinae, Palaucorinae, Bryocorinae (except in most Eccritotarsini), Deraeocorinae and Mirinae. All listed taxa have a hook-like, curved left paramere; its apical process is always well developed, while the sensory lobe is frequently reduced or completely absent. The right paramere is considerably smaller than the left one. The structure of right paramere varies, the paramere body is sometimes flattened or round in cross-section; the apical process is rather small and the sensory lobe is absent in nearly all species.

Parameres of Plagiognathus-type (Fig. 5) are distinguished by the characteristic structure of the left paramere, which has a broad body with a significantly depressed inner surface. The apical process and sensory lobe are attached to its lateral margins at the same level and both directed towards the aedeagus. The right paramere is spoon-like, with a small apical process. Parameres of Plagiognathus-type occur only in Phylinae.

KULLENBERG did not examine representatives of Halticini, but it is well known that many species of this tribe can be easily recognized by the structure of the parameres (Fig. 6, Halticus-type). The right paramere of this type is larger than the left, strongly sclerotized, flag- or spoon-like. The apical process and sensory lobe are absent, while the basal process is long. The left paramere is slender, smaller than the right one, the long apical process of the left paramere has a curved hook-like apex.

The structure of parameres within Orthotylini and Eccritotarsini is too variable to recognize morphological types for these tribes.

Generally speaking, in Miridae the parameres of Lygus-type are most common, in Phylinae and Halticini parameres are highly specialized, while in Orthotylini and Eccritotarsini the parameres are very polymorphic.



Figs 22-25. 22: apex of ventral wall of genital segment with removed aedeagus, *Isometopus* sp.
 23: genital segment with removed dorsal wall, *Isometopus rugiceps* KERZHNER, 1988. 24:
 apex of ventral wall of genital segment with removed aedeagus and parameres, *Isometopus*
rugiceps KERZHNER, 1988. 25: apex of ventral wall of genital segment with removed
 aedeagus and parameres, *Myiomma* sp. No 1.

The Aedeagus (phallus, penis) apparently originated as a two-walled tube-like outgrowth of the intersegmental membrane around the *primary gonopore*. Terminology for the whole aedeagus and its parts is confusing (Tab. 1). In this paper preference is given to the terms used by SINGH-PRUTHI (1925) (Fig. 1, 8, 11-14), who proposed a comprehensive and functional nomenclature for aedeagus parts which was widely adopted by subsequent authors.

The mesodermal *ductus ejaculatorius* runs from the testes to the basis of aedeagus and terminates with the primary genital opening (primary gonopore). A pair of robust and strongly sclerotized *basal plates* are placed around the primary gonopore at the base of the aedeagus. These plates are fused ventrally in all Miridae, forming a horseshoe-like sclerite without traces of paired origin, the so-called *phallobase*. According to SNODGRASS (1936, 1957), the term phallus is often used for the whole intromittent organ, while the term aedeagus is applied to the distal part without the phallobase. The arms of the phallobase are directed upward and connected distally with the transverse sclerotized bridge. With a few exceptions (e. g. *Mecommopsis* in the Orthotylini), the phallobase is symmetrical. Basal plates and the *basal plates bridge* encircle an opening (*basal foramen*) into the aedeagal cavity. The aedeagal and body cavities are separated by the membrane (*septum*), closing the basal foramen. The arms of the phallobase are usually developed into robust processes which are directed forward (i.e. into the body cavity). The outer surface of the arms is connected with that of the cuplike sclerite by means of *suspensory apodemes* and in this way the aedeagus is fixed in the membrane of the genital chamber like a cradle (Fig. 9-10, 23).

The aedeagus is moved by a pair of protractor and retractor muscles, both attached to the phallobase. Protractor muscles are connected to the peculiar plate-like endings (*capitate processes*) of the mushroom-like apodemes (*dorsal connectives*). Most often the *ventral connectives*, or retractor apodemes are hardly visible due to their moderate sclerotization. They are attached to the phallobase laterally, in the middle of each basal plate, while the dorsal connectives are connected to the phallobase near the apices of the phallobase arms or, occasionally, to the adjoining areas of the basal plates bridge. The septum of the basal foramen bears a ring-like sclerite around the primary gonopore. This sclerite is well developed in most mirids and was designated as *ductifer* by BONHAG & WICK (1953).

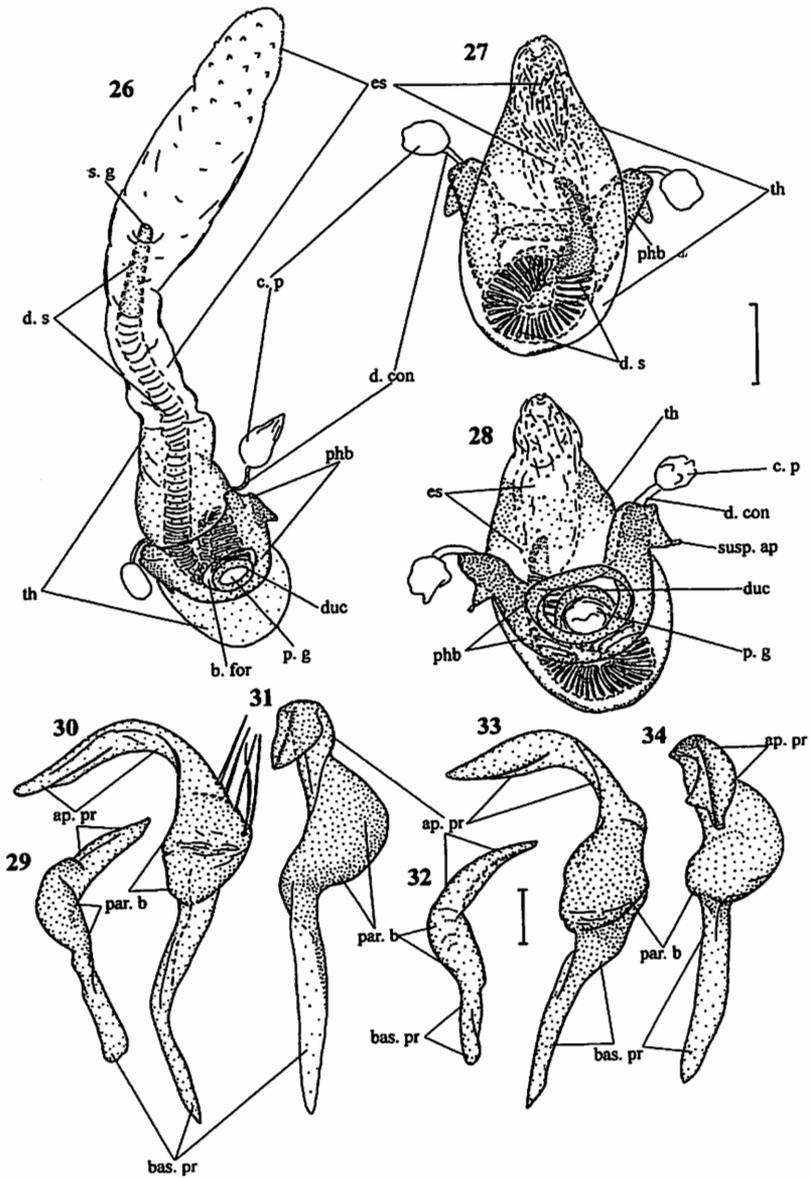
Inside the aedeagus the seminal liquid is transferred through the *ductus seminis*. The latter apparently originated when the simple tube-like aedeagus was formed as an outgrowth of the membrane around the primary gonopore. Ectodermal walls of the ductus seminis have sclerotized thickenings, similar in structure and function with tenidia in the tracheal system. They are called *sclerotized rings* in the descriptions below. The ductus seminis terminates with an orifice called the *secondary gonopore*. It often has peculiar sculpture formed by rows of thick setae incurved inside the opening. Shape and size of the secondary gonopore vary greatly from circular to oval or slit-like. The proximal part of the ductus seminis surrounded by the phallobase is usually broadened and sclerotized. In many Cylapinae, Orthotylinae and Mirinae, the

walls of the proximal part sclerotized especially well and attached to the phallobase, so that its basal opening is almost completely filled with the proximal part of the ductus seminis. In these groups the primary gonopore looks like a slit running along the basal plates bridge of the phallobase.

The aedeagus beyond the phallobase consists of two parts: the proximal (in everted condition) phallosome or phallotheca, which is most often called the *theca*, and the distal *endosoma*. The more or less tube-like theca has sclerotized walls in contrast to the sacciform and membranous endosoma. The latter aedeagal segment is fully retracted into the former in repose and thus, in the non-everted aedeagus, the theca is the external part while the endosoma became internal. The mode of sclerotization of the theca varies greatly. Usually the dorsal wall of the theca is notably more strongly sclerotized than the ventral one. In nearly all mirids, the theca has areas of weaker sclerotization at the base of the ventral wall. The apex of the theca is sometimes provided with one or few projections, teeth, or keels in the area adjacent to the opening. During copulation, the endosoma is everted through the apically or subapically placed opening, the *theca mouth*.

In the simplest case, the endosoma is single-lobed and devoid of armament, while the secondary gonopore is placed at the bottom of the endosomal sac, i.e. on the top of the fully everted aedeagus (Fig. 11). Such a structure, however, is extremely rare (some Myiommatini and Ecritotarsini). In a majority of species, the walls of the endosoma are covered with sclerotized spines, spicules and appendages of various shapes and structure, especially well developed in Cylapini and Palaucorini. In some groups the endosoma became a complicated, multilobed structure with several eversible pouches. The opening of the secondary gonopore is usually shifted from the bottom of the endosomal sac and situated laterally on the fully everted endosoma. In many groups (Isometopini, Cylapini, Halticini) the distal part of the ductus seminis is sclerotized; the ductus seminis is completely sclerotized in Bryocorini, so that the secondary gonopore is located in repose almost near the theca mouth.

In all cases discussed above, the endosoma is a functionally and morphologically integrated unit. Nevertheless, the endosoma is subdivided in the rest of the mirids into two principal sections: *conjunctiva* and *vesica*. The latter is formed by the proximal (in the state of repose, i.e. distal in the everted state) section of endosoma and encloses the distal part of the ductus seminis. The walls of the endosoma involved in the formation of the vesica are tightly attached at the base to the corresponding part of the ductus seminis. Thus, in the everted state of the aedeagus, the vesica is the well delimited distal part of the endosoma bearing the secondary gonopore. The vesica always has a narrow base and cannot be everted like undifferentiated endosoma. The distal part of the endosoma running between the base of the vesica and the theca mouth (*conjunctiva*) is membranous and wrinkles when the vesica expands through the theca mouth. In all mirids except Orthotylini, *Diphleps* (Isometopinae) and *Capsus* (Mirinae), the *conjunctiva* is devoid of any armament. The walls of the distal part of the *conjunctiva* are often fused with



Figs 26-34. 26: aedeagus with everted endosoma, *Isometopus rugiceps* KERZHNER, 1988. 27: aedeagus in repose, ventral view *Isometopus* sp. 28: aedeagus in repose, dorsal view, *Isometopus* sp. 29-31: parameres, *Isometopus rugiceps* KERZHNER, 1988. 29: right paramere, dorsal view. 30: left paramere, dorsal view. 31: left paramere, side view. 32-34: parameres, *Isometopus diversipes* LINNAVUORI, 1962. 32: right paramere, dorsal view. 33: left paramere, dorsal view. 34: left paramere, side view.

the theca walls.

Within the family the vesica varies greatly in structure and form. Nevertheless, I distinguish three main types of aedeagi with differentiated vesica. These types do not exactly coincide with the types recognized by previous authors (CARVALHO & LESTON, 1952; WAGNER, 1952; WAGNER, 1955; DUPUIS, 1955; WAGNER & WEBER, 1964). In fact, the three types described below greatly resemble Phylinae-, Orthotyliinae- and Mirinae-types of aedeagus recognized by WAGNER (1955; WAGNER & WEBER, 1964), although he did not recognize mirids without vesica as a separate group, and all mirids except Phylinae and Orthotylini were treated by him as having an aedeagus of Mirinae-type.

1. Orthotylini-type (Fig. 12) is specific for the tribe Orthotylini. The part of the conjunctiva adjacent to the vesica typically has several long sclerotized processes which are variously branched and often toothed at the margin. The vesica is small, simple and composed of the proximal part of the thin and membranous endosoma which is fastened to the sclerotized distal part of the ductus seminis. The vesica of this type is devoid of any sclerotized appendages and membranous lobes (contrary to the widespread opinion (SINGH-PRUTHI, 1925; KULLENBERG, 1947; WAGNER, 1952, 1955) that the above mentioned sclerotized processes are fastened to the vesica). A secondary gonopore with distinct opening and well developed sculpture is located at the apex of the vesica. The theca is usually moderately sclerotized and has a large oval theca mouth.
2. Phylinae-type (Fig. 13) is characteristic of all Phylinae. The vesica is comparatively long and thin, S- or C-shaped, devoid of membranous lobes, tube-like, well sclerotized and usually with one membranous wall, so that the vesica looks like a sclerotized gutter. However, in Pilophorini and some genera of Phylini the main part of the vesica is round in cross-section and completely sclerotized. The part of the ductus seminis running inside the vesica is thin-walled, membranous, and hardly visible. The secondary gonopore is located in the apical third of the vesica, sometimes apically, often surrounded by a ring with characteristic sculpture. The opening of the secondary gonopore is very small and devoid of sculpture in many Pilophorini. The theca has a membranous, very thin-walled proximal part, while the distal part is strongly sclerotized and fixed basally to the cuplike sclerite. The distal part of the theca has the peculiar shape of a curved conus and a slit-like latero-apical theca mouth. The conjunctiva is very thin and devoid of any armament.
3. Mirinae-type (Fig. 14). Aedeagus of this type is the most heterogeneous and found in Fulviini, Vanniini, Dicyphini, Deraeocorinae (except Termatophylini) and Mirinae. The vesica has a more or less sclerotized base and is composed of several (rarely single) membranous swelling lobes and armed with different sclerotized appendages. The part of the ductus seminis inside the vesica is either sclerotized (especially in Fulviini) or membranous and hardly visible (as in Dicyphini). The shape, size and sculpture of the

secondary gonopore, sclerotization of the theca and shape of the theca mouth vary greatly.

Most representatives of the tribe Ecritotarsini also have a membranous vesica composed of two membranous lobes, and the ductus seminis runs inside one of them. The distal part of the ductus seminis is strongly sclerotized, usually spine-like and in repose reaches the apex of the theca. The membrane of the lobe with enclosed ductus seminis is usually fused with the ductus along the whole length of the lobe. In some representatives, the second lobe is lost, so that the vesica slightly resembles that of Phylinae. The opening of the secondary gonopore in the above genera is apical and very small. The vesica in Bothriomirini and *Diphleps* greatly resembles that of the Ecritotarsini.

Functioning of the male genitalia

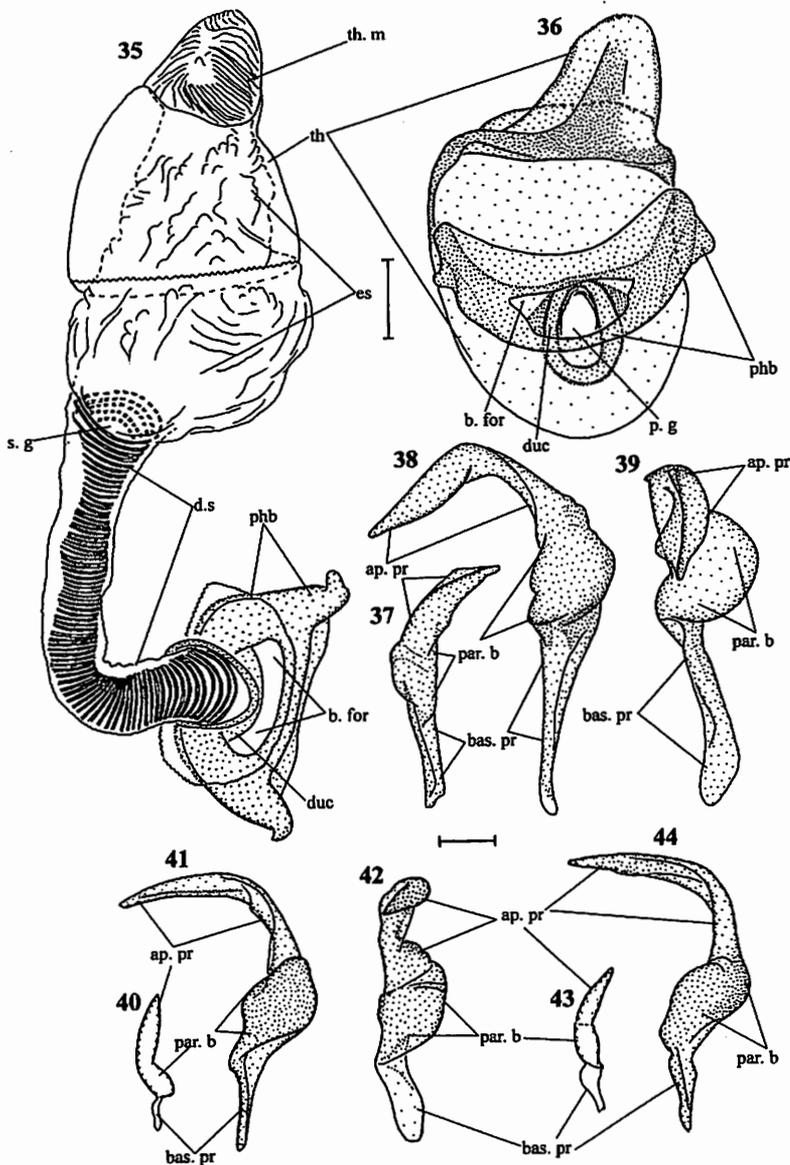
In mirids the genital capsule is always strongly sclerotized and protects the inner parts of the genital apparatus. The apical part of the genital capsule is usually densely covered with setae, some of which apparently have tactile function. The movements of the genital segment during copulation are carried out mainly by muscles of pregenital segments. The opening of the genital capsule in mirids is directed upwards and more or less turned leftward. Such a structure restricts the number of possible copulation positions. The mating behavior of European Miridae was described in details by KULLENBERG (1946, 1947) who distinguished the following three positions:

- 1) Male is placed obliquely over the female; male abdomen turns over the abdomen of female on the right side;
- 2) Male body is on the right side and more or less parallel to the female body;
- 3) Male is on the right side at various angles towards the female.

The first type of copulatory position is known in Nabidae and the second in Reduviidae, but in both families the male can be positioned at either side of the female due to the symmetry of the male genital segment. At the same time, the antagonistic position, where the male and female bodies are aligned in opposite directions was never observed in Miridae though it is rather common in Heteroptera. It was stressed by KULLENBERG (1947), that although in several species of mirids after initial coupling the partners face nearly opposite directions in fact the male and female bodies form an obtuse angle.

A great diversity of the structure of parameres within the family apparently reveals the variability of their function. According to KULLENBERG (1947), during copulation the parameres are locked on the female genital segment and direct the aedeagus while it is being inserted into the bursa copulatrix. Moreover, the parameres have tactile function and also protect the genital capsule from above by covering its opening in repose.

In species with parameres of Lygus-type the leading role in copulation apparently belongs to the left paramere. During copulation it is moved out of the paramere socket as much as possible, the apical process of the paramere is



Figs 35-44. 35: aedeagus with removed basal part of phallobase, *Myiomma* sp. No 2. 36: aedeagus in repose, dorsal view, endosoma and ductus seminis not shown, *Myiomma* sp. No 2. 37-39 parameres, *Isometopus intrusus* (HERRICH-SCHAEFFER, 1835). 37: right paramere, dorsal view. 38: left paramere, dorsal view. 39: left paramere, side view. 40-42: parameres, *Myiomma* sp. No 1. 40: right paramere, dorsal view. 41: left paramere, dorsal view. 42: left paramere, side view. 43-44: parameres, *Myiomma* sp. No 2. 43: right paramere, dorsal view. 44: left paramere, dorsal view.

fixed on the female genital segment and then the paramere is retracted into the socket. This movement results in simultaneous penetration of the apex of the theca into the vulva of the female. The right paramere, apparently, could be actively involved in anchoring only if it were well developed and had a prominent apical process. In Bryocorinae (except Eccritotarsini), Mecistoscelini and Hyalopeplini (Mirinae), Clivinemini, Hyaliodini and Termatophylini (Deraeocorinae) and several representatives of other subfamilies the right paramere is reduced to a minute rudiment, which is evidently not functioning during copulation. On the contrary, in Halticini the fixation of the female genital segment is carried out by both parameres. The larger right paramere has a long basal process, can move out of the paramere socket considerably and plays a more important role in fixation of the female genital segment and the resulting insertion of the theca apex into the vulva. In Orthotylini and Eccritotarsini the parameres (judging by their structure) evidently function as effective anchors during copulation.

Unlike parameres of *Lygus*- and *Halticus*-types, those of *Plagiognathus*-type apparently do not function as grasping organs. An observation by KULLENBERG (1947) supports this assumption. According to KULLENBERG, the copulation in Phylinae is brief and can be easily interrupted. The basal process of the left paramere is relatively short and therefore the paramere can not be moved out of the socket. The leaf-like right paramere is too small to serve as a reliable anchoring organ. The sclerotized apex of the theca lies in a depression of the body of the left paramere. The peculiar structure of the theca apex, which is attached to the genital segment and at the same time remains rather elastic, allows a change in direction of the theca apex by small movements of the left paramere.

Very unusual structure and functioning of the genital apparatus occurs in *Coridromius* (Orthotylinae) where the apical part of aedeagus lies in a gutter in the long and robust left paramere. Apparently, during copulation, the apex of the paramere is inserted into the bursa copulatrix and therefore the left paramere plays the main role in insemination.

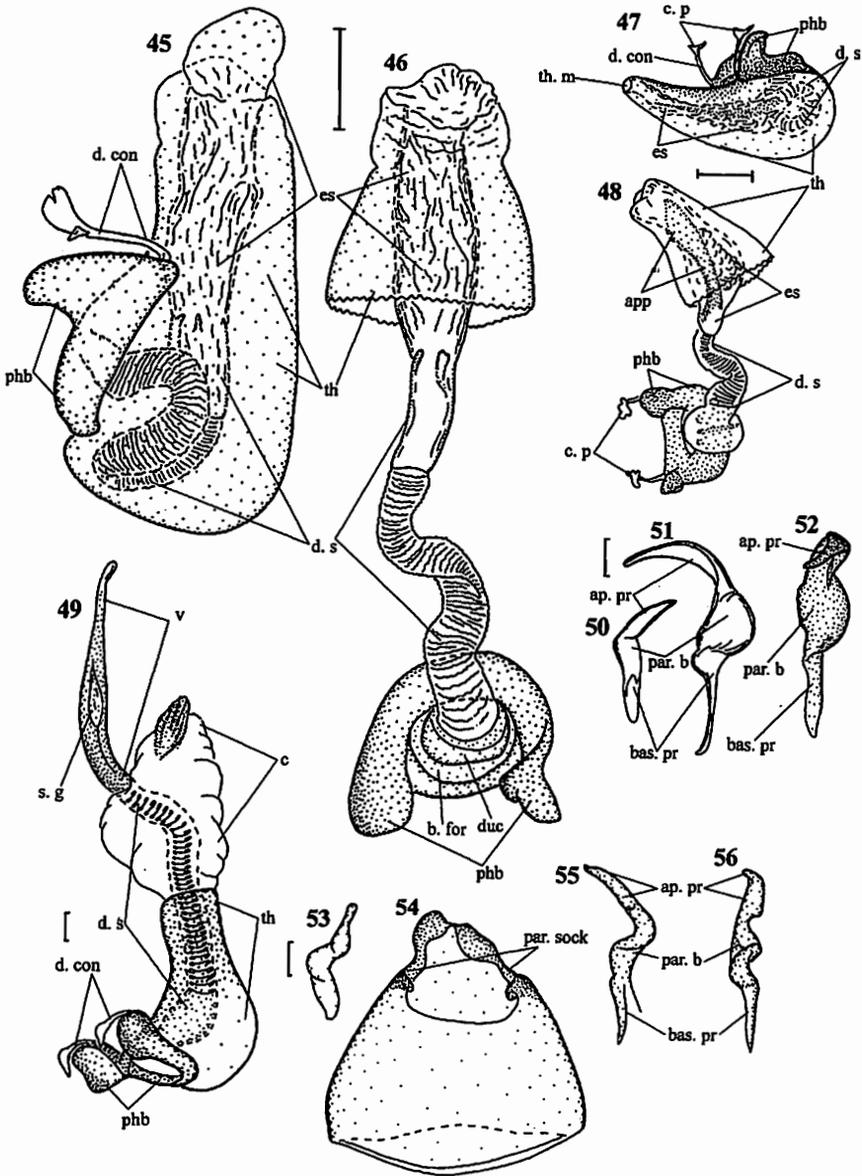
The main functions of the aedeagus are insertion of the sperm into the bursa copulatrix of the female and anchoring in the female genitalia during copulation. The arms of the phallobase are fastened to the genital segment by means of suspensory apodemes and thus the phallobase can move forward and backward like a swing. At the beginning of copulation, due to contraction of protractor muscles and probably also increased hydrostatic pressure, the phallobase is shifted backwards (Fig. 10) and the apex of theca is placed near the vulva or inserted into the vulva. Then the endosoma is hydrostatically everted out of the theca. BONHAG AND WICK (1953) described an erection fluid pump at the base of the aedeagus of *Oncopeltus* (Lygaeidae). Similar structure was found in Cydnidae and several representatives of Cimicomorpha (COBBEN, 1978). In Miridae a comparable mechanism is unknown and apparently the haemolymph is pumped into the aedeagus through a thin channels in the septum by contraction of abdominal muscles. The endosoma is everted from the theca like a glove finger (Fig. 11) and inserted into the bursa

copulatrix of the female. The internal sclerotized structures, when present, become external and come in contact with the walls of the bursa copulatrix, anchoring the aedeagus and probably stimulating the female. Additionally, the anchoring of the endosoma within the bursa copulatrix is often achieved by eversion of the membranous endosomal lobes in opposite directions. The long elastic ductus seminis is strongly lengthened and the secondary gonopore, through which the sperm is ejaculated, usually occupies an apical or subapical position in the inflated aedeagus.

In mirids with the Mirinae type of aedeagus the conjunctiva is partly everted (but usually not completely exposed) during copulation and the vesica is expanded from the theca by pressure of haemolymph within the aedeagus (Fig. 14). Apparently, the inflation of the membranous lobes of the vesica is also caused by pressure of haemolymph pumped into the vesica through a small openings in the vesica base. As in the taxa with undifferentiated endosoma, the vesica is anchored in the bursa copulatrix by means of membranous eversible lobes and various types of sclerotized appendages.

In Orthotylini, the conjunctiva is fully everted during copulation, and the short vesica is completely exposed from the theca (Fig. 12). When the conjunctiva is the everted, its branching sclerotized processes anchor the aedeagus in the bursa copulatrix. Anchoring is usually strengthened by one of the sclerotized processes which occupies a perpendicular position in everted aedeagus. Additionally, the branches of the sclerotized processes are also spread out under the pressure of haemolymph. The sclerotized processes of the conjunctiva are completely absent in some orthotylini and anchoring of the aedeagus can be brought about by the sclerotized processes of the theca (as in most species of *Ceratocapsus*).

According to observations by KULLENBERG (1947), the pumping of haemolymph into the genital segment is a result of considerable tension of the abdominal muscles and leads to anoxemia. Apparently the cataleptic rigor during copulation, typical of some mirids, is a consequence of anoxemia, but it has never been observed in Phylinae. In contrast to all other plant bugs, the pressure of the haemolymph is of minor importance in expansion of the aedeagus of Phylinae-type. During copulation, the phallobase is shifted caudad, the membranous proximal part of the theca is ruffled and the vesica is nearly entirely extended through the immovable distal part of the theca (Fig. 13). The anchoring of the Phylinae aedeagus within the bursa copulatrix of the female is carried out by the C- or S-form vesica. In some genera, especially within the tribe Hallodapini, the vesica is even more complex and has numerous bends. In many Pilophorini there is a sometimes branched process about in the middle of the vesica; the base of the process is formed by a thin membrane. During copulation, the membranous base of the process becomes more firm under pressure of haemolymph inside the vesica, and the process occupies a position more or less perpendicular to the main part of the vesica, thus promoting the anchoring. Many Phylini have 2 or 3 curved apical processes interconnected by membranous stripes and occupying parallel position in repose; during copulation these processes are turned under pressure



Figs 45-56. 45-46: aedeagus, *Isometopus kaznakovi* KIRITSHENKO, 1939. 45: in repose, side view. 46: with removed basal part of theca. 47-48: aedeagus, *Corticoris signatus* (HEIDEMANN, 1908). 47: in repose, side view. 48: with removed basal part of theca. 49: everted aedeagus, side view, *Diphleps unica*. 50-52: parameres, *Corticoris signatus* (HEIDEMANN, 1908). 50: right paramere, dorsal view. 51: left paramere, dorsal view. 52: left paramere, side view. 53-56: *Diphleps unica* BERGROTH, 1924. 53: right paramere, dorsal view. 54: genital capsule, dorsal view. 55: left paramere, dorsal view. 56: left paramere, side view.

of haemolymph within the vesica and form a true anchor with 2 or 3 branches.

After copulation, the pressure of the haemolymph decreases, the membranous lobes shrink and the sclerotized appendages turn parallel to the aedeagus. The tension of the elastic ductus seminis draws the endosoma or vesica back into the theca. The process of retraction of the vesica and especially the endosoma into the theca is a long and complex procedure, especially in species with richly sclerotized armament. Apparently the parameres are of some help in this process. According to KULLENBERG (1947), the vesica of Mirinae type cannot be drawn into the theca without constriction of intrinsic muscles. Nevertheless, the presence of internal muscles in the aedeagus seems doubtful and it has not been confirmed so far. Simultaneously with retraction of the inner aedeagal parts, the aedeagus is shifted into more proximal position by retractor muscles.

Subfamily Isometopinae FIEBER, 1860

Material examined: Isometopini: *Isometopus intrusus* (HERRICH-SCHAEFFER, 1835): Ukraine, Mleev, 45 km SSE Kiev (Grossheim) 15-21.VI.1921, 3 spec.; Ukraine, Southern coast of Crimea (E. Kiritshenko) 10.VI.1926, 2 spec.; *Isometopus kaznakovi* KIRITSHENKO, 1939: Georgia, 28 km WNW Kutaisi (Borchsenius) 18.VI.1932, 3 spec.; Russia, Dagestan, Mahachkala (Ryabov) 28.VI.1933, 3 spec.; Russia, Slavyanskaya, 30 km WNW Krasnodar, (Rysakov) 12-24.VII.1936, 2 spec.; *Isometopus diversipes* LINNAVUORI, 1962: Turkey, Sakal Sultan (Eckerlein) 23.V.1960, 1 spec.; *Isometopus rugiceps* KERZHNER, 1988: Russia, Andreevka, Khasansk. distr., Primorye (Sinev) 24.VII.1985, 2 spec.; *Isometopus sp.*: Tadzhikistan, Kondara, 40 N Dushanbe (Kerzhner) 22.VIII.1972, 2 spec.; Myiommatini: *Myiomma sp.* No 1: Vietnam, Tamdao, Vinphu prov. (Gorochov) 10.XI.1990, 1 spec.; *Myiomma sp.* No 2: Vietnam, 20 W Thanhhoa, Thanhhoa prov. (Gorochov) 04.I.1989, 1 spec.; *Corticoris signatus* (HEIDEMANN, 1908): USA, 2 mi NW Mathias, Lost River Estates (Hardy) 1-2.VIII.1997, 1 spec.; USA, Jay cea Park, N Carolina, (Stephan) 26.V.1981, 2 spec.; Diphlebiini: *Diphleps unica* BERGROTH, 1924: USA, AR Faulker Co Conway (Henry & Wheeler) 12.VI.1987, 1 spec.; AR Faulkner Co Rt. 64 nr Jst 319 NW Conway, (Henry & Wheeler) 12.VI.1987, 1 spec.

Isometopinae is a small subfamily with fewer than 150 species, distributed mainly in tropical and subtropical regions. FIEBER (1860) described the family Isometopidae to accommodate the newly erected genus *Isometopus* Fieber, 1860 which originally included *I. intrusus* (HERRICH-SCHAEFFER, 1835) transferred from *Acanthia* and *I. alienus* FIEBER, 1860. Close relations of Isometopinae and Miridae were for the first time emphasized by REUTER (1875) and the former group was treated by him as a division of Miridae. However, in subsequent versions of REUTER'S higher classification (1905, 1910) the family rank of Isometopidae was restored. Morphological data on the structure of rostrum, abdomen, wing venation (CARAYON, 1958) and female genital system (SLATER, 1950) revealed the close relationship between both groups, but the family rank was still applied to Isometopinae by several authors (WAGNER, 1973; LINNAVUORI, 1975; CARVALHO, 1984). Anyway, it is beyond question that Isometopinae is a sister group to the rest of the plant

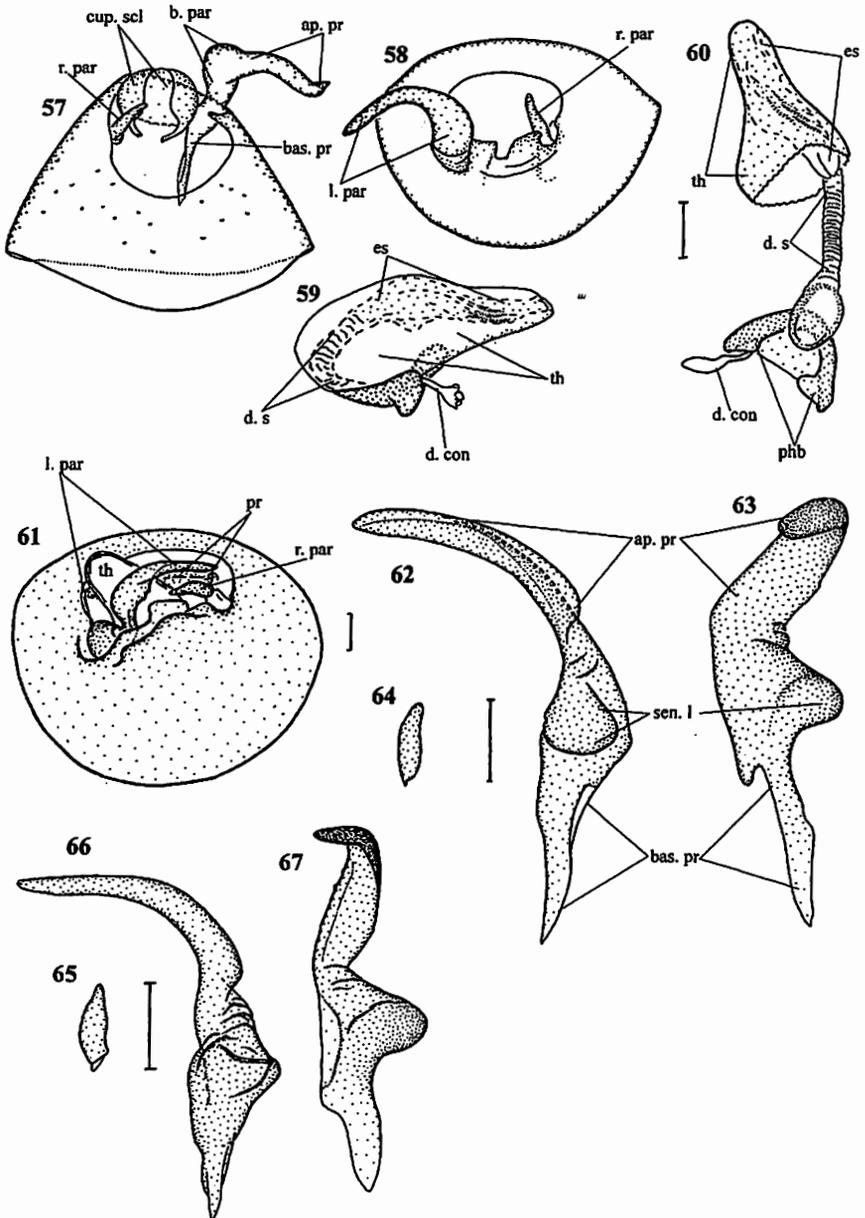
bugs (LESTON, 1961; SCHUH, 1974, 1976; HERCZEK, 1993).

For a long time the only suprageneric classification of the group was that by MCATEE & MALLOCH (1932) who distinguished in Isometopinae two tribes: Diphlebiini with a single aberrant genus and Isometopini divided into series Myiommaria and Isometoparia. Classification of Isometopinae was recently revised by HERCZEK (1993) who additionally established two new tribes: Gigantometopini for the aberrant species *Gigantometopus rossi* SCHWARTZ & SCHUH, 1990, and Electromyiommini for several fossil genera. Both Myiommaria and Isometoparia were treated by HERCZEK as separate tribes divided into three and two subtribes, accordingly, while Diphlebini were excluded from the subfamily. AKINGBOHUNGBE (1996), apparently not familiar with HERCZEK's results, revised African, European and Middle Eastern Isometopinae, also raised the rank of both series of Isometopini to the tribal level and retained Diphlebini as the third tribe within Isometopinae.

A description of genitalia of Isometopinae based on all examined taxa is given below.

Genital capsule trapeziform, more or less flattened in dorso-ventral direction and split into dorsal and ventral walls by thin membranous line in all examined representatives, except *Diphleps unica* (Fig. 54). Lateral delimiting sutures fully developed in *Isometopus* (Fig. 15, 17, 19) and in *Myiomma* (Fig. 16, 18), while in *Corticoris* (Fig. 20, 21) the sutures indistinct in basal part of genital capsule. Ventral wall larger than dorsal, so that the opening of genital capsule directed upward. In all *Isometopus* genital capsule on each side with apical projections of ventral wall and often with a lateral tooth (Fig. 23). Areas adjacent to lateral membranous lines and apex of genital capsule covered with especially dense setae. In *Isometopus* most of setae located in small rounded depressions evenly distributed on the surface of genital capsule. Genital capsule slightly asymmetrical. Plane of phallic structures turned 15-25°. Cuplike sclerite with peculiar lateral margins: ansiform in *Isometopus* (Fig. 22, 24) and formed like rounded plates in *Myiomma* (Fig. 25) and *Corticoris*. Cuplike sclerite in *Diphleps* of regular form, with uniformly sclerotized margins. Supragenital bridge absent in all species.

Parameres. Body of right paramere smoothly merging into long and straight apical process. In *Isometopus* right paramere (Fig. 29, 32, 37) larger and more strongly sclerotized than in *Myiomma* and *Corticoris*, apical process of paramere with more or less developed median rib, dividing the process into two flattened parts looking like slope of a roof. In *Myiomma* (Fig. 40, 43) and *Corticoris* (Fig. 50) right paramere nearly rounded in cross-section, in *Diphleps* (Fig. 53) slender, with remarkably turned apical process. Left paramere 2-3 times as large as right, with swollen body (except for *Diphleps*, Fig. 55, 56), robust apical process and almost undeveloped sensory lobe. Apical process of paramere as long as paramere body and basal process combined, with greatly curved apical part, spinous in examined representatives of Myiommatini (Fig. 41, 42, 44, 51, 52) and flattened, with distinct median rib in *Isometopus* (Fig. 30, 31, 33, 34, 38, 39). Paramere body with several setae on dorsal side. Basal process of left paramere shorter than



Figs 57-67. 57-58: genital segment with removed aedeagus and proctiger, *Isometocoris blantoni* CARVALHO & SALIER, 1954. 57: dorsal view. 58: caudal view. 59-60: aedeagus, *Isometocoris blantoni* CARVALHO & SALIER, 1954. 59: in repose, side view. 60: with removed basal part of theca. 61: genital segment, caudal view, *Psallops* sp. No 2. 62-64: parameres, *Psallops* sp. No 1. 62: left paramere, dorsal view. 63: left paramere, side view. 64: right paramere, dorsal view. 65-67: parameres, *Psallops* sp. No 2. 65: right paramere, dorsal view. 66: left paramere, dorsal view. 67: left paramere, side view.

paramere body, in *Myiomma* shorter than in *Isometopus*. In *Diphleps* left paramere (Fig. 55, 56) thin, with straight apical process and with hook at very apex and incision at base of the process.

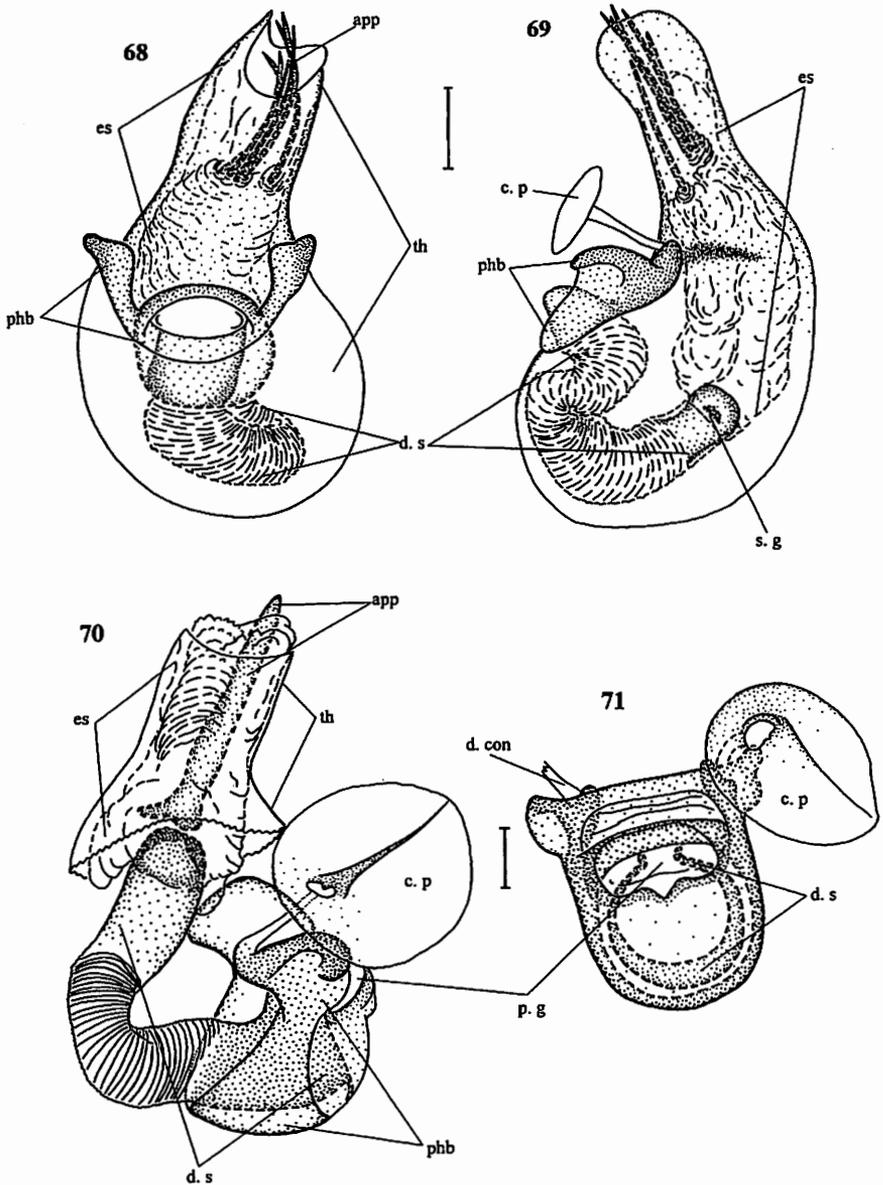
Aedeagus. Phallobase of regular form. Ductifer well developed. Dorsal connectives with weakly developed or completely reduced capitate processes. Theca usually with comparatively weak sclerotization of apical part. Dorsal wall of theca slightly (in *Isometopus* (Fig. 26-28, 45, 46) and *Diphleps* (Fig. 49)) or much (in *Corticoris* (Fig. 47, 48)) more strongly sclerotized than ventral wall while in *Myiomma* (Fig. 35, 36) dorsal wall of theca with greatly sclerotized transverse stripe prolonged into longitudinal ridge directed towards apex. Theca with rounded mouth in *Isometopus*, *Diphleps* and *Corticoris*, and with prominent apical outgrowth of dorsal wall in *Myiomma*. Vesica absent in all representatives except in *Diphleps*. Endosoma shaped like single-lobed sack, in *Myiomma* and *Corticoris* more voluminous than in *Isometopus*. Opening of secondary gonopore located in the middle of everted endosomal sac in *Isometopus* and apparently near its apex in *Myiommatini*. Apex of everted endosomal sac covered with minute spines in *Isometopus*; endosoma in *Myiomma* without any armament, in *Corticoris* with large, gutter-like and sclerotized appendage which is broadened towards apex and slightly twisted along its axis. Ductus seminis with well developed sclerotized rings. Unlike *Isometopini*, in *Myiommatini* ductus seminis with rather thick walls (distance between inner and outer walls clearly visible in fig. 35). Distal part of ductus seminis sclerotized in *Isometopus*, in contrast to examined representatives of *Myiommatini*. Specific sculpture of secondary gonopore absent in all examined species. In *Diphleps* endosoma differentiated into conjunctiva and vesica (Fig. 49). Conjunctiva voluminous, armed with conjoined sclerotized spiculae. Vesica shaped as completely sclerotized rod, nearly round in cross-section and tapering towards apex. Opening of secondary gonopore located in the middle of lateral wall of vesica. Unlike other isometopines, in *Diphleps* walls of proximal part of ductus seminis next to primary gonopore distinctly sclerotized.

Subfamily Psallopinae SCHUH, 1976

Material examined: *Psallops* sp. No 1: Singapore, Seletar Reservoir, 1° 24' N 103° 48' E (O. Martin) 7.XI.1991, 1 spec.; *Psallops* sp. No 2: East Ghana, 2° 28' W 5° 23' N (L.R. Cole) X.1965, 1 spec.; Ghana, Tafo (Leston) 2.XI.1965, 1 spec.; *Isometocoris blantoni* CARVALHO & SALIER, 1954: Panama, Fort Amador (Keenan) II.1964, 1 spec.

This small subfamily comprises three genera (including *Isometopsallus* HERCZEK & POPOV, 1992, from Baltic amber) with 9 described species. Genus *Psallops* was originally placed in Phylinae (USINGER, 1946) and later transferred to Isometopinae (EYLES, 1972). The separate subfamily Psallopinae was established as the group cannot be related to any other with certainty SCHUH (1976).

Genital capsule entire, without any sutures (Fig. 57, 58, 61), trapeziform, smoothly rounded towards apex and slightly flattened in dorso-ventral



Figs 68-71. 68-69: aedeagus, *Psallops* sp. No 2. 68: dorsal view. 69: side view. 70: aedeagus with removed basal part of theca, side view, *Psallops* sp. No 1. 71: phallobase, *Psallops* sp. No 1.

direction. Opening of genital capsule directed upward. Plane of phallic structures turned $15-20^{\circ}$. Cuplike sclerite weakly and almost uniformly

sclerotized, its apex and lateral margins sclerotized slightly stronger than the central part. Supragenital bridge absent.

Parameres of Lygus-type (Fig. 57, 58, 62-67), right paramere reduced to a hardly recognizable rudiment. Left paramere 5-6 times as large as right. Apical process of left paramere as long as paramere body and basal process combined, falciform. Sensory lobe of left paramere bud-form, located at dorsal surface of paramere body. In *Psallops* dorsal surface of body of left paramere with several wrinkle-like ridges.

Aedeagus. In *Psallops* (especially in *Psallops* sp. No 1) phallobase rather robust, with well developed arms, basal plates bridge and capitate processes (Fig. 68-71). In *Isometocoris* capitate processes reduced and basal plates bridge of phallobase poorly sclerotized (Fig. 59, 60). Saclike and membranous basal part of theca noticeably broadened. Dorsal wall of theca slightly (in *Isometocoris*) or much (*Psallops*) stronger sclerotized than ventral wall. Vesica absent. Endosoma with several eversible pouches especially well developed in *Psallops*. Armament of endosoma composed of a number of fine spiculae in *Isometocoris* (Fig. 59), six long and thin spines in *Psallops* sp No 2 (Fig. 68, 69) and single large, heavily sclerotized and pointed appendage in *Psallops* sp. No 1 (Fig. 70). This gutter-like appendage attached to the wall of endosoma near opening of secondary gonopore. Ductus seminis with strongly sclerotized distal and basal parts in *Psallops*, membranous along the whole length, but with large ductifer in *Isometocoris*. Sclerotized rings of ductus seminis well developed in all studied species. Opening of secondary gonopore indistinct, without specific sculpture in *Isometocoris*, placed laterally at the sclerotized apex of ductus seminis in *Psallops*.

Discussion

In contrast to other mirids, the male genitalia of Isometopinae have not been used either to distinguish species or for suprageneric classification. Descriptions of isometopine species are sometimes provided with figures of parameres or, most often, completely devoid of any drawings and description of genitalia structure. No representatives of Isometopinae are considered in the works on morphology of mirid genitalia (SINGH-PRUTHI, 1925; KULLENBERG, 1947; KELTON, 1959). AKINGBOHUNGBE (1996) is the only one who illustrates aedeagi and parameres of numerous species of Isometopinae and comments briefly on genitalia structure. Although it is difficult to compare his drawings with the data obtained during the present investigation, it is possible to make several remarks.

1. Sclerotization of the distal part of ductus seminis appears to be typical of all representatives of Isometopini, in contrast to Myiommatini which have entirely membranous ductus seminis.

2. Judging by described (AKINGBOHUNGBE, 1996; CARVALHO, 1976; HENRY, 1979, 1984; HENRY & HERRING, 1979; SLATER & SCHUH, 1969) and examined by me representatives of Isometopini and Myiommatini, these tribes can be also defined by the structure of the apical process of the left paramere.

3. The lack of endosomal armament in *Myiomma* found by me in examined species is not universal of the genus, as several species have sclerotized armament of minute spines or spiculae (AKINGBOHUNGBE, 1996).

4. In contrast to all representatives of Isometopinae examined by me which have undifferentiated endosoma and lack the lateral sutures, delimiting the genital capsule into dorsal and ventral walls, *Diphleps unica* has a differentiated vesica of peculiar structure, well developed conjunctiva with armament, entire genital capsule and a particular structure of parameres and cuplike sclerite, not typical for the rest of the subfamily. This supports a recent proposal (HERCZEK, 1993) to exclude *Diphleps* from the subfamily Isometopinae.

As for Psallopinae, it seems premature to make any taxonomic conclusions due to the limited examined material. Judging by the figures (YASUNAGA, 1999), the genitalia of *P. myiocephalus* and *P. nakatanii* are of the same structure as in *Psallops* No 2, while *Psallops* No 1 differs in possessing a gutter-like endosomal appendage. The genitalia of *Isometocoris* and *Psallops* seem to be characterized mostly by plesiomorphic states of characters and therefore can not be used to estimate the systematical position of the group. The male genitalia of Psallopinae are probably the closest to the Cylapini type in pattern of sclerotization of ductus seminis, comparatively moderate turning of the plane of phallic structures, structure of the cuplike sclerite, phallobase and endosoma.

Acknowledgments

I wish to thank the following persons for the loan of material: Dr. J. Gorczyca, Silesian University, Poland; Dr. Th. J. Henry, US National Museum of Natural History and Dr. M. Schwartz. I am especially grateful for discussions to Dr. I.M. Kerzhner, Zoological Institute, Russian Academy of Sciences. I also wish to thank Dr. F. Chérot, Université Libre de Bruxelles for his comments on the manuscript and Dr. V.I. Gusarov, Snow Entomological Museum, University of Kansas for improvements of the language. The study is carried out with financial support of The Russian Foundation for Basic Research, project No 02-04-49138; Federal programs "Russian Universities", project No 07.01.056 and "Leading scientific schools" project No 00-15-97934.

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