

# On the Structure of the Aedeagus in Shield Bugs (Heteroptera, Pentatomidae): 1. Subfamilies Discocephalinae and Phyllocephalinae

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**Abstract**—The paper starts a series of publications on the structure of the aedeagus Pentatomidae and its possible taxonomic significance. The structure of the aedeagus in the entire family is discussed in brief. The structure of the aedeagus in 14 species of Discocephalinae and 13 species of Phyllocephalinae is described. The Discocephalinae strongly differ from other subfamilies in the absence of differentiation in the vesica and conjunctiva and in their strong sclerotization. In Discocephalinae, the structure of the aedeagus is a valuable taxonomic character at the generic and suprageneric levels. In Phyllocephalinae, by contrast, all the species possess the common basic plan of the structure of the aedeagus. It can be treated as an autapomorphy of the group, but makes the use of this character insufficient for the phylogenetic reconstruction of the subfamily.

The structure of the male genitalia is actively used in the taxonomy of Heteroptera, and of shield bugs in particular. This complex of characters is used not only for distinguishing closely related species, but also in the supergeneric classification. First of all, this is true for the structure of the genital capsule and parameres, whereas structures of the aedeagus are used to a significantly lesser extent. It is mainly stipulated by the complicated structure of the aedeagus in Pentatomidae, in particular, by the presence of a complex of membranous lobes and sclerotized appendages, densely packed in the sclerotized theca, which are fully straightened only during copulation. The main goal of the present work was to study the structure of the fully straightened aedeagus in Pentatomidae and to reveal characters important for the supergeneric diagnostics of the group.

The inner membranous structures of the aedeagus were straightened due to the difference in the osmotic pressure (Kerzhner and Konstantinov, 1999) and by their hydraulic blowing (Gapon, 2001). Preparation of aedeagi and drawing were performed according to the standard methods. The vast basic collection of the Zoological Institute of the Russian Academy of Sciences (ZIN) was used as a source of the material for examination. The terms “proximally,” “distally,” “apically,” and “basally” in relation to the structures of the aedeagus are applied for the fully stretched organ. In shield bugs, the position of the aedeagus in relation to the body axis somewhat varies. For standardization of

descriptions, the side adjoining the ventral wall of the genital segment during copulation is designated as the ventral surface of the aedeagus. The aedeagus is pictured in dorsal, ventral, and lateral views corresponding to each other in different species. In all the cases, the scale is 0.2 mm.

The terminology of parts of the aedeagus in Heteroptera, proposed by Singh-Pruthi (1925) and later supplemented and adopted in relation to shield bugs by Baker (1931), McDonald (1961, 1966), and Gross (1975, 1976), is widespread and at present is virtually stable. It is also used in the present work, with several necessary additions.

## STRUCTURE OF THE AEDEAGUS IN SHIELD BUGS OF THE FAMILY PENTATOMIDAE

In all Heteroptera, the aedeagus consists of three main parts: phallobase, theca, and endosoma. The phallobase is formed of a pair of strong and usually strongly sclerotized basal plates, which fuse ventrally in all the bugs, forming a horseshoe-shaped sclerite without any traces of initially paired structure. Moreover, the raised up hands of this horseshoe-shaped sclerite are dorsally united by a sclerotized bridge. Suspensory apodemes, which fix the aedeagus in the membrane of the genital capsule, originate from the genital segment and are attached to the lateral surface of each basal plate near the middle. Dorsal connectives (apodemes of muscles of aedeagus protractors) origi-

nate from the apices of the basal plates of the phallobase. Their dilated and sclerotized apices are named the capitata processes. Ventral connectives, or apodemes of the retractors of the aedeagus, are attached to the basal plates ventrally. In many shield bugs, places of the attachment of the dorsal and ventral connectives are drawn into more or less developed, sclerotized processes of the phallobase, which in the present work are designated as the dorsal and ventral processes, respectively. The phallobase, fixed in the genital segment by the suspensor apodemes, can swing forward and backward during contraction of the protractors and retractors.

The semen fluid passes from spermaries to the base of the aedeagus via a mesodermic tube, named the ductus ejaculatorius, which terminates by the primary gonopore on a membrane, enveloped with the phallobase. The semen fluid passes from the primary gonopore through the entire aedeagus via an ectodermic tube, named the ductus seminis, to the secondary gonopore, situated on the straightened aedeagus apically or subapically. In all Pentatomomorpha, the ductus seminis widens in the median part, forming the ejaculatory reservoir. In Pentatomoidea, the ejaculatory reservoir possesses a very complicated structure, occupying most of the cavity of the theca. McDonald (1966) suggested designating the proximal part of the ductus seminis, running from the primary gonopore to the ejaculatory reservoir, as the seminal duct, and the distal part, running from the reservoir to the secondary gonopore, as the endophallic duct. This terminology does not seem completely suitable, but it is widespread and used in our work.

The tubular theca, the next part of the aedeagus in Heteroptera, is densely attached to the phallobase and possesses sclerotized walls. The sack-like endosoma is, by contrast, membranous. In normal state, it is placed entirely in the theca, appearing from its mouth like a glove finger under the hydraulic pressure. Distal margins of the endosoma are attached to the moth of the theca. Thus, in the resting state, the theca is the external wall and frequently a single visible part of the aedeagus. The shape, size, and character of sclerotization of the theca strongly vary. In many Pentatomidae, the base of the ventral wall of the theca bears a pair of small rounded prominences, in the following text designated as the ventral tubercles. In Asopinae, some Pentatominae, and Podorinae, the apical part of the theca is dilated, possessing a deep ventral emargination, and separated from the basal part by a band (this

modified apical part of the theca is frequently named "the thecal shield"). In some Pentatominae, the apex of the theca is supplied by a pair of titillators (dorsal sclerotized processes).

In all Pentatomomorpha, the endosoma is, in its turn, subdivided into 2 parts: conjunctiva and vesica. The vesica is a well isolated distal (in straight position) part of the endosoma, bearing the secondary gonopore. It possesses a narrow base and is unable to turn inside out like the undifferentiated endosoma. The membranous conjunctiva is the proximal part of the endosoma that turns inside out under haemolymph pressure during copulation, thus pushing the vesica off the theca.

The basic morphology of the conjunctiva and vesica strongly differ in the main groups of Pentatomomorpha. In Pentatomoidea, the vesica is formed due to the membrane of the endosomic wall, which is densely attached to the distal sclerotized part of the ductus ejaculatorius along its entire length. As a result, the vesica looks like a sclerotized process, tube-shaped and rounded in cross section, with the aperture of the secondary gonopore situated at the apex. The vesica of Pentatomoidea can be strongly developed, significantly exceeding the length of the aedeagus or even of the body of an insect, or, by contrast, reduced to a short tube-like rudiment. In the first case, the vesica is frequently smoothly bent or spirally twisted and in resting position projects from the theca.

Most frequently, the conjunctiva of Pentatomoidea is developed very well, consisting of large membranous lobes turning inside out and straightening during copulation. The number, shape, and degree of the development of these lobes, and also the presence or absence of sclerotized appendages, strongly vary. As far as the homologation of lobes of the conjunctiva in the whole family of shield bugs is impossible, the topographic nomenclature of these structures is used in our work. This nomenclature is based on the relative position of lobes and direction of their apices.

In a typical case, the vesica originates from the apex of a lobe, situated at the base of the straightened conjunctiva and directed ventrally; further, we shall call it the ventral lobe. In Pentatomidae, lateral walls of the ventral lobe are usually reinforced by more or less elongate sclerites, the so-called median penal plates. These plates can partly fuse or remain free. In most cases, the apices of the medial penal plates are dilated and terminate with a pair of apical spoon-shaped proc-

esses, enveloping the base of the vesica laterally. Apical outgrowths of the medial plates can entirely conceal the vesica laterally, when the later is strongly reduced.

In some shield bugs (Discocephalinae, some Pentatominae), the aedeagus is strongly modified, vesica and conjunctiva are undifferentiated, and a part of the aedeagus is strongly sclerotized distally to the theca and could not be rolled into it even partly. In this case, we used the term endosoma to designate the modified apical part of the aedeagus, because it is impossible to homologize it with the vesica and conjunctiva of other Pentatomidae.

The following designations of the morphological structures are given in the figures: ap.l, apical part of conjunctiva; bl.l, basolateral lobe of conjunctiva; c.p, capitate processes; d.pr, dorsal processes; ei.res, ejaculatory reservoir; en.d, endophallic duct; es, endosoma; m.l, median lobe of conjunctiva; med.pl, median penial plates; phb, phallobase; s.ap, suspensory apodema; s.g, secondary gonopore; sem.d, seminal duct; th, theca; v, vesica; v.l, ventral lobe of conjunctiva; v.pr, ventral processes; v.tub, ventral tubercle of theca; vl.l, ventrolateral lobe of conjunctiva.

## FAMILY PENTATOMIDAE

### Subfamily DISCOCEPHALINAE

Representatives of this subfamily, comprising more than 70 genera, are spread exclusively in the tropics and subtropics of the New World. The diagnosis and volume of the group were established by Rolston and McDonald (1979). In representatives of the group, the labium is shifted backwards and usually articulated to anterior eye margins; trichobothria of abdominal segment VII are situated laterally to spiracles of signets VI and VII. The subfamily includes 2 tribes: Discocephalini Fieber, 1860 and Ochlerini Rolston, 1981. The latter tribe was later revised (Rolston, 1992), whereas the nominative tribe remains insufficiently studied.

#### Tribe Discocephalini

##### *Dryptocephala obtusipes* Stål, 1872 (Figs. 1, 2)

**Material.** Argentina, Misiones Loreto, 19.XII.1930 (A. Ogloblin), 4 specimens; Paraguay, Alto Parana, P-to Bertoni, 1915 (Strelnikov, Tanasiichuk), 1 specimen.

The phallobase is weakly sclerotized, bearing strongly elongate semi-transparent ventral processes. Distally, the basal plates are supplied with strongly elongate dorsal processes. The dorsal connectives are rather short, attached to the apices of the dorsal processes; they terminate with cone-shaped sclerotized capitate processes. The ventral connectives are indistinct, articulated to the apices of the ventral processes. The suspensory apodemes are strong, attached to the lateral surfaces of the basal plates of the phallobase.

The theca is strongly and uniformly sclerotized, approximately square, possessing rounded dorsal and straight ventral walls. The ventral wall of the theca possesses a well-developed carina at the base and forms a pair of semitransparent ventral tubercles laterally. The ejaculatory reservoir is large, occupying nearly the entire cavity of the theca; it is sclerotized ventrally. The endophallic duct is also nearly entirely sclerotized.

The endosoma is entirely sclerotized and strongly reduced. It forms the apical part of the aedeagus; walls of the endosoma are immovably articulated to walls of the theca. The endosoma is bordered by a suture, corresponding to the mouth of the theca, and forms a pair of small bud-shaped lateral processes and beak-shaped central part. The secondary gonopore is very small, situated at the very apex of the endosoma.

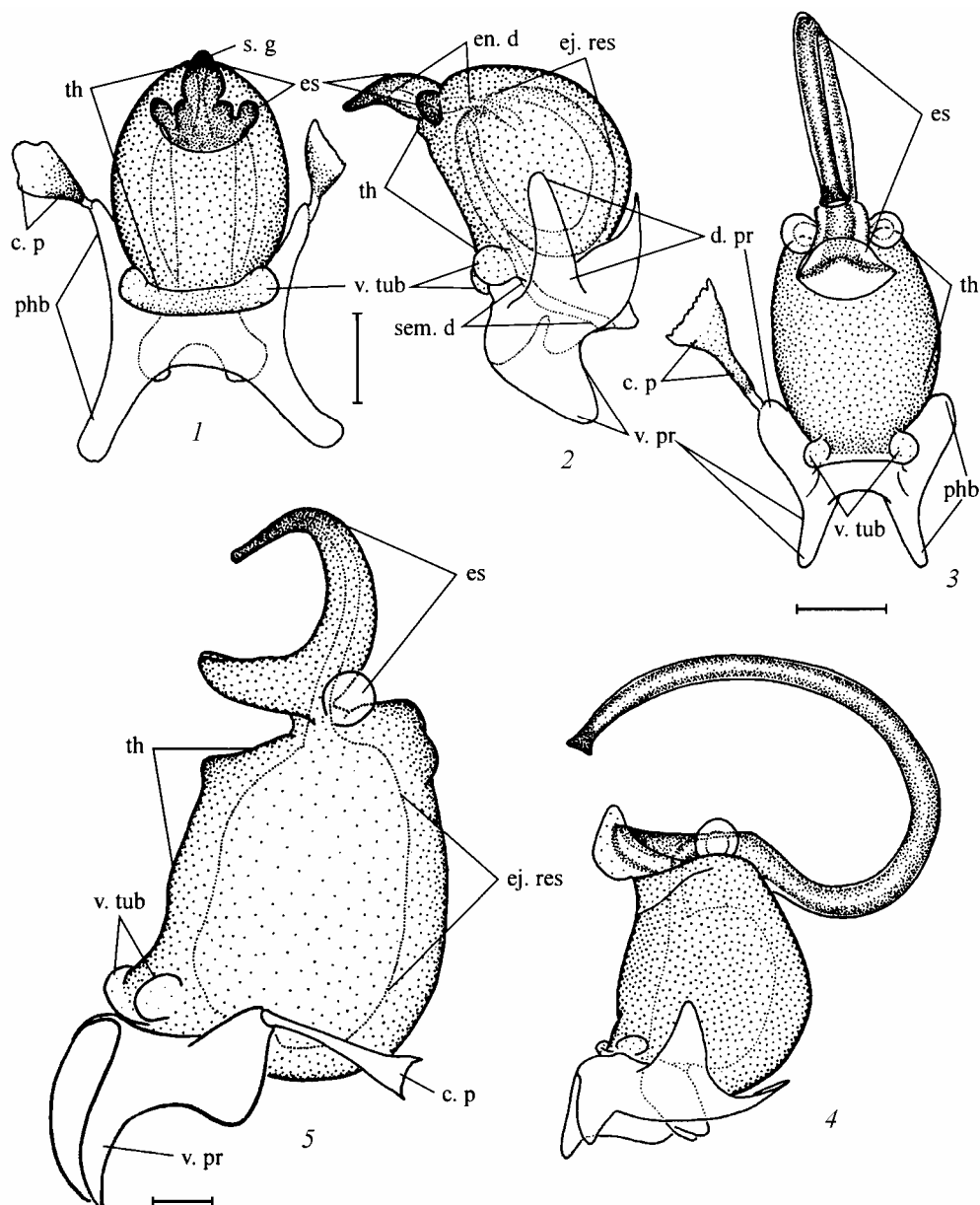
According to the published drawings (Ruckes, 1966), the aedeagus of *D. dentifrons* Latr. possesses a similar structure.

##### *Antiteuchus (Antiteuchus) tripterus* (Fabricius, 1787) (Figs. 3, 4)

**Material.** Brazil, Saõ Paulo, Piracicaba, (G. Bondar), 3 specimens; Colombia, Rio Ortegua, Hetucho, VII.1926 (Woronov), 1 specimen; 1 specimen without geographical label, "*Dinocoris (Mecistorhinus) piceus*, Oshanin det."

Other species examined in this genus: *A. (A.) sepulcealis* (Fabricius, 1803): Bolivia, Yungas (coll. I. Gudima), 1 specimen; *A. (A.) piceus* (Palisot de Beauvois, 1805): Brazil, Saõ Paulo, Piracicaba, (G. Bondar), 1 specimen; *A. (Neodine) tatei* (Ruckes, 1958): Colombia, Rio Magdalena, Penas Blancos, 3.V.1926 (Woronov), 1 specimen.

The phallobase possesses the same structure as that of *Dryptocephala*, but the dorsal and ventral processes are shorter. The theca is oblong-oval, strongly scler-



**Figs. 1–5.** Discocephalini, aedeagus in (1, 3) ventral and (2, 4, 5) lateral views: (1, 2) *Dryptocephala obtusipes* Stål; (3, 4) *Antiteuchus tripterus* F.; (5) *Callostethus guttatopunctatus* F. Scale 0.2 mm.

rotized, with rounded dorsal wall. The ventral wall is nearly straight, with a pair of rounded, weakly sclerotized tubercles at base. The ejaculatory reservoir is large, occupying virtually the entire cavity of the theca. The endophallic duct is strongly sclerotized along the entire length.

The walls of the endosoma along the entire length, except the base, adjoin C-shaped ductus seminis, forming a fine, rounded in cross-section C-shaped process exceeding the length of the theca. At the base, it smoothly passes into a small lobe of the endosoma,

directed ventrally. It is flattened and smoothly pointed apically, its upper wall is sclerotized, and the apex and lower wall are membranous. Laterally to the C-shaped process, the endosoma forms a pair of small rounded basal prominences with thick membranous walls

The aedeagus of other species investigated, including both species from the nominotypical subgenus and from the subgenus *Neodine*, is similar to that in *A. (A.) tripterus* in the structure and proportions; only in *A. sepulcralis*, the C-shaped process is slightly finer and shorter, no longer than the theca. According to the

drawing published (Ruckes, 1964), *A. (A.) mixtus* Fabr. possesses a similar aedeagus.

***Callostethus guttatopunctatus*** (Fabricius, 1803)  
(Fig. 5)

**Material.** Colombia, Rio Ortegua, Hetucho, VII.1926 (Woronov), 1 specimen.

The phallobase possesses very long and fine ventral processes. The basal plates are triangular; their distal angles are not drawn into dorsal hands. The theca is strongly and uniformly sclerotized, the base of its ventral wall is membranous, with well-developed ventral tubercles. The ventral wall is nearly straight, with a strong angle-shaped prominence at the apex. The dorsal wall is strongly convex at base; it forms 3 smoothly rounded tubercles near the mouth of theca. In addition, small tubercles are situated on the lateral walls of the theca near its middle. The theca is approximately 1.5 times as long as wide. The ejaculatory reservoir is large, occupying virtually the entire cavity of the theca. The endophallic duct is strongly sclerotized along the entire length.

The endosoma looks like a C-shaped sclerotized process, with both apices being directed ventrally and pigmented. This process is no longer than half the length of the theca. The apical part of the process becomes gradually finer toward the apex, where a small aperture of the secondary gonopore is situated.

The basal part, in contrast, is slightly dilated and possesses a bifurcated apex. The base of the endosoma is membranous, stipulating mobility of the C-shaped process in relation to the theca. Laterally to the process, the endosoma forms a pair of small vesicular prominences with membranous walls (as in *Antiteuchus*).

***Dinocoris maculates*** (Laporte, 1833)

1 specimen without geographical label, "*Dinocoris (Mecistorhinus) piceus*, Oshanin det."

The phallobase is weakly sclerotized. The dorsal processes are indistinct, dorsal connectives are attached to proximal angles of basal plates. The theca is uniformly sclerotized, oblong-oval, twice as long as wide. The ventral wall of the theca possesses a pair of weakly sclerotized rounded tubercles at the base. The ejaculatory reservoir is large, occupying nearly the entire cavity of the theca; it is sclerotized ventrally, with the apex partly projecting into the endosoma. The endophallic duct is sclerotized along the entire length.

The endosoma is small and reduced. Its walls are sclerotized at the base and immovably articulated to walls of the theca. The apical parts of the endosomic walls are membranous, densely adjoin weakly sclerotized ductus seminis, forming a small tube-shaped process. It is gently bent, so that the apical secondary gonopore is directed ventrally. Ventrally and distally, the base of the endosoma continues into a wide and short flattened lobe with membranous walls. The endosoma is about half as long as the theca.

According to the published drawings and descriptions, (Becker and Grazia, 1985), the aedeagi of all the species of the genus possess a similar basic structure; insignificant differences concern only the degree of development of the ventral lobe and, to a lesser extent, of the apical tube-shaped process.

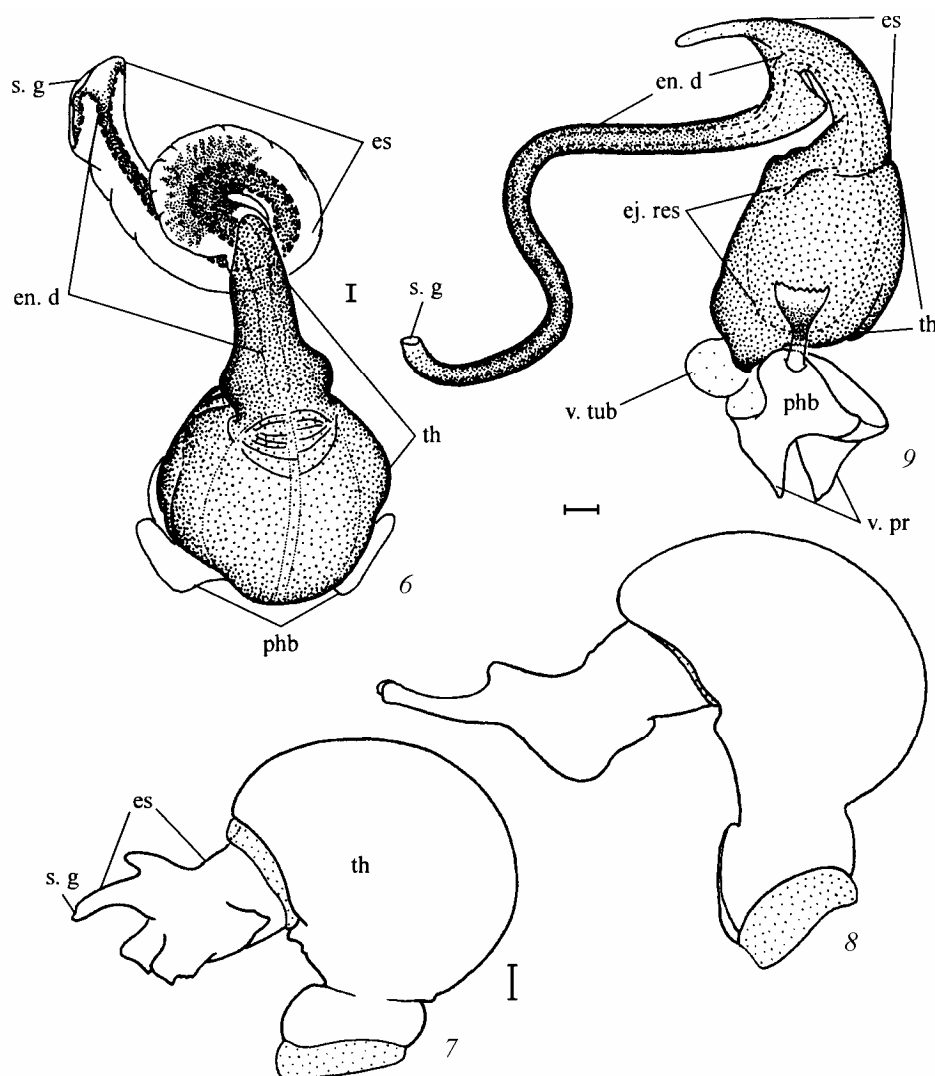
***Lineostethus clypeatus*** (Stål, 1862)

**Material.** Arizona, Baboquivaria Mts. (F.H. Snow), 1 specimen.

The phallobase is strongly reduced, similar to that in *Antiteuchus*. The theca is uniformly sclerotized, with a nearly straight ventral and strongly convex basally dorsal wall. The ventral wall of the theca possesses a pair of weakly sclerotized rounded tubercles at the base. The apex of the dorsal walls has a platen-shaped swelling, forming a pair of distinct angular prominences on the sides. The ejaculatory reservoir is large, occupying nearly the entire cavity of the theca; it is sclerotized dorsally. The endophallic duct is sclerotized along the entire length.

The walls of the endosoma are densely and immovably articulated to walls of the theca. The latter is approximately 1.5 times as long as the endosoma; it looks like a lobe, strongly flattened laterally and slightly bending dorsally. The apex of the endosoma is slightly dilated and more or less gently rounded, bearing a short straight tube-shaped process, approximately 0.25 times as long as the endosoma. The secondary gonopore is situated at the apex of the apical process. The walls of the endosoma are dense, membranous, with a sclerotized base, ventral costa, and a pair of lateral strips connected under the tube-shaped process.

According to the published drawings and descriptions (Hildebrand and Becker, 1982), the aedeagi of all the 4 species of the genus possess a similar structure; insignificant differences concern only the degree of the development of the apical tube-shaped process and dorsal wall of the theca.



**Figs. 6–9.** Ochlerini, aedeagus in (6) ventral and (7–9) lateral views: (6) *Macropygium atrum* Spin.; (7) *Lincus* sp. 1; (8) *Lincus* sp. 2; (9) *Adoxoplatys minax* Bred. Scale 0.2 mm.

### Tribe Ochlerini

**Material.** Paraguay, Alto Parana, P-to Bertoni, 18.XII.1914 (Strelnikov, Tanasiichuk), 1 specimen; Paraguay, Alto Parana, P-to Bertoni, 1915 (Strelnikov, Tanasiichuk), 1 specimen; Bolivia, Santa Kruz, 1926 (Steinbach), 2 specimens; Bolivia, Coroico (coll. I. Gudima), 1 specimen; Peru, Loreto, 40 km NE Requena, VIII–IX.1990 (Malygin), 1 specimen.

The phallobase is weakly sclerotized, rather fine; dorsal processes are short and smoothly rounded, directed dorsolaterally. The ventral processes are indistinct. The dorsal connectives are short, terminating with cone-shaped capitate processes.

The theca is strongly sclerotized and pigmented, only the ventral wall is membranous at the base; the

ventral tubercles are indistinct. The basal half of the theca is strongly dilated, rounded dorsally, with a pair of indistinct lateral tubercles. The base of the sclerotized part of the theca is bordered by a suture, especially deep and forming a pair of lobes on the ventral wall. The apical half of the theca is strongly narrowed, tube-shaped; it goes from the dilated basal part at the straight angle. The apical part of the theca bears a pair of distinct lateral tubercles at base. The mouth of the theca is oval, opening ventrally. The ejaculatory reservoir is situated in the basal part of the theca and occupies virtually its entire cavity. The endophallic duct is very strongly sclerotized along the entire length, becoming thinner apically.

The endosoma is single-lobed, membranous; only its dorsal wall is partly sclerotized at the base. It enve-

lopes ductus seminis, strongly bent at the base. The membrane of the endosoma is free along the entire length; its walls are not fused with walls of the ductus seminis. The secondary gonopore is situated on the apex of the endosoma, wide, forming a pair of lateral grooves parting over the apex of the endosoma.

*Lincus* sp. 1 (Fig. 7)

**Material.** "Egyptus,"<sup>1</sup> 1 specimen.

The phallobase with well-developed, smoothly rounded dorsal processes. The ventral processes are smaller, pointed, very weakly sclerotized. The dorsal connectives are short, terminating with large (with the diameter approximately as long as theca), lamellate capitate processes.

The base of the theca is articulated to the theca; it possesses a membranous base and a pair of rounded tubercles on the ventral wall. The rest of the theca is very strongly sclerotized and pigmented, with a narrow base, separated by a deep band, and dilated apical part. The apical part of the theca possesses nearly straight dorsal and very strongly convex and rounded ventral walls. The mouth of the theca is wide, fringed with a weakly sclerotized fold. The ejaculatory reservoir occupies nearly the entire cavity of the dilated part of theca. The endophallic duct is sclerotized along the entire length.

The entire endosoma is very strongly sclerotized and pigmented; it is immovably articulated to the theca. It is wide and rather short, rounded in cross section, bearing 2 pairs of strong flattened processes ventrolaterally and a pair of unpaired processes with common base dorsally. The ventral processes of the first pair go from the median part of the endosoma and are directed laterally and basally. The processes of the second pair are slightly serrate along the inner margin; they go from the apex of the endosoma and directly apically. Slightly bent, pointed apically and rounded in cross section dorsal processes also go from the apical part. The aperture of the secondary gonopore is small; it is situated on the apex of the distal dorsal process.

*Lincus* sp. 2 (Fig. 8)

**Material.** Peru (Staudinger), 1 specimen.

The phallobase and theca are similar to those in the previous species. The endosoma is also entirely scler-

otized, rounded in cross-section, immovably articulated to the theca. It is developed somewhat better than in the preceding species and is approximately as long as the theca. The ventrolateral processes of the endosoma are indistinct, and the dorsolateral processes are situated at the very apex. At the same time, the distal process, bearing the aperture of the secondary gonopore at the apex, is significantly longer than in the previous species.

According to the published drawings of the aedeagus in *Lincus laminatus*, *L. tumidifrons*, and *L. vandoesburgi* (Rolston, 1983), other species of the genus are also characterized by a strongly sclerotized, wide, and rather short endosoma.

*Adoxoplatys minax* Breddin, 1903 (Fig. 9)

**Material.** Peru, Marcapata (coll. I. Gudima), 2 specimens.

The phallobase is strongly sclerotized, with a pair of elongate, pointed ventral processes. The dorsal processes are undeveloped; the dorsal connectives are attached to proximal angles of the basal plates. These connectives are short, terminating with cone-shaped sclerotized capitate processes.

The theca is strongly sclerotized, except for the very base of the ventral wall. The ventral tubercles are well-developed, entirely membranous. The sclerotized part of the theca is oblong-oval, smoothly narrowing apically. The ejaculatory reservoir occupies nearly entire cavity of the theca; the endophallic duct is only slightly sclerotized along the entire length.

Nearly the entire endosoma is sclerotized; its walls smoothly pass into walls of the theca. The border between these parts of the aedeagus could be marked only conditionally along an indistinct transverse suture passing along the ventral wall distally to the apex of the semen reservoir. Apically, the endosoma smoothly narrows into a narrow and rather short membranous process, bending ventrally. Ventrally, the base of the endosoma is continued into a long, sclerotized, but retaining some flexibility S-shaped process. This process is tube-shaped; it is longer than the entire aedeagus and terminates with the secondary gonopore at the apex. The walls of this process adjoin those of the semen duct, passing to the secondary gonopore, nearly along the entire length. Its distal part is strongly pigmented. At the very base, the process is somewhat dilated, possessing a weakly sclerotized inner wall, which makes it slightly movable in relation to the basal part of the aedeagus.

<sup>1</sup> The label is distinctly erroneous, because representatives of the subfamily are known only from the New World.

*Adoxoplatys comis* Breddin, 1903

**Material.** Peru, Marcapata (coll. I. Gudima), 1 specimen.

It is similar to the previous species. The phallobase and theca are identical to those in *A. minax*. The tube-shaped process of the endosoma is also similar to that in the above species in shape and size; however, the apical membranous process in undeveloped and ventral wall of the base of the endosoma is uniformly sclerotized.

*Miopygium grossa* Ruckes, 1958

**Material.** Brazil, São Paulo, Piracicaba, (G. Bondar), 1 specimen.

The phallobase is weakly sclerotized. Dorsal processes undeveloped; dorsal connectives are attached to proximal angles of the basal plates. Ventral processes are strongly reduced, slightly distinct.

The theca is strongly and uniformly sclerotized, except for the membranous base of the ventral wall; ventral tubercles are well-developed, entirely membranous. The basal part of the theca is strongly dilated; its dorsal wall is strongly convex, bearing a pair of well-developed lateral tubercles; the ventral wall is nearly straight. The apical part of the theca is, by contrast, narrowed, tube-shaped, goes from the base under obtuse angle and is separated by a band, especially distinct dorsally. The ejaculatory reservoir occupies nearly the entire dilated part of the cavity of the theca.

The endosoma is well-developed, longer than the theca, and looks like a long, sinuate tube-shaped process with the apical gonopore at the apex. The walls of the endosoma more or less densely adjoin the ductus seminis nearly along its entire length.

The base of the endosoma is dilated; it is partly membranous, providing mobility of the process in relation to the theca.

The aedeagus of Discocephalinae is first of all distinguished by the modified endosoma, which is lacking membranous lobes in all the representatives and could not be involved into the theca in the resting state, because walls of the endosoma and endophallic duct are sclerotized.

According to the published drawings and descriptions of the aedeagi, this feature is also characteristic of all Discocephalinae, uninvestigated in the present work: *Marghita crepuscula* (Ruckes, 1964), *Paralin-*

*cus silvae* (Rolston, 1983a), *Priapismus* (Rolston, 1984; Rolston, 1992b), *Parochlerus latus* (Rolston, 1992a). Correspondingly, the absence of differentiated vesica, median plates, and reversible membranous lobes of the conjunctiva; pronounced sclerotization of walls of the endosoma and/or of the endophallic duct and some other structural features can be treated as apomorphies of the whole group.

Endosomic walls are sclerotized to various extents. For example, in *Dryptocephala* and *Lincus*, the endosoma is strongly sclerotized along the entire length and immovably articulated with the theca. In representatives of *Callostethus* and *Miopygium* examined, the basic sclerotized part of the endosoma with the secondary gonopore at the apex retains some mobility in relation to the theca, owing to a membranous base. In spite of sclerotization, the tube-shaped process, typical of many Discocephalinae (*Adoxoplatys*, *Dinocoris*, and, to a lesser degree, *Antiteuchus*), retains certain elasticity. Finally, in *Macropygium*, the walls of the endosoma are virtually entirely membranous and do not adjoin the endophallic duct. Nevertheless, a narrow endosomic lobe cannot be involved into the theca when at rest, because its shape is supported by a very strongly sclerotized ductus seminis, and any lobes, straightening under the pressure of the haemolymph, are absent.

It should also be mentioned that a great diversity in the shape of the aedeagus and, at the same time, the stable basic structure at the generic level, are characteristic of representatives of the group. For example, all the species studied in the largest genus *Antiteuchus*, including species of the nominotypical subgenus and of the subgenus *Neodine* are virtually similar in the structure of the aedeagus. The common basic structure is also characteristic of all the species of the genera *Dinocoris* (Becker and Grazia, 1985), *Lineostethus*, (Hildebrand and Becker, 1982), and the species examined of the genera *Adoxoplatys* and *Lincus*. Some common morphological features, such as the presence of a C-shaped endosomic process and a pair of membranous vesicle-shaped prominences at its base, are traced in the structure of the aedeagus in closely related genera *Antiteuchus* and *Callostethus*. Thus, the use of the structure of the aedeagus for both confirming of the monophily of the genera and supergeneric taxonomy is highly prospective.

Subfamily **PHYLLOCEPHALINAE**

Phyllocephalinae is a rather small subfamily comprising about 40 genera distributed nearly exclusively



in the Ethiopic and Indo-Malayan regions. Representatives of the group are characterized by the presence of a very short proboscis, reaching only the fore tarsi; the first and the base of the second segments are concealed laterally by non-fused buccal plates. Many authors treated Phyllocephalinae as members of the subfamily Pentatominae (Leston, 1952; Gross, 1976) or underlined the undoubted close relationship between these two groups (Linnavuori, 1982). Four tribes from the Indo-Malayan region have been described in the subfamily Phyllocephalinae: Cressonini Kamaluddin et Ahmad, 1991; Megarrhampini Ahmad et Kamaluddin, 1982; Tetrodini Ahmad et Kamaluddin, 1990; and Phyllocephalini Amyot et Serville, 1843. However, this subfamily has not been revised on the world fauna scale. Most of the genera and species of Phyllocephalinae belong to the nominotypical tribe.

#### Tribe *Phyllocephalini*

*Diplorhinus furcatus* (Westwood, 1837) (Figs. 10, 11)

**Material.** Java, Djeroelelegi, 25.XI.1931 (Lucht), 1 specimen.

The phallobase is strongly sclerotized, with strong, dorsally widening basal plates, triangular in lateral view. Ventral processes are very short, rounded, and flattened dorsoventrally; their apices are slightly retracted into the body cavity. Dorsal processes are undeveloped; dorsal connectives are attached to proximal angles of the basal plates. These connectives are short, bearing strongly sclerotized capitate processes. The bridge of the phallobase, connecting basal plates dorsally, is half as long as the theca.

The theca is densely articulated to the phallobase, possessing uniformly sclerotized walls. It is cylindrical, gently widening in the apical half and narrowing towards the base and apex. A narrow, weakly sclerotized strip is situated at the base of the ventral wall of the theca; this strip laterally widens into a pair of small, distinctly separated ventral tubercles. The ventral wall of the theca forms a smooth prominence between these tubercles. The ejaculatory reservoir occupies nearly the entire cavity of the theca, except for its apex.

The membranous conjunctiva (in straightened state) is shorter than half of the theca. It is deeply divided into 3 lobes: 1 ventral and 2 apical ones. The apical lobes are symmetric, gently pointing apically; their apices are slightly bent toward the median line. The surface of the apical lobes is covered with very small

spines. The ventral lobe is smaller than the apical lobes; its lateral walls are reinforced with strongly sclerotized medial plates of the penis, which dilate apically, terminating by a pair of spoon-shaped processes. Both apical processes are thin-walled and strongly sclerotized, with convex outer and concave inner walls. The vesica is situated between them, looking like a very short straight tube with the secondary gonopore aperture at apex. The walls of the vesica are sclerotized, densely adjoining the ductus seminis. The median plates of the penis are drawn together at the apex of the ventral plate, enveloping the base of the vesica, but not fusing. Together with 3 basic lobes, 2 small basolateral lobes are situated laterally at the base of the conjunctiva; their apices are directed towards the phallobase. The upper surfaces of each of these lobes are reinforced by narrow and strongly bent sclerites, reaching the bases of the median plates of the penis.

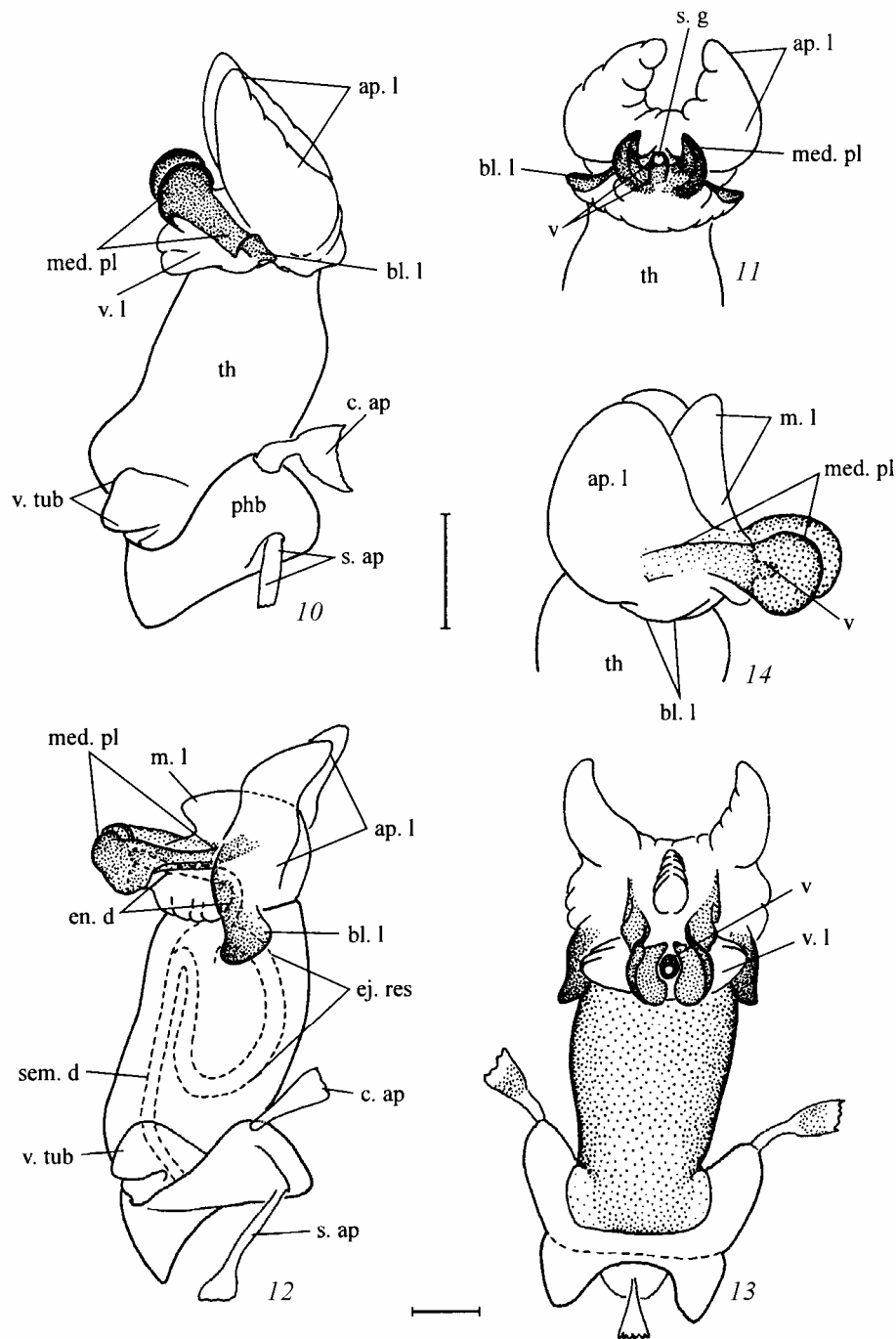
*Schyzops aegyptiaca* (Lefevre, 1831) (Figs. 12, 13)

**Material.** SE Persia [Iran], environs of Bampur, 8–12.IV.1901 (Zarudnyi), 1 specimen; Persia [Iran], Beludjistan, Kaptegin-Dukan, 26.II.1901 (Zarudnyi), 1 specimen; Egypt (P.N. Semenov), 1 specimen; 1 specimen without geographical label.

The phallobase is strong and strongly sclerotized, similar to that in *Diplorhinus*, but the basal plates are narrower and the ventral processes are more developed.

The theca is cylindrical, uniformly sclerotized, with distinct and pronouncedly separated ventral tubercles at the base, structurally similar to that of *Diplorhinus*.

The morphology of the inner structures of the aedeagus is also similar to that in *Diplorhinus*; the conjunctiva (in straightened state) is shorter than half of the theca. The ventral lobe and a pair of apical lobes are similar in structure, but, unlike in *Diplorhinus*, in *S. aegyptiaca*, apices of the apical lobes are directed sideward and somewhat dorsally. The ventral lobe, bearing vesica and median plates, is more developed, and only slightly shorter than the apical lobes. The basolateral lobes are well-developed, wide, flattened, and entirely sclerotized. Sclerites of basolateral lobes, becoming thinner and strongly bending, reach the bases of the median plates of the penis along lateral walls of the conjunctiva. In addition, conjunctiva forms a small median keel-shaped lobe, running along the median line of the aedeagus from the bases of the apical lobes to the base of the basal lobe.

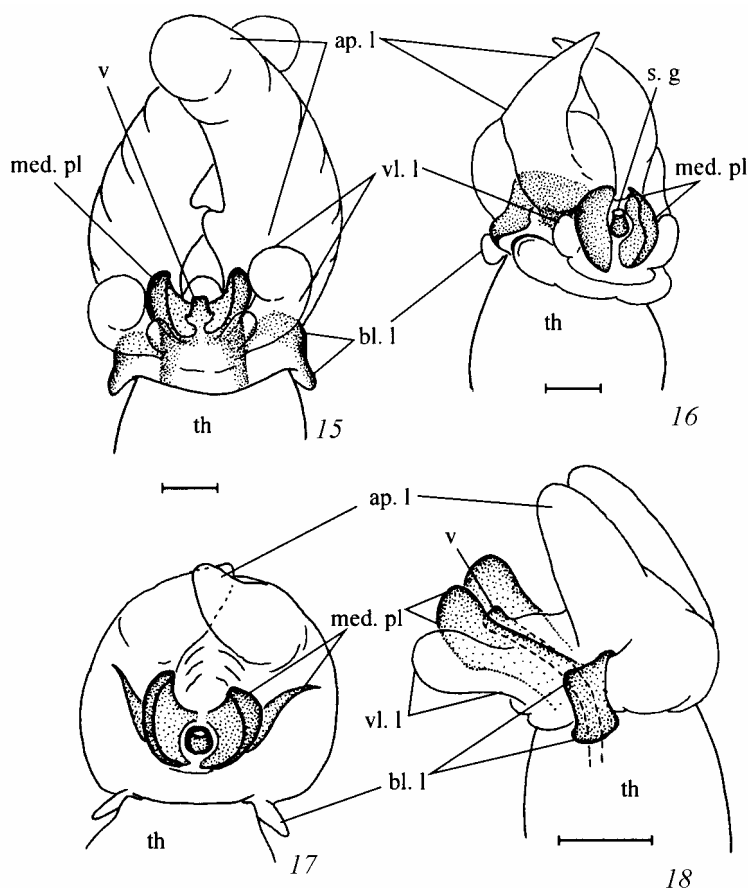


**Figs. 10–14.** Phyllocephalinae, aedeagus. (10, 11) *Diplorhinus furcatus* Westw.: (10) lateral view; (11) apex of aedeagus, ventral view; (12, 13) *Schyzops aegyptiaca* Lef.: (11) lateral, (12) ventral view; (14) *Gonopsis affinis* Uhl., apex of aedeagus in lateral view. Scale 0.2 mm.

***Macrina juvenca*** (Burmeister, 1835)

**Material.** Afrique Occidentale Française. Haute Volta, Poundou, VIII.1927 (Olsufjev), 1 specimen; Cote d'Ivoire, Bingerville (Clermont), 1 specimen; Kamerun (coll. I. Gudima), 1 specimen.

The aedeagus is virtually of the same structure as in the previous species. The phallobase possesses triangular basal plates and well-developed ventral processes. The theca is cylindrical, uniformly sclerotized, gently widening in the apical half, with distinct ventral tubercles.



**Figs. 15–18.** Phyllocephalinae, apex of aedeagus in (15, 17) ventral, (16) ventrolateral, and (18) lateral view: (15) *Salvianus lunatus* Dist.; (16) *Tantia vicina* Sign.; (17) *Megarhampus hastatus* F.; (18) *Melampodius* sp. Scale 0.2 mm.

The apical, ventral, and small median lobes of the conjunctiva are similar to those in *Schyzops*. The median plates of the penis, the vesica, and basolateral lobes are all similar to those in the previous species.

***Gonopsis affinis*** (Uhler, 1860) (Fig. 14)

**Material.** Japan, Honshu, Kunitachi, 16.VI.1936 (Zhenzhurist), 1 specimen; Japan, Honshiu, Inakashira, 4.IX.1933 (Zhenzhurist), 1 specimen; Korea, Phusan, 21.VIII.1900 (Schmidt), 1 specimen; China, Tien Tsin, 15–21.V.1915 (Vasiljev), 1 specimen.

Other species examined in the genus: *G. coccinea* (Walker, 1868): Carin Chéba, 900–1100 m, 5.XII.1888 (L. Fea), 1 specimen; *G. tonkinensis* Breddin, 1904: Vietnam, Tam Dao, 16.XI.1961 (O. Kabakov), 1 specimen; Hajiank, Tonkin, 1 specimen.

The phallobase and theca are of the same structure as in the previous species; the theca is widened apically. The membranous conjunctiva (in straightened state) is half as long as the theca. It is divided into 4

lobes: ventral, median, and 2 apical ones. The apical lobes are very widely rounded; the median lobe is situated somewhat more ventrally; its apex is obtusely pointed. Unlike the species mentioned above, the median lobe is well-developed, approximately as long as the apical lobes. The median plates of the penis and the vesica, situated on the ventral lobe are all similar to those in the previous species. The basolateral lobes are somewhat reduced, small entirely membranous; in straightened state, they diverge sideward.

In two other species examined, the aedeagus possesses a similar structure. A separate publication treats the structure of the aedeagus in *Gonopsis affinis* (Kim and Lee, 1993); however, these authors have studied the aedeagus only when at rest resting state, with the conjunctiva and vesica entirely retracted into the theca.

***Salvianus lunatus*** (Distant, 1901) (Fig. 15)

**Material.** Carin Chéba, 900–1100 m, 5.XII.1888 (L. Fea), 1 specimen.

The structure of the phallobase is typical of the group, but the phallobase is comparatively weakly sclerotized, bearing very short ventral processes. The theca is cylindrical, uniformly sclerotized, of the same structure as in previous species; however, its dorsal wall is hump-shaped, swollen in the apical part.

As in many other species of the subfamily, the conjunctiva is divided into 3 large lobes: ventral and 2 apical ones. Entirely membranous apical lobes are very well developed, so that the entirely straightened conjunctiva is as long as the theca. The apices of the apical lobes are bent ventrally; the inner wall of each lobe forms a small basal process. The ventral lobe is similar to that in previous species, but the median plates of the penis possess wide and strongly sclerotized bases. In addition, a pair of small processes, the so-called ventrolateral lobes, departs from the lower membranous wall of the basal lobe. The ventrolateral lobes are digitiform, membranous; they adjoin the outer walls of the apical processes of the median plates, projecting beyond their apices. The spoon-shaped apical processes and the vesica are of the same structure as in the other species of the subfamily. The basolateral lobes, situated at the base of the straightened conjunctiva, are well developed and sclerotized dorsally. Sclerites of the basolateral lobes, becoming thinner and strongly bending, reach the bases of the median plates of the penis along the lateral walls of the conjunctiva.

*Chalcopsis glandulosa* (Wolff, 1811)

**Material.** Hajiank, Tonkin, 3 specimens.

The phallobase and theca are similar to those in *Diplorhinus*. The phallobase is strongly sclerotized, with rather short ventral processes. The theca is uniformly sclerotized, cylindrical, with a virtually symmetric apical part.

The conjunctiva is similar to that in *Salvianus*. The apical lobes are very well developed, so that the entirely straightened conjunctiva is approximately as long as the theca. In comparison with *Salvianus*, both lobes are finer, without prominences at the base of the inner walls; their apices diverge somewhat sideward from the median line and are bent dorsally. The basolateral lobes are slightly wider than in the previous species and shifted upward, so that they are situated laterally at the base of the dorsal surface of the entirely straightened conjunctiva. As in the majority of other species, the upper surface of each basolateral lobe is

reinforced with a bent sclerite stretching from bases of median plates of the penis. The ventrolateral lobes are well-developed, slightly projecting beyond the apices of the median plates.

*Dalsira vicaria* (Linnavuori, 1982)<sup>2</sup>

**Material.** Abessinia, Adis-Abeba, 1898–1899 (Brovtsyn), 2 specimens.

The phallobase and theca are similar to those in the previous species. The conjunctiva in straightened state is less than half as long as the theca. It is divided into 4 lobes: ventral, median, and 2 apical ones. The apical lobes are very widely rounded; their obtuse apices are pointed ventro-apically. The median lobe is situated somewhat more ventrally; its pointed apex is directed apically. The ventral lobe bears very strongly sclerotized median plates of the penis. The basolateral lobes are similar to those in the previous species; they are wide, shifted dorsally, and originate from the sides of the dorsal surface at the base of the conjunctiva.

*Tantia vicina* (Signoret, 1851) (Fig. 16)

**Material.** Kamerun (Conradt), coll. I. Gudima, 1 specimen; Kongo, Kasai (Breuning), 1 specimen; Gabun (coll. I. Gudima), 1 specimen.

The phallobase and theca similar to those in the previous species. The phallobase is strongly sclerotized, with a wide bridge. The ventral processes possess rounded, flattened dorsoventrally apices, retracted into the body cavity. The dorsal processes are indistinct, dorsal connectives are attached to proximal angles of the basal plates. The theca is cylindrical, gently widening in the apical half and narrowing towards the base and apex. A narrow, weakly sclerotized strip is situated at the base of the ventral wall of the theca; this strip laterally widens into a pair of distinctly separated tubercles.

The membranous conjunctiva in straightened state is half as long as the theca. It is deeply divided into 3 equal lobes: 2 membranous apical lobes and a single ventral lobe, reinforced with median plates of the penis and bearing the vesica at the apex. Both apical

<sup>2</sup> Linnavuori (1982) described *Metonymia vicaria* with an erroneous authorship of Bergroth. According to labels of specimens from the ZIN collection, Bergroth really separated the species described, but never published the description. Later, the genus *Metonymia* was synonymized with *Dalsira* (Rider and Rolston, 1995).

lobes are similar to those in *Diplorhinus*, gently pointing apically; their apices are bent toward the median line and ventrally. The ventral lobe is similar to that in the preceding species. The ventrolateral lobes are present; they adjoin the outer walls of the apical processes of the median plates, but do not reach their apices. The apical processes of median plates of the penis and the vesica are similar to those in other species of the subfamily. Sclerites of the basolateral lobes are well developed, but the lobes themselves are reduced, possessing the membranous apices.

#### Tribe **Megarrhampini**

*Megarrhampus hastatus* (Fabricius, 1803) (Fig. 17)

**Material.** Tonkin, Hanoi, 30.VII.1917 (Jeanvoine), 1 specimen; Annam, Song-Dinh, 9.VIII.1909 (Pliginski), 3 specimens; Annam, Song-Dinh, 11.VIII.1909 (Pliginski), 1 specimen/

The phallobase, theca, conjunctiva, and vesica are similar to those in *Diplorhinus*, possessing the structure typical of the subfamily. The entirely straightened conjunctiva is slightly longer than half the length of the theca. The apical lobes are slightly longer than the ventral lobe; they are widely rounded basally and gently pointed apically. The apices of the apical lobes are pointed to the median line somewhat ventrally. The median lobe is also distinct; however, it is bud-shaped, significantly smaller than the apical lobes, and nearly entirely concealed by their approaching apices. The ventral lobe is similar to that in *Diplorhinus*; ventrolateral lobes are absent. The basolateral lobes are small, looking like entirely membranous folds.

*Megarrhampus truncatus* (Westwood, 1837)

**Material.** Java, Batavia, XI.1906 (P. Ivanov), 1 specimen; *Java occidentalis*, Buitenzorg, 1901 (Pedaschenko), 1 specimen.

The aedeagus is similar to that in the previous species; however, the theca, phallobase, and median plates of the penis are more sclerotized; basolateral lobes are also sclerotized.

#### Tribe **Cressonini**

*Melampodius* sp. (Fig. 18)

**Material.** Belgian Congo, Katanga, Kinda (coll. I. Gudima), 1 specimen.

The phallobase and theca are similar to those in *Diplorhinus*, possessing the structure typical of the

subfamily. The entirely straightened conjunctiva is shorter than half length of the theca; it is divided into a pair of the apical lobes and the basal lobe. The apical lobes are smoothly rounded; their apices are virtually parallel to each other and to the axis of the aedeagus. The ventral lobe is slightly shorter than the apical lobes. The median plates of the penis are strongly sclerotized. The ventrolateral lobes are developed; they terminate at the same level with the apices of the median plates. The vesica possesses the structure typical of the subfamily. The basolateral lobes are well-developed and flattened; they are situated laterally. Sclerites, reinforcing these lobes, reach the bases of the median plates of the penis.

In all the representatives of the subfamily Phyllocephalinae, the aedeagus possesses a similar basic structure, characterized by the following set of characters:

(1) The phallobase is strongly sclerotized, bearing triangular basal plates; short ventral processes, flattened dorsoventrally; and a wide bridge.

(2) The theca is uniformly sclerotized, undivided, cylindrical, and gently widening in the apical half. A narrow, weakly sclerotized strip is situated at the base of the ventral wall of the theca; this strip laterally widens into a pair of small, distinctly separated lateral tubercles.

(3) The conjunctiva is membranous, most frequently divided only into 3 large lobes: a pair of the apical lobes and the ventral lobe. The lateral walls of the ventral lobe are reinforced by strongly sclerotized median plates of the penis, which widen apically, terminating as a pair of spoon-shaped apical processes. The vesica is situated between them, looking like a very short straight tube with the secondary gonopore aperture at apex. The walls of the vesica are sclerotized, densely adjoining ductus seminis. The median plates of the penis are drawn together at the apex of the ventral plate, enveloping the base of the vesica, but not fusing. A pair of small digitiform outgrowths, the so-called basolateral lobes, can be situated on the lower wall of the ventral lobe. The apical lobes are entirely membranous, symmetric; both shape and direction of their apices can vary. In some species, an unpaired median lobe is situated between the apical lobes. In addition, 2 small basolateral lobes are situated laterally at the base of the conjunctiva; their apices are directed towards the phallobase or sideward. The degree of their development varies. The upper

surfaces of each of these lobes are reinforced by narrow and strongly bent sclerites, reaching bases of the median plates of the penis.

Thus, mainly only the degree of the development of the apical lobes, median lobe, digitiform ventrolateral lobes, and lateral lobes mainly vary within the subfamily. These differences could be used in the species diagnostics and, to a lesser extent, in the diagnostics of the genera; however, they could hardly be applied for isolation of groups of the higher rank.

The tribe Tetrodini, including the genera *Gelia*, *Tetroda*, and *Tetrodias*, remained unexamined in the present work; however, according to drawings of the aedeagus (Ahmad and Kamaluddin, 1992), in all the genera of the tribe, it possesses the whole complex of characters typical of the family in general. This is also true for the drawings of the aedeagus of species unexamined by us and genera of the tribe Cressonini [*Cressona* (Kamaluddin and Ahmad, 1995)], *Megarhampini* [*Megarhampus* (Ahmad and Kamaluddin, 1988)], *Bakerorandalotus* (Ahmad and Kamaluddin, 1976), and *Phyllocephalini* [*Dalsira*, *Mercatus*, *Nazeeriana* (Kamaluddin and Ahmad, 1988), and *Minchamia* (Gross, 1976)].

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