

Male genitalia in Miridae: structure, terminology and application to phylogenetic inference. Critical comments on Cheng-Shing Lin & Chung-Tu Yang's ideas (Heteroptera)

F.V. Konstantinov

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Critical analysis is given of the terminology proposed and conclusions reached in the monograph by Lin & Yang (2005) on the male genitalia of Miridae.

F.V. Konstantinov, Department of Entomology, St. Petersburg State University, Universitetskaya nab. 7/9, St. Petersburg 199034, Russia. E-mail: fkonstantinov@hotmail.com

The monograph by Lin & Yang (2005) is based on the study of the male genitalia in 121 mirid species from virtually all tribes and offers a new terminology, revised interpretation of the male genitalic structures and phylogenetic analysis of the family. Descriptions and sketchy drawings of the external male genitalia are provided for each species. Unfortunately, only a single specimen was studied as representative of a species in all cases and the phallus is mostly illustrated in the state of repose. This methodology makes it difficult to interpret the folded membranous structures of the phallus and leads to doubtful conclusions.

The book is stylistically similar to and implies the same argumentation, structure, and terminology as the comprehensive and turgid monograph by Yang & Chang (2000), which mainly focused on Auchenorrhyncha, but also concerned Sternorrhyncha, Coleorrhyncha, and Heteroptera. The ideas expressed by Prof. C.T. Yang were subsequently applied in more detail to Cydnidae (Yang, 2003a), Reduviidae (Yang, 2003b), Gerromorpha (Yang, 2003c), Coreoidea (Yang, 2003d), Pyrrhocoroidea (Yang, 2003e), and Aradidae (Yang, 2004). The reviewed monograph continues a large series of works dealing with the structure of the male genitalia in various groups of Heteroptera.

A detailed review of the whole scheme of the Rhynchotan male genitalia as depicted by Yang and co-authors is beyond the scope of the present paper. However, several new interpretations of the male genitalic structures in Miridae widely applied in the monograph by Lin & Yang require comment.

The central misconception the authors offer is a unique interpretation of the aedeagus across the Miridae. Although the term aedeagus is defined as "the median evagination tube of the segmental

membrane", it is used in a much more narrow sense when compared to the concepts of previous workers. According to the generally accepted view (Singh-Pruthi, 1925; Snodgrass, 1935, 1957; Kullenberg, 1947a; Dupuis, 1955, 1963, 1970; Bonhag & Wick, 1953; and others), the male intromittent organ, usually called the phallus or aedeagus, is considered to be a two-walled tube-like outgrowth of the intersegmental membrane surrounding the primary gonopore. Inner walls form a duct inside the intromittent tube, through which the seminal liquid is transferred to the secondary gonopore; this duct is termed the ductus seminis (which has gained wide acceptance since the excellent work by Kullenberg, 1947a). The external wall and the ductus seminis exhibit a great diversity in various taxa. However, it is accepted that this variation is differentiation of a single organ.

In contrast, Lin & Yang consider individual segments of the phallus, e.g. phallobase (termed connective) and phallotheca (termed phallobase) to be independent structures, each evolved as "bulbous growths of the membrane around the base of the aedeagus". A similar view on the nature of the phallotheca was expressed only once, in the earliest paper considering the structure of the phallus in the Heteroptera (Sharp, 1890). Sharp described the phallotheca as "a tubular or cylindrical structure, fastened to the inner face of the floor of the chamber, and completely surrounding the oedeagus; it is, in fact, a fence or hedge, open only above; I will speak of it as the theca". This idea was convincingly repudiated by Singh-Pruthi (1925) and was not taken into account by all subsequent workers.

What is the aedeagus sensu Lin & Yang then? In virtually all mirids studied, except the Phylinae, Lin & Yang apply the term aedeagus to the sclero-

tized distal portion of the ductus seminis, regardless of the actual pattern of differentiation of the inner phallic structures. This seems to be a clear misconception, as the ductus seminis, whether with partly sclerotized or entirely membranous walls, is only a duct running *inside* the phallus. No doubt, the ductus seminis proved to be a useful set of characters that can provide insight into the taxonomy of mirids, but structurally it just cannot be a separate segment of the phallus by itself. Although in most mirid taxa the distal portion of ductus seminis is more or less sclerotized, the presence of a wholly membranous ductus seminis, as for instance in Monaloniini and Dicyphini, leads Lin & Yang to conclusion that “aedeagus and gonopore wholly reduced”.

Their unique interpretation of aedeagal structure is scattered over the entire text and can be further exemplified by the genital structure in the subfamilies Mirinae and Deraeocorinae. In both groups, the distal part of phallus is formed by several membranous lobes which can inflate, a narrow, more or less sclerotized base, and the opening of secondary gonopore usually centrally located at the base of the vesical lobes. This distal part is most frequently called the vesica of the Mirinae-type (Dupuis, 1955; Wagner, 1952, 1955, 1974; Kerzhner & Konstantinov, 1999; Konstantinov, 2003), while Lin & Yang refer to this structure as “exposed phallobasal conjunctiva”. This structure again is considered as “the bulb-like growth of the phallobasal conjunctiva” (i.e. the inner wall of the phallobase sensu Lin & Yang or conjunctiva of many other authors) around the base of aedeagus. In other words, according to the proposed reconstruction, the distal part of ductus seminis is surrounded by, but not running inside one of the membranous lobes; however, this is certainly not the case. Curiously, *Felisacus longiceps* is mentioned as having the “ejaculatory duct within aedeagus visible, as the only exception among the examined Miridae”.

In contrast to mirids with membranous inner phallic structures, in the Phylinae, the distal part of ductus seminis is barely visible, thin-walled, membranous, and running inside a comparatively thin, usually almost entirely sclerotized vesica. Here, the structure of the phallus partly fits the concept of Lin & Yang and they just use the term aedeagus for what is usually called vesica.

Besides providing a new interpretation of the aedeagus, Lin & Yang discuss a number of characters “not distinguished by Singh-Pruthi (1925) or Kelton and Konstantinov (1999, 2003)”. Among others, these are the “phallobasal conjunctiva processes”, the “sheath”, and the “expanded ejaculatory duct”.

By the first character, Lin & Yang evidently meant distal projections of the phalotheca. It

is well known that the aperture of phalotheca in Miridae is seldom smoothly or regularly rounded. More often, the distal wall of the phalotheca is gradually prolonged into a linguiform projection, although the apex of the phalotheca may be differentiated in many other ways. Lin & Yang consider projections of the phalotheca as separate structures, namely “tubular evaginations of the phallobasal conjunctiva”. They are even clearly delimited by some suture or depression in all figures depicting the male genitalia of all mirines and deraeocorines, many orthotylinines and bryocorines, and several species from other subfamilies except Phylinae.

The sheath is defined as “the differentiated structure of the retracted aedeagus and associated phallobasal conjunctiva”. This enigmatic structure is usually represented in the figures by the sclerotized distal portion of the ductus seminis proximal to the point of attachment of the endosoma or conjunctiva (both named phallobasal conjunctiva by Lin & Yang). Consequently, it is absent in all groups with entirely membranous ductus seminis, or at least in species having a clearly membranous structure running outside the vesica. However, in some cases, e.g. in many mirines, the sheath seems to be just the sclerotized base of the vesica. Lin & Yang insists that the sheath “appeared only within the Miridae in the Heteroptera”, but this is not the case in both possible meanings of the term.

The expanded ejaculatory duct is a ductus seminis running between the base of the phallus and the aedeagus sensu Lin & Yang, i.e. just the membranous part of the ductus seminis. Again, this structure is believed to be “present only in the Miridae”. This conclusion is apparently based on a firm belief that all phallic structures originated as tube-like outgrowths of intersegmental membrane surrounding the so-called aedeagus as in a set of nesting dolls. Although it is not stated in the text, we may expect then that the primary gonopore was originally situated at the base of the aedeagus and subsequent lengthening of the ductus seminis is required to explain its current position. The whole idea of expanded ejaculatory duct is strange in itself for the reasons mentioned above. Moreover, its treatment as an apomorphy of Miridae not only directly contradicts the available data on the phallic structure in Heteroptera and particularly Cimicomorpha, but also seems to be in contradiction with previous papers by Yang (2003b, 2003e).

As a way of establishing homologies between all Rhynchota taxa, Prof. C.T. Yang offers a completely new terminology. As presented above, he has now extended this interpretation to the Miridae. Literally all terms proposed in the monograph are either new or used in a different sense as compared to the terminology already adopted in

the current literature. In many cases the reasons for such total aversion are difficult to comprehend. For instance, it is stated in the introduction that “The support bridge and support tube were not distinguished by Singh-Pruthi (1925), Kelton (1959), or Konstantinov (2003)”. Five pages below, in table 1, the support tube is declared as a synonym of “Basal plates bridge sensu Singh-Pruthi (1925) and Konstantinov (2003)”. In fact, the basal plates bridge (sensu Singh-Pruthi, 1925; Dupuis & Carvalho, 1956 and others, including Konstantinov, 2003) is merely a synonym of the so-called support bridge, while the support tube was previously named ductifer by Bonhag & Wick (1953) and followed by Konstantinov (2003).

In a general sense, the idea of changing the terminology whenever a new morphological interpretation sees the light of day seems unproductive. Theories on the origin of the external genitalia and assumptions concerning their homology across the main insect orders (Michener, 1944; Kullenberg, 1947b; Dupuis, 1950; Gustafson, 1950; Nielsen, 1957; Snodgrass, 1957; Smith, 1969; Scudder, 1971; Matsuda, 1976; and others) clearly illustrate this point. These papers are important milestones to deepen our understanding about structure of genitalia in insects, but at the same time most of above cited authors proposed new terms and rejected previously used ones in accordance with their theoretical views or just because a term was considered as descriptive and/or incorrect. Surely, each author considers his idea as the right one, but another theory always will be just around the corner. In contrast to morphologists, taxonomists generally adhere to the traditionally used terms and disregard new names irrespective of agreement with the morphological hypothesis. Although it is always good to know the true morphological value of the structure, a continuous change of names will merely make this task more difficult. The primary purpose of terminology, as well as any language, is to effectively communicate with colleagues, and although stability in science is ignorance, some reasonable degree of stability in names is necessary.

Application of the new ideology to the male genitalia of various mirids is rather inconsistent. For example, according to the provided description, the aedeagus and gonopore are absent in both studied species of *Halticus*. However, the secondary gonopore can be seen in Fig. 18G, located at the apex of the structure for some reason abbreviated as exposed phallobasal conjunctiva. Unfortunately, the text is rather rich in obscure interpretations of a similar nature. Even the sequence of species descriptions is hardly predictable: descriptions of *Macrolophus* are placed under the numbers 52 and 54, descriptions of *Apolygus* take number 83, than 89 till 95, and

finally 108, while *Orthops* spp. are described under the numbers 97, 109, and 110. The genus *Cylapomorpha* is transferred to the tribe Bothriomirini without any comments on this action.

Given the new interpretations and their inconsistent application it is not surprising that examined suprageneric groups of Miridae cannot be unequivocally recognized by the structure of the male genitalia according to the discussion provided for each subfamily. Even the subfamily Phylinae, a well known example of a group first and foremost diagnosed by a number of unique traits of the male genitalia, is not uniquely defined. All characters listed in “Remarks on description of the Phylinae” occur in other groups under study.

The monograph concludes with a discussion of phylogenetic relationships within the family. Lin & Yang provided a data matrix with characters and their states, as well as a dendrogram depicting phylogenetic relationships which may give an impression of using cladistic techniques. In fact, Lin & Yang merely stated “as for inferences concerning, cladistic rules did not strictly observe” and almost arbitrarily revealed three evolutionary lines, namely Isometopinae group (Isometopinae, Psallopinae, and Cylapinae), Orthotylinae group (Orthotylinae and Phylinae), and Bryocorinae group (Bryocorinae, Deraeocorinae, and Mirinae). In majority of cases, Lin & Yang coded the same trait several times as independent character within each evolutionary line. Character states were polarized arbitrarily, by means of the so-called “special judgment”. With this done, characters were evidently just arranged on the ready tree with no regard to amount of homoplasy.

Regretfully, I can only summarize that the monograph by Lin & Yang (2005) is full of confusion and can hardly bring further insight into our understanding of the structure and phylogeny of Miridae.

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