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Homology of the gonostylus parts in crane flies, with emphasis on the families Tipulidae and Limoniidae (Diptera, Tipulomorpha)

GUILHERME CUNHA RIBEIRO

Pós-Graduação em Entomologia. Departamento de Biologia, FFCLRP-Universidade de São Paulo, Avenida Bandeirantes 3900, 14040-901, Ribeirão Preto, SP, Brazil; e-mail: gribeiro@usp.br

Abstract

The study of the morphology of the gonostylus – a structure of major importance for the taxonomy and systematics of crane flies – has shown that the terminology currently applied to the branches of this organ in Tipulomorpha and its implied primary homology hypothesis are inconsistent in the different families. In this paper, such inconsistencies are discussed, some basic criteria for the proper recognition of the homologous parts are given, and a revised nomenclatural system is proposed. The terms "clasper of gonostylus" and "lobe of gonostylus" are proposed for the gonostylar branches on the basis of the known functions of these structures.

Key words: Diptera, Tipulomorpha, Limoniidae, Tipulidae, gonostylus, homology

Introduction

The Tipulomorpha (*sensu stricto*) is one of the largest groups of lower Diptera, including more than 15,000 species in four families worldwide. The Limoniidae, with more than 10,000 described species, is the largest family, followed in size by the Tipulidae (more than 4,000 species), Pediciidae (slightly more than 400 species), and Cylindrotomidae (71 species) (Oosterbroek 2005). Whether the family Trichoceridae is the sister group of the other families is still debated. But despite its great diversity and abundance, the Tipulomorpha remains a vastly unknown group, as many aspects of the morphology, biology, and consequently the phylogenetic relationships among its subgroups are poorly explored and understood.

The morphology of the male genitalia has been of major importance in the taxonomy and systematics at different levels of generality, not only in the Tipulomorpha but also in the Diptera in general. For many groups, species-level taxa can be recognized only by details of the male genitalia. In other instances, the conservative nature of some structures

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provides grounds for the proposal of inclusive monophyletic groups. However, the homology of several genital structures in different groups is not fully understood, and the issue is especially problematical when distantly related groups are compared (Wood 1991).

An example of an organ that has been useful in distinguishing similar species, as well as grouping a vast array of genera in supposedly monophyletic groups in the Tipulomorpha, is the male gonostylus. However, detailed study of the morphology of gonostylar structures in representatives of several genera in the major lineages of the Tipulomorpha has revealed inconsistencies and contradictions in the currently accepted terminology and homology of the so-called inner and outer branches of the gonostlylus in different families. As discussed below, the issue is relevant and carries important implications as far as the phylogeny of the group is concerned. The purpose of this paper is to briefly address this problem, with arguments showing why the currently adopted terminology and its implied homology hypothesis for the branches of the gonostylus in the Tipulidae and Limoniidae are equivocal. The motivation for this paper comes from the belief that a better-proposed hypothesis of primary homology for these taxonomically important structures would benefit future taxonomic and phylogenetic works.

The gonostylus of Tipulomorpha

The gonostylus of most Limoniidae and Tipulidae is divided into two branches, unlike the condition in other lower Diptera in which the gonostylus normally is a single, unbranched structure. This division of the gonostylus is clearly noticeable in the external skeletal morphology, as both branches are connected to each other at the base of the structure, where it articulates with the gonocoxite (connection indicated by arrows in Figs. 1C; 2A; 3C). Even though Paramonov (2004) considered one of the gonostylar branches of crane flies to be a lobe of the goncoxite, his observation that both branches have muscle insertions, as already demonstrated by Byers (1961), does not contradict the traditional view of a branched gonostylus.

In the Cylindrotomidae (Brodo 1967, Alexander 1929), some genera of Pediciidae (e.g., *Tricyphona*, *Ula*), and some Limoniidae (e.g., *Limonia sensu stricto*, *Cladura*), the gonostylus is not branched as in most Tipulidae and Limoniidae, but this condition probably is due to secondary loss, as a branched gonostylus is likely to be present in the Tipulomorpha groundplan (Starý 1992). These branches have been referred to by different names, depending on the author (see Table 1), but most commonly as dorsal, ventral, outer, and inner dististyli or gonostyli. Over its long evolutionary history, the Tipulomorpha have accumulated many modifications in the morphology of these structures, as seen in the great diversity of forms exhibited by the thousands of included species. The importance of the great morphological variability of the gonostylus in the Tipulomorpha is not limited to descriptive taxonomy. All of the relatively few phylogenetic studies of crane fly subgroups have scored characters from these organs (Oosterbroek 1980; Tangelder 1985; De Jong 1989, 1993, 1994, 1995a, 1995b; Starý 1992; Ribeiro 2003).

In the work of Alexander (1919), the gonostylus in Tipulomorpha is referred to as "pleural appendages", and the following statement is given (Alexander 1919: 872): "The pleural appendages are usually two in number. The outer one is more or less fleshy and is of various shapes and sizes in different groups". This simple statement seems to be precise enough for describing what is observed in most Tipulidae (Figs. 1; 3A, B), where the fleshy branch (branch I), which occupies a more proximal position on the gonocoxite compared with the more sclerotized branch (branch II), is also more lateral in position in relation to the longitudinal axis of the gonocoxite. In Alexander's subsequent papers and in the works of other authors (e.g., Oosterbroek 1980; Tangelder 1985; De Jong 1989, 1993, 1994, 1995a, 1995b, 1997), this concept of a "fleshy outer gonostylus" (branch I) versus "a more sclerotized inner gonostylus" (branch II) has been applied consistently to the family Tipulidae.

Regarding the Limoniidae, however, that has not been the case. In this family (Figs. 2, 3C-F), the more distal and normally more sclerotized branch of the gonostylus (branch II) is usually referred to as the outer gonostylus, and the fleshy, proximal branch (branch I), as the inner gonostylus, even in recently published papers (Ribeiro 2002; Starý 2003, 2004). In the Limoniidae, there is greater variability in the relative positions occupied by the gonostylar branches in relation to each other and to the gonocoxite. For example, in *Dicranomyia* (Dienske 1987: 9, figure 3) and *Rhipidia* (Alexander & Byers 1981: 155, figure 5), the great development of the so-called inner gonostylus has displaced this structure toward a more ventral position in relation to the outer gonostylus. In such cases, the terms ventral gonostylus and dorsal gonostylus have been applied (Dienske 1987). However, even the interpretation of which branch is the dorsal or ventral is not free of contradiction among different authors (Table 1).

The reversal in the application of the terms outer and inner to the gonostylar branches in most of the Limoniidae, compared with the usage of the terms in Tipulidae, has never been criticized by systematists of the group. It was proposed in the only published cladistic analysis of the major subgroups of Tipulomorpha, using characters of the imagines (Starý 1992), that the strongly sclerotized outer gonostylus (branch II) is synapomorphic for all members of the Limoniidae except *Dactylolabis* Osten Sacken (subfamily Dactylolabidinae).

In the Limoniidae, a strongly sclerotized distal branch (branch II) is absent not only on the gonostylus of *Dactylolabis*, but also on that of *Metalimnophila* Alexander (Fig. 2C, D). Moreover, some primitive members of the Tipulidae (e.g., *Leptotarsus* and *Ptilogyna*, Fig. 3A, B), in which the gonocoxite and gonostylus have characters that are probably plesiomorphic for crane flies (e.g., the cone-shaped gonocoxite) (Oosterbroek 1980), also have the distal branch of the gonostylus (branch II) more sclerotized than the basal one (branch I). These observations combined place doubt on the sclerotization of the distal branch of the gonostylus (branch II) as synapomorphic for all limoniids except *Dactylolabis*. Given the present knowledge of the phylogeny of the Tipulomorpha, it is difficult to decide which condition more likely corresponds to the plesiomorphic condition for the group: the condition similar to *Metalimnophila* and *Dactylolabis* (both branches of gonostylus weakly sclerotized) or that of most Limoniidae and certain Tipulidae (distal branch II more sclerotized than basal branch I).

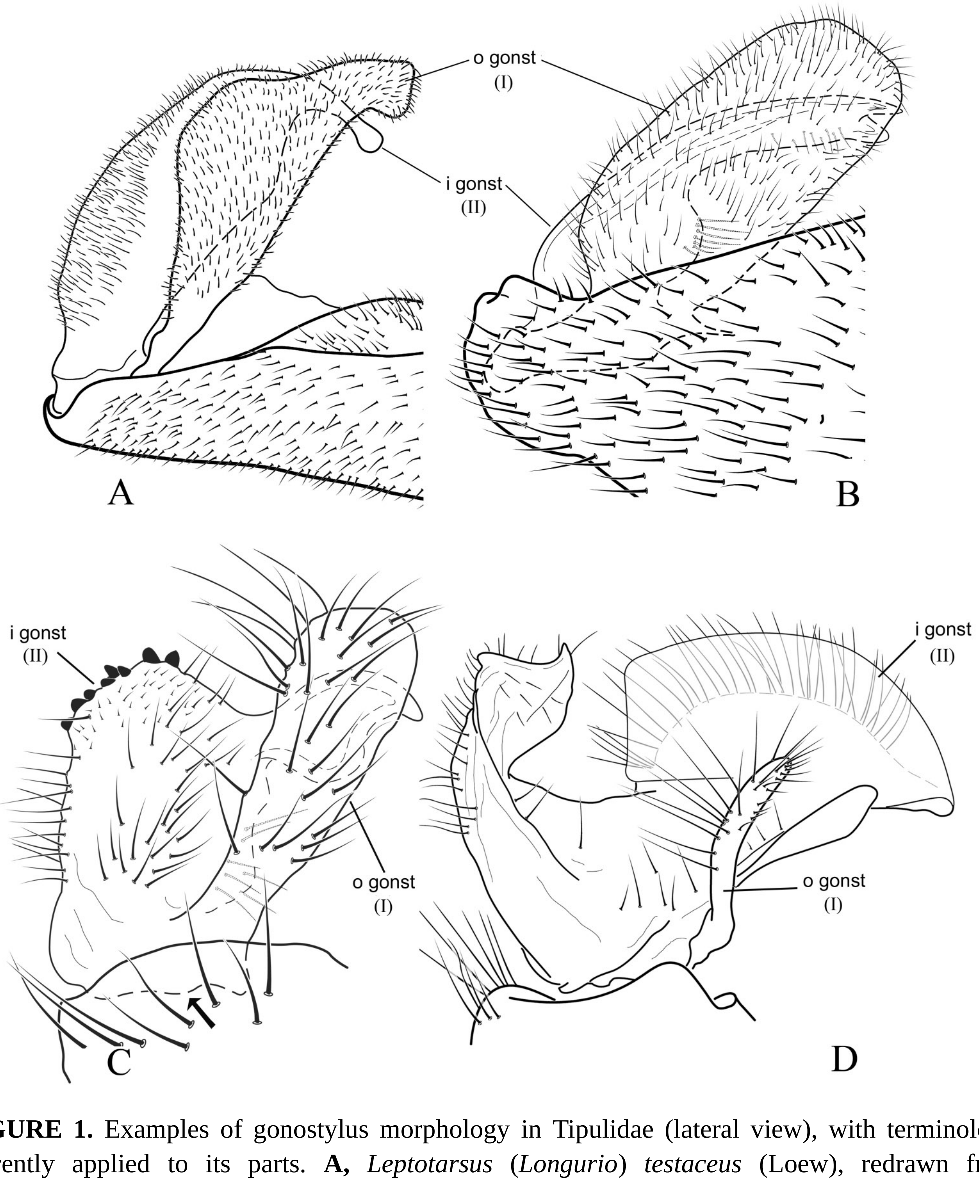

FIGURE 1. Examples of gonostylus morphology in Tipulidae (lateral view), with terminology currently applied to its parts. **A,** *Leptotarsus* (*Longurio*) *testaceus* (Loew), redrawn from Oosterbroek (1980). **B,** *Ptilogyna* sp. **C,** *Leptotarsus* (*Longurio*) *gymnocerus* (Alexander). **D,** *Tipula* (*Lunatipula*) *bullata* Loew, redrawn from De Jong (1995b). Abbreviations: I, branch I of gonostylus; II, branch II of gonostylus; i gonst, inner gonostylus; o gonst, outer gonostylus.

TABLE 1. Compendium of terms applied to the gonostylar branches in Tipulidae and Limoniidae in some selected publications, compared with the system proposed herein (in bold).

Source	**Family Tipulidae**		**Family Limoniidae**	
	Lobe of gonostylus (branch I)	**Clasper of gonostylus (branch II)**	**Lobe of gonostylus (branch I)**	**Clasper of gonostylus (branch II)**
Alexander (1919)	outer pleural appendage	inner pleural appendage	ventral pleural appendage	dorsal pleural appendage
Tokunaga (1930)	-	-	harpe	clasper
Edwards (1938)	-	-	dorsal or inner style	ventral or outer style
Alexander (1966)	outer dististyle	inner dististyle	ventral dististyle (*Dicranomyia*, *Rhipidia*) inner dististyle (other genera)	dorsal dististyle (*Dicranomyia*, *Rhipidia*) outer dististyle (other genera)
Alexander & Byers (1981)	outer gonostylus	inner gonostylus	inner gonostylus	outer gonostylus
Dienske (1987)	-	-	ventral gonostylus (*Dicranomyia*) dorsal or inner gonostylus (other genera)	dorsal gonostylus (*Dicranomyia*) ventral or outer gonostylus (other genera)
De Jong (1997)	outer gonostylus	inner gonostylus	-	-
Paramonov (2004)	lobe of gonocoxite	gonostylus	lobe of gonocoxite	gonostylus

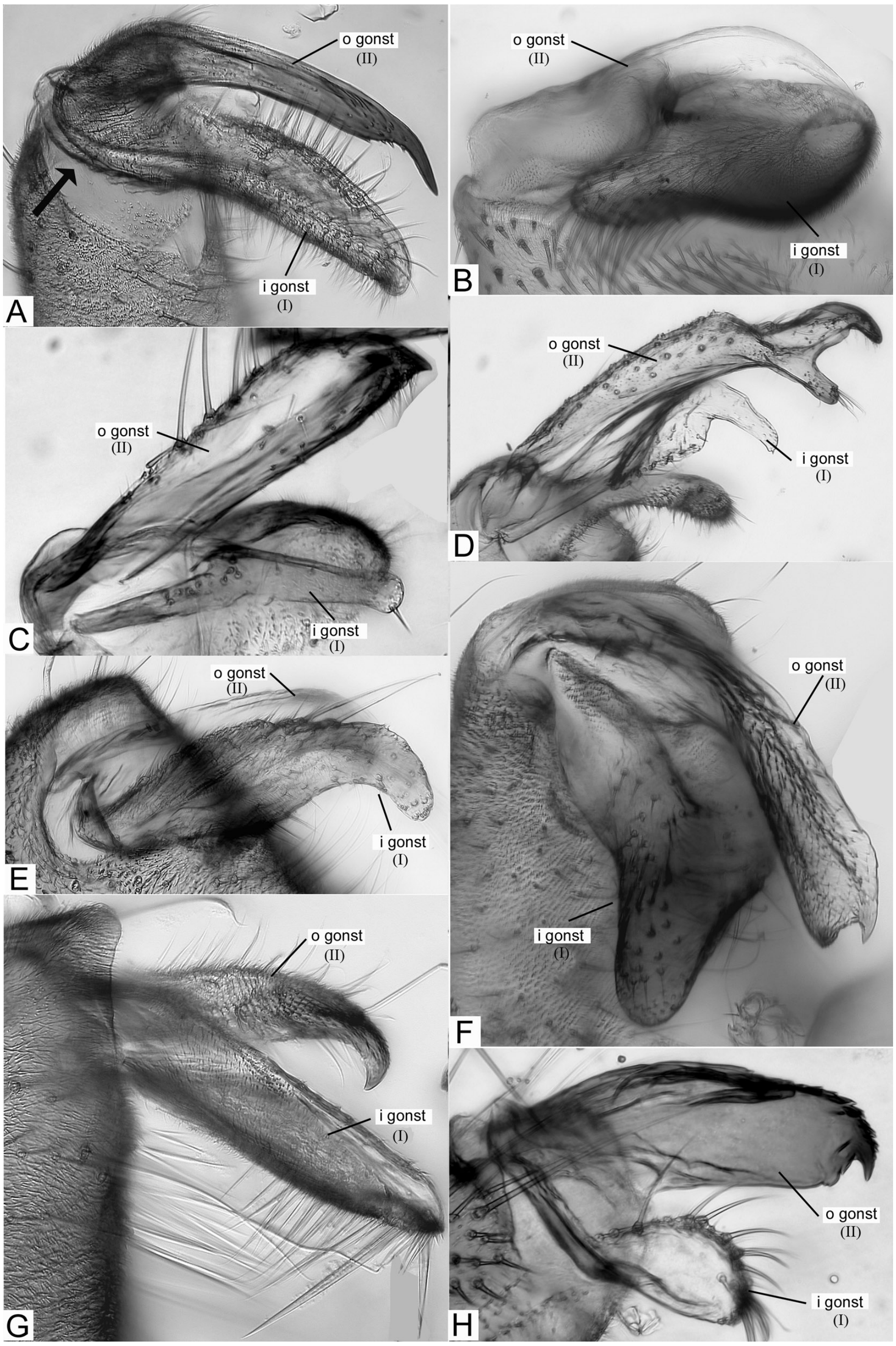

FIGURE 2. Examples of gonostylus morphology in Limoniidae (dorsal view), with terminology currently applied to its parts. **A,** *Hexatoma* (*Eriocera*) *aegle* Alexander. **B,** *Hexatoma* (*Eriocera*) *austera* (Doane). **C,** *Metalimnophila howesi* (Alexander). **D,** *Metalimnophila productella productella* Alexander. **E,** *Conosia* sp. **F,** *Lecteria* (*Lecteria*) sp. **G,** *Tinemyia margaritifera* Hutton. **H,** *Eloeophila aldrichi aldrichi* (Alexander). Abbreviations: I, branch I of gonostylus; II, branch II of gonostylus; i gonst, inner gonostylus; o gonst, outer gonostylus.

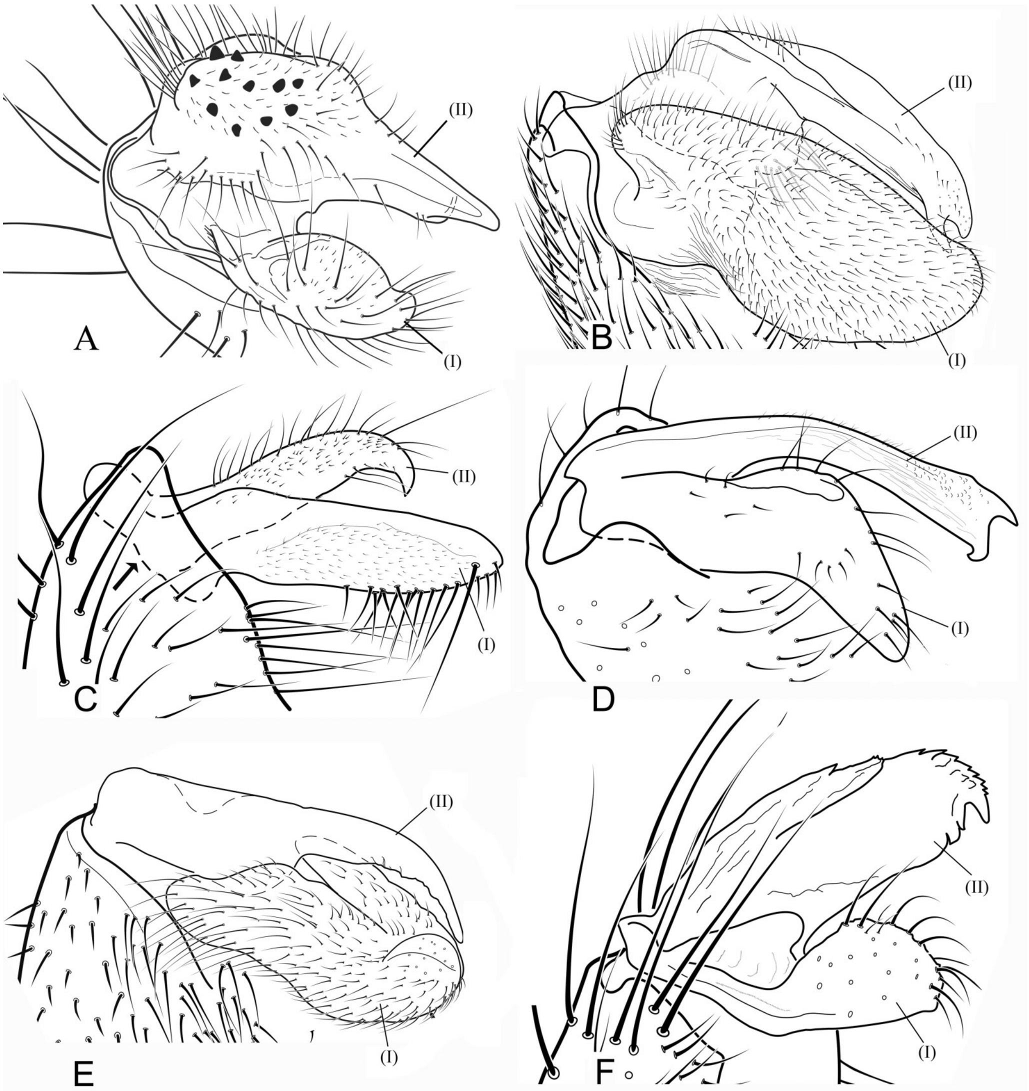

FIGURE 3. Gonostylus morphology in Tipulidae and Limoniidae (dorsal view), with revised homology between branches as proposed here. **A,** *Leptotarsus* (*Longurio*) *gymnocerus* (Alexander) (Tipulidae). **B,** *Ptilogyna* sp. (Tipulidae). **C,** *Tinemyia margaritifera* Hutton (Limoniidae). **D,** *Lecteria* (*Lecteria*) sp. (Limoniidae). **E,** *Hexatoma* (*Eriocera*) *austera* (Doane) (Limoniidae). **F,** *Eloeophila aldrichi aldrichi* (Alexander) (Limoniidae). Abbreviations: I, branch I of gonostylus (lobe of gonostylus); II, branch II of gonostylus (clasper of gonostylus).

In Figure 2, the morphology of the gonostylus in several representatives of the family Limoniidae is shown. The homology system and nomenclature currently applied to the structures is given. As shown in the figures, the so-called inner branch of the gonostylus in the Limoniidae (branch I) actually occupies a more lateral position in relation to branch II in some species, as for example in *Conosia* sp. (Fig. 2E) and *Tinemyia margaritifera* (Fig. 2G). It also can be situated ventrally in relation to branch II, as in the case of *Rhipidia* and *Dicranomyia*. More commonly, however, branch I is not situated either more lateral or medial in relation to branch II, but more or less is aligned with it, though positioned more proximally in relation to the apex of the gonocoxite.

Figure 3 compares the gonostylar morphology in the Tipulidae (*Leptotarsus* (*Longurio*) and *Ptilogyna*) and some of the Limoniidae genera previously shown in Figure 2. From this comparison, a correspondence can be seen for the relative positions of the branches of the gonostylus in the different families, and that the inner gonostylus in the Tipulidae is more probably the homologue of the distal, strongly sclerotized branch of the gonostylus in the Limoniidae, normally referred to as the outer gonostylus in this family. This relationship is supported by the more distal position on the gonocoxite occupied by this branch in both families. Its relatively higher degree of sclerotization in some Tipulidae, as in *Leptotarsus* and *Ptilogyna*, adds compelling evidence for this view. With respect to the condition found in *Rhipidia* and *Dicranomyia*, in which one branch is positioned dorsally relative to the other, the evidence that the dorsal branch is the homologue of branch II comes not only from its higher degree of sclerotization, but also by having, at least in *Dicranomyia*, the same muscles in this branch as in other Limoniidae and Tipulidae (Paramonov 2004).

A description of the mechanism of copulation in the Tipulidae is provided by Tangelder (1985), with examples taken from the genus *Nephrotoma*. According to her, during copulation, gonostylar branch II moves inside and hitches to the sclerotized folds on the inner surface of the female hypogynial valves, thus acting as a clasper, while branch I embraces the hypogynial valves from the outside. She also quotes Neumann (1958, cited therein) saying that males of *Tipula paludosa* can copulate without gonostylar branch I, which would have no special function other than protection.

Conclusions

A basic criterion for primary homology assessments in comparative morphology is topographic correspondence, or position within the whole (de Pinna 1991, Hawkins et al. 1997). The examples and arguments given above demonstrate that the nomenclatural system currently in use for the branches of the gonostylus in Tipulomorpha and its implied primary homology hypothesis contradict this basic principle and is contradictory when its usage in different families is compared. The issue is relevant because the situation can lead to the comparison of homonymous, albeit nonhomologous, structures. Because a false hypothesis of homology usually produces false topologies, the issue gains more relevance as far as the phylogeny of the major lineages of the Tipulomorpha is concerned.

Naming the gonostylar branches of crane flies based on their relative positions, as implied in the use of the terms ventral, dorsal, inner, and outer, might not only cause confusion due to eventual shifts in the position of the structures, but also impose practical limitations, as these terms cannot be applied to every crane fly taxon with the same accuracy. Considering the relative positions of these structures as an important step for the recognition of homology, I propose the use of terms that can be applied to the gonostylar branches of crane flies, without relying solely on this criterion. The known functions of the structures could provide a solution for a nomenclatural system. Available functional morphological studies (e.g., Tangelder 1985) suggest that the primary function of branch II is clasping; therefore, I suggest the term “**clasper of gonostylus**” for this branch. The name “**clasper**” has been used to refer to this organ by previous authors (e.g., Tokunaga 1930). Given the lobular nature of branch I, which is never strongly sclerotized, I propose the term “**lobe of gonostylus**”. This term is proposed here for the first time.

From a modern phylogenetic perspective, legitimizing a primary homology hypothesis requires testing its congruence with other characters (De Pinna 1991, Hawkins et al. 1997). A comprehensive phylogenetic framework for crane flies is still wanting, and the confirmation of the ideas presented here will require a wider phylogenetic framework. On the other hand, the proposal of a unified nomenclatural system embodying a homology proposition is a necessary step toward that goal.

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