

A new reconstruction of the origin of eremoneuran hypopygium and its implications for classification
(*Insecta: Diptera*)

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Motto. "Die Deutung der Genital- und Postgenitalsegmente der *Cyclorrhapha* gehört zu den schwierigsten und wichtigsten unter den noch offenen Fragen der Dipteren-Morphologie" [The interpretation of the genital and postgenital segments of the *Cyclorrhapha* are among the most difficult and important of the still open questions in dipteran morphology].

W. HENNIG (1973: 215)

The article is dedicated to the memory of Prof. Dr. Willi HENNIG, the author of the motto, who contributed excellent studies on the taxonomy and phylogenetic system of various dipteran taxa and of the whole order *Diptera*.

ABSTRACT. Previous ideas on the origin of the male terminalia in higher *Diptera* are presented (including original citations) and classified in two groups: surstylar and gonostylar. The former explain the origin of clasping lobes as derivatives of epandrium, internal sclerite, proctiger, pregenital, or genital sclerite. The latter include concepts of gonocoxites reduction, gonocoxites retention, fusion and periandrial hypotheses. The concept of gonocoxites retention in higher *Diptera* is developed as a "hinge hypothesis", which is explained and documented. The mechanics of the transformation of clasping lobes suggests, that the arrangement of the male genitalia of *Orthogenya* and *Cyclorrhapha* developed in the same way. The essence of the so-called "hinge hypothesis" is that the gonocoxites in the ancestors of both groups included in *Eremoneura* fused under epandrium and become attached to the antero-medial margin of gonocoxite apodeme, permitting articulation of gonocoxite remnants with the hypandrium. Possibly such a connection of genital structures allowed its folding underneath and circumversion of hypopygium in *Cyclorrhapha*. Origin of each component of the ventral hypopygial complex is discussed. A new concept of the origin of cyclorrhaphan phallapodeme as a fusion of ejaculatory apodeme with postero-medial portion of hypandrium is suggested. Three new terms are proposed. The sclerite situated ventrally in epandrial complex is called medandrium, the dorsal bridge connected with it is called transandrium, and eremoneuran "ejaculatory apodeme" is termed ejacapodeme. The new interpretation of hypopygial transformation supports the monophyly of *Eremoneura*, *Orthogenya* and *Cyclorrhapha*, as well as the division of *Orthogenya* into five families. The general phylogeny of the latter group could be characterized by separation of subsequent lineages (*Acroptera*, *Platyzezoidea*, *Hypocera* and *Syrphoidea*) leading to *Schizophora*.

Key words: entomology, morphology, evolution, classification, eremoneuran hypopygium, *Diptera*.

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1. INTRODUCTION

My initial interest in the eremoneuran hypopygium was connected with my studies on the taxonomy of shore flies (*Ephydriidae*), and then developed during the examination of additional material and influenced by reading dipterological literature. This article was prepared under direct impression of the third volume of Manual of Nearctic *Diptera* (edited by McALPINE, 1989) and a paper of HENNIG (1976a). While reading HENNIG's (1976a) brilliant paper, I realized that one more explanation of the origin of eremoneuran hypopygium could be proposed. My astonishment was even greater, when after reconstructing possible transformations, I found unexpectedly that such an explanation already existed, however not supported by any evidence before and not considered in recent literature, at least in the years 1924-1995. In my opinion the presented interpretation of the origin of gonopods in *Eremoneura* combines the merits of the remaining theories and eliminates their deficiencies.

The structure of the male terminalia of the higher *Diptera* defined as the *Eremoneura* was a great challenge for many entomologists during the second half of our century. In the *Eremoneura* hypopygial organs are highly modified. They are not easily homologized with those existing in lower flies, and the distinct gap in hypopygial structure between the lower *Brachycera* and *Eremoneura* was the reason for suggesting various possible transformations. Several theories of the origin of

eremoneuran hypopygium were formulated. Each hypothesis assumes different origin of particular components and, consequently, different names are used by various specialists. At the time of preparation of this paper five of the nine theories, contradicting each other, trying to explain the origin of the dorsal hypopygial complex (epandrial complex) in higher *Diptera*, caused permanent controversies. All of them seem to have faults, which are pointed out by the opponents and merits stressed by their followers. The discussion in recent literature might suggest an existence of two opposite theories - epandrial and periandrial, which is misleading. Such a simplification caused erroneous systematic conclusions drawn by DISNEY (1986a), WIEGMANN et al. (1993) and CUMMING et al. (1995).

The main discrepancies and controversies pertain to the transformation of gonopods. Already LOWNE (1895) assumed, that in *Cyclorrhapha* clasping lobes originated as epandrial lobes, but the hypothesis is often attributed to CRAMPTON (1936). Two years later BRÜEL (1897) homologized clasping lobes with the eleventh tergite. BERLESE (1909) supposed that the internal sclerite was the tenth sternite and clasping lobes - its derivatives. Similar ideas were published by METCALF (1921), as well as by ZUMPT and HEINZ (1949). According to AWATI (1915) clasping lobes were represented by gonostyli, but gonocoxites were reduced. A similar idea was presented by HENDEL (1928). The clasping lobes in *Musca domestica* L. were regarded by HEWITT (1914) as pregenital sternite. EDWARDS (1920) conjectured that clasping lobes were derivatives of the ninth sternite. The author who proposed homology of the internal sclerite (subepandrial sclerite) with the gonocoxites was probably CRAMPTON (1923). HENNIG (1936a) constructed the theory of gonocoxite fusion with the saddle-shaped sclerite. The same year CRAMPTON (1936), independently from LOWNE (1895), considered clasping lobes as derivatives of epandrium. Some of those hypotheses were forgotten by contemporary researchers, or resigned by their authors. HENNIG (1958) abandoned his fusion theory in favour of epandrial theory. During thirty years (1942-1972) the situation remained stable. The terminology proposed by CRAMPTON (1923, 1936) became commonly accepted. In 1972 GRIFFITHS' periandrial theory enforced the usage of different terminology, which divided dipterologists into two camps. One kept defending the classical concept and terminology, the other (especially European) accepted the periandrial hypothesis and the new terminology. A reply to GRIFFITHS (1972) was a HENNIG's (1976a) paper, very broadly considering the origin of clasping lobes from the tenth tergite (here considered together with the concept of BRÜEL, 1897 and called proctiger hypothesis - see chapter 6c). Despite its novelty, Hennig's hypothesis followed CRAMPTON's terminology and therefore painlessly replaced the epandrial hypothesis. For OVTSHINNIKOVA (1993, 1994) clasping lobes were derived from subepandrial sclerite (her tenth sternite). Recently CUMMING et al. (1995) rejected HENNIG's hypothesis in favour of epandrial hypothesis (the so called "revised epandrial hypothesis"), accepting the criticism of proctiger hypothesis by GRIFFITHS (1981).

Discussion on the homology of hypopygial structures has been intensified since publication of periandrial theory by GRIFFITHS (1972). The argument of GRIFFITHS'

opponents pertained mostly to the question of origin of the saddle-shaped sclerite (developed by arising of gonopods, or formed by epandrium). The question of the origin of clasping lobes was considered to be of secondary importance and the two concepts (epandrial and periandrial) started to compete. Actually, the demarcation line between the various theories proposed is the question of clasping lobes homology, whereas the origin of other structures is to a certain degree a secondary question. The situation caused by discussion is, however, strange. The author of periandrial theory presents suitable and concrete arguments, on the other hand his opponents, proponents of the surstylar theory, exchange general metaphors and inadequate insinuations (see chapters 6a-6c). Opponents of GRIFFITHS modified their hypothesis to accommodate each new argument mostly - and possibly also in this case GRIFFITHS was right - to save their usual terminology. It is easy to say without evidence that genital claspers are of secondary origin. However, with the sclerites are connected also muscles, nerves and tracheal system and in reality such a replacement concept brings with it an avalanche of transformations. The suggestion that secondary appendices developed in other taxa of flies is not satisfactory. Below I will argue that, it is possible to imagine a gonostylar theory in which epandrium is completely retained. We can construct a surstylar theory, in which the periandrium comes into existence. To those persons, who can not imagine it, I give a recipe. The transformations start with extrusion of the anterior portion of epandrium by gonopods and its fusion along posteromedial margin. The next step is reduction and disappearance of gonostyli. The posterior portion of epandrium begins to elongate posterolaterally, then divides and forms surstyli. In my opinion, this strange-looking hypothesis (which is not maintained any further) has a similar explanatory power as epandrial hypothesis, while it includes two replacements of structures.

An idea of testing all the existing theories against independent characters would be very interesting. Two hypotheses (epandrial and periandrial) were compared by WIEGMANN (1990) and WIEGMANN et al. (1993) against the external characters, but the results gave no clear indication, which hypothesis better explained the relationships among the taxa of higher flies.

We can make a mind experiment and try to imagine how an other process concerning the male terminalia in *Cyclorrhapha* is evidenced. This process, namely hypopygium circumversion, or rotating the postabdomen by 360°, is not questioned anyway. This will help us understand how the hypothesis of the origin of male terminalia in higher *Diptera* should be evidenced. The concept of circumversum was suggested by BRÜEL (1897), who was the first to observe the ejaculatory duct looping over hindgut in *Calliphora vicina* ROB.-DES. (= *erythrocephala* (MEIGEN)); then it was developed by SCHRÄDER (1927). In most *Cyclorrhapha* no trace of circumversion of the sclerites can be observed and the whole postabdomen is ideally symmetrical. The phenomenon of asymmetrical seventh and eighth sclerites in some families could be explained as secondary, and insertion of postabdomen during copulation in *Platypezidae* as an adaptation to copulation in flight. Even turning of the ejaculatory duct around the hindgut could be explained without resorting to

circumversion. It is possible, that not postabdomen, but testes changed their position and they made the complete turn around the hindgut. There are single observations contradicting the circumversion in *Cyclorrhapha*: BLACK (1966) in *Eucalliphora lilaea* and DISNEY (1987) in *Opetia nigra* MEIGEN (the latter corrected by CUMMING et al., 1995). What is the reason for the common acceptance of postabdomen circumversion? The evidence for the concept comes from the structure of neural and tracheal systems, as well as from ontogenetic observations. According to RIVOSECCI (1958), in the seventh segment, the tracheal system on both body sides is crossed. This means that from that segment the postabdomen sides were dorso-ventrally reversed. SALZER (1968) presents the position of tracheal and neural systems, which in the eight segment turn around the hindgut. FEUERBORN (1922) and SCHRÄDER (1927) in *Calliphora* and GLEICHAUF (1936) in *Drosophila* observed the rotation of postabdomen by 360° during the embryonic development. To sum up, it is not the sclerites themselves, but anatomical and ontogenetical observations, that document ultimately the circumversum in *Cyclorrhapha*.

The phenomenon of circumversum provides also examples of transformations exclusive to each other. One of these involves the position of the eighth segment sclerites. The muscular connection between the last three abdominal segments contradicts the inversion of pregenital segment, which is documented by the tracheal system. The muscular connections provided by HENNIG (1976b) are: a) muscle designated as M 25 connecting dorsal sclerites of prehypopygial (eighth or fusion of seventh and eighth tergite) and ninth segment, as well as its homologue M 23 connecting prehypopygial sclerite with the preceding one, indicate that all these sclerites match all the tergites, not prehypopygial as an inverted sternite; b) muscle designated as M 33 in *Calliphora* (*Calliphoridae*) and *Delia* (*Anthomyiidae*) connecting hypandrium (ninth sternite) with prehypopygial dorsal sclerite is homologous with the muscle designated as M 176 in *Tabanus* (BONHAG, 1951), which means that the prehypopygial dorsal sclerite in those genera corresponds with the eighth tergite, not sternite; c) in some Calyptrate the muscle designated as M 32 connects hypandrium with the remnant of the preceding sclerite, which corresponds to the eighth sternite, but not tergite. Because of accepting the muscular connection of prehypopygial tergite with epandrium and other connections, HENNIG (1976b) denied the possibility of inversion of the eighth segment in *Calliphora* and assumed that the circumversum moved the postabdomen from the ninth segment. However, assumption that the tracheal system truly reflects the position of sclerites implies that the muscular connections between adjacent sclerites must have originated secondarily. All those facts indicate again, that the muscular connections are very plastic and relatively large translocation of their attachment points (at least on one side) are possible.

If the same process was responsible for the development of empidoid and cyclorrhaphan dorsal hypopygial complex, it must have taken place earlier than the circumversion in *Cyclorrhapha*. Thus the traces of "great transformation" should be less distinct than the traces of circumversion. Consequently, the similarities between

the sclerites known in recent taxa cannot provide convincing evidence for this change; it is necessary to consider the structure of neural, muscular and tracheal systems. Also characteristics of ontogenetic development of the hypopygium, and evolutionary trends could aid the confirmation procedure. It should be remembered that in some cases these features could be secondarily modified, and thus disturb the general pattern of hypopygial evolution. So far these data are insufficient for a univocal designation of precise homologies of the male genitalia in higher flies, because they are known only in single cases. Unfortunately, most concepts were proposed as statements or conjectures, not supported by any sound evidence.

2. MATERIAL AND METHODS

The new hypothesis and the critique of the previous theories are based on the literature data with addition of *Cyclorrhapha* material from my collection, and *Empidoidea* from the private collection of Mr. Andrzej PALACZYK (Institute of Systematics and Evolution of Animals, Cracow). Totally about 120 male terminalia of eremoneuran species of 33 families other than *Ephydriidae* were examined. Male genitalia were dissected in KOH and placed in plastic microvials with glycerine. They were examined in light microscope and camera lucida drawings were made.

There are several questions concerning the development of hypopygium of higher flies. Not all of them are discussed here. The basic goal of this contribution is to present and criticize the existing concepts of the origin of eremoneuran hypopygium and to make phylogenetic remarks on major sublineages within *Eremoneura*. Some basic questions of dipteran morphology, although controversial in the past, are at present explained, or generally agreed upon. The precise explanations of these problems have no direct influence on my studies. Thus, in this paper I do not discuss direction of circumversion, the numbering of abdominal segments, homology of cerci and gonopods of *Diptera* with those of other holometabolic insects. I accept that the genital segment bears number nine. EMDEN and HENNIG (1956) suggested that the clasping lobes arose from the precoxae and styli of the *Thysanura* and called them gonopods. SNODGRASS (1957) believed that clasping lobes in *Diptera* and all *Holometabola* originated from the primary lobes of the *Thysanura*, but this point of view is not maintained here.

3. TERMINOLOGY

Those students who dealt with the names of genital structures in old literature know how difficult it is to understand misleading terms and how important is a clear, consistent and explicit terminology. In this paper the terminology is especially important and therefore explained in detail (Fig. 2). While evaluating the opinions in cases where the name of a structure suggests its homology, I use neutral terms, not connected with any hypothesis; e.g. I prefer the term "saddle-shaped sclerite", to

“ninth tergite”, “epandrium” or “periandrium”; “clasping lobes”, to “surstyli”, “dististyli”, or “gonostyli”; “dorsal complex” to “epandrial complex”; “ventral complex” to “hypandrial complex”, “internal sclerite” for the sclerite of *Eremoneura* placed ventrally to saddle-shaped sclerite, if it is homologized (in my opinion erroneously) with the tenth sternite of lower *Brachycera*. I realize that this unusual terminology could be difficult for those accustomed to the commonly accepted terms, however it is the only way to be objective in my criticism. Otherwise, explaining details of concepts I try to use specific terminology, which was proposed or used by advocates of the respective hypotheses, thus the terms “epandrium” or “periandrium”, “surstyli” or “gonostyli” are used equivalently, and depend on how the contents of the hypothesis is treated.

I found it difficult to find names for two different structures in non-cyclorrhaphan and cyclorrhaphan flies, both called ejaculatory apodeme. The homology of both apodemes is unclear, and even if they are fully homologous, their shape and function are completely different (see chapters 8.b.4-5), hence I suggest the term ejacapodeme for the cyclorrhaphan “ejaculatory apodeme”. Two hypopygial structures have descriptive names, consisting of two words, which is not very convenient. In those cases I propose to use a short, one-word terms:

- medandrium for the sclerite called “bacilliform sclerite”, “subepandrial plate”, “processus longi” or sometimes erroneously “tenth sternite”.
- transandrium for the structure situated dorsally to aedeagus, connected with or attached to hypandrium and called “dorsal bridge”.

For details see descriptions of the above structures in chapter 8.

The terms hypopygium or, equivalently, the male terminalia used here refer to the ninth segment and associated proctiger. For the true clasping lobes of lower *Diptera* several terms were proposed - “styli” (with basistyli and dististyli as its components), “parameres” (with telomeres and basimeres as its parts), “claspers”, or “forceps”, but I prefer the term gonopod and gonocoxite for its basal segment and gonostylus for its distal segment. When I write that the clasping lobes of *Eremoneura* are homologous to gonostyli, I always mean that the clasping lobes of *Eremoneura* and the gonostyli of lower *Diptera* have the same origin as homologous structures. The same pertains to other structures. Folding of hypopygium caused the change of relations among the structures. I follow GRIFFITHS’ (1972) approach to establish the direction of the respective structures of cyclorrhaphan hypopygium in the same way as in lower *Diptera*, i.e. the cerci and hypopygial tergite indicate the “dorsal” side of the hypopygium and the sternite is regarded as “ventral”.

MCALPINE (1981) proposed to adopt a uniform terminology for the “postgonites” as parameres throughout the order, but I still hesitate to accept the homology of the structure in higher flies, following GRIFFITHS (1981), who suggested to avoid the term parameres in *Diptera*. The term was originally proposed for the genital structures of *Coleoptera* by VERHOEFF (1893), and its homology with the structures in other holometabolous insects is not clear. It is thought that true gonopods in

Coleoptera are reduced, and the term used for gonopods or for postgonites in *Diptera* could be misleading. The postgonites presumably represent paraphyses of lower *Diptera*, but the homology of pregonites is still disputed. Therefore I prefer the neutral terms pregonites and postgonites for *Cyclorrhapha*, as proposed by CRAMPTON (1944). After reaching the consensus on the homology of clasping lobes it would be easier to solve the problem of origin and terminology of hypandrial processes.

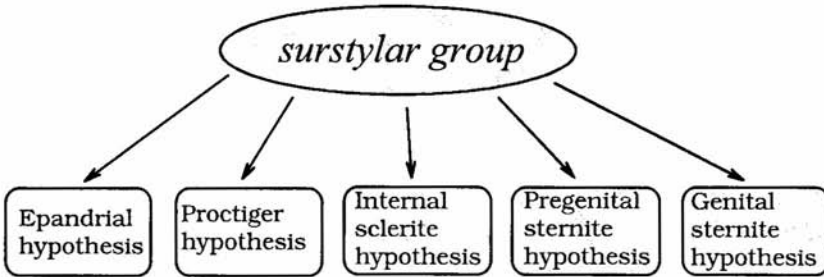
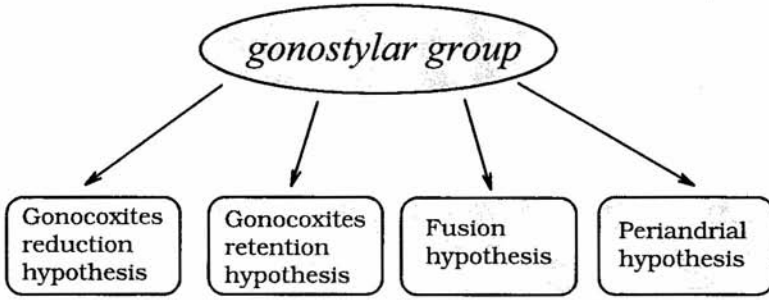
Some common taxonomic names denote non-monophyletic groups and therefore I try to avoid them. Thus, instead of "*Nematocera*" I use the term lower *Diptera* (flies other than *Brachycera*), lower *Brachycera* instead of "*Orthorrhapha*" without *Orthogenya* (other than *Eremoneura*), lower *Schizophora* instead of "*Acalyptatae*" and also higher *Diptera*, when initial meaning is not clear and it may mean *Brachycera*, *Eremoneura* or *Cyclorrhapha*.

4. HYPOTHESES OF THE ORIGIN OF MALE TERMINALIA (DORSAL COMPLEX) IN *EREMONEURA*

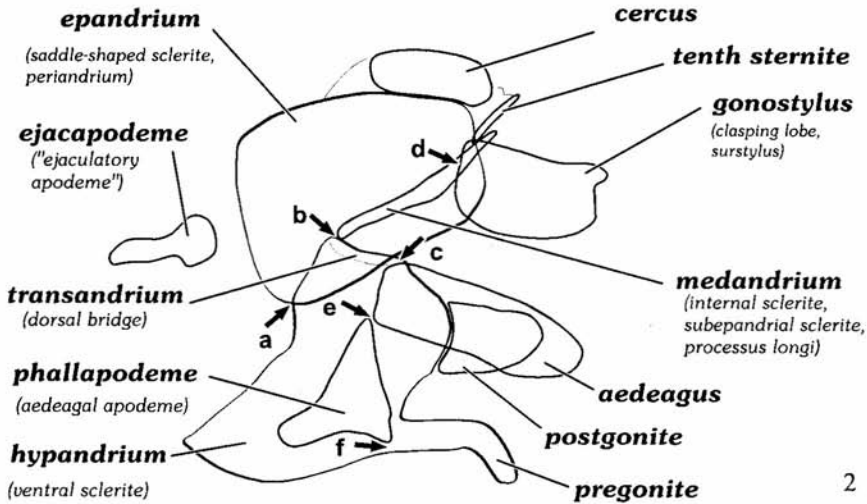
The studies on the male terminalia of *Diptera* started very early and the work of J. SWAMMERDAM "*Biblia Naturae*" published in 1752 can be mentioned as the first. The terms for the genital structures of *Diptera* were often adopted from the other orders of insects. Since realizing the diagnostic importance of the male terminalia, the amount of papers dealing with this problem has stated to increase. Naturally, some authors proposed their own terms, others tried to adopt the existing terminology to the respective structures. The mere usage of terms does not amount to a hypothesis on the origin of hypopygium in higher *Diptera*. An example of such an action is the work of WESCHÉ (1906), who investigated the male terminalia throughout the order *Diptera*.

Various hypotheses were advanced concerning the eremoneuran hypopygial structures, to explain their origin to various extent - some pertain to all the components, some - to one or several elements. This makes them sometimes difficult to compare. I propose to begin with the extraordinarily contradictory problem of the origin of clasping lobes. The question implies further homology of dorsal hypopygial structures and therefore I decided to present these concepts for the whole dorsal complex. On the other hand, I discuss the concepts of the origin of ventral complex of each structure separately. Additional reason for such a division is the similarity of dorsal hypopygial complex of *Orthogenya* and *Cyclorrhapha* and strong differences in the shape of ventral complex, and the concept of these structures pertains to *Cyclorrhapha* only (ejaculatory structures of *Orthogenya* are similar to those of lower *Brachycera*).

Early concepts were proposed to explain the origin of genital structures of some taxa of higher *Diptera*, e.g. genera *Musca*, *Calliphora*, *Eristalis*, or *Glossina*, and here I extend them to all *Eremoneura*. To prevent any misunderstanding I cite the concepts in their original form (sometimes with necessary additions or explana-



1



2

1 - Hypotheses on the origin of the ermoneuran clasp ing lobes; 2 - The groundplan scheme of the cyclotrhaphan hypopygium in lateral view. Arrows with letters indicate available articulations: a) between hypandrium and epandrium; b) between transandrium and medandrium; c) between aedeagus and transandrium; d) between medandrium and gonostylus; e) between phallapodeme and aedeagus; f) between phallapodeme and hypandrium

tions). I have divided the hypotheses of origin of dorsal eremoneuran hypopygial complex of higher flies in two groups (Fig. 1): in one the clasping lobes are treated as secondary structures and gonopods were modified - surstylar hypotheses; gonostylar hypotheses consider the clasping lobes as homologous to gonostyli. The surstylar theories can be further divided into five groups: 1) epandrial hypothesis; 2) internal sclerite hypothesis; 3) pregenital sternite hypothesis; 4) genital sternite hypothesis; 5) proctiger hypothesis. In the gonostylar group I recognize four concepts, in which the clasping lobes in *Eremoneura* are homologized with gonostyli of lower *Diptera*. The concepts differ in transformation of gonocoxites and saddle-shaped sclerite. The following hypotheses belong here: 1) gonocoxites reduction hypothesis; 2) gonocoxites retention hypothesis; 3) fusion hypothesis and 4) periandrial hypothesis. The hypotheses are presented below in chronological order.

4.A. SURSTYLAR CONCEPTS

I consider here all the hypotheses in which clasping lobes are of secondary origin and separated from epandrium or other sclerites, but true gonopods are reduced or associated with hypandrium. CRAMPTON (1923) proposed the term surstyli for the "lobe-like process of the ninth tergite" of *Mecoptera*, *Bittacomorpha* (*Ptychopteridae*) and *Ptecticus trivittatus* (*Stratiomyidae*). Later the term was transferred to epandrial appendices of cyclorrhaphous flies. The name of each theory designates the structure from which the secondary clasping lobes (surstyli) originate.

4.a.1. Epandrial hypothesis

The hypothesis is commonly attributed to CRAMPTON (1936), but already LOWNE (1895) explained the origin of *Calliphora* clasping lobes in tergal way: "I do not think that either the external or internal valves [clasping lobes and postgonites] are true appendages, but believe both to be prolongations of the posterior edge of the terga of their respective segments" (LOWNE, 1895: 744). The hypothesis was more precisely explained by CRAMPTON (1936, page 147): "The surstyli in the higher *Diptera* are appendages of the ninth tergite, and should not be homologized with the coxites and styli in a lower dipteran, as is done by AWATI, 1915, HENDEL, 1928, PATTON, 1932, and other students of the higher *Diptera*. It [coxite] is not the surstyli, but rather the anterior and posterior gonapophyses in the higher *Diptera*, that represent the segments of genital forceps coxites and styli in the lower dipteran, as may be seen by comparing the corresponding parts in one of the lower representatives of the *Cyclorrhapha*, such as a syrphid, etc., with the parts in a bombyliid, lepidid and other lower forms leading back to the *Nematocera*." (references to illustrations removed).

The suggestions of OVTSHINNIKOVA (1993, 1994), CUMMING et al. (1995), and WHEELER (1995) that epandrial hypothesis was formulated by HENNIG (1936a) were

based on a misunderstanding. W. HENNIG changed his opinion on the homology of hypopygial structures several times, he himself was the author of two concepts - fusion and proctiger hypotheses (1936a and 1976 respectively), however, in the meantime he accepted epandrial hypothesis, probably based on CRAMPTON's (1942) suggestions. If any doubt remains, see repetition of the concept in HENNIG (1937).

4.a.2. Proctiger hypothesis

Two hypotheses belong here, which are superficially distinct because of different numbering of the post-andrial segments. BRÜEL (1897) homologized clasping lobes with the appendices of the eleventh segment, and HENNIG (1976a and b) with the divided tenth tergite. BRÜEL (1897) treated the chitinization around the anus of *Calliphora* as the tenth tergite, so to both authors it was essentially the same segment. BRÜEL (1897) criticized LOWNE's (1895) work, disagreed with his concept of the clasping lobes as derivatives of saddle-shaped sclerite and suggested that the clasping lobes originated from the eleventh segment. The citation from BRÜEL (1897: 531) clearly presents his opinion: "Denn bei einem Geschöpf, dessen Segmente so sehr umgebildet sind, bei dem man insbesondere überall auf Spuren von Reductionen trifft, steht es m. E. [meines Erachtens] vorläufig frei, diese Chitinstücke [valvulae mediales und valvulae laterales, which means cerci and clasping lobes] für Anhänge eines 11. Segments oder Theile eines Analstücks zu halten für Cerci also oder für Valvulae anales und subanales (Heymons, 95a)." [Then in the formation, which segments are so rebuild, that one may everywhere fall upon the traces of reduction, in my opinion temporarily remain the choice of these chitinized pieces as the appendices of eleventh segment or parts of anal portion for cerci or for Valvulae anales or subanales (HEYMONDS, 95a)]

Eighty years later, and a few years after formulation of the periandrial hypothesis, HENNIG (1976a and b) proposed an explanation, which was alternative to GRIFFITHS' (1972) idea. HENNIG (1976a and b) assumed, that the tenth tergite was secondarily divided into clasping lobes. The citation from HENNIG (1976a, page 6): "Ich halte es für möglich, dass bei den *Empidiformia* und *Cyclorrhapha* das 10. Tergit in 2 Teile gespalten ist (ähnlich wie das 9. Tergit bei vielen *Empidiformia* und *Asiliformia*), und dass diese beiden Teile als Aussenwände der Surstyli dem 9. Tergit beweglich (nur in abgeleiteten Fällen unbeweglich) angegliedert sind." [I think it possible, that in *Empidiformia* and *Cyclorrhapha* the 10. tergite is divided into two portions (similar to 9. tergite in many *Empidiformia* and *Asiliformia*), and these both portions as external edges of surstyli are articulated movable with 9. tergite (only in derived cases unmovable)].

4.a.3. Internal sclerite hypothesis

The so called "internal sclerite" was often called "tenth sternite" or "subepandrial sclerite" and in the hypothesis the clasping lobes should derive from the sclerite.

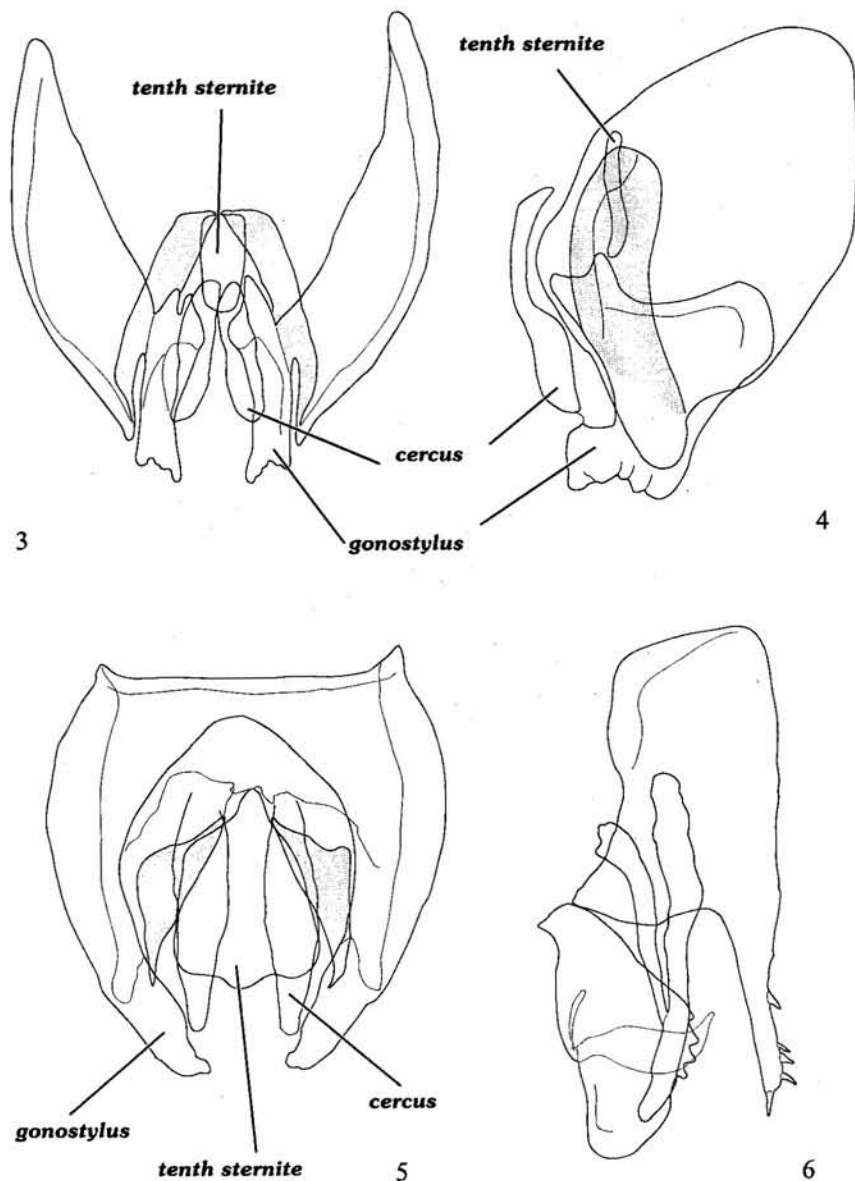
Probably the concept was first suggested by BERLESE (1909), as he termed the internal sclerite and genital claspers of *Eristalis tenax* (L.) and *Musca domestica* L. "10 sternite". BERLESE's (1909) concept can be found on the page 327 in his description of the male terminalia of *Eristalis tenax*: "Il 10.° sternite, molto ridotto e si mostra rappresentato da due pezzi laterali, triangolari, saldati in parte, o meglio articolati sui lati sel corrispondente tergite, ed essi recano una parte articolata apicale, larga, rotondeggiante che, un vero mesostilo" [10. sternite is much reduced, and composed of two lateral triangular fragments, partly fused or rather articulated with sides of the respective tergites, and these consist of an apical articulated portion, large and broadly rounded, which is the true mesostyli (= claspings lobe)].

For BERLESE (1909) the sclerite called "tenth sternite" belongs to the same segment as the saddle-shaped sclerite (his tenth tergite). Actually, it is the ninth segment, and hence he did not recognize hypandrium as a sclerite, but as a part of aedeagal complex (his "organo copulatore"), which could mean the ninth sternite. Also in METCALF's (1921) opinion the claspings lobes constitute appendages of the tenth segment. According to ZUMPT and HEINZ (1949) the saddle-shaped sclerite belongs to the tenth segment, which consists of a tergite and a sternite. These authors interpret the claspings lobes as new structures, derived from the tenth sternite.

OVTSHINNIKOVA (1993, 1994) compared the musculature of lower *Brachycera* and *Cyclorrhapha* and suggested the internal sclerite origin of the claspings lobes (page 264): "The epandrial musculature suggests the homologization of the surstyli of *Cyclorrhapha* with the ventral proctiger plate (10th sternum) of *Orthorrhapha*". For her the sclerite is a part of proctiger, and does not belong to the genital segment. Although the interpretation of the internal sclerite by OVTSHINNIKOVA (1993, 1994) differs from that of BERLESE (1909), both of them suggest the same structure, as ancestral to claspings lobes.

4.a.4. Pregenital sternite hypothesis

In his description of the genitalia of *Musca domestica* L., HEWITT (1914: 434) expressed his view on the origin of claspings lobes as follows: "The ventral arch of the seventh sclerite has been completely withdrawn into the abdomen, and consists of a pair of curved sclerites (fig. 9, vii, v.), somewhat rhomboidal in shape, lying dorsal to the fifth ventral arch and ventral to the penis (P.); they form the secondary forceps." (=claspings lobes). HEWITT (1907, 1914) called the posterolateral processes of the fifth sternite "primary forceps", and to him the saddle-shaped sclerite was the eighth tergite, thus the seventh ventral sclerite (because of indication "v.", i.e. ventral in figure caption) was to him the pregenital sternite.



3-4. Epandrial complex of *Empis (Anacrostichus) lucida* ZETTERSTEDT, 1838 (*Empididae*): 3 - ventral view, 4 - lateral view (Sweden, Gällivare, VII, leg. T. BECKER, Museum of Natural History, Wrocław). 5-6. Male terminalia of *Bicellaria nigra* (MEIGEN, 1824) (*Hybotidae*): 5 - epandrial complex, ventral view (medandrium shaded), 6 - hypandrial complex, lateral view (Poland, Carpathian Mts., Babia Góra, 30. VI. 1989, leg. A. PALACZYK)

4.a.5. Genital sternite hypothesis

This is a conjecture rather than a statement, however, it was treated as such by CRAMPTON (1942). EDWARDS (1920: 26) wrote: "In *Cyclorrhapha* it is said by AWATI (1915) to be [the ninth sternite] absent, but may possibly be represented by his vesiculum or by the editum by NEWSTEAD (1911)." Probably EDWARDS (1920) erroneously called vinculum of AWATI (1915) vesiculum, which term, suggested by AWATI (1915) for *Biblio*, was also adopted to denote cyclorrhaphan hypopygial structure. In this case the ventral sclerite was homologized by EDWARDS (1920) with the ninth sternite. The second possibility is that the ninth sternite could be homologized with clasping lobes (named as "editum" in *Glossina* by NEWSTEAD, 1911).

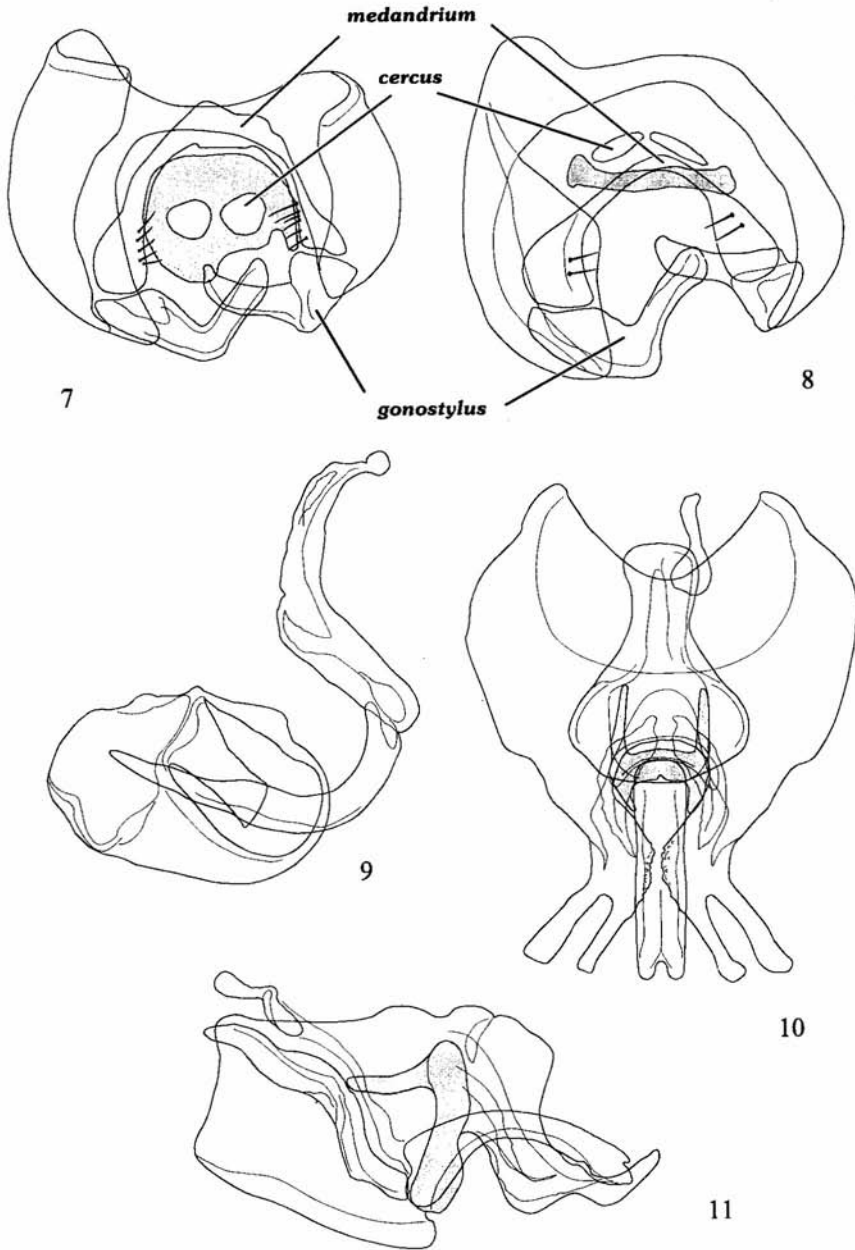
4.B. GONOSTYLAR CONCEPTS

All the hypotheses, in which clasping lobes are homologized with the gonostyli of lower *Diptera*, despite transformation of other structures, belong here. A major difference between these hypotheses is the transformation of gonocoxites. In two hypotheses the gonocoxites take part in formation of the saddle-shaped sclerite, in the other two the gonopods remain as separate structures.

4.b.1. Gonocoxites reduction hypothesis

The idea was presented independently by several authors. It was first suggested by AWATI (1915). He assumed that not only gonocoxites, but also the ninth sternite in higher *Diptera* were lost; he homologized the ventral sclerite (his "body of theca") with the sclerite called "vinculum" in *Biblio* (it is probably the tenth sternite or the so called parameral sheet). AWATI (1915), analyzing the genitalia of *Biblio*, presumed that "Appendages of the genital segment" (i.e. gonostyli) are set on "Sternite of the genital segment", and homologized them with the structures in a "Syrphid", *Glossina*, *Musca*, *Calliphora* and *Lispe*. He stated, that the genital sternite (i.e. also gonocoxites) underwent reduction, and the clasping lobes (his "appendages") were displaced dorsally, as compared to *Biblio*.

Presenting his opinion, AWATI (1915) described two "types" of hypopygia. *Glossina* type (p. 517): "The tergite of the genital segment is highly developed and incurved to give attachment to the body of the theca [=ventral sclerite]. Its sternite has completely disappeared. The appendages of this tergite are also reduced and are enveloped by it. The edita of Newstead seem to be these reduced appendages". *Musca* type (p. 517): "The inner claspers of HEWITT, which he thinks are formed by the modifications of the seventh sternite seem to be the appendages of the genital segment and to be homologous with those of the first two types [=Syrphid and *Glossina* type]. ... The sternite of this segment [=genital segment] has, according to my view, disappeared as in the last type, while HEWITT thinks that it is represented by



7-9 - Male terminalia of *Ocydromia glabricula* (FALLÉN, 1816) (*Hybotidae*): 7-8 - epandrial complex: 7 - ventral view, 8 - posterior view (tenth sternite shaded); 9 - hypandrial complex, dorso-lateral view (Poland, Carpathian Mts., Babia Góra, 30. VI. 1989, leg. A. PALACZYK); 10-11 - Hypandrial complex of *Lonchoptera nigrociliata* DUDA, 1927 (*Lonchopterygidae*): 10 - dorsal view, 11 - lateral view (transandrium shaded) (Poland, Chojnów env., 22. VI. 1979, leg. T. ZATWARNICKI)

those pieces of chitin which, according to my view, represent the cerci of the anal segment”.

Also FEUERBORN (1922), probably independently from AWATI (1915), suggested the same idea on his page 206: “Ich möchte die Valv. laterales als Gonopoden deuten, die allerdings hier (wenn nicht der »Processor brevis« BRUELS als 2. Glied aufgefaßt wird) nur 1gliedrig sind.” [I will term “Valv. laterales” gonopods, which here (if “Processor brevis” of BRUEL is not understood as the second segment) is only one-segmented]. Another proponent of the concept was HENDEL (1928) (p. 49): “Sie [=Styli] gehören dem 9. Segment an, inserieren bei niederen *Nematoceren*, z. B. bei Tipuloiden, scheinbar an dem dort noch sichtbaren 9. Sternit (mit den gonocoxites CRAMPTON), rücken aber mit der Reduktion des 9. Sternits dorsalwärts, und bei den Schizophoren ist der 9. Tergit der Träger der Gonopoden”. [They (=styli) belong to the 9. segment, attached in lower *Nematocera*, e.g. in *Tipuloidea*, to the still visible 9. sternite (with the gonocoxites of CRAMPTON), but moved dorsally with the reduction of the 9. sternite, and in the *Schizophora* the 9. tergite bears the gonopods]. It is likely that the concept was presented earlier, but I do not regard denoting clasping lobes as “gonostyli” or corresponding terms as a clear indication of the origin of the structure.

4.b.2. Gonocoxites retention hypothesis

I include here two apparently similar opinions, which however are based on very different assumptions. PATTON's (1932) concept is a hybrid between the view of METCALF (1921) on the existence of the tenth sternite under the epandrium, and AWATI's (1915) opinion on retaining the gonocoxites by higher *Diptera*. PATTON (1932) observed the presence of a process attached to the clasping lobe in the Muscidae; the process to him represented a remnants of the gonocoxite. His explanation of the origin of the clasping lobes is the following (PATTON 1932: 370): “Awati regarded them as the appendages of the ninth segment, and I believe that this is correct interpretation of their true nature, and they would then be homologous with the coxites of the ninth segment (claspers, forceps, ect.) of mosquitoes. It is possible then, if this view be accepted, that the small hairy sclerite on the outer side represents the basal, and the larger sclerite the distal segment of the coxite.” Because the sclerite attached to the “distal segment of coxites” was interpreted by PATTON as a part of the clasping lobes (internal sclerite or “processus longi” was regarded as the tenth sternite), I think that he thus concluded that all the gonopod (gonocoxite and gonostylus) was transformed into the clasping lobe.

CRAMPTON's (1923, p. 214) interpretation differs slightly but significantly; for him the gonocoxites are homologous with the internal sclerite: “In the syrphid shown in the figure 22 [illustration of the genitalia of *Eristalis tenax* (L.)], the distal segment of the genital style is flat and broad, while the basal segment is more membranous, and becomes quite closely applied to the pleural region of the ninth

abdominal segment.” Such a concept was completely neglected by CRAMPTON and other authors during the last seventy years. This short statement is treated here as a correct explanation of the transformation of gonopods in *Eremoneura* and a basis for the new reconstruction of the origin of eremoneuran hypopygium; it is discussed in chapter 7 as “hinge” hypothesis.

4.b.3. Fusion hypothesis

Though the hypothesis is attributed to ULRICH (1972), already HENNIG (1936a) suggested the idea, writing on p. 359: “Bei den Cyclorrhaphen sind die eingliedrigen Gonopoden schon von CRAMPTON (1922) mit dem Dististylus der *Nematocera* verglichen worden. Es liegt nun die Annahme sehr nahe, das bei den erwähnten *Nematocera* schon sehr schmale 9. Segment bei den Cyclorrhaphen als gänzlich mit dem 10. verschmolzen anzunehmen. Ausserdem ist wahrscheinlich das Basalglied der Gonopoden in seiner Längsrichtung mit dem 10. Segment verwachsen, ähnlich wie ich das oben von Weibchen von *Pachyrrhina* beschrieb”. [In *Cyclorrhapha* the one-segmented gonopods were compared with the dististylus of *Nematocera* already by CRAMPTON (1922). It is close to the accepting, that the narrow 9. segment, mentioned in the *Nematocera*, is completely connected with 10. segment in *Cyclorrhapha*. Besides it is possible, that basal segment of gonopods is fused lengthwise with 10. segment, as described above in the female of *Pachyrrhina*], and then on page 367 he concluded that “Das 9. Segment ist mit dem 10. und dem Basalglied der Gonopoden verschmolzen.” and “Die Gonopoden gehören daher auch bei dem Cyclorrhaphen zum 9. Segment, doch sitzt ihr Distalglied, wie aus der Lage der männlichen Geschlechtsöffnung hervorgeht, dem 10. Segment auf, mit dem ihr Basalglied verschmolzen ist.” [The ninth segment is fused with the tenth segment and with the basic segment of gonopods. Therefore also the gonopods in *Cyclorrhapha* belong to the ninth segment, however, as indicated by the position of the male genital opening, their distal segment is set on the tenth segment, with which their basal article is connected]. The view that gonopods became fused with epandrium was applied to *Orthogenya* by ULRICH (1972). HENNIG (1976a) and McALPINE (1981) suggested that the concept was the same as that proposed by GRIFFITHS (1972) - periandrial hypothesis - however, both views are in my opinion essentially different.

4.b.4 Periandrial hypothesis

While presenting the phylogeny of *Cyclorrhapha* based on the male terminalia, GRIFFITHS (1972) suggested a reduction of the true epandrium in *Cyclorrhapha* and a dorsal expansion of the gonopods, a condition being a prelude to loss of the epandrium and fusion of the gonopods along their lateral margins to form a replacement sclerite. The citation from his p. 32 is as follows: “My view is that the

true epandrium (9th tergum) is completely absent in the *Cyclorrhapha*, and that the so-called 'epandrium' of this group is formed by upward growth of the basimeres (basal articles of the parameres) and their fusion along the centre of the dorsum. Since the term epandrium should be applied only to the 9th tergum, I therefore propose for this sclerite the new term periandrium." He also explained the origin of processus longi (p. 35): "It is possible that the processus longi of some *Calyptratae* arose as apodemes from the base of the telomeres [gonostyli], since they bear muscles apparently homologous with those inserted on the base of the telomeres [gonostyli] in other groups."

On the basis of CHVALA's (1983) work, GRIFFITHS (1983) verified his interpretation of the lost epandrium in the groundplan of the *Eremoneura*: "CHVALA interprets the structure of *Hormopeza* as indicative of the groundplan condition in this respect, a view with I concur. Thus I was not correct in stating in my 1972 book that the epandrium was "either lost or fused with cerci" in the groundplan of the *Eremoneura*. *Hormopeza* illustrates exactly the intermediate condition needed to verify my interpretation of the structure of the *Cyclorrhapha* and of other families of *Orthogenya* (reduction of the epandrium and dorsal expansion of the gonocoxites, a condition precursory to the elimination of the epandrium and fusion of the gonocoxites across the dorsum which I postulated)."

For the sclerite linking the hypandrium and clasping lobes GRIFFITHS (1972) proposed the term "interparameral sclerite". ROZKOŠNY (1984) proposed to change the term "interparameral plate", as illogical, to the interperiandrial plate or sclerite, and in his opinion the structure represented probably a vestige of the ninth tergum. GRIFFITHS (1983) called it intergonopodal sclerite.

5. CONCEPTS OF THE ORIGIN OF VENTRAL COMPLEX (=HYPANDRIAL COMPLEX) IN CYCLORRHAPHA

The so called ventral complex (or hypandrial complex) consists of the following structures: transandrium (dorsal bridge), ventral sclerite (hypandrium), gonites, aedeagus, phallapodeme and ejacapodeme ("ejaculatory apodeme"). All these components are evidently changed, as compared with lower *Brachycera*.

5.A. TRANSANDRIUM

This is a component of constant position and therefore in various hypotheses the question of the transandrium (dorsal bridge) origin is not a matter of controversies. The sclerite often fused with hypandrium, was called in English literature "dorsal bridge", and by HENNIG (1976a) "Dorsalbrücke". It is agreed that it originated from the gonocoxite apodemes fused to each other (GRIFFITHS, 1972; HENNIG, 1976a).

According to WOOD (1991) its mid portion should be derived from the postero-dorsal remnants of parameral sheet. The view was subsequently followed by SINCLAIR et al. (1994) and CUMMING et al. (1995). In my opinion the function of the structure in transformation of eremoneuran hypopygium is important (see chapter 7) and the question, if the parameral sheet was involved in forming transandrium, has no great influence on the matter.

5.B. PRE- AND POSTGONITES

Two pairs of appendices attached to the ventral sclerite can be found in *Cyclorrhapha*; sometimes one or both pairs are reduced. The origin of those projections, called here gonites, mostly depends on the interpretation of the clasping lobes transformation. Most followers of the surstylar hypotheses conceive the gonites (or one of them) as derived from gonopods. For those students who accept the homology of clasping lobes as gonopods the interpretation is different - they are derivatives of hypandrium or homologous to the structures called "paraphyses", "hypophyses" or sometimes "parameres" in lower *Diptera*.

The author of the first surstylar theory (LOWNE, 1895) suggested that the pregonite (his "anterior gonapophyses") in *Calliphora* was the homologous to gonopod. The same view was adopted by CRAMPTON (1942), and VAN EMDEN and HENNIG (1956). The concept of CRAMPTON (1936a), who homologized the pregonite with the gonocoxite and the postgonite with the gonostylus was more developed. A similar proposal was presented by MICHELSEN (1988), although according to that author also other structures should originate from the gonocoxite (phallapodeme and dorsal bridge). CHILLCOTT (1958) interpreted the pregonites as lobes of the basal segment, and the postgonites as distal segments of the gonopods. The same origin of the pregonite was proposed by OVTSHINNIKOVA (1993, 1994), but she suggested a different origin of the postgonites. COLE (1927) designated pre- and postgonites as anterior and posterior gonapophyses of lower *Diptera*, but I am not sure, if such a statement can be accepted as an indication of homology. BRÜEL (1897) viewed the pregonites as a modified posterior margin of the eight sternite (additionally the phallapodeme should originate from the rest of it). Apparently, to him postgonites were transformed gonopods and he called them "Parameren" (in his argumentation BRÜEL (1897) refers to another work on general entomology, unavailable to me). Probably CRAMPTON (1942) was the first to consider pre- and postgonites as new structures of the *Cyclorrhapha* and therefore gonopods as lost. A similar opinion was presented by HENNIG (1976b), who, based on muscular connections, could not accept the direct homology of the gonites with gonopods. HENNIG (1976b) regarded the gonites as secondary attachments, separated from the posterior margin of the ventral sclerite, the latter resulting from fusion of the hypandrium and gonocoxites (see chapter 6.c).

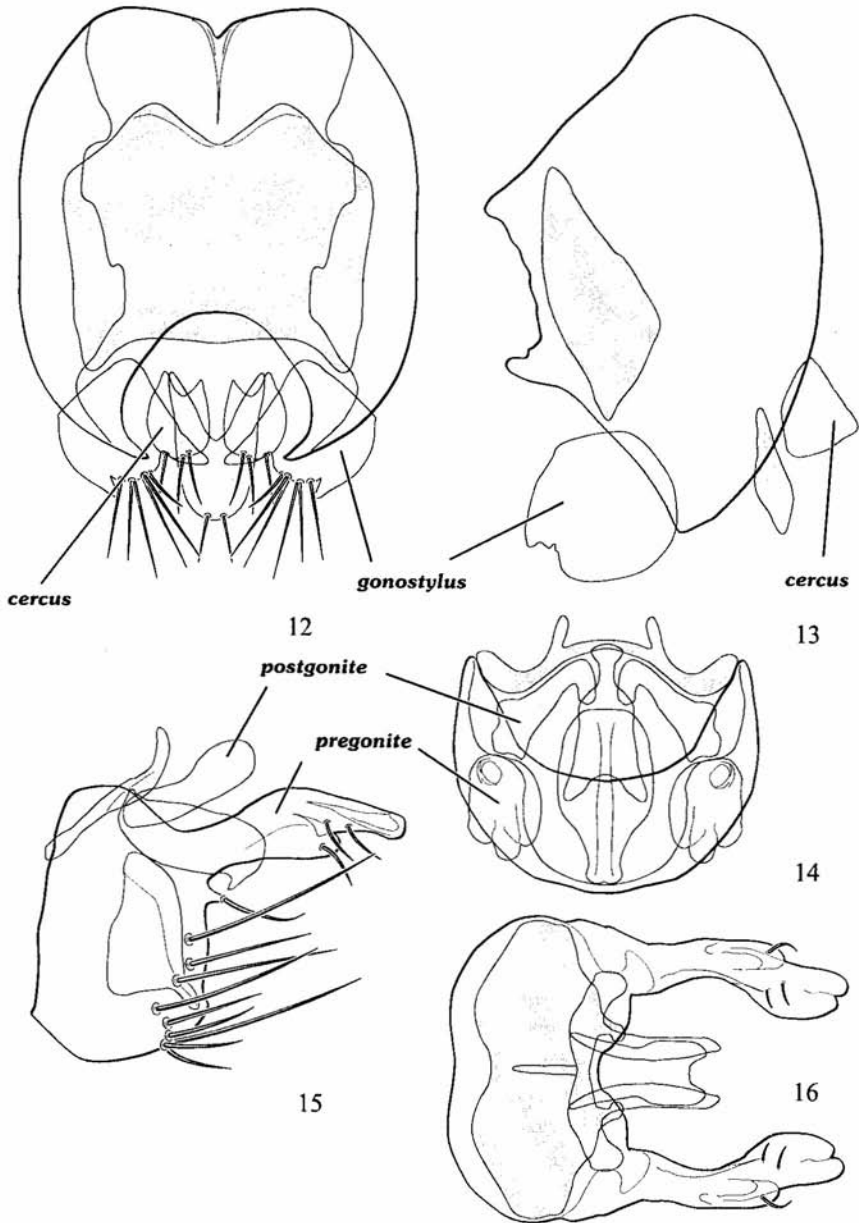
I follow GRIFFITHS' (1972) interpretation of the postgonites as paraphyses of lower *Diptera*, but I do not accept his view that the pregonites represent additional

paraphyses. According to BLACK (1966), pregonites and postgonites of *Eucalliphora* develop as lobes from the same posterior papillae of the dorsal wall of the genital disc. I doubt if ontogenetic investigations can really be decisive in the matter, because after all ontogeny is neither a complete nor an unchanged recapitulation of phylogeny. Since in primitive *Cyclorrhapha* pregonites are attached to the hypandrium, but not articulated with it, I think that they are posteroventral processes of hypandrium. I disagree with an argument of OVTSHINNIKOVA (1993, 1994), that the pregonite derived from the gonocoxite (basistyli), because the muscle M42 connecting the pregonite with the hypandrium in *Calyptata* is homologous with M33 (longitudinal to hypandrium and attached also to gonocoxites) of lower *Brachycera*. The muscle connects not only the hypandrium with the gonocoxite, but mostly the anterior and posterior edges of hypandrium, and the homology (M42 with M33), which I also accept, does not exclude the possibility of hypandrial origin of the pregonite.

5.C. EJACAPODEME ("EJACULATORY APODEME") AND PHALLAPODEME

In the groundplan of both the *Nematocera* and the non-cyclorrhaphan *Brachycera*, the sperm pump is enclosed within the base of the aedeagus and is closely associated with what is often referred to as the ejaculatory apodeme in these groups. That apodeme arises from, and is firmly attached to the inner walls of the aedeagus; the muscles that operate the sperm sac are attached to it. According to SCHRÄDER (1927) the phallapodeme develops ontogenetically as an ingrowth of the integument at the base of the aedeagus. There are three characters, which distinguish the *Cyclorrhapha* from other *Diptera*: the presence of the sperm pump, which is separated from the phallapodeme, the membranous articulation between the phallapodeme and hypandrium, and the articulation phallapodeme and aedeagus. The latter character was also observed by HENNIG (1976a) in some *Orthogenya* (e.g. in *Empis borealis* L.). The articulation of the phallapodeme with the aedeagus in *Acroptera* (*Lonchopterygidae*) is not completely developed, despite the fact that they possess the ejacapodeme ("ejaculatory apodeme"). Therefore the transformation is pertains to *Atriata*, and not to all the *Cyclorrhapha*.

Thus in *Atriata* a rather complicated pattern of interconnected structures can be observed, which allows protrusion of aedeagus during the bending of hypopygium. The transformation of phallapodeme is related to different movements of aedeagus. In lower *Diptera* the musculature causes shifting of the aedeagus in sagittal surface - forward and backward, whereas in *Atriata* the aedeagus during protrusion moves upward. This enables it to lean on the phallapodeme and on the margin of hypandrium, and makes possible an oblique or transverse position of the phallapodeme relative to aedeagus. The phallapodeme articulates with the postero-ventral margin of aedeagus. Its postero-dorsal margin is usually articulated with the medial portion of medandrium (dorsal bridge). The sperm pump is only loosely joined to the base of the aedeagus by means of ejaculatory duct, and the ejacapodeme ("ejaculatory apodeme") is com-



12-16 - Male terminalia of *Callomyia amoena* MEIGEN, 1824 (*Platypezidae*): 12-13 - epandrial complex, 12 - ventral view, 13 - lateral view (medandrium light shaded, tenth sternite dark shaded); 14-16 - hypandrial complex, 14 - lateral view, 15 - dorsal view, 16 - posterior view (transandrium shaded) (Poland, Wrocław-Osobowice, 21. VI. 1979, leg. T. ZATWARNICKI)

pletely separated from the body wall. I agree with HENNIG (1976b) that the possession of a separate sperm pump independent from the phallapodeme, and the presence of a striking connection (at least partially sclerotized) between the phallapodeme and hypandrium are interrelated features.

HENNIG (1976a) proposed three possible interpretations of this transformation.

1. The ejacapodeme ("ejaculatory apodeme") in association with the sperm pump of the *Atriata* is homologous with the ejaculatory apodeme of the non-cyclorrhaphan flies, and the phallapodeme of the *Atriata* represents a neomorphic structure of the group.

2. The phallapodeme is homologous with the ejaculatory apodeme of the non-cyclorrhaphan flies, and the ejacapodeme ("ejaculatory apodeme") represents a neomorphic structure.

3. Both the phallapodeme and the ejacapodeme ("ejaculatory apodeme") are parts of the ejaculatory apodeme of the non-cyclorrhaphan flies, developed by its division and both of them took over its functions.

Theoretically one more possibility exists, namely that both the apodemes are neomorphic structures (which can not be totally excluded).

BRÜEL (1897) was a follower of the first concept, that the phallapodeme was a novelty. He homologized the phallapodeme (his "Gabelplatte") with the remnant of the eight sternite; this view was also maintained by FEUERBORN (1922), who homologized the ejacapodeme ("ejaculatory apodeme") with the seventh sternite. To ZUMPT and HEINZ (1949) the phallapodeme was a new acquisition, not homologous with the hypopygial components of lower *Diptera*. GRIFFITHS (1972) identified the phallapodeme with ejaculatory apodeme, and regarded the ejacapodeme as a neomorphic structure. Later he changed his view (GRIFFITHS, 1981) and conjectured that it originated from the gonocoxite apodemes. He recognized two kinds of apodemes: endophallic apodemes, formed as outgrowths of the invaginated integument of the endophallus with ejaculatory duct, and exogenous apodemes, formed as ingrowths from the external body wall. According to GRIFFITHS (1981) the phallapodeme of *Cyclorrhapha* is an exogenous apodeme and cannot be homologous with the ejaculatory apodeme of the non-cyclorrhaphan *Diptera*, since the latter is endophallic in origin. Nor can it have arisen by the splitting process suggested by HENNIG (1936a), since splitting of an endophallic apodeme could produce two endophallic apodemes. Finally the ejacapodeme of *Cyclorrhapha* could be homologous with the ejaculatory apodeme, which lost its muscular connections with the outer body wall and come withdrawn into the body cavity. GRIFFITHS' (1981) opinion on the origin of phallapodeme was maintained also by MICHELSEN (1988), who also homologized the phallic guide (intermedium) with the gonocoxites. HENNIG (1976a and b) concluded that the phallapodeme was homologous to the ejaculatory apodeme.

In *Lonchopterygidae* both the phallapodeme and ejacapodeme occur together, but the phallapodeme is curved and narrow, distinctly separated from the aedeagus.

In my opinion this contradicts the possibility of the origin of the ejacapodeme from the ejaculatory apodeme. Also in *Opetia*, characterized by a reduced phallapodeme, the ejacapodeme is present (see figures in HENNIG, 1976a and CUMMING et al., 1995). Therefore I think that ejacapodeme is a neomorphic structure.

I suggest a new concept of the phallapodeme origin. According to TREHEN's (1960, 1962) and ULRICH's (1972, 1975, 1988) studies, the muscles of the ejaculatory apodeme ("aedeagal apodeme") in *Empidoidea* are inserted at the base of aedeagus, or on the hypandrium, in the same way as in cyclorrhaphous flies. Not only the criterion of similarity of musculature, but also the criteria of continuity of function and similarity of position indicate homology of the phallapodeme with the ejaculatory apodeme. GRIFFITHS (1981) was opposed to this view, since he interpreted the ejaculatory apodeme as an endogeneous apodeme and the phallapodeme as an exogeneous apodeme. In my opinion the problem could be solved, if a mixed origin of the phallapodeme was accepted. I presume that the posterior and external margins are of hypandrial origin, and the internal portion is of ejaculatory apodeme origin. Most probably, an expansion of its anterior portion took place and this portion came to lean on the antero-ventral edge of the remaining portion of hypandrium. Such an arrangement makes it possible to move the aedeagus upwards with bending of the epandrium.

5.D. VENTRAL SCLERITE (HYPANDRIUM)

The sclerite is commonly treated as the ninth sternite and called hypandrium even though the gonopods are fused with it, but there are also other concepts. Already BRÜEL (1897), based on a comparison with the representatives of other insect orders, correctly homologized the sclerite (his "Tragplatte") with the ninth sternite (despite this, he designated the saddle-shape sclerite as eight segment). AWATI (1915) supposed that the ninth sternite in higher *Diptera* was reduced and homologized the ventral sclerite with the structure called "Vinculum" in *Biblio*. According to METCALF (1921) (the concept later accepted by PATTON, 1932, 1934, PATTON & CUSHING, 1934, PATTON & GIBBINS, 1934, PATTON & WAINWRIGHT, 1935, ZUMPT & HEINZ, 1949) hypandrium and epandrium originated from different segments (ninth and tenth respectively). The hypandrium, being the ninth sternite, was supplied by parts of the ninth tergite, together forming the "ninth tergosternum". Based on the investigations on *Platypezidae* and *Pipunculidae*, CHILLCOTT (1958) suggested that the ninth sternite was reduced or absent and the ventral sclerite was formed chiefly by fused gonocoxites. A remnant of the 9th sternite would be found only at the proximal margin. It is widely accepted that the hypandrium is the ninth sternite.

6. CRITIQUE OF THE HYPOTHESES ON THE ORIGIN OF EREMONEURAN DORSAL HYPOPYGIAL COMPLEX

In this chapter I discuss the arguments presented in order to explain the origin of clasping lobes, saddle-shaped sclerite and internal sclerites of the *Eremoneura*. Several hypotheses were presented without any substantiating evidence (pregenital sternite, genital sternite, and gonocoxites reduction hypotheses) and these, according to the present knowledge, are not very probable and thus not taken into consideration here. As a key to the explanation of transformation of the eremoneuran hypopygium I accept the gonostylar concept of gonocoxites retention, which is developed below as "hinge" hypothesis. As regards the gonostylar concepts, I criticize the secondary character of the saddle-shaped sclerite in the periandrial theory. The idea of gonopods fusion is rather speculative, and difficult to verify. Neither HENNIG (1936a), nor ULRICH (1972) mentioned any sound evidence, which might either support or refute it. No sign of the fusion of the ninth tergite with other structures was observed in recent primitive *Eremoneura*. The loss of gonopods forced the origin of this theory, and only the lack of separated gonopods in *Eremoneura* motivates maintaining the hypothesis. Since 1972 the concepts of ULRICH and GRIFFITHS, being so similar and complementary, have converged (ULRICH used the term "periandrium", and GRIFFITHS postulated the possibility of retaining the epandrium in some "primitive" *Orthogenya* - e. g. *Hormopeza*, *Idaelaphia*). My remarks on periandrial hypothesis (chapter 6.d) could apply also to the fusion hypothesis.

To introduce order in my reasoning, I recognize five kinds of arguments given for justification of surstylar concepts:

- rejecting the continuity of function (expressed as repeatedly occurring replacement of one structure by others).
- substantiating the secondary origin of clasping lobes.
- substantiating the transformation of gonopods into the hypandrial complex.
- presence of a single muscle of clasping lobes.
- suggesting the direction of gonopodal modification in gonostylar hypotheses.

Separately, I consider the arguments common to all the surstylar hypotheses, especially those evidencing the secondary origin of clasping lobes and fusion of the gonopods with the hypandrium. The remaining arguments, presented by authors or defenders of individual theories, are discussed in the separate chapters concerning epandrial, proctiger and internal sclerite hypothesis.

6.A. DISCUSSION ON SURSTYLAR HYPOTHESES

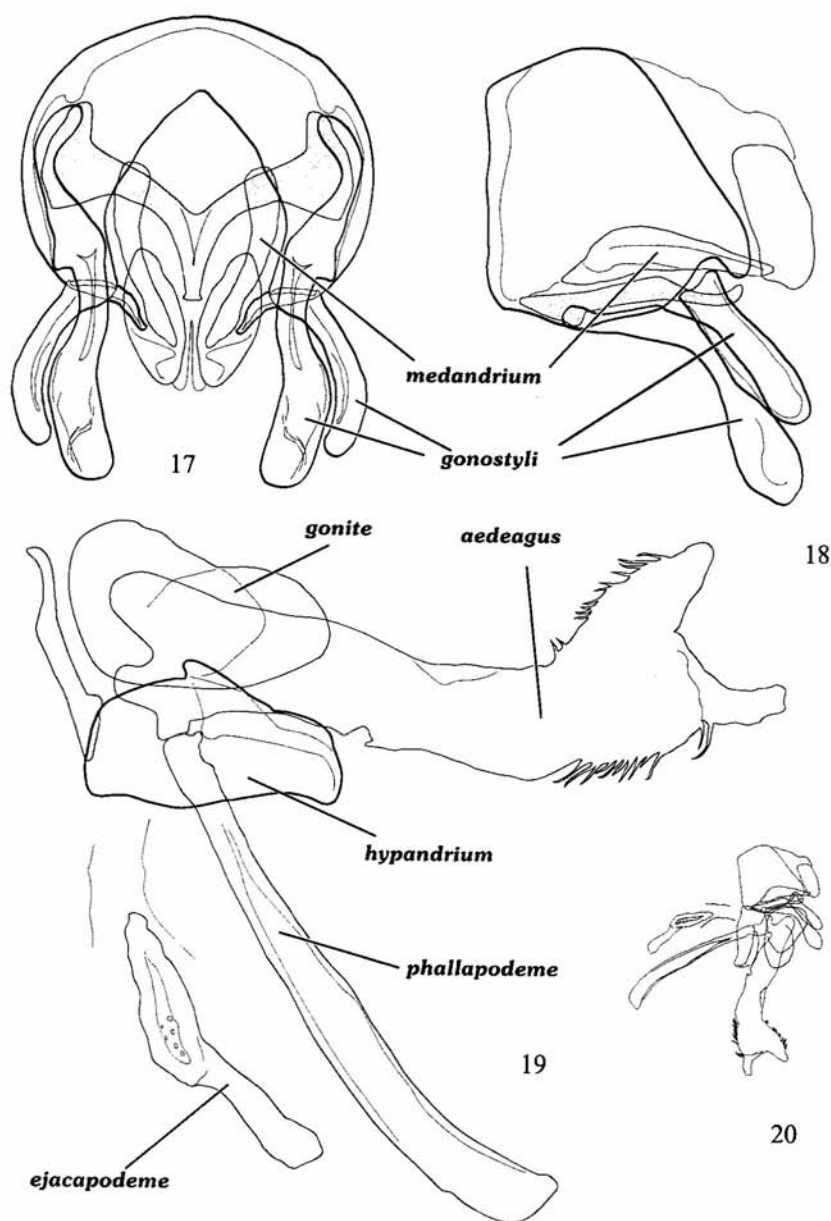
Irrespective from which hypothesis explaining the evolutionary processes we analyze, certainly a hypothesis maintaining the continuity of function has a better explanatory power than a hypothesis in which such a continuity is not maintained.

Only when evidence is found against the homology of clasping lobes with gonostyli, the continuity of function may be rejected. In the case when arguments in favour of replacement are doubtful, or result from erroneous assumptions, it should be accepted, that the function continuity is an additional argument in each gonostylar hypothesis. When a direct homologization of structures is possible, there is no need to resort to replacement of one structure by another. The proponents of epandrial hypothesis (CUMMING et al., 1995) argue that even the lack of function continuity can be understood as its advantage, since they criticize GRIFFITHS' (1972) assumption of a priori continuity of function, when considering various hypotheses. Analyzing the evidence, I do not have the impression that the question was presupposed by GRIFFITHS (1972), or by others. In his methodology, GRIFFITHS (1972, 1981, 1990, 1991) employs valuable and verified rules of homology, and one of such rules is the continuity of function. In my opinion this should not raise objections, and everybody (including GRIFFITHS himself) would reject the rule of continuity in the face of unquestionable evidence for structural replacement. It should be stressed, however, that such a rejection could be accepted only after presenting reliable evidence for the replacement of structures. Unless this happens, questioning the continuity of function is pointless and only obfuscates the real problem. The so called "morphological evidence based on extensive outgroup comparison" presented by CUMMING et al. (1995), or interpretations provided by other authors, are not arguments strong enough to refute the rule of continuity.

Advocating structural replacement requires presenting reasons and the way, in which such a replacement could be effected, as well as direct indications testifying to the process. Hitherto the following indications of gonostylar replacement have been given:

- secondary clasping lobes (surstyli) exist in lower *Diptera*.
- clasping lobes can be replaced by other structures.
- possibility of the change of gonopodal action, also relative of other structures.

CRAMPTON (1923, 1936, 1942) supported the secondary origin of clasping lobes with the cases of *Bittacomorpha* (*Ptychopteridae*) and *Ptecticus trivittatus* (*Stratiomyidae*), whose male terminalia have distinct gonopods and true epandrial lobes. According to OVTSHINNIKOVA (1989) there exist muscular connections between the tenth sternite and the "epandrial lobes" in *Ptecticus tenebrifer* WALKER, hence the latter structures should be interpreted as elongated cerci, not appendices of epandrium. The secondary clasping lobes (surstyli) are known not only in *Bittacomorpha* (cf fig. in WOOD, 1991), but also in the *Apsilocephalidae* (NAGATOMI et al., 1991b; SINCLAIR et al., 1994), various *Asilidae*: *Leptogaster cylindrica* (DE GEER) presented by KARL (1959) and OVTSHINNIKOVA (1989); *Neoitamus navasardiani* RICHTER and *Trypanoides testaceipes* MCQ. presented by OVTSHINNIKOVA (1989); even among the *Cyclorrhapha* - genus *Limnellia* (*Ephydridae*), according to ZATWARNICKI (1992). The fact, that in lower *Diptera*, and even within the *Eremoneura* epandrial lobes are developed, does not indicate, that such a process was responsible



17-20 - Male terminalia of *Dryomyza analis* (FALLEN, 1820) (*Dryomyzidae*): 17-18 - epandrial complex and transandrium, 17 - ventral view, 18 - lateral view; 19 - hypandrial complex, lateral view (transandrium shaded); 20 - general view, lateral view (Poland, Chojnów, 22. VI. 1979, leg. T. ZATWARNICKI)

for the origin of deflected hypopygium. This had to happen in the ancestors of *Eremoneura* and traces of the process should persist in the groundplan of the group. In all the mentioned cases the phenomenon could be treated as exceptional, and even in the *Asilidae* the taxa with surstyli belong to derived lineages, and the presence of surstyli is not a part of the groundplan of the family. In all known cases the surstyli of lower *Diptera* have no muscular connection with the saddle-shaped sclerite, contrary to the eremoneuran clasping lobes (exceptionally attachment shifted in a few advanced sublineages).

According to CUMMING et al. (1995) cerci (the structures of "undisputed homology") in the *Empididae* (presented in illustration no. 7) and some *Hemerodromiinae* (ULRICH, 1975 in *Chelifera*) are known to function as horizontal claspers. The illustration no. 7 (a and b) in CUMMING et al. (1995) shows left lateral and terminal view of *Empis borealis* L. and in my opinion the clasper designated as cerci represents a clasping lobe (gonostyli), not cerci. In this case cerci are reduced. If it is true, no structures of "undisputed homology" functioning as horizontal claspers will be left. CUMMING & SINCLAIR'S (1990) and CUMMING'S et al. (1995) assumption that the lobes attached to the saddle-shaped sclerite in most *Orthogenya* (*Empidoidea*) are cerci and not clasping lobes, implies that, although clasping lobes are present in the groundplan of the *Cyclorrhapha*, they are not found in most empidoid groups (i.e. all *Oreogetoninae*, as well as groundplans of *Empidinae*, *Hemerodromiinae*, *Clinocerinae*, *Ocydromiinae*, *Hybotinae*, *Trichopezinae*, and *Brachystomatinae*). CUMMING & SINCLAIR (1990) interpreted this as an indication that the clasping lobes developed independently in several lineages of the *Empidoidea*. As far as I remember, listening to the lecture presented at the Second Dipterological Congress, the "several" means that in *Empidoidea* surstyli should originate independently up to six or seven times in each sublineage, and another time in *Cyclorrhapha*. If this were true, we would have to do with an incredible phenomenon, unknown in other groups.

Paradoxically, the argument on the variable direction of gonostylar movement and even the clasping movement, as opposed to the gonocoxites in the asilid genus *Proctacanthus* (see figure in KARL, 1959 on p. 641) presented by CUMMING et al. (1995), better supports the gonostylar hypotheses, than the surstylar ones. According to the surstylar hypotheses the clasping function is provided not by claspers, but by secondary structures, hence the presence and/or position of gonopods are not important at all. On the other hand, in the gonostylar hypotheses the gonopods retain their clasping function, but the direction of their movement is shifted to the ventralo-dorsal direction in most *Eremoneura*. All arguments that a non-horizontal gonopodal action is possible, support the gonostylar hypotheses.

HENNIG'S (1976a and b) and McALPINE'S (1981) indications, that the gonopods have been transferred to the hypandrial complex, are the following:

- acceptance of homology of the relative position of transandrium (dorsal bridge) and the sclerite underneath in lower *Brachycera* and *Eremoneura*.
- muscular connection between epandrium and hypandrium.

- acceptance of existence in primitive *Cyclorrhapha* of two-segmented appendices attached to hypandrium.

The support for HENNIG's (1976a) thesis, that gonopods moved to the hypandrial complex is the sclerite, which lies on the ventral side of epandrial complex, and its relation to transandrium (dorsal bridge). He admitted the presence of this sclerite in the groundplan of the *Brachycera* all the way to *Schizophora*. In other words, HENNIG (1976a) homologized the tenth sternite in *Rhagio scoliopaceus* (L.) and other lower *Brachycera* (called by him "ventrales Epandrialsklerit" and by KARL (1959) in *Asilidae* "Ventrale Lamelle des Analkegels") with the internal sclerite in the *Syrphidae* and lower *Schizophora*. He suggested that in these cases where the sclerite was paired, it originated through the division of a single structure. It is indisputable that if the internal sclerite were paired, the posterior portion would represent the tenth sternite. Let us analyze the origin of anterior portion of the internal sclerite. Apart from HENNIG (1976a), also OVTSHINNIKOVA (1993, 1994) accepted that both portions (including clasping lobes) originated from a single sclerite, being homologous to the tenth sternite of lower *Brachycera*. GRIFFITHS (1972) homologized the internal sclerite (medandrium) with ventral edges of gonocoxites and then (GRIFFITHS, 1981) presented evidence against the homology of the sclerite with the tenth sternite (see chapter 6c). Accepting the evidence, CUMMING et al. (1995) proposed the secondary origin of the internal sclerite (medandrium), through sclerotization of membranes. Whichever homology is accepted, if we deny that the internal sclerite (medandrium) represents the tenth sternite, nothing will prevent us from accepting that gonopods could move to the dorsal complex (epandrial complex), and that medandrium originated by fusion of the gonocoxites (see chapter 7).

For HENNIG (1976a) the presence of eremoneuran muscle connecting the saddle-shaped sclerite (epandrium) with the hypandrium was an important indication of the link of the gonocoxites with the hypandrium. He homologized the muscle with those connecting the epandrium with the gonocoxal apodeme (M34a and possibly also M 34b) in *Rhagio*. The same homology was suggested by OVTSHINNIKOVA (1993, 1994) for her muscles M5 of lower *Brachycera*. I partially agree with the above homology, but I do not think that it supports the fusion of the gonocoxites with the hypandrium. The muscle connecting the saddle-shaped sclerite (epandrium) with the hypandrium could have originated by shifting its attachment from the gonocoxal apodeme to the hypandrium, or by fusion with the muscle connecting the gonocoxite with the hypandrium (Figs. 29-32). HENNIG (1976a) himself presented the hypopygial musculature in *Lonchoptera lutea* PANZER, with the muscle M34 attached to the anterodorsal margin of the hypandrium. HENNIG (1976b) homologized the muscles connecting the epandrium and hypandrium in *Calliphora* M34 (in *Anthomyiidae* such a muscle is attached to the hypandrial dorsal lobe) and ULRICH's (1972) M3 and M5 (ULRICH, 1974) in *Empidoidea*. ULRICH (1972) homologized it with the transverse muscle of the hypandrium in *Tabanus* (no. 186 in BONHAG, 1951; no. M33 in OVTSHINNIKOVA, 1989). HENNIG correctly homologized this muscle with the muscle

connecting the epandrium with the gonocoxal apodeme (no. 184 in BONHAG, 1951, no. M5 in OVTSHINNIKOVA, 1989).

Proponents of the surstylar theories reached no agreement as to what happened with the gonopods, and they allow all the possibilities, from disappearing, through the homology of gonopods with the pregonites or postgonites, to homologization of gonostyli with both gonites (gonocoxite as pregonite, gonostylus as postgonite). Probably only the variant in which the gonocoxite is the postgonite, and the gonostylus the pregonite, was not considered. This indicates, that the appendices of ventral sclerite (hypandrium) could not be easily homologized with the gonopods. In two cases the authors attempted to homologize the gonopods with the pregonites, suggesting that they were two-articled structures. CHILLCOTT (1958) concluded, that true two-segmented pregonites (his "gonopods") which are supposedly still present in *Platypezidae* and *Pipunculidae* could be regarded as evidence for the connection of gonopods with the hypandrium. Also according to McALPINE (1981) the pregonite (regarded as gonopod) is usually reduced to a simple lobe on the hypandrium and only rarely is the primitive two-segmented condition apparent, e.g. in *Callomyia* (*Platypezidae*). In my opinion the designation of the distal portion of pregonite as gonocoxite and the basal as gonostylus on illustrations 132 and 133 in McALPINE (1981) is only theoretical, since the pregonite bears no sign of articulation or fusion of two portions and is completely uniform, as can be demonstrated also in related species (Figs. 15-16).

According to CUMMING et al. (1995) the structure of the male terminalia of *Apsilocephala* illustrates the major flaw of the gonostylar hypothesis. Both genera of *Apsilocephalidae* - *Apsilocephala* and *Clesthentia* - are characterized by clasper-like modifications of the posterolateral margin of epandrium (NAGATOMI et al. 1991b) which are virtually identical to the clasping structures found in *Eremoneura*, including being abducted by a pair of "bacilliform sclerites". However, imputation that "these clasping lobes would certainly be considered homologous to gonopods by proponents of the periandrial hypothesis" is a misuse. Because the two genera have distinct gonopods attached to the hypandrium, I interpret the sentence as an attempt at depreciating the proponents of the periandrial and other gonostylar hypotheses. The periandrial hypothesis was originally proposed for *Cyclorrhapha*, its proponents even accepted the different transformation of orthogenyan male terminalia; the hypothesis has nothing to do with lower *Brachycera*. Actually, GRIFFITHS (1994) interpreted the clasping lobes of *Apsilocephalidae* as secondary and I do not think anyone would consider differently.

HENNIG'S (1973) argument in favour of the surstylar theory turned out to be outdated. He, presumably basing on SALZER'S (1968) study on *Calliphora*, provided evidence that the clasping lobes had no motoric musculature of their own, which speaks against their homology with the gonostyli of the lower *Diptera*. At present it is known that the hypopygium of *Calliphora* represents a relatively advanced structure; in less derived groups the musculature of clasping lobes is present.

6.B. COMMENTS ON EPANDRIAL HYPOTHESIS

The main argument in support of the origin of the clasping lobes from the epandrium, besides those discussed in the previous chapter, refers to the muscular connections of the epandrium with the clasping lobes. The presence of secondary clasping lobes in lower *Diptera* is an indirect evidence that the clasping lobes differentiated from the epandrium. Very characteristic for the reasoning of the followers of epandrial theory is a sentence from CUMMING et al. (1995), which I repeat here, in order to analyze this way of reasoning: "Presence of both sets of claspers in this genus [*Apsilocephala* KRÖBER] indicates that the dorsal pair actually represent de novo structures of tergal origin as postulated by an epandrial hypothesis."

The fact that in the genus *Apsilocephala* there are two pairs of clasping lobes - both surstyli and gonopods of course, actually means, that surstyli are neomorphic structures. This is only one consequence of the above fact. This hypothesis of the origin the structure could be called "epandrial": secondary lobe - surstyli develop as processes of the epandrium. I find it fully convincing and I do not know anyone, who has a different opinion on the matter. The problem, however, is that the genus discussed above does not belong to the *Eremoneura*, but to the *Pleroneura* (*Asiloidea*). In CUMMING's et al. (1995) sentence quoted above, the epandrial theory means an explanation of the origin of eremoneuran hypopygium. The fact that the "epandrial theory" explains the origin of secondary claspers (here surstyli) in one group does not mean at all, that this theory equally well explains the origin of these structures in other group. In this way CRAMPTON (1923, 1936) historically developed the epandrial theory: from the explanation of the origin of secondary claspers in lower flies and then extending it to *Cyclorrhapha*. I do not doubt, that the concept explains the case of *Apsilocephala* very well, but it is only an indication, not a direct evidence for the followers of the epandrial theory in *Eremoneura*. The position of *Apsilocephala* is not stable and has been recently disputed - SINCLAIR et al. (1994) placed it in *Therevidae*, and NAGATOMI et. al (1991a) in a separate family *Apsilocephalidae*, but all of them agree that *Apsilocephala*, on account of a peg on the anterior margin of the hind coxa belongs to *Pleroneura* (*Asiloidea*), together with *Therevidae*, *Bombyliidae* and a few groups of *Tabanomorpha* (feature discovered by YEATS, 1994). All the above authors agree that the "surstyliar condition" in *Apsilocephala* arose independently from that in the *Eremoneura*.

CUMMING et al. (1995, p. 125) assumed that there was a single muscle connecting the clasping lobes with the epandrium and objected to GRIFFITHS' (1991) accepting the single muscle inserted to the clasping lobe as a basis of homologization of the muscle involved in clasping throughout the *Diptera*. Two pages below they interpret the existence of one muscle attached to the postgonite in a completely different way. Although those muscles can not be homologized in the same way in epandrial hypothesis, those authors managed to find the way to turn them into an argument in their favour. They suspect that the second muscle of the postgonite could be

discovered after examining of postgonital musculature in members of the basal lineages of the *Cyclorrhapha*. What, if such a second muscle is not found? Why should the loss of one postgonital muscle speak in favour of rejection of the epandrial theory to a lesser degree, than the loss of one muscle of clasping lobes in the periandrial theory? In most eremoneuran taxa the clasping lobe bears a single muscle, there are, however, species with a double (*Scatophila stercoraria*, see OVTSHINNIKOVA, 1993, 1994), or even triple (*Delia*, see HENNIG, 1976b) muscle of the clasping lobes. Since in the *Orthogenya* there is also a single muscle of the clasping lobe, probably the former muscles developed by splitting of the single muscle and represent an advanced condition associated with the reduction of medandrium. In chapter 7 I suggest the transformation of dorsal hypopygial complex, which explains the loss of one gonopodal muscle (Figs. 29-32).

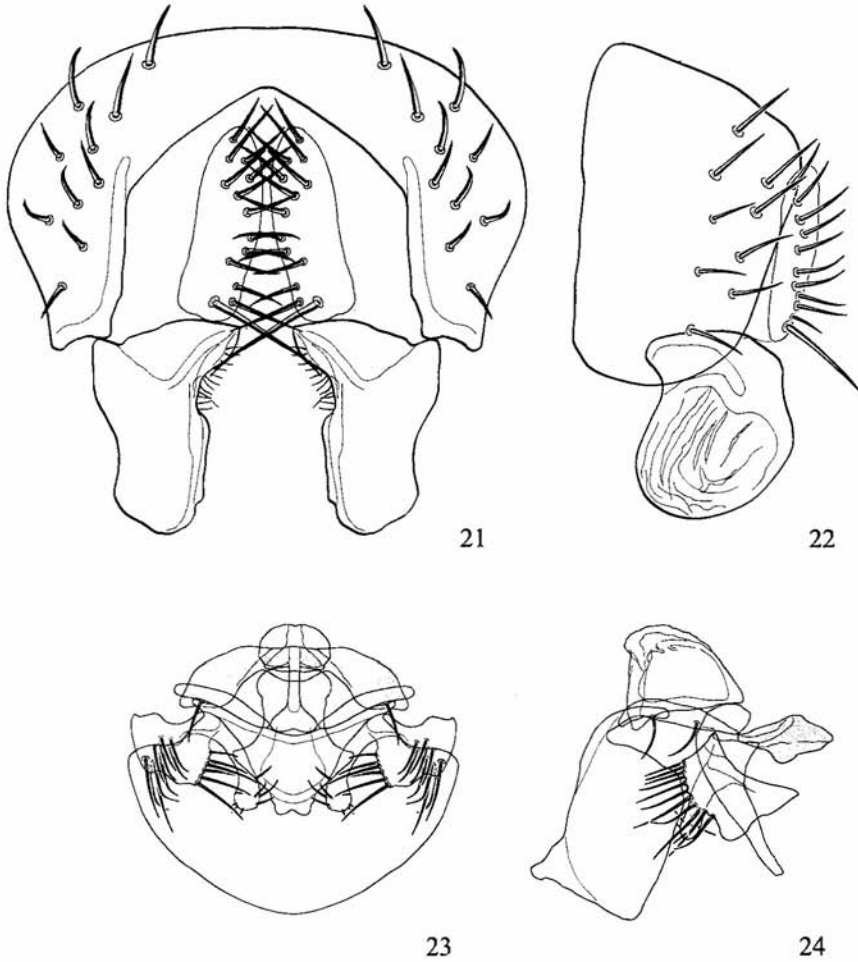
6.C. COMMENTS ON PROCTIGER HYPOTHESIS

This group includes two very similar hypotheses, formulated by BRÜEL (1897) and HENNIG (1976a and b). BRÜEL's (1897) hypothesis was presented without any supporting evidence. On the other hand, HENNIG's (1976a and b) hypothesis homologizing the clasping lobes with the tenth tergite was supported by numerous arguments and the following are discussed below:

- homology of "laminae supraanales" of *Pleroneura (Asiloidea)* with the divided tenth tergite.
- membranous connection between the internal sclerite and clasping lobes.
- shifting of the attachment of epandrial muscle from the internal sclerite to the clasping lobes.

The tenth tergite is present in the most primitive representatives of *Rhagionidae*. According to NAGATOMI (1984) the tenth tergite exists in six of the nineteen illustrated genera of the family. HENNIG's (1976a) figures of *Rhagio (Rhagionidae)* show the tenth tergite in ventral view, as lobate appendices of the epandrium, but in the figure in lateral view they are less distinct. As an argument, HENNIG (1976a) assumed the homology of the lobes called by KARL (1959) "laminae supraanales" of *Pleroneura (Asiloidea)* with the divided tenth tergite, and therefore suggested that the division of the tenth tergite might be a part of the groundplan of the *Asiloidea* and *Eremoneura* (the group called "Heterodactyla"). Those lobes were interpreted by OVTSHINNIKOVA (1989) as cerci, because their muscular connections with the tenth sternite (muscle nr. 29). I think that this is the only possible interpretation of the lobes.

According to HENNIG (1976a), if clasping lobes were derivatives of the tenth segment, a membranous zone between the internal sclerite and the clasping lobes in relatively primitive forms could be expected. Therefore the articulation between the proximal margin of clasping lobes and the internal sclerite or its derivative should be a novelty, for the first time acquired by the *Schizophora* and still absent e.g. in the



21-24 - Male terminalia of *Heleomyia petrolei* (COQUILLET) (Ephydriidae): 21-22 - epandrium, cerci and gonostyli, 21 - ventral view, 22 - lateral view; 23-24 - clasper, medandrium and hypandrial complex (medandrium shaded) (USA, California, Montebello, 1950, leg. A. H. STURTEVANDT, National Museum of Natural History, Washington)

Platypezidae. HENNIG (1976a) supposed that the origin of the articulation between the internal sclerite (medandrium) and the clasping lobes was a part of the groundplan of the *Schizophora*. The non-articulated connection of the internal sclerite with the clasping lobes provided CUMMING et al. (1995) with an argument against the gonostylar hypothesis. They suggested, that if the clasping lobes were homologous with the gonostyli, there should exist some character states resulting from this homology, namely that primitive members of *Eremoneura*, such as the most generalized empidoids (like *Hormopeza*, *Oreogeton*, and *Trichinomyia*) should possess plesiomorphic articulated dorsoapical clasping lobes; however, the actual situation is the opposite - in primitive *Eremoneura* the clasping lobes are not articulated with the saddle-shaped sclerite or the internal sclerite. In my opinion those three genera are really generalized within the *Empididae*, in having not completely divided epandrium, but the whole family is characterized by advanced structure of the epandrial complex in comparison with the groundplan of *Eremoneura*. The argument, that primitive *Eremoneura* do not have articulated clasping lobes, has a reasonable explanation, even if we accept one of gonostylar hypotheses. The character is not widely distributed in the primitive *Eremoneura*. Not in all the *Platypezidae* and *Orthogenya* the clasping lobes are fused with the internal sclerite. HENNIG (1976a) incidentally examined the representatives of platypezid genera *Platypezina* and *Agathomyia*, which have postero-lateral epandrial projections and the clasping lobes fused with the internal sclerite (medandrium). According to KESSEL & MAGGIONCALDA (1968) in two additional genera (*Grossovena* and *Protoclythia*) the clasping lobes could be fused with the medandrium, but in 8 other platypezid genera the clasping lobes are articulated with the medandrium, like in *Callomyia*, presented in figs. 15-16, or in McALPINE et al. (1987, p. 685). In my opinion the connection of the clasping lobes with the internal sclerite (gonostyli with medandrium) developed in an opposite way: from articulated connection to the fusion, even when it took place in primitive forms. Thus, in the groundplan of the *Eremoneura* there are separate genital claspers, and their connection with the medandrium (internal sclerite) represents a specialized state, derived as a homoplastic character in several groups.

HENNIG (1976a) suggested that the muscular connection of the epandrium with the clasping lobes in *Fucellia tergina* (ZETT.) (*Anthomyiidae*) was a specialized condition in comparison with the connection of the muscle with the medandrium (his "processus longus") in other anthomyiid genera. In *Delia platura* (MEIG.) and *Fucellia tergina* (ZETT.) three muscles M31, M42 and M43 are attached to the epandrium and the margin of clasping lobes, whereas in *Calliphora* those three muscles are inserted on the medandrium (processus longus), or near it. In *Craspedochaeta pullula* (ZETT.) the muscle M42 is attached to the margin of clasping lobes, whereas the muscles M42 and M31 to the medandrium. HENNIG (1976b) did not follow ULRICH's (1972) homology of the muscles connecting the epandrium and the clasping lobes with the gonopodal muscles. HENNIG (1976b) homologized those muscles with those which connected the epandrium with the tenth sternite in *Rhagio*. Various arrangements of muscles and the change of their

position in the investigated species induced him to accept the possibility of separation and translocation of insertion points of the muscles. Therefore he suggested, that the plesiomorphic state was the connection of muscles with the internal sclerite (medandrium), but not with the clasping lobes. The changes should proceed from *Calliphora* through *Craspedochaeta* to *Delia* and *Fucelia*. In my opinion the direction of the transformation is the reverse - from muscular connection in *Fucellia* and *Delia* through mixed connection in *Craspedochaeta* to *Calliphora*, which represents the most specialized condition.

GRIFFITHS (1981) summarized the ontogenetic evidence, which made the homologies of both the internal sclerite and the clasping lobes in *Eremoneura* with the proctiger (tenth sternite and tenth tergite respectively) of lower *Brachycera* unparsimonious. The argument was accepted even by the followers of surstylar hypotheses (CUMMING et al., 1995). In *Eucalliphora* BLACK (1966) found the medandrium (processus longi) developing in the membrane of the ninth segment at a late stage of development of the genital disc, the same was demonstrated for the clasping lobes which differentiated from the saddle-shaped sclerite distinctly later than the proctiger, which became separated from the genital segment at a very early stage of development. LAUGÉ's (1968) reconstruction of a series of transitions between the male-type and female-type intersexes in *Drosophila* clearly shows that the female and male proctiger are homologous and originate from the same segment. The clasping lobes never border with the proctiger. Also studies of DOBZHANSKY (1930) documented the origin of the clasping lobes of *Drosophila* in the same way.

6.D. COMMENTS ON INTERNAL SCLERITE HYPOTHESIS

OVTSHINNIKOVA (1993, 1994) tried to provide evidence for the hypothesis based on the muscle connections. It follows from the concept that the tenth sternite of lower *Brachycera* should divide in *Cyclorrhapha* into four (sometimes five) variously shaped structures - a pair of clasping lobes, the tenth sternite (sometimes divided), and subepandrial plate (in *Cyclorrhapha* a pair of "processus longi"), each with its own musculature. Generally, the tenth sternite is relatively small (sometimes transversely divided), and only members of the *Tabanidae* (*Pangoniinae*) have an enormously large tenth sternite, reaching to the posterior margin of epandrium (NAGATOMI, 1984). OVTSHINNIKOVA (1993, 1994) extrapolated the scheme of musculature of lower *Brachycera* to *Cyclorrhapha*, supporting the secondary origin of the clasping lobes, and suggested that other explanations of muscular homologies were improbable, or too intricate. Is it true, that - accepting the internal sclerite hypothesis - there are no new muscles or sclerites in primitive *Cyclorrhapha* in comparison to lower *Brachycera*, as concluded by OVTSHINNIKOVA (1994)? I could agree that the clasping lobes are not new structures, as they are present in the *Apsilocephalidae*. However, in primitive *Cyclorrhapha* (*Platyzezoidea*, primitive *Hypocera*) and *Orthogenya* (nota bene, not examined by her at all) there are two subepandrial sclerites (medandrium and tenth sternite). OVTSHINNIKOVA (1993, 1994)

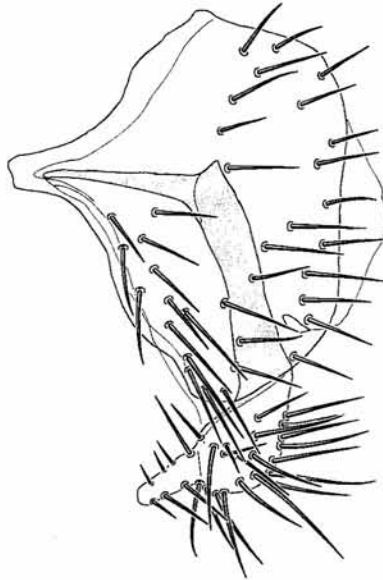
examined several representatives of *Cyclorrhapha*, but all of them belong to the *Schizophora*, and *Eristalis interrupta* PODA (*Syrphidae*) seems to be the most primitive; thus she did not notice the additional sclerite (medandrium). OVTSHINNIKOVA (1994) interpreted the origin of muscles connecting the clasping lobes and the saddle-shaped sclerite (epandrium) (M3 and M4), as a recent splitting of one muscle. Even, if the muscles M3 (also designated as M25 on illustration of *Scatophaga stercoraria*) and M4 originated by splitting of muscle M21 (the fact is not precisely expressed in her papers) the statement, that there are no new muscles in *Cyclorrhapha*, would be too far-reaching. The split muscles M21 (M21₁, M21₂, M21₃) in the asilid *Trypanoides testaceipes* Mcq. connect the epandrium and clasping lobes with the tenth sternite and can not be homologous with the three muscles (M21, M3 and M4) in *Cyclorrhapha*. We must accept the split muscle M21 in *Trypanoides testaceipes* as a unique condition, since she herself (OVTSHINNIKOVA, 1989) presented the musculature of five other asilids with a single muscle M21. Thus in this case, there is a simple indication, that if the epandrium was distinctly protruding, the muscle M21 could split, and the same process could occur, when the tenth sternite became broad, or separated.

The concept including homologization of clasping lobes with the derivatives of medandrium (her "ventral proctiger plate") is, however, not in "excellent agreement with epandrial hypothesis", but only provides a confirmation of the tergal origin of epandrium. With respect to the proposed origin of the clasping lobes, the two concepts differ considerably. OVTSHINNIKOVA (1994) designated clasping lobes and internal sclerite as "surstyli" and her muscle pair (M29) connecting the cerci with the surstyli means the connection between the cerci and medandrium (internal sclerite). Adhering to the term surstyli, OVTSHINNIKOVA (1994), when writing about the periandrial hypothesis, adopted the term dististyli for surstyli, suggesting, that accepting the periandrial hypothesis "*Cyclorrhapha* have muscles connecting the cerci with the dististyli". In reality *Cyclorrhapha* have muscles connecting the cerci with the medandrium (for her they are surstyli), but not with the gonostyli. The case of *Scatophaga stercoraria* (L.) is probably an exception and could be explained by the fusion of medandrium with the clasping lobes, or by shifting the muscle from the medandrium to the clasping lobe. The difference between our views consists in my accepting the attachments as secondary, which is also accepted by proponents of epandrial hypothesis (CUMMING et. al., 1995). If the shifting of the muscle were so unlikely, how could we explain the muscular connections of three (7-9) abdominal segments (see introduction). OVTSHINNIKOVA's (1994) argumentation that the fusion of gonocoxites and hypandrium occurred in several families of lower *Brachycera* is of the same category as the origin of surstyli in lower *Brachycera*. It must be regarded as an indirect indication, not as evidence for the transformation of eremoneuran hypopygium.

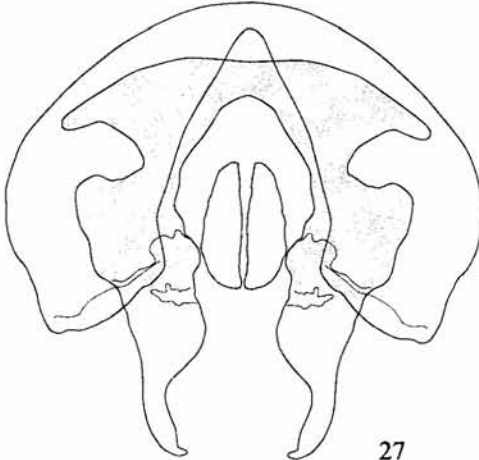
For those readers, which still accept the replacement of clasping lobes, I repeat HENNIG's (1976b, page LI) sentence: "Die Muskelverbindungen mit dem Phallapodem schliessen auch die Möglichkeit aus, dass die Prä- oder Postgonite (oder beide) mit dem Telomeren homolog sei könnten." [The muscular connections with the



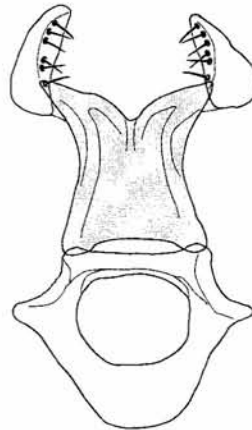
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25-26 - Epandrial complex of *Trixoscelis obscurella* (FALLÉN, 1823) (*Trixoscelidae*): 25 - ventral view, 26 - lateral view (Poland, Wrocław-Leśnica, 9. VII. 1984, leg. T. ZATWARNICKI); 27 - Epandrial complex of *Pherbelia argyra* VERBEKE (*Sciomyzidae*) (Poland, Wrocław-Wojnów, 16.IX. 1982, leg. T. ZATWARNICKI); 28 - hypandrium, medandrium and gonostyli of *Schoenomyza litorella* (FALLÉN, 1823) (*Muscidae*) (Poland, Milicz, 15. VII. 1981, leg. T. ZATWARNICKI) (medandrium shaded)

phallapodeme excludes also the possibility, that the pre- or postgonite (or both) could be homologous with telomeres (=gonopods)]. He accepted, that the muscular connections of the gonites with the phallapodeme and also ontogenetic development ("euphallische Organe") excluded regarding them as gonopods. This means, that followers of any surstylar theory have to accept also the secondary origin of gonites, and this implies accepting, that all appendices of cyclorrhaphan hypopygium have to originate secondarily. I personally think that it is very little probable, and completely unnecessary in view of the fact that other hypotheses exist, that do not assume any replacement and allow an easy homologization of almost all genital structures between the lower and higher flies.

6.E. DEBATE ON PERIANDRIAL HYPOTHESIS

Basically, periandrial hypothesis can be divided into two independent components, 1) the saddle-shaped sclerite is of gonopodal origin and 2) the clasping lobes are homologous to gonostyli. To me, the essence of the hypothesis is the first point, while also other hypotheses include the homology of the clasping lobes with the gonostyli. My criticism of the periandrial theory refers to the origin of saddle-shaped sclerite, whereas I completely agree with the arguments on gonopodal homology of the clasping lobes, because they are compatible with my interpretation. Those arguments are discussed in chapter 7.

The hitherto critique of periandrial hypothesis presented by its opponents is, in my opinion, very little valuable. MATSUDA (1976) argued that the periandrial idea was not acceptable, because both the gonopods and epandrium occurred together in *Brachycera*. ANDERSSON (1977) claimed that the true nature of the gonites and of the interparameral sclerites had not been convincingly demonstrated and the occurrence of microchaetae on the gonites suggested their tergal origin. DISNEY (1986a) mentioned comparative studies suggesting, that the saddle-shaped sclerite was represented by the ninth tergite and not by the periandrium. DISNEY (1986a) suggested that the plesiomorphic condition of the "gonopods" and their relation to the hypandrium were well exemplified by *Chonocephalus blackithorum* DISNEY (*Phoridae*). In his figure 1(e) DISNEY (1986a: p. 79) presented the male terminalia of *Chonocephalus blackithorum* "viewed from below" with a pair of large pregonites (designated as left and right gonopods), being not very distinct from those of platypezids *Callomyia amoena* MEIG. presented in fig. 15-16. DISNEY (1988) denied the "affinity between *Cyclorrhapha* and *Empidoidea*" and, on the other hand, accepted CHVALA'S (1983) suggestion, that in the groundplan of *Empidoidea* the epandrium had not been replaced by the periandrium, which resulted in an opinion, that the epandrial theory better applies to the *Cyclorrhapha*, than the periandrial.

GRIFFITHS (1972) provided three kinds of evidence to support his concept - transformation of saddle-shaped sclerite in *Orthogenya*, the process of ontogenetic development of the saddle-shaped sclerite and the presence of muscles inserted to the base of clasping lobes. The latter character is a good evidence for every

gonostylar theory and does not support the transformation of the epandrium and gonocoxites, therefore I discuss only the first two points.

a) Transformation of saddle-shaped sclerite in *Orthogenya*.

For GRIFFITHS (1972) and CHVALA (1983) the laterally placed dorsal sclerites in *Empididae* (s. str.) represented the gonocoxites, and the condition is plesiomorphous. It is an important argument, but it could be re-interpreted and then the direction of the transformation series would be the reverse, thus not suggesting formation of the periandrium. Such an interpretation was already proposed by BÄHRMANN (1960), who interpreted the shape of epandrium in *Hybotidae* with moderately incised posterior margin as a plesiomorphous condition. BÄHRMANN (1960) suggested, however, the presence of gonocoxites within *Orthogenya*. In my opinion the structures designated by BÄHRMANN (1960) as gonocoxites ("basistyli") represent epandrium. In case of the presence of undivided epandrium and two pairs of lamellae, BÄHRMANN (1960) designated dorsal as cerci and ventral as surstyli. In case of the presence of divided epandrium with posterior lamella, he interpreted the complex as the epandrium with cerci, but the divided epandrium with dorsal lamella as gonocoxite (ventral) and epandrium (dorsal). This explains, why BÄHRMANN (1960) wrote, that he never found gonostyli in the empidoid species available for his studies. I also interpret all the sclerites designated by CHVALA (1983) as gonocoxite as a lateral portion of epandrium (sometimes so deeply incised, that almost separated). In some cases CHVALA (1983) designated the sclerite as epandrium and in the case of *Hormopeza* the plate situated posterodorsally really denotes epandrium together with lateral plates; the remaining designations referred to cerci. This is extremely well visible, if we compare figures 89 and 90 in CHVALA (1983), showing the lateral view of hypopygium in *Hormopeza copulifera* MELANDER and *Iteaphila nitidula* ZETTERSTEDT, respectively. Looking as homological structures, they are once indicated as cerci (fig. 89), and then as epandrium (fig. 90). Such indications can be found in several places in his paper. CHVALA (1983) defined small lamellae situated ventral to his "epandrium" as cerci. In my opinion they represent paired appendices of the tenth sternite.

CHVALA (1983) hesitated to homologize the "dorsal lamellae" with the cerci, because of their complicated shape. In my opinion the degree of the structure's complication shown in figs. 95-97 of *Gloma fuscipennis* MEIGEN, 118-119 of *Hemerodromia lineata* ZETT. and in figs. 128-130 of *Ceratomerus mediocris* COLLIN does not depart significantly from the shape of the structures designated as cerci in fig. 105 of *Oreogeton scopifer* (COQUILLET) and fig. 138 of *Brachystoma esiculosum* (FABRICIUS). Curved cerci are also found in *Stylogaster neglecta* WILLISTON (*Conopidae*), presented by McALPINE et al. (1989). If the epandrium and gonopods were present also in primitive *Empidoidea* (*Oreogetoninae*, genus *Hormopeza*), one should admit the presence of epandrium as a part of the groundplan of *Eremoneura* and then the process of epandrium reduction in *Cyclorrhapha* would have to occur separately from that in the *Empidoidea*, which should be possible to prove without resorting to analogy with the related groups.

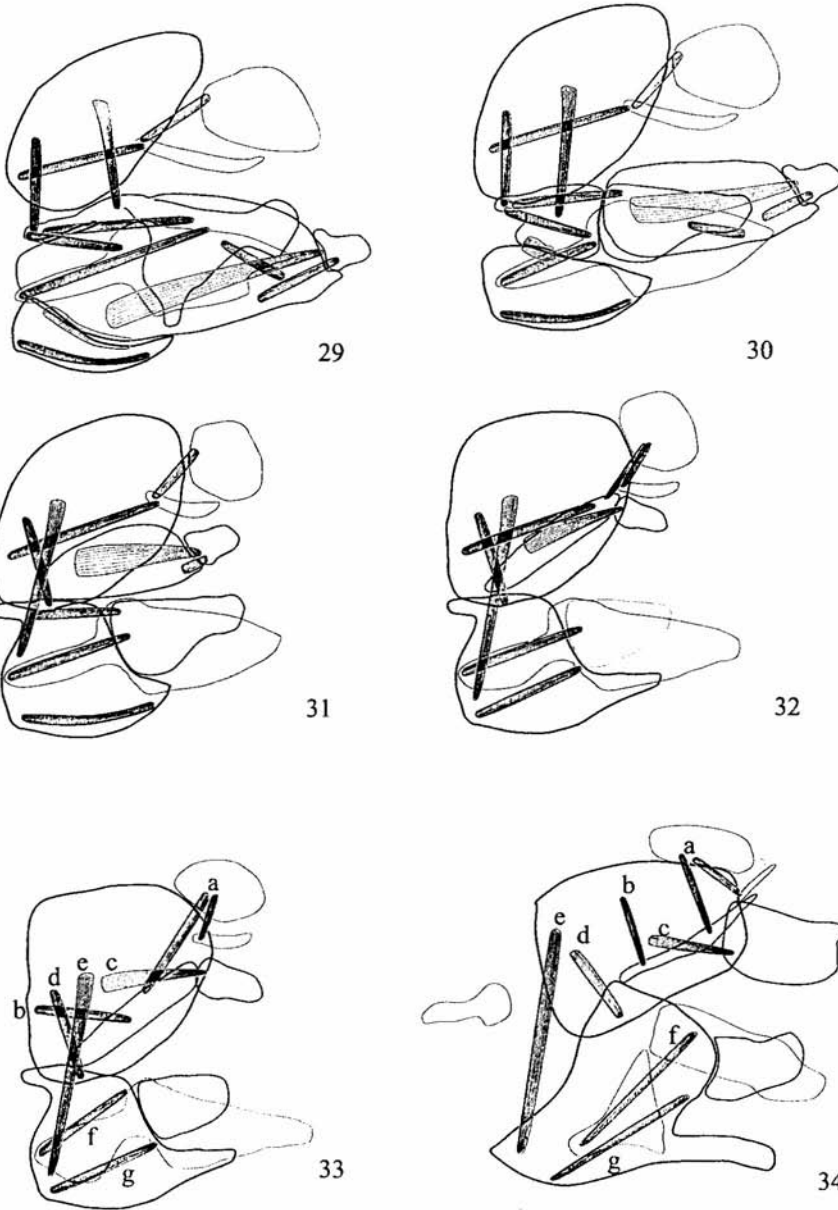
b) The process of ontogenetic development of saddle-shaped sclerite

GRIFFITHS (1972) identified the evolutionary process of periandrium formation through the fusion of gonocoxites over the dorsum with the process of epandrial ontogenesis in *Cyclorrhapha*, which is similar. The evidence would be stronger, if it turned out that in lower *Brachycera* epandrium arose in another way and/or drawing aside the germ of epandrium were an adaptation to the structure of wide sclerite. Probably the process is typical for the ontogeny of all dipterous abdominal tergites, which was described by ZUMPT and HEINZ (1949, footnote on p. 304): "The sterna are the first to be formed in the embryological development of the segments. The terga, on the other hand, are attached as lateral protuberances which approach each other dorsally in their growth until they meet and close the segmental ring. It can easily be envisaged that the sternum was forced in a ventral direction out of its original position between the VIII and X segments. The terga, on the other hand, were fused as reinforcing edges with the sidewalls of the sternum."

Assuming the continuity of clasping functions, the periandrial theory does not maintain the continuity of dorsal sclerite and its muscular connections. However, not all the evidence presented by HENNIG (1976a, 1976b) to demonstrate that the *Cyclorrhapha* retained true epandrium, which was emphasized by McALPINE (1981), can be repeated here. The muscle connection of the saddle-shaped sclerite and the prehypopygial sclerite could be questioned, because its anterior attachment had to develop secondarily (see introduction). There are evident muscles, presented by SALZER (1968) connecting the ventral surface of saddle-shaped sclerite with the posterior margin of cerci (= mesolobus) (SALZER's muscle no. M 44) and with the anal region (M 30), which was interpreted also by GRIFFITHS (1991) as an evident weakness of this hypothesis. The muscle M 44 can be homologized with the muscles connecting the epandrium and proctiger in lower *Brachycera* (OVTSHINNIKOVA's muscle no. 21).

7. "HINGE" CONCEPT OF THE ORIGIN OF DORSAL COMPLEX OF EREMONEURAN HYPOPYGIUM

All arguments, which were presented to support the surstylar hypotheses are repeated and very precisely commented. There are no unresolved phenomena, remnant structures, transformation series, ontogenetic evidence, evolutionary reconstruction or other sound reasons, which would allow us to refute the rule of function continuity. This is an a posteriori conclusion, not a priori assumption (first evidence, or its lack, then the opinion). I have shown here, that any surstylar theory corresponding to ontogeny, or anatomical structure of hypopygium, then all its appendices (clasping lobes and gonites) and a part of muscular connection had to originate secondarily. This leads to the homology of the eremoneuran clasping lobes with the gonostyli of lower *Diptera*. The next question is how to explain such a different structure of lower *Brachycera* and *Eremoneura*, and especially in



29-34 - Scheme of hypothetical development of eremoneuran hypopygial structures and muscular system according to "hinge" hypothesis: 29 - groundplan of brachyceran ancestor, 30 - stage of transandrium separation, 31 - stage of fusion of transandrium with hypandrium and leaning of gonocoxites on transandrium, 32 - stage of fusion of gonocoxites, 33 - groundplan of *Orthogenya*, 34 - groundplan of *Cyclorhapha* (the letters indicate muscles listed in chapter 7)

Cyclorrhapha, without causing excessive perturbations. In my opinion the gonocoxites retention hypothesis of CRAMPTON (1923) in a correct way explains the origin of dorsal complex of eremoneuran hypopygium, but unfortunately the concept was never documented. In my explanations I put emphasis mostly on the explanation of the way of genital structures transformation, and not on presenting simple homologies. Because in the concept I stress the origin of the movable connection of the medandrium (internal sclerite) and the transandrium (dorsal bridge), which function on the hinge principle, I propose the name "hinge hypothesis" for the explanation.

The evolutionary process in the ancestors of *Eremoneura* began from the transformation of dorsal hypopygial complex and involved both *Orthogenya* and *Cyclorrhapha*. In order to form an advanced structure of hypopygium in *Atriata*, first the gonocoxites had to separate from their apodemes (Figs. 29-34). The apodemes, being fused to each other (possibly also to the antero-medial part of aedeagal sheet), accreted to the hypandrium, forming a ring. I do not exclude, that the attachment of the apodemes to the hypandrium involved also the anterior portion of the gonocoxites. A subsequent stage of evolution should be a translocation of the anterior margin of gonocoxites (possibly with the reduction of its anterior portion) posteriorly, to lean on the posterior margin of transandrium. Then, a fusion of gonocoxites to the ventral side of epandrium took place, anteriorly to the tenth sternite and the shift of the plane of gonostylar action in dorso-internal direction. The fusion of gonocoxites enabled the gonostylar abduction through the uplift of epandrium and shifting of medandrium posteriorly. The origin of such a hinge of the medandrium and transandrium enabled the reduction of abductor of gonostylus, which turned out to be useless. Possibly already before the gonocoxal fusion, gonostylar adductor shifted from the gonocoxite to the ventral side of epandrium. The connection of gonostylar adductor had to function after the fusion of the gonocoxites. I recognize the presence of articulation between the clasping lobes and the medandrium as a component of the groundplan of *Eremoneura*. In a part of *Orthogenya*, as well as in some *Cyclorrhapha*, chitinous connection was formed between the medandrium and the gonostyli. Usually the connection medandrium - gonostyli is associated with epandrial sides protruding posteriorly, and/or the fusion of gonostyli with the postero-lateral margins of epandrium. In my opinion, this caused the protection or immobilization of gonostyli, therefore the gonostyli could connect with the medandrium. Such a condition can be found in *Empididae* (s. str.), *Atelestidae*, some *Platypezidae* (*Agathomyia*, *Grossovena*, *Platypezina* and *Protoclythia*).

The movable articulation between the dorsal bridge and the medandrium constituted a preadaptation of great significance, accelerating the rate of evolutionary changes and opening new adaptive possibilities. This articulation enabled hiding of the hypopygium under the abdomen, with the possibility of its upward movement and protrusion of aedeagus during copulation. It is difficult to evaluate the adapting significance of hypopygial folding, but it had to be very important, since it led to the origin of a large group of insects (circa 90 thousand species), at present

flourishing, occupying various habitats and displaying an astounding richness of shapes and colors. In most *Orthogenya* (*Hybotidae*, *Atelestidae*, *Microphoridae* and *Dolichopodiidae*) rotation of the hypopygium by 180° took place. In ancestors of *Cyclorrhapha* also inversion of male terminalia had to occur, since they are rotated by 360°. Before circumversum occurred in such an inverted hypopygium, the hypandrial complex had to transform. The ejaculatory apodeme separated from the aedeagus, and its postero-dorsal edge produced articulation with the ventralo-basal margin of aedeagus. The posterior margin of ejaculatory apodeme connected with the postero-medial portion of hypandrium and formed the structure called phallapodeme. In my opinion the arrangement, which allowed bending of the aedeagus during its protrusion, developed in this way. The aedeagus is usually articulated basalo-ventrally with the phallapodeme, and basalo-dorsally with the medial portion of transandrium (dorsal bridge). The spatulate plate, called ejacapodeme (“ejaculatory apodeme”) could possibly arise from the dorsal margin of the apodeme, or as a novelty through partial sclerotization of the sperm sac. It was only after the formation of hypandrial complex, that circumversum could happen in the ancestors of *Cyclorrhapha*, i.e. rotation of hypopygium by 360°. HENNIG (1976b) only supposed, but I am sure that the separated medandrium in *Calyptata* and the development of lateral rods connected with membrane (so called “processus longi”) are specialized characters. In *Calyptata* the mechanism of hypopygial function is modified, enabling the separation between the phallapodeme and the hypandrium, and in some taxa the medandrium got reduced (e.g. *Delia platura* of *Athomyiidae*).

Two authors considered the theoretical possibilities of the formation of cyclorrhaphan hypopygium and for different reasons none of them took the presented explanation into consideration. GRIFFITHS (1981) specified three possible interpretations of the clasping structures of *Cyclorrhapha* and they are compatible with the ontogenetic evidence. According to him the interpretations of the saddle-shaped sclerite could be as follows:

- it is the ninth tergite (epandrium) and the clasping lobes have differentiated from it (epandrial hypothesis).
- it represents a fusion of the gonopods and epandrium and the clasping lobes are the gonostyli (fusion hypothesis).
- it is formed by growth of the gonopods across the dorsum (following loss of the true epandrium) and the clasping lobes are the gonostyli (periandrial hypothesis).

GRIFFITHS (1981) did not realize that there was another possible interpretation, which assigned all sclerites to their correct segments, namely the saddle-shaped sclerite was the ninth tergite and the clasping lobes were the gonostyli (“hinge hypopygium”). On the other hand, HENNIG (1976a) presented three possibilities of hypopygial transformation, in which gonopods could be:

- completely reduced
- translocated to the epandrial complex
- translocated to the hypandrial complex

HENNIG (1976a and b) opted for the third possibility, even having the troubles with the homology of cyclorrhaphan gonites and phallapodeme. HENNIG (1976a) assumed, that the comparison of hypopygial structures in primitive *Brachycera* (in his case *Rhagio*) with those of *Eremoneura* made it possible to find stable reference points and thus also reconstruct the changes, that occurred between these groups. The dorsal hypopygial complex in primitive *Eremoneura* (eg. *Atelestus*) differs from that in *Rhagio* in two respects: a) between transandrium (dorsal bridge) and internal sclerite the relatively broad membranous zone is absent and both skeleton elements are connected by a membranous joint, b) clasping lobes are attached to the margin of internal sclerite. To him the transandrium (dorsal bridge) and the tenth sternite constituted two reference points for further considerations on the transformation of gonopods. Based on the homology of the relative position of the internal sclerite and transandrium (dorsal bridge), HENNIG (1976a and b) rejected the translocation of gonopods to the epandrial complex. His false basic conclusion (transferring gonopods to hypandrium) caused a chain reaction of inconsequencies and extorted acceptance of pregonites as transformed gonopods, although no articular connection could be found in primitive *Eremoneura*, which might correspond to the connection between the gonocoxite and gonostyli. HENNIG (1976a and b) had to find an explanation for the origin of genital claspers. Because he hesitated to admit that the appendices were more associated with the subepandrial sclerite (his tenth sternite), than with the epandrium, he drew the next extorted conclusion, that the genital claspers derived from a transformed, divided tenth tergite (see chapter 4.a.2). In my opinion the great achievement of HENNIG (1976a) was the statement, that the clasping lobes in primitive *Eremoneura* were attached to the medandrium (subepandrial sclerite), and not to the epandrium. For HENNIG (1976a and b) the joint between the transandrium (dorsal bridge) and the internal sclerite (his "tenth sternite") (the latter also connected with postero-ventral margin of clasping lobes) was a possible synapomorphy of *Eremoneura*, but for me both characters are unquestionable synapomorphies resulting from the hypopygial transformations.

The musculature of eremoneuran hypopygium was presented by HENNIG (1936a, 1976a and b); FERRIS (1950); OVTSHINNIKOVA (1989, 1993, 1994); POPHAM (1982); ULRICH (1972, 1975, 1988); SALZER (1968); TREHEN (1960, 1962); VALDEZ-CARRASCO & PRADO-BELTRAN (1990); and ZAKA-UR-RAB (1979a, b, c). Their studies make it possible to reconstruct the groundplan of eremoneuran musculature and to interpret its homology with lower *Brachycera*. The epandrial complex is characterized by the epandrial muscles attached to the medandrium and to the gonostyli (single or double). One muscle connects the medandrium with the cerci. Two muscles connect the epandrial and hypandrial complexes. Both originated from the epandrium - one is attached to the transandrium (dorsal bridge), and the other to the hypandrium. In the hypandrial complex two groups of muscles could be recognized. The muscle(s) running from the top of phallapodeme to the hypandrium and/or transandrium (dorsal bridge), and the muscle(s) connecting the anterior edge of hypandrium with the postero-dorsal portion of hypandrium and/or adjacent structures. These connections (Figs. 33-34) are discussed separately:

a) muscular connection of cerci with medandrium and tenth sternite: designated by ULRICH (1972 - 8 and 9 of *Empis*, 9 of *Wiedemannia*); ULRICH (1988 - 9 b and c); and OVTSHINNIKOVA (1989, 1993, 1994 - M29).

In my opinion the pair of muscles are homologous to the muscle connecting the tenth sternite with the cerci (muscle MC of HENNIG, 1976a), which got additionally attached to medandrium. Possibly this stage of muscle transformation was presented by ULRICH (1972) for *Empis borealis*, which has two muscles connected to the base of cercus - one attached to the tenth sternite and the other to the medandrium ("Proctigersklerit"). CUMMING et al. (1995) claimed the shift of the muscle attachment from the tenth sternite to medandrium (Figs. 32-33). Possibly both muscles are present in primitive *Cyclorrhapha*, those having the tenth sternite and existed in the ancestors of the group.

b) muscular connection of the epandrium with the medandrium: designated by ULRICH (1972 - 5 for *Empis*); ULRICH (1975 - 4); ULRICH (1988 - 9a); SALZER (1968 - M42); and OVTSHINNIKOVA (1989, 1993, 1994 - M21).

HENNIG (1976a) homologized muscles attached to the medandrium (processus longi) in *Calyptрата* (no. M31, M42 and M43) with the muscle connecting the epandrium with the tenth sternite in *Rhagio*. The same interpretation was suggested by OVTSHINNIKOVA (1993, 1994) for her muscle M21. I also accept such a homology of the muscle, assuming the medandrium being not the tenth sternite; then the muscle shifted its attachment from the tenth sternite to the medandrium.

c) muscular connection of the epandrium with the clasping lobes; usually a single muscle, in *Calyptрата* double: designated by ULRICH (1972 - 4); ULRICH (1975 - 7); SALZER (1968 - M44); and OVTSHINNIKOVA (1989, 1993, 1994 - M4 and M3).

I homologize the muscle with the adductor of gonostylus, which shifted its attachment from the gonocoxites to the epandrium. Perhaps we could observe the shift of one muscle from the medandrium to the epandrium in primitive *Orthogenya*. ULRICH (1972) presented the muscle no. 4 in *Empis* connecting the clasping lobe with the medandrium (his "Skleritsteg") and the same muscle in *Wiedemannia* connecting the clasping lobes with the epandrium. I interpret the presence of double musculature of the clasping lobes in *Calyptрата* as a secondary development.

d) muscular connection of the anterior edge of epandrium with the transandrium: designated by ULRICH (1972 - 5 for *Empis*); ULRICH (1975 - 4); ULRICH (1988 - 9a); and OVTSHINNIKOVA (1989, 1993, 1994 - M5₂).

Here there is an agreement, that it corresponds to the muscle connecting the epandrium with the gonocoxal apodeme in lower *Brachycera* (M5₂ of OVTSHINNIKOVA, 1989 and M34b of HENNIG, 1976a; M6a of HENNIG, 1936b).

e) muscular connection of the epandrial anterior edge with the anterior edge of hypandrium: designated by ULRICH (1972 - 5 for *Empis*); ULRICH (1975 - 4); ULRICH (1988 - 9a); and OVTSHINNIKOVA (1989, 1993, 1994 - 5₁).

Because in lower *Brachycera* there is no direct connection between the epandrium and hypandrium, the muscle is an evident novelty in the *Eremoneura*. It could originate from the connection of the long muscle attached to the epandrium and antero-dorsal portion of gonocoxite (muscle M34a of HENNIG, 1976a; M5₁ of

OVTSHINNIKOVA, 1989) and the short muscle connecting the ventral edge of gonocoxite with the hypandrium (Mv2 of HENNIG, 1976a; lateral parts of M33 of OVTSHINNIKOVA, 1989).

f) muscular connection of the top of phallapodeme with the hypandrium and/or transandrium (dorsal bridge): designated by TREHEN (1960, 1962 - 1-3); ULRICH (1972; 1975 - 1 and 2); OVTSHINNIKOVA (1989 - M2); and ZAKA-UR-RAB (1979a - 7; 1979c - 13).

Possibly there are three muscles of the ejaculatory apodeme in the groundplan of *Orthogenya*, although the presence of two muscles was noticed by ULRICH (1972, 1975) in *Empis borealis* L., *Wiedemannia ouedorum* VAILLANT and *Chelifera precabunda* COLLIN. On the other hand, TREHEN (1960) presented three muscles of the ejaculatory apodeme in *Empis tessellata* FABR. There is a single muscle in *Syrphoidea* (*Sphaerophoria*), lower *Schizophora* (*Dryomyza*: *Dryomyzidae*, *Ceratitis*: *Tephritidae*, *Lipara*: *Chloropidae* and *Drosophila*: *Drosophilidae*), and *Hippoboscidae* (*Basilina*), or a complex consists of four muscles in the remaining *Calypttrata* (*Scatophaga*: *Scatophagidae*, *Delia* and *Fucelia*: *Anthomyiidae*, and *Calliphora*: *Calliphoridae*) all of them running from the phallapodeme (top, basalo-dorsal or basalo-ventral portion) to the anterior edge of transandrium (M35 of SALZER, 1968; M2₁ of OVTSHINNIKOVA, 1993, 1994), the base of aedeagus (M36 of SALZER, 1968; M2₃ of OVTSHINNIKOVA, 1993, 1994), posterodorsal edge of hypandrium (M37 of SALZER, 1968; M1 of OVTSHINNIKOVA, 1993, 1994), and the base of pregonites or both gonites (M38 and M39 of SALZER, 1968; M2₂ of OVTSHINNIKOVA, 1993, 1994). In my opinion all those muscles originate from the muscles connecting the ejaculatory apodeme with the postero-lateral edge of aedeagal sheet in lower *Brachycera* (muscle M31 in OVTSHINNIKOVA, 1989; MP1 and MP2 in HENNIG, 1936b; M37-39 in HENNIG, 1976a; m1 and m2 in REICHARDT, 1929; m5 in BLASCHKE-BERTHOLD, 1994). A similar homology of the group of muscles was proposed by HENNIG (1976b), though he postulated a different origin of the muscle connection of pregonite with basalo-ventral part of phallapodeme in *Calypttrata* (see below). In my opinion the muscle belongs to the group which does not correspond with the longitudinal muscle of hypandrium or gonopods. HENNIG (1976a) homologized two muscles connecting the phallapodeme and the hypandrium in *Lonchoptera* with SALZER's muscles of the phallapodeme M40 and M41 in *Calypttrata*. According to him the muscles Mv1 and Mv2 in *Rhagio*, connecting the hypandrium with the postero-internal edge of gonocoxite and longitudinal muscle of hypandrium are their homologs. I think that muscles in *Lonchoptera* are homologous to all the muscles of phallapodeme (M35-M41) in *Calypttrata*, but not homologous to the muscle connecting the hypandrium with the gonocoxite of lower *Brachycera* (Mv2).

g) muscular connection of the hypandrial anterior edge with the postero-dorsal portion of hypandrium and/or adjacent structures: OVTSHINNIKOVA (1989 - M1); ZAKA-UR-RAB (1979a - 6, 1979c - 14).

There is a single muscle attached to the base of phallapodeme in *Dryomyza*, *Lipara*, and *Calypttrata*; to the base of aedeagus in *Sphaerophoria*; to the base of

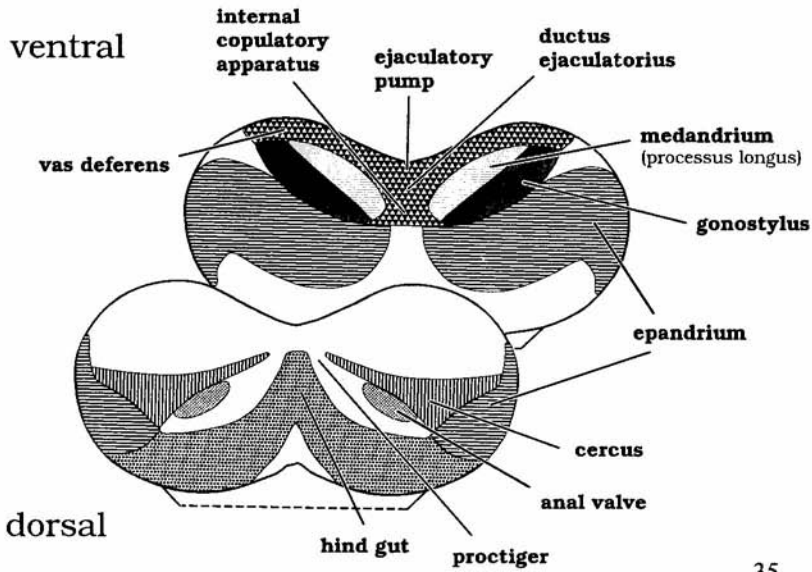
gonites in *Basilis* and *Ceratitis*. In *Drosophila* and the remaining *Calyptata*, there is a pair of muscles, attached to the base of pregonites and aedeagus, modified in *Calliphora* - running to the baso-ventral part of phallapodeme and postero-dorsal edge of hypandrium. Probably also muscle no. 3 of *Microphor holosericeus* (*Microphoridae*, *Orthogenya*) presented by ULRICH (1988) belongs to the group. I would homologize it with the longitudinal muscle of hypandrium (M33 of OVTSHINNIKOVA, 1989, Mv1 of HENNIG, 1976a) in lower *Brachycera*. HENNIG (1976b) mentioned that an explanation of the origin of muscular connection of the pregonite with the baso-ventral part of phallapodeme (M40) could be important for verification of the pregonite homology and suggested that the connection could originate from the longitudinal muscle of hypandrium, but he also allowed the possibility of its origin from the muscle connecting the intero-ventral surface of gonocoxite with the latero-ventral edge of aedeagal sheet, suggesting the origin of pregonites from gonopods. Since the muscle of pregonite and basalo-ventral part of phallapodeme is absent in lower *Aschiza*, its homology with the gonocoxal muscle is implausible and it should thus belong to the phallapodemal group of muscles.

There are five other muscles in lower *Brachycera*, which are regarded as lost, and not preserved in recent *Eremoneura* (in parentheses the numbering of OVTSHINNIKOVA, 1989) - adductor of gonostyli (M28), two muscles of gonocoxite apodeme running to the aedeagal complex: one to the ejaculatory apodeme (M30) and one to the lateral edge of aedeagal sheet (M1), muscle of ejaculatory sclerite (M32) and internal adductor of gonocoxites (M2).

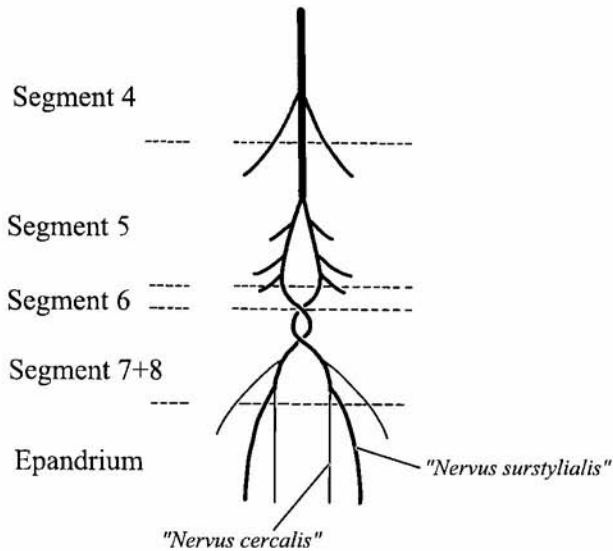
In terms of the available evidence the gonostylar interpretation of the origin and homology of genitalia has a much greater explanatory power than the surstylar concepts. The clasping mechanism in *Eremoneura* does not differ substantially from that of lower *Diptera* and all criteria of homology (function, placement and development) remain fulfilled. A significant, but not considered, argument is the presence and route of the nerve controlling the clasping lobes (Fig. 36). The nerve called by SALZER (1968) "Nervus surstylialis", presented for *Calliphora vicina* passes close to the medandrium (processus longi) between muscles M43 and M44, or closer to the top, externally to M44. The nerve "Nervus cercalis" runs internally to muscle M42 and M44, while "Nervus surstylialis" runs ventrally to muscles M42 and M44. If gonopods moved to the hypandrial complex, then the nerve should run to the gonites (regarded as the remainder of gonostyli), not to the clasping lobes. As was already mentioned in the previous chapter, the ontogenetic data indicate that the clasping lobes belong to the andrium (ninth segment). Those data provide also evidence that the development of clasping lobes is more connected with the medandrium (internal sclerite) than with the saddle-shaped sclerite. This can be noticed especially in EMMERT'S (1972) reconstruction of *Calliphora*, where the clasping lobes and medandrium (processus longus) develop from a separate germ (Fig. 35). In my opinion, this confirms evidently the origin of medandrium (processus longus) from the gonocoxites. Even a different reconstruction of genital imaginal disc in *Drosophila* illustrated by BRYANT (1978) does not contradict with this statement, since in this genus medandrium is absent (GRIMALDI, 1990).

The "hinge hypothesis" implies minimal changes in the structure of hypopygium, that is, the clasping lobes are homologous with gonostyli, internal sclerite is a transformed gonocoxite, also sclerite connected with hypandrial appendices is transformed gonocoxite apodemes, and dorsal tergite is completely homologous with the epandrium. The only weakness of the presented explanation in comparison with other gonostylar theories is the necessary assumption of the shift of the attachment of gonostylar muscles from the gonocoxite to the epandrium. In the case of fusion or periandrial theory the gonostylar muscles do not shift their attachment points. I console myself, that the muscular system is known from its plastic abilities of shifting its attachment points from one structure to another. The transformation of clasping lobes musculature in *Calyptрата* demonstrates the plasticity of the muscular system. In the group there exists a muscle connecting the epandrium with cerci (M44 of SALZER, 1968), which HENNIG (1976a) could not explain. Possibly *Scatophaga* correspond to the groundplan of muscular connections for *Calyptрата*. It is characterized by two muscles running to the base of clasping lobes (OVTSHINNIKOVA, 1993, 1994). In higher *Calyptрата*, whose cerci are associated (sometimes even articulated) with the clasping lobes, a translocation of these muscles could happen - the insertion of one was shifted to the base of cerci and of the other - to the distal portion of medandrium (processus longi).

As opposed to the surstylar concepts, the four known gonostylar hypotheses differ very slightly from each other, mainly in the postulated transformations of gonocoxites. Two of them (periandrial and fusion hypotheses) assume participation of gonocoxites in formation of the saddle-shaped sclerite. Of the remaining two hypotheses, one assumes transformation of gonocoxites into the medandrium (internal sclerite), the other - reduction of gonocoxites. Which criteria should be applied to select the better one? The criterion, which allows the selection according to the first division (contribution of gonocoxites to formation of the saddle-shaped sclerite or lack of such a contribution) is the explanation if a single process caused the origin of dorsal hypopygial complex in the *Eremoneura*, or if it happened independently in *Orthogenya* and *Cyclorrhapha*, as well as the polarity of shape of saddle-shaped sclerite in *Orthogenya*. If the polarity of the saddle-shaped sclerite transformation from moderately incised to deeply incised were more plausible, the fusion and periandrial hypotheses should be rejected. If the opposite were true, then the gonocoxite reduction and retention hypotheses would be useless. The distinction between the last two hypotheses is the question of origin of the internal sclerite. The secondary origin of the medandrium would speak in favour of the gonocoxites reduction hypothesis; the data confirming the homology of the medandrium with gonocoxites would support the gonocoxites retention hypothesis. Surprisingly, besides the same treatment of epandrium, there is one more component of the "hinge hypothesis", which fits even with the surstylar concept (revised epandrial hypothesis). It is the homology of the muscle connecting the anteromedial portion of ventral epandrial surface with the tenth sternite, suggested by CUMMING et al. (1995). Apparently the muscle shifted its insertion from the tenth sternite to the medandrium.



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36

35 - Predetermination map of the male genital disk of *Calliphora vicina* (after EMMERT, 1972); 36 - Scheme of the male neural system in posterior abdominal portion of *Calliphora vicina* (after SALZER, 1968)

8. SHAPE AND ARRANGEMENT OF HYPOPYGIAL STRUCTURES

The hypopygium (term proposed by WESTHOFF, 1882) is situated at the tip of abdomen and its components belong to the ninth segment (andrium) and proctiger (term proposed by CRAMPTON, 1923). The latter is a posteriormost component of the postabdomen, and usually consists of cerci (sometimes tenth sternite). The hypopygium with its appendices has to perform two different functions: transfer the sperm properly and protect the internal copulatory organs, when in resting position. The hypopygium is commonly divided horizontally in two sections: epandrial and hypandrial (above called ventral complex).

8.A. EPANDRIAL COMPLEX

The complex comprises the anus and two parts, which are situated dorsally and ventrally relative to hindgut, are recognized. The epandrium and cerci are placed dorsally to the hindgut. Ventrally to the hindgut, there are usually medandrium, gonopods and tenth sternite. Even, if in the groundplan of the *Diptera* the gonostyli were double and articulated separately with the gonocoxites, I would follow HENNIG'S (1936a) interpretation, that it is a secondary character in *Eremoneura*. Double or divided gonostyli are found only in a few families of *Eremoneura*.

In his figures of the male hypopygia in *Diplonevra* (*Phoridae*), DISNEY (1986b) indicated structures which are characteristic of primitive *Brachycera*: not only the ninth tergite and cerci, but also the tenth tergite, tenth sternite and hypoproct. The genitalia are presented in lateral view, which makes it impossible to see which structures are paired or how they are connected. However, I think that most of the designations are erroneous, and the hypopygia presented by DISNEY (1986) in figures 13-14 (p. 421) are not so exceptional, as that author thinks. The arrangement is typical for primitive *Cyclorrhapha* and needs to be re-interpreted. In fig. 13, representing *Diplonevra nitidula* (MEIGEN), designations of the tenth tergite, tenth sternite and hypoproct pertain to a single sclerite, presumably tenth sternite, folded up laterally (possibly it is a part of cerci). In fig. 14, representing *Dorniphora cornuta* (BIGOT), the term hypoproct is used for the tenth sternite, tenth tergite probably for the clasping lobe and tenth sternite for the medandrium (subepandrial sclerite).

8.a.1. Epandrium

The sclerite is also called periandrium, saddle-shaped sclerite, or ninth tergite. It surrounds a pair of cerci, and in primitive members of *Eremoneura* also the tenth sternite, posteroventrally articulated with hypandrium (Figs. 3, 5, 7-8, 12-13, 17-18, 21-22). It represents a modified ninth tergite. Epandrium (term proposed by CRAMPTON, 1923) carries clasping lobes (gonostyli) on its posteroventral margin. Sometimes the gonostyli are firmly joined with the epandrium (e. g. in *Sepsidae* and *Chamaemyiidae*), or completely reduced. In the groundplan the form of epandrium is elongated, U-

shaped, in dorsal view forming cercal cavity, and strongly concave. In primitive taxa the epandrium is distinctly convex, but in more specialized forms it becomes flat or/and fused indistinguishably with other structures (cerci and/or gonostyli).

8.a.2. Cerci

They are usually haired lappets on both sides of the anal orifice. The cerci are a part of proctiger, belonging to the twelfth segment. They are sometimes fused to each other, forming the so called "mesolobus" in *Anthomyiidae* and *Muscidae*, partially fused to the epandrium, or reduced, but they can be also modified, as extended appendages, sometimes connected with gonostyli (e. g. in *Calliphoridae*). They get reduced only in some members of a few families, e.g. *Empididae*, *Sphaeroceridae* and *Chloropidae*. In Calypttrata there exists an unpaired muscle (Nr. M45 by SALZER, 1968) connecting both cerci, and possibly originated from the fusion of muscles running between cerci and tenth sternite of lower *Cyclorrhapha* (MC of HENNIG, 1976a).

8.a.3. Gonostylus (= surstylus)

I interpret the presence of a one gonostylus on each side, as a part of the groundplan of *Eremoneura*. The structure is present in many families, only rarely absent, or indistinguishably fused with the epandrium (in some *Chloropidae*, *Ephydriidae*, *Lauxanidae*). In some primitive *Schizophora* two pairs of closely associated gonostyli are present. In my opinion they originated by a secondary division of a single structure, and do not represent a plesiomorphic condition in *Eremoneura*. In this case, it is easy to recognize the appendix as an internal gonostylus, not a gonite. It is situated basally to medandrium, as the external gonostylus, not attached to hypandrial complex. Double gonostyli are characteristic of the following families: *Platystomatidae*, *Pyrgotidae*, *Richardiidae*, *Carnidae*, *Dryomyzidae*, *Sciomyzidae*, *Heleomyzidae*, *Chiropteromyzidae*, *Diastatidae*, part of *Ephydriidae*, and probably also *Clusiidae* and *Periscelididae*. Also McALPINE (1981) gives two examples, of the conopid genus *Zodion* and of the chamaemyiid genus *Cremifania*, bearing double clasping lobes.

In the Manual of Nearctic *Diptera* (McALPINE et al., 1987) the division of gonostylus is accepted in certain cases, designated as the inner and outer surstylus in *Rivellia inaequata* (*Platystomatidae*), *Sphecomyiella valida* (*Pyrgotidae*) and *Automala rufa* (*Richardiidae*), but in other cases the posterior gonostylus is called "inner lobe of epandrium" (*Dryomyza flaveola* (*Dryomyzidae*) and *Masoniella richardsi* (*Tethinidae*)), as well as "process of sternite 10" in *Amoebaleria helveola* (*Heleomyzidae*).

8.a.4. Medandrium (subepandrial sclerite)

Several names have been proposed for this structure in *Cyclorrhapha*, e.g. bacilliform sclerites, processus longus (original term proposed by BRÜEL, 1897 "Processus longus der Valvula lateralis"), deca sternum, intergonopodal sclerite, interparameral sclerite, intraepandrial sclerite, interperiandrial sclerite. In *Calyptrata* the structure is paired and the plural form of "processus longus" is "processus longi", not "processi longi" (the latter term used by McALPINE, 1981). Thus, GRIFFITHS (1981), in his review of Nearctic Manual, is right in correcting the error. The sclerite situated ventrally to the epandrium and anteriorly to the tenth sternite exists also in *Orthogenya*, named "Verbindungssteg zwischen Cercibasis und Aedoeagusbasis" by BÄHRMANN (1960), "ventrale Proctigersklerite" by ULRICH (1972), "Proctigersklerit" by ULRICH (1975). In my opinion all the terms indicate structures, which are homologous to each other, called here shortly medandrium.

It was sometimes erroneously designated as "tenth sternite" (term proposed by METCALF, 1921 for *Syrphidae*), or as its derivative. The authors using the term before 1976 were probably not conscious that it was based on two erroneous concepts: BERLESE's (1909), who presumed that the first abdominal segment in flies was lost and therefore the genital segment with the tergite and sternite bore number ten, and METCALF's (1921), assuming that the pregenital tergite disappeared and the hypandrium was the ninth sternite. He considered epandrium to be the tenth tergite and the sclerite under the epandrium to be the tenth sternite. The designation of the "tenth sternite" by HENNIG (1976a) was based on a too widely interpreted homology between the sclerites in lower *Brachycera* and *Eremoneura*. The indication, based on the homology, was subsequently used by McALPINE (1981), McALPINE et al. (1987). The use of the term "10th sternite" for the sclerite is clearly groundless, since it belongs to the ninth segment, and it is not a part of the proctiger. WHEELER (1995) adopted various names for the parts of sphaerocerid internal sclerite - the posterior part: subanal plate, postero-lateral: bacilliform sclerite, finally medial and anterior: subepandrial sclerite. The terms were proposed for the same structure in various taxa and the usage of all of them to denote a single sclerite seems to be incorrect.

According to BRÜEL (1897) the medandrium (his "processus longus") is a new structure. The same opinion was presented by CUMMING et al. (1995). HENNIG (1973) interpreted the medandrium as a specialization of the inner wall of the epandrium. In my opinion this sclerite originated from the fusion of both gonocoxites; besides the transandrium (dorsal sclerites) no other components are involved in formation of the connection of gonocoxite in *Eremoneura* (and not only margins, as GRIFFITHS, 1972 postulate). It is not homologous to, nor did it originate, by a division of the tenth sternite of lower *Brachycera*. In *Cyclorrhapha* the true tenth sternite is present only in four primitive families (see paragraph below).

The medandrium was illustrated in some families, and probably it occurs widely in most cyclorrhaphous flies. HENNIG (1971a: 54, fig. 54) figured it in *Apetaenus littoralis* (*Tethinidae*), McALPINE (1967: 229, figs 9-10) for *Ironomyia nigromaculata*

(*Ironomyiidae*), and also on p. 233 (fig. 18) for *Platypezina pacifica* (*Platypezidae*). HIPPA (1968) presented the structure for *Syrphus torvus* O. S. This structure is present in most genera of *Chloropidae* (ANDERSSON, 1977). McALPINE et al. (1987) figured the medandrium as "10 sclerite" in *Syrphidae*, *Neriidae*, *Diopsidae*, *Clusiidae*, *Anthomyzidae*, *Carnidae*, *Dryomyzidae*, *Ropalomeridae*, *Heleomyzidae*, *Sphaeroceridae*, *Drosophilidae*, *Chloropidae*, *Tethinidae*, and as "bacilliform sclerite" in *Calliphoridae*, *Sarcophagidae*, *Rhinophoridae*, and *Tachinidae*. In the genus *Cerodontha* (*Agromyzidae*) the internal epandrial sclerite is U-shaped; for its transverse portion NOWAKOWSKI (1973) used the name "Stabförmige Sklerite", and for the elongate part "Langfortsatz". In the family *Ephydriidae* (subfamily *Discomyzinae*) the medandrium is also present, as shown in figures 23-24 of "oil-fly" *Heleaomyia petrolei* (COQUILLET). From the descriptions of the male terminalia included in GRIFFITHS (1972) and additional data mentioned above, it follows that only in 17, mainly small and highly specialized families (*Muscidae* are the exception) this sclerite has not been found so far. It appears to be evident that the structure can be treated as a part of the groundplan of *Eremoneura* (Figs. 3-5, 7-8, 12-13, 17-18, 25-28).

8.a.5. Tenth sternite

The tenth sternite in *Eremoneura* is a simple, usually triangular plate, situated ventrally to the cerci and posteriorly to the medandrium. The sclerite is sometimes erroneously called "epiproct" (KESSEL & MAGGIONCALDA, 1968), or "hypoproct", both terms denoting the elements of eleventh segment, recognized in female genitalia. Tenth sternite occurs in primitive families of *Atriata* - *Platypezidae*, *Sciadoceridae* and *Ironomyiidae* and primitive *Phoridae* (e.g. in the genera *Diplonevra* and *Dornivora*, see DISNEY, 1986b; *Phora* see GOTÔ, 1984) only. The indication of the "tenth sternite" or "hypoproct" in the figures of *Spelobia clunipes* (*Sphaeroceridae*), *Meoneura obscurella* (*Carnidae*), *Aulacigaster leucostoma* (*Aulacigastridae*) in McALPINE et al. (1987) is evidently erroneous and probably refers to medandrium. Because McALPINE (1967) designated medandrium (subepandrial sclerite) as the tenth sternite for hypopygium of *Ironomyiidae*, he had to call the posteriormost sclerite "11 sternite". HENNIG (1976a) doubted the existence of the eleventh sternite, and assumed rather a division of the tenth sternite.

8.B. HYPANDRIAL COMPLEX

The complex in primitive *Eremoneura* consists of aedeagal complex, which is posteriorly completely surrounded by the sclerite called transandrium. Other parts of the complex are phallapodeme and ejacapodeme in *Cyclorrhapha*, ejaculatory apodeme in *Orthogenya*, hypandrium, gonites, and aedeagus.

8.b.1. Transandrium

The structure in *Cyclorrhapha*, in English literature usually called dorsal bridge, interperiandrial fold (GRIFFITHS, 1972), "Brückenartige Verbindung über dem Aedoeagus" (BÄHRMANN, 1960), or "Dorsal-Brücke" (HENNIG, 1976a), is in my opinion an important sclerite in the transformation of eremoneuran hypopygium.

The transandrium is made of gonocoxal apodemes extended posteromedially behind the aedeagus and fused with each other (presumably also with the aedeagal sheet) turning the hypandrial complex into a closed ring. It is always the postero-dorsal portion of the hypandrium, close to the point of articulation with the epandrium. The structure is present in rather primitive families of *Atriata*. In *Platypezidae* it is well developed as a rectangular sclerite, in *Dryomyzidae* it has a Y-shaped form (fig. 17). HENNIG (1976b: fig. A80) presented in *Fucellia tergina* (*Anthomyiidae*) the sclerite between the hypandrial process and dorsal margin of aedeagal base, which could be the remnant of transandrium. He called it "Vertikalsklerit". The sclerite is placed distinctly under the termination of ductus ejaculatoris and does not have any muscle attachments, but close to it there is a sclerotized strengthening of epandrial ventral margin (Figs. 10-11, 14-20). Probably the structure called "metaphallic plate" in *Heleomyzidae* (cf. figs 11-14 in GORODKOV, 1959), as well as the structure called "epiphallus" in *Neottiophilidae*, *Ropalomeridae*, *Clusiidae* and *Piophilidae* represent a modified transandrium (dorsal bridge).

8.b.2. Gonites

The gonites (term proposed by CRAMPTON, 1944) are widespread among the *Cyclorrhapha*, associated with posterodorsal margin of hypandrium, as one or two pairs of appendices. The orthogenyan hypandrial appendices occur rarely, e.g. those presented in the genus *Microphor* (*Microphoridae*) by HENNIG (1976a) and ULRICH (1988) are presumably not homologous to cyclorrhaphan gonites. In the lower *Atriata* (*Platypezidae*) a pair of lobes (postgonites) is attached to transandrium (dorsal bridge) and to posterodorsal margin of hypandrium. The second pair of lobes (pregonites) forms an elongation of posteroventral margin of hypandrium. Such a condition is typical for several families of *Atriata*. In some advanced sublineages also pregonites are articulated with the hypandrium, having a finger-like form, or as sclerotized plates.

8.b.3. Hypandrium

The hypandrium (term proposed by CRAMPTON, 1923), being the ninth sternite, is a horse-shoe-shaped structure, whose postero-lateral arms have sockets at their tips, providing articulation with the anterior epandrial arms. In some cases postero-dorsal lobes of hypandrium are united by a sclerotized connecting bar (transandrium), and the hypandrium in these forms becomes a closed ring around the aedeagus. In *Atriata* hypandrium is articulated posteromedially with the phallopodeme. In

Calyptrata the base of phallapodeme is relatively narrow and between the anteroventral margin of phallapodeme and hypandrium there is a membrane, the so called "phallic guide" (intermedium).

8.b.4. Ejacapodeme ("Ejaculatory apodeme")

The structure is present in *Cyclorrhapha*. It is an elongate, mostly spatulate, loose structure situated anteriorly to the aedeagus on a prolongation of ductus ejaculatoris. Most probably it developed as a chitinized margin of ejaculatory sac, or as a part of phallapodeme. Only in 11, mostly specialized, families such a structure was not found (after GRIFFITHS, 1972 with additions): *Camillidae*, *Cnemosphatidae*, *Odiinidae*, *Fergusonidae*, *Ropalomeridae*, *Fannidae*, *Braulidae*, *Glossinidae*, *Hippoboscidae*, *Nycteriibidae*, and *Streblidae*. Perhaps the structure could be found in some of those families. Even the Manual of Nearctic *Diptera* (McALPINE et al., 1987) presented the absence of ejacapodeme as the autapomorphic character of the *Ephydriidae*, but the structure was recently observed in representatives of several dozen of shore-fly genera (ZATWARNICKI, 1992).

8.b.5. Ejaculatory apodeme

The internal structure occurs in *Orthogenya*, and is usually attached to the base of aedeagus (Figs. 6, 9). In *Dolichopodidae* the ejaculatory apodeme is articulated with the aedeagus. Free ejaculatory apodeme exists also in *Stratiomyoidea*, but despite McALPINE's (1989) suggestion, that the character is shared by *Stratiomyoidea* and *Cyclorrhapha*, it is undoubtedly a homoplastic modification, originated independently in both groups. In dorsal view, it is a narrow structure, but in lateral view, the ejaculatory apodeme is posteriorly rounded, directed antero-ventrally, narrowed posteriorly. The homology of the structure with that of the lower *Brachycera* is unquestionable.

8.b.6. Phallapodeme

The structure occurs in *Cyclorrhapha* and it has a very variable shape, from much elongate, with a narrow anterior margin, through triangular and semicircular, to band-like with a broad base. Its postero-dorsal margin has to connect with the base of aedeagus, and its antero-ventral margin is usually attached to the middle portion of the posterior margin of hypandrium (secondarily not attached in *Calyptrata*, and some lower *Schizophora*, e.g. *Sphaeroceridae*, *Dryomyzidae* (figs. 19-20), and *Agromyzidae*). Like HENNIG (1976a), I assume that the rod-like phallapodeme, which is not articulated with the hypandrium, is a specialized condition in *Schizophora*.

8.b.7. Aedeagus

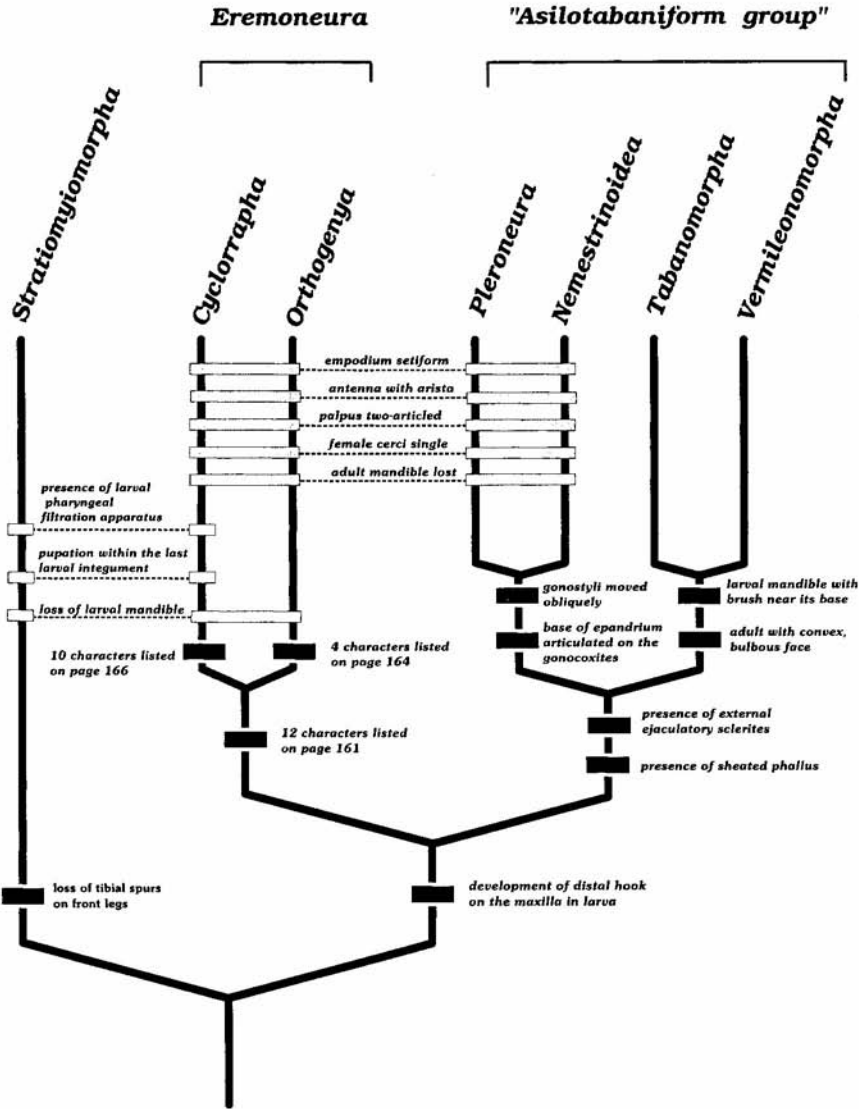
The copulatory organ is situated ventrally to the transandrium, sustained by phallapodeme. Usually it is symmetrical, elongated, and tapered apically. In *Orthogenya* the aedeagus bears ejaculatory apodeme posteriorly and in lateral view is arcuate or distinctly arched; in *Cyclorrhapha* the aedeagus articulates with the apodeme called phallapodeme and variously shaped, mostly uniform and nearly straight. In some advanced taxa aedeagus is highly modified - it bears scales, or teeth on its surface, consists of differentiated sections and/or is curved.

9. PHYLOGENETIC CONSIDERATIONS

The gonostylar concept, which I accept, supports most of the proposals following from other gonostylar hypotheses (especially periandrial hypothesis). The main disagreement between GRIFFITHS' (1972) and me is the direction of the development of epandrium in *Orthogenya* (see chapter 6.d). The concept of the origin of eremoneuran male hypopygium imposes the polarization of characters, which are used for the reconstruction of the phylogeny of higher *Brachycera*. Accepting some hypotheses, which assume a connection of the gonopods with the hypandrium, the development of *Brachycera* passes fluently to *Eremoneura*, as the most advanced group and *Pleroneura* (*Asiloidea*), as its sister group. But accepting the homology of the clasping lobes with the gonostyli implies changing the position of *Eremoneura*. Because in most lower *Brachycera* the gonopods are connected with the hypandrium, *Eremoneura* have to be assumed as the sister group to most of them, or it has to be accepted, that the connection of gonopods with the hypandrium in lower *Brachycera* occurred repeatedly.

9.A. PLACEMENT AND MONOPHYLY OF *EREMONEURA*

Orthogenya (*Empidoidea*) were initially placed closer to other lower *Brachycera*, than to *Cyclorrhapha*, and were included in the group called *Orthorrhapha Brachycera*. LAMEERE (1906) was the first to suggest a close relationship between *Orthogenya* and *Cyclorrhapha*, and classified both of them in the group *Eremoneura*. The concept of *Eremoneura* was adopted by HENNIG (1952, 1954), but later he (HENNIG, 1971a) rejected the recognition of the group on the basis of the articulation of antennal arista. He claimed that the antennal arista was two-articulated in the *Pleroneura* (*Asiloidea*) and *Orthogenya* (*Empidoidea*), but three-articulated in the *Cyclorrhapha*. Finally HENNIG (1976a) once again adopted the *Eremoneura*, having found a two-articulated arista in *Opetia*. The monophyly of *Eremoneura* was widely argued by GRIFFITHS (1972, 1984), and the discussion on the question is in my opinion out of date. The hesitation of WOODLEY (1989), who presented an unresolved trichotomy among *Pleroneura* (*Asiloidea*), *Orthogenya* and *Cyclorrhapha* resulted probably from HENNIG's (1971a, 1976a) change of opinion on the placement of



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Orthogenya. WOODLEY (1989) was not sure, which point of view he should adopt, and left *Orthogenya* as related to both *Asiloidea* and *Cyclorrhapha*.

Based on his principles of 'ancestral' and 'derived' taxa, DISNEY (1988) tried to demonstrate that, if the groundplan of the *Phoridae* (primitive members of *Cyclorrhapha*) was plesiomorphic compared with the groundplan of the *Empidoidea*, the latter taxon could not be 'ancestral' to the *Cyclorrhapha*. He denied the sister group relationship between the *Empidoidea* and *Cyclorrhapha* under the name *Eremoneura*, and envisaged that *Orthogenya* (*Empidoidea*) and *Cyclorrhapha* represented separate clades, whose ancestors diverged nearer the base of the "heterodactylan" *Brachycera*. DISNEY (1986a) rejected even the monophyly of *Brachycera*, suggesting that the *Cyclorrhapha* could represent a lineage independent from *Bibionomorpha*. His argumentation (DISNEY, 1988) seems to be strange in view of modern methodology. The taxa could have "primitive" or "advanced" characters, but the recent taxa could not be 'ancestral' or 'derived' relative to each other. It is not excluded that the taxa commonly treated as "primitive" (eg. *Empidoidea*) have several 'advanced' characters, which are absent in their more derived sister groups, and I see nothing illogical in this fact. Even the fact that the *Empidoidea* are characterized by several 'derived' characters, does not imply that "*Empidoidea* evolved from the *Cyclorrhapha*", as both *Empidoidea* and *Cyclorrhapha* have evolved independently, at least since the middle of Cretaceous period (HENNIG, 1971b; WATERS, 1989).

Both *Eremoneura* and *Pleroneura* were placed together in a group named *Heterodactyla*. Several synapomorphies were presented to support its monophyly: empodium setiform, much narrower than pulvilli; antenna with five articles, the terminal section slender, forming arista; maxillary palpi of adult with two articles; female cerci with single article; mandibles in adults lost. According to RÖDER'S (1984) dissertation (after GRIFFITHS, 1994), in the groundplan of both *Eremoneura* and *Pleroneura* the empodium is short and weakly developed. Therefore the setiform empodium had to develop independently in both groups, and does not constitute a reliable synapomorphy. The polarity of other constitutive characters linking *Nemestrinoidea*, *Pleroneura* and *Eremoneura*: absence of true tibial spurs, at most four flagellomeres of antenna, reduction of female second cercal article, are doubtless, but often reductions are subject to homoplasy and should be supported by other characters.

Assuming that the "distal hook" of the larval mouthparts of lower *Brachycera* is of mandibular, not maxillar, origin GRIFFITHS (1994) regarded its presence as plesiomorphous. To him the development of distal hook on the maxilla could be a synapomorphy of *Brachycera*, excluding *Stratiomyomorpha*, and the loss of mandible became a possible synapomorphy of *Stratiomyomorpha* and *Eremoneura*. SINCLAIR (1992) stated, that the lack of the larval pharyngeal filtration apparatus belonged to the groundplan of *Brachycera*, but GRIFFITHS (1994) considered the presence of the apparatus as an independent apomorphy in the *Stratiomyomorpha* and *Cyclorrhapha* and proposed the presence of external ejaculatory sclerites, and sheathed intromittent organ (phallus) as synapomorphies of the so called asilotabaniform group

(*Tabanomorpha*, *Vermileonomorpha*, *Nemestrinoidea* and *Pleroneura*). The relationships between the major sublineages of *Brachycera*, based on the characters suggested by GRIFFITHS (1994), are shown in the cladogram (Fig. 37).

Eremoneura are undoubtedly monophyletic, since they have complicated but uniform groundplan of hypopygium, which developed as a result of a unique process of gonopods transformation. *Orthogenya* and *Cyclorrhapha* share so many progressive characters, that the assumption of a closer relationship between *Orthogenya* and *Pleroneura* (*Asiloidea*) could not be wider supported.

The *Eremoneura* are characterized by the following synapomorphies (in this and other cases, the authors who first proposed the respective characters, are provided, if known to me):

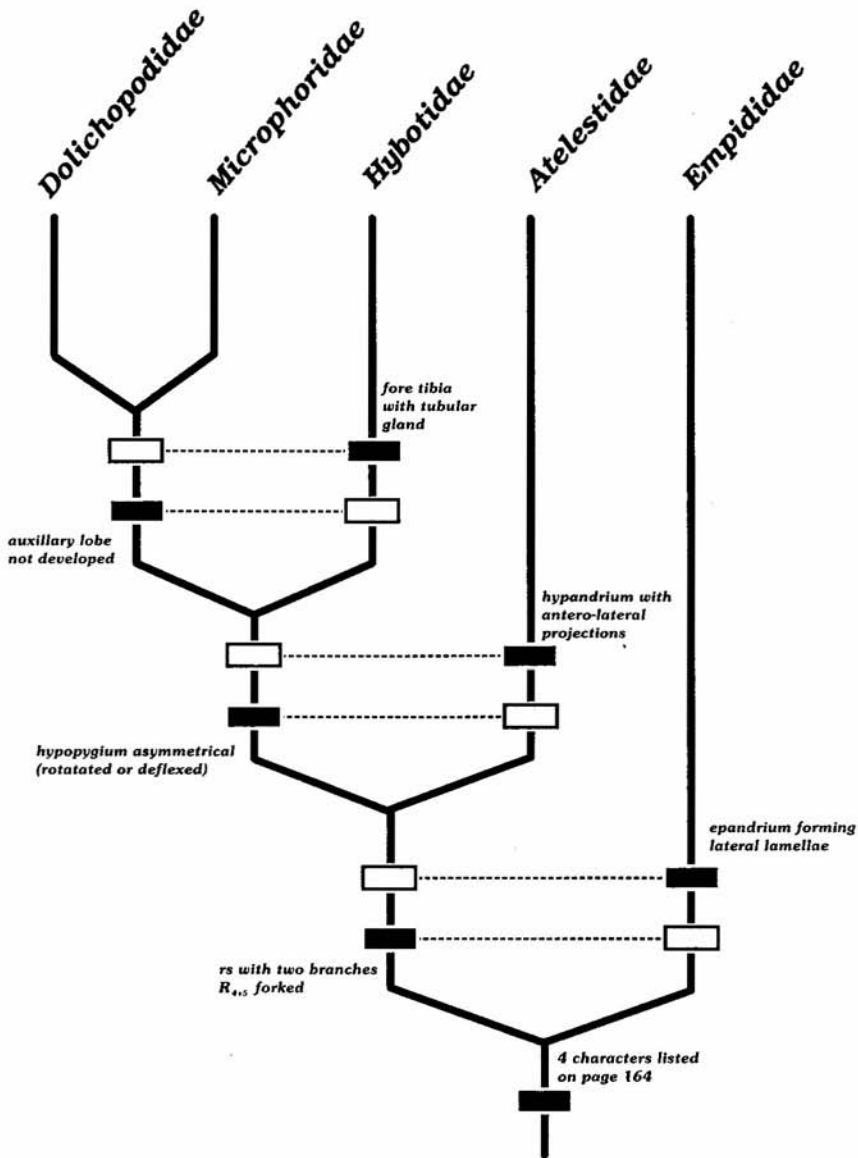
- (1) Gonocoxites folded under epandrium.
- (2) Gonocoxal apodemes separated from the gonocoxites and attached to the hypandrium.
- (3) Tenth tergite lost (occurs independently in other groups).
- (4) Complete loss of sclerites of the female ninth segment (secondarily developed in a few genera of *Syrphidae*).
- (5) Aedeagus slender, upcurved distally (GRIFFITHS, 1972).
- (6) Cerci single-articled.
- (7) Wing with medial veins with only 3 branches (M_3 fused with M_4) (HENNIG, 1952, 1954).
- (8) Wing with anal cell closed apically (HENNIG, 1952, 1954).
- (9) Palpus one-segmented.
- (10) Three larval instars.
- (11) Hypopharyngeal skeleton of larvae V-shaped (HENNIG, 1952, 1954).
- (12) Larval maxilla reduced to an elongate, primarily membranous lobe (SINCLAIR, 1992).

9.B. COMMENTS ON THE MAJOR SUBGROUPS OF *EREMONEURA*

In this chapter I discuss the monophyly and status of the major eremoneuran subgroups: *Orthogenya*, *Cyclorrhapha*, *Acroptera*, *Atriata*, *Platypezoidea*, *Hypocera*, *Eumuscomorpha*, *Syrphoidea*, and *Schizophora*.

9.b.1. *Orthogenya*

The taxon called also *Empidoidea* or *Empidiformia* was proposed by BRAUER (1883). Although some genera, at present placed within *Orthogenya*, were included by KESSEL (1968) in the *Platypezidae*, the monophyly of *Orthogenya* was not seriously questioned during the last forty years. The exception was the proposal of CHVALA (1983), who divided the *Eremoneura* into two phylogenetic lineages: *Empididae* with a complete wing venation (rs three-branched) and the rest with a reduced wing venation (rs two-branched). The latter lineage led to the assemblage



(more primitive in CHVALA's (1983) opinion) with symmetrical male terminalia, producing the *Atelestidae* and *Cyclorrhapha*, and another lineage, characterized by asymmetrical male terminalia, consisting of *Hybotidae*, *Microphoridae* and *Dolichopodidae* ("hybotid line"). In such a classification the sister-group of *Cyclorrhapha* was the family *Atelestidae*. The phylogeny of *Eremoneura* proposed by CHVALA (1983) is a result of application of periandrial hypothesis to the polarization of saddle-shaped sclerite transformation.

The correctness of CHVALA's (1983) phylogeny was questioned already by GRIFFITHS (1983), who noticed that *Cyclorrhapha* could not separate from ancestors of *Atelestidae*, since, like the remaining *Orthogenya*, *Atelestidae* had only one spermatheca (as observed by CHANDLER, 1981), and in the groundplan of *Cyclorrhapha* there were three spermathecae. There are also other characters (see below), which support the monophyly of *Orthogenya*, and the character shared by the "hybotid line" and *Cyclorrhapha* (reduced wing venation - rs two-branched) could be easily interpreted as homoplasy.

Accepting *Cyclorrhapha* as a sister group to *Orthogenya*, we can analyze the synapomorphies provided by CHVALA (1983) for the sublineages of *Orthogenya*. A major weakness of his reconstruction is the lack of synapomorphy for *Empididae* (sensu stricto), while four apomorphic characters occurring in the *Empididae*, presented in fig. 141 (p. 61) are not shared by all their subfamilies. Also BÄHRMANN (1960) easily separated the hybotid line with inverted and asymmetrical male hypopygium. He stated also, that the lack of gonopods characterized the "hybotid line" and in the *Empididae* gonopods (gonocoxites) were retained (see chapter 6.e), therefore the *Empididae* remained without synapomorphic characters. As a follower of the periandrial hypothesis CHVALA (1983) accepted the *Empididae* (sensu stricto) as the most primitive representatives of *Orthogenya* (*Empidoidea*). Adopting the hypotheses with retained epandrium (all the hypotheses excluding fusion and periandrial hypothesis) implies that the first synapomorphic character of the *Empidoidea* other than *Empididae*, mentioned by CHVALA (1983) - gonopods fused basally and forming periandrium, after reversal of its polarization - becomes a character describing the shape of epandrium, as a synapomorphy of *Empididae* (epandrium posteromedially incised) and therefore each phylogenetic lineage is based on derived characters (Fig. 38). In this sense the "hinge hypothesis" supports CHVALA's (1983) classification, which was originally based mainly on external characters, but it reverses the direction of character polarization, resulting from the concept of dorsal hypopygial complex. Assuming that the shape of the empidid epandrium is a specialized state, the shape of the "hybotid" epandrium must be interpreted as primitive and the placement of the "hybotid" sublineage (*Hybotidae*, *Atelestidae*, *Microphoridae* and *Dolichopodidae*) close to *Cyclorrhapha* is no longer necessary.

Although I disagree with CHVALA's (1983) phylogeny of *Eremoneura*, I understand his reasons for reclassification of *Orthogenya*. Several authors, prior to CHVALA's (1983) publication pointed out, that the former "*Empididae*" constituted a

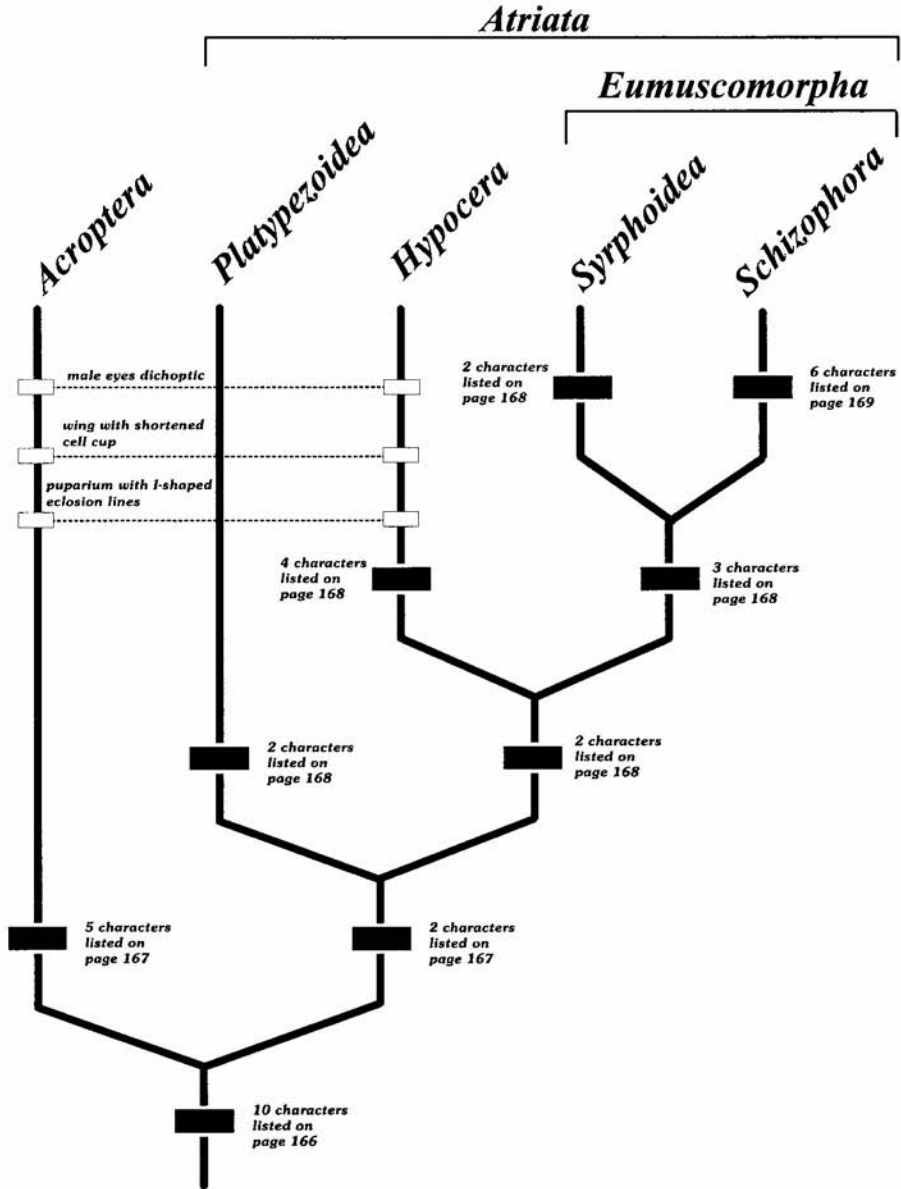
paraphyletic and unnatural unit. Both *Cyclorrhapha* and *Orthogenya* (*Empidoidea*) separated from each other relatively early. WATERS (1989) mentioned a fossil hybotid from the Cretaceous, and suggested that the empidid and hybotid lineages were well established at a much earlier date, than that accepted. If *Dolichopodidae* constituted a family-level taxon, and the remaining *Empidoidea* were not their sister group, but only a component-group, the only logical consequence would be the acceptance of each group, equivalent to *Dolichopodidae*, as a family. The proposal of CHVALA (1983) could be rejected after finding a character restoring the status of the two sister groups: *Dolichopodidae* (possible with *Microphoridae*) and the rest of *Empidoidea*. Conservatism and aversion to accept changes proposed by other scientist could be the only explanation, why WOODLEY (1989) and CUMMING et al. (1995) did not accept CHVALA's (1983) proposal of the five families within *Orthogenya*. When reading the above works, I expected some definite arguments, which would contradict CHVALA's (1983) classification. I am not satisfied with WOODLEY's (1989) statement, that the classification of CHVALA (1983) could not be accepted, because he did not examine the primitive *Oreogetoninae* from Chile. If case of doubt, it is necessary to explain exactly, which characters of Chilean *Oreogetoninae* prevent the acceptance of the taxonomic status of empidoid families. Instead, WOODLEY (1989) marked the monophyly of the *Empididae* (s. lato) with a question mark in his cladogram (p. 1374). The main difference between the relationships of orthogenyan taxa presented by CHVALA (1983) and CUMMING et al. (1995) is the position of the assemblage of three subfamilies (*Ceratomerinae*, *Trichopezinae* and *Brachystomatinae*), which according to CUMMING et al. (1995) form a sister group to *Dolichopodidae*-"*Microphorinae*", but in CHVALA's (1983) opinion the assemblage belongs to the *Empididae* (s. str.).

The *Orthogenya* are characterized by the following synapomorphies:

- (1) Female with single spermatheca.
- (2) Wing with vein cu1 recurved.
- (3) Larva with postcranium modified into a pair of slender metacephalic rods (SINCLAIR, 1992).
- (4) Final instar larval distal hook composed of four components (SINCLAIR, 1992).

9.b.2. *Cyclorrhapha*

The group was recognized by BRAUER (1863) based on the position of the ecdysial lines in the puparium, and later confirmed by several other characters. The monophyly of the group has never been questioned since its description, although some genera, which belong to *Atelestidae* (*Orthogenya*), were placed in a relatively primitive family of *Cyclorrhapha* - *Platypezidae*. DISNEY (1987) doubted if *Opetia* was a cyclorrhaphan fly, but CUMMING et al. (1995) demonstrated, that in the genus the ejaculatory duct was looping over hindgut. Likewise, my own studies, do not



39 - Phylogeny of major sublineages of *Cyclorhapha*

confirm the division of *Cyclorrhapha* into *Aschiza* and *Schizophora*. Only the *Schizophora* form a monophyletic group (Fig. 39).

The *Cyclorrhapha* are characterized by the following synapomorphies:

- (1) Ejacapodeme free.
- (2) Hypandrium with a pair of postero-dorsal processes (gonites).
- (3) Hypopygium rotated to an inverted position within puparium, then rotated by further 180° to a circumverse resting position soon after emergence; the eighth abdominal segment rotated by 180° (half angle of hypopygial rotation).
- (4) Eight male tergum (normally in ventral position in mature adult) reduced to a narrow band (also in *Atelestus* and some *Empididae*) (GRIFFITHS, 1972).
- (5) Antenna with flagellum composed of the first flagellomere and three arisomeres.
- (6) Radial sector two-branched; R₄₊₅ not forked (HENNIG, 1954).
- (7) Costa reduced on posterior margin of wing.
- (8) Larval head capsule reduced: individual parts of cephalic and pharyngeal skeleton fused into a uniform "cephalopharyngeal skeleton".
- (9) Larva with pharyngeal ridges, functioning as a filter device (SINCLAIR, 1992).
- (10) Pupa enclosed within puparium formed by contraction and hardening of integument of the third larval instar.

9.b.3. *Acroptera* (*Lonchopterygidae*)

The first branch of *Cyclorrhapha* are *Lonchopterygidae*, separated by de MEIJERE (1900), but already earlier called *Acroptera* by BRAUER (1883). A small remnant of the larval capsule visible in dorsal view justifies the separation. Also my studies reveal that in *Lonchopterygidae* hypopygium is of a shape different from that found in the remainder of *Cyclorrhapha*. At first sight, the family is much more specialized than the *Platyezidae*, but the former have primitive characters of hypopygium (phallapodeme, if present, functioning as ejaculatory apodeme in lower *Brachycera* (Figs. 10-11); aedeagus in lateral view curved). I agree with the division of *Cyclorrhapha* into *Acroptera* and *Atriata*, agreeing with HENNIG (1952, 1976b), and GRIFFITHS (1972), that *Lonchopterygidae* are the sister-group to the remaining *Cyclorrhapha*. For CUMMING et al. (1995) the *Opetidae* and the *Platyezidae* were separately sister-groups to the rest of *Cyclorrhapha*, and they placed *Lonchopterygidae* within the third branch, as a sister group to *Phoroidea*. The dichoptic male eyes, wing with shortened cell cup, and puparium with I-shaped eclosion lines, should support such a placement.

The *Lonchopterygidae*, having some specific features, are much distinct from the remaining *Cyclorrhapha*. Their external characters allow an easy recognition of the group. Besides the characters presented by GRIFFITHS (1972), I suggest several

new pertaining to hypopygial structures (marked with asterisks). All the characters mentioned above provide evidence that *Atriata* have found a specific way of hypopygial movement and evolved in way different from *Cyclorrhapha*.

The *Acroptera* are characterized by the following synapomorphies:

- * (1) Anterior margin of epandrium straight, posteriorly adjoined by cerci, therefore cercal cavity absent.
- * (2) Gonostyli and medandrium reduced, consequently clasping function abandoned.
- * (3) Posterior margin of epandrium fused ventrally, forming the closed ring.
- (4) Folding of hypopygium occurs between the ventral epandrial arch and the sixth segment.
- (5) Shape and venation of wing modified (GRIFFITHS, 1972).

9.b.4. *Atriata*

The *Atriata* were divided by GRIFFITHS (1972) into *Hypocera* and the rest (*Platypezoidea*, *Syrphoidea* and *Schizophora*). The monophyly of the sister group to *Hypocera* was supported by the wing venation (veins M_1 and M_2 forked beyond discal cell or at least at its distal corner). In my opinion *Platypezoidea* constitute a more primitive group, and although the characters supporting the monophyly of *Hypocera*, *Syrphoidea* and *Schizophora* are homoplasies acquired independently by *Lonchopterygidae* (see paragraph below), at present it seems to be the right solution.

The *Atriata* (*Cyclorrhapha*, excluding *Lonchopterygidae*) are characterized by the following synapomorphies:

- (1) Phallapodeme articulating with aedeagus and hypandrium.
- (2) Larval head capsule reduced: atrium developed (GRIFFITHS, 1972).

9.b.5. *Platypezoidea* and their sister group

It is the most primitive family of *Atriata*. In the *Platypezidae* copulation takes place in flight (KESSEL, 1968) when the hypopygium is inverted, but after the copulation it returns to the resting position, rotating by further 180° to fold underneath. It is obviously a plesiotypic character. The *Platypezidae* have separate tergites 7 and 8 (in other families they are connected and there is a typical sixth sternite). After the correction of CUMMING et al. (1995), that in *Opetia* also the ejaculatory duct is coiled around the hindgut, there is no reason to separate *Opetidae* from the remaining *Cyclorrhapha*, as done by WIEGMANN et al. (1994) and CUMMING et al. (1995). The synapomorphic (absence of female abdominal spiracles 5-7 and spermathecae) and plesiomorphic characters (antenna with two-article arista, costa circumambient) do not support such a high position of *Opetia*, and it is better placed

in *Platypezoidea*. *Opetia* is a unique genus with two-article arista within *Cyclorrhapha*, but the three-article arista evolved also in *Acarteroptera* and *Meghyperus* (*Atelestidae*), hence the character is not conclusive.

The *Platypezoidea* are characterized by the following synapomorphies:

- (1) Hind tarsi expanded.
- (2) Acrostichal setae uniserial.

The rest of *Cyclorrhapha* (without *Acroptera* and *Platypezoidea*) is characterized by the following synapomorphies:

- (1) Antennal pedicel with thumb-like condyle inserted on the first flagellomere (HENNIG, 1976a).
- (2) Pupal respiratory organ projecting through puparium (KEILIN, 1944).

9.b.6. *Hypocera* (*Phoroidea*)

The *Hypocera* comprising *Phoridae*, *Ironomyiidae*, and *Sciadoceridae* are characterized by the following synapomorphies (after HENNIG, 1954, and McALPINE & MARTIN, 1966):

- (1) Subcosta partially fused to R_1 at mid-length.
- (2) Wing with shortened anal cell.
- (3) Only a single dorsal sclerite between the sixth segment and the hypopygium (also in *Lonchopterygidae*).
- (4) Apex of the second antennal article deeply inserted into the base of the third (also in *Lonchopterygidae*).

9.b.7. *Eumuscomorpha*

The term *Eumuscomorpha* (*Syrphoidea* and *Schizophora*) was proposed by WADA (1991), who demonstrated their separate status. The taxon is characterized by the following synapomorphies:

- (1) Hypopygial circumversion completed within puparium.
- (2) Mono-type of retina of the compound eyes (WADA, 1991).
- (3) Dorsobasal position of arista on the first flagellomere.

9.b.8. *Syrphoidea*

The *Syrphoidea* (*Syrphidae* and *Pipunculidae*) are characterized by the following synapomorphies:

- (1) Frons without macrochaete.
- (2) Sixth and seventh abdominal segments asymmetrically developed on the left side, with reduced terga; eighth sternum enlarged and asymmetrical; hypopygium strongly deflexed, directed anteriorly.

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- (3) Dorsobasal position of arista on the first flagellomere.

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- (1) Frons without macrochaete.
- (2) Sixth and seventh abdominal segments asymmetrically developed on the left side, with reduced terga; eighth sternum enlarged and asymmetrical; hypopygium strongly deflexed, directed anteriorly.

9.b.9. *Schizophora*

The taxon was first recognized and named by BECHER (1882), who discovered a complex organ (ptilinum), which enabled emergence of imago from the puparium. The division of the group into *Acalyprata* and *Calyprata* is in my opinion artificial. Probably *Calyprata* form a monophyletic group, distinguished by the divided second antennal segment.

The *Schizophora* are characterized by the following synapomorphies (GRIFFITHS, 1972):

- (1) Ptilinum and temporary musculature present.
- (2) First abdominal segment with "adventitious suture" (YOUNG, 1921).
- (3) Lunule discrete
- (4) Wing with M_{1+2} not forked.
- (5) Wing with shortened anal cell (retrograde in *Conopidae* and *Micropezidae*).
- (6) Two pairs of vertical bristles present.

10. CONCLUDING REMARKS

At present I may not be in a position to convince the opponents of the gonostylar hypothesis, and this is not the main purpose of the paper. I am not able to provide final answers to all the controversial questions, but I have paid attention to some problems, so far not adequately worked out.

Perhaps there are some facts, that justify acceptance of surstylar hypothesis. But I have discussed all arguments given in the papers of their defenders, especially HENNIG (1976a and b), McALPINE (1981), CUMMING et al. (1995); OVTSHINNIKOVA (1993, 1994) and WHEELER (1995). Their duty is to ultimately justify the hypothesis they follow. If they find sources that they have previously overlooked, or discover new facts, which they can interpret to their advantage, I am ready to analyze them. The structure of "hinge" concept implies many regularities, particular homologies, the way of explanation of several transformations and the direction of development of respective characters. All of them may be subject to verification.

I have selected the following topics, which could advance the explanation of the origin of the eremoneuran male terminalia:

- recognition of muscular connections of the *Platypezidae* and other primitive *Cyclorrhapha*.
- explanation, if sclerites attached to the epandrium in the *Empididae* are gonostyli (ninth segment), or cerci (part of proctiger).
- reconstruction of the male hypopygial ontogeny in members of primitive *Brachycera*.
- studies on muscle connections in the epandrial complex of *Apsilocephalidae*.

While preparing this paper, my intention was three-fold: first, to expose the weak bases of the commonly accepted surstylar hypotheses, as well as the secondary

origin of epandrium in periandrial hypothesis; second, to introduce some order in the discussion on the origin of eremoneuran male terminalia; third, to suggest criteria, which could falsify the existing hypotheses, and finally to select a better one. If the article contributes to these questions in any way, the objective of my work will be fulfilled.

11. ACKNOWLEDGMENTS

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