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On the Evolution of the Genitalia in Male Insects.

Særtryk af Ent. Medd. XXVIII 1957

On the Evolution of the Genitalia in Male Insects.

By
Anker Nielsen.

In male insects the copulatory apparatus typically consists of an intromittent organ, the phallus, often carrying a pair of appendages, the parameres, and surrounded by various periphallic structures. The phallus arises from a depression, the genital chamber, on the posterior end of segment IX (the genital segment). The genital chamber is roofed over by the small segments X and XI. The periphallic organs comprise a pair of gonopods, more or less firmly articulated to the posterior border of the sternal region of segment IX, and various appendages on segments X (socii) and XI (epiproct and paraprocts). Rarely, if ever, all these structures are present in the same insect. On the other hand, accessory copulatory structures may be formed of processes from segment IX and sometimes also from some of the pregenital segments. In the present paper the phallus and the gonopods only will be discussed.

As to the morphological value of these structures opinions have varied considerably. A current view is that the gonopods are true limbs of segment IX, whereas the phallus is a secondary development of the ventral intersegmental membrane between segments IX and X. It has, however, been claimed that the phallus is formed of parts of the limbs of segment IX (Klapálek 1904), or of the limbs of segment X (Sharif 1937, Else 1934, Qadri 1940). But an entirely contrary opinion has also been put forward, namely that the phallus is a secondary outgrowth from the intersegmental membrane, and that the gonopods are differentiations of this outgrowth, and thus have nothing to do with abdominal limbs. In re-

cent years the latter view seems to have gained ground (Crampton 1942, p. 85; Snodgrass 1941, pp. 9—10, and 1946, p. 52).

The starting point for the considerations below is a study of the male genitalia of Trichoptera carried out by the author on the initiation of Dr. S. L. Tuxen, Copenhagen, in order to include a summary of the results in his book: Taxonomist's Glossary of Genitalia; a detailed account of this study will be published elsewhere. The original condition in Trichoptera (fig. 1) is that the phallus is divided into a proximal, membranous phallobase (5) and a distal, more or less sclerotized ædeagus (6). The latter arises from a depression, the endotheca, on the distal end of the phallobase. It is flanked by a pair of parameres (7; titillators of most trichopterists). The phallobase is lowered into a tubular phallocrypt (4), the anterior part of which has fused with the proximal end of the phallobase to form a sclerotic phallic apodeme (3). The gonopods are divided into two joints: the coxopodite (8) and the harpago (9). The two coxopodites (right and left) are united by a basal plate (11). The relations between this and the phallocrypt vary. In some cases (shown in fig. 1 A) it lies ventrally in the entrance of the phallocrypt, in others (shown in fig. 1 B) it lies in a special pocket below the entrance to the phallocrypt. In some Trichoptera the coxopodite is divided into a dorsal and a ventral branch, the latter carrying the harpago. Comparative studies indicate that this condition is the primitive one within the order. (In order not to complicate the drawing too much, it is not shown in fig. 1).

The gonopod has an intrinsic flexor muscle originating in the coxopodite and inserted medio-proximally in the harpago. There are four pairs of extrinsic muscles: two pairs (13 and 14) originate orally, two pairs (15 and 16) anally in segment IX. (In most Trichoptera the ven-

tral anterior muscles actually fuse to an unpaired muscle). The anterior muscles are inserted on the coxopodite itself, the posterior on the basal plate. The phallus has intrinsic muscles (retractors of the ædeagus, originating in the phallic apodeme) and two pairs of extrinsic muscles: an anterior (13a) and a posterior pair (15a). The two extrinsic phallic muscles appear, so to speak, as twins of the anterior and the posterior dorsal muscle of

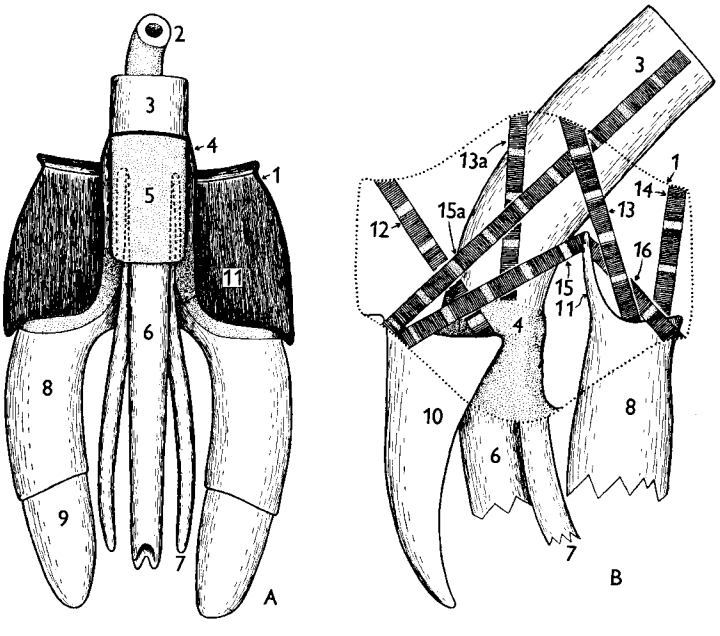


Fig. 1. Trichoptera; diagrams. A: Gonopods and phallus, dorsal view. B: Showing musculature of gonopods and phallus, lateral (right) view. (Actually the muscles are several times thicker than shown). 1: in A cut edge, in B outline of segment IX. 2: ejaculatory duct. 3: phallic apodeme. 4: in B phallocrypt, in A cut edge of same. 5: phallobase. 6: ædeagus. 7: paramere. 8: coxopodite of gonopod. 9: harpago. 10: segment X. 11: basal plate of gonopods. 12: intersegmental dorsal muscle IX/X. 13: anterior dorsal m. of gonopod. 13a: anterior phallic m. 14: anterior ventral m. of gonopod. 15: posterior dorsal m. of gonopod. 15a: posterior phallic m. 16: posterior ventral m. of gonopod.

the gonopod, resp., and thus may be interpreted as portions of these muscles. This is especially obvious as regards the posterior phallic muscle (15a), which originates immediately above the posterior dorsal muscle of the gonopod (15). Furthermore, in some Trichoptera the anterior ventral muscle of the gonopod (14) looses its connection with the gonopod and becomes transformed into a phallic muscle, and in others the same is the case with the posterior ventral muscle (16). This means that the gonopods and the phallus have a musculature in common, and this again indicates that these organs have a common origin. As shall be shown below, the development of the gonopods and the phallus during metamorphosis corroborates this view. The musculature of the gonopods and the phallus agrees exactly with the musculature of the typical arthropod limb. This musculature comprises four muscles (or four groups of muscles): anterior and posterior dorsals, and anterior and posterior ventrals. (The anterior dorsal muscle of the gonopod has a latero-ventral origin, it is true, but much weight cannot be attributed to this, since segment IX is synscleritous). The musculature thus gives evidence that the gonopods really are the limbs of segment IX, and that the phallus is composed of parts of these limbs, or that it contains parts of the limbs. (The extrinsic muscles of the phallus are inserted on the phallic apodeme or the phallocrypt. Also in the former case they are, strictly spoken, inserted on the phallocrypt. This must be considered as an inverted part of the phallobase).

Gonopods which, no doubt, are homologous with those of Trichoptera in Endopterygota are found in the Mecoptera and the lower Diptera. In the Mecoptera the two coxopodites are united basally, though sometimes by membrane only (Crampton 1931). In *Panorpa* the coxopodites, though distinctly delimited, are sclerotically continuous with segment IX. The harpago is moved by a

flexor and an extensor muscle originating in the coxopodite (Grell 1942). In some Nematocera the coxopodite has fused with the sternal part of segment IX, the harpagones thus appearing as appendages of segment IX. In the Brachycera this condition is prevailing. In the Cyclorrhapha, finally, the harpagones are reduced. The appendages ("surstyli" and "cerci") flanking the entrance to the genital chamber cannot be considered as gonopods (Crampton 1942).

In the Megaloptera and the Neuroptera the gonopods are much complicated, and from the point of view of comparative morphology they are very poorly known. The best account is given by Tjeder (1954). In the Raphidioidea true coxopodites seem to be present, in the Raphidiidæ provided with small, stylus-like harpogones. In the Coniopterygidæ the coxopodites have united into an unpaired plate ("the hypandrium") behind the sternal region of segment IX. In the other forms they have fused completely with segment IX.

In the Lepidoptera the sclerotization of segment IX is divided into a dorsal and a ventral part ("tegumen" and "vinculum", resp.). There is a pair of large, plate-like "valvæ", articulating dorsally with the "tegumen", ventrally partly with each other, partly with an unpaired plate (the "juxta") lying in the floor of the genital chamber. The bases of the "valvæ" are overlapped by the posterior border of the vinculum. "In some of the lower Lepidoptera (e. g. Hepialidæ) the valvæ are wholly attached to the juxta" (Beirne 1942). The "valvæ" are moved by three pairs of muscles (Forbes 1939); two extensors originate on the "tegumen" and the "vinculum", resp., one flexor on the "juxta". Phallus has an anterior and a posterior muscle. On the median side of the "valva" there are, in most Lepidoptera, a small appendage (the "harpe"), movable by a flexor muscle originating in the "valva". The genital musculature practically is identical

with that of the Trichoptera. Two differences may be noted. 1: The posterior dorsal muscle is lacking. The same is the case in some Trichoptera. 2: The phallic muscles originate in the "vinculum". The division in "tegumen" and "vinculum", however, probably is secondary, since it is very unlikely that so generalized a feature as a primary division of segment IX into tergum and sternum should occur in the Lepidoptera. There is, therefore, good evidence that the "valvæ" are homologous with the coxopodites in Trichoptera, and the "harpes" with the harpagones. As mentioned above the posterior ventral muscle in the Lepidoptera originates on the "juxta". In a great many Trichoptera it stretches between the basal plate and the lateral proximal edge of the coxopodite. The "juxta" thus is homologous with the basal plate in the Trichoptera. In *Bombyx mori* the "juxta" has fused with the "valvæ" (Forbes 1939).

In the Aphaniptera (Snodgrass 1946) segment IX has a tergum and a sternum (fig. 2 C). The external parts are very short, but the tergum has a large apodemal part (t IXa). Laterally the posterior edge of the tergum is produced into a pair of wings, the "claspers" (1), each carrying a "finger" (2), movable by muscles originating in the "clasper" or in tergum IX. The position of the finger varies from subdistally on the inferior edge to proximally on the median side. In the latter case there may be an extra, more dorsal "finger" (without muscles?). The "clasper" possibly is homologous with the coxopodite in the Trichoptera, the "finger" with the harpago. One thing might seem inconsistent with this theory: the "clasper" is associated with the tergum instead of the sternum. It is, however, highly probable that the division into tergum and sternum is secondary in the Aphaniptera.

In two orders of Endopterygota, viz. the Hymenoptera and the Coleoptera, the existence of gonopods gene-

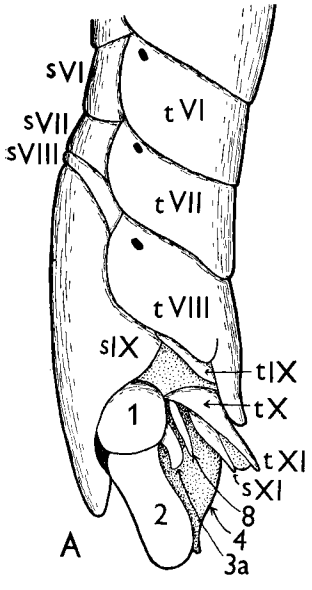
rally has been disputed by those who consider the gonopods of Mecoptera etc. as true limbs.

In the Coleoptera (Verhoeff 1893, 1895) the copulatory apparatus (fig. 2 D) in the state of repose is concealed due to the reduction of segments IX—XI and their withdrawal into the preceding segments. (In some cases segment VIII also is concealed by segment VII). It consists of a phallus (5, 6) flanked by a pair of "parameres" (1, 2). The latter may to a greater or less extent fuse and thus form a tube around the phallus. In some forms the "paramere" is divided into a proximal (1) and a distal joint (2), and at least in the Coccinellidæ the latter is movable by a muscle originating in the proximal joint. In *Hyphydrus ferrugineus*, in which the paramere of the imago shows no signs of a bipartition, it temporarily is divided into two joints during the pupal stage (Heberdey 1928, p. 545). This indicates that the two-jointed condition is the primitive one, and this again indicates that the "parameres" are homologous with the gonopods of the Trichoptera. Further evidence for this point of view is given by the development of the copulatory apparatus (see below). The extrinsic muscles of the copulatory apparatus originate in segment IX or the remnants of this segment (Verhoeff 1893). In some few cases the parameres seem to be entirely reduced (Metcalf 1932).

In the Hymenoptera (Snodgrass 1941) the copulatory apparatus (fig. 2 B) consists of a common basal piece, the "caulis", and a tripartite distal part. Proximally on the caulis a, sometimes incomplete, "basal ring" or "cardo" (1a) is seen. More distally there are lateral "parameral plates" (1) and a pair of medio-ventral "volsellar plates" (3). The former are produced into a pair of valve-like "parameres" (2), the lateral elements of the tripartite distal part of the copulatory apparatus. The "volsellar plate" carries a small movable appendage, the "digitus" (3a), which together with an immovable process, the

"cuspis" (3b), form a pair of pincers. Between the "parameres" the distal part of the phallus is seen. The proximal part is included in the "caulis". In some forms, especially among the Symphyta, the paramere is divided into a proximal (1) and a distal joint (2). The latter is movable by flexor and extensor muscles originating in the proximal joint. This gives the "parameres" a great resemblance to the gonopods in Mecoptera and Trichoptera, and hence I consider the "parameres" as gonopods. In the Tenthredinidæ (fig. 2A), in which the parameres have similar relations to the large sternum IX as have the gonopods of the Trichoptera, the immediate likeness also is great. In the higher Apocrita there is an increasing tendency for the posterior segments to become reduced and, together with the copulatory apparatus, withdrawn into the preceding segments. This makes the similarity less obvious. The "cardo" possibly may be regarded as a secondary division of the proximal joint of the "paramere", analogous with the trochantin in the thoracic limbs. In forms with an especially well developed "cardo", it may resemble a segment. In the higher forms it is reduced (Zander 1900). The copulatory apparatus has a much complicated intrinsic

Fig. 2. A: Posterior end of *Pteronidea ribesi* ♂ (Tenthredinidæ); lateral (left) view. (Redrawn from Snodgrass 1941). B: diagram of copulatory apparatus of Hymenoptera, ventral view. (Based upon Snodgrass 1941). C: Genitalia and postgenital segments of an Aphanipteron ♂; lateral (left) view. (Redrawn from Snodgrass 1946. The highly complicated "endophallus" has been omitted). D: diagram of copulatory apparatus of Coleoptera; ventral (or dorsal) view. (Based upon Verhoeff 1893). VI—XI: abdominal segments VI—XI; s sternum, t tergum. (tIXa in C: apodemal part of tergum IX; tXI: epiproct; sXI: paraproct). 1: coxopodite of gonopod. 2: harpago. 3: in B "volsella", in C "ædeagal hook". 3a: "digitus"; (when this in A is seen above the "paramere", it is due to a torsion of 180° of the copulatory apparatus taking place in many Tenthredinidæ). 3b: "cuspis". 4: phallus. 5: phallobase. 6: ædeagus. 7: phallic apodeme. 8: socius (passively movable appendage on segment X).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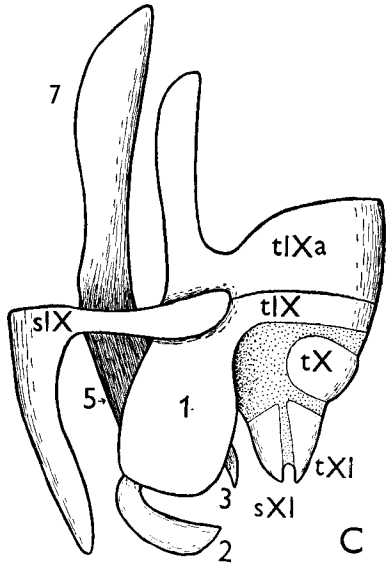
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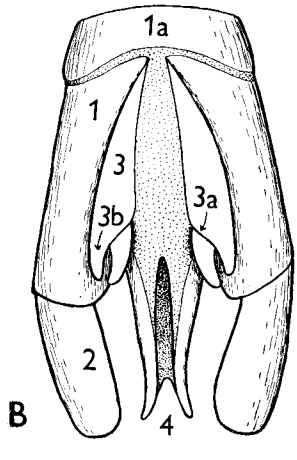
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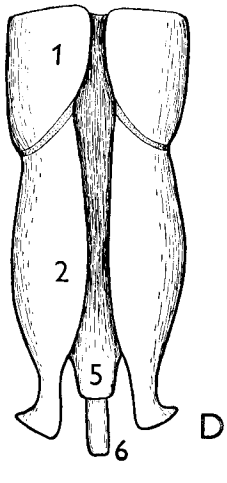
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musculature. The comparatively few extrinsic muscles originate in sternum IX (Snodgrass).

What is known about the development of the external genitalia in the Endepterygota supports the views advanced on the preceding pages. 1: That the gonopods in Mecoptera, Trichoptera and primitive Diptera are homologous with the "valvæ" + "harpes" in Lepidoptera, the "claspers" + "fingers" in Aphaniptera, and the "parameres" in Coleoptera and Hymenoptera. 2: That the endopterygotan phallus is formed by parts of, or include parts of, the gonopods.

During metamorphosis the first rudiments of these structures appear in an unpaired peripodial cavity ("Herold's pouch"), anally on the ventral side of abdominal segment IX of the larva as a pair of small processes (Primitivzapfen, Zander). Each process later on is divided into two by a sagittal cleft. The two median processes fuse to form the phallus; the laterals give rise to the gonopods. This development has been described in the Trichoptera (Zander 1901), Lepidoptera (*Paraponyx*, Zander 1903; *Solenobia*, Florin 1945), Coleoptera (*Sitodrepa*, Metcalf 1932a), Hymenoptera (Zander 1900) and Nematocera (Christophers 1922). A little different process of formation has been described in the Coleoptera by Kershner (1913) and Heberdey (1928), and in the Lepidoptera by Mehta (1933): In *Tenebrio* and *Hyphydrus* (Coleoptera) the lateral pair of processes is first formed, and the median processes (the rudiments of the phallus) later on arise by a sort of proliferation basally on the median sides of the lateral processes. This mode of formation may be regarded as a minor variation of that first described. In *Hepialus, Earias, Bombyx* and *Pieris* (Lepidoptera) there are formed two pairs of processes at the very beginning. Nor can this be considered as an important variation, since both pairs of processes are formed

in close proximity, and probably from the same imaginal disc. A considerably diverging mode of formation has been described in the Aphaniptera by Sharif (1937): The phallus is formed in one peripodial cavity by a pair of processes, which later on are divided into two pairs. The two median processes fuse to form the phallus, whereas the "parameres" are developed from the two laterals. The gonopods ("subgenital plates") are formed in another peripodial cavity. According to Snodgrass (1946), however, Sharif's "parameres" are the rudiments of the "claspers" + "fingers", and his "subgenital plates" are secondary processes on the sternal region of segment IX, structures of great functional, but little morphological significance. It means that the formation of the gonopods and the phallus in the Aphaniptera thus is exactly the same as in the Trichoptera etc.

It thus may be concluded that if the gonopods really are the limbs of segment IX (and their musculature in the Trichoptera and Lepidoptera gives evidence for this assumption), then the endopterygotan phallus is formed by parts of, or contains parts of, these limbs. The question now is how the gonopore has acquired this relation to the limbs of segment IX.

There is an overwhelming evidence that the genital ducts of male insects originally discharged through paired openings on venter X, medially to the limbs of this segment; both from embryology (Heymons, Wheeler, a. o.) and from morphology (the relations between the cercal nerve and the vas deferens; Snodgrass 1936 and 1937, p. 96; Brinck 1956, pp. 98—99).

In the Machilidæ (fig. 3 A) the posterior edge of abdominal sterna I—IX are produced into backward directed, more or less pronouncedly bilobed plates (c), which — no doubt justly — have been regarded as abdominal limbs. On segments II—IX they carry, laterally on the

posterior border, movable styli (2), probably homodynamous with corresponding structures on the meso- and metathoracic coxæ (though the latter lack muscles). Styli are found also on the coxæ of the Symphyla. On segments II—VII one or two pairs of thin-walled, eversible sacs (1) generally are found medially to the styli. Such sacs occur also on the coxæ of some Diplopoda and Symphyla and even in the Onychophora (Lawrence 1953). It thus may be justified to consider the posterior sternal lobes in the Machilidæ as coxopodites, and to designate the whole sternal structure a coxosternum. Faint impressed lines demarcate a small medio-oral part of the coxosternum. Snodgrass considers this triangular part as the true sternum (eusternum). Another faint furrow, stretching in the median line of the body from the apex of the triangle to the bottom of the anal indentation, probably indicates the line of union between the two coxopodites. The muscles of the styli and of the eversible sacs originate in the coxopodite, which again may be moved by muscles originating in the tergum.

From the following it will appear (I hope) that there is good reason to believe that the coxopodites and the styli of segment IX in the Machilidæ are homologous with the coxopodites and the harpagones, resp., of the gonopods in the Endopterygota.

On segment IX the posterior, V-shaped, indentation is very deep, almost reaching the anterior border of the segment. The two coxopodites slope much towards the indentation. From the anterior end of the membranous area between the coxopodites an unpaired phallus arises. Between its base and the posterior end of segment X a fold is seen, which on the ventral side continues the posterior edge of tergum IX. The phallus thus might make the impression to arise from venter IX. Since, however, the proximal end of the membranous upper side of the coxopodites certainly must be considered as

the posterior border of segment IX, and since no muscles are attached to the fold mentioned, it probably is a secondary structure of no morphological value. Hence, the phallus arises from the anterior end of the elongated, membranous venter X.

In (most) Machilidæ a pair of gonapophyses arises proximally and medio-dorsally on the coxopodites of segment IX. In the species figured they take the shape of lanceolate plates (3) covering the proximal part of the phallus ventrally. They are movable by muscles originating in the coxopodite (Snodgrass 1936). (In the ♀ there is a pair of gonapophyses on segment VIII also; the two pairs together form a long ovipositor. In some machilids the ♂ has rudimentary gonapophyses on segment VIII).

In the Lepismatidæ the pregenital segments are more like those of the Pterygota, and styli generally are confined to some of the posterior segments. Segment IX, however, is built as in the Machilidæ, though the male gonapophyses are rudimentary in many genera. As to the phallus see below.

Verhoeff (1896) considers the gonapophyses as telopodites, and by Gustafson (1950) they are regarded homodynamous with the eversible sacs of the preceding segments (there are never eversible sacs on segments VIII and IX). The gonapophyses may be telopodites, or they may be homodynamous with the eversible sacs; but it must be considered certain that the eversible sacs are not telopodites, since they are present in some Diplopoda and Symphyla together with typical telopodites.

In the ontogeny of the Thysanura the unpaired phallus is formed by fusion of a pair of processes (Qadri 1940). In *Lepisma* it is a slightly bilobed structure with a pair of gonopores (Gustafson 1950, p. 47). In the Machilidæ the gonopore is unpaired. It seems justified to regard the thysanuran phallus as arisen by fusion of the limbs of segment X, shifted forwards on the membra-

nous venter. Originally the two genital ducts opened at the bases of these limbs. Through the formation of a gutter on the median side of the limbs, and the subsequent closure of these gutter, each limb became penetrated by an ectodermal ejaculatory duct. By fusion of the limbs an unpaired phallus arose with two ectodermal ducts (*Lepisma*), which later on united to an unpaired duct (Machilidæ; cp. below: Dermaptera).

In the Ephemeroptera (Snodgrass 1936) segment IX shows a condition which in some respects is even more primitive than in the Thysanura (fig. 3 B). The posterior edge of sternum IX generally carries an unpaired plate (c), movable by muscles originating on the sternum. This plate possibly represents the united coxopodites. In a few forms the two coxopodites are separate, in some others they are united at their bases only (Walker 1922. On the other hand, the unpaired coxal plate may fuse with the sternum). Laterally and distally the coxal plate carries a pair of jointed appendages (2), movable by muscles originating on the coxal plate. It is the secondarily jointed styli; (in *Cœnis* they are unjointed). Medially to the styli a pair of, often rather complicated, appendages (4) are seen, the bases of which are concealed by the coxal plate. It is the paired phalli. Sometimes they are united basally, but the gonopore always is paired. The ejaculatory duct generally penetrates the whole phallus, but in some forms, e. g. *Ephemera,* the gonopore is on the base of the phallus (Qadri 1940), which must be considered as a more primitive condition. The phalli are carried by a paired or unpaired sclerotic bridge, which is situated between the dorsal base of the coxal plate and the paraprocts (s XI), and the lateral end of which is intercalated between the posterior corner of tergum IX and the anterior corner of tergum X. It seems justified to consider the phalli as the limbs of segment X (as does Qadri). Or, at least, they contain these limbs

(see below). The sclerotic bridge mentioned possibly is a part of the phallus. In younger nymphal instars the two phalli are widely separated; later on they approach each other in the median line. It will be seen that venter X (contrary to conditions in the Thysanura) is much reduced in length. By the mutual approach of the two phalli it is reduced in width also, and eventually entirely obliterated as an external structure. It is probable that a part of the ectodermal ejaculatory ducts is formed by venter X. Structures corresponding to the gonapophyses of the Thysanura are not seen. However, Snodgrass pictures in *Ephemera simulans* a muscle originating on sternum IX and inserted on the sclerotic bridge laterally to the phallus proper, and Levy (1948) describes in *Siphlurus* a similar muscle which is inserted dorsolaterally in the phallus. (In the vast majority of Ephemeroptera the phallus has no extrinsic muscles). This indicates that in the Ephemeroptera the gonapophysis of segment IX has fused with the limb of segment X, the phallus thus being a composite structure. (Cp. below: Dermaptera). The slightly bilobed shape of each phallus exhibited by *Ephemera simulans* may be a reminescence of the double origin.

Plecoptera (Snodgrass 1936, Qadri 1940, Brinck 1956). Coxopodites and styli are lacking, but in most forms sternum IX is produced posteriorly as a subgenital plate, which may represent the fused coxopodites, though it is entirely continuous with the anterior part of the sternum. The genital ducts open into a "genital cavity" (Brinck) above this plate. (In the Leuctridæ the genital cavity is poorly developed, and in the Nemuridæ it is entirely lacking). Paired gonopores are found in some (not all) Perlodidæ and Perlidæ (Brinck), but in most Plecoptera the gonopore is unpaired. In *Isoperla* Bks. (= *Chloroperla* Newm.) the two gonopores are flanked by a pair of lobes, and perhaps there is a rudiment of an unpaired

dorsal lobe ("penial armature", Brinck). In *Diura* Billberg and *Perlodes* Bks. three lobes are seen, a pair of laterals and an unpaired one. In *Diura* the latter is ventral, in *Perlodes* dorsal in position. It is obvious that the unpaired lobe cannot be homologous in the two genera. A probable inference is that originally there were two pairs of lobes, representing the gonapophysis of segment IX and the limbs of segment X, resp. In *Diura* the former, in *Perlodes* the latter have fused into an unpaired lobe. In other Perlodidæ and Perlidæ and in the Tæniopterygidæ all lobes have united to form a very short phallus. In the families mentioned above the phallic structures, no doubt, have been subjected to some reduction. The functional copulatory organ is formed chiefly by eversion of the genital cavity and — in forms with unpaired gonopore — of the posterior part of the ejaculatory duct. In the Leuctridæ, Capniidæ and Nemuridæ the phallic lobes are very much reduced and the sperma is transferred to the ♀ by secondary "sperm conveyors". In the first mentioned family the conveyor is a pair of spear-like valves ("specillum"; Brinck, p. 85), which possibly represents parts of the paraprocts. In the Capniidæ and Nemuridæ the epiproct acts as conveyor. In the former family a sclerotic process ("fusion plate", Brinck) from the dorsal wall of the genital cavity also play a rôle; it may perhaps represent an unpaired dorsal phallic lobe.

Dermaptera (Walker 1922, Snodgrass 1936). Neither coxopodites nor styli are seen, but probably it is justified to suppose that the coxopodites have fused with sternum IX (as it has in most Orthoptera), which is much larger than the preceeding sterna and forms a subgenital plate. The phallic organs are concealed above this plate. They arise from a short area between segment IX and the paraprocts. In the Labiduroidea (fig. 3 D) there is a pair of phalli, closely approached in the median line.

Each consists of a membranous shaft and two distal branches. The median, membranous branch carries distally the gonopore. The lateral branch (the paramere) is sclerotized. The paired, ectodermal ejaculatory ducts are very long and anastomose anteriorly for some distance. In *Hemimerus* the two median phallic branches have fused, but there are still two gonopores. In the Forficuloidea (fig. 3 E) the phallus superficially resembles that of *Hemimerus,* but the condition has arisen by a suppression of the median branch of the left phallus (Qadri 1940), and likewise the left ejaculatory duct beyond the anastomosis has atrophied. In the Forficuloidea, also, the first rudiments of the phallic organs are paired, and in younger nymphal instars the two rudiments are widely separated (Qadri 1940). By their approachal the short venter X is obliterated as an external structure. It probably is represented by parts of the ejaculatory ducts. To me it seems a reasonable assumption that the phallic organs of the Dermaptera have arisen by fusion of the gonapophyses of segment IX and the limbs of segment X, the parameres representing the distal parts of the former. The union of the two structures, belonging to two different segments, has been made possible by the reduction of venter X.

It will be seen that in the Thysanura, Ephemeroptera and Dermaptera there is no structure which may be regarded as sternum X (as to the Plecoptera: see below). In the Thysanura venter X is large, but entirely membranous. In the Ephemeroptera and the Dermaptera it has been obliterated as an external structure. Nor is there any true sternum X in other insects. What sometimes has been regarded as such a one is the united anterior ends of the paraprocts. In cases where there is a membranous ventral region corresponding in position to tergum X, it possibly is due to a reduction of the anterior parts of the paraprocts. A synscleritous "seg-

ment X", which is seen in some forms (e. g. some Plecoptera), may have arisen by union of a secondary sclerotization in this region with tergum X.

In all insects, apart from the four orders mentioned, there is an unpaired gonopore leading into a long unpaired ectodermal ejaculatory duct, in the anterior end of which the paired genital ducts open. Since no external region rightly can be considered as venter X, and since the ejaculatory duct is innervated from abdominal ganglion X (Snodgrass 1936, 1937), it seems reasonable to assume that the ejaculatory duct represents the invaginated venter X. It is of course impossible to say whether venter X originally has evolved as an unpaired invagination, carrying the paired, primary gonopores in the deep, or it has evolved as paired invaginations, which later on have united. Some things speak in favour of the latter possibility: As mentioned above there is an anastomosis between the two ejaculatory ducts in the Dermaptera, and the same is the case in the Ephemeropteron *Hexagenia* (Levy 1948). Conditions in the Plecoptera also point in this direction. In the Pterygota (apart from Ephemeroptera and Dermaptera) the ejaculatory ducts probably never have penetrated the limbs of segment X.

Orthoptera (Walker 1922, Snodgrass 1937). In the Grylloblattidæ (fig. 3 C), only, a condition is found like

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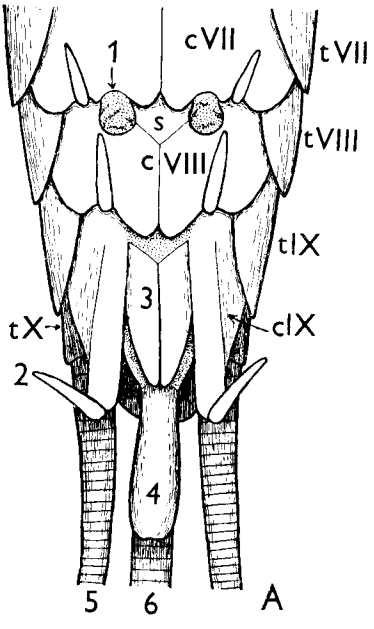
Fig. 3. A: Posterior end of *Petrobius brevistylis* Carp. ♂ (Machilidæ); ventral view. B: Same of *Ephemera simulans* ♂. C: Same of *Galloisiana nipponensis* Caudell & King ♂ (Grylloblattidæ). D: Diagram of phallic organs of Labiduroidea. E: Same of Forficuloidea. (B redrawn from Snodgrass 1936, D and E from Walker 1922). VII—XI: abdominal segments VII—XI; c coxopodite, s sternum, t tergum, sXI paraproct, tXI epiproct. 1: eversible sac (on segments II—VI there are two pairs in this form). 2: stylus (in *Petrobius* the styli are directed downwards, forwards and outwards, and hence are seen much fore-shortened). 3: gonapophysis of segment IX; (in D and E: paramere). 4: phallus. 5: cercus. 6: "terminal filum" (annulated process of the epiproct).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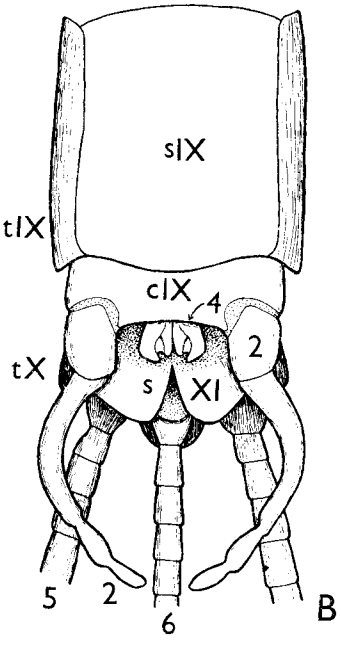
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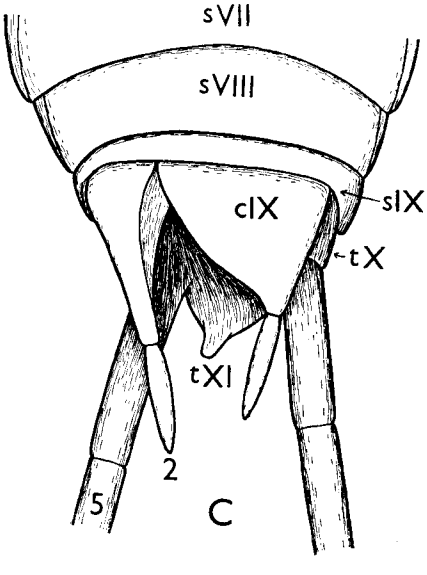
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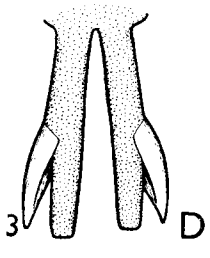
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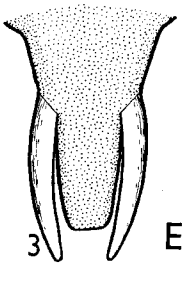
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that in the Thysanura: segment IX is provided with well developed coxopodites (c IX), carrying styli (2) and movable by a pair of muscles originating on the tergum. The coxopodites even are better developed, separated from the sternum by true articulations, but the styli are not musculated. In the other Orthoptera the coxopodites possibly have fused with the sternum. This appears from the facts that the posterior edge of the large sternum IX in the Blattidæ and most Tettigoniidæ carries a pair of (non-musculated) styli, and the posterior edge of the sternum is bilobed in younger nymphs of the Tettigoniidæ and the Acridiidæ (Qadri 1940). In the Phasmidæ the sternum is divided into an oral and an anal plate (Walker, Snodgrass). The latter, which forms a subgenital plate, may represent fused coxopodites. The phallic structures in the Orthoptera consist of a various number of, often much complicated and asymmetric, "phallomeres". These sometimes fuse to a greater or less extent to a sort of phallus, which serves as a mould for the spermatophore. A true copulatory organ probably never is formed. In all cases the first rudiments are one pair of lobes (Qadri 1940), and this number is retained in the Grylloblattidæ. Else (1934) thinks that these lobes are the limbs of segment X, whereas Roonwal (1937) claims that they are formed by fusion of the limbs of segment IX and X. Since there has been disposed of the coxopodites IX in another way (see above), "limbs of segment IX" in this connection must mean the gonaphyses. In favour of Roonwal speaks the fact that the phallomeres in the Mantidæ and the Tettigoniidæ receive muscles both from sternum IX and from tergum X. (In the other families — as far as is known — only from sternum IX). Hence, I am inclined to join Roonwal's view (as modified above), though he does not give much positive evidence.

In the Isoptera and the Embioptera both coxopodites and phallic structures are lacking, but in the former

order the posterior edge of sternum IX may carry a pair of styli without muscles (Walker 1922, Snodgrass 1937), which indicates that the coxopodites have fused with the sternum.

Hemiptera Heteroptera (Pruthi 1925a, Ludwig 1926, Larsén 1938, Bonhag & Wick 1953). Segment IX forms the so-called genital capsule, which in some families is withdrawn into the preceding segments. The genital capsule is an annular sclerotization with a very long ventral side and an extremely short dorsal side, so that the entrance to the large genital chamber opens upwards or (Gerrididæ) obliquely upwards and backwards. Between the dorsal side of the genital capsule and the much reduced segment X a small plate is seen. It is generally regarded as tergum IX. Since, however, it has no connection with the musculature, it probably is merely a secondary sclerotization. On the edge of the entrance to the genital chamber a pair of one-jointed "genital hooks" or "gonostyli" is found. The phallus, more often entirely concealed within the genital chamber, may assume a much complicated shape. Typically it is divided into a phallobase ("phallosoma" + "conjunctiva", Pruthi; "phallosoma" + "Schwellkörper", Larsén) and an ædeagus ("vesica", Pruthi; "flagellum", Larsén). The latter may reach an enormous length, and then is wound up spirally in the state of repose. Bonhag & Wick have described the genital musculature of *Oncopeltus* (Lygæidæ). There are six pairs of strong muscles, three inserted into the "genital hooks", the three others into the phallus. The musculature has some similarity to that of the Trichoptera. During ontogenetic development the phallus and the "genital hooks" are formed by the same rudiment. Hence, it is reasonable to assume that the "genital hooks" represent the coxopodites (the styli having been lost), and the gonapophyses form the phallus or a part of the phallus.

Hemiptera Homoptera. In the Aleyrodidæ (Weber 1930, fig. 230) and especially in the Psyllidæ (l. c., fig. 229) segment IX has a considerable resemblance to that of Heteroptera. On the edge of the entrance to the genital chamber there is a pair of appendages, movable by muscles originating in segment IX. The phallus is undivided as in other Homoptera. Its muscles take their origin partly in segment IX, partly in segment X. The latter indicates that the limbs of segment X take part in the formation of the phallus.

In most Auchenorhyncha (Pruthi 1925b, George 1928, Metcalf 1932b) the ventral part of segment IX is shorter, but carries a pair of large processes ("subgenital plates"), sometimes delimited by distinct articulations. In the Cicadidæ they are lacking, but in return the ventral portion of the segment is of considerable length. The undivided phallus proximally carries a pair of appendages or processes, the parameres. Possibly the "subgenital plates" (by Weber called "parameres") are homologous with the genital hooks in the Heteroptera, though — contrary to conditions in the latter suborder — the "subgenital plates" and the phallus (with the parameres) are stated to develop from two separate pairs of rudiments. It seems, however, that the youngest nymphal instars have not been studied, which means that the ontogeny of the organs in question is imperfectly known.

Mallophaga (Schmutz 1955). In the Amblycera the phallus is divided into a phallobase, carrying a pair of parameres, and an extremely complicated ædeagus. In the Ischnocera the ædeagus is reduced. In the Anoplura (Mjöberg 1910, Nuttall 1917) the copulatory apparatus consists of a mighty phallobase and a small ædeagus. Structures ("lateral spurs on dilator", Nuttall) which may be considered as parameres are also present.

To me it appears most likely that the parameres in the two last mentioned orders represent the gonapophy-

ses of segment IX, and that the coxopodites have fused entirely with sternum IX as in most Orthoptera.

In the Odonata every trace of phallic structures is lacking. The unpaired gonopore is situated on a membranous area and is flanked by a pair of small sclerotic plates. In the nymphs of some Zygoptera these plates carry vestigial styli (Walker 1922), indicating that they are to be considered as coxopodites. The gonopore and the plates are situated on a membranous area anteriorly to the middle of what might be considered as sternum IX. The sclerotic bridge behind the genital area, however, probably is a secundary sclerotization in the intersegmental membrane between the coxopodites of segment IX and the synscleritous "segment X" (cp. above p. 43).

As already mentioned the phallus of the Trichoptera is divided into a phallobase and an ædeagus. The same division is found in the Coleoptera and the Aphaniptera. In the former order the ædeagus ("virga", Verhoeff 1893) is slender and sometimes spiral. In the latter it is very short. In the Lepidoptera (in which the phallus is lowered into a phallocrypt as in the Trichoptera) and in the Hymenoptera the ædeagus is reduced and functionally replaced by the eversible endotheca ("vesica" in Lepidoptera; "endophallus" in Hymenoptera, Snodgrass 1941). This condition is found also in many Trichoptera. In the Lepidoptera the phallocrypt is very deep. Its entrance is surrounded by a short, generally membranous, tubular projection (the "anellus"), on the ventral side of which the "juxta" is situated, and the edge of which is often produced into a pair of "anellus lobes". Beirne (1942) consider the "anellus" as the phallobase, the "anellus lobes" as parameres, and the copulatory organ s. str. as the ædeagus. The musculature (Forbes 1939), however, does not conform with this idea. The phallic muscles

are inserted into Beirne's "ædeagus", showing that it actually is the phallobase.

Structures homologous with the parameres of Trichoptera probably are the "volsella" in Hymenoptera (fig. 2 B, 3) and the "crochets" or "ædeagal hooks" in Aphaniptera (fig. 2 C, 3). In the Lepidoptera and the Coleoptera parameres (in this sense of the word) are lacking — and the same is actually the case in most Trichoptera.

A condition which I think is representative of primeval Endopterygota is found in the Mecoptera. Grell (1942) has given an excellent description of the genital apparatus in *Panorpa communis* L. As in other members of the order there is no true phallus, but the opening of the ejaculatory duct, situated on the dorsal wall of the genital chamber, is flanked by three pairs of longitudinal folds. The lateral pair is the most complicated and covers the two other pairs. The two median folds (right and left) have fused partly, and a part of the cavity thus formed has developed into a sperm pump. Conditions in *Panorpa*, however, no doubt are specialized. The original condition in the Mecoptera (Crampton 1931) is that the opening of the ejaculatory duct is flanked by two pairs of processes ("dorsal" and "ventral valves"). The former (fig. 4, 5) have also a median position, the latter (3 and 4) have unmistakable relations to the coxopodites (1). In most Mecoptera the "ventral valve" is divided into two branches, ("upper" and "lower valve"; 4 and 3, resp. Cp. the three pairs of folds in *Panorpa*). In the Bittacidæ the "lower valves" are much lengthened and mutually apposed to form a "penis filum". In *Panorpodes* all processes appear to have fused to a "penis". In *Boreus* the processes are very much reduced and inverted into a tubular pocket. Through eversion of this pocket a long, membranous "penis" may be formed.

To me it appears to be a plausible theory to assume that the phallobase of the higher Endopterygota have

evolved by fusion of the proximal parts of all processes in the Mecoptera, and that the ædeagus is formed by fusion of the distal parts of the two "dorsal valves". The distal parts of the "ventral valves" then form the parameres.

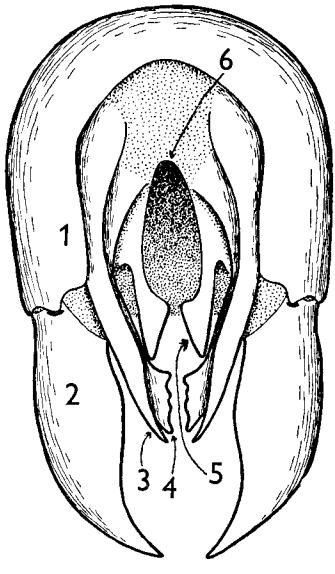

Fig. 4. Gonopods and phallic structures of a hypothetical primeval Mecopteron ♂. (Based upon Crampton 1931). 1: coxopodite. 2: harpago. 3: "lower valve". 4: "upper valve". 5: "dorsal valve". 6: gonopore.

Conditions in the Trichoptera may indicate that the bifurcation of the ventral valve is an original feature in the Endopterygota. The interpretation then is that the dorsal branch of the coxopodite in Trichoptera represents the "lower valve", whereas the paramere represents the "upper valve". In the other Endopterygota, however, no structure is seen which may be homologized with the dorsal branch of the coxopodite in Trichoptera, though the "cuspis" and the "digitus" in Hymenoptera perhaps indicate that the whole "volsellar" structure

(fig. 2 B, 3) has evolved from a bifurcated "valve". (Cp. also below: Diptera).

It seems justified to consider the "ventral valve" in Mecoptera as a homologue of the gonapophysis in Thysanura, and it seems probable that the "dorsal valves" are the limbs of segment X. The mutual position of the "ventral" and the "dorsal valve" are the same as those of the gonapophysis and the phallus in Thysanura. Some things, however, speak against considering the "dorsal valves" as the limbs of segment X. In *Panorpa* (Grell 1942) all muscles attached to the phallic apparatus originate in the coxopodites. (They may be homologous with those muscles which move the gonapophyses in the Thysanura). The ædeagal retractor of the Trichoptera stretches between parts which must be referred to the "ventral" and the "dorsal valve", resp. In the Hymenoptera the "parameres" (i. e. the gonopods), the "volsella" (i. e. the parameres) and the phallus are connected by a much complicated musculature. The interpretation of the "dorsal valves" as the limbs of segment X thus involves that muscles stretch between limbs belonging to two successive segments. However, the fusion of the pairs of limbs first having been accomplished, made possible by the reduction of venter X as an external structure, such a condition perhaps may have arisen through a shifting of the origins and the insertions of the muscles. Perhaps it even is not a unique condition. According to Robinson (1939), in the highly specialized mouthparts of *Anopheles maculipennis* the retractor præmenti (a labial muscle) originates on the stipes (a part of the maxilla).

In the Megaloptera and the Neuroptera a phallic structure seems to be present in some forms and lacking in others (Killington 1936). When present, it more often is membranous (Tjeder 1954). It probably is a structure analogous with the "penis" in *Boreus*. It, or the simple gonopore, is flanked by a pair of so-called "parameres",

which may represent the gonapophyses of segment IX.

In the Diptera the phallus may reach a high degree of complexity. Since many things indicate a close relationship between the Mecoptera and the Diptera, it is possible that the dipteran phallus has evolved independently of that of the other Endopterygota. In the Cyclorrhapha it is flanked by an anterior and a posterior pair of gonapophyses(?), which may be homologous with the "lower" and the "upper valves" in Mecoptera. (The phallus in this case would be formed exclusively by the "dorsal valves"). Two pairs of appendages on the median side of the coxopodites in some Nematocera may be homologues of the dorsal branches of the coxopodites and the parameres, resp., in Trichoptera.

Conclusions. The coxopodites and the styli of segment IX in the Thysanura and the Grylloblattidæ evolve to the gonopods of the Pterygota; the stylus forms the distal joint, the harpago. The so-called "parameres" in the Coleoptera and the Hymenoptera are gonopods. In the Trichoptera (and partly in the Lepidoptera and the Heteroptera also) the extrinsic musculature of the gonopods has been preserved in a generalized condition. In other forms either the dorsal or the ventral musles have been obliterated. The latter is the case in the Thysanura and the Grylloblattidæ, the former in most Pterygota. In many cases the coxopodite unites with the sternal part of segment IX (as probably has happened in the pregenital segments). This being the case, the stylus may either be preserved in a simple state on the posterior edge of segment IX, it may have evolved to a clasping organ (Aphaniptera), or it is lost. The last mentioned possibility is the prevailing condition in the Exopterygota.

The genital chamber of the Pterygota is formed, partly of the anterior part of segment XI (the paraprocts), partly perhaps also of the intersegmental membrane be-

tween terga IX and X. To the greatest extent, however, its wall is homologous with the membranous dorsal side of the coxopodites in the Thysanura.

The phallus in the Thysanura is formed by the limbs of segment X. In the Pterygota the phallic structures are formed by the gonapophyses of segment IX and the limbs of segment X. They may be developed as "phallomeres", or — more often — they have united to a true copulatory organ. In the Ephemeroptera and the lower Dermaptera the latter is paired, in the majority of Pterygota it is unpaired. In the class Insecta a copulatory organ, a phallus, has evolved independently several times. The exopterygotan and the endopterygotan ædeagus thus are not strictly homologous. In those cases where phallic structures are entirely lacking, it probably is due to reduction.

The term endophallus has been used in many senses. I. a. about the endotheca in the case the ægeagus being reduced (e. g. Hymenoptera). Or about a posterior, specialized part of the ejaculatory duct. It seems to have been used in other senses too. It probably would be better entirely to avoid this term.

The term parameres ought to be reserved for structures which may be considered as homologous with (a part of) the gonapophyses in the Thysanura.

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