Genital structures and terminology in the order *Neuroptera*.

By

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The genitalia and the terminal abdominal structures of the Neuroptera have been dealt with in many papers but hitherto no account comprising representatives throughout the order seems to have been rendered. Almost all authors have used their own terminology and this fact has caused a great confusion, especially for the taxonomists. When the editor of the "Taxonomists' Glossary of Genitalia in Insects", Dr. S. L. Tuxen, Copenhagen, entrusted me with the task of composing a paper on the Neuroptera for the glossary I found it necessary to make a thorough examination of representatives of the genera and families, which were available to me, and this study has shown the necessity of inventing a partly new terminology which I have tried to make neutral and fit for use in papers in any language. As there exist, especially in the σ genitalia, from the standpoint of phylogeny obscure, not yet cleared cases, for instance the origin of the structures, named gonarcus and hypandrium internum, I have tried to make the terminology neutral also in this respect.

Some hitherto unknown or undescribed structures have been termed and other structures have in several cases received new, neutral denominations. As an example: the "superior appendages" = "anal plates" = "paraprocts", etc., a pairy piece of the anal segment, has been termed ectoproct. The old terms have been rejected because the structure is not always appendage-similar, because it is not always plate-like, and because it cannot be true paraprocts (each ectoproct is composed by three fused structures, the anoprocessus, the cercus, and the catoprocessus, which latter possibly can be identified as the paraproct in the phylogenetic sense of this term). The denomination ectoproct, i. e. a structure bordering the anus from the outside, seems to me to be neutral and suitable for taxonomic purposes.

This paper may be considered as an attempt to elucidate the leading feature in the shape of the genitalia of this order and to apply a terminology, usable for taxonomists. When time and access to material will allow a more extensive examination no doubtalso other structures, worthy of special terms may be discovered.

The J genitalia.

The 9th segment is either synscleritous or discleritous. In many genera (e. g. in the families Sisyridae, Chrysopidae, Myrmeleontidae, Ascalaphidae) the 9th tergite is divided in its dorsal middle-line into a lateral plate on each side of the abdomen. The 9th tergite has in some genera (e. g. Psectra and Annandalia, fam. Hemerobiidae) on each side a backwards directed projection, the lateroprocessus, *prl* (fig. 1) and has in few cases also a single, median, backwards directed process, the dorsoprocessus, prd (fig. 2) or other dorsal projections or outgrowths (e. g. some Osmylidae). The 9th sternite carries in the Raphidiidae, the Inocelliidae, and the Coniopterygidae a pair of gonocoxites, qx (fig. 3-4), often reduced or even fused with the 9th sternite. Each gonocoxite carries in the Raphidiidae a stylus, st (fig. 3) which is one-segmented, movably attached to a list or tooth of the gonocoxite. The sternal region of the 9th sternite is in the Raphidiidae, in Polystoechotes (fam. Polystoechotidae), in some *Mantispidae*, and *Chrysopidae* produced posteriorly to form a more or less large plate, the hypovalva, hyv (fig. 3). The gonocoxites of most *Coniopterygidae* are fused with one another and form an external hypandrium, hy (fig. 5), which frequently has a median apical incision. The apices on each side of this incision are called processus terminales, tpr, and frequently there is also on the hind margin of the hypandrium on each side a tooth-like process, called the processus lateralis, lpr (fig. 5).

The majority of the Neuroptera have a simple plateor half-ring-shaped, often elongate 9th sternite, covered from above by the membrane that forms the hind body wall of the lower part of the abdominal end. In many *Chrysopidae* this dorsal membrane of the 9th sternite has a single or a pair of sclerotized plates, carrying strong teeth, which structure is dealt with as the gon ocristae, gcr (fig. 6). In some species of the same family there is an internal arched structure, fused to the under side of the membrane and to the gonocristae and with a central, strong apex extending through the membrane which structure is called the gonapsis, gap (fig. 6).

The \mathcal{J} genitalia proper are situated in the 9th sternite. The penis, p, is generally mostly membranous, sclerotized and distinct only in few genera, e. g. several *Coniopterygidae* (fig. 5) and *Mantispidae*. A kind of penisfilum, pf, is present in the *Berothidae* (fig. 7) and some *Mantispidae*, consisting of a single thread-like organ or of several such threads, closely adpressed, separated only at their bases and apices.

A pair of parameters, pa^{1}), is always present or can be traced, cf. fig. 1-5, 7-10, 12-15, arising close to the base of the penis. They are paired, either free or fused. Free parameres have the Sialidae, the Raphidiidae, the Inocelliidae, several Hemerobiidae, Sisyridae, Berothidae, etc. Parameres fused distally are present in Nemopterella (fam. Nemopteridae), several Chrysopidae, and in some *Mantispidae*, in which the apices occasionally are fused into a very long, sharp and narrow distal part, extending far out of the abdominal apex. A median fusion is present in some *Coniopterygidae*. In other genera they are proximally connected, e.g. Protohermes (fig. 8) or fused, e.g. many Hemerobiidae (fig. 9). In some Corydalidae they are wholly fused into a single plate, e.g. Neochauliodes. When proximally fused their proximal ends form in some genera an adpressed apophysis proximus, app (fig. 9). Apophyses laterales, apl (fig. 9) may also be present and frequently each paramere has a dorsal, backwards directed superproces-

¹) J. G. Ferris (Microentomology, Vol. 5, 2, 1940) thinks that the parameres (he has examined one species of *Raphidiidae* and two of *Mantispidae*) are lobes of the coxopodite, secondarily cut off, and names them fragmenta of the coxopodite of the 9th sternite.

sus, *spp* (fig. 9, 14). In certain *Coniopterygidae* the parameres have each an immovable apical, upwards directed processus apicalis, *pap*, connected with the main stem of the paramere by means of a sclerotized membrane (fig. 5). In *Osmylops* (fam. *Myiodactylidae*) each paramere is bulbous with a weak dorsal surface in which a very long, dorsally directed process, called the adscensio, *ads* (fig. 10) is movably inserted.

A pair of hypomeres, *hm* (fig. 7) are present in *Spermophorella* (fam. *Berothidae*). They are placed ventrally of the aedeagus and project downwards over the hind margin of the 9th sternite.

Many *Chrysopidae* have a peculiar, tube-like, unpairy organ, the pseudopenis, *psp*, situated centrally between a pair of membranous sacs, from the inner surfaces of which arise a number of setae (fig. 11). In such species the parameres are absent, the pseudopenis apparently being developed from them.

A peculiar organ, the hypandrium internum, hyi, or internal hypandrium is present in most families. It is situated below the bases of the parameres and has almost always the shape of the stem of a boat. It is generally a relatively very small and unpigmented structure but in the *Berothidae* (fig. 7) and in some *Myrmeleontidae*, e. g. *Acanthaclisis*, it is a large structure. In the latter genus it is also dark-pigmented.

Another organ which seems common to all male Neu-

Fig. 1. Psectra diptera Burm. \mathcal{J} (fam. Hemerobiidae), lateral. Hairs not drawn. — Fig. 2. Dilar burmanus Tjed. \mathcal{J} (fam. Dilaridae), lateral. Hairs not drawn. — Fig. 3. Raphidia notata F. \mathcal{J} (fam. Raphidiidae). Hairs not drawn. A, from behind. B, lateral. — Fig. 4. Inocellia crassicornis Schumm. \mathcal{J} (fam. Inocelliidae). Hairs not drawn. A, lateral. B, from behind. — Fig. 5. A. Coniopteryx borealis Tjed. \mathcal{J} (fam. Coniopterygidae), lateral. B. Coniopteryx tullgreni Tjed. \mathcal{J} , gonarcus and aedeagus from behind. Hairs not drawn. — Fig. 6. Chrysopa sensitiva Tjed. \mathcal{J} (fam. Chrysopidae). 9th sternite, dorsal.



gs.

1





prd

spap рг ent рa

roptera is the gonarcus¹), gs (fig. 1–8, 10–15). It is situated between the anal segment and the 9th sternite, in some genera very close to the anal segment, e.g. Sialis, Inocellia, Nymphes. Its upper part may in these genera serve as a subanal plate. In Nymphes its upper part is hollowed into a furrow for the rectum and the anus opens in a broadened apical excavation of this furrow (fig. 14). In other genera the gonarcus is distinctly median, e. g. Raphidia (fig. 3), Hemerobius, and Protohermes (fig. 8). In others it is situated very closely above the aedeagus (fig. 7) and in others, e.g. many Myrme*leontidae* it is so fused with the parametes that it forms together with them a central, huge, penis-like organ (fig. 12). The gonarcus thus is very heterogenously developed but may be described as a generally archformed structure with its arches directed downwards or inwards. In some *Coniopterygidae* the arch is split in its dorsal middle-line. The median upper part of the organ ends frequently in a backwards directed process, the mediuncus, mu (fig. 12-14). The genus Nymphes has on the under side of the mediuncus a downwards directed, unpaired but twice forked, immovable process, called the hypocuspis, hyc (fig. 14). Some Sialis have a pair of weak, tube-like utriculi, u, close to the mediuncus (fig. 13). Each arch of the gonarcus may have a

Fig. 7. Spermophorella maculatissima Till. ♂ (fam. Berothidae).
A, lateral. B, from behind. C, hypandrium internum, dorsal. —
Fig. 8. Protohermes xanthodes Nav. ♂ (fam. Corydalidae), dorsal. —
Fig. 9. Neuronema sinensis Tjed. ♂ (fam. Hemerobiidae), parameres, dorsal. — Fig. 10. Osmylops pallidus Banks ♂ (fam. Myiodactylidae), lateral. Hairs not drawn. Left portion of 7th—9th segments removed. — Fig. 11. Chrysopa formosa Br. ♂ (fam. Chrysopidae), gonarcus and pseudopenis from behind.

¹⁾ J. G. Ferris (Microentomology, Vol. 5, 2, 1940) considers as a really tenable assumption that this peculiar arch is composed of remainders of the coxopodites of the 9th sternite which are fused over the penis-base.











lateral process, the entoprocessus, ent (fig. 2, 5, 10, 11, 14, 15). The entoprocessus are very varying in shape and size; either they are narrow simple or forked rods or they are hugely developed as broad, hairy plates (Polystoechotes, etc.) or they form a pair of large claspers, dominating the abdominal apex (Sisyra) (fig. 15). In some genera there is an additional structure, movably attached below the uppermost part of the gonarcus, which organ is called the arcessus, ar, and is of very varying shape in different genera. It may be developed as a plate, as a thin rod-like, sometimes forked structure, or even as a bladder-like, echinate, large organ, e.g. Osmylops (fam. Myiodactylidae), cf. fig. 10, or as a pair of movably attached spine-like appendages, e.g. Hemerobius. In Polystoechotes it is club-shaped and has both spines and long hairs. In Nymphes (fam. Nymphidae) there is another additional organ, belonging to the gonarcus, movably attached to the lowest part of each arch by means of a real joint, the hypostylus, *hst* (fig. 14). Some Osmylidae have on either side of the gonarcus an additional narrow strut, the baculum, the upper end of which fits into a socket of the respective end of the arch.

The anal segment is in primitive *Corydalidae* present as three processes on each hind lateral margin of the 9th tergite, bordering the anus laterally. The uppermost of these processes is denominated the anoprocessus, *apr*, the lowermost the catoprocessus, *cpr*, while the middle process is the one-segmented cercus, *c*, which bears a number of trichobothria, *tr*. This condition

^{Fig 12. Cueta sp. ♂ (fam. Myrmeleontidae). Fused, tube-like gonarcus and parameres. A, lateral. B, ventral. C, dorsal. — Fig. 13. Sialis sordida Klingst. ♂ (fam. Sialidae), lateral. Hairs not drawn. — 14. Nymphes myrmeleonoides Leach ♂ (fam. Nymphidae), lateral. Hairs not drawn. Left portion of 7th—9th segments and ectoproct removed. — Fig. 15. Sisyra fuscata F. ♂ (fam. Sisyridae). A, lateral. B, dorsal; hairs not drawn.}





of the anal segment is represented in the figured Platyneuromus soror (fig. 16). In other Corydalidae, e.g. Protohermes xanthodes (fig. 8) the anoprocessus and the cercus are fused and included in the 9th tergite while the catoprocessus is free. In most Neuroptera, however, the three processes have united into a single lateral plate, here called the ectoproct, epr (fig. 1, 3, 4, 5, 10, 13, 14, 15, 17, 18). The cercus is reduced to a callus cerci, cc, bearing the trichobothria, or is totally wanting. In some genera there are no traces of a callus but a number of trichobothria are retained (Sialis, fig. 13, and Raphidia, fig. 3). In the Raphidiidae and the Inocelliidae these trichobothria are placed in a transverse row, the portion before the row having been identified as the 10th tergite while the portion behind the row has been supposed to be the 11th tergite. In these families and in several others, e.g. the Sisyridae (fig. 15), the Polystoechotidae, the Osmylidae, the Chrysopidae, the two ectoprocts are united to form a dorsal half-ring, covering the anus also dorsally. In the *Sialidae* the ectoprocts are frequently a somewhat depressed, transverse plate with the anus opening on its dorsal surface. The ectoproct has frequently two (many Hemerobiidae) or one prong, representing the anoprocessus and the catoprocessus or either of them. Very often all traces of prongs are absent. Other processes, spines or teeth, occur in many species on the surface of the ectoproct or on the prongs. No traces of the ectoprocts are visible in the genera Spermophorella and Acroberotha (fam. Berothidae), cf. fig. 7. Perhaps the ectoprocts in these genera are fused with the 9th tergite, which is very large and covers the anus dorsally and laterally. The figured species of *Dilar* (fig. 2) has a very differently shaped anal segment. The 9th tergite is huge, covering the anal segment and the genitalia from the sides. No ectoprocts are present and the anal segment consists of a strongly sclerotized and pigmented supraanale, *spap*, and below this a less strongly sclerotized proctiger, *pr*, through which the anus opens.

It was intended that this paper should deal only with the external genitalia and the terminal abdominal structures. There are, however, in many *Myrmeleontidae*, paired anteapical structures which possibly have a function



16. Platyneuromus soror Hag. ♂(fam. Corydalidae), lateral. Hairs, parameres and gonarcus not drawn. — Fig. 17. Lopezus fedtschenkoi Mc Lachl. ♂ (fam. Myrmeleontidae), lateral. Hairs and internal genitalia not drawn. — Fig. 18. Grocus inconspicuus Ramb. ♂ (fam. Myrmeleontidae), lateral. Hairs and internal genitalia not drawn.

during copulation and which organs I will not omit. In many genera there are thus one or two pairs of pleuritosquamae, *pls* (fig. 17), a kind of intersegmental organs of the 7th or 6th and 7th segments, formed as large hook-like structures, as round plates, or even as ridges, always clothed with long hairs. In other genera, e. g. *Myrmeleon* and *Grocus* there are instead of pleuritosquamae pocket-like, inwards turned, perhaps eversible

organs between the same segments, but they are placed more dorsally, between the tergites. These pockets may be denominated pleuritocava, *plc* (fig. 18). It should be noted that they are not homologous with the eversible sacs, present on the lateral sides of the 2nd—8th sternites in certain \mathcal{J} and \mathcal{Q} *Coniopterygidae* (subfam. *Aleuropteryginae*). The 7th and 8th tergites of the genus *Annandalia* (fam. *Hemerobiidae*) bear prongs or teeth.

The Q genitalia.

The 8th segment frequently consists of a dorsal halfring, the tergite, with often downwards prolonged sides. A sternite is generally missing but in some Corydalidae and Coniopterygidae a secondary 8th sternite has been developed. A distinct median longitudinal suture is occasionally present, indicating that the sternite at least in such cases may have been developed from two plates or pieces (?remainders of the gonapophyses anteriores), cf. fig. 19. Below the 8th tergite there is frequently a subgenital plate, subgenitale, sqp, cf. fig. 20-25, 28. This plate is of very varying shape in different genera or even different species. It is certainly developed from the gonapophyses anteriores. In many Myrmeleontidae the gonapophyses anteriores are present as long, finger-like lateral appendages, projecting considerably downwards, cf. fig. 27. Occasionally there is a second, single or paired plate present, situated proximally to the subgenitale closely behind the distal lower apex of the 7th sternite, for which structure the term prae-

Fig. 19. Protochauliodes cinerascens Blanch. Q (fam. Corydalidae), lateral. Hairs not drawn. — Fig. 20. Porismus strigatus Burm. Q(fam. Osmylidae), lateral. — Fig. 21. Boriomyia baltica Tjed. Q(fam. Hemerobiidae). Subgenitale, dorsal. — Fig. 22. Inocellia crassicornis Schumm. Q (fam. Inocelliidae), lateral. — Fig. 23. Chrysopa septempunctata Wesm. Q (fam. Chrysopidae). Praegenitale, subgenitale, and spermatheca, lateral. — Fig. 24. Spermophorella maculatissima Till. Q (fam. Berothidae), lateral. Hairs not drawn.









genitale, prg, may be used (fig. 23). In some Myrmeleontidae the praegenitale has the shape of a small tooth.

The 9th tergite forms a half-ring or is longitudinally split in its dorsal middle-line, in some Chrysopidae situated distant from the dorsum and fused with the ectoprocts on their under border, forming a kind of lateral plates. In the Sisyridae and the Ithonidae (fig. 25) they are almost sternite-similar, reaching the lower surface of the abdomen. The downwards prolonged sides of the tergite have rarely processes or other modifications. In some species of Micromus (fam. Hemerobiidae) a lateroprocessus is developed; in Sisyra there is an apical internal tooth and in the figured species of Spermophorella (fam. Berothidae) they end in two sharp prongs (fig. 24). In the latter species, however, the 9th tergite forms the dorsal end of the abdomen and is - I think - fused with the ectoproct. If so is the case the prongs may belong to the ectoproct.

The two gonapophyses-pairs of the 9th sternite are present in some families, most distinctly in the *Raphidiidae* and the *Inocelliidae*, in which they form a long ovipositor (fig. 22). The gonapophyses laterales, *gl*, form the lateral sides of the ovipositor. They are membranously connected dorsally to near the apex and have a longitudinal, ridge-like apodeme, *ap*, giving rigidity to the ovipositor. The gonapophyses posteriores, *gp*, proceed from the membranous structure above the apex of the subgenitale and fuse in their proximal part to a long, narrow process, which runs between the gonapo-

Fig. 25. Ithone fusca [Newm. \heartsuit (fam. Ithonidae), lateral. — — Fig. 26. Coniopteryx tineiformis Curt. \heartsuit (fam. Coniopterygidae), lateral. — Fig. 27. Lopezus fedtschenkoi Mc Lachl. \heartsuit (fam. Myrmeleontidae). A, dorsal. B, right gonapophysis posterior, lateral (to show the digging hairs). — Fig. 28. Acroberotha xiphophora Tjed. \heartsuit (fam. Berothidae). A, lateral. B, oviduct with ovipilum and spermatheca with glandula accessoria from the right side.



physes laterales and reach their apex. The gonapophyses laterales carry each one stylus, *st*.

The gonapophyses laterales form also in the family *Dilaridae* a long ovipositor. The gonapophyses posteriores are in that family short and the gonapophyses laterales are membranously connected also ventrally; the styli are lacking. Also *Symphrasis* and *Plega* (fam. *Mantispidae*) have a long ovipositor and the *Sisyridae* have a short but distinct ovipositor, formed by the gonapophyses laterales; the apodemes are strong and remainders of styles are present between the apices of the gonapophyses laterales in *Sisyra*.

Remainders of the gonapophyses posteriores are often present, situated either at the apex of the subgenitale, behind that plate, or between the bases of the gonapophyses laterales, e. g. many *Hemerobiidae*. In *Boriomyia* (fig. 21) they are membranously connected to the subgenitale. In other *Hemerobiidae* they are often fused into a plate below the 9th tergite or between the proximal ends of the gonapophyses laterales and in the *Osmylidae* they form an occasionally small, occasionally very large plate- or bladder-like organ, often with long prongs or processes. I name the structure in question the postgenital plate or postgenitale, *pop* (fig. 20, 24, 28).

The most common condition of the mentioned gonaphyses pairs is that the gonapophyses posteriores are lacking and the gonapophyses laterales are present as a pair of short or elongate plates, proceeding from the lower hind margin of the 9th sternite. Styli are present in some families or genera (*Sialidae, Osmylidae, many Corydalidae* and *Hemerobiidae*). The lateral gonapophyses of *Ithone* (fam. *Ithonidae*) have on the under margin each a strongly sclerotized, plug-like process, the pseudostylus, *pst*, for digging purposes (fig. 25). The highly specialized *Berothidae* have from the under margin of each gonapophysis lateralis a slender, finger-like organ, the hypocauda, *hyp* (fig. 24, 28). Each hypocauda is somewhat movable, the gonapophysis being very weak at the place, where the hypocauda is inserted. The hypocaudae are generally somewhat diverging.

The gonapophyses laterales of the *Coniopterygidae* are frequently placed closely together (in one of the known species fused into a single broad plate) on a weakly sclerotized plate-like structure distally of an internal structure which is possibly a bursa copulatrix, bc (fig. 26). A sclerotized bursa copulatrix is also present in the Sialidae. Many other Neuroptera have a strongly sclerotized spermatheca, spm, very different in shape in the different families. It may have the shape of a long tube (many Myrmeleontidae), a long duct, coiled to a ball (Spermophorella, fig. 24), a more or less twisted sac (many Hemerobiidae), or a round, flattened box with dorsal triangular processes, the vela, v, and a ventral impression (many Chrysopidae, cf. fig. 23). It may also be twofold and may have paired vesicles (Raphidia) or a single glandula accessoria, aq (e. g. Acroberotha, fam. Bero*thidae*, cf. fig. 28).

A very peculiar type of ovipositor is present in the genus *Acroberotha* (fig. 28). In the figured species the very long and beautifully curled oviduct is strongly sclerotized and ends as a dilated, downward projecting, very long, sabre-formed and strong tube. Such a structure may be called the ovipilum, *ovp*.

The anal segment is shaped much as in the male. There is thus an ectoproct, situated laterally on each side of the anus. The primitive Corydalid Archichauliodes diversus Walk., from New Zealand, has a long one-segmented cercus, extending from the middle of the ectoproct (figured by D. E. Kimmins, Ann. Mag. Nat. Hist. Vol. II, p. 354, f. 5, 1938). Distinct remainders of the cercus are present also in other Corydalidae, e. g. Protohermes and Protochauliodes (fig. 19). In the last species a dorsal prong, the anoprocessus, *apr*, is very distinct. In other species, e. g. *Protohermes*, also the catoprocessus is distinct. Generally, however, the ectoproct is a plate without processes and with or without a callus cerci, *cc*, with trichobothria (fig. 20, 22, 25—27). A subanal plate, subanale, *sap*, is distinct in *Ithone* (fig. 25) and *Coniopteryx* (fig. 26) but else absent or indistinct, being occasionally a small ill-defined sclerotization with some small hairs. No distinct ectoproct is present in the *Berothidae* (fig. 24, 28), presumably being fused and included in the 9th tergite.

List of abbreviations.

a, anus ads, adscensio ag, glandula accessoria ap, apodeme apl, apophyses laterales app, apophysis proximus apr, anoprocessus ar, arcessus ba, baculum bc, bursa copulatrix c, cercus cc, callus cerci cpr, catoprocessus ent, entoprocessus epr, ectoproct ga, gonapophyses anteriores gap, gonapsis gcr, gonocristae gl, gonapophyses laterales gp, gonapophyses posteriores gs, gonarcus gx, gonocoxites hm, hypomeres hst, hypostylus hy, hypandrium hýc, hypocuspis hyi, hypandrium internum

hyp, hypocauda hyv, hypovalva lpr, processus laterales mu, mediuncus ovp, ovipilum p, penis pa, parameres pap, processus apicalis pf, penisfilum pg, proctiger *plc*, pleuritocava pls, pleuritosquamae pop, postgenitale prd, dorsoprocessus prg, praegenitale prl, lateroprocessus psp, pseudopenis pst, pseudostylus sap, subanale sgp, subgenitale spap, supraanale spm, spermatheca spp, superprocessus st, stylus tpr, processus terminales u, utriculi v, vela

1-9, 1st-9th tergites. I-IX, 1st-9th sternites. (VIII), secondary 8th sternite.