A Comparative Description of the Male Terminalia in Thereva Latr., Dialineura Rond., and Psilocephala Zett. (Diptera, Therevidae)

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The male terminalia of Therevidae have been little studied. The only brief notes are those given by Cole (1923: 6—8, 1927: 423—24) and Karl (1959). Several other authors have figured and briefly described the outlines of the external "hypopygium", which often affords distinct characters for the separation of the species. Also the tip of aedeagus which is normally visible without dissection, has been found useful for the separation of species of *Thereva* Latr. (Collin, 1948). The present author (1965) published figures of the male terminalia of all the Danish species of Therevidae.

It is the present author's opinion that the male terminalia of Therevidae provide characters of great importance. Some pilot testings in a number of species of many genera from all regions have given the impression that the male terminalia combined with other characters can be used for a suprageneric division of the family. Besides this, the male terminalia also possess excellent characters for the separation of closely related species, or, vice versa, the male terminalia often show more correctly the relationship between species which by use of other characters have been placed far from each other.

In order to have a starting point, it was found of value to describe and figure in detail the male terminalia of *Thereva* Latreille, 1796, represented by its type-species: *plebeja* Linné, 1758; *Dialineura* Rondani, 1856, represented by its type-species:

anilis Linné, 1761, and finally *Psilocephala* Zetterstedt, 1838, as fixed by its type-species: *imberbis* Fallén, 1814. All three species occur in Northern Europe. As will be understood from the above remarks, these three species do not by any means show the range within the family. They may, on the other hand, be taken as representing three closely related genera constituting together with other genera a suprageneric group on subfamily or tribe level. As is known, the two genera *Thereva* Latr. and *Psilocephala* Zett. include a great number of species, and are thus apparently very heterogenous genera. When in the following description the generic names *Thereva, Dialineura,* and *Psilocephala* are used, these names are to be understood in the most strict sense, namely as representing their respective type-species only.

In the following description an attempt has also been made to homologize the terminalia of the three therevid-genera with the terminalia of the Asilidae represented by the generalized genus *Dioctria* Meig. The terminalia of this genus were described by Hennig (1936) and Karl (1959).

Segment 8

In all three therevid-genera both the tergal and sternal elements of the last pregenital segment 8 are developed, though normally not visible without dissection. Tergite 8 (figs. 2, 4, 6) is a broad sclerite which is very narrow for a considerable distance on the middle part. Its shape is practically identical in the three genera. There are some differences in the distribution and length of the pubescence. In *Dialineura* and *Psilocephala* (figs. 2 and 4) the hairs are rather short and confined to the lateral parts of the tergite. In *Thereva* (fig. 6) the hairs are longer and are also distributed along the fore margin to mid line.

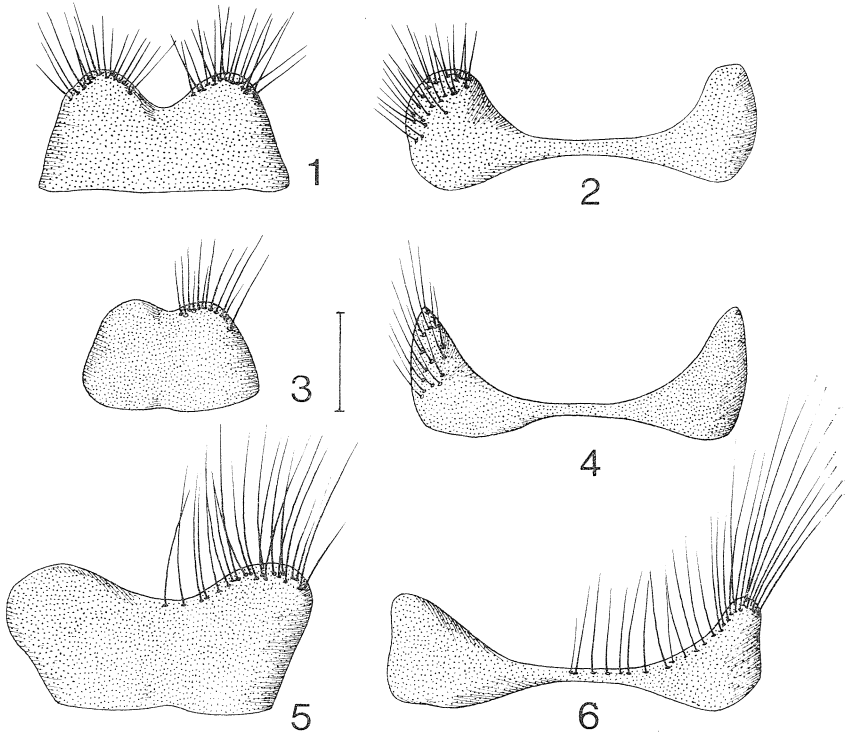
Sternite 8 (figs. 1, 3, 5) is rhomboid with a more or less deep and evenly curved incision on hind margin. The length of the pubescence varies somewhat, and the hairs are distributed along the hind margin, mainly laterally.

In *Dioctria* the tergite 8 is much larger than in the three therevid genera, while the sternite 8 is completely reduced.

Tergite 9—10 (epandrium)

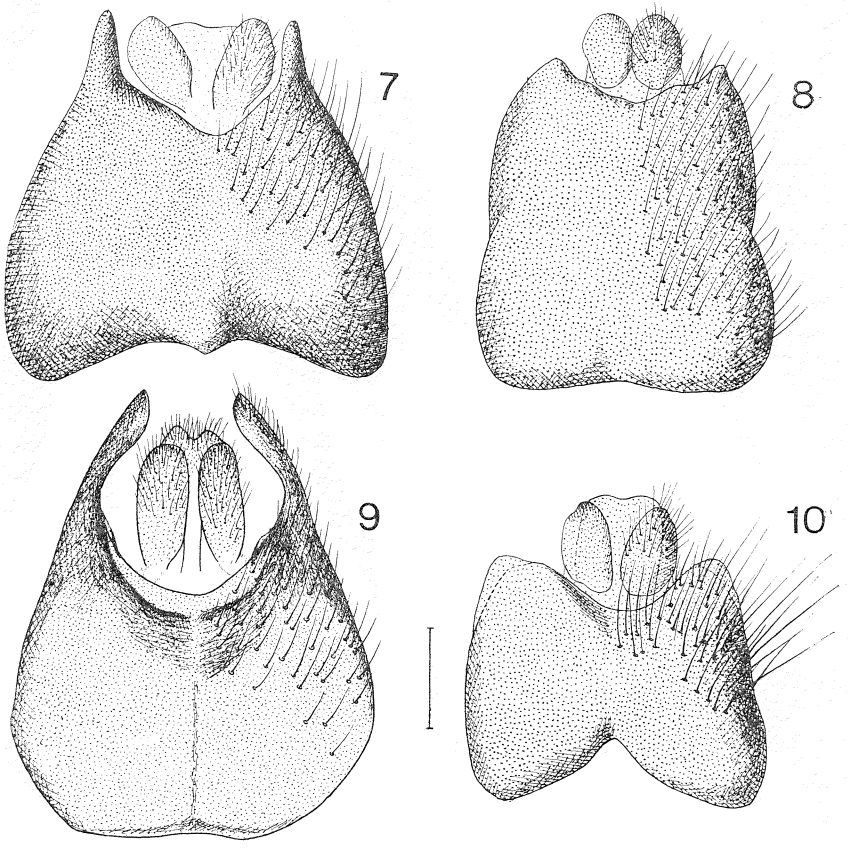
The dorsal part of the so-called "hypopygium" is formed by an unpaired sclerite covering the other parts of the terminalia. Seen

dorsally it is shown for *Dioctria* in fig. 7 and for the three therevid-genera in figs. 8—10. This sclerite is often termed epandrium, in Asilidae also "superior forceps", this term then indicates a cleavage of the epandrium as found in many asilid-genera. There can be no doubt about the homology of the epandrium of *Dioctria* and of the three therevid-genera, though Karl (1959) found that the epandrium of *Dioctria* most certainly represents a secondary fusion of a clefted epandrium. This seems an unlikely and unnecessary interpretation. Hennig (1936) has shown that the epandrium certainly represents a fusion of both tergite 9 and tergite 10. The constriction about middle of the epandrium in *Dialineura anilis* (fig. 8) thus probably indicates its bisegmental nature. This constriction is still more pronounced in the males of four species of *Dialineura* from the East Palaearctis (Lyneborg, in print).



Figs. 1—8. Sclerites of segment 8 in (1—2) *Dialineura anilis* L., (3—4) *Psilocephala imberbis Fall.* and (5—6) *Thereva plebeja* L. Figs. 1, 3 and 5 show sternite 8; 2, 4 and 6 tergite 8. Scale : 0.2 mm.

The epandrium shows a considerable degree of variation in shape. In *Dialineura* (fig. 8) it is nearly square, with a very inconspicuously incurved fore margin, and a more distinctly incurved hind margin. The epandrium of *Thereva* (fig. 10) is broader than long, with a deep, acute incision on fore margin, and a more evenly curved incision on hind margin. Finally, in *Psilocephala* (fig. 9), the epandrium has an evenly convex fore margin, while the hind margin has a very deep incision. The hind corners of the epandrium in the three genera are provided with thin rims, bearing no hairs. These rims are especially distinct in



Figs. 7—10. Tergite 9, or epandrium, and its appendages in (7) *Dioctria oelandica* L., (8) *Dialineura anilis* L., (9) *Psilocephala imberbis* Fall., and (10) *Thereva plebeja* L. All seen in dorsal view. Scale : 0.2 mm.

Thereva. The epandria of all three genera bear an evenly distributed pubescence.

Cerci, paraprocts and sternites 10+11.

The anal opening is surrounded by dorsal and ventral sclerites which are attached to the incised hind margin of the epandrium. This complex is in the Therevidae termed proctiger by Cole (1923:7), and the same term is used for the homologous structure in the Asilidae by Hull (1962:12). Later, Cole (1927:424) clearly distinguishes between the dorsal part which he terms cerci, and the ventral part which he terms proctiger, then obviously in a more strict sense than in 1923. It is important to distinguish between the dorsal and ventral part, as it is done in the Asilidae by Karl (1959). He terms the dorsal appendages cerci, and the same term will be used here for the Therevidae. In the three therevid-genera under discussion the cerci constitute two separate oval sclerites, which bear fine pubescence dorsally. A fusion of the cerci as observed by Karl (l.c.: 633) in some asilid-genera has not been observed in other therevid-genera studied.

In the Asilidae the ventral part is termed "ventral lamella" by Karl (l.c.: 633). He states that this sclerite is normally undivided in the Asilidae, and that a more or less distinct cleavage as found in some genera is an apomorph condition. In the three therevid-genera the conditions are as in most Asilidae, i.e., a complete sclerite. In *Psilocephala* this sclerite has a very deep cleft proximally and a shorter incision distally. *Thereva* has the same incision distally and the median area is less distinctly pigmented and thus leaving the appearence of two separate sclerites. In *Dialineura* the sclerite is short trough-shaped with the convex surface ventrally, and there are no indications of incisions. Without being able to demonstrate it, the present author is of the opinion that this ventral sclerite represents the paraprocts.

The paraprocts continue proximally in an intersegmental skin situated close to the underside of epandrium. This intersegmental skin is more or less distinctly grown-together with the proximal margin of the aedeagus (=the distal margin of the so-called dorsal apodeme, vide p. 557), and shows sometimes some sclerotizations which seem to be of great importance for an understanding of the segmentation of the therevid-terminalia. In *Dialineura* the intersegmental skin has two oval sclerites which are well-separat-

ed and without any connection with the hind margin of the epandrium. *Thereva* has the same two sclerites, but these are linked to the hind margin of epandrium and can be folded out by help of a pin. In *Psilocephala* the intersegmental skin is without any sclerotizations. It seems naturally to take these sclerites as representing sternal elements from segment 10 and/or 11. It is probably the same morphological element as is found in the anal segments of *Panorpa,* where it is termed sternum 10 by Tjeder (1956: fig. 100). If these sclerites as represented in *Thereva* are of real segmental nature they may certainly also be taken into consideration when forming ideas about the nature of the so-called surstyli in Cyclorrhapha.

Sternite 9, gonopods and appendages.

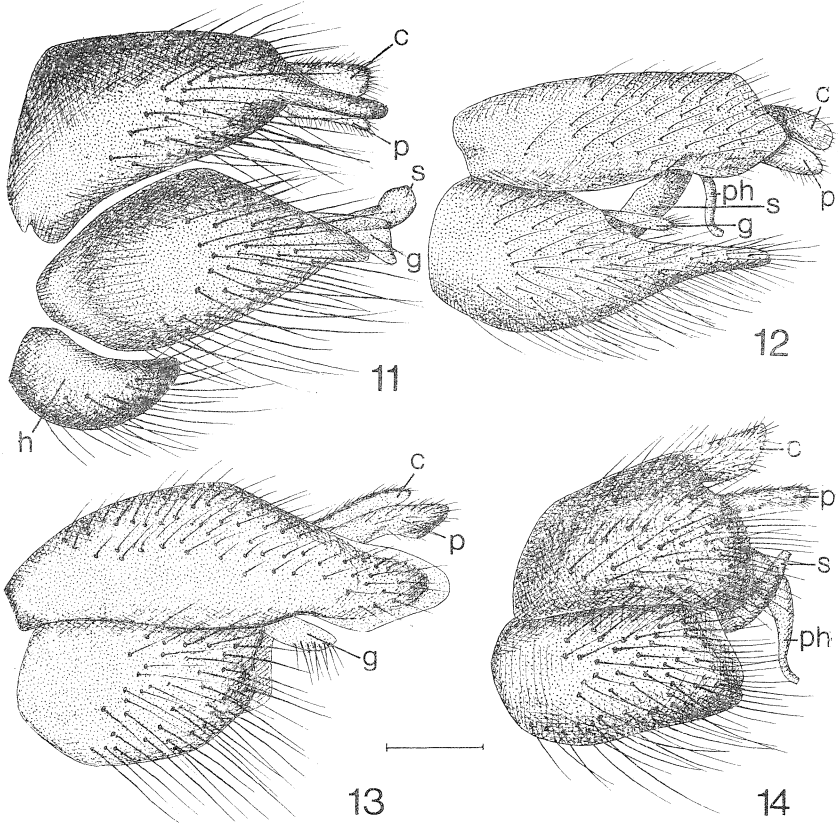
The ventral portion of the "hypopygium" is formed mainly by two large sclerites of nearly semiglobular shape. The margin surrounding the lumen of these sclerites lies in a nearly sagittal plane. The two sclerites are entirely separated in the three genera examined, and show a more or less distinct tendency to send out a process from the hind part. This process is less distinct in *Psilocephala* (fig. 13), more distinct in *Thereva* (fig. 14), while *Dialineura* (fig. 12) has the hind margin provided with a long process. This hind, projecting, part bears the longest and strongest of the hairs on these sclerites.

The two ventral sclerites mentioned were in the Therevidae generally taken as representing the sternite 9 or hypandrium (Cole 1923: 6, 1927: 424), but were correctly interpreted as representing the gonopods by Karl (1959:673). The homology is clearly known when comparing figs. 15 and 16, showing *Dioctria* and *Thereva* respectively, both figures giving a dorsal view of the aedeagus and left portion of the "hypopygium" after removing epandrium. The gonopod of *Dioctria* has the same shape and the same attached elements as the gonopod of *Thereva.* The attached elements are as follows: 1) An element (s) arising from the lumen; 2) An element (g) fused to the dorsal margin for a long distance; and 3) A ventral excrescence (vl).

The only real difference between these structures in *Dioctria* and *Thereva* is the presence of a large sternite 9 (hypandrium) in *Dioctria* (see also fig. 17), while this is seemingly absent in *Thereva.* In fact, *Thereva* also has a sternite 9, formed as a narrow and

weakly sclerotized band connecting the bases of the two gonopods at the anterior margin of their ventral surfaces. It is shown in fig. 18. In *Psilocephala* (fig. 19) there is still a smaller triangular sclerite representing sternite 9, while in *Dialineura* (fig. 21) there is no indication of it. A tendency to a reduction of sternite 9 (hypandrium) is also found within the family Asilidae (Karl, 1959: 628).

The problem now arises to try to homologize the three elements attached to the gonopods. The gonopod in its morphological definition consists of two segments, the gonocoxite basally, and the



Figs. 11—14. Lateral views of the "hypopygium" of 11: *Dioctria oelandica* L., 12: *Dialineura anilis* L., 13: *Psilocephala imberbis* Fall., and 14: *Thereva plebeja L.* All seen from left side. Abbreviations: c = cerci, g = gonapophysis, h = hypandrium or sternite 9, p = paraprocts, ph = phallus, s = stylus. Scale: 0.2 mm.

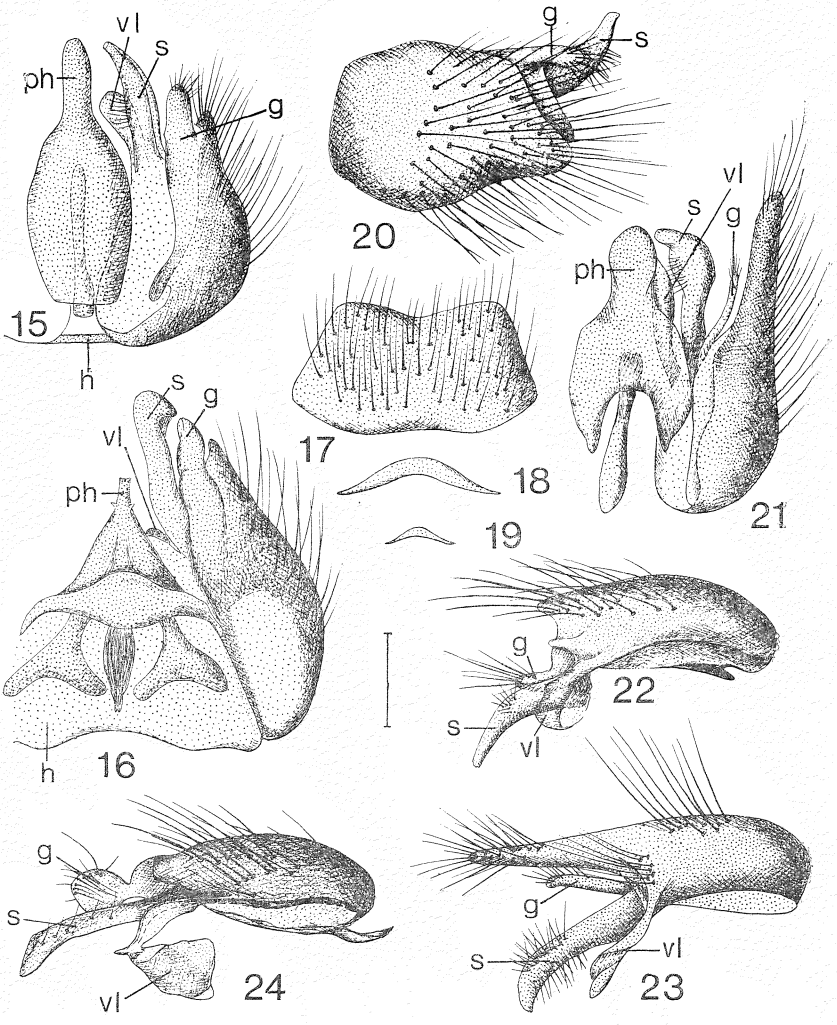


Fig. 15. Left gonocoxite with its appendages and the aedeagus of *Thereva plebeja* L., seen dorsally after removing the epandrium. Fig. 16. The same in *Dioctria oelandica* L. Figs. 17—19. Hypandrium, or sternite 9, in (17) *Dioctria oelandica* L., (18) *Thereva plebeja* L., and (19) *Psilocephala imberbis* Fall. Fig. 20. Left gonocoxite with its appendages of *Thereva plebeja* L., seen laterally. Fig. 21. Left gonocoxite with its appendages and the aedeagus of *Dialineura anilis* L., seen dorsally after removing the epandrium. Figs. 22—24. Right gonocoxite with its appendages, seen ventrally, of (22) *Thereva plebeja* L., (23) *Dialineura anilis* L. and (24) *Psilocephala imberbis* Fall. Abbreviations: g = gonapophysis, h = hypandrium, ph = phallus, s = stylus, vl = ventral lobe. Scale: 0.2 mm.

stylus distally. There seems to be clear evidence for the fact that both elements are represented in the three therevid-genera as well as in many asilid-genera, the large, semiglobular sclerite then being the gonocoxite, and the staff-shaped element arising from the lumen being the stylus. Other terms used for the same structures are basistylus and dististylus (Emden & Hennig, 1956: fig. 140; Karl, 1959). In the Asilidae the stylus is termed "claspers" by Oldroyd (1938) and Hull (1962), and "Parameren" by Reichardt (1929). The styli certainly always join the intromittent part of the aedeagus into the female postabdomen during copulation (cf. Reichardt, l.c.). The "anterior gonapophysis" in the sense of Cole (1927: 424) is homologous to the stylus of the present paper.

The stylus is generally similar in the three therevid-genera examined (and also in *Dioctria),* formed as a slightly curved staff with small differences in shape. It is inserted in the lumen of the gonocoxite near to its hind margin. The styli are provided with groups of hairs in all the genera.

The sclerite fused to the dorsal margin of the gonocoxite for a long distance is found in the therevid-genera and also in many asilid-genera. It is most clearly seen in fig. 15 of *Thereva,* where it appears as an elongated sclerotization with a free terminal end provided with hairs, and a basal rod which is formed as a strongly sclerotized process. Hennig (1936) has shortly commented on this structure in *Dioctria* and termed it "Hakenfortsätze" (hf? in figs. 3—4 of Hennig, l.c.), and Karl (1959) terms it "lateral Fortsatz des Basistylus". This structure is not present in the higher asilids (Asilinae). In many therevid-genera (e.g. *Phycus* Walk.) it seems also "absent". This means that its free terminal end is absent, while the basal rod shows a strongly sclerotized connection to the aedeagus. This character is no doubt very valuable for a division of the Therevidae. Based on these facts the present author finds it reasonable to take, at least provisionally, this sclerite as representing a gonapophysis.

The gonapophysis shows some variation in *Thereva, Dialineura,* and *Psilocephala.* In a lateral view of the terminalia of *Thereva* and *Dialineura* this appendage is often difficult to see without dissection, either because, as in *Thereva* (compare fig. 14 and fig. 20), it is hidden so that only the extreme apex is visible, or, as in *Dialineura* (fig. 12), it is weakly pigmented. The shape of the free part is like a finger in these two genera. In *Psilocephala* (fig.

13) it is more distinct externally, arising as a lamellate sclerite from the corner formed by the latero-ventral edge of the epandrium and the gonocoxite. In all three genera the apical part of the gonapophysis bears hairs. Its nature as a morprological element separate from the gonocoxite is most clearly seen in fig. 15 of *Thereva. Psilocephala* shows practically the same feature as *Thereva,* but the connection between the free part and the basal rod is less distinct. Finally, in *Dialineura* (fig. 21) the gonapophysis has a more rudimentary nature, with the free part placed near the middle of the dorsal margin of the gonocoxite and with only weakly sclerotized indications of a rod.

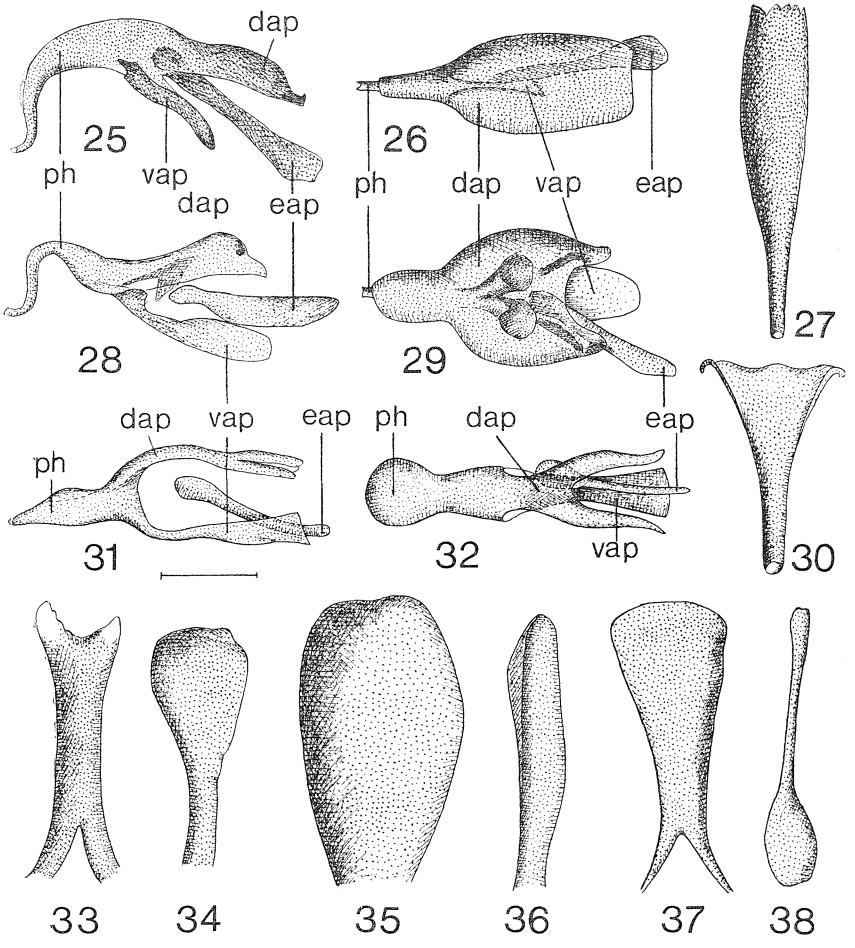
The third element earlier mentioned as a ventral excrescence is the "posterior gonapophysis" of Cole (1927). It is certainly not a morphological element in its proper sense, but simply an excrescence from the ventral surface of the gonocoxite. It must therefore have a non-commital name, and it is proposed to name it simply: ventral lobe. Similar excrescenses are found for example in the Culicidae ("apical lobe" in fig. 138 by Emden & Hennig, 1956) and also in the Asilidae ("ventral Fortsatz des Basistylus" in Karl, 1959).

The shape of the ventral lobe varies considerably in the three genera in question. In *Thereva* (fig. 22) it is nearly circular, while in *Dialineura* (fig. 23) it is a long and narrow, lamellate structure; in both genera the ventral lobe is free. *Psilocephala* (fig. 24) shows a different picture. Here, this ventral lobe consists of two different parts, the part most distal to the gonocoxite forming a flat, semitriangular structure which is united to the lateral part of the aedeagus by its dorsally placed margin.

Aedeagus.

The term aedeagus is used here for the entire copulatory organ situated ventrally to the epandrium and flanked by the gonocoxites and their attached elements. The elements forming this complicated organ have been found to vary considerably in shape in the three therevid-genera examined and in other representatives of the family. It has, therefore, been found desirable to have some terms to be used for the various elements forming the aedeagus. Reichardt (1929) describes in detail the aedeagus (called by him penis) of the asilid: *Machimus atricapillus* Meig., and Karl (1959) gives further details, but none of these attempt to give any terms

to the various parts which were found taxonomically useful in the therevid-genera. The following proposed terms are simply descriptive and are used provisionally. The intromittent part of aedeagus will be termed: phallus. In *Thereva* (figs. 25—27) and



Figs. 25—32. Aedeagus of (25—27) *Thereva plebeja* L., (28—30) *Dialineura anilis* L., and (31—32) of *Psilocephala imberbis* Fall. Figs. 25, 28 and 31 lateral view; 26, 29 and 32 dorsal view, and 27 and 30 caudal view. Figs. 33—38. Ventral apodeme and ejaculatory apodeme of (33—34) *Thereva plebeja* L., (35—36) *Dialineura anilis* L., and (37—38) *Psilocephala imberbis* Fall. All ventral view. Abbreviations: dap = dorsal apodeme, eap = ejaculatory apodeme, ph = phallus, vap = ventral apodeme. Scale: 0.2 mm for figs. 25—26, 28—29, 31—32, and 0.1 mm for the rest.

Dialineura (figs. 28—30) it is formed as a gradually narrowing tube which in lateral view curves downwards. Its shape has been found variable in British and Danish species of *Thereva* (Collin, 1948; Lyneborg, 1965), and therefore useful for specific separation. In *Psilocephala* (figs. 31—32) the phallus has a different shape, being almost circular in dorsal view (fig. 32) and flat in lateral view (fig. 31).

The proximal end of the phallus is fused to an arched plate forming the rest of the dorsal portion of the aedeagus. This will be termed: the dorsal apodeme, but is apparently not a separate morphological element. It is not possible to give an exact limit between the phallus and the dorsal apodeme. This latter portion was also found useful as a distinguishing character because it varies much in shape. In *Thereva* (fig. 26) and *Dialineura* (fig. 29) this so-called dorsal apodeme is much wider than the proximal part of the phallus, and the free end of the dorsal apodeme has a distinct incision in *Dialineura,* but none in *Thereva.* Seen laterally (fig. 25 and 28) the dorsal apodeme is high in both genera, i.e. arched. In *Psilocephala* (fig. 32) the dorsal apodeme is not much wider than the proximal part of the phallus, and its free end is deeply incised, so that it appears bifurcate. In lateral view (fig. 31) it is flat, i.e. slightly arched.

On the ventral part of the aedeagus is found a flat or slightly trough-shaped sclerite, which in the following will be termed: ventral apodeme. It arises from the ventral, proximal end of the tubular phallus, and its rod indicates the above-postulated limit between the phallus and the dorsal apodeme. In *Thereva* (fig. 33) and *Psilocephala* (fig. 37) this ventral apodeme is rather narrow and widens gradually, while in *Dialineura* (fig. 35) it is much wider.

The fourth and last element of the aedeagus to be termed here is the ejaculatory apodeme, a term also used for the same morphological element in other families. In the three therevid-genera this element is inserted into the space formed by the dorsal apodeme and the ventral apodeme, its proximal end being situated rather near the proximal end of the phallus. The shape of the ejaculatory apodeme varies in the three genera in question. In *Thereva* (fig. 34) and *Dialineura* (fig. 36) it gradually becomes wider towards the distal end, while in *Psilocephala* (fig. 38) the proximal end is the most thickened.

Summary

The male terminalia of the three therevid-genera: *Thereva* Latr., *Dialineura* Rond., and *Psilocephala* Zett. are described on the basis of their type-species. An attempted homology is made between these structures and the terminalia of the Asilidae. Both the tergal and sternal elements of the segment 8 are well developed. Tergite 9 (+ 10), or epandrium, is present as a large, dorsal shield. Attached to the hind margin of the epandrium is a dorsal pair of small sclerites, here called the cerci, and ventrally to these an additional sclerite. The latter is probably also paired in its disposition and is called the paraprocts.

The two large, semiglobular sclerites constituting the ventral part of the "hypopygium" represent the gonopods (the gonocoxites). The gonocoxite bears a sclerite attached to its dorsal margin which is interpreted as representing a gonapophysis. In the genera examined the gonapophysis has a free distal end bearing some setae. The basal rod of the gonapophysis has no connection with the aedeagus. Sternite 9, or hypandrium, is small or completely reduced. The rod-like sclerite arising from the lumen of the gonocoxite represents a stylus. A ventral lobe arises as an excrescence from the ventral surface of the gonocoxite in all three genera. In *Psilocephala* the distal margin of the ventral lobe is attached to the lateral part of the aedeagus. The aedeagus is otherwise free in the genera examined, i. e. there is no strongly sclerotized connection between the aedeagus and the basal rod of the gonapophysis (as found in other therevid-genera, e.g. *Phycus* Walk.). The intromittent part of the aedeagus is called phallus. This is proximally fused with a so-called dorsal apodeme. A sclerite termed: ventral apodeme arises from the postulated limit between the phallus and the dorsal apodeme. An ejaculatory apodeme is inserted between the dorsal and ventral apodemes.

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ANMELDELSE

Victor Hansen: BILLER XXIV. SANDSPRINGERE OG LØBEBILLER. Larverne ved *Sv. G. Larsson.* — Danmarks Fauna 76, Kbhv. 1968. 451 pp. Pris ib. kr. 65,25.

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F. Bangsholt.