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'Retournement' of the aedeagus in Chrysomelidae (Coleoptera, Phytophaga)

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Key to lettering of figures.

AED :	aedeagus.
GA :	terminal abdominal ganglion, compound.
LS :	position of the last spiracle.
LT :	lateral longitudinal tracheal trunk.
MED :	median ejaculatory tract.
NA :	right and left aedeagal nerves fused basally.
NAL :	left aedeagal nerve.
NAR :	right aedeagal nerve.
PS :	position of the penultimate spiracle.
SP :	spiculum.
SPA :	accessory spiculum.
SPA2 :	second accessory spiculum.
ST :	last visible sternum.
TAL :	left aedeagal trachea.
TANL :	left nerve/nerves for terminal portion of the abdomen.
TANR :	right nerve/nerves for terminal portion of the abdomen.
TAR :	right aedeagal trachea.

The rotation of the aedeagus about its longitudinal axis in ontogeny has been referred to as 'torsion' by Lindorth & Palmén (1956), as 'version' by Jeannel & Paulian (1944), and as 'retournement' by Jeannel (1955). Jeannel (1955) has carefully distinguished 'retournement' from such other phenomena as a temporary tilting of the ventrally curved aedeagus on one side in repose, or 'déversement', which is undone every time the aedeagus is protruded for copulation, and which has often been confused with the ontogenetic 'retournement'.

'Retournement' of the aedeagus is known in some Coleoptera (in certain Silphidae, Staphylinidae and probably also Oedemeridae, Jeannel, 1955; in *Tenebrio*, Kerschner, 1913; and in the Dytiscid *Hydroporus*, Heberdey, 1928). The first definite record of this phenomenon in Phytophaga is in the work of Verma (1958, 1969), who has observed 'retournement' through 180° in the clock-wise direction, when seen from behind, taking place in the pupa of the Chrysomelid *Galerucella birmanica* Jac., and who has pointed out the anatomical effects of this developmental change in the adult, including twisting of the tracheal and nervous supply reaching the aedeagus base.

The present authors have examined the adults of the various Chrysomelid beetles, which could be locally collected during the period from May 1968 to May 1969 for the above mentioned anatomical effects of 'retournement' ; and

the observations are presented below. In all cases freshly killed males were dissected.

Before coming to the observations it would be profitable to consider theoretically what is expected in the adult if the aedeagus has turned about its axis through 180° in the clock-wise direction, when seen from behind, during ontogeny. This would obviously make the paired tracheal and nervous supply for the aedeagus twisted. When the aedeagus is small in development and has rotated, the aedeagal trachea coming from the left side would be seen passing beneath the right trachea in a dissection from the ventral side (fig. 1 (*b*)). But

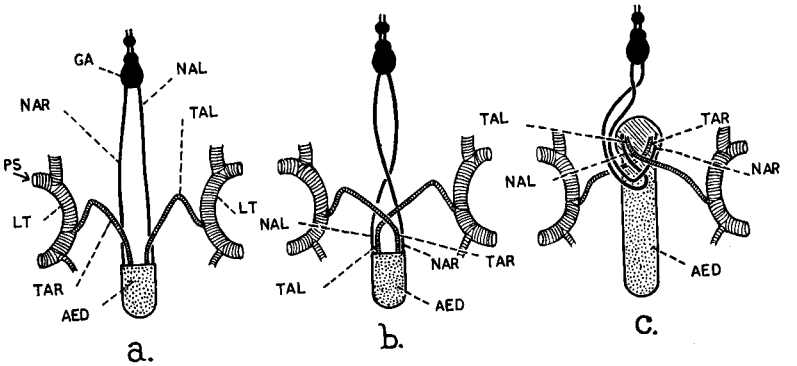


FIG. 1. Theoretical diagrams showing the effect of the 'retournement' on the tracheal and nervous supply for the aedeagus. (*a*) The aedeagus is without 'retournement' and is small in development. (*b*) The young and small aedeagus has undergone 'retournement'. (*c*) The aedeagus with 'retournement' has grown forward in length. (In all cases it has been imagined that the male has been dissected from the ventral side.)

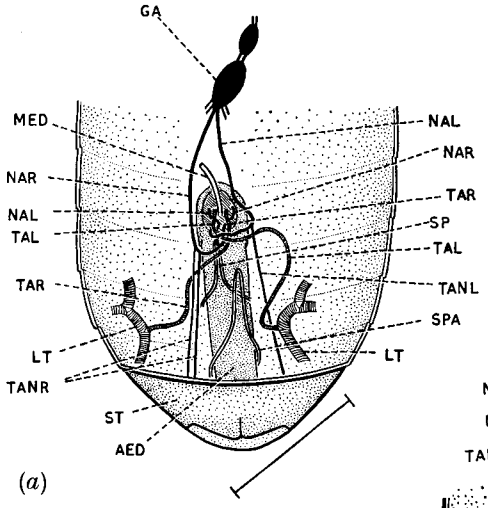
when the aedeagus has grown forward, the tracheal inter-crossing would be inverted ; and now the left trachea would be passing over the right one, when examined from the ventral side (fig. 1 (*c*)). Such a situation should be taken as indicative of a clock-wise rotation through nearly 180°. A similar change in the nature of the nervous inter-crossing during the growth of the aedeagus is not expected, as the aedeagal nerves arise in these insects far anteriorly, from the terminal abdominal ganglion, which is a compound ganglion, having resulted from forward shifting and fusion of several abdominal ganglia. If, however, in a dissection the point of crossing between the aedeagal nerves is shifted posteriorly, close to the aedeagal base, where the nerves are looping forward to reach the basal orifice of the aedeagus, the pattern of cross seen would be the inverted form of that shown in fig. 1 (*c*). The looping forward of the nerves may eliminate an obvious nervous inter-crossing, as ample looping of the nerves will permit crossing of each nerve to the opposite side without creating a typical pin-point crossing of the nerves in a particular aspect, say when seen from the ventral side. Also the left aedeagal trachea and the left nerve may get wound round the dorsal side of the aedeagus base, so that a typical chiasma is again eliminated. (Here by 'dorsal' is meant the upper surface of the aedeagus after 'retournement'.)

Observations

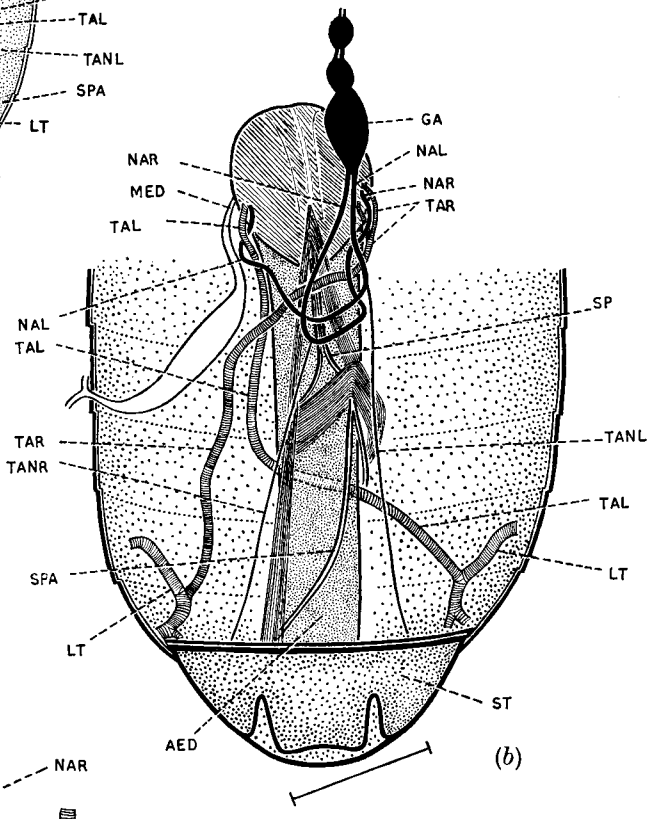
Material No.	Species	Nature of the tracheal supply reaching the aedeagus base	Nature of the nervous supply for the aedeagus
1	*Altica coerulea* Ol. (Halticinae)	As in fig. 1 (*c*) (fig. 2 (*c*)).	As in fig. 1 (*c*) (fig. 2 (*c*)).
2	*Pachnephorus bistriatus* Muls. (=*impressus* Rosenh.) (Eumolpinae)	As in fig. 1 (*c*) (fig. 3 (*b*)).	No satisfactory dissection for the nervous supply could be made because of limited supply of the material and its small size.
3	*Aulacophora foveicollis* Luc. (Galerucinae)	As in fig. 1 (*c*) (fig. 2 (*f*)).	As in fig. 1 (*c*) (fig. 2 (*f*)).
4	*Aspidomorpha miliaris* F. (Cassidinae)	As in fig. 1 (*c*).	As in fig. 1 (*c*).
5	*Aulacophora intermedia* Jac. (Galerucinae)	As in fig. 1 (*c*).	As in fig. 1 (*c*).
6	*Colasposoma auripenne* Motsch. (Eumolpinae)	As in fig. 1 (*c*) (fig. 3 (*c*)). (The spiculum is like a broad plate. The aedeagal tracheae and nerves, after crossing over to the other side, enter the aedeagus close to the sides of the plate-like spiculum.)	As in fig. 1 (*c*) (fig. 3 (*c*)).
7	*Cassida* sp. (Cassidinae)	As in fig. 1 (*c*) (fig. 2 (*d*)).	As in fig. 1 (*c*) (fig. 2 (*d*)).
8	*Medythia suturalis* Motsch. (Galerucinae)	As in fig. 1 (*c*) (fig. 3 (*d*)).	No satisfactory dissection for the nervous supply could be made because of limited supply of the material and its small size.

Observations—(*continued*)

Material No.	Species	Nature of the tracheal supply reaching the aedeagus base	Nature of the nervous supply for the aedeagus
9	*Monolepta signata* Ol. (Galerucinae)	As in fig. 1 (*c*) (fig. 2 (*b*)).	As in fig. 1 (*c*) (fig. 2 (*b*)). However, in most specimens dissected the two aedeagal nerves are fused together for a considerable distance from the terminal abdominal ganglion. Such separate nerves, as shown in fig. 2 (*b*), have been seen only in one out of ten specimens dissected. In those cases, in which the aedeagal nerves are fused basally, the twisted nature of the nervous supply may be inferred on comparing the aedeagal nerves with their branches, supplying the posterior part of the abdomen, e.g. the branch of the nerve entering the basal orifice of the aedeagus on the left side, supplies the posterior part of the abdomen on the right side.
10	*Crepidocera* sp. (Halticinae)	As in fig. 1 (*c*) (fig. 2 (*e*)).	The aedeagal nerves are basally fused as in material No. 9, in all the specimens studied. The fine branches of these nerves supplying the posterior part of the abdomen could not be made out satisfactorily.
11	*Cryptocephalus ovulum* Suffr. (Cryptocephalinae)	As in fig. 1 (*c*).	No satisfactory dissection of the nervous supply could be made, as only one male could be collected and studied.
12	*Phyllotreta chotanica* Duviv. (Halticinae)	As in fig. 1 (*c*) (fig. 3 (*a*)).	The nerves are fused together basally. This situation has been found in all the specimens studied. However, the twisted nature of the nervous supply could be inferred in the same way as in case of material No. 9 (fig. 3 (*a*)).
13	*Cryptocephalus sehestedti* F. (Cryptocephalinae)	As in fig. 1 (*c*) (fig. 3 (*e*)).	As in fig. 1 (*c*) (fig. 3 (*e*)).
14	*Aphthona kanaraensis* Jac. (Halticinae)	As in fig. 1 (*c*) (fig. 2 (*a*)).	As in fig. 1 (*c*) (fig. 2 (*a*)).



(a)



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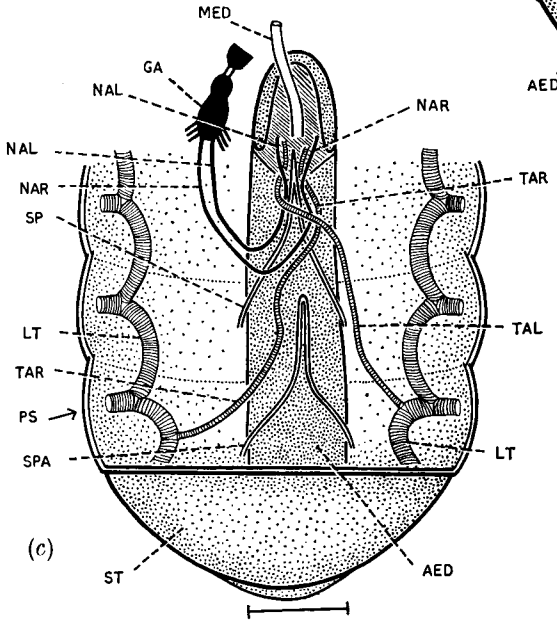

(c)

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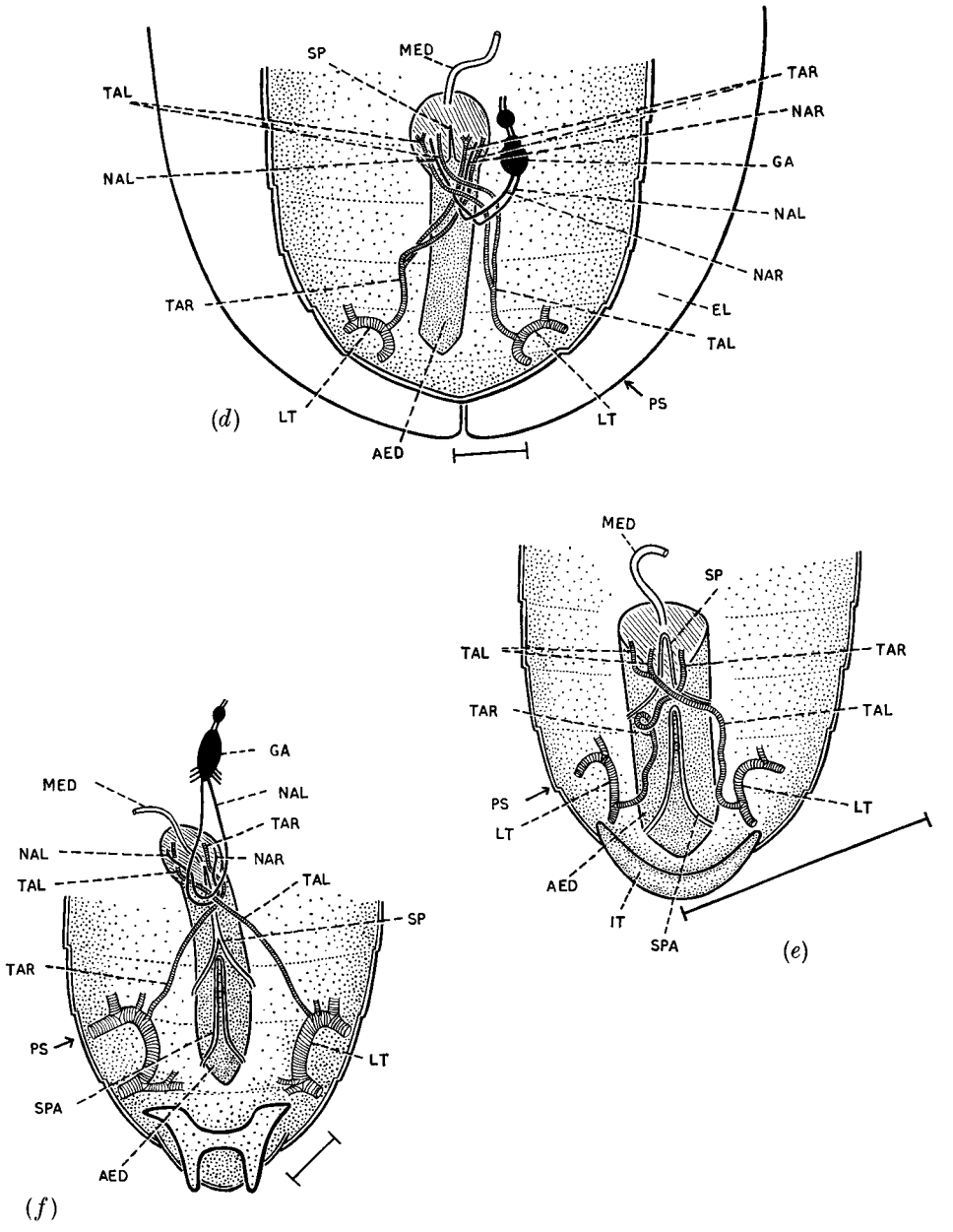

FIG. 2. Figures of dissections of the abdomens of the males of certain Chrysomelid beetles to show the tracheal and the nervous supply for the aedeagus. In all cases the abdomen has been dissected from the ventral side. The scale accompanying each figure denotes 0·5 mm. (*a*) *Aphthona kanaraensis* Jac. (material No. 14). (*b*) *Monolepta signata* Ol. (material No. 9). (*c*) *Altica coerulea* Ol. (material No. 1). (*d*) *Cassida* sp. (material No. 7). (*e*) *Crepidocera* sp. (material No. 10). (*f*) *Aulacophora foveicollis* Luc. (material No. 3).

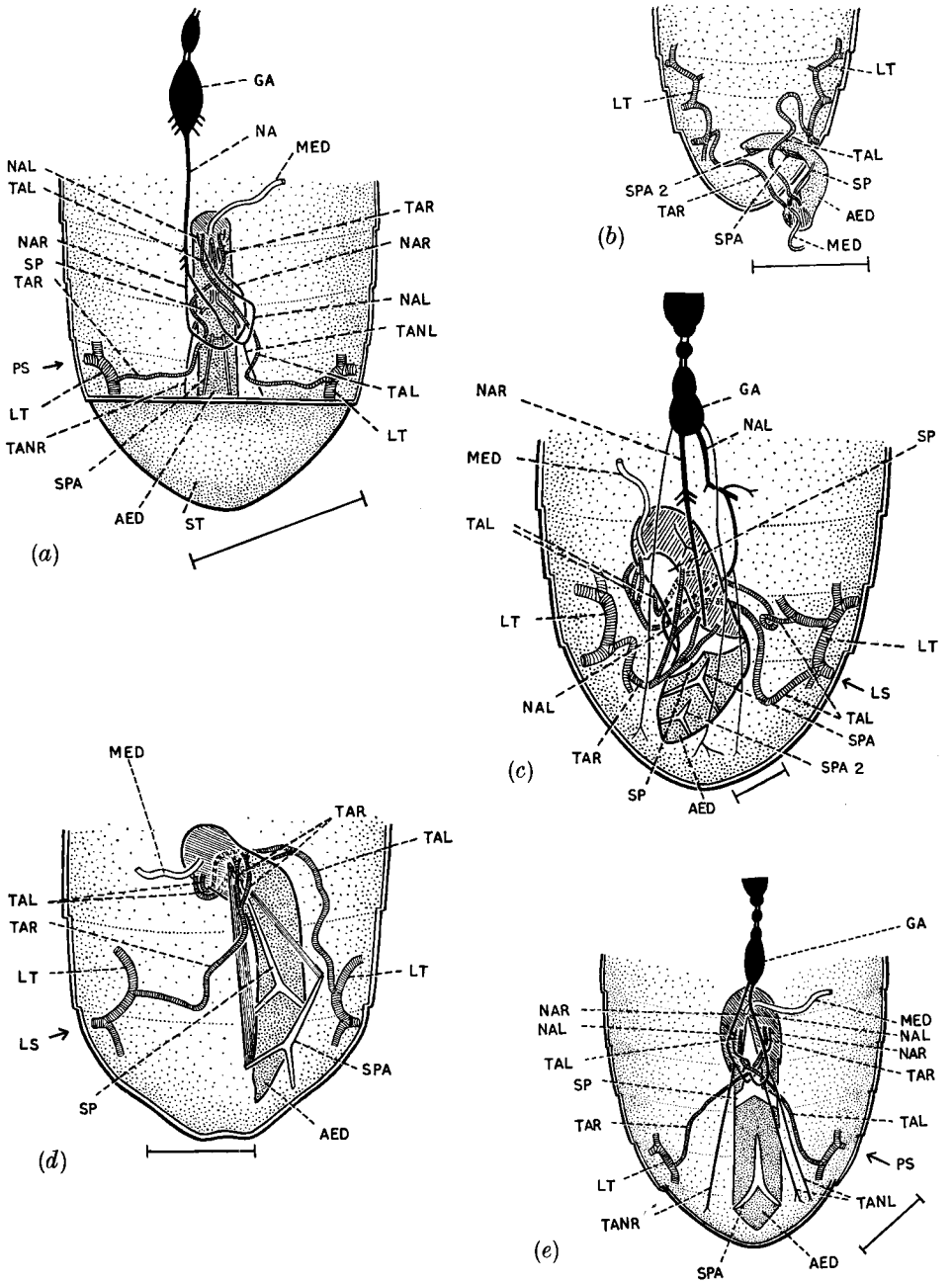

FIG. 3. Figures of dissections similar to those included in fig. 2. (*a*) *Phyllotreta chotanica* Duviv. (material No. 12). (*b*) *Pachnephorus bistriatus* Muls. (material No. 2). (The aedeagus has been lifted and then tilted towards the left of the animal to show the tracheae entering the aedeagus. To visualize the natural position of the aedeagus imagine that it is brought into the median position and then pushed back into the abdomen.) (*c*) *Colasposoma auripenne* Motsch. (material No. 6). (*d*) *Medythia suturalis* Motsch. (material No. 8). (*e*) *Cryptocephalus sehestedti* F. (material No. 13).

Thus in all these species, it may be inferred that the aedeagus has undergone 'retournement' through 180° in the clock-wise direction, when seen from behind. In none of the species has any asymmetry of the terminal abdominal sclerites been noted, and in all cases the anus has been observed as situated above the opening of the genital pocket in the ano-genital vestibule. It may also be inferred for the species in question that (contrary to the situation in Diptera) the torsion of the aedeagus in Coleoptera is independent of the terminal part of the abdomen, inferred earlier by one of the present authors (Verma, 1969) on the basis of the facts then available.

In addition to *Galerucella birmanica* Jac., 'retournement' of the aedeagus through 180° in the clock-wise direction, when seen from behind, actually taking place in ontogeny has been seen in *Aspidomorpha miliaris* F. (Verma & Kumar).

Though the number of the species examined in the present study is small in relation to the size of the family, it may be inferred that the 'retournement' of the aedeagus is a fairly common phenomenon among Chrysomelidae, if not universal, as it has been invariably detected in the various species examined.

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