

Phylogenetic significances of the ventral nerve cord in the Chrysomeloidea (Coleoptera: Phytophaga)

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ABSTRACT. The ventral nerve cord of adult Chrysomeloidea exhibits variation in the degree of fusion of the meso- and metathoracic ganglia. Similar variation occurs also in the ganglia of the abdominal chain, and in the single or double connectives between them. In adult Chrysomeloidea (and Curculionoidea) there never seem to be more than five separate abdominal ganglia, the first two being more or less fused to the metathoracic ganglion and the last two more or less connate; the supposed primitive condition is retained in some Cerambycidae. Trends toward the fusion of additional abdominal ganglia appear in several different lines in Chrysomelidae (and in Cerambycidae), and in more than one line a condition is reached in which only the ganglion in the third abdominal segment remains free. Structures possibly representing 'perisymphatic organs' have been observed in a few of the seventy-eight European and Indian species studied. Systematic and phylogenetic conclusions are drawn.

Introduction

The ventral nerve cord in the superfamily Chrysomeloidea consists of the suboesophageal, thoracic and abdominal ganglia. Various degrees of fusion of the thoracic and abdominal ganglia occur. The first two abdominal ganglia are always fused with the metathoracic ganglion and the last two abdominal ganglia are always fused in a terminal mass. Connectives may be single or double.

Blanchard (1846) and Brandt (1879) studied the nerve cord of adult and larval Coleoptera and stated that the basic number of the abdominal ganglia in polyphagan larvae is eight as in *Chrysolina hyperici* (Forster) and *Phaedon cochleariae* (F.) (Hamnett, 1944). Brandt's (1879) study of the metamorphic changes in the nerve cord of *Coccinella septempunctata* L. provides a basis for the morphological interpretation

of the nerve cord of Cucujiformia (Crowson, 1960).

Structures similar to the perisymphatic organs (Grillot, 1976) have been observed in some subfamilies of Chrysomelidae.

Materials and Methods

The specimens studied were collected from Northern India (1975–78) and from the Glasgow area (1980). The specimens were preserved in Pampel's fluid and dissected in 70% alcohol under a stereo-binocular microscope. Living beetles were narcotized with ethyl ether and dissected in 2% saline solution. Specimens of *Exosoma lusitanica* (L.), *Orsodacne cerasi* (L.) and *Syneta betulae* (F.) were supplied by Professor Manuel G. de Viedma (Spain), Dr W. Wittmer of Basle (Switzerland) and Dr Hans Silfverberg (Finland), respectively. Alcohol-preserved specimens of many species from the personal collections of Dr R. A. Crowson were also studied. Figures were drawn using a squared eyepiece graticule.

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Observations

The nerve cord of most of the species studied is figured; descriptions of the brain are avoided for the sake of brevity, and emphasis is laid upon descriptions of the thoracic and abdominal ganglia. The arrangement of the subfamilies of Chrysomelidae is according to Mann & Crowson (1981).

ORSODACNINAE (Fig. 1)

The nerve cord of *Orsodacne cerasi* has all the thoracic and abdominal ganglia 3–5 free. Abdominal ganglion 6 is partly detached from the terminal nerve mass of 7 and 8. All the abdominal nerve connectives are apparently single (Mann & Crowson, 1981).

SYNETINAE (Fig. 2)

The nerve cord of *Syneta betulae* has all the thoracic and abdominal ganglia 3–5 free, with double nerve connectives in between (Mann & Crowson, 1981). [In Fig. 2 there should be a fine line separating the double connectives between ganglia 3–4, 4–5 and 5–6 + 8.]

EUMOLPINAE (Figs. 3–7)

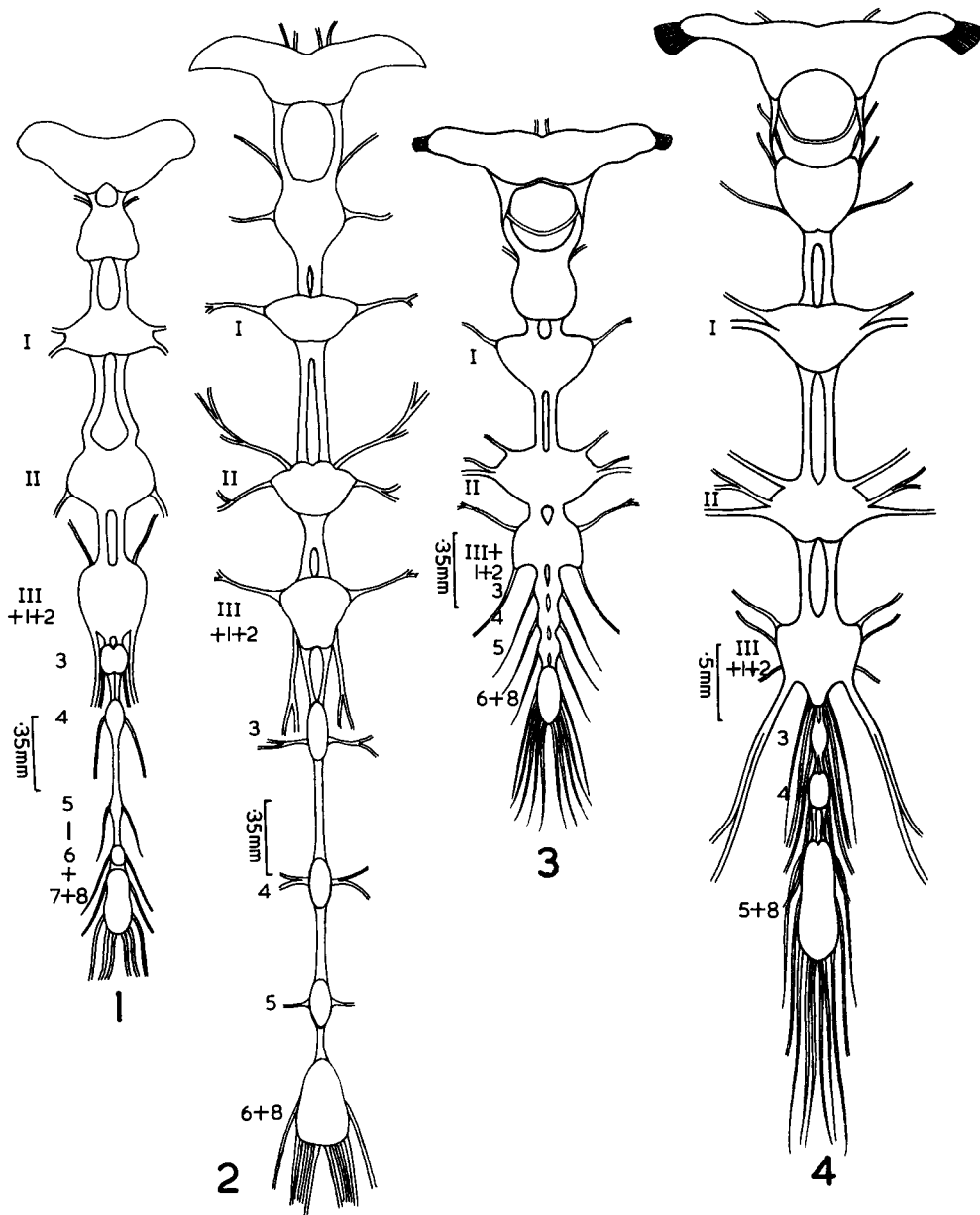
The representative forms studied show various degrees of fusion of the abdominal ganglia. We found three, two, one and no free abdominal ganglia in our present observations. There are three free abdominal ganglia in *Adoxus obscurus*, *Scelodonta indica*, *Spilopyra sump-tuosa* (Kasap, 1979) and *Colasposoma semi-costatum*; two in *Platycorynus peregrinus*, *Eubraxis indica*, *Pseudopiomera andrewesi* and *Tricliona* sp.; one in *Basilepta variable* and none in *Nodina crassipes* and *Abirus rubripes*. Of the thoracic ganglia, the meso- and metathoracic ganglia are contiguous to each other in *Basilepta variable*, fused in *Abirus rubripes* and *Nodina crassipes* and discrete in the rest of the species studied. The nerve connectives are double in all the species studied by us or others.

GALERUCINAE (Figs. 8–22)

The number of free abdominal ganglia in the species studied varies considerably, the maximum being three in *Exosoma lusitanica*. There are two free abdominal ganglia in *Aulacophora foveicollis*, *Gallerucida rutilans*, *Macrima armata*, *Monolepta signata*, *Lochmaea suturalis*, *Luperus longicornis*, *Paridea octomaculata* and *Phyllobrotica quadrimaculata* (three free abdominal ganglia according to Kasap, 1979); and one in *Diorhabda lusca*, *Gallerucida bicolor*, *Merista quadrifasciata*, *Galerucella regosa*, *G. birmanica*, *G. nymphaeae*, *Mimastra quadripartita*, *M. oblonga* and *Sermylassa halensis*. In all the species studied the mesothoracic ganglion is closer to the metathoracic than to the prothoracic ganglion. The nerve connectives are double. The nerve connectives between the first free abdominal ganglion (No. 3) and the metathoracic nerve complex are the shortest of the abdominal nerve connectives.

HALTICINAE (Figs. 23–26)

The nerve cord in the representatives of this subfamily tends to be more concentrated than in Galerucinae. The number of free abdominal ganglia varies; there are two in *Haltica cyanea*, *H. ericeti*, *Derocrepis rufipes*, *Crepidodera transversa*, *Chalcoides fulvicornis*, *Psylliodes marcida*, *P. cuprea*, *Podagrica menetriesi* and *Aphthona coerulea*; one in *Apteropeda orbiculata*, *Chaetocnema concinna*, *Phyllotreta undulata*, *Hespera nigripes*, *Luperomorpha nigripennis*, *Longitarsus melanocephalus* and *Hyphasoma nigricorne*; in *Mantura obtusata* and *Sphaeroderma testaceum*, the abdominal ganglia are fused with no distinguishable connectives in between. Of the thoracic ganglia, the meso- and metathoracic ganglia are connate in *Luperomorpha nigripennis* and contiguous in *Hespera nigripes*. According to Kasap (1979), *Longitarsus melanocephalus* shows a very unusual condition with the prothoracic ganglion fused to the suboesophageal one and the mesothoracic with the metathoracic one. The abdominal connectives are double in all the species studied.

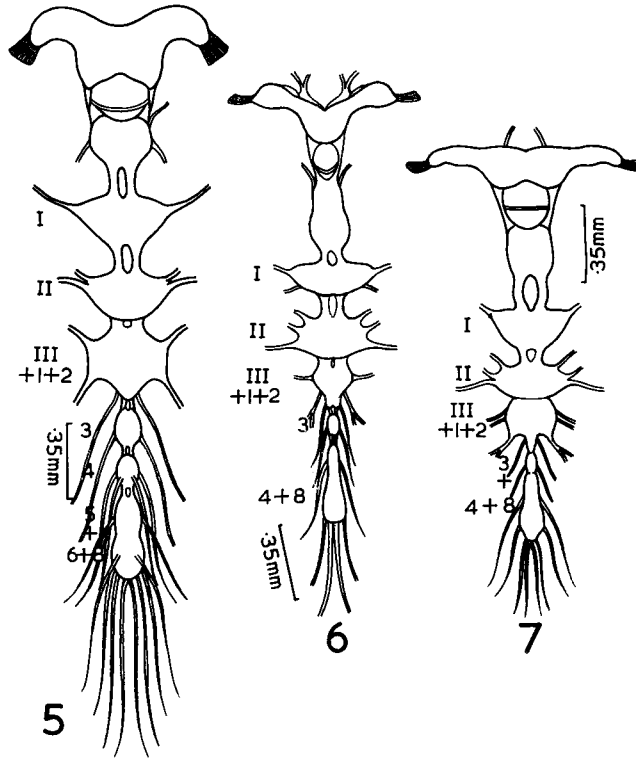


FIGS. 1-4. Ventral nerve cord of: 1, *Orsodacne cerasi* (L.); 2, *Syneta betulae* (F.); 3, *Colaspodoma semicostatum* Jacoby; 4, *Platycorynus peregrinus* (Herbst).

CHRYSOMELINAE (Figs. 27-33)

The number of free abdominal ganglia in the species studied here varies from one to three. Abdominal ganglia 3-5 are free in *Timarcha tenebricosa*, *Entomoscelis adonidis*, *Phyto-*

decta pallida and *Phyllocharis cyanicornis*; abdominal ganglion 6 is partially detached in *Timarcha tenebricosa*. There are two free abdominal ganglia (Nos. 3 and 4) in *Chrysolina polita*, *Ch.exanthematica*, *Ch.varians*, *Ch.staphylea*, *Ch.hyperici*, *Ch.americana* and



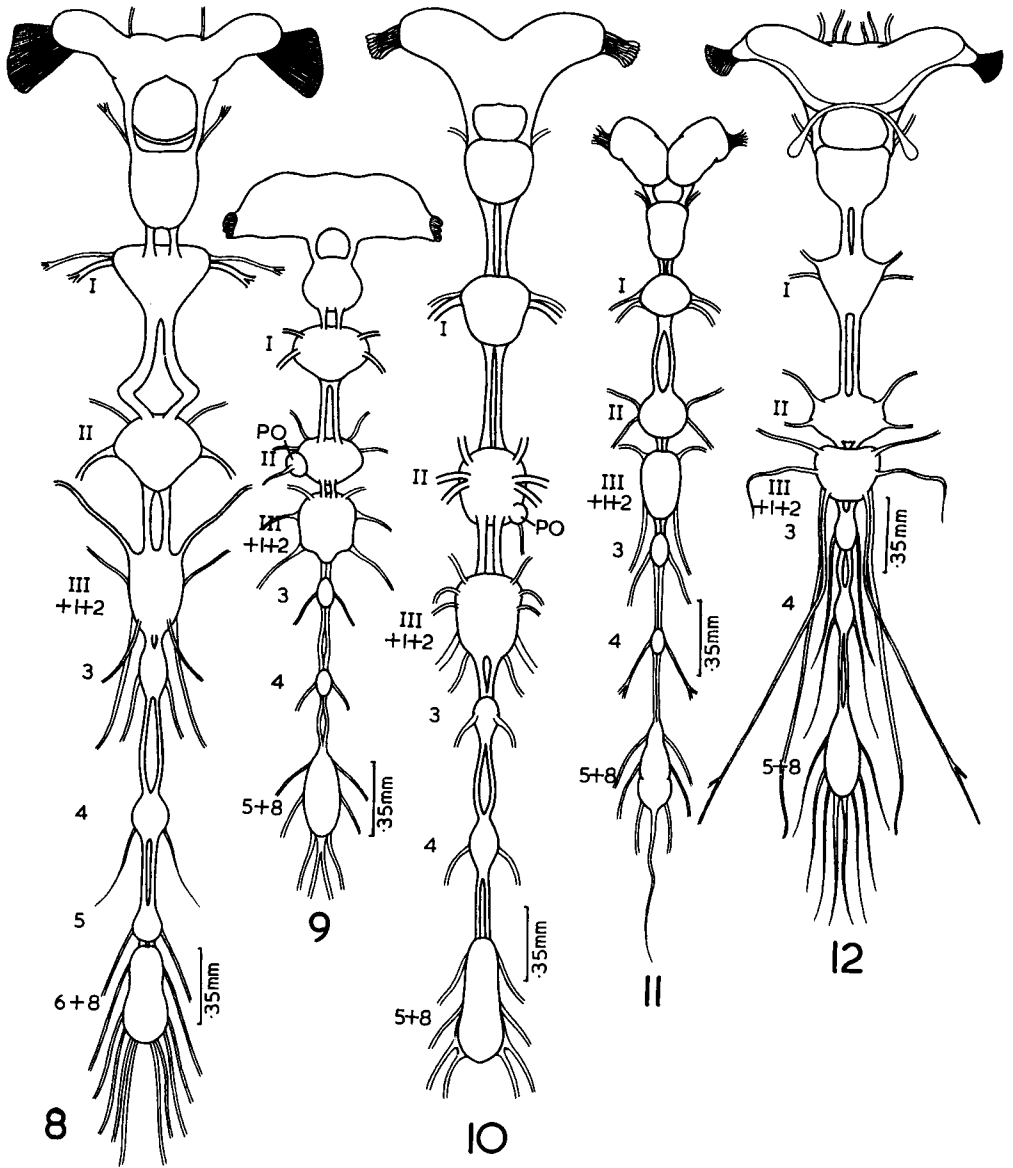
FIGS. 5–7. Ventral nerve cord of: 5, *Eubrachis indica* Baly; 6, *Basilepta variabile* (Duvivier); 7, *Nodina crassipes* Jacoby.

Paropsis sp.; in *Chrysomela aenea*, *Ch. populi* and *Prasocuris phellandrii* there is only one free abdominal ganglion (No. 3) and ganglion 4 is partially detached, while ganglion 4 is fused with the terminal nerve mass in *Gastroidea viridula*, *Hydrothassa marginella*, *Phaedon tumidulus*, *Ph. cochleariae*, *Phyllo-decta vulgatissima*, *Phytodecta olivacea* and *Plagioderia versicolorea*. In *Leptinotarsa decemlineata* the abdominal ganglia are fused (Pavlovsky & Teravsky, 1958). The thoracic ganglia are all free. The mesothoracic ganglion is closer to the metathoracic than to the prothoracic ganglion. In *Gastroidea viridula*, structures which may correspond to the peri-sympathetic organs (Grillot, 1976) were found on the suboesophageal ganglion and the fused nerve mass of abdominal ganglia 4–8 (Fig. 31, PO). On the basis of the number of free abdominal ganglia and the presence or absence of larval glands, it is possible to form two natural groups of the representatives

studied; one is with defensive larval glands and one free abdominal ganglion (i.e. genera *Chrysomela*, *Gastroidea*, *Hydrothassa*, *Phaedon*, *Phyllo-decta*, *Phytodecta*, *Plagioderia* and *Prasocuris*), others without defensive glands, and with two or three abdominal ganglia (i.e. genera *Chrysolina*, *Entomoscelis* and *Timarcha*). The nerve connectives are double in all the species studied.

DONACIINAE (Figs. 34–35)

The nerve cords of the species of *Donacia* and *Plateumaris* studied here have three free abdominal ganglia (Nos. 3, 4 and 5). Ganglia 6–8 are fused into the terminal nerve mass. The abdominal nerve connectives are single in *Plateumaris discolor* and double in *Donacia crassipes*. Of the thoracic ganglia, the meso-thoracic is closer to the meta- than the pro-

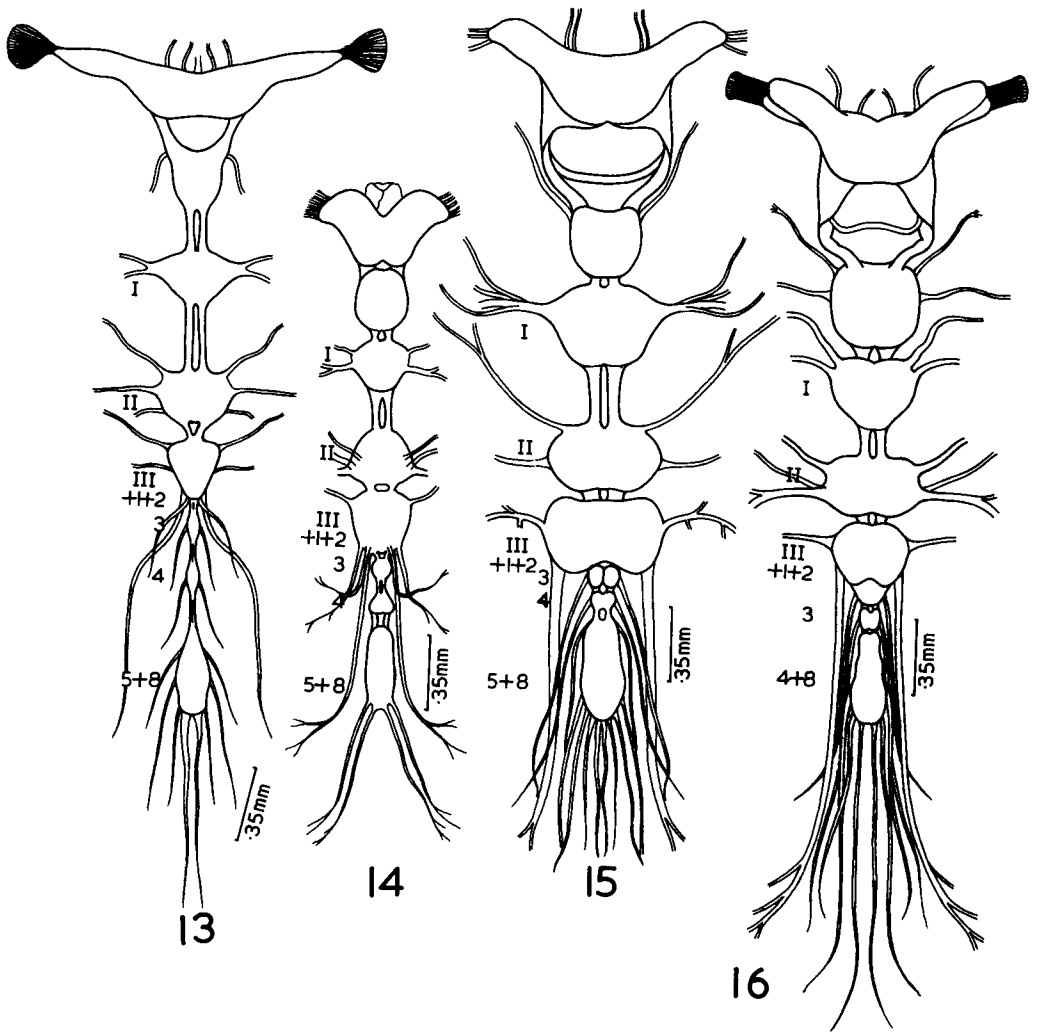


FIGS. 8–12 Ventral nerve cord of: 8, *Exosoma lusitanica* (L.); 9, *Lochmaea suturalis* (Thunberg); 10, *Phyllobrotica quadrimaculata* (L.); 11, *Luperus longicornis* (F.); 12, *Aulacophora foveicollis* (Lucas).

thoracic ganglion. Structures which might correspond to Grillot's (1976) perisymphatic organs were found on either side of the meso-thoracic ganglion and ventral to the terminal abdominal nerve mass in *Donacia crassipes* (Fig. 34, PO).

CRIOCERINAE (Figs. 36–39)

The nerve cords of the species are basically similar to those of Donaciinae. There are three free abdominal ganglia (Nos. 3, 4 and 5) in all the species of *Lema*, *Oulema*, *Crioceris*



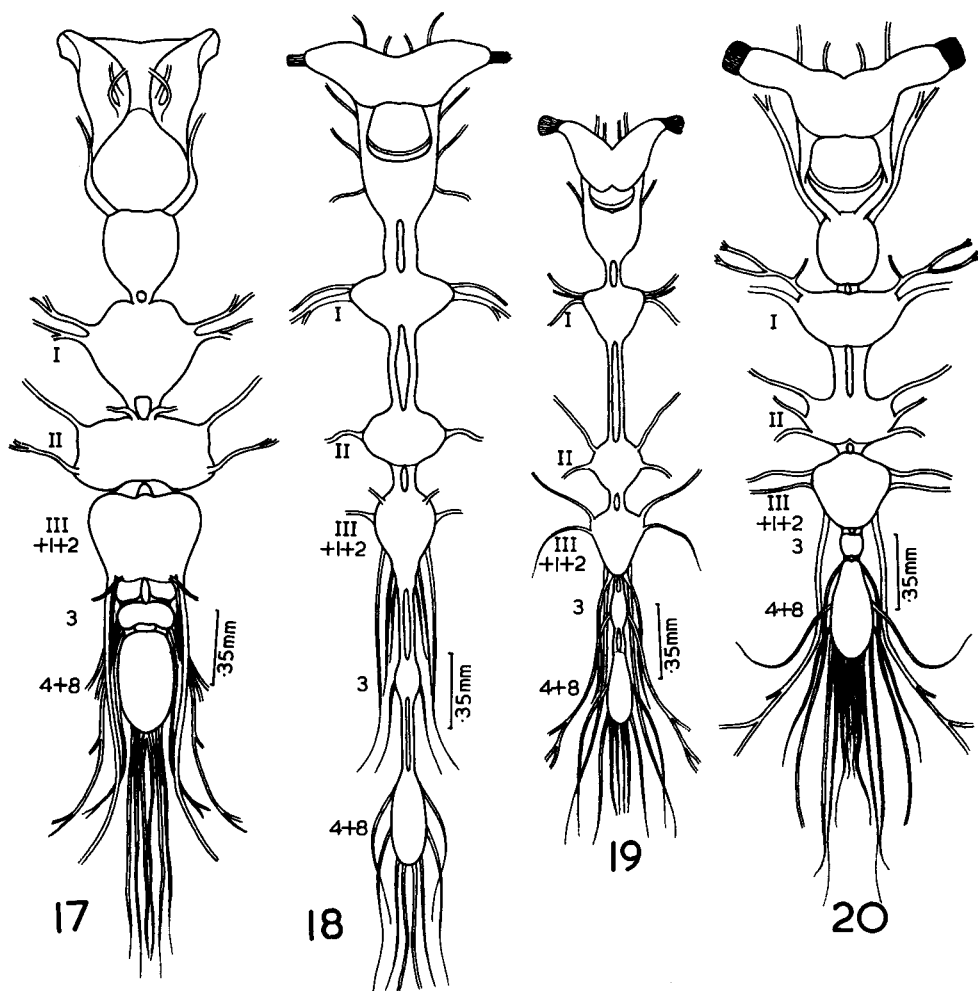
FIGS. 13–16. Ventral nerve cord of: 13, *Macrima armata* Baly; 14, *Monolepta signata* (Olivier); 15, *Gallerucida rutilans* (Hope); 16, *Merista quadrifasciata* (Hope).

and *Lilioceris* studied by us and others (Blanchard, 1846; Kasap, 1979). The abdominal connectives are double in all species included in this study.

HISPINAE (Figs. 40–42)

Of the species of this subfamily studied here, there are three free abdominal ganglia (Nos. 3, 4 and 5) in *Dactylispa peregrina*, *Rhadinosa*

laghua and *R. reticulata*; two (Nos. 3 and 4) in *Aproidea balyi* (No. 5 being partially detached from the terminal nerve mass of 6–8) and six (Nos. 3–8) in *Hispa testacea* (Kasap, 1979). In Chrysomelidae it is quite unusual to have six ganglia free as reported by Kasap (1979) in *Hispa testacea*. We assume the condition to be abnormal. The abdominal nerve connectives are double in all the species studied, being unusually long between the metathoracic and the first free abdominal ganglion (No. 3).



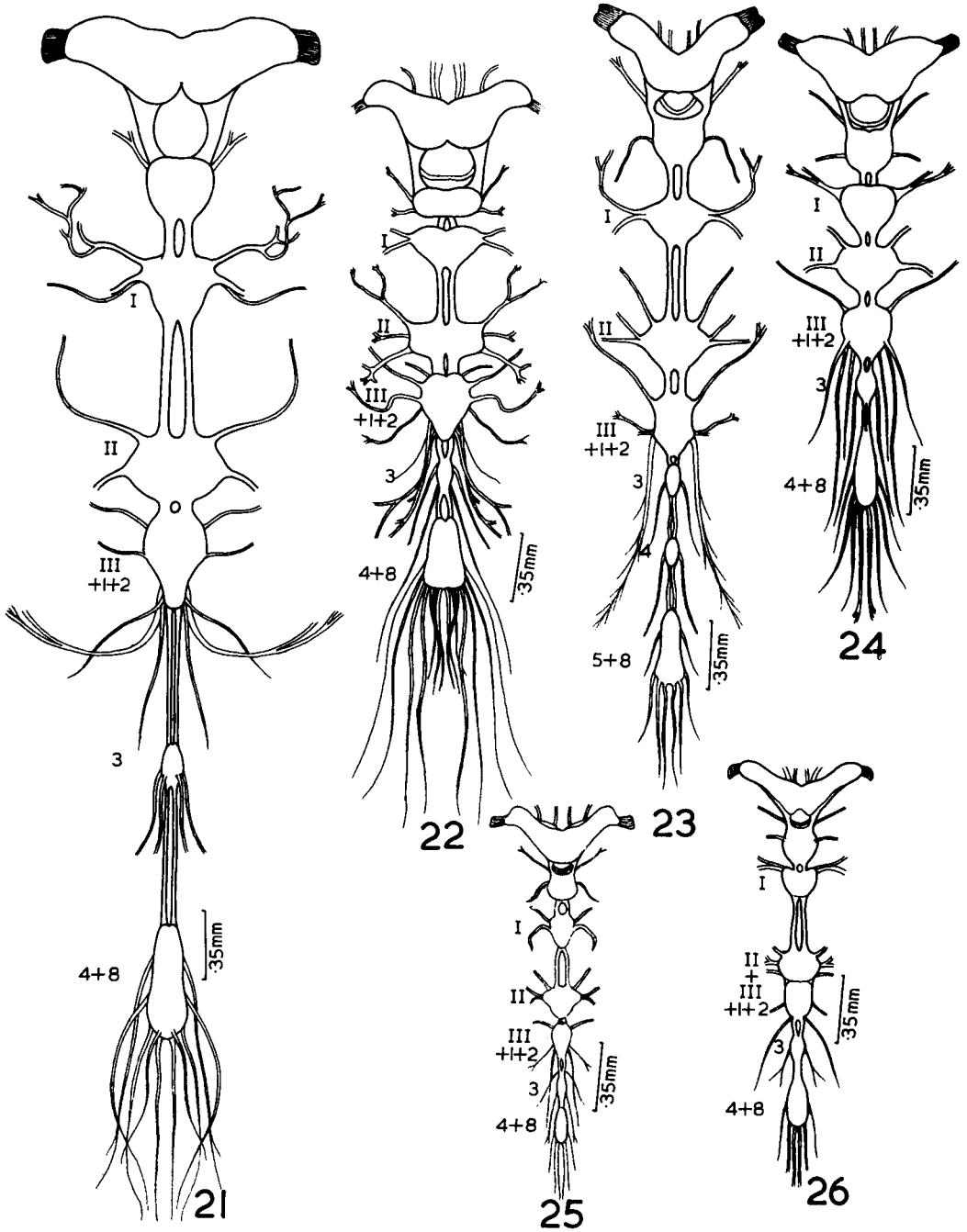
FIGS. 17–20. Ventral nerve cord of: 17, *Paridea octomaculata* (Baly); 18, *Mimastra quadripartita* Baly; 19, *Galerucella rugosa* Jacoby; 20, *Gallerucida bicolor* (Hope).

CASSIDINAE (Figs. 43–46)

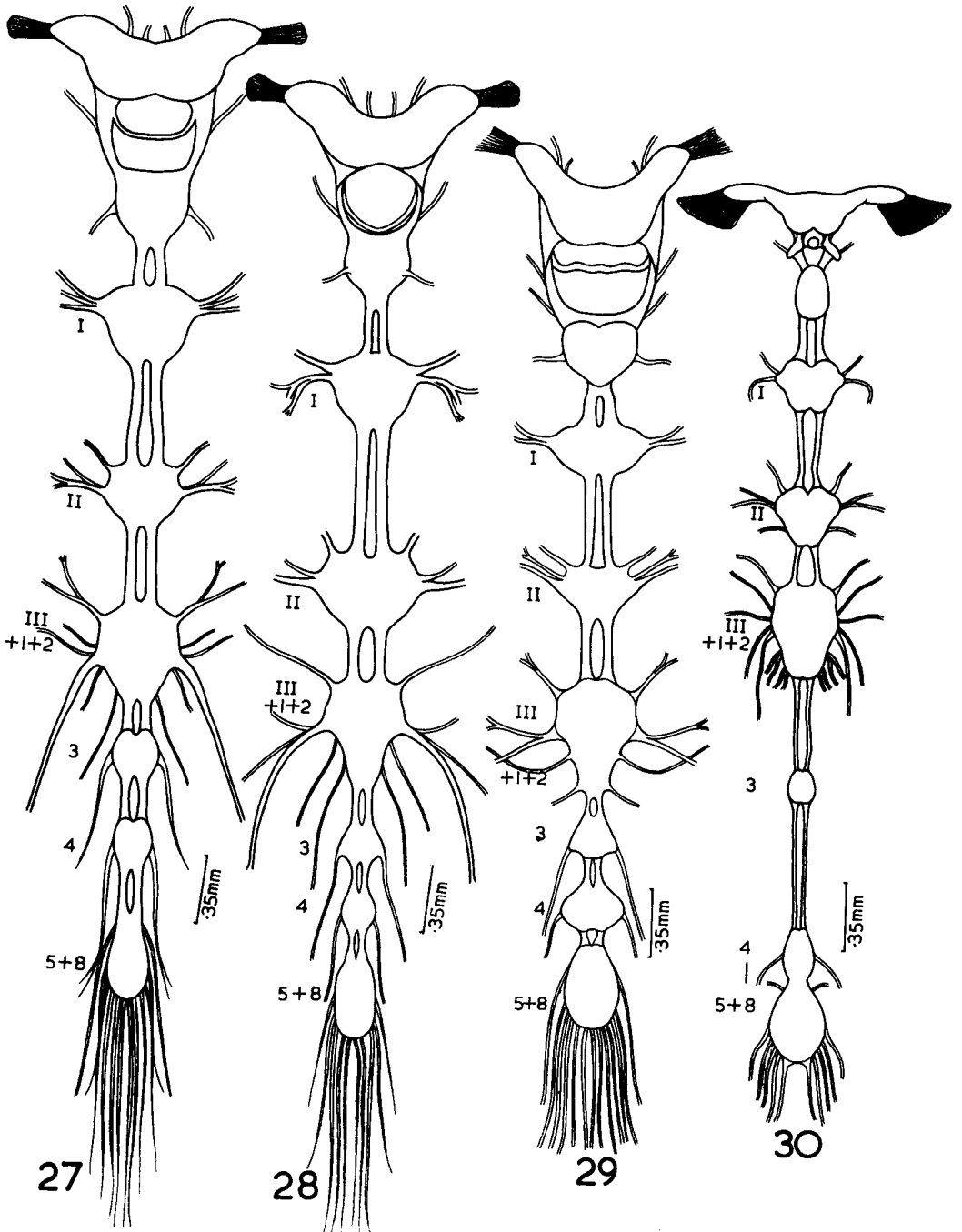
The nerve cord of *Cassida nobilis*, *C.rubiginosa*, *Glyphocassis trilineata* and *Laccoptera quadrimaculata* has two free abdominal ganglia (Nos. 3 and 4). The connectives are double in all the species studied. The thoracic ganglia are discrete. Abdominal ganglia 5–8 fuse to form the terminal nerve mass in all the species mentioned here.

CRYPTOCEPHALINAE (Figs. 47–51)

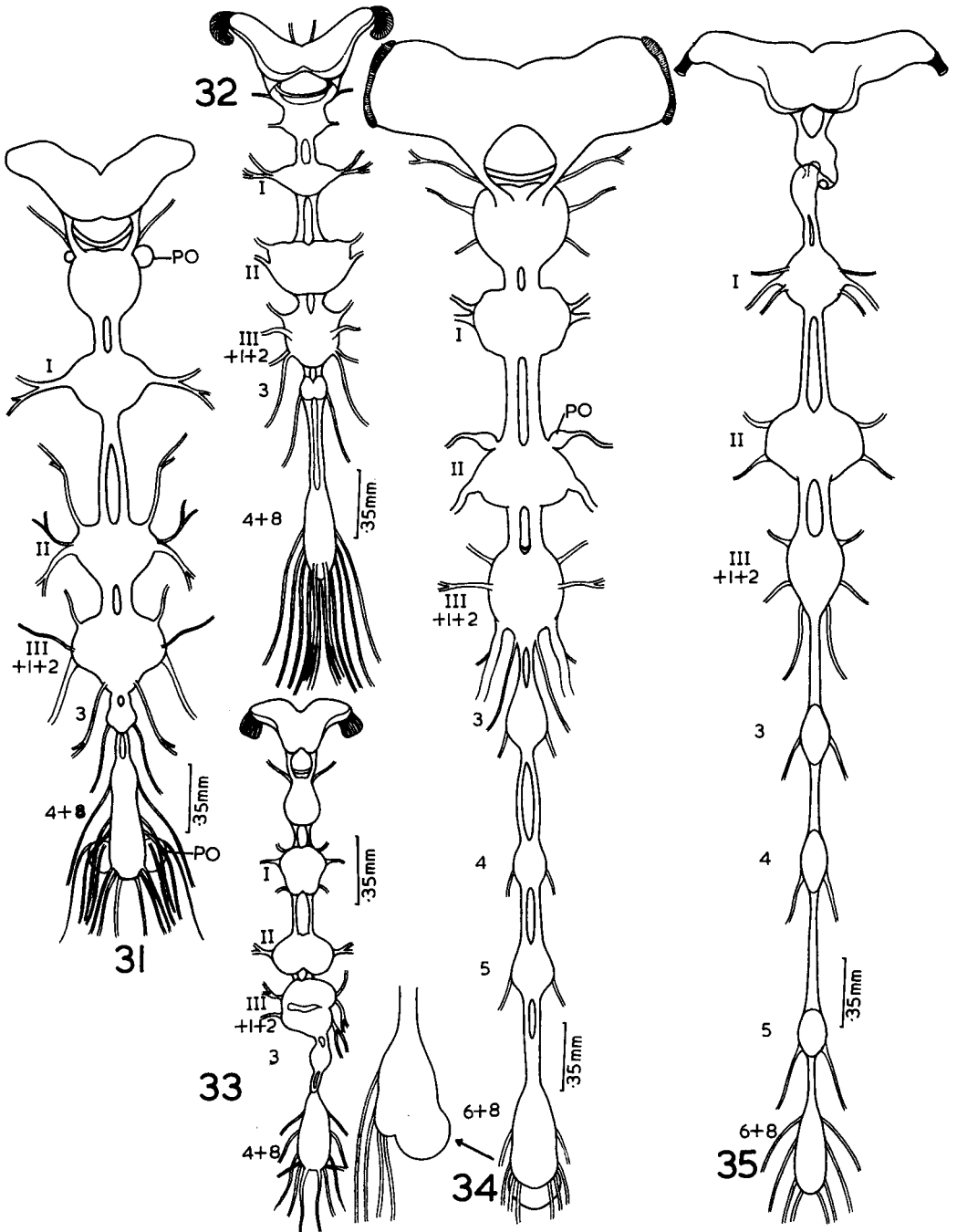
In all the seven species of *Cryptocephalus* studied here, there is only one entirely free abdominal ganglion (No. 3). There are slight differences in the nerve chain among the species studied here. Abdominal ganglia 2 and 4 are partially detached from the metathoracic and the terminal nerve mass, respectively, in *Cryptocephalus herbsti* and *C.sericeus*, and



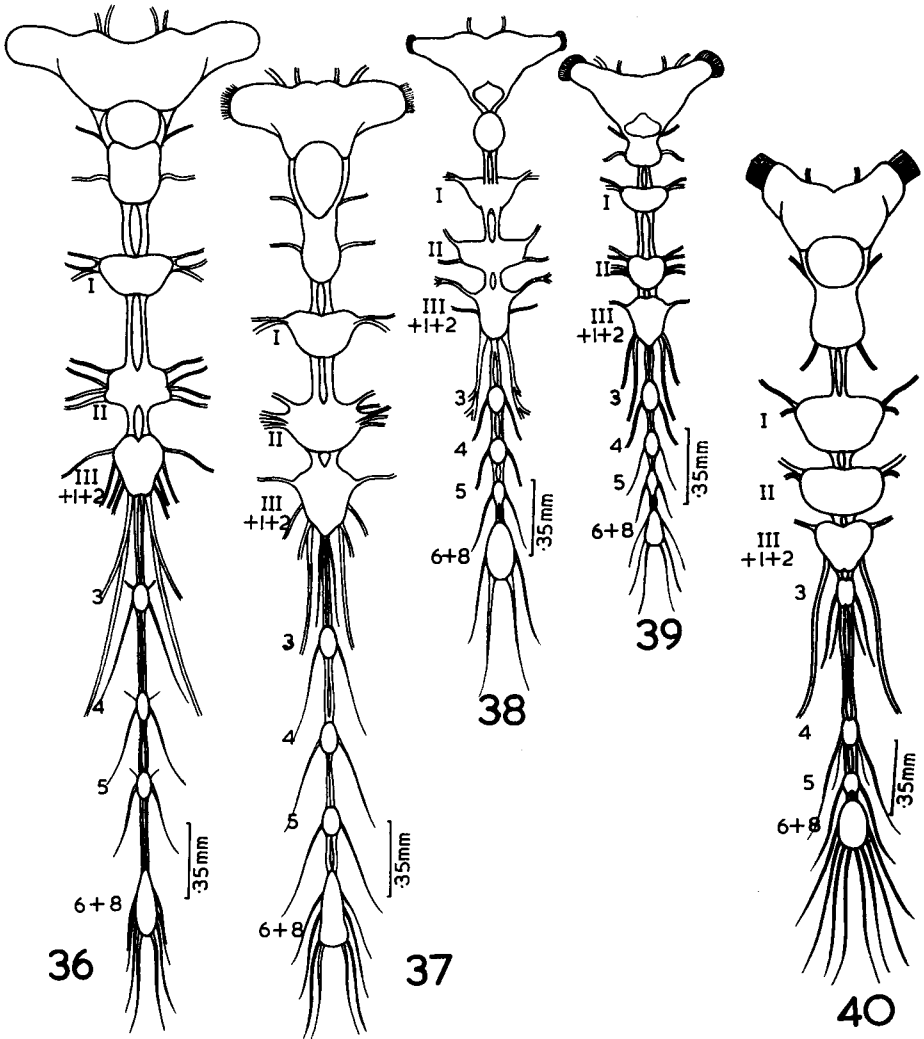
FIGS. 21–26. Ventral nerve cord of: 21, *Mimastra oblonga* (Gyllenhall); 22, *Diorhabda lusca* Maulik; 23, *Haltica cyanea* (Weber); 24, *Hyphasoma nigricorne* Baly; 25, *Hespera nigripes* Maulik; 26, *Luperomorphia nigripennis* Duvivier.



FIGS. 27–30. Ventral nerve cord of: 27, *Chrysolina exanthematica* (Wiedemann); 28, *Chrysolina polita* (L.); 29, *Chrysolina staphylea* (L.); 30, *Chrysomela aenea*, L.



FIGS. 31–35. Ventral nerve cord of: 31, *Gastroidea viridula* (DeGeer); 32, *Phyllosecta vulgatissima* (L.); 33, *Phaedon tumidulus* Germar; 34, *Donacia crassipes* F.; 35, *Plateumaris discolor* (Panzer).



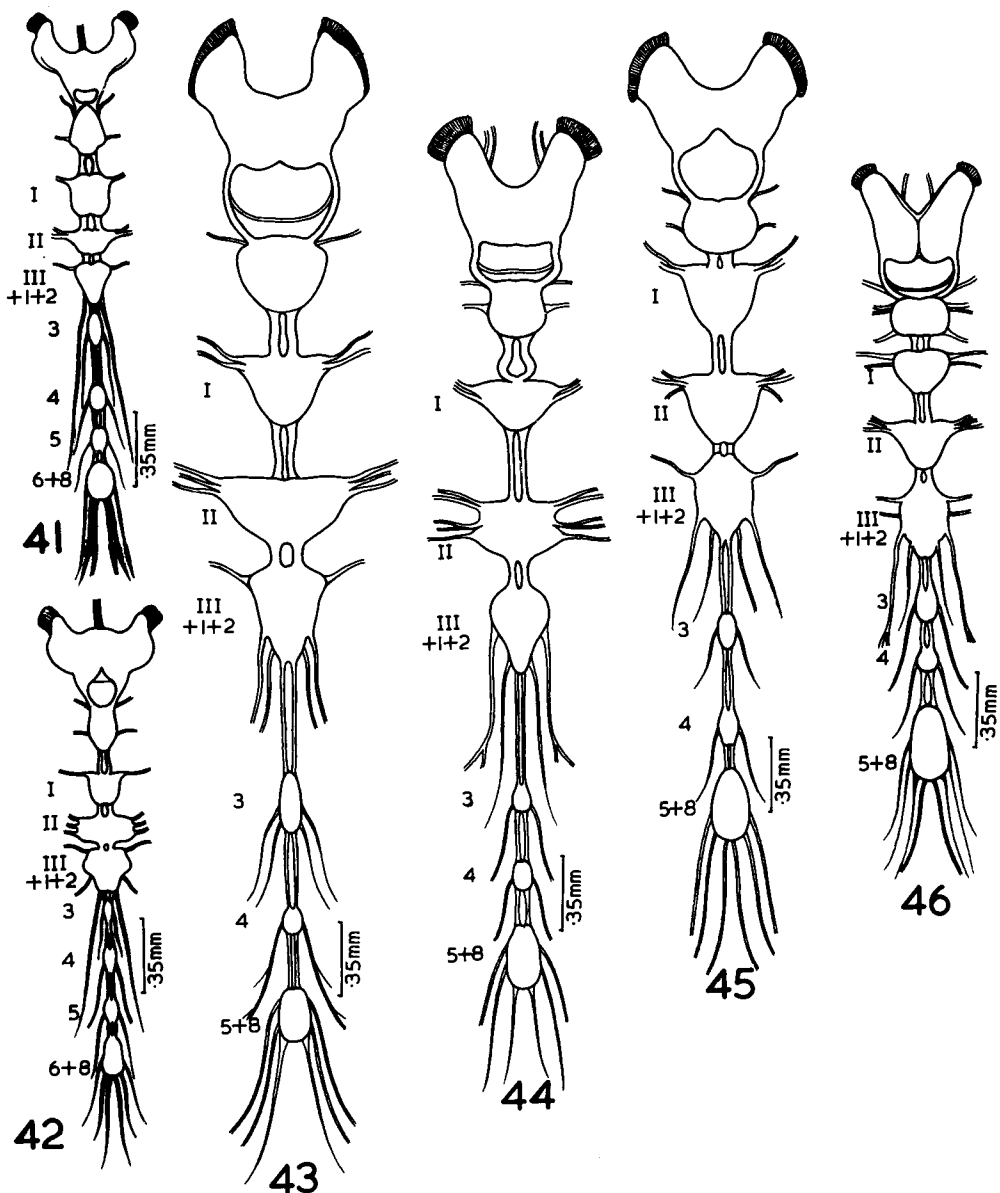
FIGS. 36–40. Ventral nerve cord of: 36, *Lema coromandeliana* (F.); 37, *Lema terminata* Lacordaire; 38, *Oulema cyanella* (L.); 39, *Oulema downesi* (Baly); 40, *Dactylispa peregrina* Maulik.

ganglion 4 is partially detached from the terminal nerve mass in *C.rugicollis*. The thoracic ganglia are contiguous with each other, with only a suture of connation between the pro-, meso- and metathoracic ganglia in *C.divisus*. The meso- and metathoracic ganglia are connate in *C.analis*, *C.sehestedi* and *C.sexsignatus*. The nerve connectives are double.

CLYTRINAE (Figs. 52–54)

As in Cryptocephalinae, there is only one free

abdominal ganglion (No. 3) in *Clytra quadripunctata*, *Diapromorpha turcica* and *Smaragdina* sp. The meso- and metathoracic and the first two abdominal ganglia (Nos. 1 and 2) are fused into a thoracic nerve mass, and abdominal ganglia (Nos. 4–8) form the terminal nerve mass in all the species here. The abdominal nerve connectives are double in *D.turcica* and *Smaragdina* sp. and single in *C.quadripunctata*, in which the meso- and metathoracic nerve complex bears structures which might correspond to Grillot's (1976) perisymphatic organs (Fig. 52, PO).



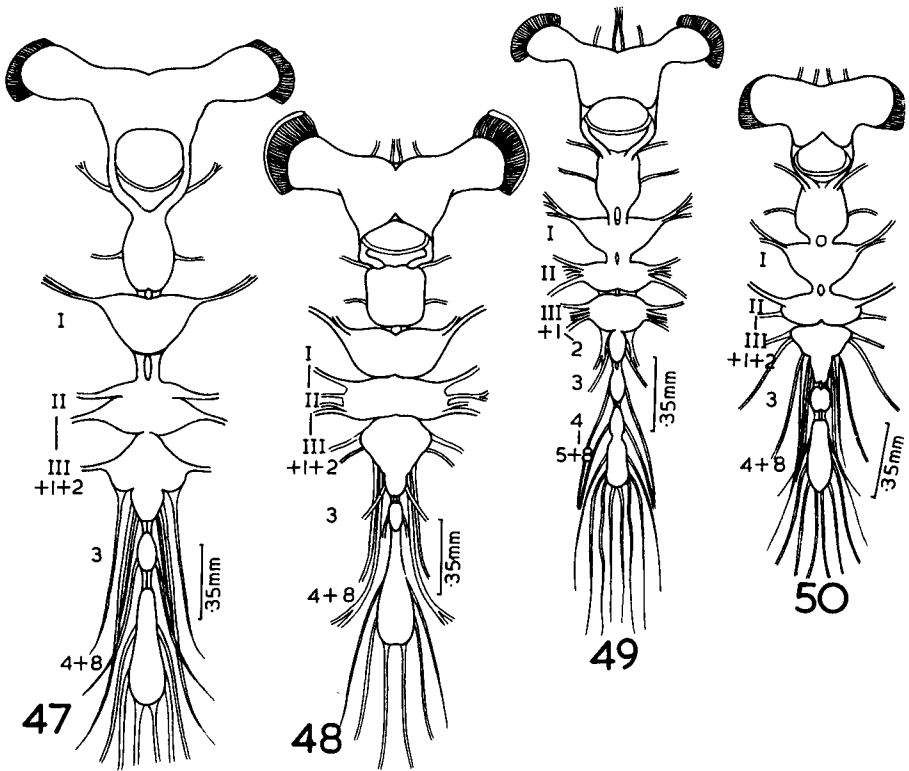
FIGS. 41–46. Ventral nerve cord of: 41, *Rhadinosa laghua* Maulik; 42, *Rhadinosa reticulata* Baly; 43, *Laccoptera quadrimaculata* (Thunberg); 44, *Glyphocassis trilineata* (Hope); 45, *Cassida rubiginosa* Müller; 46, *Cassida nobilis* L.

LAMPROSOMATINAE (Fig. 55)

The nerve cord of *Oomorplus concolor* has two free abdominal ganglia (Nos. 3 and 4). The thoracic ganglia are discrete. Abdominal ganglia 5–8 form the terminal nerve mass. The connectives are double throughout the nerve cord.

ZEUGOPHORINAE

Kasap (1979) studied the nerve cord of *Zeugophora flavicollis* Marsh. and recorded the presence of three free abdominal ganglia (Nos. 3, 4 and 5) with double nerve connectives in between.



FIGS. 47–50. Ventral nerve cord of: 47, *Cryptocephalus analis* Olivier; 48, *Cryptocephalus divisus* Jacoby; 49, *Cryptocephalus herbsti* Suffrian; 50, *Cryptocephalus sehestedi* (F.).

Phylogenetic conclusions

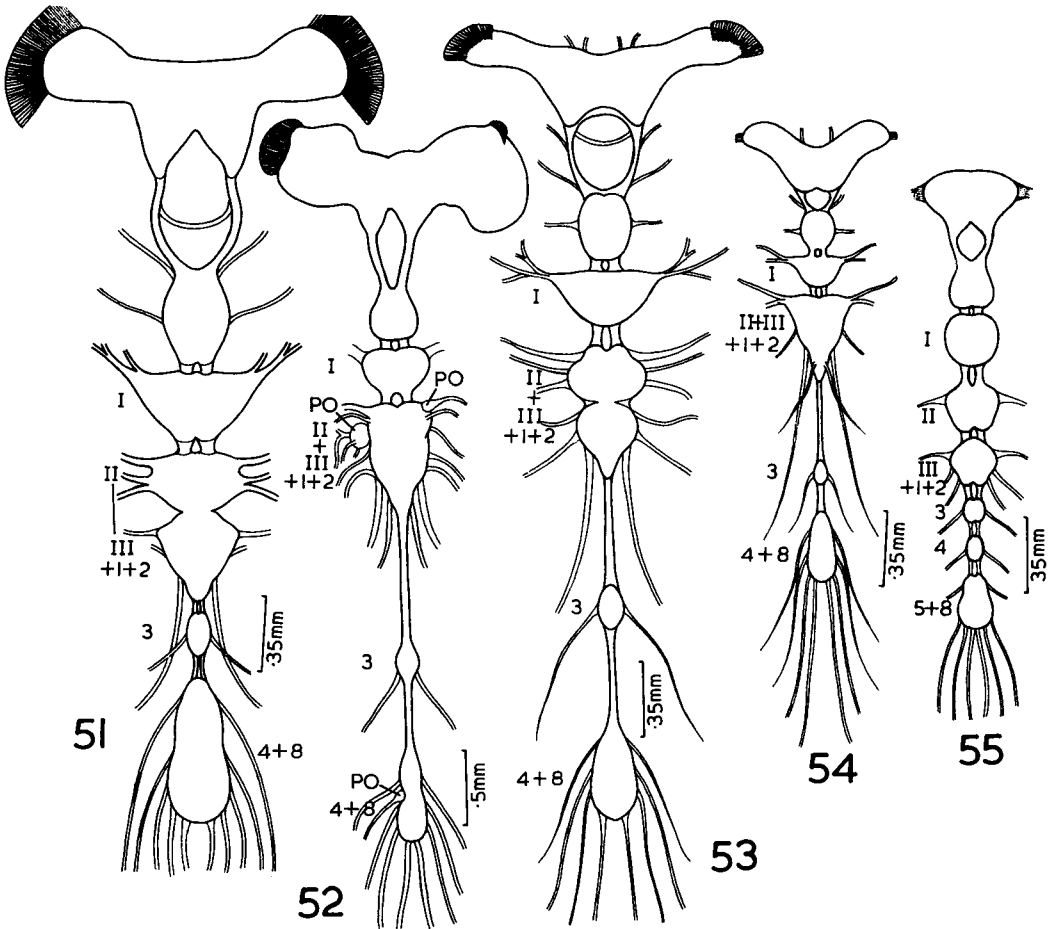
In adult beetles, eight separate abdominal ganglia have been recorded in certain larviform females of Cantharoidea. In such primitive forms as *Dascillus* the first abdominal ganglion is fused with the metathoracic one and the seventh and eighth are fused into a common mass, a condition which may well be ancestral for adult Coleoptera, or at least for Polyphaga. In adults of Chrysomeloidea and Curculionoidea, there never seem to be more than five separate abdominal ganglia, the first two being more or less fused to the metathoracic one. Such a condition is retained in at least some Cerambycidae. In Chrysomelidae, abdominal ganglion 6 is always more or less closely attached to the terminal mass formed by 7 and 8, while in Curculionoidea even the primitive *Rhinotia* has ganglion 5 of the abdominal chain fused into the terminal mass and in the large majority of species ganglion 4 is also incorporated in the mass. In both

superfamilies there seems to be a general trend towards increasing fusion of ganglia in the ventral chain, and such a trend seem to operate even within individual families or subfamilies (Table 1). In all cases it seems that the ganglion of abdominal segment 3 is the last one to remain separate when all the others have become fused.

A major phylogenetic question is whether fusions of adjacent ganglia in the chain are subject to Dollo's Law, i.e. are effectively irreversible in evolution, or whether secondary separation of ganglia has occurred in any lines. The data considered here tend to suggest that secondary separations of previously fused ganglia, if they have occurred at all, are rare and exceptional events. The Chrysomelidae appear to be basically separable from Cerambycidae by the at least partial fusion of abdominal ganglion 6 to the terminal mass (as in *Orsodacne* and *Timarcha*), the Camptosomata proper (excluding *Zeugophora*) by the fusion of ganglion 5 with the terminal mass,

TABLE 1. The degree of fusion of the ventral nerve cord ganglia in Chrysomeloidea and Curculionoidea

Serial no.	Super-family Subfamily	Nerve cord ganglia																		
		I	II	III	1	2	3	4	5	6	7	8								
1.	Chrysomeloidea																			
	I. Cerambycidae	I	II	III+	1+	2	3	4	5	6	7+	8							(<i>Rhagium bifasciatum</i>)	
	II. Chrysomelidae																			
	(i) Orsodacninae (---)	I	II	III+	1+	2	3	4	5	6-	7+	8							(<i>Orsodacne cerasi</i>)	
	(ii) Synetinae	I	II	III+	1+	2	3	4	5	6+	7+	8							(<i>Syneta betulae</i>)	
	(iii) Eumolpinae																			
	(a)	I	II	III+	1+	2	3	4	5	6+	7+	8								
	(b)	I	II	III+	1+	2	3	4	5+	6+	7+	8							(<i>Basilepta variabilis</i>)	
	(c)	I	II-	III+	1+	2	3	4+	5+	6+	7+	8							(<i>Nodina crassipes</i> , <i>Abitus rubripes</i>)	
	(d)	I	II+	III+	1+	2+	3+	4+	5+	6+	7+	8								
	(iv) *Galerucinae																			
	(a)	I	II	III+	1+	2	3	4	5	6+	7+	8							(<i>Exosoma lusitanica</i>)	
	(b)	I	II	III+	1+	2	3	4	5+	6+	7+	8								
	(c)	I	II	III+	1+	2	3	4+	5+	6+	7+	8								
	(v) Halticinae																			
	(a)	I	II	III+	1+	2	3	4	5+	6+	7+	8								
	(b)	I	II	III+	1+	2	3	4+	5+	6+	7+	8								
	(c)	I	II-	III+	1+	2	3	4+	5+	6+	7+	8							(<i>Luperomorpha nigripennis</i>)	
	(d)	I	II+	III+	1+	2	3	4+	5+	6+	7+	8							(<i>Longitarsus melanocephalus</i>)	
	(e)	I	II	III+	1+	2+	3+	4+	5+	6+	7+	8							(<i>Sphaeroderma testaceum</i> and <i>Mantura obtusata</i>)	
	(vi) Aulacoscelinae																			
	(vii) *Chrysomelinae																			
	(a)	I	II	III+	1+	2	3	4	5	6-	7+	8							(<i>Timarcha tenebricosa</i>)	
	(b)	I	II	III+	1+	2	3	4	5	6+	7+	8							(<i>Entomoscelis adoniae</i> , <i>Phytodecta pallida</i> and <i>Phyllochartis cyanicornis</i>)	
	(c)	I	II	III+	1+	2	3	4	5+	6+	7+	8								
	(d)	I	II	III+	1+	2	3	4-	5+	6+	7+	8								
	(e)	I	II	III+	1+	2-	3-	4+	5+	6+	7+	8								(<i>Leptinotarsa decemlineata</i>)



FIGS. 51-55. Ventral nerve cord of: 51, *Cryptocephalus sexsignatus* F.; 52, *Clytra quadripunctata* (Olivier); 53, *Diapromorpha turcica* (F.); 54, *Smaragdina* sp.; 55, *Oomorplus concolor* (Sturm).

and the Clytrinae-Cryptocephalinae by the fusion of ganglion 4 with the terminal mass and at least partial fusion of the meso- and metathoracic ganglia. In the Chrysomelinae, *Timarcha* is separable from other genera studied by abdominal ganglion 6 not being completely fused to 7+8, a presumably primitive condition shared with *Orsodacne* and *Caryedon* (Bruchinae) and paralleling the primitive forms of the aedeagus (Sharp & Muir, 1912) and ovipositor (Wandolleck, 1906) in this genus. *Timarcha* also has ganglion 5 quite free from 6, a condition found also in *Entomoscelis* and *Phyllocharis* but not in other Chrysomelinae studied. *Entomoscelis* and *Phyllocharis* have other probably primitive features in common with *Timarcha*, notably the closed front coxal cavities of the adults,

the absence of defensive glands in the larvae, and larval claws not toothed at the base. The degree of fusion of the abdominal ganglia may provide useful evidence for phylogenetic classification in this subfamily.

In the Hispinae-Cassidinae, the separation of the two subfamilies is notoriously difficult; from our data it might appear that *Hispinae* are distinguishable by having abdominal ganglion 5 separated from 6+7+8, but we have not been able to study the more primitive and Hispinae-like types of Cassidinae, such as *Delocrania*, the Hemisphaerotini or even Priopterini. Kasap's record of six free abdominal ganglia in *Hispa* is very anomalous and we can only suggest that he studied a teneral or otherwise abnormal specimen.

The fusion of the meso- and metathoracic

ganglia, being found in the otherwise primitive *Caryedon*, is likely to be a basic feature of Bruchinae, clearly developed quite independently of Camptosomata. The separation of abdominal ganglion 6 from the terminal mass may be one of the primitive features separating Pachymerini from the Bruchini proper.

The presence of apparently single connectives between the abdominal ganglia in Orsodacninae, *Plateumaris* and Clytrinae studied is almost certainly a polyphyletic derivative feature; in Camptosomata it seems to provide a distinction between the closely allied Cryptocephalinae and Clytrinae, with the former group retaining the primitive double connectives. This is one of several characters which suggest that Clytrinae may have arisen from primitive Cryptocephaline ancestors rather than vice versa. It also supports the sharp separation of *Plateumaris* from *Donacia*, which is manifest in several other features of internal anatomy.

In Eumolpinae, the differences we have observed in the ventral nerve cord show no evident correlation with recognized systematic characters of either adults or larvae; further study of this group is needed. Of the Galerucinae–Halticinae, *Exosoma* retains what may be the most primitive condition of the nerve cord; the genus has other probably primitive features, e.g. the presence of a well-marked prosternal process between the front coxae and the bicameral spiracles of the larva (Böving & Craighead, 1931). The Halticinae tend to show more modified conditions than typical Galerucinae, but in the nerve cord, as in other characters, we have found no clear division between the two subfamilies.

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