

INTERNATIONAL
Review of Cytology

EDITED BY

G. H. BOURNE

*St. George's University School of Medicine
St. George's, Grenada
West Indies*

J. F. DANIELLI

*Worcester Polytechnic Institute
Worcester, Massachusetts*

ASSISTANT EDITOR

K. W. JEON

*Department of Zoology
University of Tennessee
Knoxville, Tennessee*

VOLUME 57

ACADEMIC PRESS New York San Francisco London 1979
A Subsidiary of Harcourt Brace Jovanovich, Publishers

INTERNATIONAL Review of Cytology

EDITED BY

G. H. BOURNE

*St. George's University School of Medicine
St. George's, Grenada
West Indies*

J. F. DANIELLI

*Worcester Polytechnic Institute
Worcester, Massachusetts*

ASSISTANT EDITOR

K. W. JEON

*Department of Zoology
University of Tennessee
Knoxville, Tennessee*

VOLUME 57

ACADEMIC PRESS New York San Francisco London 1979
A Subsidiary of Harcourt Brace Jovanovich, Publishers

COPYRIGHT © 1979, BY ACADEMIC PRESS, INC.
ALL RIGHTS RESERVED.

NO PART OF THIS PUBLICATION MAY BE REPRODUCED OR
TRANSMITTED IN ANY FORM OR BY ANY MEANS, ELECTRONIC
OR MECHANICAL, INCLUDING PHOTOCOPY, RECORDING, OR ANY
INFORMATION STORAGE AND RETRIEVAL SYSTEM, WITHOUT
PERMISSION IN WRITING FROM THE PUBLISHER.

ACADEMIC PRESS, INC.
111 Fifth Avenue, New York, New York 10003

United Kingdom Edition published by
ACADEMIC PRESS, INC. (LONDON) LTD.
24/28 Oval Road, London NW1 7DX

LIBRARY OF CONGRESS CATALOG CARD NUMBER: 52-5203

ISBN 0-12-364357-0

PRINTED IN THE UNITED STATES OF AMERICA

79 80 81 82 9 8 7 6 5 4 3 2 1

List of Contributors

Numbers in parentheses indicate the pages on which the authors' contributions begin.

J.-C. BISCONTE (75), *Laboratoire de Neurobiologie Quantitative, Centre Hospitalier et Universitaire de Bobigny, Université de Paris XIII, France*

PIERRE CASSIER (1), *Université Pierre et Marie Curie, ERA 620, Cytophysiologie des Arthropodes, 105 Boulevard Raspail, 75006 Paris, France*

HUGH J. CLARKE (185), *Department of Zoology, University of Toronto, Toronto M5S 1A1, Ontario, Canada*

F. G. GRIBAKIN (127), *The Laboratory of Evolutionary Morphology, Sechenov Institute of Evolutionary Physiology and Biochemistry, Academy of Sciences of the USSR, 194223 Leningrad, USSR*

A. A. MANINA (345), *Laboratory of Cytology, Institute of Experimental Medicine, USSR Academy of Medical Science, Leningrad, USSR*

YOSHIO MASUI (185), *Department of Zoology, University of Toronto, Toronto M5S 1A1, Ontario, Canada*

JACQUES TAXI (283), *Laboratoire de Neurocytologie, Université Pierre et Marie Curie, 12 Rue Cuvier, 75005 Paris, France*

Contents

LIST OF CONTRIBUTORS	vii
----------------------------	-----

The Corpora Allata of Insects

PIERRE CASSIER

I. Introduction	1
II. The Embryonic Origin of Corpora Allata	4
III. Morphological Types	6
IV. Innervation and Tracheal Supply of Corpora Allata	9
V. Histological Characteristics and Types	11
VI. Cytological and Infrastructural Characteristics of Corpora Allata	21
VII. Conclusions	65
References	66

Kinetic Analysis of Cellular Populations by Means of the Quantitative Radioautography

J.-C. BISCONTE

I. Introduction	75
II. Quantitative Radioautography	77
III. Kinetics of Cell Proliferation	92
IV. Migration and Chronoarchitectony	112
V. Concluding Remarks	118
References	118

Cellular Mechanisms of Insect Photoreception

F. G. GRIBAKIN

I. Introduction	127
II. The Compound Eye and Photoreceptor Optics	128
III. Electrical Basis for Insect Photoreception	159
IV. Conclusion	177
References	178
Note Added in Proof	184

Oocyte Maturation

YOSHIO MASUI AND HUGH J. CLARKE

I. Introduction	186
II. Hormonal Control of Maturation	191

III. Progression of Maturation	205
IV. Initiation of Oocyte Maturation	222
V. Cytoplasmic Control of Oocyte Maturation	240
VI. Nucleocytoplasmic Interaction during Oocyte Maturation	256
VII. Control of Meiosis and Mitosis—Concluding Remarks	267
References	271

The Chromaffin and Chromaffin-like Cells in the Autonomic Nervous System

JACQUES TAXI

I. Terminology	283
II. Techniques	285
III. CCL Cells in Mammals	287
IV. CCL Cells in Nonmammalian Vertebrates	327
V. Concluding Remarks	335
References	336

The Synapses of the Nervous System

A. A. MANINA

I. Introduction	345
II. The Mechanisms of Synaptic Transmission	347
III. General Principles of the Synapse Ultrastructure	351
IV. Classification of Synapses	351
V. Structural-Functional Properties of the Synaptic Contact	352
VI. The Role of Neurospecific Proteins	357
VII. The Role of Glycoproteins	359
VIII. The Enzymic Activity of ATPase and Adenyl Cyclase Reactions in Synapses	361
IX. Autoradiographic Investigations of the Synthesis of Biopolymers in the Synapses ..	364
X. The Structural-Functional Features of the Axospinal Apparatus	368
References	379
SUBJECT INDEX	385

The Corpora Allata of Insects

PIERRE CASSIER

*Université Pierre et Marie Curie,
Cytophysiologie des Arthropodes,
Paris, France*

I. Introduction	1
II. The Embryonic Origin of Corpora Allata	4
III. Morphological Types	6
A. The Lateralized Type	6
B. The Distal Lateralized Type	7
C. The Semicentralized Type	8
D. The Centralized Type	9
E. The Annular Type	9
IV. Innervation and Tracheal Supply of Corpora Allata	9
A. Innervation	9
B. The Tracheal Supply of Corpora Allata	10
V. Histological Characteristics and Types	11
A. Histological Types	11
B. Volume of the Gland, Mitosis, and Pycnosis	14
C. Sexual Dimorphism	19
VI. Cytological and Infrastructural Characteristics of Corpora Allata	21
A. Basal Lamina	23
B. Gland Cells	25
C. Neurosecretory Fibers	63
VII. Conclusions	65
References	66

I. Introduction

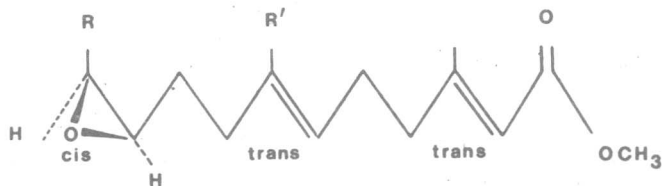
Insect *corpora allata* (Heymons, 1897a,b, 1899) or *corps allates* (Cazal, 1948) are endocrine glands which were previously called paired posterior visceral ganglia (Hofer, 1887), ganglia allata (Heymons, 1895), or corpora incertae (Meinert, 1861), owing to their being confused with the sympathetic cerebral structures constituting the stomatogastric system.

These glands were first identified in the ant (Meinert, 1861; Forel, 1874); however, the endocrine function of these structures was first reported by Nabert (1913), Ito (1918), and Müller (1829), and was experimentally demonstrated by Wigglesworth (1935), Bouhniol (1936a,b, 1937a,b,c, 1938a,b,c,d,e,f), Pflug-

felder (1937a,b), Piepho (1938a,b,c,d), Bodenstein (1938a,b,c.), and Weed-Pfeiffer (1936a,b). Since these early experiments corpora allata glands have been found in many insect species. In his comprehensive topographic, histological study, which is still often referred to, P. Cazal presented both the data of previous workers and his own personal observations on more than 130 species (Cazal and Guerrier, 1946; P. Cazal, 1948). The definitions of structural types are used even today, although Cazal admitted that he lacked certain knowledge about Grylloblattidae, Zoraptera, Strepsiptera, Raphidioptera, and Plecoptera. His observations on Apterygota, which often were lacking in details, were later completed by other workers (Chaudonneret, 1949; Bitsch, 1962; Watson, 1964; Rohdendorf, 1965; Cassagnau and Juberthie, 1967; Rohdendorf and Watson, 1969; Palevody, 1976; Palevody and Grimal, 1975).

The secretion of corpora allata is designated by the generic name "juvenile hormone" (JH) (Table I). Actually, three different JHs have been identified (Röller *et al.*, 1967; Dahm *et al.*, 1967; Meyer *et al.*, 1968; Judy *et al.*, 1973a,b). With one exception (Lanzrein *et al.*, 1975; Lüscher and Lanzrein, 1976) it is not yet clear, however, whether any one of these hormones has a particular morphogenetic or gonadotropic effect. A possible explanation of the physiological effects that have been established (Röller and Dahm, 1968) may be that, for the criteria measured, there are different activity thresholds or different induction capacities for these three hormones (Table II). Thus, in the final larval stage of *Galleria*, the injection of 1 μ l of JH-I caused a larval molt in more than 50% of the cases, 10 μ g of JH-II was less effective, and following an injection of 100 μ g of JH-III most of the larvae had a normal pupal molt. Such an estimation

TABLE I
THE JUVENILE HORMONES



Source	R	JH ^a
<i>Hyalophora cecropia</i>	R = R' = CH ₃ CH ₂	JH-I (C ₁₁ JH)
<i>Hyalophora cecropia</i>	R = CH ₃ CH ₂ ; R' = CH ₃	JH-II (C ₁₇ JH)
<i>Manduca sexta</i>	R = R' = CH ₃	JH-III (C ₁₆ JH)

^a JH-I: methyl-2(E),6(E)-10(R),11(S)-10,11-epoxy-7-ethyl-3,11-dimethyl-2,6-tridecadienoate (trans-trans-cis). JH-II: 7-methyl analog of JH-I. JH-III = methyl-2(E),6(E)-10(R), 11(S)-10,11-epoxy-3,7,11-trimethyl-2,6-dodecadienoate.

TABLE II
SPECIFIC ACTIVITIES OF RACEMIC JHS IN THE *Galleria* WAX TEST AND IN THE *Tenebrio* Test^a

Juvenile hormone	<i>Galleria</i> units per microgram ^b	<i>Tenebrio</i> units per microgram ^c
JH-I	200×10^3	8.00
JH-II	200×10^3	30
JH-III	2×10^3	0.05

^aFrom Dahm *et al.*, 1976.

^b*Galleria* unit: Amount required to elicit a positive response in 50% of the animals scored.

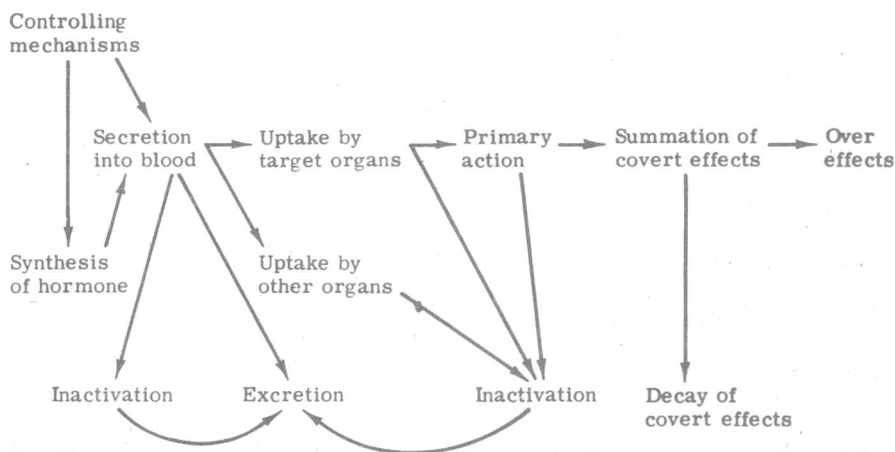
^c*Tenebrio* unit: Amount required to elicit a positive response in 40% of the treated pupae.

is a delicate one and varies according to the tests being used. With a single exception (Lanzrein *et al.*, 1975) JH-I and JH-II have been identified only in Lepidoptera (Röller *et al.*, 1967; Meyer *et al.*, 1968; Dahm *et al.*, 1976; Dahm and Röller, 1970; Röller and Dahm, 1970; Schooley *et al.*, 1973; Judy *et al.*, 1973a; Jennings *et al.*, 1975a,b). JH-III alone was found in orthopteran, coleopteran, and hymenopteran species (Judy *et al.*, 1973b; Trautmann *et al.*, 1974b, 1976) and also in cultures of orthopteran and coleopteran corpora allata (Judy *et al.*, 1973b, 1975; Peter and Dahm, 1975; Müller *et al.*, 1974; Dahm *et al.*, 1976). These findings suggest that the original JH of insects is JH-III and that JH-I and JH-II are special evolutionary achievements in Lepidoptera and possibly in other insect orders.

In adult insects JH-III is the most common form. This may indicate which is the first form in the biosynthetic system of terpenoids; the synthesis of JH-I and JH-II, which are noteworthy since they contain ethyl radicals, requires the presence of enzyme systems and particular precursors.

These JHs are transported in the hemolymph, presumably by lipoprotein carriers (Gilbert, 1974).

The endocrine activity of the corpora allata and the mode of action of the different forms of JH are well known and retain a central position in entomological research (Scheme 1). They are concerned with morphogenesis (inhibition of metamorphosis), activation of follicular cells and sexual accessory glands, control of polymorphism, and so on, general physiology (synthesis of proteins, respiration, effect on fat body, oenocytes, water balance, imaginal diapause, coloration, pheromone secretion), behavior, and so on. The different aspects of classic endocrinology have been extremely well documented in several reviews which the reader should consult (Wigglesworth, 1964, 1965; Engelmann, 1968, 1970; Novak, 1966; Cassier, 1967; Gilbert, 1963, 1964, 1974, 1976; Menn and Beroza, 1972; Wyatt, 1972; Gilbert and King, 1973; Doane, 1973; de Wilde, 1964; de Wilde and de Loof, 1973; Sláma *et al.*, 1974; Willis, 1974; Steel, 1975). The interest in this field of research is further demonstrated by the amount of research



SCHEME 1. Mechanisms of control of the activity of corpora allata (Williams, 1976; Ohtaki *et al.*, 1968). The activation may be neuroendocrine and the inhibition of a neural nature (Sehnal and Granger, 1975). An inhibitory factor from the blood (see Williams, 1976) and an antigonadotropin (Liu and Davey, 1974) may be also involved.

carried out on juvenoids, growth regulator and juvenile hormone mimetics with specific short-range action affecting insects which are economically important (cf. Henrick *et al.*, 1976; Zurflueh, 1976).

However, histological and, even more important, cytological observations, whether they are based on optical or electron microscopy separately or combined, have not been subjected to comparative analysis. They are therefore presented here in the hope that this article will provide a better understanding of corpora allata activities and of their regulatory modalities, since in spite of all the efforts made, the formation and excretion of JH have not yet been clarified with regard to binding modalities of precursors, the site of synthesis, sites of release, and functional cooperation between the organelles, namely, between the chondriome and endoplasmic reticulum.

The number of species investigated by electron microscopy is limited; thus attempts at interpretation and, even more so, at generalization might be subject to error and must be treated with caution.

II. The Embryonic Origin of Corpora Allata

That the corpora allata are ectodermal in origin is definite; this was established by Heymons in 1895 and since then has been frequently verified (cf. Haget,

1977, in *Traité de Zoologie*). The site of appearance of the buds (Fig. 1), at first paired and symmetrical, differs slightly from species to species. The corpora allata may be formed by invaginations at the anterior part of the mandibular somite (*Corynodes*; Paterson, 1936), at its posterior part (*Pieris*; Eastham, 1930), between the mandibular and the maxillary segments (*Silpha*; Smereczyński, 1932; *Locusta*, Roonwald, 1936, 1937; Maltête, 1962; *Carausius*, Wiesmann, 1926; Pflugfelder, 1937a) or even in the maxillar somite (*Forficula* and *Gryllus*, Heymons, 1895). In *Apis* they appear to be derived from lateral outgrowths of the epithelium of the transverse bar of the tentorium (Pflugfelder, 1937a; Nelson, 1915).

The conspicuous differences are due, first, to the amplitude of morphogenetic movements which affect the ventral part of the gnathal region and, second, to the timing of bud formation or appearance. Examination of the available data allowed Haget (1977) to confirm that the corpora allata are intersegmental organs originating in a region anterior to the maxillar segment.

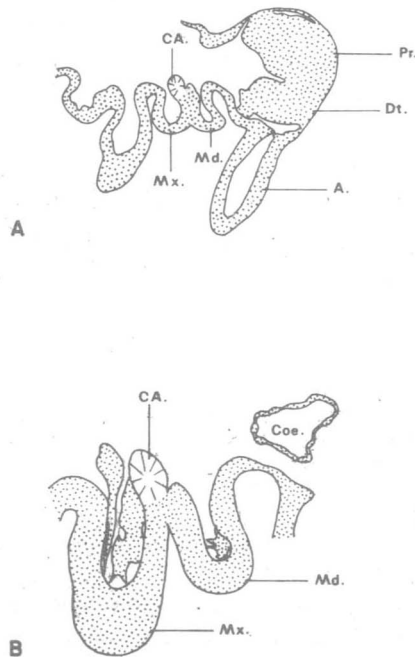


FIG. 1. The embryonic origin of corpora allata in *C. morosus*. (A) Sagittal section showing corpora allata (C.A.) bud. (B) Corpora allata bud becoming vesiculous. Mx., maxillae; Md., mandible; A., antenna; Dt., deutocerebrum; Pr., protocerebrum; Coe., antennal celom (after Pflugfelder, 1937).

Subsequently, the buds of the corpora allata form two coherent cellular masses. During the time they are in contact with the ectoderm from which they originate they become pediculous; then they subsequently become globular and migrate in dorsal and mesal directions. They follow the anterior branch of the tentorium and finally attach themselves at the ventrolateral angles of the celomic sacs of the antennal segment. At this level the corpora allata fuse with the hypocerebral ganglia and the corpora cardiaca.

Throughout the class Insecta and throughout its various orders, the more highly evolved the species, the more marked the migration of the corpora allata. Thus, in Thysanura, the corpora allata or *corps jugaux* (Chaudonneret, 1946, 1949; Bitsch, 1962) still occupy the ventral position. In Odonata they are anterior and ventral (Hanström, 1940a,b; Cazal, 1948; Schaller, 1968), in contact with the circumesophageal connectives and even between the connectives and the esophagus. In the majority of Heterometabola they flank the esophagus laterally and remain distinct. However, in numerous species of Dermaptera, Hemiptera, and Holometabola the corpora allata fuse on the ventral surface of the aorta. Last, in superior Diptera they form a single mass above the aorta.

Exceptionally, the corpora allata are situated extremely posteriorly. Thus in *Sialis*, *Japyx*, and the larvae of *Lampyrus* they are located in the prothorax.

In the embryo of *Carausius* (Wiesmann, 1926) the buds of corpora allata very rapidly become vesiculated (Figs. 4 and 5).

III. Morphological Types

At the moment of hatching the corpora allata occupy different positions according to the group or species. Their mutual relations, as well as those with neighboring organs, also vary considerably.

Following his numerous observations P. Cazal (1948) described five important morphological types whose essential characteristics are presented in Fig. 2.

A. THE LATERALIZED TYPE

The lateralized type is the most common and is found in the primitive forms of most groups. It is characterized by the presence of two corpora allata, symmetrically arranged on each side of the digestive tube, connected by completely individualized allatocardiac nerves (N.C.A. 1).

Beginning with this type, the evolution always follows the same pattern. The corpora allata reach the dorsal surface of the esophagus, join side to side and fuse either beneath or above the aorta. Thus two corpora allata beneath the aorta

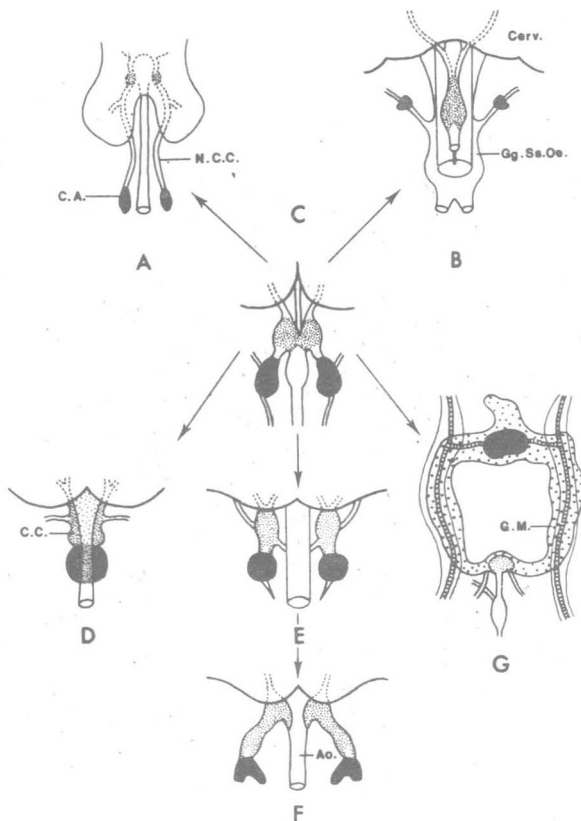


FIG. 2. Retrocerebral glands in various groups of insects. (A) The lateralized type (e.g., *Japyx*); (B) the ventral type (e.g., *Ephemera vulgata*); (C) the semicentralized type (e.g., *Blatta orientalis*); (D) the centralized type (e.g., *Pyrrhocoris apterus*); (E) the distal lateralized type, primitive stage (e.g., *Sphinx ligustri*); (F) the distal lateralized type, evolved stage (e.g., *Hydrous piceus*); (G) the annular type (e.g., *C. erythrocephala*). Solid areas, corpora allata (C.A.); densely dotted areas, corpora cardiaca (C.C.); lightly dotted areas, peritracheal glands, molting or prothoracic glands (G.M.); Ao., aorta; N.C.C., nervi corporis cardiaci; Gg.Ss.Oe., subesophageal ganglia; Cerv., cerebral ganglia.

may still be observed in Isoptera, Phasmidae, Heteroptera, Cryptocera, and Cicadidae.

B. THE DISTAL LATERALIZED TYPE

The distal lateralized type seen in several Diptera and Coleoptera differ from the lateralized type by the attachment of homolateral corpora cardiaca and corpora allata.

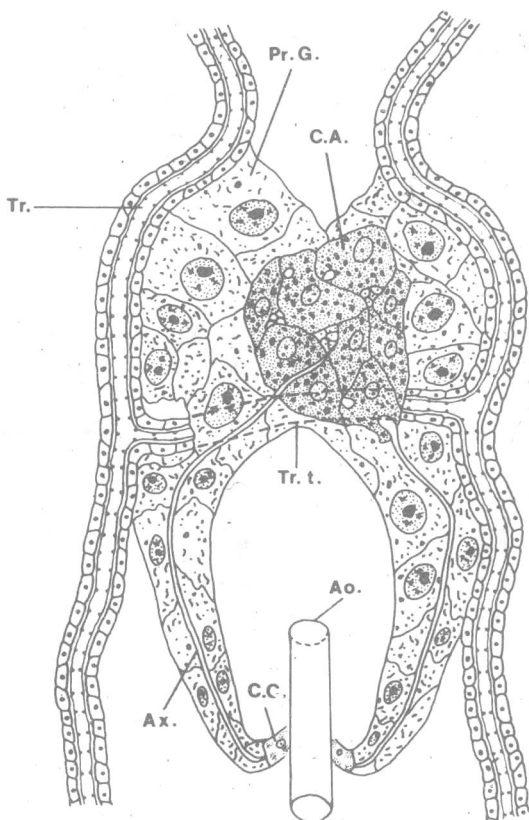


FIG. 3. Diagram of an ideal transverse section through the ring gland of a third-instar larva of *Drosophila*. Ao., aorta; Ax., axons from corpus cardiacum to corpus allatum; C.A., corpus allatum; Tr.t., transverse trachea; Tr., trachea; Pr.G., prothoracic gland; C.C., corpus cardiacum (after King *et al.*, 1966a).

C. THE SEMICENTRALIZED TYPE

This type, found in Paleoptera and primitive Neoptera (Dictyoptera, Orthoptera, and so on), is characterized by a sagittal fusion of the corpora cardiaca (or corpus paracardiacum) which are attached directly to the aorta and the hypocerebral ganglia; the corpora allata remain distinct, while the N.C.A. 1 may remain separate (Orthoptera) or not (Dictyoptera), depending on the closeness of the relationship between the corpora cardiaca and corpora allata.

This semicentralized type, which is very common, seems to be the most primitive.

D. THE CENTRALIZED TYPE

In this type (Embioptera, Plecoptera, Dermaptera, Psocoptera, various gymnocerate Heteroptera, Cicadidae, Aphididae) there is a development of the previous type, since the corpora allata also fuse and form a separate mass located beneath the aorta, in direct contact with the corpora cardiaca so that it seems as if they were actually inside the corpora cardiaca.

In *Oncopeltus* the incomplete fusion of corpora allata may give rise to a bilobed structure (Novak, 1951; Unnitham *et al.*, 1971).

E. THE ANNULAR TYPE

The annular type (ring-shaped type; Fig. 3) characteristic of higher Diptera (Brachycera, Cyclorhapha) results from a fusion above the aorta of the corpora allata, which together with the ventral corpora cardiaca and the lateral peritracheal glands form a ring around the aorta known as Weissmann's ring.

Formation of this ring takes place in the larval stage, and the N.C.A. 1 are not visible; they become apparent during metamorphosis, from the onset of the imaginal molt as the ecdysial glands (peritracheal glands) degenerate. Furthermore, the corpora allata in contact with the brain of the larvae migrate posteriorly to reach the prothorax of the imago.

IV. Innervation and Tracheal Supply of Corpora Allata

A. INNERVATION

The most complex innervation of the corpora allata is double. In fact, these glands are connected both to the brain, by the superior allatocardiac nerve (N.C.A.1), and to the subesophageal ganglion (N.C.A.2), either directly or by means of the tritocerebral paracardiac nerve (N.C.C.IV).

The superior allatocardiac nerve (N.C.A.1) is formed from ordinary fibers and neurosecretory fibers which arise in the protocerebrum and traverse the corpora cardiaca. In *Schistocerca cancellata* (= *paranensis*) (Strong, 1965a,b) the neurosecretory fibers arise exclusively from lateral protocerebral neurosecretory cells via the external paracardiacal nerves (N.C.C.II). In *Locusta* (Cassier and Fain-Maurel, 1970) they arise also from median protocerebral neurosecretory cells (pars intercerebralis) along the slope of the internal paracardiacal nerves (N.C.C.I).

The relationships between the pars intercerebralis (a neurosecretory center), the corpora cardiaca (a neurohemal organ), and the corpora allata (an endocrine gland) are frequently compared with those in the hypothalamic-hypophyseal complex, particularly at the level of the adenohypophysis.

In insects with the lateralized type and some semicentralized type (Paleoptera, Orthoptera) the N.C.A.1 are completely individualized. They enter the corpora allata at the level of the hilum, they lose their sheath, and then the fibers ramify between the glandular cells. However, in Dictyoptera and in species of the centralized and annular types, the N.C.A.1 are morphologically indiscernible because of the coalescence of the corpora allata and corpora cardiaca. It is only by histological studies that the constitutive fibers may be recognized. They frequently form a periglandular plexus and then enter the gland by several hila and ramify between the glandular cells (Schultz, 1960; Fukuda *et al.*, 1966; Tombes and Smith, 1970; Dorn, 1973; Baehr *et al.*, 1973; Melnikova and Panov, 1975; Paledovy and Grimal, 1975; Morohoshi *et al.*, 1976a). In *Hyalophora* (Waku and Gilbert, 1964) only one part of corpora allata is covered by the neurosecretory fibers.

Since the origin of corpora allata is ventral, the relationship with the superior centers must be acquired secondarily.

However, the subesophageal innervation (N.C.A.2) is primitive; it exists only in Ephemeroptera (Hanström, 1940; Cazal, 1948, Bouhniol *et al.*, 1953), Thysanura (Cazal, 1948), Collembola (Cassagnau and Juberthie, 1967), and in young stages of Odonata where the cerebral innervation appears only in aged larvae (Cazal, 1948). In *Locusta* the N.C.A.2 consist of neurosecretory fibers which emerge from the subesophageal cells (Chalaye, 1965, 1966), and the pattern is the same in Blattidae and Culicidae (Füller, 1960; Harker, 1960). In Thysanura (Chaudonneret, 1949) the *corps jugaux* are entirely covered with maxillary nerves but are directly innervated by the subesophageal ganglion.

In Machilidae (Bitsch, 1962) the corpora allata are innervated by both maxillary and mandibular neuromers.

The afferent and efferent nerves are surrounded by a thick (3–4 μm), stratified neural sheet and by a perilemma consisting of a layer of thin (1–3 μm) glial cells (the lemmoblasts of Edwards *et al.*, 1958; the Schwann cells of Hess, 1958; the neuroglial cells of Trujillo-Cenoz, 1962). Extensions of these cells enclose the isolated fibers or bundles of fibers. They are united by septate desmosomes. Their ovoid nucleus (4–6 μm in diameter) contains in general only one nucleolus; the fragmented chromatin clumps are attached to the nuclear membrane.

B. THE TRACHEAL SUPPLY OF CORPORA ALLATA

Corpora allata are abundantly supplied with tracheae; their distribution seems to follow the same pattern as that of the nerve fibers. Thus, where N.C.A.1 are

entirely individualized (e.g., *Locusta*), they run side by side with the nerve and enter the gland at the level of the hilum and ramify between the gland cells. However, when these nerves lose their individuality there is a network of tracheae surrounding the gland, which then ramify and run into the glandular parenchyma (Cazal, 1948; Busselet, 1968; Baehr *et al.*, 1973). In the latter example the tracheae are often enclosed between the basal laminae and the allata cells.

V. Histological Characteristics and Types

A. HISTOLOGICAL TYPES

Structural study of corpora allata shows that there are at least six distinguishable types of cells which correspond mainly to glandular cells (undifferentiated, normal, polyploid; Özbas, 1957; Joly, 1976; Mendes, 1948) and to associated elements (axons, neurosecretory fibers, glial cells, tracheoblasts, peripheral conjunctive cells). Furthermore, these glands are often surrounded by fat-body tissue and pericardial cells.

The distribution of these different cellular types, their abundance, and their morphometric and histological characteristics provide so many criteria that P. Cazal (1948) was able to identify four principal types of corpora allata.

1. *The Pseudolymphoid (or Lymphoid) Type*

The pseudolymphoid type is found in Paleoptera (Ephemera, Odonata) and is characterized by the presence of many cells packed closely one against another. They have a reduced amount of cytoplasm, which is slightly basophilic, and do not have any apparent secretory activity. The small nuclei (7–9 μm in diameter) are round or oval. There are a few mitochondria; the Golgi apparatus is not well developed, and it is difficult to distinguish any secretory products or secretion-related phenomena.

2. *The Small-Cell Type*

The small-cell type is fairly common, appearing in Blattidae, Mantidae, Orthoptera, Dermaptera, Paraneoptera, and in numerous Oligoneoptera. It is characterized by the presence of many gland cells which are small, irregularly shaped, and particularly rich in mitochondria, Golgi apparatus, and secretory grains.

In Acrididae and Coccinellidae the peripheral cells are more or less palisade, whereas the central cells are irregularly shaped; many intercellular cavities whose size varies according to the physiological state of the insect and size of the gland may also be seen.