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THE COMPARATIVE MORPHOLOGY OF THE DORSAL
VESSEL AND ACCESSORY STRUCTURES OF THE
LEPIDOPTERA AND ITS PHYLOGENETIC IMPLICATIONS.**

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THE COMPARATIVE MORPHOLOGY OF THE DORSAL
VESSEL AND ACCESSORY STRUCTURES OF THE
LEPIDOPTERA AND ITS PHYLOGENETIC IMPLICATIONS

by
John H. ^{ofman} Hessel

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DOCTOR OF PHILOSOPHY

In the Graduate College
THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my
direction by John H. Hessel
entitled THE COMPARATIVE MORPHOLOGY OF THE DORSAL VESSEL
AND ACCESSORY STRUCTURES OF THE LEPIDOPTERA AND
ITS PHYLOGENETIC IMPLICATIONS
be accepted as fulfilling the dissertation requirement of the
degree of Doctor of Philosophy

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John H. Hensel

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ABSTRACT

The dorsal vessels of adult representatives from 34 ditrysian families of Lepidoptera were examined with the aid of vital staining. A pair of incurrent ostia was found in the mesothorax (except in the Papilionidae), metathorax, and each abdominal segment (seven in females, eight in males). Since no excurrent openings were found in the dorsal vessel, it is suggested that the dorsal vessel may act principally as a phagocytic organ, and that accessory structures have assumed the role of haemolymph circulation. A transverse muscular septum, of unknown function, was found between the first and second abdominal segments. Metathoracic and abdominal cardiac variations, such as the loss of the eighth pair of abdominal ostia in females and modifications in the metathoracic aortal pathway, are considered as secondary reflections of integumental developments. Therefore, systematic affinities and phylogenetic relationships are proposed based on mesothoracic aortal characters. The proposed phylogeny involves several modifications of previously suggested relationships based on venational and other external characters. The higher-moth relationships are in essential agreement with a nineteenth century work based on pupal and oval characters.

INTRODUCTION

This is the second part of a comparative morphological study of the adult heart of the Lepidoptera. In the previous investigation (Hessel 1966) primary emphasis was placed on the comparative anatomy of the mesothoracic aorta of the Rhopalocera; the present investigation deals primarily with the heart and the more prominent accessory pulsatile structures of the Heterocera.

The scope of the present study has had to be limited because of the overwhelming number of heteroceran taxa. Except for the Calliduloidea, representatives from all the ditrysian superfamilies of Remington (1954) are included. However, only about one third of the nominal families are represented. With the exception of the Castniidae, only families present in the fauna of the United States are included. No monotrysian superfamilies were included in this study. The omission of these primitive taxa is due partly to the limitations of the techniques used and partly to the unavailability of the few suitably large species.

Because of the limited number of species investigated, and the representation of only a minority of the conservatively recognized families, the proposed phylogenetic

arrangement must be considered tentative. Hopefully, this arrangement will provide a framework useful in the placement of some lepidopteran taxa whose systematic affinities are unsettled.

Previous Anatomical Work

Previous anatomical studies of the lepidopteran heart have been largely restricted to single species or, at most, to a cursory examination of a few species. Workers such as Selvatico (1887), Verson (1909), Gerould (1938), and Schneider and Kaissling (1959) worked out the details of the dorsal vessel in the silkworm moth Bombyx mori L. Brocher (1919, 1920) dealt with the morphology of the sphingid heart. Burgess (1880), and Ehrlich and Davidson (1961) examined the internal anatomy of Danaus plexippus L., but neither study greatly emphasized the heart of this butterfly.

Burgess (1881), in a brief and superficial study, compared the mesothoracic aortas of a hesperiid, a nymphalid, a pierid, a sphingid, a geometrid, an agaristid, and a tortricid. With the exception of Hessel (1966), Burgess' work constitutes the sole comparative anatomical study of the lepidopteran heart.

Larval hearts have been investigated even less than those of imagines. Verson (1909) and Gerould (1938)

dealt briefly with the heart of B. mori, and Peterson (1912) with the larval heart of Phlegethontius sexta Johanssen.

A few broad comparative studies of other internal systems have been made. Notable among these are the studies of the ventral diaphragm (Richards 1963), the malpighian tubules (Ishimori 1924), the peritrophic membrane (Waterhouse 1953), and the tympanic organs (Kiriakoff 1963). With the above exceptions, almost all comparative anatomical work on the Lepidoptera has been confined to skeletal or reproductive structures, or has been limited in scope to a single superfamily.

No attempt will be made to summarize the non-lepidopteran cardiological studies. The literature has been recently reviewed by Jones (1964), and the reader is referred to that source for information on other insect orders.

MATERIALS AND METHODS

In most instances several specimens of each species were examined. In so far as possible, an attempt was made to dissect both sexes of each species. However, since most of the Heterocera were collected at black-light, to which a preponderance of males is attracted, in many cases only males were examined. All species were investigated for head, thoracic, and basal abdominal cardiac variations. With the exception of the Gelechiidae at least one species from each family was examined for possible abdominal modifications.

In almost all cases vital staining with a saturated solution of trypan blue in insect Ringer's was utilized (Hershberger 1948). Injection was made through an abdominal intersegmental membrane using sufficient material to cause slight abdominal distention. The dye was rapidly aspirated by the heart and colored the entire organ, associated pericardial cells, trabeculae, and alary muscles.

If dissections could not be made immediately, the left wings were removed, a small ventral abdominal incision was made, and the live insect was fixed in 10% formalin or Kahle's fluid. The former preservative is preferred since the delicate dorsal vessel does not become so brittle

as when solutions containing alcohol are used. Formalin offers the further advantage of not wetting the tracheal system so that the distinctive silvery appearance of that tissue is retained.

Lateral dissections of the abdomen and thorax, and dorsal dissections of the head, proved to be the most enlightening approaches to reveal details of the heart. Since most Heterocera and many Hesperioidea possess translucent thoracic integument, the accessory diaphragms are best seen in dorsal views of intact living specimens, in which the contractions are readily visible. Because these diaphragms are extremely delicate and, after death, tend to adhere to the notum or muscles, they are most difficult to distinguish in preserved specimens.

Several attempts were made to utilize stained whole mounts of the abdominal heart to demonstrate the ostia. The uniform failure of these attempts was likely due to the unique structure and dorsal location of lepidopteran ostia. The pressure of a cover slip forced the ostium closed and made it virtually invisible by transmitted illumination. Ostia were generally discernible in unmounted, preserved specimens because they tended to gape.

List of Species Studied

The classification of species which follows will be used throughout the text. The superfamilial categories

were chosen primarily for convenience of discussion based on comparative heart anatomy, and do not reflect the author's opinions on the higher systematics of the Lepidoptera. The higher categories of the Heterocera are those of Remington (1954), except that the Aegeriidae and Yponomeutidae have been removed from the Tineoidea and placed in the superfamily Yponomeutoidea. Also the Saturniidae have been separated from the Bombycoidea and raised to superfamily rank. Both these modifications are in accordance with Forbes (1923) and McDunnough (1938, 1939). The generic and trivial nomenclature of the Heterocera follows McDunnough (1938, 1939). For the Rhopalocera, nomenclature through the generic level follows dos Passos (1964). The higher classification of the Hesperioidea conforms to dos Passos (1964), and that of the Papilionoidea follows Ehrlich (1958).

For convenience, names of higher categories will be used throughout the text. However, it should be understood that extrapolation and generalization beyond the species listed may be inadvisable. This is especially true for those taxa in which only one or two species were examined.

Pyralidoidea

Pyralididae

Terastia meticulosalis Guenée
Laniifera cyclades Druce
Galleria mellonella L.
Melitara parabates Dyar
Cactobrosis fernaldialis Hulst

Pterophoridae

Platyptilia grandis Walsingham

Yponomeutoidea

Aegeriidae

Melittia gloriosa Hy. Edwards

Yponomeutidae

Atteva punctella Cramer

Tineoidea

Acrolophidae

Acrolophus sp.

Psychidae

Oiketicus townsendi Townsend

Tineidae

Dorata sp.

Gelechiidae

Pectinophora gossypiella Saunders

Castnioidea

Castniidae

Castnia mygdon Dalman

Tortricioidea

Tortricidae

Archips sp.

Zygaenoidea

Eucleidae

Parasa chloris Herrich-Schaeffer
Prolimacodes badia Hübner

Megalopygidae

Norape tener Druce
Megalopyge bisessa Dyar
Trosia obsolescens Dyar

Pyromorphidae

Harrisina brillians Barnes & McDunnough

Cossoidea

Cossidae

Givira mucida Hy. Edwards
Givira cornelia Neumoegen & Dyar
Zeuzera pyrina L.
Hamilcara atra Barnes & McDunnough
Prionoxystus robiniae Peck

Saturnioidea

Saturniidae

Telea polyphemus Cramer
Automeris pamina Neumoegen
Adelocephala heiligbrodti Harvey
Adelocephala hogei Druce
Citheronia splendens Druce
Eacles imperialis Druce

Bombycoidea

Lasiocampidae

Gloveria arizonensis Packard
Dicogaster coronado Barnes

Lasiocampidae (Continued)

Tolyte distincta French
Malacosoma fragilis Stretch

Eupterotidae

Apatelodes pudefacta Dyar

Sphingoidea

Sphingidae

Phlegethontius quinquemaculata Haworth
Phlegethontius florestan Stoll
Sphinx chersis Hübner
Smerinthus jamaicensis Druce
Smerinthus cerisyi Kirby
Pachysphinx modesta Harris
Erinnyis ello L.
Pholus typhon Klug
Celerio lineata F.

Geometroidea

Geometridae

Lygris diversilineata Hübner
Galenara sp.
Amphidasis cognataria Guenée
Phaeoura mexicanaria Grote
Caripeta aequaliaria Grote

Noctuoidea

Ctenuchidae

Ctenucha venosa Walker

Lithosiidae

Eudesmia arida Skinner
Gardinia magnifica Walker

Arctiidae

Bertholdia trigona Grote
Hemihyalea labecula Grote
Apocrisias thaumasta Franclemont
Estigmene acrea Druce
Apantesis proxima Guérin

Agaristidae

Misa cosyra Druce

Lymantriidae

Hemerocampa vetusta BoisduvalOlene sp.Liparis dispar L.

Nyctemeridae

Gnophaela latipennis Boisduval

Notodontidae

Phoesia rimosa PackardPseudhapigia brunnea SchausCargida pyrrha DruceHeterocampa averna Barnes & McDunnoughCerura scolopendrina BoisduvalGluphisia septentrionalis Walker

Noctuidae

Chorizagrotis incoccina HarveyHeliothis zea BoddieTrichoplusia ni HübnerMelipotēs indomita WalkerSiavana rigida Smith

Hesperioidea

Megathymidae

Agathymus aryxna DyarAgathymus polingi Skinner

Hesperiidae

Urbanus dorantes StollPyrrhopyge araxes Hewitson

Papilionoidea

Papilionidae

Parnassius phoebus F.Battus philenor L.Papilio polyxenes F.

Papilionidae (Continued)

Papilio zelicaon Lucas
Papilio multicaudata Kirby

Pieridae

Colias eurytheme Boisduval
Colias caesonia Stoll
Phoebis sennae L.

Lycaenidae

Emesis zela Butler
Hypaurotis cysalus Edwards

Libytheidae

Libytheana bachmanii Kirtland

Nymphalidae

Limenitis bredowii Geyer
Speyeria atlantis Edwards
Euptoieta claudia Cramer
Danaus plexippus L.
Danaus gilippus Cramer
Oeneis uhleri Reakirt

General Considerations

For convenience during the introductory remarks, the term "heart" has been used to denote an organ more properly termed the dorsal vessel. The classical division of the dorsal vessel into "heart" and "aorta" seems of dubious value or significance. In the Lepidoptera the dorsal vessel is contractile throughout its entire length, and the exotic arrangement in the cephalic region seems incompatible with the traditional view of the "aorta" as an undifferentiated tube cephalad of the most anterior

pair of ostia. As a matter of pure convenience, in the account which follows, the term "aorta" will be used to denote that portion of the dorsal vessel, unsupported by alary muscles, which lies ventral or anterior to the first pair of alary muscles in the abdomen. In effect, the "aorta" refers to the thoracic and cephalic portions of the dorsal vessel.

The term "chamber", variously defined in insect cardiological literature, seems of limited significance in reference to the dorsal vessel of the Lepidoptera. Since no interventricular valves are present (with the possible exception of the tissue mass in the antennary vessel), the term will be used principally in reference to the prominent swellings in the pterothorax and first abdominal segment of some Lepidoptera.

With the exception of modifications in the mesothoracic aorta, no primary cardiac variations were found in the Lepidoptera. Differences in the number of pairs of ostia between males and females, displacement of the first abdominal or metathoracic ostia, and variations in the pathway of the metathoracic aortal segment, are all considered to be secondary developments due to integumental modifications.

The lepidopteran aorta consists of a cephalic portion with branched antennary and optic vessels, an

undifferentiated prothoracic segment, a mesothoracic portion which (except in the Papilionidae) bears a pair of ostia, and an osteolated metathoracic segment. Paired ostia and alary muscles, corresponding to the number of abdominal tergites, are present in the abdominal heart. The modification of the eighth abdominal tergite in females has resulted in the loss of the corresponding pair of ostia and alary muscles. The failure of early workers to recognize this secondary sex difference may well account for the conflicting reports as to the number of pairs of abdominal ostia present in this order.

THE AORTA AND THE FIRST ABDOMINAL CHAMBER

The aorta, like the abdominal heart, appears to be composed mainly of obliquely oriented muscle fibers. Observations of live-heart preparations have led to the conclusion that the aorta is actively contractile throughout its entire length. This finding is in agreement with Gerould (1938), and would seem necessary in an organism in which heartbeat reversal is an integral part of the cardiac cycle.

For purposes of discussion, the aorta has been divided into "segments". It should be emphasized, however, that this fragmentation is artificial, and that the entire dorsal vessel functions as a single, highly coordinated organ.

Ostia

All adult ostia, wherever found, follow the same basic incurrent plan. The ostial apparatus, first described from the mesothoracic chamber of the Rhopalocera by Hessel (1966), consists of a thickened anterior lip and a posterior lip from which a thin, membranous sheet of tissue extends anteriorly. This sheet passes beneath the anterior lip and, together with the vessel wall, forms the definitive ostium. The relatively huge ostial apparatus

found in the first abdominal chamber of the Papilioninae (Fig. 25) clearly demonstrates this construction.

Despite the difficulty of ascertaining ostia in small specimens, and in the pregenital segments of all specimens, it seems likely that the basic lepidopteran plan consists of one pair of ostia in the mesothorax, a pair in the metathorax, and a number in the abdomen which corresponds to the number of abdominal tergites and paired alary muscles. In females due to the modifications of the eighth abdominal segment, only seven pairs of ostia are present in contrast to eight pairs in males. The loss of the mesothoracic ostia in the Papilionidae represents the only clear exception to the above arrangement.

The ostia may be situated in distinct swellings or in otherwise undifferentiated segments of the dorsal vessel. The ostia are located dorsally or dorsolaterally and are always directed posteriorly. Abdominal ostia are generally located in a transverse plane near the anterior fibers of the alary muscles, although the precise location is variable. The metathoracic ostia are exceedingly variable in their location and may be found almost anywhere in the aortal segment between the first pair of alary muscles of the abdominal heart and the point where the aorta passes through, or under, the second phragma.

There is a tendency for some of the normally paired ostia in the abdomen to fuse internally. Gerould (1938) first noted this phenomenon in Bombyx mori. In Givira mucida the fusion of the metathoracic ostial apparatus is complete, and only a single large ostium is present.

Hessel (1966) proposed a mechanism for the passive operation of the ostia in response to haemolymph pressures. The construction of the ostial apparatus militates against active opening or closing of the ostia by muscular contraction. Briefly summarized, the ostial mechanism operates as follows: during systole, the increased pressure within the dorsal vessel causes the membranous sheet to be closely applied to the inner wall of the vessel, thus forcing the ostium closed. If, during diastole, the pressure external to the ostium exceeds the internal pressure, the ostium is forced open and blood is forced into the dorsal vessel.

The above hypothesis is invoked to explain not only the impossibility of detecting ostial operation in living preparations when the integrity of the haemocoel was disrupted, but also to explain the rapid uptake of injected material by the heart as due to the increased extracardiac pressure caused by the injection.

Cephalic Termination

The cephalic termination of the aorta in all specimens was essentially similar (Figs. 2, 26). The

aorta, upon entering the head, passes between the circum-esophageal connectives, dorsal to the esophagus, and abruptly widens into a well-developed dorsoventral frontal sac (Fig. 1, FS). A pair of dorsolateral vessels originates in the dorsal region of the frontal sac. Each bifurcates into an optic vessel and an antennary vessel. The optic vessel (Fig. 2, OpV) passes to the optic lobe where it terminates as an encircling flattened sac. The basal region of the antennary vessel (AntV) consists of a more or less prominent ampulla (Amp) which contains a spherical mass of tissue (TM). The antennary vessel extends to the distal end of the antenna.

The frontal sac, and the antennary vessels with their basal ampullae and tissue masses, were first described in Bombyx mori by Selvatico (1887). Brocher (1920) found a similar arrangement in Herse convolvuli L., and described the optic vessel. More recently, Schneider and Kaissling (1959) confirmed the findings in B. mori.

Gerould (1938), in his investigation of the dorsal vessel of B. mori, described the frontal sac, and the antennary and optic vessels, but did not note the antennary ampullae or the enclosed tissue masses. Gerould also reported vessels leading to the maxillae. No maxillary vessels have been reported by previous or subsequent

workers, and none were found in any of the species examined in this study.

The presence of a tissue mass within the lumen of the heart is most unusual. With the exception of endocardial cells, the only other intracardiac organs known from the Insecta are the intracardiac cords found by Miall and Shelford (1897) in the larva of the dipteron Phalacrocer replicata L. The function of the spherical tissue mass is unknown. Selvatico (1887), and Schneider and Kaissling (1959) suggested that the mass acts as a valve for the antennary vessel. The latter authors do not rule out a possible endocrine function for the structure, but the spindle-shaped cells, reminiscent of connective tissue, tend to rule against this interpretation.

The ampulla and tissue mass are particularly well developed in the Noctuoidea and Bombycoidea, and less well developed in most other groups, but the variation in degree of development or precise location is not considered as a useful clue to phylogenetic relationships. Minor variations in shape and muscular development of the frontal sac were found, but again, no inter-superfamilial trends were discernible. The basic similarity of arrangement in all the Lepidoptera suggests that the cephalic arrangement developed early and has remained essentially unchanged during the evolution of the order.

No ostia were found in any part of the cephalic aorta. One specimen of Megalopyge bisessa did demonstrate configurations on the posterior surface of the frontal sac suggesting ostia, but failure to find comparable signs in other specimens of this species has forced the conclusion that these were artifacts.

Both the antennary vessel and the optic vessel appear to end blindly with neither a terminal opening nor a return vessel. Observations of living specimens failed to reveal any flow of blood emanating from the base of the antenna, the sac which encircles the optic lobe, or the frontal sac itself. The author is in agreement with Gerould (1938) in his conclusion that the cephalic arrangement comprises a closed system which does not contribute appreciably to the circulation of blood in the hemocoel. The implications of the closed system in the head of the adult Lepidoptera will be discussed in the section on the function of the dorsal vessel.

Accessory Structures and Circulation

The circulation of blood within the hemocoel in the head appears to be accomplished by accessory structures. In several groups, a richly tracheated sheet of tissue lying between the brain and vertex was seen to contract. In addition, observations of the living aorta were often made difficult due to pulses of stained blood which entered

through the foramen magnum and flowed into the head. These pulses were likely due to the activity of the mesothoracic subscutellar diaphragm driving the blood anteroventrally. In an intact specimen it seems likely that the expansion and contraction of the frontal sac would also serve as a device for random mixing of the blood in the cephalic hemocoel.

Prothorax and Mesothorax

Upon passing posteriorly through the foramen magnum, the aorta continues ventrally through the cervix and prothorax attached to the dorsal surface of the esophagus. The aorta is unosteolated, and no evidence of alary muscles exists in this region. After passing beneath the first phragma, the aorta may follow one of several pathways. These pathways are characteristic of various groups. It is the pattern of the heart in the mesothorax which provides the most convincing and definitive characters for unraveling phylogenetic affinities within the Lepidoptera. Four basic patterns exist with variations of each. These will be discussed in detail below.

Ventral Arrangement

In the ventral arrangement (Fig. 6) the aorta passes through the mesothorax closely applied to the esophagus and never rises dorsally into the region of the

dorsal-longitudinal muscles. This pattern has been observed in all specimens examined from the families Pyralididae, Pterophoridae, Pyromorphidae, Megalopygidae, Yponomeutidae, Aegeriidae, and Acrolophidae.

A pair of dorsolaterally situated ostia was found in the postfurcal region of the aorta in all of the larger representatives of each of the above families. It is now felt that all species from this assemblage probably possess a pair of mesothoracic ostia and that failure to observe them in small species such as Galleria mellonella (Hessel 1966) was due to the small size of the moth and the limitations of gross dissection in resolving extremely small structures. In the Pyromorphidae, and especially in the Megalopygidae, the ostia are located in a distinct aortal swelling or chamber. In other families the aorta is not differentiated in the ostial region.

Dorsal Arrangement with Transverse Chamber

In the dorsal, transverse chamber arrangement, the aorta anterior to the ostia rises to the notum where it is attached to the scutellum immediately posterior to the scutoscuteellar suture. The ostial region is located at this point, and the ostia are oriented horizontally immediately beneath the tergum with the openings directed posteriorly. The ostia are generally situated in a chamber with transverse expansions (Fig. 5). In sagittal view,

the apposition of anterior and posterior aortal segments may give the illusion of a vertically oriented chamber. However, the longest dimension of the chamber is in a transverse plane, and the term transverse chamber will be used in preference to vertical chamber (cf. Hessel 1966). The aorta posterior to the ostia travels postero-ventrally or in a more direct ventral path depending on whether it passes through or beneath the second phragma.

The above general description applies to all the remaining Heterocera except some of the Cossidae. The variations of aortal arrangement will be discussed in the sections which follow. The anatomy of the chamber does not appear to vary appreciably in any of the five types.

Tineoid Type. This arrangement (Fig. 7), in which the anterior and posterior segments (Fig. 3, AAo, PAo) are strongly divergent, is typical of the Tineidae, Psychidae, Gelechiidae, Tortricidae, and Castniidae. The posterior segment of the aorta passes beneath the mesothoracic phragma or lies in a shallow groove in the ventral portion of the phragma. In the Tineoidea the segment of the aorta anterior to the chamber traverses obliquely anteroventrally across the dorsal-longitudinal muscles. In the Tortricidae the anterior aorta follows a more directly ventral course.

Saturnioid Type. In contrast to the tineoid type, this aortal configuration (Fig. 8) involves a more vertically oriented anterior segment, and a posterior segment which perforates the second phragma near its dorsoventral midpoint. The Eucleidae and Saturniidae demonstrate this arrangement, while the cossid Prionoxystus robiniae (Fig. 13) approaches it except for a more obliquely oriented anterior segment.

Geometroid Type. In this arrangement, which is characteristic of most Geometridae and the sphingid genus Smerinthus, the aortal segments are parallel but separated (Figs. 9, 10). As in all but the saturnioid type, the posterior aortal segment passes beneath the second phragma. Bombyx, according to the figure of Gerould (1938), demonstrates this geometroid pattern.

Jones (1964, Fig. 34A), in redrawing Gerould's figure, has increased the divergence of the anterior and posterior mesothoracic aortal segments so that they approach a tineoid-type arrangement. Other errors in this figure will be discussed below.

Noctuoid Type. The Noctuoidea, Eupterotidae, and the Lasiocampidae, (Figs. 1, 3, 12) exhibit a pattern like the above except that the anterior and posterior segments are closely apposed. The two segments generally follow a posteroventral course from the transverse chamber.

Sphingoid Type. This arrangement is restricted to the Sphingidae. In Pholus, Erinnyis, and Celerio (Fig. 11), a distinct loop is formed in the anterior segment of the aorta, and the two aortal segments are apposed for a considerable distance in the dorsal part of the mesothorax. It was this apposition of segments which was misinterpreted by Brocher (1919, 1920) as comprising a single diverticulum. Phlegethontius, Sphinx, and Pachysphinx have less distinct anterior aortal loops than Pholus, Erinnyis, and Celerio, and exhibit a pattern intermediate between that of the latter three genera and the geometroid-type arrangement of Smerinthus.

Dorsal Arrangement with Horizontal Chamber

The horizontal chamber, first described by Burgess (1880) in Danaus plexippus, is a large, muscular, antero-posterior expansion in the aorta. The chamber bears a pair of dorsolateral ostia (Fig. 21). The horizontal chamber is found in the cossid genera Zeuzera, Hamilcara, and Givira, in the Hesperioidea, and in all Papilionoidea except the Papilionidae. In the Cossidae the chamber is situated ventral to the scutellum, in contrast to the Rhopalocera in which it extends for a considerable distance beneath the scutum as well as the scutellum.

The aortal patterns vary among the three genera of Cossidae, and all present a striking contrast to the

transverse chambered, saturnioid type of Prionoxystus. Although the basic aortal patterns of the Hesperioidea and chambered Papilionoidea are remarkably constant, the Hesperioidea and Lycaenidae possess elongate narrow chambers in contrast to the more ellipsoidal chambers of the Pieridae, Nymphalidae, and Libytheidae.

Cossoid Type. The arrangement found in Zeuzera (Fig. 14) and Hamilcara is similar to the modified saturnioid type of Prionoxystus except for the shape and orientation of the chamber and ostia. As in the latter genus, the mesothoracic phragma is perforated near its middle, and the anterior aortal segment traverses obliquely anteroventrally.

Species of Givira (Fig. 15) exhibit an anterior aortal pattern similar to Zeuzera except that the aorta parallels the scutum for some distance anterior to the chamber before passing ventrad. The posterior aortal segment in Givira does not perforate the phragma, but rather passes beneath it or lies in a shallow groove in the ventral portion of the phragma.

Rhopaloceran Type. The Hesperioidea and Papilionoidea (except for the Papilionidae) present a highly characteristic arrangement (Figs. 16-18). In these taxa the anterior aortal segment contains a loop (Fig. 21, RhAo) formed as the aorta traverses horizontally

caudad beneath the chamber. Upon reaching the posterior aortal segment, this recurrent-horizontal aortal segment turns ventrad and continues apposed to the posterior aortal segment for a variable distance before turning cephalad. The posterior aortal segment passes beneath the second phragma or lies within a shallow phragmal groove. The minor variations on this pattern have been discussed by Hessel (1966) and will not be considered further. The aortal loop, although differing in some respects, recalls the analogous arrangement in some of the Sphingidae.

Dorsal Arrangement with Unchambered Aorta

No chamber or ostia are present in the Papilionidae. In this family the aorta rises into the central region of the flight muscles where a variety of patterns are exhibited. In the Parnassiinae (Fig. 20) the aorta describes a smooth curve through the mesothorax. In the Papilioninae (Fig. 19) a sigmoid segment is often, but not always, present in the anterior portion of the aorta. For a more extensive discussion of the variety of aortal patterns to be found in the Papilionidae the reader is referred to Hessel (1966).

Accessory Structures and Circulation

In all Lepidoptera a subscutellar accessory diaphragm is present (Fig. 3, 2Dph). This diaphragm is supported by trabeculae (Tr) which are attached to the scutellum. The anterior edge of the diaphragm is connected to the posterior surface of the transverse chamber, or to the dorsal surface of the horizontal chamber. The presence of the accessory diaphragm in those groups with a ventral aortal arrangement suggests that the diaphragm has developed independently from the heart and has secondarily become attached to it in those groups in which the aorta assumes a dorsal chambered configuration.

In observations on Celerio and several species of Noctuidae, the dorsal diaphragm appeared to contract synchronously with the transverse chamber. In the pyralidid, Laniifera cyclades, with its ventral aortal arrangement, the diaphragm contracted more rapidly than the abdominal heart. It would seem, from this observation, that the rate of diaphragm contraction may be modified and become synchronous with that of the dorsal chamber.

The subscutellar diaphragm forces blood anteriorly from the subscutellar sinus. Relatively little blood is forced into the ostia of the transverse chamber, the major portion being channelled beneath the scutum in well-defined subnotal pathways. The blood is subsequently conveyed

pleurally and ventrally to the sinus in which lie the nerve cord, esophagus, and salivary glands. This ventral sinus communicates directly with the head anteriorly, and the abdomen posteriorly. Further discussions of the circulation in the mesothorax are beyond the scope of this investigation, and the reader is referred to Brocher (1919, 1920) and Gerould (1938) for more extensive discussions.

It is the conclusion of the author that the accessory mesothoracic diaphragm is the principal organ for governing the circulation of blood in the mesothorax. In addition, however, changes in mesothoracic configuration and volume due to contraction and relaxation of the flight muscles doubtless contribute to an active mixing of the blood during flight. The possibility further exists that a directed flow of blood in the deep sinuses may be caused by flight activity.

Metathorax and First Abdominal Segment

The decision to discuss the metathoracic aortal segment and the anterior portion of the abdominal heart in the same section was made because both pairs of ostia drain the subdivision of the haemocoel bounded by the second phragma anteriorly, and by the septum posteriorly (Fig. 3). The metathoracic aortal segment, first abdominal chamber, metathoracic air sac, septum, and accessory diaphragm will be discussed separately below.

Metathoracic Aortal Segment

The metathoracic aortal segment shows considerable superficial variation, both in the pathway it follows, and in the location of ostia. However, the pathway is always determined by integumental considerations, and therefore represents a reflection of non-cardiac modifications. The location of the ostia is a specific or generic variable and is of no significance to higher systematics or phylogeny.

The aorta passes posteriorly from the second phragma to the septum (Fig. 3, 2Ph, Sm). In all taxa except those in which the aorta perforates the second phragma near its middle, the aorta is applied to the dorsal surface of the esophagus. Depending on the relative positions of the second phragma and the antecosta of the second abdominal sternite, this aortal segment may be very short (Fig. 1) or quite long (Fig. 3).

A pair of ostia are generally located in this horizontal portion of the aorta. In some species, however, the metathoracic ostia are located in the dorsoventrally oriented portion of the metathoracic aortal segment (Figs. 6, 20). The ostia may be situated in a well-developed chamber or in an otherwise undifferentiated portion of the aorta. In those taxa with a saturnioid- or zeuzera-type mesothoracic aortal arrangement (Figs. 8,

13, 14), the aorta possesses a distinct chamber bearing a pair of dorsal ostia. This chamber occupies a space between the second phragma and the ventral portion of the third phragma. In such saturnioid types the aorta passes through a ventral notch in the third phragma and continues posteriorly to the septum.

When the aorta reaches the septum, it turns dorsally and follows that structure. The dorsal vessel occupies a medial position slightly posterior to the septal muscle fibers, and is loosely attached to the septum laterally.

Air Sac

A large air sac (Fig. 3, AS), which opens to the metathoracic spiracles, occupies much of the space within the metathorax and first abdominal segment. When inflated, the sac is closely applied to the dorsal (anterior) surface of the metathoracic aorta, the first abdominal segment of the heart, and the anterior surface of the septum.

It was the metathoracic air sac which was mistakenly connected to the aorta and made a part of the dorsal vessel by Jones (1964, and personal communication). Jones' figure was redrawn after Gerould (1938). The latter misinterpreted the air sac as an accessory vessel, and his figure is most unclear. However, Gerould states: "...the pulsatile metathoracic vessel not being directly connected with the aorta." The misinterpretation by Gerould is rather

surprising since Brocher (1919) had clearly delineated the air sac and the metathoracic subscutellar diaphragm in Herse convolvuli.

Septum

One of the most remarkable structures encountered in this study was the transverse muscular septum (Figs. 4, Sm, 27) which lies between the first and second abdominal segments. The tergosternal muscle fibers which comprise the septum are attached dorsally to the ventral portion of the fourth phragma (Fig. 4, 4Ph) and ventrally to the sternal apophyses (FA). The septum is incomplete medially where the dorsal vessel is situated (Fig. 27). The esophagus, ventral diaphragm, and nerve cord all pass through a small space ventral to the septum (Figs. 4, 27).

As mentioned above, the inflated metathoracic air sac is closely applied to the anterior surface of the septum. In addition, a large abdominal air sac is applied to the posterior surface producing a sort of "septal sandwich" (Fig. 3).

The anteroposterior inclination of the septum depends on the relative widths of the first abdominal tergite and the much-reduced first abdominal sternite. Based on these integumental considerations, the septum is canted more or less anteroposteriorly. It is, then, the shape and orientation of the first abdominal segment

which determines the position of the septum. The relative locations of the septum and second phragma, in turn, determine the pathway of the dorsal vessel in the metathoracic-basal abdominal region of the insect.

First Abdominal Segment

In most Geometroidea, Hesperioidea, and Noctuoidea (except Lithosiidae and Notodontidae) the fourth phragma (Fig. 4, 4Ph) possesses lobular ventral expansions. In the above groups the first abdominal ostia are displaced ventrally, and the heart segment is not attached to the first abdominal tergite. In all other groups investigated, the first abdominal chamber is attached to the tergum by trabeculae. It should be emphasized that the ventral (posterior) part of the first abdominal chamber is always attached to the septum, and only the dorsal (anterior) enlargement extends into the first abdominal segment (Fig. 1). The first pair of alary muscles lies immediately posterior to the septum (Fig. 4, AM), and is often less developed than the more posterior alary muscles.

Metathoracic Diaphragm

All Lepidoptera possess a metathoracic subscutellar diaphragm (Fig. 3, 3Dph) analogous to that in the mesothorax. The contractile rhythm of this diaphragm is considerably more rapid than the contraction rate of the dorsal vessel.

The circulation pathways regulated by this accessory structure were not investigated in this study. The reader is referred to Brocher (1919) for a brief discussion of the metathoracic circulation in Herse convolvuli. It seems likely that the metascutellar diaphragm, like that in the mesothorax, partially serves as an aid to circulation in the wings.

THE ABDOMINAL HEART

The abdominal heart (Fig. 1) posterior to the first segment is remarkably uniform in all species. It possesses a pair of ostia and supporting alary muscles corresponding to the number of abdominal tergites. As mentioned above, the reduction of the eighth tergite in females has resulted in the loss of the corresponding ostia and alary muscles.

The dorsal surface of the heart closely parallels the dorsal integument. In many instances this produces a "chambered" appearance due to the overlap of successive tergites. The heart is supported dorsally by trabeculae which are attached to the tergum. These trabeculae are especially numerous in the ostial region where they probably serve to maintain the ostial apparatus in a fixed or relatively rigid condition.

The caudal segment of the heart generally dips ventrally away from the tergum and approaches the rectum. The mass of tracheae intimately associated with this region of the heart makes detailed observations very difficult. Gerould (1938) found that several tracheae generally penetrated the heart wall in this region, and that during heartbeat reversal haemolymph often passed from the dorsal vessel at these points of tracheal perforation.

Especially in females, in which the seventh pair of ostia are situated near the midpoint of the long seventh abdominal segment, the heart tapers conspicuously posterior to the ostia. In many cases this "tail" was packed with endocardial cells and trypan blue following heartbeat reversal.

Dorsal Diaphragm

While no attempt was made to study the dorsal diaphragm in a comparative manner, certain general statements concerning this structure seem appropriate. In most species the dorsal diaphragm is incomplete, being restricted to the alary muscles. However, a dorsal diaphragm sufficiently complete to more or less delimit a dorsal sinus was found in some of the Hesperioidea.

Considerable variation in the relative development of alary muscles was observed. These variations range from structures containing half a dozen or so thin fibers (Fig. 28) to relatively massive sheets composed of many anastomosing fibers. In all cases the alary muscles are more or less triangular in shape with the base attached ventrally to the heart and the distal apex originating on the antecostal ridge of each segment. No histochemical tests of the alary muscles were made, but they appear to be composed of muscle fibers through most of their length.

Pericardial Cells

Pericardial cells were always found associated with the abdominal heart and, in some cases, with the mesothoracic aorta. The distribution of these cells may be confined to the lateral surfaces of the heart, or may extend to the surfaces of the alary muscles as well. The pericardial cells vary greatly in size and shape in different species, and a comparative study of these conspicuous elements might prove enlightening. The unusually large spherical pericardial cells of Harrisina (Fig. 28) comprise one of the more unusual variations to be found in the Lepidoptera.

Ventral Diaphragm

The principal accessory circulatory structure in the abdomen of adult Lepidoptera is a well-developed ventral diaphragm (Fig. 4, VDph). Richards (1963) examined the ventral diaphragms from a number of species in various lepidopteran families. In the Ditrysia which he examined, he found the ventral diaphragm typically extended from the posterior portion of the mesothorax to the region of the terminal abdominal ganglion. The diaphragm is attached to the dorsal surface of the nerve cord by connective tissue from which muscle fibers extend laterally to origins on the sternites. The multiplicity of origins is in marked

contrast to the usual wing-shaped muscles which comprise the ventral diaphragms in other insect groups.

The separate origins of the muscle fibers presumably permit a fine control of diaphragm movement. Such fine control would be impossible in arrangements where all fibers from one side of a segment arise at a common point. The attachment of the fibers to its dorsal surface makes the nerve cord a sort of keel extending medioventrally into the ventral sinus. As the muscle fibers contract sequentially, a sinuous movement of the nerve cord is produced which drives the blood in a more or less directed fashion in the ventral sinus.

Although Richards questions the efficiency of circulation in those Lepidoptera in which the subneural space is packed with adipose tissue, directional flow was observed by Brocher (1920). Gerould (1938) reported that the movement of the nerve cord produced an extensive mixing action. In this study a distinct caudal flow of haemolymph was noted in the ventral sinus of Celerio, although no reversal of flow as found by Brocher was detected.

Richards found that a ventral diaphragm was present only in lepidopterous adults and never in larvae. The implications of this finding will be discussed further in the following section devoted to the function of the dorsal vessel in the adult Lepidoptera.

THE FUNCTION OF THE DORSAL VESSEL

The traditional view of the insect heart is one of a simple structure which aspirates blood from posterior portions of the organism and sweeps it forward where the blood escapes freely into the head anterior to the brain. Even in those orthopteroids with exotic cardiac modifications, such as phagocytic organs, lateral segmental vessels, or excurrent ostia (Nutting 1951), the dorsal vessel terminates anteriorly as an open funnel.

In marked contrast to this arrangement, the dorsal vessel of the Lepidoptera possesses no obvious means for the haemolymph to leave the heart, either anteriorly or posteriorly. Even if small quantities of blood escape caudally at points where tracheae perforate the dorsal vessel (Gerould 1938), or escape anteriorly through perforations at the terminations of the optic or antennal vessels in the head, no extensive circulatory currents are produced.

This conclusion has been reinforced by observations of several living preparations of mesothoracic aortas during both forward- and backward-beating phases of the cardiac cycle. In such preparations it was possible to follow the "progress" of particulate inclusions in the

lumen of the aorta. During systole, particles were seen to move in the direction of the peristaltic contraction. However, at diastole, the particles returned to points near their original positions. Apparently, little net movement occurs during a single cycle.

Furthermore, the tendency for endocardial cells and particles of trypan blue to pack the lumen of the caudal segment following backward beating, strongly suggests that no large excurrent opening exists in that portion of the dorsal vessel. When very small quantities of trypan blue were injected, the colored material was seldom found in the anterior portions of the aorta as would be expected if the haemolymph were being rapidly expelled from the cephalic portion of the aorta.

The presence of accessory structures such as ventral and subscutellar diaphragms in adults and the reported absence of these structures in larvae, the free opening of the aorta in the larval head, and the absence of heart-beat reversal in normal larvae, all suggest that the circulation in larva and adult is fundamentally different. The evidence further suggests, albeit circumstantially, that the adult circulation has been assumed by accessory structures, and that the dorsal vessel has taken on some alternative role. Although it is not possible to present any specific evidence from this study as to what this alternative

function might be, there is a possibility that the dorsal vessel functions principally as a blood filter.

Phagocytic organs which function as blood filters are present as heart diverticula in some subfamilies of Gryllidae and Tettigoniidae (Nutting 1951). Accessory phagocytic organs, not connected to the dorsal vessel, are known from some dipterous larvae (see Jones 1964). The presence of phagocytic organs in other insect orders suggests that some advantage accrues to insects which possess such systems.

The presence of large numbers of endocardial cells which rapidly absorb trypan blue, and the periodic reversal of peristalsis which facilitates the mixing of the contents of the dorsal vessel, suggest a system well suited to perform a phagocytic function. In addition, the intracardiac pressure produced by peristalsis creates relatively high pressures which would promote outward diffusion of the plasma through the thin walls of the dorsal vessel. The intracardiac blood supply would presumably be replenished by aspiration of haemolymph through the incurrent ostia as the internal pressure fell due to the outward diffusion of plasma through the vessel walls.

It is possible that the conversion of the dorsal vessel in the Lepidoptera into a phagocytic organ occurred in response to pressures introduced by the functional

specialization of the adult. Since most adult Lepidoptera either do not feed or restrict their diet to small quantities of sugar and water, metabolism in the adult is confined largely to the catabolism of material stored during the larval period. To an organism undergoing extensive tissue histolysis, a phagocytic organ might prove useful, and accessory structures and muscular movement during flight might suffice to maintain adequate circulation.

Although alternative functions of the dorsal vessel can not, and should not, be ruled out, the possible role of the dorsal vessel as a haemolymph filter in the adult Lepidoptera seems worthy of future investigation.

PHYLOGENETIC RELATIONSHIPS

The criteria for inferring phylogenetic affinities are based on the principal of homology. However, the homology of end products of gene expression, whether they be enzymes or aortal chambers, can only be guessed at by investigators. It is the continuity of DNA which is the keystone of evolution and phylogeny, and it is the similarity of DNA base sequence which constitutes ultimate homology. In the future it may be practical to compare base sequences in appropriate chromosomal segments. Until such a time arrives, phylogenies will continue to be inferred from phenotypic characters.

Recently, technological advances have made comparative biochemical studies practical. Isozyme studies, such as that by Burns and Johnson (1967), may provide new sets of characters to help in reconstructing phylogeny. However, it should be clear that such sets of molecular characters do not differ in essence from sets of anatomical characters since all are phenotypic in nature. If molecular studies provide new phylogenetic clues, these clues will be significant because of their "newness" and not their "molecularness". By the same reasoning, studies of internal characters in the Lepidoptera can provide useful clues to

phyletic relationships, not because internal characters are more significant, but because they have not been investigated in the past, and therefore can provide new sets of characters.

Within this broad philosophical framework, however, differences may exist in the relative usefulness of types of characters. Evolutionarily tachytelic characters are especially useful in detecting affinities between closely related taxa which have recently diverged from a common ancestral stock. Relatively slowly changing characters are more informative in revealing affinities of higher taxa such as families or superfamilies.

It is the author's belief that, in general, internal characters tend to be more conservative than external characters. The conservatism is likely due to the nature of the selective pressures exerted on internal systems. Whereas external structures often represent ecomorphological adaptations to new or changing niches or other extrinsic factors, internal systems evolve in a relatively homeostatic environment where selective pressures are primarily directed towards increased physiological efficiency or other intrinsic considerations. The fact that internal systems are concerned with basic life processes may severely limit freedom to deviate widely from existing functional arrangements.

Since it is widely accepted that the Lepidoptera are of monophyletic origin, it follows that phylogenetic relationships must exist between the various taxa within the order. Determining phylogenetic relationships from extant forms, however, is analogous to reconstructing an oak tree from the slash left after the trunk and large limbs have been removed and burned.

Under ideal conditions, the phyletic sequence of n taxa can be inferred from $n-1$ mutually exclusive characters. In such a system each character must be shared by two taxa, and each member of the pair must share a second character with one member of another pair of taxa. In practice such conditions are seldom fulfilled, and far more than the theoretical minimum number of characters are required to elucidate the relationships between a given number of taxa.

Even when sufficient numbers of characters are available to the systematist, additional difficulties exist in the evaluation of their validity. The problem of determining true homology is, perhaps, the greatest difficulty. In general one can say that, the more elaborate or complex a structure, the more likely that it is homologous in those taxa in which it occurs. Of course, a very simple structure may be equally homologous in its manifestations. However, the likelihood of establishing

polyphyletic taxa and erroneous phylogenies is increased when very simple anatomical characters are used.

The loss or degeneration of characters presents the second major difficulty in inferring phyletic relationships. The absence of a structure is often considered to represent the primitive condition, and its presence to represent the advanced condition. If a structure is lost in a taxon derived from an ancestor which possessed such a structure, a pseudoprimitive phenotype results. Based on the absence of a character, it is not possible to distinguish such a secondarily primitive condition from one that is truly primitive. The decision that a character represents a secondarily primitive condition in one taxon, and a truly primitive condition in a second taxon, is highly subjective.

The obvious solution to the problems of homology and secondary primitiveness lies in the use of large numbers of characters in constructing higher taxa or deriving phylogenies. Since relatively few variable characters were found in the dorsal vessel, it is not possible to reconstruct a phylogeny of the Lepidoptera based on purely cardiac considerations. Therefore, the method described in the following section was used to reconstruct what is felt to be a reasonable phylogenetic sequence for the ditrysian superfamilies of the Lepidoptera.

Procedure

Certain modifications of the dorsal vessel, such as the loss of the eighth abdominal ostia in females, the ventral displacement of the first abdominal chamber in some taxa, and the variations in the pathway of the metathoracic aorta, clearly indicate that the dorsal vessel "gives way" to integumental considerations. It is these integumental modifications, rather than the passive response of the dorsal vessel, which may properly be considered valid indications of phyletic relationships. It seems possible that the positional variations of the dorsal vessel in the metathorax and first abdominal segment are not, in themselves, genetically controlled. The absurdity of basing phylogeny on non-genetically determined characters requires no further comment.

Therefore, the relationships which will be proposed are based on mesothoracic aortal considerations, for it is in the mesothorax alone that cardiac variations are not clearly attributable to integumental modifications.

In order to minimize bias and subjectivity, the following procedure was adopted. Assemblages of taxa were produced, comprising groups whose members possess nearly identical mesothoracic aortal characteristics. The seven assemblages which resulted correspond to the "aortal types" previously discussed. Fortunately, the

assemblages shared genera from the same family, or families from the same superfamily, in such a way that all the assemblages could be interconnected. These interconnections are based on the higher systematic conclusions of other workers, notably Forbes (1923), Remington (1954), and Ehrlich (1960). Therefore, the phylogeny which resulted from the application of the above procedure is based partly on cardiac and partly on non-cardiac characters (Fig. 22).

By using non-cardiac characters to connect the cardiac-based assemblages, the evolutionary sequence of aortal modifications was revealed. It should be emphasized that this information is a by-product of the method and did not form the basis for constructing the phylogeny.

For convenience of the reader, the cardiac-based assemblages are summarized in Table 1.

Assemblage Affinities

The ventral aortal arrangement has been taken as representing the primitive condition in the Lepidoptera. The Trichoptera (the insect order generally considered most closely related to the Lepidoptera), the Megaloptera, and the Mecoptera all possess a similar arrangement. Since no monotrysian Lepidoptera were examined in this study, confirmation of the ventral arrangement as primitive must await the examination of representatives from monotrysian taxa.

Table 1. Summary of mesothoracic aortal variations and interassemblage relationships.

ASSEMBLAGES	Group	Ventral	Tineoid	Saturnioid	Geometroid	Noctuoid	Cossoid	Rhopaloceran
		Type	Type	Type	Type	Type	Type	Type
		Transverse Chamber						Horizontal Chamber
	PYRALIDOIDEA	X						
	YPONOMEUTOIDEA	X						
	TINEOIDEA (1) ¹							
	Acrolophidae	X						
	ZYGAENOIDEA ²							
	Megalopygidae	X						
	Pyromorphidae	X						
	TINEOIDEA (1)							
	Psychidae		X					
	Tineidae		X					
	Gelechiidae		X					
	CASTNIOIDEA		X					
	TORTRICOIDEA (2)		X					
	ZYGAENOIDEA							
	Eucleidae			X				
	SATURNIOIDEA (3)			X				
	COSSOIDEA (2)							
	<u>Prionoxystus</u>			X				
	BOMBYCOIDEA (3)							
	Bombycidae				X			
	GEOMETROIDEA				X			
	SPHINGOIDEA ³							
	<u>Smerinthus</u>				X			
	BOMBYCOIDEA (3)							
	Lasiocampidae					X		
	Eupterotidae					X		
	NOCTUOIDEA					X		
	COSSOIDEA (2)							
	<u>Zeuzera</u>						X	
	<u>Hamilcara</u>						X	
	<u>Givira</u>						X	
	HESPERIOIDEA							X
	PAPILIONOIDEA ³							X

¹Arabic numerals refer to systematic overlaps of cardiac assemblages (see text).

²The Zygaenoidea included here are considered to represent a secondarily primitive condition (see text).

³This taxon contains some members with unique aortal arrangements.

Because of their clear association with the Eucleidae on the basis of non-cardiac characters, the ventral arrangement found in the zygaenoid families Megalopygidae and Pyromorphidae is considered as secondarily derived. Since both ventral and dorsal transverse-chamber arrangements occur in the Tineoidea and the Zygaenoidea, it is clear that convergent evolution has occurred. Therefore, three alternative interpretations exist.

The least likely of these alternatives is that the transverse chamber evolved twice, once in the Tineoidea and again in the Zygaenoidea. As discussed previously, the probability that a complex structure, such as the transverse chamber, represents true homology is greater than the probability that a simple or null arrangement does so.

Since the Eucleidae demonstrate a clear relationship to the Saturniidae and through this stirps, to the higher moths, it seems unlikely that the Zygaenoidea are on a branch of very early origin. The Tineoidea and Yponomeutoidea show no such association with the higher moths. It is more likely that the Yponomeutoidea and Acrolophidae are truly primitive and that the two zygaenoid families represent a derived condition.

The assemblage possessing the primitive ventral arrangement is associated with the tineoid-type assemblage through the Acrolophidae. The Acrolophidae are widely considered to be a family of the Tineoidea. Remington (1954) and Ehrlich (1960) also considered the Yponomeutidae and Aegeriidae to be Tineoidea.

The tineoid-type assemblage is associated with the Cossidae through the Tortricoidea. Forbes (1923) considered the Cossidae as a family of the Tortricoidea, and the general association of the Cossidae and Tortricidae is widely accepted. (See Powell, 1964, for discussion.) The Cossidae, through Prionoxystus, serve to connect the saturnioid-type assemblage, and through Zeuzera, Hamilcara, and Givira, connect to the Rhopalocera. The assemblage associations, thus far discussed, are illustrated in Figure 24 and are designated by arabic numerals (1) and (2) in Table 1.

Most systematists recognize the association of the Saturniidae and the Bombycoidea. Both Remington and Ehrlich place the Saturniidae, Bombycidae, Lasiocampidae and Eupterotidae in the same superfamily. Forbes, although he raised the Saturniidae to superfamily rank, clearly showed their close relationship to the Bombycoidea in his phylogenetic diagram.

Based on aortal considerations, two distinct types are found in the Bombycoidea. The Bombycidae (Gerould 1938) possess a geometroid-type, and the Lasiocampidae and Eupterotidae demonstrate a noctuoid-type arrangement. Therefore, it is suggested that the Geometroidea-Sphingoidea stirps originated from a bombycid-like ancestor, and that the Noctuoidea stirps diverged from a lasiocampid- or eupterotid-like ancestor at a later time. The associations of these "higher" moths are illustrated in Figure 23, and the systematic overlap of the aortal types is designated in Table 1, (3).

Discussion

The derivation of the Rhopalocera from a cossid-like ancestor was suggested by Forbes (1923), based on the upright egg of the Cossinae. Hessel (1966) discussed the relationship of the Rhopalocera to the Cossidae, based on the horizontal aortal chamber of Zeuzera. The examination of additional cossid genera in this study has clarified the picture considerably. The aortal polymorphism found in the Cossidae is not approached in any other taxon except the Papilioninae (Hessel 1966). In this latter group, however, the polymorphisms constitute intraspecific variations of no systematic significance.

It appears that the horizontal chamber developed from a transverse chamber at some time between the branching

of the Prionoxystus and Zeuzera stirpes. It further appears that at some time between the branching of the Zeuzera and Givira stirpes, the point at which the posterior aortal segment passes into the metathorax shifted to a rhopaloceran arrangement. The sequence of changes in the chamber and aortal configurations is shown in Figure 24.

There is little cardiac evidence to indicate the precise interrelationships between families of the Hesperioidea and Papilionoidea, although both superfamilies are obviously related through the rhopaloceran-type aortal arrangement. The elongate horizontal chamber common to the Hesperioidea and the Lycaenidae was noted by Hessel (1966), but this character was considered of doubtful significance. A recent study by Ehrlich and Ehrlich (1967) indicates a close phenetic relationship between the Hesperiidae and the Lycaenidae. It would seem, at least in this instance, that the chamber shape may be of some significance.

The proposed phylogeny of the higher moths is in striking agreement with that of Chapman (1896). In this early study of the phylogeny of the Lepidoptera based on characters of the egg and pupa, Chapman proposed relationships between the Eucleidae and Saturniidae, the Lasio-campidae and Notodontidae, and the Bombycidae and Geometridae. These relationships are strongly supported by the aortal characters used in this study.

The derivation of the Castnioidea has long been a topic of discussion and disagreement among phylogenists. Some, such as Forbes, have considered them to be derived from the Cossidae and ancestral to the Hesperioidea. Ehrlich (1960) suggested that the castnioids are of earlier origin and that the clubbed antennae and diurnal habits of this group were evolved independently from the analogous characteristics in the Rhopalocera. The mesothoracic aortal pattern of the Castnioidea offers support for this latter view. The aortal pattern is clearly of the tineoid type.

The Pyralidoidea are considered by Ehrlich as a stirps of uncertain basal attachment but located near the base of the zygaenoid branch. Forbes considered the pyralidoids to be derived from the yponomeutoid line. On the basis of the ventral-type aortal arrangement, either view could be correct. If the ventral arrangement is truly primitive in the Pyralidoidea, then the evidence supports Forbes. If, on the other hand, the aortal arrangement is secondarily primitive, the Pyralidoidea could have been derived from a proto-zygaenoid ancestor.

Since a ventrally located tympanic organ is found in the first abdominal segment of the Geometridae and some Pyralididae, Ehrlich's view possesses considerable

initial appeal. However, if the pyralidoids are considered as secondarily primitive and related to the Geometroidea, the resulting phylogeny requires the destruction of either the Saturnioidea-Bombycoidea relationship or that between the Bombycoidea and the Geometroidea. Strong evidence has been presented in support of these two relationships. Therefore, the author favors Forbes' interpretation and considers the Pyralidoidea to be of truly primitive derivation.

Concluding Remarks

It is hoped that the findings of this investigation will provide a basis for elucidating the affinities of certain taxa which were not available for inclusion in this study. It is anticipated that specimens of Euschemon and Doa, and representatives of the Dalceridae, Hyblaeidae, and Uraniidae can be examined in the near future.

Furthermore, suitable material from the presumed primitive monotrystian superfamilies and the Micropterygidae, which some workers have considered as deserving of ordinal rank (Zeugloptera), should be examined to ascertain the affinities of these taxa.

KEY TO ABBREVIATIONS

AAo	anterior aortal segment
AbOst	abdominal ostium
AM	alary muscles
Amp	ampulla
AntNv	antennary nerve
AntV	antennary vessel
AS	air sac
1Br	protocerebrum
2Br	deutocerebrum
Cx	coxa
DM	dorsal-longitudinal muscles
2Dph	mesothoracic accessory diaphragm
3Dph	metathoracic accessory diaphragm
Es	esophagus
FA	furcal arm
FS	frontal sac
Ht	heart
NC	nerve cord
OpL	optic lobe
OpV	optic vessel
Ost	ostium
PAo	posterior aortal segment
2Ph	second phragma

3Ph	third phragma
4Ph	fourth phragma
RhAo	recurrent-horizontal aortal segment
Sc1_2	mesoscutellum
Sc1_3	metascutellum
Sct_2	mesoscutum
Sm	septum
2ThOst	mesothoracic ostium
3ThOst	metathoracic ostium
TM	tissue mass
Tr	trabeculae
VDph	ventral diaphragm
vs	scutoscutellar suture

- Fig. 1. Cerura (Notodontidae), parasagittal view of dorsal vessel.
- Fig. 2. Ctenucha (Ctenuchidae), dorsal view of head showing aortal terminations.
- Fig. 3. Apantesis (Arctiidae), parasagittal view of portion of mesothorax, metathorax, and first abdominal segment.
- Fig. 4. Malacosoma (Lasiocampidae), posterior view of septum.
- Fig. 5. Transverse mesothoracic chamber, dorsal view.

1. *Cerura* 2. *Ctenucha* 4. *Malacosoma* 3. *Apantesis*

5. Transverse chamber

- Fig. 6. Laniifera (Pyrallidae), parasagittal view of pterothorax and first abdominal segment, ventral type.
- Fig. 7. Archips (Tortricidae), parasagittal view of pterothorax and first abdominal segment, tineoid type.
- Fig. 8. Automeris (Saturniidae), parasagittal view of pterothorax and first abdominal segment, saturnioid type.
- Fig. 9. Phaeoura (Geometridae), parasagittal view of pterothorax and first abdominal segment, geometroid type.
- Fig. 10. Smerinthus (Sphingidae), parasagittal view of pterothorax and first abdominal segment, geometroid type.
- Fig. 11. Celerio (Sphingidae), parasagittal view of pterothorax and first abdominal segment, sphingoid type.
- Fig. 12. Chorizagrotis (Noctuidae), parasagittal view of pterothorax and first abdominal segment, noctuoid type.
- Fig. 13. Prionoxystus (Cossidae), parasagittal view of pterothorax and first abdominal segment, saturnioid type.
- Fig. 14. Zeuzera (Cossidae), parasagittal view of pterothorax and first abdominal segment, cossoid type.
- Fig. 15. Givira (Cossidae), parasagittal view of pterothorax and first abdominal segment, cossoid type.

6. *Laniifera* 11. *Celerio* 7. *Archips* 12. *Chorizagrotis* 8. *Automeris* 13. *Prionoxystus* 9. *Phaeoura* 14. *Zeuzera* 10. *Smerinthus* 15. *Givira*

- Fig. 16. Pyrrhopyge (Hesperiidae), parasagittal view of pterothorax and first abdominal segment, rhopaloceran type.
- Fig. 17. Emesis (Lycaenidae), parasagittal view of pterothorax and first abdominal segment, rhopaloceran type.
- Fig. 18. Colias (Pieridae), parasagittal view of pterothorax and first abdominal segment, rhopaloceran type.
- Fig. 19. Battus (Papilionidae), parasagittal view of pterothorax and first abdominal segment, papilionid type.
- Fig. 20. Parnassius (Papilionidae), parasagittal view of pterothorax and first abdominal segment, papilionid type.
- Fig. 21A. Horizontal chamber and aortal configuration of rhopaloceran type, lateral view.
B. Horizontal chamber, dorsal view.
- Fig. 22. Superfamily relationships.

16. *Pyrrhopyge* 19. *Battus* 17. *Emesis* 20. *Parnassius* 18. *Colias*

21. Horizontal chamber

22. Superfamily Relationships

Fig. 23. Higher-moth relationships showing modifications and transitions of mesothoracic aortal patterns.

Fig. 24. Lower-moth and hesperioid relationships showing modifications and transitions of mesothoracic aortal patterns.

23. Higher-moth Relationships

24. Lower-moth Relationships

Fig. 25. Lateral view of first abdominal chamber of Papilio zelicaon showing ostial apparatus. Refer to Figure 21.

Fig. 26. Dorsal view of head of Ctenucha venosa showing optic vessels and ampullae. Refer to Figure 2.

Fig. 27. Posterior view of septum of Malacosoma fragilis with the dorsal vessel removed. Refer to Figure 4.

Fig. 28. Ventral view of portion of abdomen of Harrisina
brillians showing pericardial cells and alary
muscles.

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