THE METENDOSTERNITE IN COLEOPTERA: A COMPARATIVE STUDY

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With Plates 1–13.

1. Introduction.

According to Snodgrass (1927) the endoskeletal structures of insects are elaborations of the primitive intersegmental invaginations of a *Peripatus*-like ancestor. With the development of an exoskeleton, these internal ridges become sclerotised, and attached to the segmental ring before or behind, with an obvious gain in mechanical stability. Thus the functional intersegmental membrane comes to lie before or behind the ridge. At the same time, however, the somites have been divided into terga and sterna, which thereafter pursue their evolution more or less independently. In the thoracic sterna of beetles, the primitively intersegmental muscle-bearing ridges are represented by the endosternites. These have become wholly incorporated in the sterna that primitively were anterior to them; instead of a complete ridge across the sternum we have a specialised structure, consisting in the pro- and mesothorax of a pair of apophyses, and in the metathorax having much more varied forms. The variations of the metendosternite are the subject of the present paper.

The primitive intersegmental ridges, when attached to a segment and sclerotised, are called pre- or post-phragmata according to whether attached to the segment behind or before. In the thoracic sterna the furcae are morphologically post-phragmata. The non-genital abdominal segments possess prephragmata both in terga and sterna. There are dorsal and ventral longitudinal muscle-bands running from each phragma to the next. Both series are recognisable through the thorax too. In beetles, a band of muscle runs from the posterior coxal fold to the arms of the metafurca. The muscle helps to move the abdomen on the thorax. From the front of the metafurca arise a pair of tendons—conspicuous in my diagrams—that run forward into the mesothorax, where they are connected by very short muscles to the mesofurcal arms. It will be remembered that, in beetles, mesothorax and metathorax are immovably fused together; correspondingly the mesofurco-metafurcal muscle has degenerated; its only conceivable function nowadays is to even out the tensions on the endosternites by giving a forward pull when the working stroke of the hind leg is pulling back on the metafurca. In the abdomen there is also a series of dorso-ventral muscles between the tergal and sternal phragmata of each segment. These are represented in the metathorax by the *furco-dorsalis* muscles, which run from the sides of the metafurca to the post-phragma of the metatergum. The sterno-pleural muscles of the abdomen may be represented in the metathorax by the *furco-lateralis* muscles that run from the sides of the furca to the pleural ridges. The functions of these small muscles are problematic; they may be respiratory—perhaps help in directing flight, or merely give additional stability to the furca. The remaining muscles that are attached to the metafurca are leg-muscles, and have no representative in the abdomen of Coleoptera. There are the promotors and remotors of the hind coxae, and the *depressor trochanteris metathoracis.* XThe hind coxae in Coleoptera are fixed at the outer end to a process from the end of the pleural ridge, and at the inner end to a sternal process; thus they rotate about an axis through these fixed points. XThe *remotor metacoxae* is one of the chief locomotor muscles of the hind leg; it runs just under the *furco-abdominalis* muscle from the furcal arm to the top of the coxa. The promotor makes the recovery stroke; it runs from under the posterior part of the furca to the lower edge of the coxa. There remains the most important muscle of all—the *depressor trochanteris.* This large muscle attaches on the furcal arm, under the *furco-abdominalis* and *remotor coxae* muscles, and runs through the metacoxa to be inserted on the trochanter of the hind-leg. It turns the trochanter about a hinge on the coxa, and produces the working-stroke of the hind femur (which is fused to the trochanter).

The dorso-ventral wing-muscles of the metathorax lie before and beneath the furca; where wide furcal arms are present, it is evident that a large development of these muscles throws the whole furca backwards and upwards. This is well seen in such beetles as CISTELIDAE and many Lamellicornia.

The furca arises from a ridge on the posterior part of the metasternum. In some beetles there is a suture in front of the ridge which is probably what Snodgrass calls the sternal suture—in *Cupes*, some Adephaga, many Serricornia, Silphoidea, etc.—and the part of the sternum behind it should be called the furcisternum. The sternal suture is shown in a few (pl. 12, fig. 11) of my figures.

Where the furca arises on a single stem, it has a ventral median rib to strengthen it. The normal structure of this region is represented in the two diagrams pl. 13, figs. 8 and 9. An enigmatic and variable character is the development of a longitudinal suture extending forward from the middle of the hind margin of the metasternum, represented internally by a sharp ridge. It may be entirely absent, or extend the whole length of the sternum, and all intermediate conditions can be found. The side view of the base of the furca will show how this ridge is continuous with the ventral ridge of the furca.

Where the coxae are far apart, the furca rises on a broad base; where they are close, its base is correspondingly narrow. The proximity or otherwise of the hind coxae has long been used as a taxonomic character in Coleoptera, and most systematists would quite naturally tend to say that a character so intimately bound up with it could have no independent taxonomic value. I think that one should, however, picture the metathorax evolving as a whole —the slow changes in relative development and manner of use of the various muscles being reflected in the transformations of the endosternite, of which the position of the coxae is only an incomplete and misleading external manifestation.

In large beetles, a relatively stronger musculature is mechanically necessary to produce the same activity; hence the furca is relatively larger and stouter than in smaller beetles.

2. TECHNIQUE.

The drawings of furcae in the present paper were made from specimens boiled in potash, decolorised with hydrogen peroxide, and cleared in xylol. The terga being removed, and the elytra spread, a dorsal view of the furca can be drawn. The smaller beetles can be conveniently mounted in Canada balsam on a ringed slide (taking care to use excess of balsam). These preparations can be used for a detailed study of the whole skeleton of the beetle; a representative set of them would, in my opinion, be of great value to systematists and morphologists. The drawings pl. 13, figs. 6 and 7 were made from dissections; pl. 13, figs. 4 and 5 are reconstructions from serial sections of fixed freshly emerged beetles. I made reconstructions thus of the following beetles: *Araecerus fasciculatus* Deg., *Bruchidius obtectus* Say, *Caulophilus latinasus* Say, *Calandra granaria* L., *Lasioderma serricorne* Jab., *Oryzaephilus surinamensis* L., and *Trogoderma granarium.*

In those genera where I examined more than one species, no significant differences were found. In certain families, where the furca is unusually variable (CHRYSOMELIDAE, SILPHIDAE), it would probably be advisable to study several species in each of the larger genera. It is not improbable that results of taxonomic value might be obtained. Here, however, where I am concerned with the broad lines of variation of a previously uninvestigated character in a large order, my interest is rather in resemblances and homology than in taxonomic differentiation.

3. DESCRIPTIVE.

The order in which I have described my results must seem very arbitrary to an orthodox taxonomist. The main peculiarity is that I have described the furcae of Adephaga last. For the rest, the arrangement adopted is intermediate between Böving's classification (as revised by de Peyerimhoff) and Ganglbauer's. The LYMEXYLONIDAE are admittedly an archaic and isolated family, and might as well be placed first as anywhere. After *Hylecoëtes* sp. I have described the Heteromera and the Clavicornia, and then the Phytophaga–Rhynchophora. For all these types the furca of *Hylecoëtes* supplies a convenient ground-plan. The Serricornia and the Malacodermata follow, then the Lamellicornia. The Staphylinoidea and the Palpicornia complete the suborder Polyphaga.

The Lymexylonid *Hylecoëtes* has a furca that seems one of the most primitive in the order (pl. 1, fig. 1). The hind coxae in this insect are close together, and the endosternite arises as a slender stalk, which broadens out forward into a lamina, with a narrow front whence arise the two anterior tendons (*t*) close together. From the base of the lamina rise a pair of strongly sclerotised arms. The notable features are (1) the freedom of the arms (2) the extensive lamina (3) the anterior tendons, *t*, arising close together, supported merely by a median thickening of the lamina. All of the forms (pl. 1, fig. 1 to pl. 7, fig. 4) may be derived from a furca very like that of *Hylecoëtes.* For instance, *Oedemera nobilis* Scop. (pl. 1. fig. 2) has a furca with a similar long slender stalk, but a considerable fusion of arms and lamina has occurred, and the tendons *t* have become separated. To support them a rib has been developed along the front of the lamina, between the central ridge and the fusion with the arms. Another species of *Oedemera* was studied; the Australian *Pseudolycus* sp. and *Sessinia* sp. have similar furcae but with wider tendons and rather less free arms, thus approaching the MELOIDAE.

The form in pl. 1, fig. 3 (*Rhinosimus planirostris* F. PYTHIDAE) is anomalous. The considerable freedom of the arms looks primitive, but the strengthening of the anterior edge of the lamina, and above all the position of the anterior tendons, point to an origin from something like the furca of *Oedemera.*

Aegestria sp. (pl. 1, fig. 4) also represents a small family of dubious affinities. The lamina is considerably modified and the arms shortened; it is clearly related to *Oedemera*.

Plate 1, fig. 5 shows a furca directly derivable from that of *Oedemera*. The beetle is the Australian *Palaestra* sp.—a Meloïd. *Zonitis* sp. and *Mylabris* sp., European representatives of the family, also the African *Cylindrothorax melanocephala*, are similar. *Meloë violaceus* Marsh. is remarkable in not possessing any free lamina; this may follow from its peculiar habit. In those MELOÏDAE with a differentiated lamina, the anterior tendons arise at the point of its fusion with the arms. The Pyrochroïd *Pyrochroa coccinea* L. (pl. 1, fig. 7) is a step beyond this, having the tendons just on the arms. *Melandrya caraboides* L. (pl. 1, fig. 6) is evidently of the same type.

The two Tenebrionid beetles figured produce a difficulty. *Derosphaera foveostriata* Thoms. (pl. 1, fig. 8), and most ordinary Tenebrionids (*Helops striatus* Geof., *Zopherus nodulosus*, *Diaperis* sp., *Tribolium navale* F. (pl. 2, fig. 1), *Gnathocerus cornutus* F., *Tenebrio molitor* L., *Saragus* sp., *Adelium* sp., *Helaeus* sp., *Uloma* sp., etc.) are evidently from the same stock as the preceding Heteromera, all having laminae reduced, and anterior tendons on the arms, but *Amarygmus* sp. (pl. 1, fig. 11) has little trace of lamina, yet its anterior tendons arise comparatively close together. Now if *Amarygmus* is a true Tenebrionid, the proximity of the tendons must be secondary. However, I do not think that this necessarily invalidates any taxonomic conclusions based on the position of the tendons; the projection bearing the tendons in *Amarygmus* is itself unusual in Heteromera. When the lamina has become as extensively fused to the arms as it is in the higher TENEBRIONIDAE (*Helops*, etc.), a re-approach of the tendons is not inconceivable. Among the TENEBRIONIDAE, it is interesting to note that *Lyprops* sp. (pl. 1, fig. 10) has something like the median projection of *Amarygmus*, without the approximation of the tendons, while *Lagria hirta* L., and a larger Australian species have the tendons unusually close (pl. 2, fig. 2). LAGRIIDAE and CISTELIDAE (*Anaxo* sp., *Chromomoea* sp. (pl. 1, fig. 9), *Cteniopus sulphureus* L., *Ectenostoma* sp.) both have some trace of a median projection.

Trictenotoma childreni Gray may belong here. The furca is about the shape of that of *Arthropterus* (pl. 2), and very heavily sclerotised; it rises almost vertically from the sternum, and the anterior tendons—fairly widely separated—are at right angles to its general plane (*i.e.*, parallel to the sternum).

The family MORDELLIDAE has a very unusual type of furca (*Anaspis*—pl. 1, fig. 13), quite unlike any other heteromerous form studied. Both Sharp (1912) and Böving (1931) place *Anaspis* with *Anthicus*, leaving *Mordella*, *Mordellistena*, and *Tomoxia* in the MORDELLIDAE. The furcae of *Anaspis* sp., *Mordella* sp., and *Mordellistena* sp., are closely alike, and none of them shows any resemblance to *Anthicus*.

The RHIPIDOPHORIDAE are usually placed near the MORDELLIDAE; the furca of an Australian species of *Euctenia* is figured on pl. 1, fig. 12. The lamina has disappeared as in *Meloë*.

Two of the forms figured (pl. 2, fig. 9 and pl. 3, fig. 7) merit particular attention. They belong to families usually put some way apart; both are recognised as aberrant forms. *Rhizophagus depressus* F. (pl. 2, fig. 9) is a distinct subfamily of the NITIDULIDAE, and *Hectarthrum* sp. (pl. 3, fig. 7) of the CUCUJIDAE, in the orthodox classification. In both of them the anterior tendons are very close together. *Rhizophagus* has a modified lamina, but the close placing of its tendons is primitive—as will be seen later, the NITIDULIDAE proper have rather close tendons. *Hectarthrum* also is undoubtedly primitive in this character—and the great median elongation of the lamina is probably another archaic character. The furca of *Hectarthrum* is very distinct from those of other CUCUJIDAE studied. With the furca of *Hectarthrum* should be compared the Australian Clerid *Pylus* sp. figured on pl. 4, fig. 5. In this form the arms are thrown farther back than in any of the genera examined so far, and they are rather short. The large tendon (*h*) of the furco-lateralis muscle is conspicuous. The lamina and anterior tendons are in much the same condition as in *Hectarthrum*. Other CLERIDAE—*Necrobia rufipes* De G., *Scrobiger* sp., *Trogodendron fasciculatum* Schreib., and others—were examined, and had furcae much like that of *Pylus*. Two other subfamilies of the CUCUJIDAE have furcae comparable with *Hectarthrum* and *Pylus*. These are the BRONTINAE (*Hyliota dubia* F., pl. 3, fig. 6) and the HEMIPEPLINAE (*Hemipeplus rodericensis*, pl. 3, fig. 5). The metendosternite in *Hyliota* closely resembles the EROTYLIDAE and other lower Clavicorns, while *Hemipeplus* is equally clearly Nitiduloid.

The true NITIDULIDAE—I examined endosternites of *Meligethes aeneus* F., *Omosita colon* L., *Glischrochilus* 4-*punctatus* L., *Prometopia* sp., *Soronia grisea* L., *Pityophagus* sp., *Carpophilus hemipterus* L., *Diphyllus lunatus* F.—are not obviously related to any other Coleoptera in the character under investigation. Pl. 3, figs. 9, 11 are typical forms. *Pityophagus* (pl. 3, fig. 10) alone shows a distinct lamina, and is otherwise aberrant. This furca is rather more definitely Cleroid than the picture would suggest. In the rest of the family, it may be assumed that arms and lamina have either fused or have never been distinct—what that implies will be seen later. In *Leperina* sp. (pl. 4, fig. 1) and *Tenebroides mauretanicus* L. the furcae are essentially similar to *Pityophagus*, CLERIDAE, *Hectarthrum* etc.; *Thymalus limbatus* F. (pl. 4. fig. 2) and *Helota gemmata* Gorh. (pl. 4, fig. 3) have less primitive furcae (unless the lack of arms-lamina differentiation is primitive) not very like each other. In the proximity of the tendons, *Thymalus* may retain an archaic character, and the general Bostrychoid appearance is suggestive. The Derodontid beetle *Laricobius erichsoni* Rosenh. seems to belong near these forms; I hope to be able to publish a figure of its metendosternite soon.

Pl. 2, fig. 3, *Tetralanguria elongata* F. has a primitive Hylecoëtoid metendosternite, with a significant resemblance to the primitive Phytophagan *Orsodacne*.

Triplax russica L. (pl. 2, fig. 4) belongs to the family EROTYLIDAE, and is therefore a Clavicorn. Its furca could be easily derived from that of *Oedemera* by a general shortening and thickening. Other EROTYLIDAE examined—*Thallis* sp. and *Dacne* sp.—are of the same type. *Coccinella* 7-*punctata* L. (pl. 2, fig. 5) shows an endosternite more modified than that of *Triplax* and clearly derivable from it. The anterior tendons are in the same position as with *Oedemera* and *Triplax*, but the lamina is more reduced, and the shortening more extreme than in the EROTYLIDAE. Most COCCINELLIDAE studied (*Adalia* 2-*punctata* L., *Micraspis* 16-*punctata* L., *Thea* 22-*punctata* L., *Halyzia* 18-*guttata* L., *Rhizobius* sp., *Coccidula rufa* Hbst.) have less shortened furcae than *Coccinella* 7-*punctata*. A step farther leads to the ENDOMYCHIDAE, in which the stalk is hardly distinguishable, and the whole structure begins to look like a pair of arms. A similar line of evolution has led to the furca of *Bothrideres* sp. (pl. 3, fig. 1), which rather resembles that of *Endomychus coccineus* L. *Olibrus* sp. (pl. 3, fig. 3) (PHALACRIDAE) is very like *Dacne* and *Thallis* in the EROTYLIDAE. The endosternite of *Bothrideres* is most probably derived from one like that of *Ditoma crenata* F. or *Orthocerus clavicornis* Lat. (COLYDIIDAE

—pl. 2, fig. 7); the same may be true of *Cerylon* sp. (pl. 3, fig. 4). In all these COLYDIIDAE the anterior tendons are wide apart, and arms and lamina are not distinct. The furca has a complicated arrangement of thickened bars which give it a very distinctive facies. The MYCETOPHAGIDAE are the only family with which the COLYDIIDAE seem comparable. The furca of *Mycetophagus 4-pustulatus* L. is shown on pl. 2, fig. 6. The arms are strongly developed, while the lamina is small. *Litargus connexus* Geof. and *Typhaea stercorea* L. of the same family have closely similar endosternites; and *Byturus tomentosus* F., *Telmatophilus* sp., *Cryptophagus* sp., *Micrambe vini* Pz., *Atomaria analis* Er., and *Ephistemus globulus* Pk. all resemble *Triplax* and *Rhizophagus* in the character under discussion. *Anthicus floralis* L. is very similar to these forms rather than to Heteromera. CIIDAE (*Cis boleti* Scop., pl. 8, fig. 11 and *C.* sp., also *Ennearthron affine* Gyll.) have a furca with a pair of arms of a special type, giving no hint of their systematic position.

Among the small CUCUJIDAE and LATHRIDIIDAE a furca with a pair of arms is likewise found, with no indication of its origin from a Hylecoëtoid form. *Oryzaephilus surinamensis* L. (pl. 3, fig. 8) was studied, together with *Laemophloeus minutus* Ol. and *Psammoecus bipunctatus* F.; *Melanophthalma gibbosa* Hbst. (pl. 3, fig. 2) (LATHRIDIIDAE) is figured, while *Lathridius nodifer* West., *Enicmus minutus* L., and *Corticaria pubescens* Gyll. were also examined.

Monotoma testacea Mots. (pl. 2, fig. 8) is remarkable in combining both a furca with a pair of arms and anterior tendons arising in close proximity; it seems to have been derived from an endosternite something like that of *Rhizophagus.*

Phytophaga–Rhynchophora.

Orsodacne lineola Pz. (pl. 5, fig. 1) figures a metendosternite that reminds one of *Hylecoëtes* and *Tetralanguria* for a comparison. The lamina is well developed, the tendons separated as in *Oedemera*, and the arms are fairly free, though somewhat short. This beetle is admittedly primitive, and a member of a great, homogeneous group whose outside relationships are debatable. *Orsodacne* is certainly a member of the Phytophaga, though of uncertain family position. Some of the Phytophaga, and especially the weevil *Rhinomacer*, evidently link to *Orsodacne.* The great family CERAMBYCIDAE is, if one exclude the PRIONIDAE *Distenia* and *Parandra*, very uniform in the furca, which is not greatly removed from that of *Orsodacne. Spondylus buprestoides* was the most primitive form studied (pl. 4, fig. 7) and stands close to the ancestral furca of the Longicorns.

In the CERAMBYCIDAE proper *Clytus* (pl. 4, fig. 11) and *Tetropium* (pl. 4, fig. 8) were figured from a number of species studied : *Phoracantha* sp., *Rhagium mordax* De G., *Monohammus* sp., *Phyllocnema latipes* De G., *Tetropium gabrieli* Weise, *Grammoptera ruficornis* F., *Strangalia armata* Brit. Cat., *Clytus arietis* L., *Bethelium* sp.—and differ as widely as any of these. In all of them the tendons are about as close as in *Orsodacne*, the arms have rotated far back, there is an extensive free lamina, and a stalk of moderate length. *Distenia undata* F. (pl. 4, fig. 10) is a form whose isolation has met with growing recognition ever since Leconte and Horn drew attention to it. Yet the general facies of the beetle is so typically Cerambycoid that I was greatly surprised by its extraordinary furca.

The PRIONIDAE, or at least those I examined (*Prionus coriarius* L., an undetermined African species, and *Pathocerus wagneri* Waterh.), do not show the typical Hylecoëtoid furca. *P. coriarius* and the African species resemble

Trictenotoma closely, except that they have the anterior tendons close together; *Pathocerus* is probably more primitive, and might be described as a Hylecoëtoid furca with no recognisable lamina. *Hypocephalus armatus* Desm. (pl. 4, fig. 9) is reputed to be near *Pathocerus*; its furca is fused to the mesendosternite as in *Brachycerus*, *Cebrio*, and *Gibbium*. It is a peculiar form, quite unlike any other examined. There remains *Parandra glabra* De G. (pl. 5, fig. 10) with almost as doubtful a right to be considered here. The furca has a longicorn-like shape, but the characteristic separation of arms and lamina is not present. On the other hand, the general shape, and position of the tendons, separate it sharply from the PRIONIDAE and *Distenia*. It is not obviously comparable with any of the CUCUJIDAE examined by me.

Mecynodera coxalgica Boisd. and *Sagra* sp. among the CHRYSOMELIDAE could well be described with the CERAMBYCIDAE, for their furcae are of essentially the same type (pl. 5, fig. 6). Of the remaining CHRYSOMELIDAE, the Cyclica (CHRYSOMELINAE and EUMOLPINAE) have apparently the most modified furcae. The residue can be roughly lumped in three groups: Trichostomes, Camptosomata, Eupoda–Cryptostomes–LAMPROSOMINAE. The Trichostome furca as typically developed in *Haltica* (pl. 6, fig. 5) has the tendons in the *Orsodacne* position, no free lamina, and a fairly long stalk. *Oides collaris* Baly. from Africa is more like *Orsodacne* than usual, but recognisably Galerucine. *Sermyla halensis* L. (pl. 6, fig. 6), GALERUCINAE, differs from *Haltica*, but no general difference can be found between the two subfamilies. The smaller HALTICINAE tend to lose the stalk, and the most extreme forms studied (*Longitarsus*, pl. 6, fig. 4) look by themselves quite unlike other CHRYSOMELIDAE. Forms studied: *Lochmaea suturalis* Th., *Galerucella* sp., *Oides collaris* Baly., *Sermyla halensis* L., *Spilocephalus viridipennis* Jac., *Luperus longicornis* F., *Haltica* sp., *Hyphasoma* sp., *Sphaeroderma rubidum* Graells, *Phyllotreta cruciferae* Goez., *Chaetocnema hortensis* Geof., *Chalcoides aurata* Marsh., *Longitarsus* sp., *Apteropeda globosa* Ill., *Diamphidia flexuosa* Baly.

Crioceris asparagi L. (pl. 5, fig. 4) and *Donacia* sp. have fairly close tendons, and some vestige of lamina remaining. The position of the arms is characteristic of them. The endosternite of *Lema cyanella* L. (pl. 5, fig. 2) suggests that the Galerucine furca is derived from a Eupodan form. The CASSIDINAE (*Cassida rubiginosa* Müll. (pl. 5, fig. 7) and *Aspidomorpha* sp.) likewise may be derived from the Eupoda, and possibly HISPINAE too. The furca of *Hispa testacea* L. (pl. 5, fig. 8) has a considerable resemblance to that of *Lamprosoma concolor* Stm. (pl. 5, fig. 5). The diagrams (pl. 6, fig. 1, a, b, c, d,) are of the ends of the furcal arms in *Cassida*, *Aspidomorpha*, *Hispa*, and *Lamprosoma* respectively.

The CHLAMYDINAE (*Chlamys natalensis* Jac., pl. 5, fig. 3) are apparently related to the Camptosomata, but also to the HISPINAE and LAMPROSOMINAE (pl. 5, fig. 3, cf. figs. 5 and 8).

Clytra quadripunctata L. and *C. interrupta* Lacord. among the Camptosomata have a furca surprisingly like those of Lamellicornia (pl. 5, fig. 9; pl. 9, fig. 4). The close tendons, borne on a median elongation of the lamina, are a perplexing character, though it is hinted at in some other forms (*Chlamys*, *Hispa*, *Lamprosoma*). *Cryptocephalus aureolus* Sut. is very like *Clytra*; *Labidostomis tridentata* L. alone approaches the Eupodan furca appreciably. *Megascelis viridis* Ill. probably belongs here; the furca has a somewhat longer stalk than in *Cryptocephalus*, and is somewhat suggestive of GALERUCINAE. The subfamily MEGALOPODINAE, represented by *Mastostethus nigrocinctus* Chevr., is not at all Camptosomatan in the metendosternite, but shows a close resemblance to SAGRINAE.

The Cyclica form a uniform group whose furcae have reached the " pair of arms " condition (leaving little trace of the ancestral form), just as has happened in many Clavicorns. The tendons are widely separated on the arms (cf. *Lamprosoma*). Genera studied: *Timarcha tenebricosa* F., *Phytodecta viminalis L.*, *Phyllodecta vulgatissima* L. (pl. 6, fig. 2), *Phaedon cochleariae* F., *Hydrothassa marginella* L., *Colasposoma metallicum* Clark (pl. 6, fig. 3), *Prasocuris junci* Brahm.

Anthonomus (pl. 6, fig. 11) is as nearly as possible typical of weevil furcae. Most weevils have quite long arms; many (*Baris, Sciaphilus, Calandra,* etc.) have shortened stalks or verge on a "pair of arms" condition. *Brachycerus congestus,* a very rotund Rhodesian weevil, has the metafurca fused to the mesofurca in the same way as *Gibbium,* which it resembles in general form. Apart from this, the furca is a rather primitive one. *Belus* (pl. 6, fig. 12) is remarkable in having a furca very like those of CERAMBYCIDAE. Forms studied: *Anthonomus pomorum* L., *Baris lepidii* Germ., *Balaninus nucum* L., *Belus* sp., *Brachycerus congestus* Gerst., *Calandra granaria* L., *Caulophilus* sp., *Ceuthorrhynchus* sp., *Cylas formicarius* F., *Epipolaeus caliginosus* F., *Hylobius abietis* L., *Mecinus pyraster* Hbst., *Orchestes* sp., *Pissodes pini* L., *Polychlaeis equestris* Bohem., *Otiorrhynchus atroapterus* De G., *Rhynchites betulae* L., and *R.* sp., *Sciaphilus asperatus* Bons., etc. *Cordus* sp. (BRENTHIDAE—pl. 6, fig. 9) is easily referable to the primitive weevil type.

The Hawaiian genus *Proterhinus* is notably aberrant in many ways. The furca is of the specialised " pair of arms " type, and gives no help to the placing of this family. In the SCOLYTIDAE the weevil tendency to have long arms is carried further. *Ips typographus* (pl. 7, fig. 2) is typical. *Platypus cylindrus* F. (pl. 7, fig. 1) appears in the figure to have no anterior tendons and no lamina; they are probably present, but I could not be sure. I also studied *Xyleborus dryographus* Ratz. and *Hylastes* sp. Plate 6, figs. 8 and 10—figuring *Rhynchites* and *Rhinomacer*—are primitive furcae, the latter in particular being very close to *Orsodacne*. In both of them the anterior tendons are unusually close. Leconte and Horn (1883) cite the genus *Urodon* as transitional from ANTHRIBIDAE to BRUCHIDAE; *U. lilii* Sch. (pl. 7, fig. 4) is certainly primitive, but appears nearer to *Araecerus* than to *Bruchidius*. *Araecerus fasciculatus* Say (ANTHRIBIDAE—pl. 7, fig. 3) has short arms, otherwise it has an ordinary weevil furca.

The furca of *Bruchidius obtectus* Say (pl. 6, fig. 7) is by no means primitive; it is perhaps derived from a weevil-like type.

Before leaving the series of forms ultimately referable to " Hylecoëtoid " or " Cleroid " furcae, there is one odd form to be noticed. On pl. 4, fig. 4 a furca is figured which recalls that of *Pylus* (pl. 4, fig. 5) and others. The beetle is *Dasytes* sp., usually put in the MELYRIDAE. A comparison with pl. 4, fig. 6 (*Malachius bipustulatus* L.) reveals a surprising difference, in no way bridged by *Balanophorus* sp. or *Melyris rufiventris* Boh. This family raises difficulties. *Dasytes* is now usually placed in a distinct family.

The furca of *Telephorus* sp. (pl. 7, fig. 5) cannot be derived from a Hylecoëtoid stock, but must be placed as a primitive representative of a different evolutionary line. There is a well-developed stalk that broadens out forward into a sort of lamina; in front it narrows again to an apex whence arise the anterior tendons in close proximity. The " lamina " is more or less diamond shape. The whole thing has a deep central indentation with a wide ventral median flange, giving it a **Y**-shaped cross-section. The central and posterior part of the lamina is a heavily sclerotised area, sending forth two fine ridges to the bases of the anterior tendons. A similar state of affairs holds for the furca of *Agriotes lineatus* L., though the tendons have parted a little and the thinly sclerotised part of the lamina is larger (*Agriotes* is figured on pl. 7, fig. 6). *Rhagonycha lignosa* Müll. and *Malthinus fasciatus* Ol. resemble *Telephorus* very closely; the furca of *Lycus trabeatus* Guèr. (pl. 7, fig. 7) is probably a shortened version of the Telephorid furca. Most Coleopterists think of *Agriotes* as belonging to a compact, isolated group of families—ELATERIDAE, BUPRESTIDAE, EUCNEMIDAE, THROSCIDAE, CEBRIONIDAE, etc. The English Elaterids *Limonius aeruginosus* Ol. and *Prosternon holosericeus* Ol., *Nematodes* sp. and *Melasis buprestoides* L. among the EUCNEMIDAE; *Sternocera orissa* Buquet, *Ethon* sp. and *Sphenoptera gossypii* Cotes (pl. 7, fig. 9) of the BUPRESTIDAE, were also examined. The Buprestids and *Melasis* have much less elongate furcae than *Agriotes*; they all show a clear division of the lamina into membranous and sclerotised areas. *Nematodes*, on the other hand, has a very elongate furca, with the anterior tendons arising close together on a long median projection; the division of the lamina is faint but distinct. *Limonius* is shortened like BUPRESTIDAE, while *Prosternon* has a peculiar-looking furca with sclerotised lateral arms something like *Throscus* (*v. infra*) and peculiar postero-ventral projections at the bases of these arms, rather like *Attagenus* (*v. infra*). Though all these furcae have the same ground plan as those of *Agriotes* and *Telephorus*, their dissimilarities are complex and puzzling. It will be necessary to study many more forms in the Elateroidea before the relationships of the furcae become clear. *Cebrio gigas* F.—the genus has met with various adventures at the hands of American taxonomists—has an indubitably Elateroid furca. As in *Brachycerus* and *Gibbium*, the anterior tendons have been consolidated to fuse the metafurca on to the mesofurca (pl. 7, fig. 8). *Throscus* sp. and *Aulacothroscus elongatus* Bonv. (pl. 8, fig. 4), usually placed as *primitive* ELATERIDAE, exhibit a striking superficial unlikeness to the previous " Serricorns," but their furca is easily derivable from that of (say) *Telephorus* by a lateral extension of the heavily sclerotised part of the lamina, forming a pair of somewhat backward-directed arms. This is a natural consequence of the shortened form of these beetles. As will be seen later, there are parallels for this process. Included with the " Serricorns " by many recent systematists are the HETEROCERIDAE. In this family I examined the furcae of *H. marginatus* F. (pl. 8, fig. 3) and an undetermined Australian species. The relationship to the previously mentioned Serricorns is clear. The sternal suture conspicuous in the diagram is found, or at least suggested, in various Elateroids—*Sternocera, Ethon, Sphenoptera,* but not *Agriotes, Nematodes,* or *Throscus*—in *Dryops*, and notably in *Cupes*. When I made the drawings, I was not at all interested in the character, and unfortunately neglected to represent it systematically in my diagrams.

Dryops luridus Er. (PARNIDAE, pl. 8, fig. 5) is commonly thought to be " in the neighbourhood of " HETEROCERIDAE. The furca is peculiar; there is a posterior central sclerotised region on the lamina comparable with that of *Agriotes*. Lateral arms occur much as in THROSCIDAE. The anterior tendons are separated by a deep median cleft. Just behind the " head " of the furca, there is a wide, downward projection from the top of the stalk. It is not clearly shown in the diagram—what is shown appears as broken lines. This structure is apparently homologous with a smaller one in a similar position on the furca of *Agriotes* (pl. 7, fig. 6), and vestigially present in many furcae of this series. From its position I should imagine it supports the muscle, labelled P in my diagrams, that effects the recovery stroke of the coxa. The structure is rather unstable in position; it may arise under the lamina itself, or behind it on the stalk. In BYRRHIDAE (*Byrrhus pilula* L., pl. 7, fig. 10) (also examined, *Simplocaria semistriata* F. and the Australian *Microchaetes* sp.) a rather primitive furca of the same series is found. The tendons are not very close; the central sclerotisation of the lamina noticeable in all the preceding forms (except possibly Buprestidae) is absent, but the afore-mentioned ventral structure is well developed and shown in the diagram by broken lines. As befits so rotund an insect, the whole structure is short and wide. *Dascillus cervinus* L. (pl. 8, fig. 1) has a central sclerotisation, but little trace of the ventral structure; the tendons are separated as in *Byrrhus*. Cyphonidae (*Cyphon variabilis* Thunb., pl. 8, fig. 2) is a related family, with a furca of a similar type. The ventral structure is well developed. *Macrohelodes* sp. from Australia has a shorter and wider version of the Cyphon furca, thus becoming rather like the Byrrhidae (which it otherwise resembles). *Eucinetus infumatus* Lec. has a very peculiar furca, which I hope to figure in a future paper. The furca of *Attagenus pellio* L. (pl. 8, fig. 6) has all the features of this series—with a lateral extension of the sclerotised part of the lamina forming arms as in the Throscidae. The ventral process is perceivable though not shown in the diagrams, but there is an enigmatic flap at the posterior base of the arms that looks like a vestige of differentiated lamina. However, I think this must be secondary. *Trogoderma granarium* Ev. has a short stalk, and noticeable ridges connecting the heavily sclerotised back of the lamina with the anterior tendons as in *Dryops*. In *Anthrenus verbasci* L. the arms have turned forward to produce a Y-shaped furca.

To this series belong the furcae of the Bostrychoid group, too. *Anobium* sp. (pl. 8, fig. 8), for instance, has a furca of similar shape to *Anthrenus*—and the ridges to the bases of the tendons are present though not shown in the diagram. *Ptilinus pectinicornis* L. appears to have the most primitive endosternite of any examined in this superfamily, with close tendons on a long median elongation, and the general facies of some of the Lamellicornia. *Lasioderma serricorne* F., *Ptinus* sp., *Niptus* sp., *Lyctus linearis* Goez. (pl. 8, fig. 9) and sp., *Sitodrepa panicea* L., *Dinoderus* sp. (pl. 8, fig. 7), *Rhizopertha dominica* F. are hardly worth separate description, having furcae all of the same type. The furca of *Gibbium* sp. is, as one would expect, much modified (pl. 8, fig. 10); by consolidation of the anterior tendons, the metendosternite has become fused to the mesendosternite.

Lamellicornia.

The superfamily Scarabaeoidea is as uniform in the furca as in other characters. The most primitive furca might be expected to be that of *Trox scaber* L. figured on pl. 9, fig. 3. It is conceivably derivable from the Byrrhoid–Elateroid type, though lacking strong positive points to prove this. *Onthophagus fracticornis* Pk. shows, if anything, stronger resemblances that way (pl. 9, fig. 1). In all the Lamellicorns the furca is heavily thickened, and the tendons arise close together on a median projection. The lateral projections are particularly strongly sclerotised—probably this is needed to support the immense muscles of the hind legs of these beetles. There are a few obvious differences between the furcae of the various families of this group. In *Trox* and the coprophilous Scarabaeids the furcae have long stalks and are very stout. In *Lucanus cervus* L., *Dorcus parallelopipedus* L., and *Sinodendron cylindricum* L. (pl. 9, fig. 4) the structure is more slender than usual, and the projection bearing the tendons is unusually long. A Passalid examined has the usual Lamellicorn furca, with the stalk very short—a character shared with the Cetoniines, Genera studied: *Trox scaber* L., *Lucanus cervus* L., *Dorcus parallelopipedus* L., *Sinodendron cylindricum* L., *Geotrupes stercorarius* L., *Aphodius* sp., *Onthophagus fracticornis* Pk., *Phyllopertha horticola* L., *Serica brunnea* L., *Pachnoda impressa* and two other Cetoniines; *Passalus* 2 spp. (pl. 9, fig. 3).

The basal type whence Malacoderm, Serricorn and Lamellicorn furcae may be derived is, I think, the most primitive in the order, and serves also as a basal type for the Staphylinoid–Silphoid association. In the more primitive members of the Silphoidea the derivation from this type of metendosternite is easily seen. *Hydnobius perrisi* Fair. (Anisotomidae—pl. 9, fig. 6) is a good example. The " arrow-head " shape of this furca, which recalls *Crioceris*, is an unimportant secondary character, much less marked in other Anisotomidae (*Liodes* sp. and *Agathidium* sp.). *Choleva angustata* F., *Choleva* sp., and *Nargus fumatus* Spence all resemble this family; a species of *Ptomaphagus* has the arms thrown more forward, while the median projection is reduced. The Silphi and Necrophori are more primitive than most of their allies in this character. In *Phosphuga atrata* L. (pl. 9, fig. 8) there are backward-pointing arms developed from the posterior sclerotisation of the primitive lamina; the front part has disappeared except for a central strongly sclerotised projection bearing the forward tendons. The musculature of this type of furca is illustrated on pl. 13, fig. 7. *Thanatophilus rugosus* L. (pl. 9, fig. 7) is unexpectedly different for so similar a genus; the central projection is obsolete in this furca. *Necrophorus humator* F. is like *Phosphuga*. *Clambus armadillo* De G. has a superficial resemblance to *Agathidium*, and undoubtedly belongs in the present series. The furca could hardly be said (pl. 9, fig. 11) to resemble Anisotomidae, or indeed any other studied in this investigation. The much-disputed genus *Syntelia* (*S. histeroides* Lewis, pl. 9, fig. 10) has no Clavicorn features in its endosternite, neither does it resemble the Histeridae. I am convinced that it is closely related to the Silphidae.

In the more modified Silphids (I mean more modified in this character) the structure tends to become a featureless Y. In *Leptinus testaceus* Müll. the stalk is evanescent, and the furca is V-shaped. The Staphylinidae in typical forms show little furcal resemblance to the Silphidae, but one genus—*Megalopsidia*, pl. 10, fig. 1—shows how they are related to the forms I have been studying.

Two major subfamilies of the Staphylinidae have a common furcal type that most observers would admit to be comparable with that of *Megalops*. The subfamilies are the Omaliinae and the Oxytelinae; the furcal type is figured on plate 10, fig. 6, the actual form being *Haploderus coelatus* Gr. From *Haploderus* other Oxytelinae exhibit departures in two directions—exemplified by *Siagonium quadricorne* Kirb. (pl. 10, fig. 7) and *Platystethus arenarius* Geof. (pl. 10, fig. 4). *Coprophilus striatus* F. and *Bledius* sp. are very like *Haploderus*, while *Trogophloeus* inclines towards *Platystethus*. Among the Omaliines, *Omalium rivulare* Pk. (pl. 10, fig. 2), *O.* sp., *Lesteva* sp., *Lathrimaeum unicolor* Marsh., *Olophrum piceum* Gyll., and *O.* sp., *Coryphium angusticolle* Steph. are all similar to *Haploderus*; *Acidota cruentata* Man. has probably the most primitive furca in the subfamily (pl. 10, fig. 3), from which that of *Phyllodrepa vilis* Er. (pl. 10, fig. 5) is probably derived. *Proteinus macropterus* Gyll. and *Megarthrus affinis* Müll. are also aberrant (pl. 10, fig. 8), perhaps from a similar type. *Oxyporus* I have unfortunately not been able to examine, but prophesy that the furca will be found to be near those of *Megalopsidia* and *Acidota*. *Piestus* sp. is transitional in its furca from the Omaliine type to that of higher Staphylinidae.

The subfamilies Staphylininae, Paederinae, Tachyporinae, and Aleo-

CHARINAE—containing the most familiar and "typical" STAPHYLINIDAE—share a furca that is like a roman T with the serifs on the cross piece (pl. 10, fig. 9) inverted. Some genera (*Amischa*, an indeterminate "*Atheta*" sp., *Stilicus*) have a central projection, apparently *not* bearing the anterior tendons. In *Bolitobius*, the form shows similarities to the Oxyteline type, and *Piestus* resembles *Bolitobius* (pl. 10, fig. 10), rather closely. Most of the ALEOCHARINAE and *Hypocyptus* have a short stout stalk. Forms examined: *Philonthus* sp., *Quedius* sp., *Baptolinus affinis* Pk., *Paederus littoralis* Gr., *Stilicus orbiculatus* Pk., *Ontholestes murinus* L., *Amischa analis* Gr., *Myrmedonia* sp., "*Atheta*" sp., *Piestus* sp., *Tachyporus hypnorum* F. and *T.* sp., *Tachinus rufipes* De G. (pl. 10, fig. 9), *Bolitobius trinotatus* Er., *Hypocyptus longicornis* Pk.

In the preceding account of Staphylinid metendosternites, one familiar subfamily has been designedly omitted. Pl. 11, fig. 3, the furca of *Stenus cicindeloides* Gr., will explain this omission. Until recently, I knew of no transitional forms connecting *Stenus* with the rest of the family; in fact I felt that *Stenus* and *Euasthetus bipunctatus* Gr. (pl. 11, fig. 7) ought to form a separate family, but a transitional form was later discovered, and is figured on pl. 11, fig. 1. The furca of *Phloeocharis subtilissima* Man. has a very short stalk, and forward-curving arms, supplying a midway stage between *Stenus* and *Siagonium*. The furca of *Micropeplus staphylinoides* Marsh. (pl. 10, fig. 11) is much reduced; a vague resemblance to some ALEOCHARINAE, and also to *Hypocyptus*, may or may not indicate a similar origin.

One genus each of the small families PSELAPHIDAE and SCYDMAENIDAE is figured—*Bibloporus bicolor* Den. (pl. 11, fig. 2) and *Stenichnus collaris* Müll. (pl. 11, fig. 9). *Tychus niger* Pk. is like *Bibloporus*. All three furcae are made up of "pairs of arms" similar to the furca of *Euaesthetus*. TRICHOPTERYGIDAE have also a pair of nearly parallel arms (*Trichopteryx* sp. (pl. 11, fig. 6), *Pteryx* sp., *Ptenidium* sp.). *Hister* sp. and *Saprinus* sp. (pl. 9, fig. 9) have also a furca of the "pair of arms" type; whether this indicates a relationship to the derived Staphylinid types is dubious. The figure (pl. 11, fig. 6) for TRICHOPTERYGIDAE would serve as well for the furca of *Hydroscapha natans* Lec., and I am satisfied that these insects are TRICHOPTERYGIDAE adapted for an aquatic life as stated by Imms.

One major group of the Polyphaga remains to be considered—the HYDROPHILIDAE and their allies. These appear to have the same fundamental type of furca as the Silphoid–Staphylinoid group. *Hydrobius fuscipes* L. (pl. 11, fig. 12) and *Laccobius* sp. have typical furcae, a shorter and more heavily sclerotised version of that of *Thanatophilus*. *Hydrochus elongatus* Schal., *Helophorus aquaticus* L., *H.* sp., and *Limnebius truncatellus* Thunb. (pl. 11, fig. 10) exhibit a variant of this type. The Helophori have a quite long stalk, while *Hydrochus* and *Limnebius* have a short one like *Hydrobius*. The Sphaeridiines have stout furcae more or less intermediate between these two types. *Sphaeridium lunatum* F., *Cercyon* sp., *Megasternum boletophagum* Marsh. were examined. *Hydraena* sp. (pl. 11, fig. 8), examined with particular interest, shows no resemblance to the other Hydrophiloids. The metendosternite is a Y with a short stalk, suggesting comparison with the derived Staphylinoids and Silphoids. *Scaphidium 4-maculatum* Ol. (pl. 11, fig. 5) is usually thought to be related to the derived Staphylinoid families; its furca is rather Hydrophiloid-looking, with particular resemblances to the Helophori. The general facies also recalls that of *Ditoma* and *Orthocerus*. *Scaphisoma boleti* Pz. of the same family exhibits in yet another group the specialised "pair of arms" furca, and illustrates the great advisability of studying several forms in each family, so that a better idea can be gained of the primitive form of the structure in the group (pl. 11, fig. 4; cf. pl. 11, fig. 5, also pl. 3, fig. 8 and pl. 3, fig. 7 in the CUCUJIDAE, and pl. 6, fig. 2 with pl. 5, fig. 2 among CHRYSOMELIDAE).

Archostemata is a recently erected suborder, containing the family CUPIDAE and *Micromalthus debilis* Lec. which are believed to have split off from the main Coleopterous stem before the Adephaga–Polyphaga division occurred. *Cupes clathratus* Solsky (pl. 13, fig. 3) has a furca which might well be the ancestral form of the order. It is exceptionally elongate, and the anterior tendons arise on a very long median projection. The lamina is thinly and evenly sclerotised, without a posterior sclerotisation such as is universal in Elateroids. There is also a well-developed ventral process as in *Byrrhus*. The sternum has a sternal suture, and a complete median longitudinal suture. *Micromalthus*, not figured, has a small, heavily sclerotised furca, with fairly close tendons, and a median projection. It might be near the ancestor of Bostrychoidea–Cleroidea–Cucujoidea.

From the CUPIDAE, one naturally turns to the almost equally interesting family RHYSODIDAE. Pl. 13, fig. 1 shows the furca of *Rhysodes* sp. There is a median elongation bearing the close anterior tendons as before, but the stalk is much shorter. The lateral projections also are much modified; the whole thing is lightly sclerotised except for the central ridge and a sort of nodule near the base. This furca is rather puzzling. Some of its characters point strongly to a derivation from a Cupoid endosternite, yet there is a disquieting suggestion of *Pityophagus* about it. It is generally agreed that *Rhysodes* belongs with the Adephaga, and indeed the development of a process on the inner edges of its hind coxae is an Adephagan character. But it does little to bridge the gap between the CARABIDAE and CUPIDAE.

Among the Caraboidea proper, CICINDELIDAE (*Cicindela compestris* L., pl. 13, fig. 3) show the clearest traces of their origin. The strength and width of this furca are probably adaptions for swift running. The "lamina" facies is preserved, and the anterior tendons remain fairly close. The step from this furca to that of *Carabus monilis* F. (pl. 12, fig. 1) is not very great but if one go a stage farther to a small, specialised Carabid such as *Adelotopus* sp. (pl. 12, fig. 7) it may be seen that the lamina facies has gone altogether and there is a Y furca. This sort of furca is found in all the smaller Carabids, also in the PAUSSIDAE, HALIPLIDAE, and *Omophron*. *Pelobius* (pl. 12, fig. 3) has a modified version of it. DYTISCIDAE, generally believed to be evolved from early CARABIDAE, have furcae quite in keeping with this conception. In all the DYTISCIDAE studied, the lateral process (L.P.) of small terrestrial Carabids is drawn out in a characteristic manner. Various modifications of the plan are found. *Dytiscus*, like the large Carabi, has a broad strong furca, figured by Korschelt (1923–4); *Hydroporus*, figured on pl. 12, fig. 11, is typical of the HYDROPORINAE; *Copelatus* seems primitive, and unmistakably resembles the CARABIDAE. In *Laccophilus* the furca is little modified, resembling that of *Copelatus*. *Noterus* is as specialised as one would expect it to be.

Gyrinus (pl. 12, fig. 5) has a very remarkable furca, unparalleled in the order. Little needs to be said save that it could be derived from a modified Caraboid type.

Adephaga studied: *Rhysodes* sp., *Cicindela campestris* L., *Carabus monilis* F., and *C. violaceus* L., *Harpalus* sp., *Pterostichus strenuus* Pz. (pl. 12, fig. 9), *P. madidus* F., *Notiophilus rufipes* Curt., *N. substriatus* Wat. (pl. 12, fig. 6), *N. palustris* Duft., *Bembidion lampros* Hbst., *B.* sp., *Brachinus crepitans* L., *Pheropsophus lafertei* Arrow, *Lebia chlorocephala* Hoff., *Dromius melanocephalus* Dej., *Demetrias atricapillus* L., *Clivina fossor* L., *Trichocellus cognatus* Gyll., *Amara* sp., *Badister bipustulatus* F., *Elaphrus riparius* L., *Leistus spinibarbis* F., *Loricera pilicornis* F. (pl. 12, fig. 8), *Adelotopus* sp. (pl. 12, fig. 7), *Omophron* sp., *Haliplus* sp., *Dytiscus marginalis* L., *Copelatus ruficollis* Schal., *Ilybius ater* De G., *Agabus bipustulatus* L., *Hydroporus* 2 spp., *Hyphydrus ovatus* L., *Laccophilus hyalinus* De G., *Noterus clavicornis* De G., *Pelobius tardus* Hbst., *Gyrinus substriatus* Steph., *Arthropterus brevis* Westw.

PHYLOGENETIC DISCUSSION.

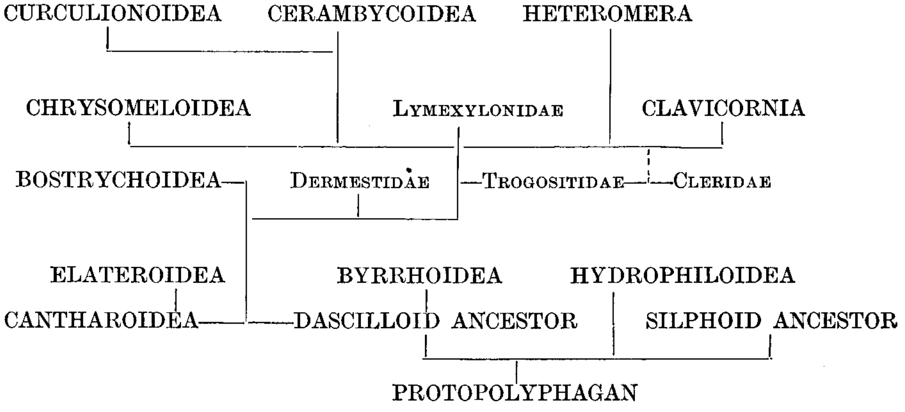
The most important previous phylogenetic conclusions seem to me to be those of Ganglbauer and the larval system of Böving and Craighead. The various other comparative studies—the works of Forbes (1922, 1926), Sharp and Muir (1912), Tanner (1927), etc.—are individually of less importance but often the coincidence of several lines of evidence suggests new groupings. The wide divergence between Ganglbauer's system and the larval classification of Böving and Craighead is partially due, no doubt, to the influence of American taxonomic traditions on the authors of the " Illustrated Synopsis." Larvae studied (*e.g.* by van Emden, de Peyerimhoff) in a European environment seem as amenable to the Ganglbauerian classification as those studied by Böving and Craighead were to the system of Leng's Catalogue.

In suggesting certain changes in the larval system which would enable me to present a coherent account of furcal evolution, I have tried to avoid such geographical tendencies. Meixner, the author of the recently-published Coleoptera section *in* Kukenthal and Krumbach *Handbuch der Zoologie*, seems to me to have been disproportionately influenced by central European work, so that his classification cannot be taken as an adequate summary of recent work.

After the now familiar separation of three suborders—Adephaga, Archostemata, Polyphaga—Böving somewhat obscurely suggests a threefold division of the largest suborder. He postulates a Staphylinoid ancestor, a Cucujoid ancestor, and a Byrrhoid ancestor, without giving names to the implied groupings. These large and shadowy divisions are resolved into groups—Staphylinoidea, Hydrophiloidea, Cucujoidea, Byrrhoidea, Dascilloidea, Cleroidea, etc., respectively—which he calls series. I prefer the well-established term superfamily for these groups, reserving the " series " as a larger grouping.

In discussing the relations of the three series (*sensu meo*) of Polyphaga, Böving observes that the series Byrrhoidea and the series Staphylinoidea " probably have ancestors in common " (!) but are not linked by any known larvae. " However," he adds, " some of the derived families of the Byrrhoid type and some belonging to a third distinct polyphagous type, the Cucujoid type, approach one another, and about the direct affinities between the Cucujoidea and the Staphylinoidea there can be no doubt. Rather isolated as the series [*sensu* Böving] Byrrhoidea appears in the polyphagous suborder, it does not seem necessary to rank it and the families derived from it as a separate suborder." These indubitable direct relations between the Cucujoidea and the Staphylinoidea are said to be exemplified in *Eucinetus*, which larvally is intermediate between LEPTINIDAE–LIMNEBIIDAE–ANISOTOMIDAE–TRICHOPTERYGIDAE and LATHRIDIIDAE–DERODONTIDAE–RHIZOPHAGIDAE. The approach between Cucujoid- and Byrrhoid-derived groups seems to refer to some Heteromerous families and TROGOSITIDAE, CLERIDAE, " BOTHRIDERIDAE," " CATOGENIDAE." The latter family is the equivalent of CUCUJIDAE–PASSANDRINAE of older authors; it will be seen that the " convergence " is very marked in the furca of *Hectarthrum*; as Forbes groups CUCUJIDAE and CLERIDAE together on the wings, and TROGOSITIDAE resemble both on adult characters, there seems evidence of a real relationship between Cucujoidea and Cleroidea. The heteromerous families with the exception of MELOIDAE, RHIPIDOPHORIDAE, and MORDELLIDAE, are placed by Böving in Cucujoidea with the comment that they can only indirectly be traced to the primitive Cucujoid type of larva through rather advanced Cucujoid types like the larvae of COLYDIIDAE (he puts *Bothrideres* in Cleroidea) or MELANDRYIDAE. MORDELLIDAE he is in doubt whether to link to MELANDRYIDAE or Cleroidea. MELOIDAE and RHIPIDOPHORIDAE are placed immediately after Cleroidea with a relation to Cantharoidea also suggested. LYMEXYLONIDAE he places alternatively in a separate superfamily or immediately before OEDEMERIDAE in Cucujoidea—adding that the larvae appear to converge toward Archostemata. The Phytophaga, Rhynchophora, and Bostrychoidea are all said by Böving to be related to Cleroidea.

My main conclusion—that the Hylecoëtoid furca is not likely to be polyphyletic—involves the jettisoning of Böving's indubitable Cucujoid–Staphylinoid relation. Its main pillar is the Cucujoid position accorded to *Eucinetus*. The furca of *E. infumatus* I have recently examined; it has no suggestion of Hylecoëtoid characters, but is derivable from the *Cyphon* furca. On adult characters it is absolutely impossible to put the genus anywhere but near HELODIDAE; if the larvae are near the primitive Staphylinoid type, they may help to connect Byrrhoidea and Staphylinoidea. The accompanying diagram of relationships will, I think, combine with the appropriate figures to give a clear idea of furcal evolution—and is probably more generally acceptable than the " trees " of Böving and Meixner.



The diagram illustrates my phylogenetic conclusions well enough, but needs a little elucidation. The superfamily names are taken from Böving, except that I have resuscitated Heteromera and Clavicornia as convenient though perhaps not entirely natural groups. The principal families of Cleroidea are represented separately. The broken line between TROGOSITIDAE–CLERIDAE and the Clavicornia is a possible alternative to the full line leading to LYMEXYLONIDAE; there is undoubtedly some kind of relationship there, but whether polyphyly in the Cucujoidea or Cleroidea (by abolishing the direct Dermestid–Trogositid link) is implied is a problem for future work. It is possible that as the diagram stands, LYMEXYLONIDAE might better be replaced by *Dasytes*, or perhaps LANGURIIDAE. One feature of the figure—the placing of Curculionoidea—is frankly more caprice than judgement. No doubt the orthodox Chrysomeloid origin for weevils will easily square with my evidence; but I believe that the lower forms (*Sagra*, *Orsodacne*, *Spondylus*, *Rhinomacer*, *Belus*, *Cordus*) in the phytophagous groups are more closely related to each other than to the higher forms with which they are usually placed, and each of the three superfamilies as now constituted is to be suspected of polyphyly.

The lower right-hand side of the diagram could be expanded into a large and complicated arrangement showing the relationships of the "Haplogastran" groups; but the furcal evidence is not strong, and it seems impossible to obtain any agreement with the results of other workers. There does seem to be a suggestion that *Syntelia* is a form linking HISTERIDAE, SILPHIDAE, HYDROPHILIDAE, and Lamellicornia; the Dascilloid resemblances in the larvae of the latter group may not be wholly spurious, and the furcae are quite consistent with a descent for the Scarabaeoids between Hydrophiloidea and Dascilloidea.

Having discovered a type of furca that seems primitive for the whole order, one is tempted to look for some other group of insects with a similar one. The furca of the Strepsipteron *Dacyrtocora* (male) is of an undoubtedly Coleopterous type, though not resembling the Heteromera. I examined metafurcae of four insects, representing four different theories of the origin of the beetles. *Sialis*, *Forficula*, *Sirex*, and a winged Eupsocid alike failed to show the sort of furca for which I was looking. This negative result proves little, for at least *Forficula* and the Eupsocids are highly-modified members of their own groups. A perusal of morphological literature reveals that BLATTIDAE, Isoptera, Mecoptera, Trichoptera, Lepidoptera, Psocoptera, and Heteroptera—or rather the species of these groups described in recent literature—do not approach the Proto-Coleopteran furca envisaged above. The isolation of the beetles is emphasised, and I believe that if one could understand why the ancestors of Coleoptera developed such an unusual type of furca, the essential nature of the largest order of insects would be better understood.

ACKNOWLEDGEMENTS.

Of the beetles I studied, perhaps two-thirds of the British ones I collected myself. The remaining—usually rarer—third were supplied by Dr. O. W. Richards from his own collection. A valuable collection of Australian forms was received from Mr. J. W. T. Armstrong of Nyngan, N.S. Wales. Most of the African forms studied I owe to the kindness of Dr. E. B. Edney of the National Museum, Buluwayo, S. Rhodesia. Material of *Micromalthus* was very courteously forwarded by the U.S. National Museum, Washington. The rest of my specimens came either from the Entomological Department's collection at the Imperial College of Science or from the British Museum. I am indebted to Dr. K. G. Blair and Dr. Hugh Scott for very many rare beetles, for expert assistance in identifying many forms, and for some fruitful suggestions. Most of the work was carried out at the Department of Entomology, Imperial College of Science, for the facilities of which I am indebted to Prof. J. W. Munro.

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INDEX TO LETTERING.

L.P.	Lateral Process.	In CARABIDAE.	i	Mesendosternite.
F.P.	Forward Process.		k	Hind coxa.
Ab.	S1 1st Abdominal Sternite.		l	*Furco-lateralis* muscle or its tendon.
Cx3	Hind Coxa.		m	Metasternum.
St3	Metasternum.		n	*Furco-dorsalis* muscle.
Est3	Metendosternite.		r	Retractor muscle of Trochanter.
Cxp	Coxal Process.		s	Extensor muscle of Trochanter.
G	Gut.		t	Metafurca-mesofurcal muscle or its tendon.
g & p	Coxal Muscles.			
h	lamina.		u	Muscle to 1st Abdominal Sternite.

EXPLANATION OF PLATES.

Plate 1.

FIG. 1. *Hylecoëtes* sp.
2. *Oedemera nobilis.*
3. *Rhinosimus planirostris.*
4. *Aegestria* sp.
5. *Palaestra* sp.
6. *Melandrya caraboides.*
7. *Pyrochroa coccinea.*
8. *Derosphaera foveostriata.*
9. *Chromomoea* sp.
10. *Lyprops* sp.
11. *Amarygmus* sp.
12. *Euctenia* sp.
13. *Anaspis* sp.

Plate 2.

FIG. 1. *Tribolium navale.*
2. *Lagria hirta.*
3. *Tetralanguria elongata.*
4. *Triplax russica.*
5. *Coccinella 7-punctata.*
6. *Mycetophagus 4-pustulatus.*
7. *Orthocerus clavicornis.*
8. *Monotoma testacea.*
9. *Rhizophagus depressus.*

Plate 3.

FIG. 1. *Bothrideres* sp.
2. *Melanophthalma gibbosa.*
3. *Olibrus* sp.
4. *Cerylon* sp.
5. *Hemipeplus rodrigensis.*
6. *Hyliota dubia.*
7. *Hectarthrum* sp.
8. *Oryzaephilus surinamensis.*
9. *Omosita colon.*
10. *Pityophagus* sp.
11. *Diphyllus lunatus.*

Plate 4.

FIG. 1. *Leperina* sp.
2. *Thymalus limbatus.*
3. *Helota gemmata.*
4. *Dasytes* sp.
5. *Pylus* sp.
6. *Malachius bipustulatus.*
7. *Spondylus buprestoides.*
8. *Tetrops* sp.
9. *Hypocephalus armatus.*
10. *Distenia undata.*
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2. *Lema cyanella.*
3. *Chlamys natalensis.*
4. *Crioceris asparagi.*
5. *Lamprosoma concolor.*
6. *Sagra* sp.
7. *Cassida rubiginosa.*
8. *Hispa* sp.
9. *Clytra 4-punctata.*
10. *Parandra brunnea.*

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FIG. 1. *a. Cassida.* *c. Aspidomorpha.*
b. Hispa. *d. Lamprosoma.*
2. *Phyllodecta vitellinae.*
3. *Colasposoma metallicum.*
4. *Longitarsus* sp.
5. *Haltica* sp.
6. *Sermyla halensis.*
7. *Bruchidius obtectus.*
8. *Rhinomacer attelaboides.*
9. *Cordus* sp.
10. *Rhynchites betulae.*
11. *Anthonomus pomorum.*
12. *Belus* sp.

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2. *Ips typographus.*
3. *Araecerus fasciculatus.*
4. *Urodon lilii.*
5. *Telephorus* sp.
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7. *Lycus trabeatus.*
8. *Cebrio gigas.*
9. *Sphenoptera gossypiella.*
10. *Byrrhus pillula.*

Plate 8.

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4. *Throscus* sp.
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6. *Attagenus pellio.*
7. *Dinoderus* sp.
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9. *Lyctus linearis.*
10. *Gibbium* sp.
11. *Cis boleti.*

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2. *Passalus* sp.
3. *Trox scaber.*
4. *Sinodendron cylindricum.*
5. *Choleva angustata.*
6. *Hydnobius perrisi.*
7. *Thanatophilus rugosus.*
8. *Phosphuga atrata.*
9. *Hister* sp.
10. *Syntelia histeroides.*
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5. *Phyllodrepa vilis.*
6. *Haploderus coelatus.*
7. *Siagonium quadricorne.*
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9. *Tachinus rufipes.*
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2. *Bibloporus bicolor.*
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5. *Scaphidium 4-maculatum.*
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7. *Euaesthetus bipunctatus.*
8. *Hydraena* sp.
9. *Stenichnus collaris.*
10. *Limnebius truncatellus.*
11. *Helophorus* sp.
12. *Hydrobius fuscipes.*

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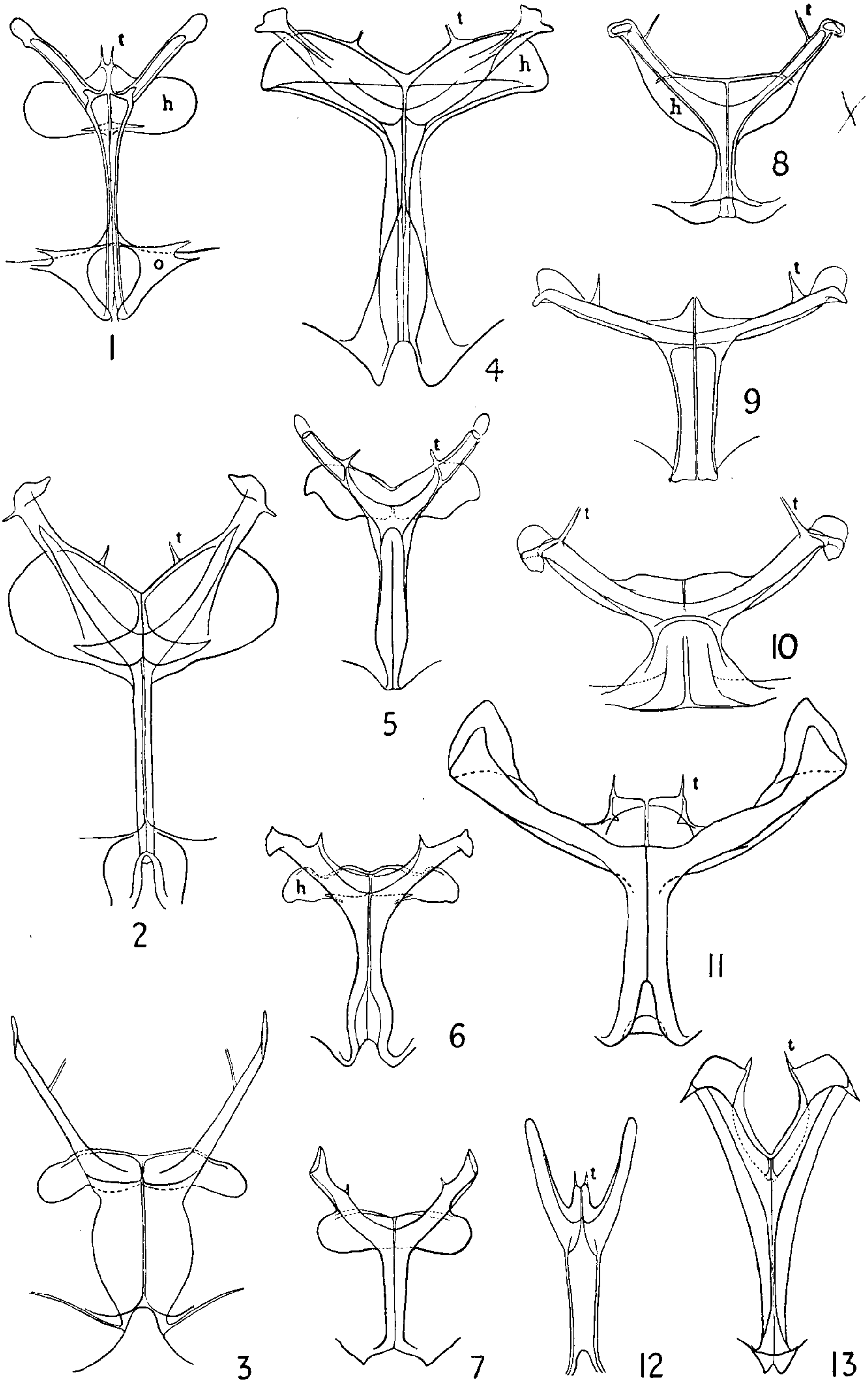
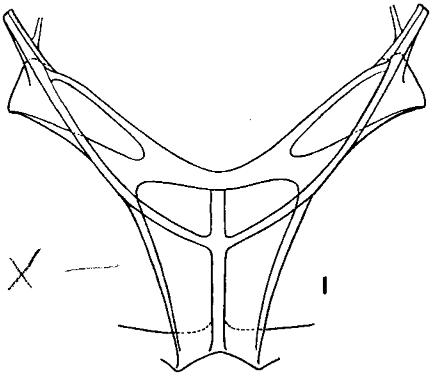
FIG. 1. *Carabus monilis.*
2. *Haliplus* sp.
3. *Pelobius tardus.*
4. *Arthropterus brevis.*
5. *Gyrinus substriatus.*
6. *Notiophilus substriatus.*
7. *Adelotopus castaneus.*
8. *Loricera pilicornis.*
9. *Pterostichus strenuus.*
10. *Omophron* sp.
11. *Hydroporus* sp.

Plate 13.

FIG. 1. *Rhysodes* sp.
2. *Cicindela campestris.*
3. *Cupes clathratus.*
4. *Oryzaephilus* } Reconstructed
5. *Tribolium* } musculature.
6. *Carabus* } Dissected
7. *Phosphuga* } musculature.
8. Base of furca dorsally } Dia-
9. ,, ,, laterally } grams.



The metendosternite in Coleoptera.



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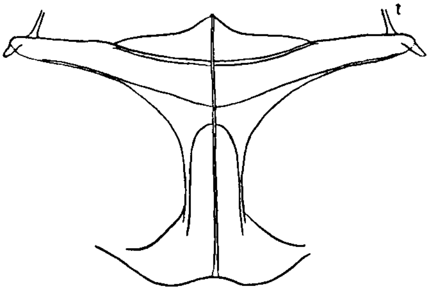

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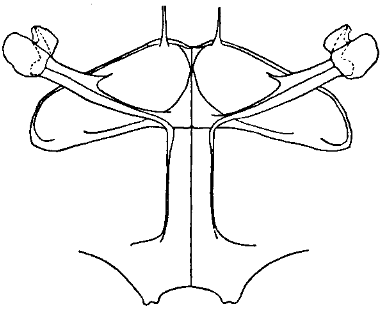

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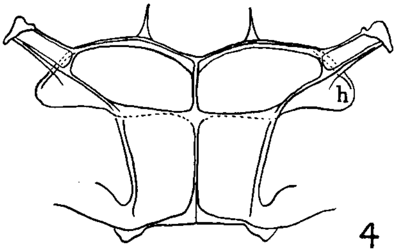

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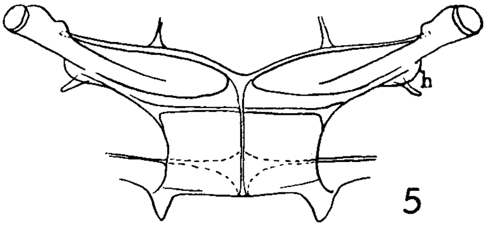

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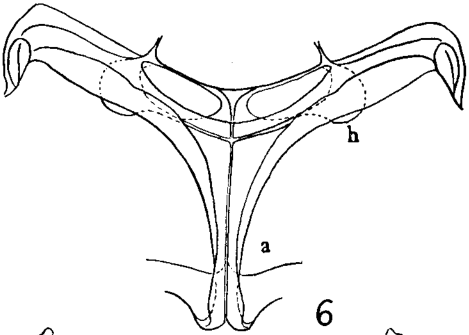

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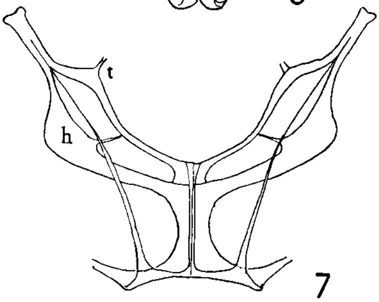

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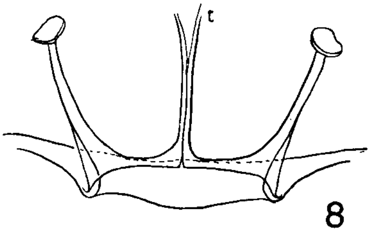

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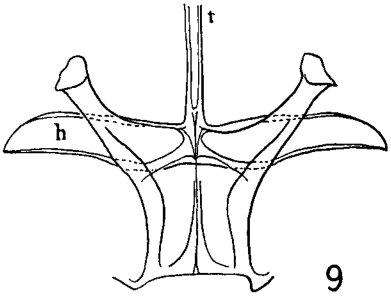

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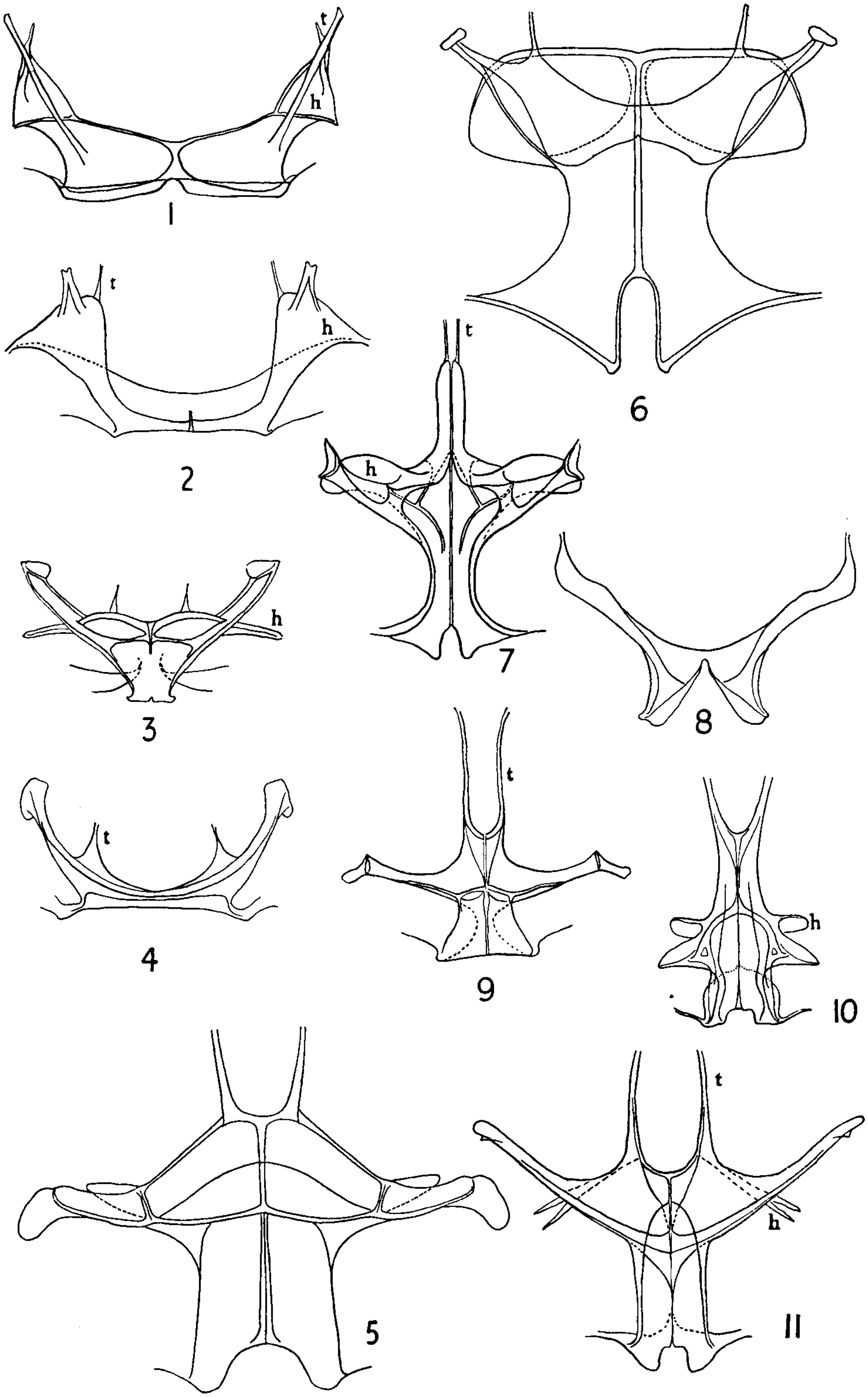

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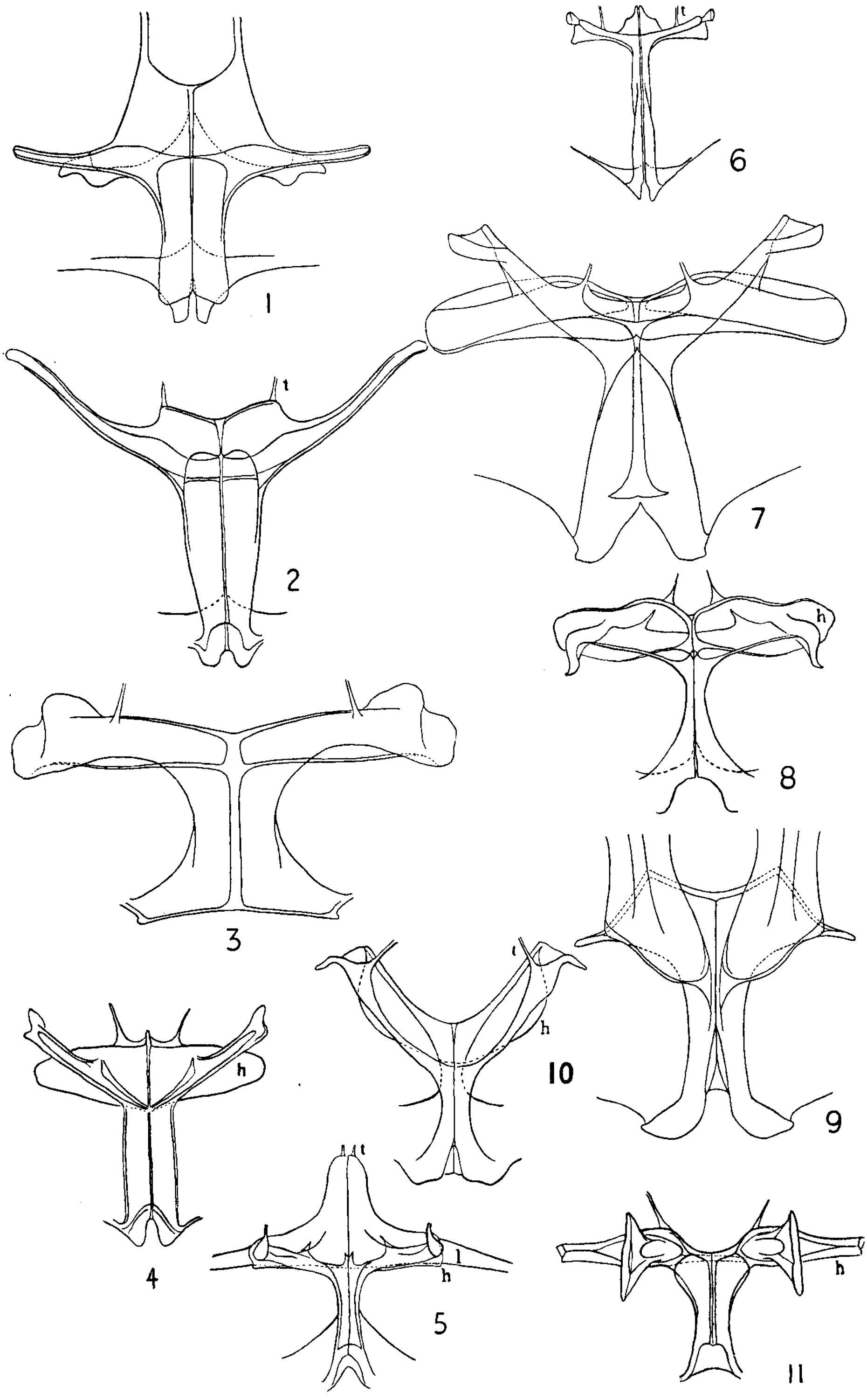

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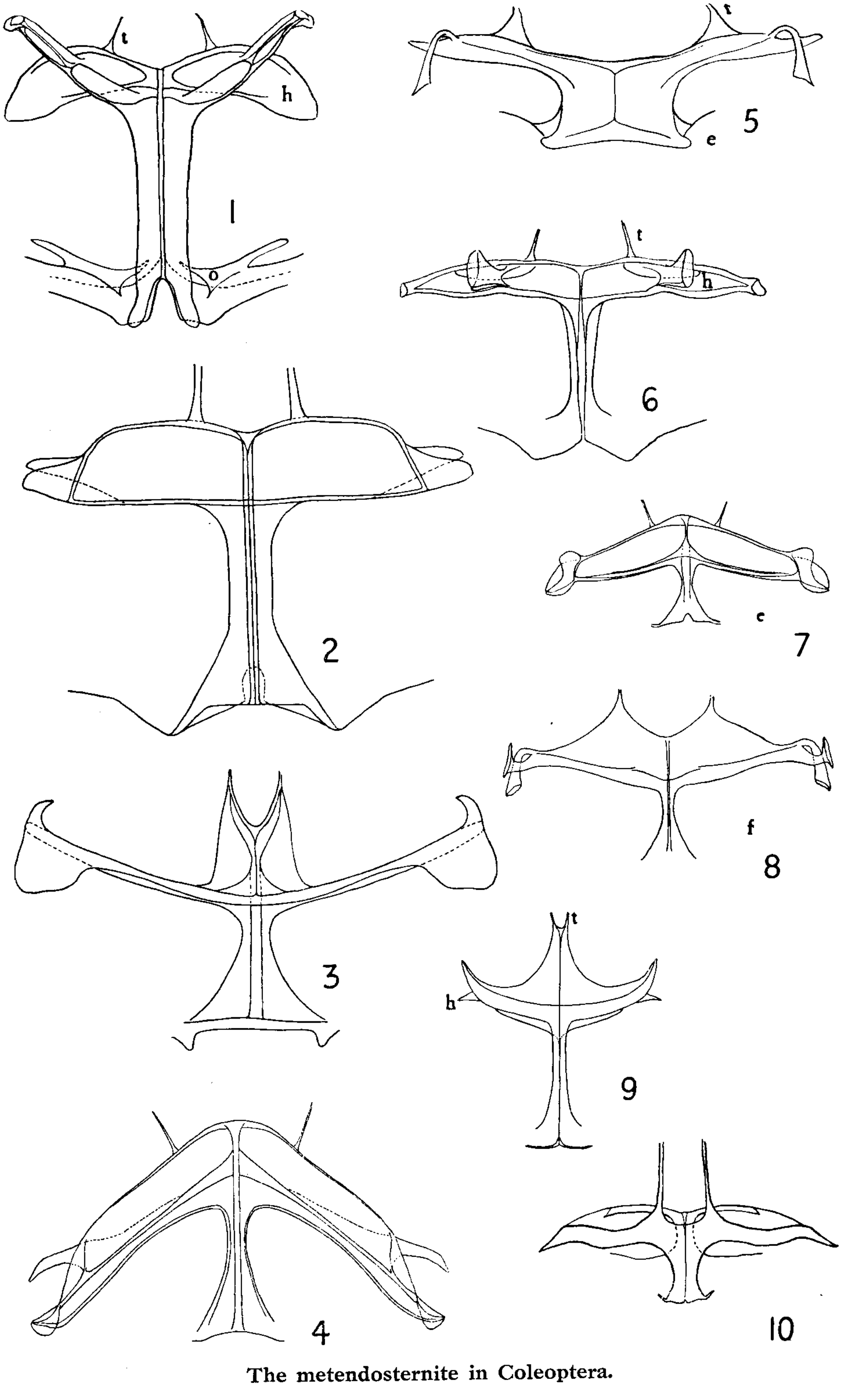

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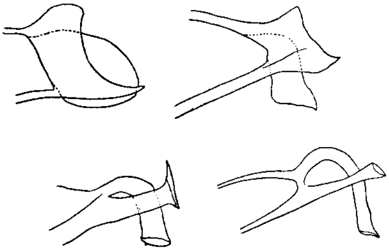
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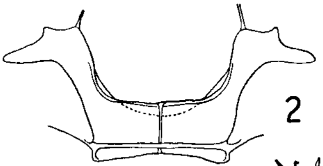
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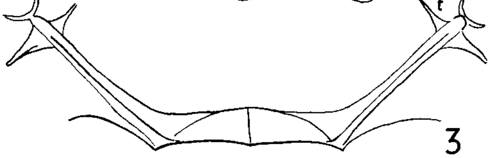

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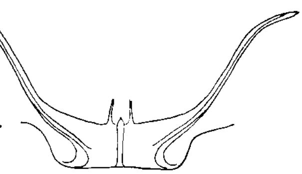
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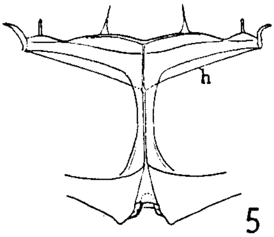

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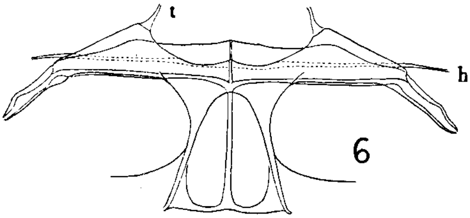

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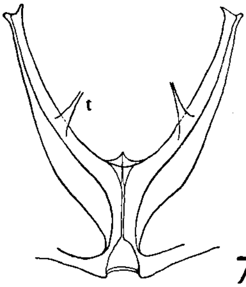

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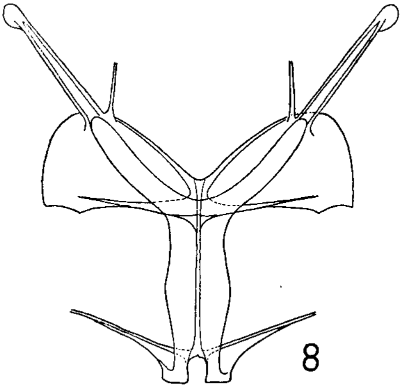
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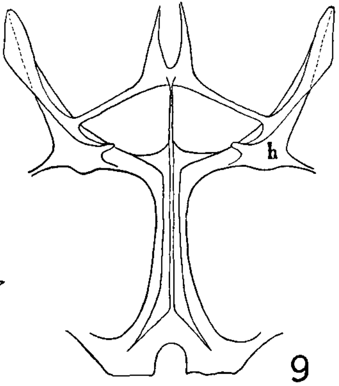

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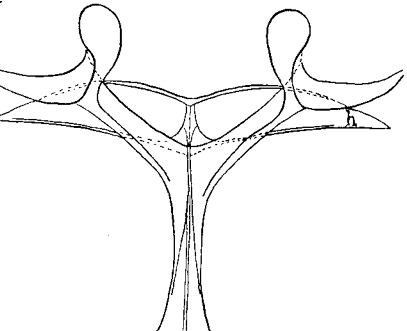

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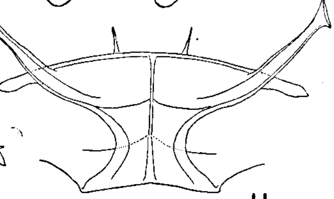
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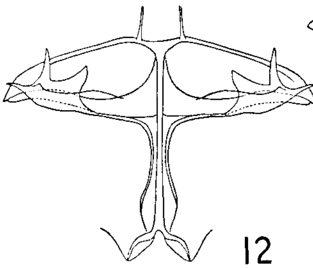
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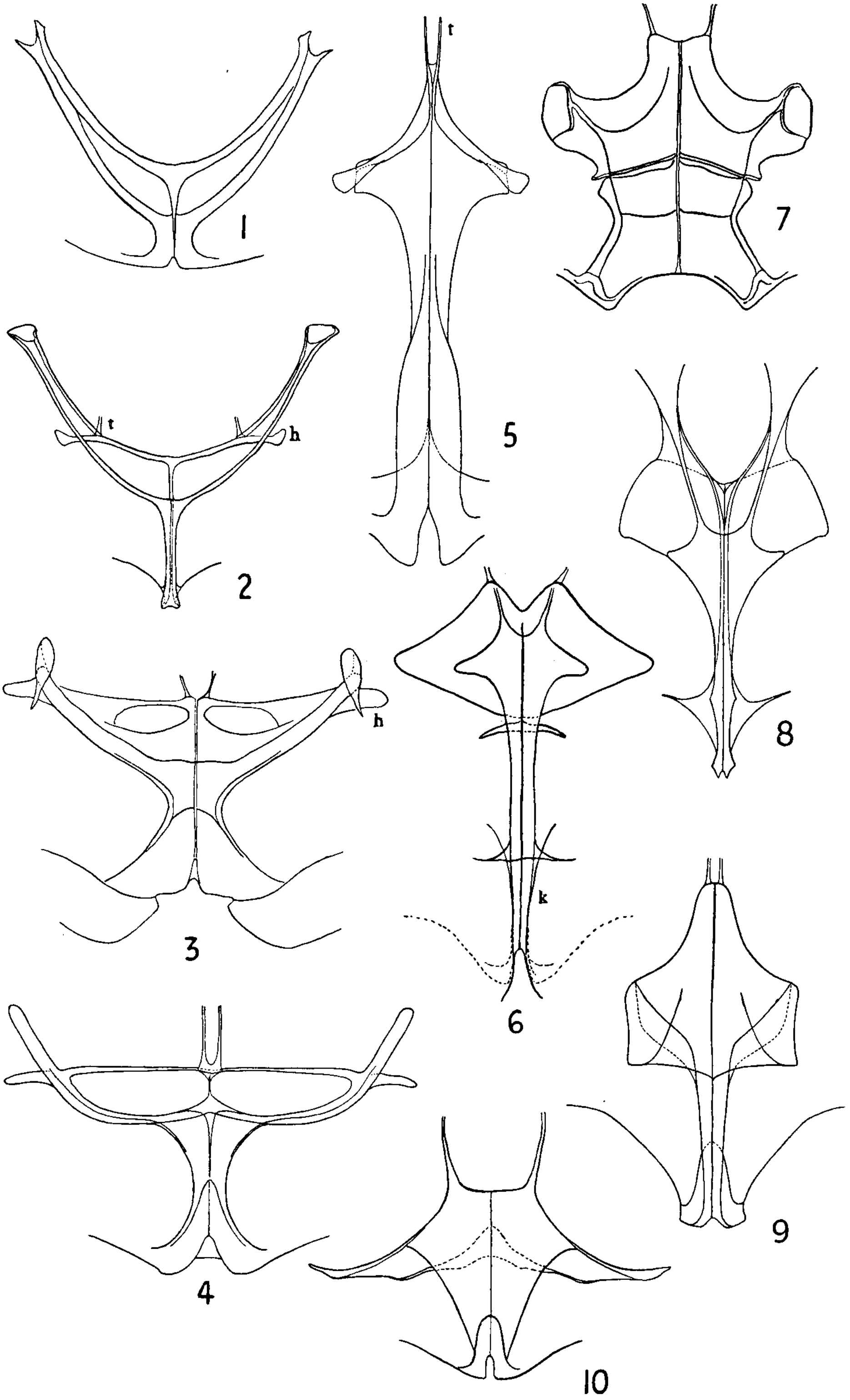

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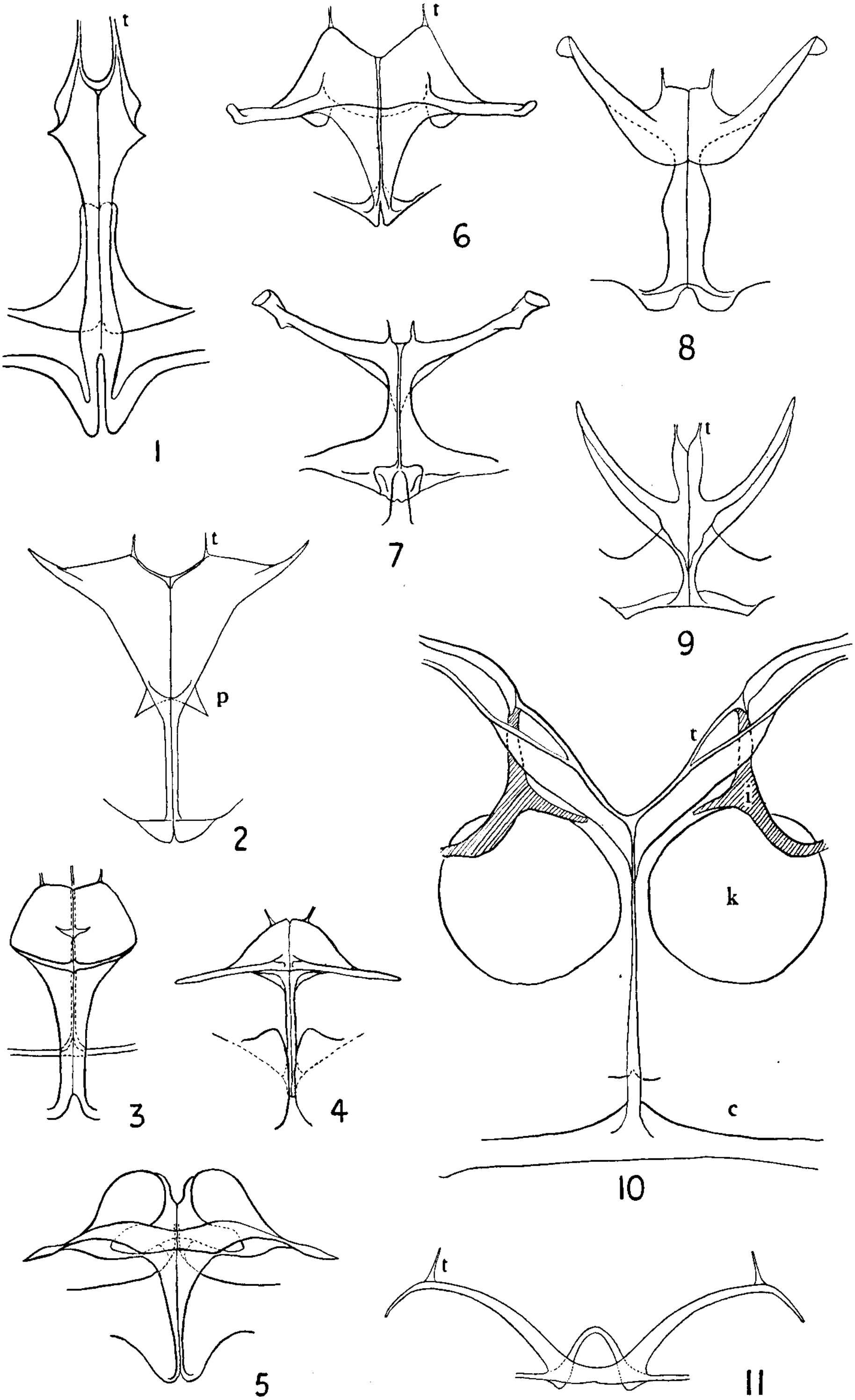

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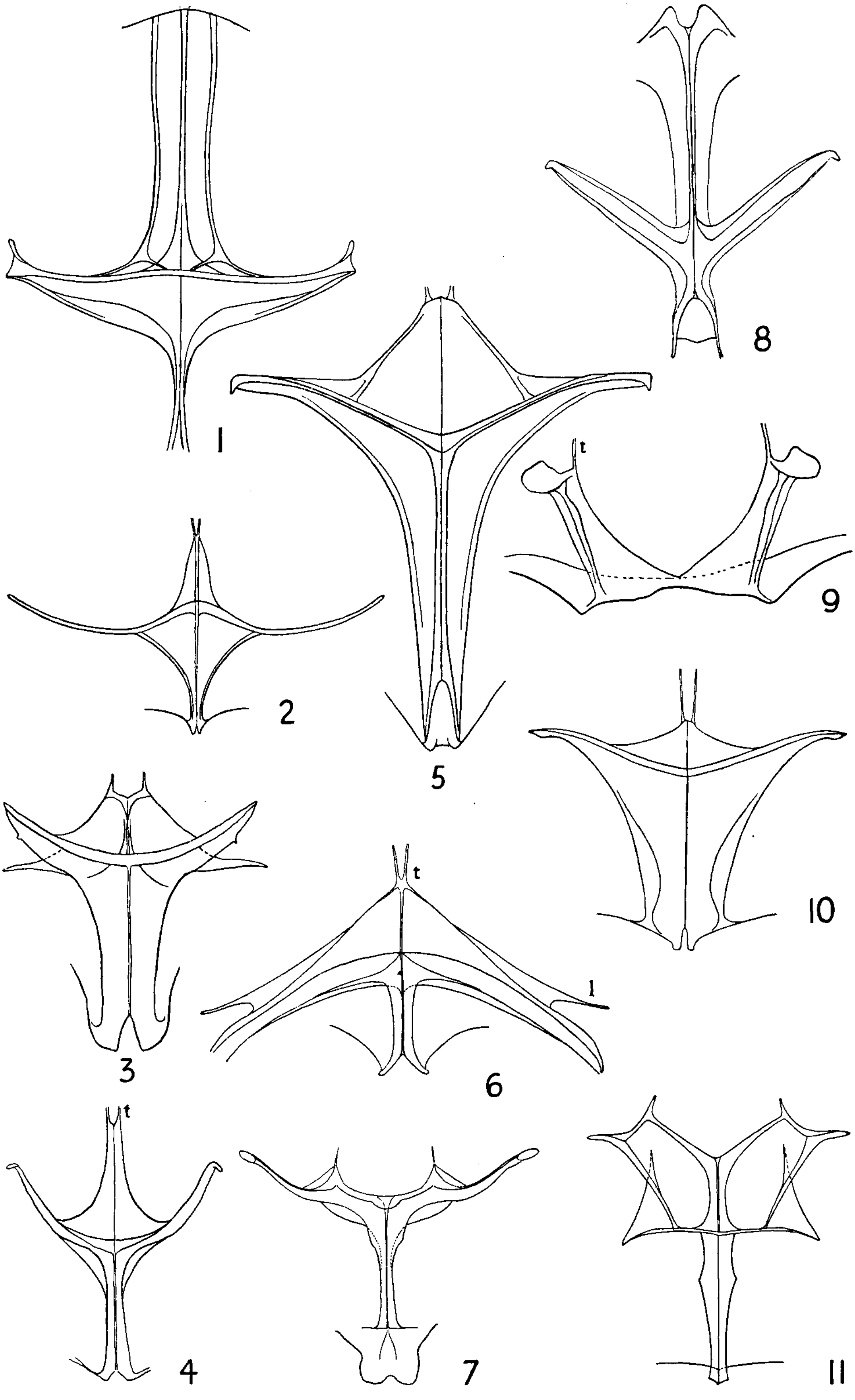
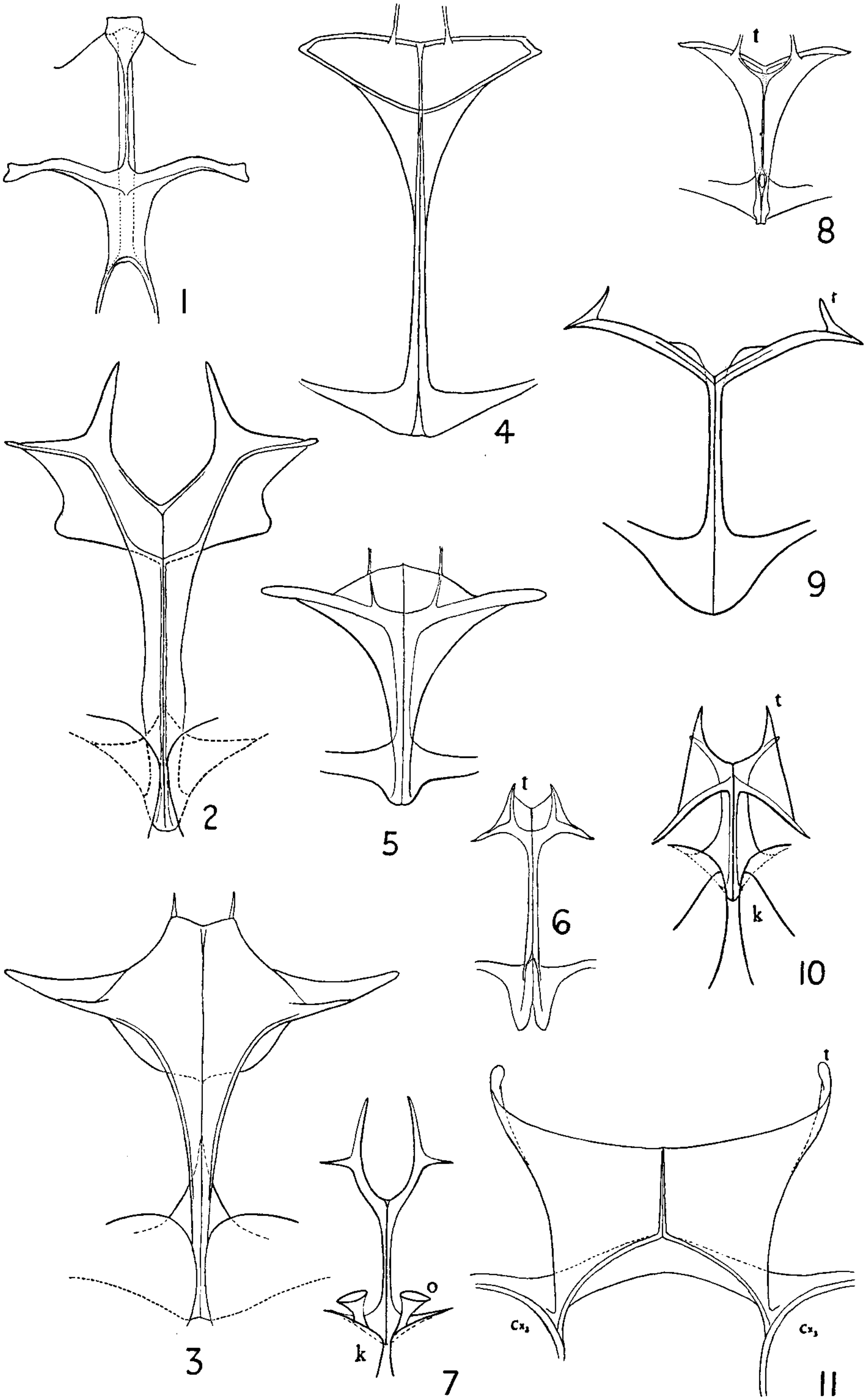


The metendosternite in Coleoptera.



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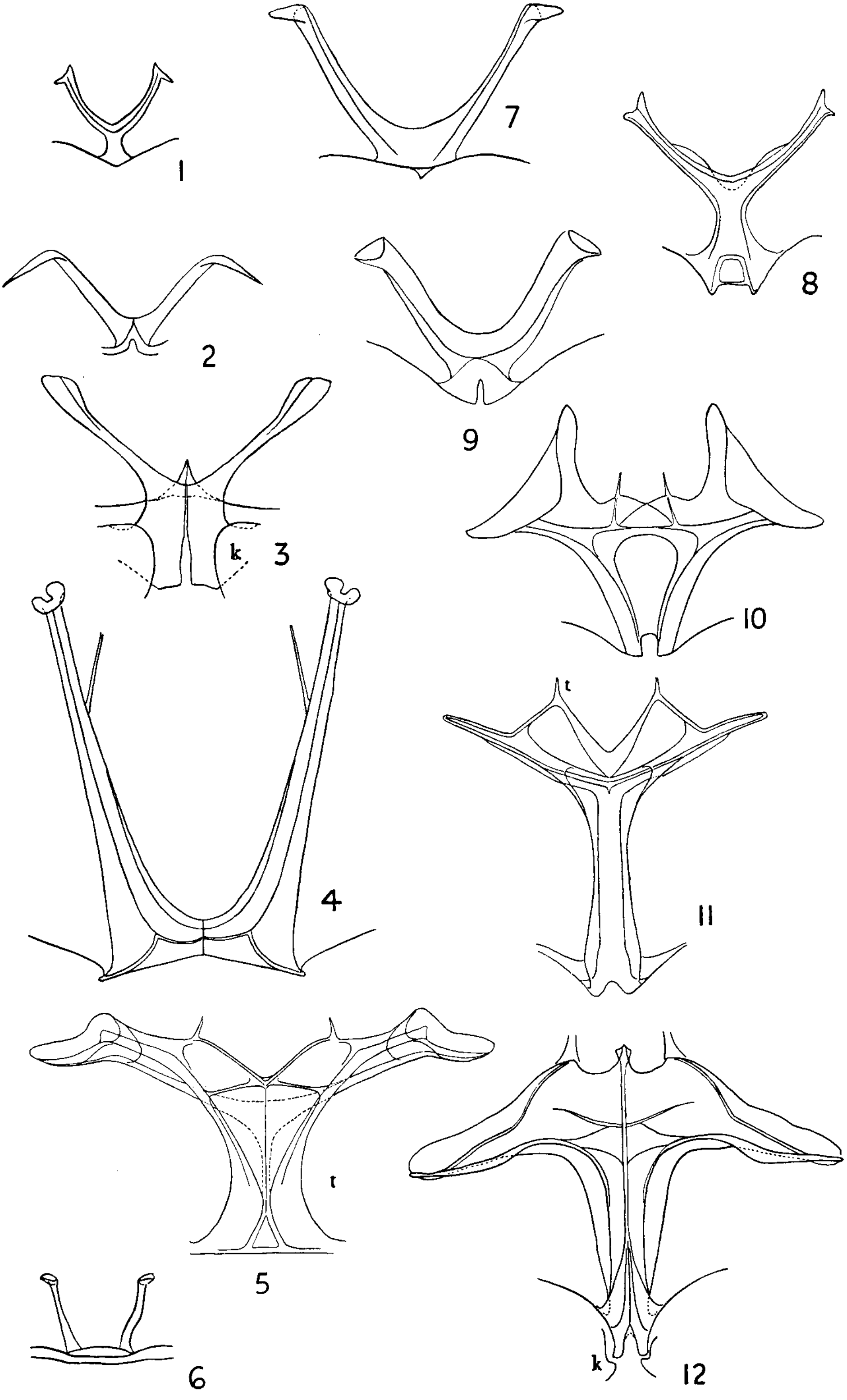

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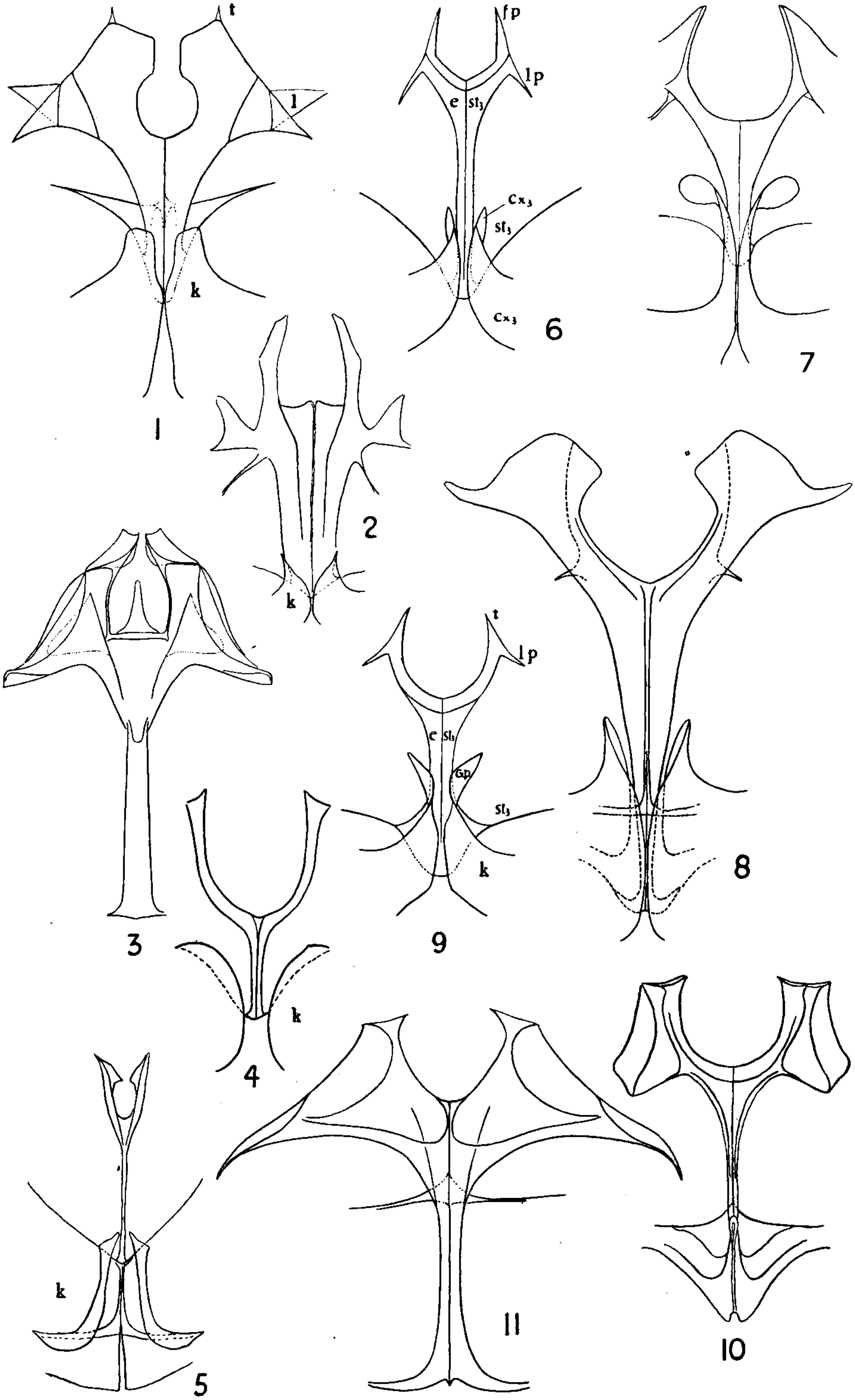

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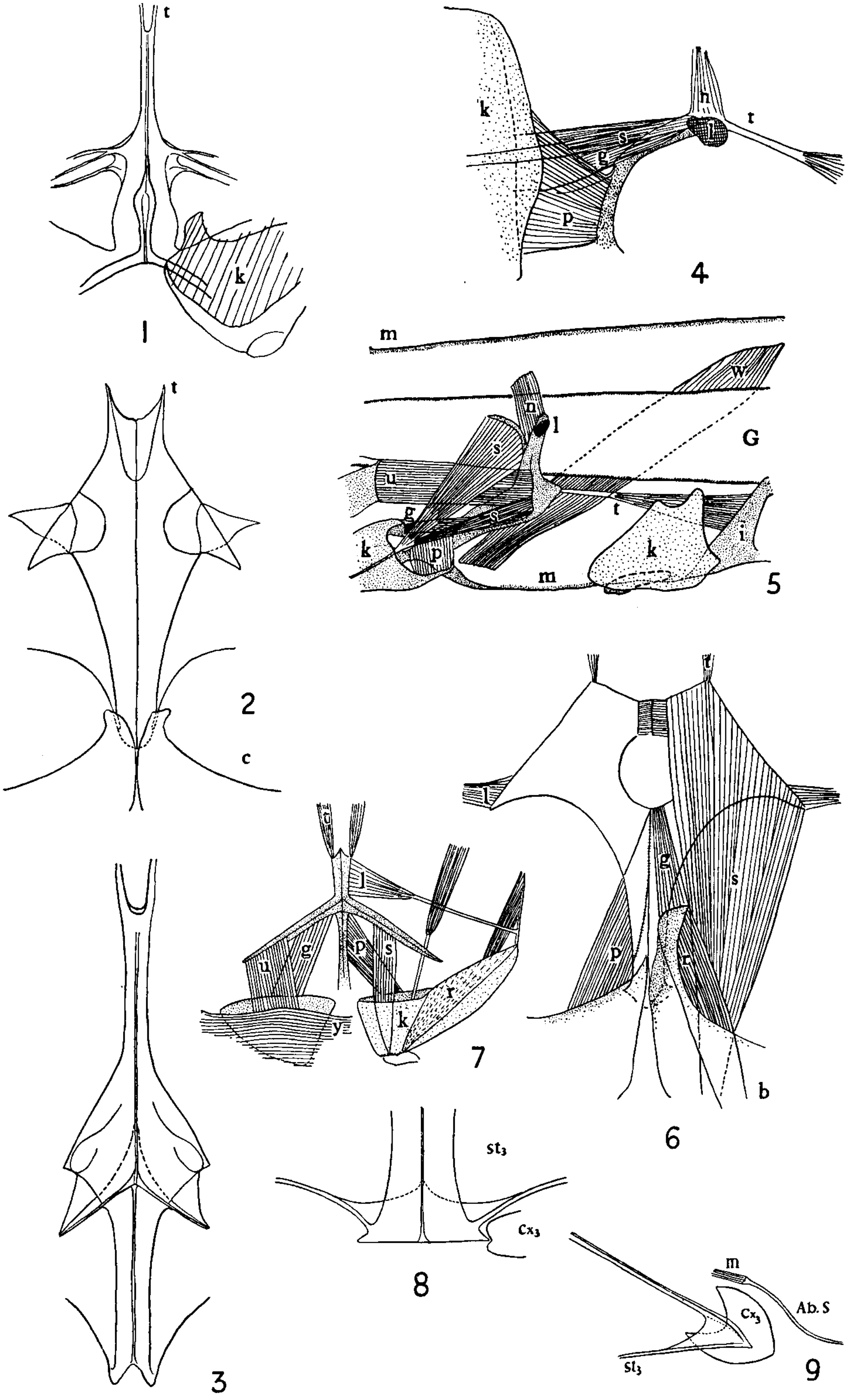

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