THE GENITALIA AND TERMINAL STRUCTURES OF
THE MALE OF THE ARCHAIC MECOPTERON,
NOTIOTHAUMA REEDI, COMPARED WITH
RELATED HOLOMETABOLA FROM THE
STANDPOINT OF PHYLOGENY

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For the rare privilege of studying the hitherto undescribed male of the intensely interesting archaic Mecopteron Notiothauma reedi, McL. (which is in some respects a "living fossil"—the last remnant of a primitive relict fauna, representing as closely as any living form, the type ancestral to the rest of the Mecoptera) I am deeply indebted to Professor Dr. C. E. Porter, who has done so much to advance the study of Entomology in Chile, and to Dr. E. P. Reed, the distinguished Chilean surgeon, who has been more than generous in supplying me with a wealth of material for morphological study. To both of these gentlemen I would express my profound gratitude for their aid in enabling me to carry out this investigation.

The abdominal structures of the male of Notiothauma are the most remarkable and primitive to be found within the order Mecoptera, and could readily serve as the archetypes of these structures for the rest of the order. The primitive character of these structures is thus in harmony with the evidence of the archaic character of Notiothauma indicated by other features such as the wings, which have been discussed in Psyche, Vol. 37, p. 83, for 1930, where
the male here described was designated as the allotype of Notiothauma reedi, McL.

The greater portion of the abdomen of the male of Notiothauma is of a castaneous color, but segments eight and nine (see fig. 1), and the gonopods labelled cx and st in fig. 1, are somewhat fulvous hued. The abdomen is rather broad and is somewhat flattened, and does not taper as the abdomen does in the Panorpidæ (sensu stricto), being more like the abdomen in the closely related family Meropidæ in this respect, although the genitalia are much more primitive than those of Merope (which are elongated and rather highly specialized), and the genitalia of Notiothauma might readily serve as the archetype of the genitalia of the Panorpidæ. On the other hand, the abdominal structures of Notiothauma present some remarkable modifications, which, with the general archaic character of Notiothauma, make it the most interesting and striking representative of the Mecoptera. Starting with the structures of the third abdominal segment and taking up the structures of the following segments in turn, I shall briefly describe the striking features of the abdomen, and point out wherein the structures of Notiothauma may serve as the starting point for tracing the evolutionary developments occurring in the other Mecopterous families.

In the posterior region of the third abdominal tergite of the male of Notiothauma there occurs a median unpaired structure labelled n in figs. 1 and 5, which, for the sake of convenience, may be referred to as the notorganus or notal organ. A conical median tergal structure labelled po in figs. 1 and 5, borne on the following (i. e., the fourth) tergite, abuts against the notorgan n, on the third tergite. I have followed Felt, 1896 (Rept. N. Y. State Entomologist for 1894, p. 463) in regarding the notorgan n as an alluring organ which gives out an exudate licked up by the female prior to mating. The notorgan n (and the posterior structure po) is not developed in other primitive Mecoptera such as Merope, Chorista and Panorpodes, (and it is likewise absent in the Bittacidæ, Nannochoristidæ and Boreidæ), so that Notiothauma furnishes the only starting point for tracing the development of these structures in the Pan-
orpidæ, in which the structures in question may become hugely developed. In Panorpa stigmalis (fig. 27) the notorgan \( n \) has become elongated and extends posteriorly to the cone \( po \), which is located further back in segment four, while in Neopanorpa cornuta (fig. 26) the orthogenetic tendency for the notorgan \( n \) to become further elongated becomes more pronounced, since in the latter insect (fig. 26) the notorgan \( n \) projects posteriorly over the fourth tergite and nearly reaches the middle of the fifth tergite. In such Panorpids as \( P. \) takenouchii (fig. 29) the orthogenetic tendency for the notorgan \( n \) to become more and more elongated, reaches its culmination. Since Notiothauma furnishes the only starting point, among the lower Mecoptera, for the development of such a notorgan (\( n \) of fig. 1 and 5) this very clearly indicates that Notiothauma is the most like the ancestor of the Panorpidae.

On the fifth tergite of Notiothauma there occurs a remarkable median unpaired tergal process labelled \( mo \) in figs. 1 and 5. This process is apparently peculiar to Notiothauma, although a shorter process, resembling it in some respects, is borne on the sixth (instead of the fifth) tergite of \( P. \) cornigera, shown in fig. 32. This process of the sixth tergite of \( P. \) cornigera, abuts against the dorsal portion of the seventh abdominal segment, when the end of the abdomen is turned forward on top of the abdomen, while in Notiothauma, the tips of the genital styles \( st \) of figs. 1 and 5 apparently lie on each side of the median process \( mo \) when the tip of the abdomen is turned up over the top of the abdomen of the male insect.

The sixth abdominal tergite of Notiothauma bears a pair of lateral tergal processes labelled \( bc \) in fig. 1, which are somewhat suggestive of the paired lateral tergal processes borne on the sixth tergite of Neopanorpa cornuta shown in fig. 26. Dorso-mesad of the processes \( bc \) on the sixth tergite of Notiothauma shown in fig. 1, are two smaller processes (paired) which may have developed as enlarged “setigera” or seta-bearing protuberances of the segment. These setigera bear dinotrichia or powerful bristles like those shown on the seventh and eighth tergites in fig. 1,
but most of the setae and bristles have been omitted in fig. 1, to avoid making the figure too complicated to show the more important structures readily.

The seventh tergite in *Notiothauma* bears a pair of remarkable tergal processes labelled *bc* in fig. 1, which appear to correspond in a general way to the structures called the "bicorna" in the male Plecopteron shown in fig. 17, plate 2, of vol. 13 of the Bulletin of the Brooklyn Ent. Society for 1918, and this term has therefore been applied to the structures labelled *bc* in fig. 1 of *Notiothauma*. The "bicorna" of the seventh tergite in *Notiothauma* (*bc* of fig. 1) apparently serve to support the genital structures when the tip of the abdomen is turned forward over the top of the abdomen in the male insect. Since there are no such structures on the seventh tergite of the other Mecoptera I have examined, it is possible that these remarkable processes are peculiar to *Notiothauma* among the Mecoptera.

The abdominal segments (with the exception of the first) as far back as the eighth segment, in *Notiothauma*, are "disceritous"—i.e., the tergal and sternal sclerites are distinct and separate (the tergites are denoted by the letter *t* and the sternites by the letter *s* in fig. 1)—and the spiracles labelled *sp*) are located in the pleural or lateral membrane between the tergites and sternites. The fulvous-colored eighth and ninth abdominal segments, however, are "synscleritous"—i.e., the tergites and sternites have united to form a complete ring or continuously sclerotized surface from dorsal to ventral sclerite, and the spiracle of the eighth segment (which is larger than the preceding ones) is surrounded by the sclerotized surface, instead of being located in a pleural membrane.

In *Panorpodes* the eighth and ninth segments are synscleritous (tergites and sternites fusing completely) and the seventh segment is partially synscleritous, the fusion of the tergite with the sternite being complete in the anterior half of the segment, but the posterior half retains a partial division between tergite and sternite. *Panorpodes* thus presents an intermediate stage between *Notiothauma* (in which only the eighth and ninth segments are synscleritous) and the Panorpidae in which the seventh, and
sixth segments also, are synscleritous. *Panorpodes* likewise presents an intermediate condition between the posterior abdominal segments of *Notiothauma*, which are broad and flattened, and the narrow more cylindrical segments of the postabdomen (narrowed region) of the Panorpidae, since the segments in *Panorpodes* are somewhat narrower than those of *Notiothauma* but are not as narrow as those of the Panorpidae, in the postabdomen. As was mentioned above the sixth, seventh, eighth and ninth segments are synscleritous in the Panorpidae; the sixth is discleritous, the seventh partially so, the eighth is synscleritous and the ninth is synscleritous in *Panorpodes*; the sixth and seventh abdominal segments are discleritous and the eighth and ninth are synscleritous in *Nannochorista* and *Notiothauma*. In *Chorista* and *Merope* the sixth and seventh abdominal segments are discleritous and the eighth and ninth are weakly so. In *Boreus* and *Harpobittacus* the sixth, seventh, eighth and ninth (reduced in *Harpobittacus*) abdominal segments are discleritous.

The ninth segment of the male has been termed the andromere (since it is the genital segment "par excellence") and the ninth segment together with the genitalia constitute the androecium, or as the Dipterists term it, the hypopygium. The andromere or ninth segment presents some intensely interesting modifications in *Notiothauma*. Its tergal region or epiandrium labelled *ep* in fig. 1, bears a remarkable median dorsal process (labelled *g* in fig. 1 and fig. 4) which is turned slightly forward. The lateral portions of the epiandrium on each side of the median process *g* are produced posteriorly to form two lobe-like projections labelled *e* in figs. 1, 4, 5 and 37, and these epiandrial processes bear lesser lateral projections as is shown in figs. 1 and 4 of *Notiothauma*. These epiandrial processes are apparently homologous with the processes and lobes of the ninth tergite variously termed the surgonopods, surstyli, epivalvae, epiprocessi, etc., in different insects. The condition exhibited by *Notiothauma*, in which the epiandrium is produced posteriorly to form the epiandrial lobes *e* above the anus-bearing structures *pg* of fig. 37, apparently
represents the starting point of the development of the epandrial processes and lobes of other Mecoptera.

In *Merope* the epandrial processes *e* of fig. 36 are broad, flat, pointed plates clearly demarked from the tergite behind them. In the Bittacidæ represented by *Harpobittacus* (fig. 35) the epandrial lobes become highly developed, and in some Bittacidæ they are extremely large and are provided with roughened areas suggesting that they may play a part in mating (as claspers), and on this account they were referred to as the "copulalobi" in the Bittacidæ, but it is preferable to designate all of these lobes and processes of the ninth tergite as the epandrial processes (or lobes). In *Harpobittacus* the first abdominal segment (which is provided with a huge spiracle) is very small, so that the ninth segment might be counted as the eighth if the true first segment were overlooked, but by counting the eight pairs of abdominal spiracles one can determine the corresponding segments, even when the first segment has fused with the metathorax as in *Boreus*, and when there has been a fusion or suppression of segments, the spiracles furnish the clews for determining whether the fusion has been in the anterior or posterior region of the abdomen, since if there are eight distinct, spiracle-bearing segments in the abdomen when the number of segments has been reduced, it is evident that the fusion has occurred posterior to the eighth segment. In the Boreidæ, the epandrial lobes *e* of fig. 33 are rather densely beset with small protuberances giving a roughened appearance to their dorsal surfaces. The epandrial processes are not developed in *Chorista* (fig. 34) or *Panorpodes* (fig. 31) or most Panorpidæ (fig. 31), and the character of the epandrium *ep* of *Chorista* and *Panorpodes* (figs. 34 and 31) points to a rather close relationship between these insects, and *Panorpodes* is apparently closely related to the ancestral Panorpidæ among the Mecoptera. In *Chorista* and *Panorpodes* (figs. 34 and 31) the anus-bearing structure *pg* is not covered by the epandrium *ep*, but in the Panorpid shown in fig. 28, the epandrium *ep* is produced posteriorly and completely hides the proctiger beneath it.
The hypandrium or sternal portion of the ninth segment (andromere) is extremely interesting in Notiothauma (i.e., ha of figs. 7 and 21), and its condition in Notiothauma might be taken as the starting point for tracing the modifications of the hypandrium of other Mecoptera (see ha in the different figures), although the hypandrium ha of Chorista shown in fig. 18 might also be taken as the starting point in tracing the development of the hypandrium in other Mecoptera. The hypandrial processes labelled h in figs. 18, 21, etc., have been termed the hypovalvae, hypoprocessi, etc., but in the following discussion they will be referred to simply as the hypandrial processes. In Notiothauma (figs. 1, 7 and 21) the hypandrium ha (which is divided into a basal and distal area) bears an unpaired median process and two lateral processes, while in Chorista (fig. 18) the median process is not developed, and there are small secondary mesal processes on the lateral hypandrial processes labelled h in fig. 18. In Merope (fig. 19) and Boreus (fig. 17) the hypandrial projections h are very slightly developed. In Panorpodes (fig. 20), however, the hypandrial processes h are well developed (and are provided with peculiar outgrowths, as shown in fig. 20), and in the development of its hypandrial processes, Panorpodes approaches the Panorpidae more closely than any other lower Mecoptera do. In most Panorpidae, such as the one shown in fig. 22, the hypandrial processes are well developed and in the Indian Panorpid shown in fig. 23, which has the most peculiar hypandrium of any Mecopteron I have seen, the hypandrial processes h curve about a somewhat circular basal opening, and are produced posteriorly into elongated processes which are modified apically to form the peculiar distal structures shown in fig. 23. The hypandrium is not prolonged posteriorly in the Bittacidae or Nannochoristidae.

The male genitalia proper consist of the gonopods ex and st of fig. 13 and the structures comprising what the Dipterists call the phallosome, made up of the valvae and other projections about the penis or the genital opening—i.e., the central structures labelled ps in fig. 13. It is very difficult to interpret the homologies of the male genitalia in the
different orders of insects, and the homologies of the parts in Diptera, Mecoptera, etc., are still in dispute.

In a discussion of the male genitalia of Diptera, Mecoptera, and related forms, published in Vol. 25, p. 47, of *Psyche* for 1918, the structures labelled *st* and *cx* in figs. 3, 7, 8, etc., were designated as the gonopods; but in attempting to homologize the gonopods of sawflies (which are fundamentally like those of Diptera and Mecoptera, but are of a more primitive type) with the gonopods of male Ephemerids, etc., which have retained the parts in practically the original condition for insects in general (see Canadian Entomologist, Vol. 52, p. 178, for 1920), I was misled by the fact that the bilobed basal plate (called the "cardo" by Hymenopterists) of some sawflies' genitalia resembles the fused coxites in the male genitalia of certain mayflies and the two-segmented forceps of these sawflies resemble the styli of certain mayflies, in which the styli are composed of two or more segments. Using the condition exhibited by these sawflies as the basis for determining the homologies of the parts in Diptera and Mecoptera, I consequently homologized the segment labelled *st* in figs. 3 and 7, of the Diptera and Mecoptera with the distal segment of the stylus (i.e., with the dististyle) and homologized the basal segment labelled *cx* with the basal segment of the stylus (i.e., with the basistytle), and interpreted the demarked basal areas of these basistyles as the reduced coxites in Diptera and Mecoptera (see also Vol. 48, p. 207, of the Transactions of the American Ent. Soc. for 1923). In his review of Dr. Alexander's "Craneflies of New York," however, Walker, 1920 (Canadian Entomologist, Vol. 52, p. 190), states that in the Diptera the distal portion of the claspers (i.e., *st* of fig. 3, represents the entire stylus, while the basal portion *cx* of fig. 3 represents the coxite instead of the basal segment of the stylus, and Eyer, 1924, (Annals Ent. Soc. of America, Vol. 17, p. 275) applies this interpretation to the Mecoptera and other Holometabola. Mr. R. E. Snodgrass, who has been making a detailed study of the musculature of the genital claspers, etc., of male insects, informs me that the musculature bears out the view that the basal segment of the gonopods (labelled *cx* in the
Structure of Notiothauma reedi

different figures) is the coxite, and the distal portion (st in the different figures) represents the entire stylus, so that I have provisionally adopted this view of the interpretation of the parts of the gonopods in the present paper. Mr. Snodgrass is inclined to regard the basal collar called the "cardo" in the genitalia of Hymenoptera, as a detached basal portion of the coxites, which has united with its fellow from the opposite side to form a basal collar-like sclerite in these insects, while the basal segment of the (outer) claspers represents the remainder of the coxite, and the outer claspers themselves represent the styli, in the Hymenoptera, and this view seems to be as reasonable as any, since it is in accord with the evidence of the musculature of the structures in question. It should not be forgotten, however, that Emery, Wheeler, and other students of the ants, interpret the basal and distal portions of the outer claspers (i.e., the gonopods) as parameres, and the question of the homologies of the parts of the gonopods is by no means settled as yet. In the following discussion, I shall refer to the claspers st of figs. 3, 7, 8, etc., as the gonostyles, and shall designate the basal portions cx as the gonocoxites, terming them both together, the gonopods.

The gonopods st and cx of Notiothauma (figs. 1, 5 and 7) not only furnish the prototypes from which the gonopods of the Panorpidae and other Mecoptera could be derived, but they are also surprisingly like the gonopods of primitive Diptera such as Trichocera (fig. 3), suggesting that the ancestors of the Diptera were very like Notiothauma in the character of their genitalia. Thus, the gonostyle st of Trichocera bituberculata Alex., shown in fig. 3, has a mediotubercle m and a basitubercle b astonishingly like the medi- tubercle m and the basitubercle b of the gonostyle of Notiothauma shown in fig. 7, but I have not found any Dipteron in which the gonostyle (st of fig. 3) bears a peculiar stylorganus (or stylar organ) like that labelled o in the gonostyle st of Notiothauma shown in fig. 7, although such a stylar organ is not found in all of the Mecoptera either, being apparently absent in Chorista and Panorpodes (figs. 12 and 13) and in all of the Panorpidae and Bittacidæ that I have examined. A stylorgan o is present in Notiothauma.
(figs. 1, 5 and 7), in *Merope* (fig. 13), in *Nannochorista* (fig. 10) and in *Boreus* (fig. 9), however, and this may indicate that *Notiothauma* is very like the common ancestors of all of these Mecoptera, since the ancestors of these forms must have had a stylorgan, if this structure is developed in these families.

Aside from the presence of stylorgans o in both *Notiothauma* (fig. 7) and *Merope* (fig. 16) the gonostyles st themselves are not very similar in the Notiothaumidæ and Meropidæ, since the gonostyli of Merope (fig. 16) are long and slender and resemble those of certain Chironomid Diptera in contour, while the gonostyli of Notiothauma are more like those of the Dipteron *Trichocera bituberculata* in contour, and it is amazing that the gonostyli of these closely related families of Mecoptera (the Notiothaumidæ and Meropidæ, should resemble the gonostyli of Diptera more than they resemble each other.

The gonostyli st of *Notiothauma* (figs. 5 and 7) are more normal, and therefore furnish better starting points for tracing the development of the gonostyles of other Mecoptera than is the case in other primitive Mecoptera such as *Chorista* (fig. 12) in which the basitubercle b and the medi- tubercle m are modified in a peculiar manner, and the gonostyle is not as much like those of *Panorpodes* (fig. 13) and the Panorpidæ (fig. 23) as the gonostyle of *Notiothauma* is.

The gonostyle st of the Indian Panorpid from Mysore, shown in fig. 23, is so astonishingly hairy that this remarkable Panorp should be called “Panorpa hirsuta" if it should prove to be new to science, and an appropriate name is desired for it! The Panorpid shown in fig. 8 has remarkably “thin,” leaf-like gonostyli st with a peculiar basituber cle b and meditubercle m, and with a very peculiar mesal process en or “endostyle” which may represent the inner branch of the divided gonostyli in Diptera (i. e., the so-called inner basistyle in certain Diptera). In comparison with the size of the coxites which bear them, the gonostyli st are rather short in the Boreidæ (fig. 9) and Nannochoristidæ (fig. 10); and in the Bittacidæ represented by *Harpobittacus* (fig. 11) the gonostyli st become tremen-
dously reduced—a feature which serves to set apart the Bittacidae from the rest of the Mecoptera very sharply.

In *Notiothauma*, the gonocoxites *ex* of figs. 5 and 7, are more like the prototypes of the gonocoxites of the Panorpidae (figs. 8, 23, etc.) than is the case in Chorista (fig. 12), although Chorista and Panorpodes are not sharply set off from the Panorpidae in this respect. In *Notiothauma* (fig. 5) there is an intercrater *cc* or intercoxal region which is hollowed out and sclerotized in a fashion suggesting the prototype of the condition met with in primitive Diptera, and all of the features of the genitalia of *Notiothauma* suggest that the ancestors of the Diptera resembled *Notiothauma* in many respects.

In *Boreus* (fig. 9) the gonocoxites *ex* are quite large in proportion to the size of the gonostyles *st*, and there is a wide posterior, or ventral, intercoxal area *ic* of membrane between the gonocoxites *ex*. In *Nannochorista* (fig. 10) the gonocoxites *ex* are likewise very large in proportion to the length of the gonostyli *st*, but the intercoxal area has become sclerotized and the gonocoxites appear to be quite solidly united. In the Bittacidae (fig. 11) the intercoxal area has likewise become sclerotized, but a partial suture remains to demark the distal region of the gonocoxites, which are hugely developed in proportion to the size of the gonostyli *st*.

In the Panorpid shown in fig. 8, the posterior intercoxal area contains a pair of membranous lobe-like valves, the postvalvae labelled *p* in fig. 8. These are apparently homologous with the posterior valve-like structures labelled *p* in fig. 12 of Chorista and a similar pair of valves labelled *p* in fig. 15 of *Notiothauma*. The function and significance of these postvalvae is not clear.

In the Panorpid shown in fig. 8, the intercoxal area contains a pair of ventral phallic valves labelled *v*, which are received in a flanged groove of the gonocoxite *ex*, and the Panorpid shown in fig. 8 likewise has a pair of dorsal phallic valves labelled *d*, which lie on each side of the meatus or gonopore, as the genital opening of the male is called. These valves may represent the penis valves of sawflies which form the ædeagus or chitinous parts about the penis in
higher insects. The penis valves have been homologized with the endopodites of the genital limbs of the ninth segment, while the gonostyli have been homologized with the exopodites of the genital limbs (gonopods) whose protopodites are represented by the gonocoxites, but the homologies of the genital valves of the male insect have not been definitively determined, and it is preferable to refer to them as parts of the phallosome, as is done by the Dipterists. The ornate valves labelled d in fig. 15 of Notiothauma, lie on each side of the gonopore and apparently represent the dorsal valves d of the Panorpid shown in fig. 8, while the ventral valves v of fig. 15 of Notiothauma may represent the ventral valves v of the Panorpid shown in fig. 8, although the ventral valves v of Notiothauma are poorly developed, and were difficult to make out in the dried specimen available to me for study.

In such Panorpids as Panorpa lugubris, shown in fig. 25, the dorsal valve d of each side is not divided, but the ventral valve of each side is divided into an upper ventral valve labelled u and a lower ventral valve labelled l in fig. 25. The ventral valves of Notiothauma are not thus divided into an upper and lower branch, but in Chorista (fig. 12) one of the branches of the lower valves forms one of the penisfilum valves labelled pv in fig. 12, and this pair of valves becomes greatly elongated to form the so-called penisfilum pf of the Bittacidæ (fig. 11), so that in this, and certain other respects, Chorista is more like the ancestor of the Bittacidæ, while Notiothauma is more like the ancestor of the Panorpodidæ and Panorpidæ. The phallosome ps of Nannochorista shown in fig. 10 is much reduced and in Boreus (fig. 9) the parts are usually retracted, although in the specimens shown in figs. 31 and 34 of plate 10, in Vol. 48 of the Transactions of the Amer. Ent. Soc. for 1923, a large eversible membranous penis was visible, being apparently extruded at the time of mating. The parts are as much alike in the Boreidæ and Nannochoristidæ as any, but the resemblance is not very marked in these two families, and it is difficult to determine where they branched off in the phylogenetic tree of the Mecopteran families.
Following the usage proposed in Vol. 13, p. 60, of the Bulletin of the Brooklyn Ent. Society for 1918, the terminal abdominal segments may be referred to as the terminalia, and the anus-bearing portion may be termed the proctiger, while the set-off papilla with the anal opening at its tip, may be called the anal papilla. In Notiothauma (figs. 1, 2 and 5) the anal papilla ap is surmounted by a process labelled sr, and below it is a lower process labelled sb. The condition exhibited by Notiothauma (fig. 2) suggests the beginning of the development of the parts of the proctiger and its processes exhibited by the Bittacid shown in fig. 24, in which the dorsal process labelled sr may have developed from one like that labelled sr in fig. 2, while the ventral process labelled sb in fig. 24 may have developed from a ventral process like that labelled sb in fig. 2. Although the cerci ce and proctiger of the Bittacid shown in fig. 24 are hugely developed, these features are more normal in such primitive Bittacids as Harpobittacus (fig. 35), in which the tenth tergite appears to be well developed and sclerotized, and in such a highly specialized Mecopteron as Nannochorista, the tenth segment (or the tenth and eleventh together) is remarkably well developed and sclerotized. The cerci are apparently lost in Boreus, and the peculiar character of the proctiger pg of fig. 33 bears out the view that the Boreidæ are rather isolated Mecoptera. The proctiger pg of Merope (fig. 36) is long and slender, and is not as much like that of Notiothauma (figs. 1, 2 and 5), as would be expected from the fact that the Meropidæ and Notiothaumidæ are very closely related, and the character of these parts is therefore of no great significance in attempting to determine the closest affinities of the Mecopterous families. The proctiger pg, short cerci ce and other features are quite similar in Chorista (fig. 34) and Panorpodes (fig. 31), and this may possibly indicate that Panorpodes is related to Chorista as well as to Notiothauma among the primitive representatives of the Mecoptera. In the Panorpid shown in fig. 28, the epiandrium ep, or ninth tergite, is produced posteriorly and hides the proctiger, etc., which lies rather far back beneath the epiandrium.
In general, the abdominal structures of *Notiothauma* would indicate that this remarkable insect is a remnant of the ancestral Mecoptera, and is the nearest living representative of the ancestors of the Panorpidae. The Panorpidae, however, are somewhat nearer the immediate ancestors of the Panorpidae, occupying a position intermediate between the Notiothaumidae and Panorpidae, and they are also related to the Choristidae. The Choristidae occupy a position at the base of the lines of descent leading to the Bittacidae. Certain features suggest a relationship between the Boreidae and Nannochoristidae, but these insects are too highly modified to determine their closest relatives among the other Mecopterous families, although the Panorpidae may represent the types from which the Boreidae were descended, judging from characters other than the male genitalia, and the Nannochoristidae exhibit some affinities with the Panorpodidae.

**ABBREVIATIONS**

- **a** Apical portion of genital style (stylapex).
- **ap** Anal papilla (anopapilla).
- **b** Basal tubercle of genital style (basotuberculus).
- **be** Paired tergal processes (bicurnua).
- **bs** Basal portion of phallus (basiphallus).
- **c** Dorsal and ventral stylocondyles, or pivotal processes of genital styles.
- **cc** Coxal hollow (coxocrater).
- **ce** Cerci.
- **cx** Genital coxites (gonocoxites or gonocoxae).
- **d** Dorsal phallic valves.
- **e** Epiandrial processes or lobes (surgonopods, surstyli, epiprocessi, etc.)
- **en** Endostyle.
- **ep** Epiandrium or ninth tergite.
- **es** Epistyle, or process of genital style to which the extensor muscles are attached.
- **g** Dorsal epiandrial process.
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<thead>
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<th>Symbol</th>
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<tr>
<td>h</td>
<td>Hypandrial processes (Hypoprocessi, hypovalvae, etc.).</td>
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<td>ha</td>
<td>Hypandrium or tenth sternite.</td>
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<td>ic</td>
<td>Intercoxal area.</td>
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<td>l</td>
<td>Lower ventral phallic valves.</td>
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<td>m</td>
<td>Median stylar tubercle (meditubereulus).</td>
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<td>mo</td>
<td>Unpaired median tergal process (monocornus).</td>
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<td>n</td>
<td>Notoorganus or notal alluring organ of male.</td>
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<td>o</td>
<td>Styloorganus or organ on genital style.</td>
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<tr>
<td>p</td>
<td>Posterior phallic valves and lobes.</td>
</tr>
<tr>
<td>pa</td>
<td>Parandrium.</td>
</tr>
<tr>
<td>pf</td>
<td>Penisfilum valves, forming penisfilum in Bittacidae.</td>
</tr>
<tr>
<td>pg</td>
<td>Proctiger (anus-bearing region).</td>
</tr>
<tr>
<td>po</td>
<td>Conical posterior tergal process (postorganus).</td>
</tr>
<tr>
<td>ps</td>
<td>Phallosome or parts about genital opening.</td>
</tr>
<tr>
<td>sb</td>
<td>Subpapilla.</td>
</tr>
<tr>
<td>sp</td>
<td>Spiracles.</td>
</tr>
<tr>
<td>st</td>
<td>Genital styles (gonostyli).</td>
</tr>
<tr>
<td>sr</td>
<td>Surpapilla or suprapapilla.</td>
</tr>
<tr>
<td>u</td>
<td>Upper ventral phallic valves.</td>
</tr>
<tr>
<td>v</td>
<td>Ventral phallic valves.</td>
</tr>
</tbody>
</table>
Crampton—Notiothauma.
Structure of Notiothauma reedi


Crampton—Notiothauma.
Crampton—Notiothauma.
Structure of Notiothauma reedi


Crampton—Notiothauma.
EXPLANATION OF PLATES I—IV

Fig. 1. Lateral view of abdomen of male *Notiothauma reedi*, McL.

Fig. 2. Lateral view of terminal structures (terminalia) of *Notiothauma*.

Fig. 3. Ventral view of genital style and coxite of the Dipteron *Trichocera bituberculata*, Alex.

Fig. 4. Lateral view of epiandrium of male *Notiothauma*.

Fig. 5. Dorsal view of abdomen of male *Notiothauma*.

Fig. 6. Dorsal view of genital style and coxite of Dipteron *Trichocera garretti* Alex.

Fig. 7. Ventral view of terminal structures and genitalia of male *Notiothauma*.

Fig. 8. Ventral view of sinistral genital style, coxite and phallosome of a Panorpid.

Fig. 9. Same of *Boreus* sp.

Fig. 10. Same of *Nannochorista dipteroïdes*, Till.

Fig. 11. Same of *Harpobittacus* sp.

Fig. 12. Same of *Chorista australis*, Tillyard.

Fig. 13. Same of *Panorpodes* sp. from Japan.

Fig. 14. Ventral view of phallosome and basal coxites of *Merope*.

Fig. 15. Same of *Notiothauma*.

Fig. 16. Mesal view of genital style of *Merope*.

Fig. 17. Ventral view of end of hypandrium of *Boreus*.

Fig. 18. Same of *Chorista*.

Fig. 19. Same of *Merope*.

Fig. 20. Same of *Panorpodes* (from Japan).

Fig. 21. Same of *Notiothauma*.

Fig. 22. Same of *Neopanorpia opthalmica* (redrawn from Miyaké).

Fig. 23. Ventral view of sinistral half of genitalia of *Panorpa* sp. from India.

Fig. 24. Lateral view of proctiger of *Bittacus strigosus*.

Fig. 25. Lateral view of phallic valves of *Panorpa lugubris*. 
Fig. 26. Lateral view of segments three to six of *Neopanorpa cornuta*, after Miyaké.

Fig. 27. Lateral view of notal organ and conical process of *P. stigmalis*, after Miyaké.

Fig. 28. Dorsal view of epandrium of *P. lugubris*.

Fig. 29. Lateral view of third and fourth abdominal segments of a Panorpid related to *P. takenouchii*.

Fig. 30. Lateral view of terminal region of seventh segment of *P. bicornuta*, after Miyaké.

Fig. 31. Dorsal view of epandrium and proctiger of Japanese *Panoropodes*.

Fig. 32. Lateral view of terminal region of sixth segment of a Panorpodid related to *P. cornigera*.

Fig. 33. Dorsal view of epandrium and proctiger of *Boreus*.

Fig. 34. Dorsal view of epandrium and proctiger of *Chorista*.

Fig. 35. Same of *Harpobittacus*.

Fig. 36. Same of *Merope*.

Fig. 37. Same of *Notiothauma*. 