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Comparative morphology and taxonomy of the Capniidae (Plecoptera)

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COMPARATIVE MORPHOLOGY AND TAXONOMY OF SOME [illegible] (COLEOPTERA)

COMPARATIVE MORPHOLOGY AND TAXONOMY OF THE CAPNIIDAE (PLECOPTERA)

By

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COMPARATIVE MORPHOLOGY AND TAXONOMY OF THE CAPNIIDAE (PLECOPTERA)

As originally planned, this work was intended to treat only of thoracic morphology. However, as the work progressed, significant characters of other parts of the body came to my attention and prompted me to attempt a comparative study of the complete external anatomy of all available material in the Capniidae. I now consider myself very fortunate to have made this decision, since characters of significance in determining family, generic, and specific relationships are to be found in all regions of the body. Thus it is now apparent to me that in no other manner than through a comparative study of all body parts could one arrive at a thorough understanding of family, generic, and specific relationships within this particular group of insects.

It is probable that the interrelationships of no group of insects can be determined with certainty and with any degree of finality until a complete comparative study has been made. Studies of external anatomy of various widely differing species of insects have been published; but detailed comparative studies, particularly within the lower taxonomic categories (genera and species), are few. Not until one compares all of the structures of any given species with all of the structures of other species do we begin to understand fully the phylogenetic and taxonomic relationships of the insects concerned.

Capnia nigra (Pictet) is the type species of the typical genus of the Capniidae. Consequently all conclusions concerning family and generic characters are ultimately based upon it. It is appropriate, therefore, that a study of the comparative morphology of the family Capniidae be introduced by a detailed discussion of the anatomy of this species.

Figures of nearly all external anatomical features of Capnia nigra are included to supplement the discussion. The treatment of the comparative morphology of other genera of Capniidae is supplemented by figures wherever characters of any considerable generic significance occur.

PART I.

EXTERNAL ANATOMY OF CAPNIA NIGRA (PICTET)

The study of this species was made possible through the loan of material from Professor N. Banks of the Museum of Comparative Zoology at Cambridge. The identity of the specimens studied is unquestionably in agreement with Capnia nigra as used by European workers. Morton especially (1929) has figured the species in detail. As far as I can determine no author has studied the genitalia of the type specimens. It is even doubtful that the types still exist.

GENERAL APPEARANCE

Capnia nigra, like most other species of the genus, is a relatively small, slender, darkly colored stonefly which varies in length from 5 to 6 mm. in the male sex and from 6 to 8 mm. in the female. The female is fully winged but the male is extremely brachypterous, having practically veinless wings, which are reduced to one millimeter or less in length. In both sexes the wings and most of the sclerotized body parts are covered with tiny light-colored setae.

HEAD

Figs. 1-3, 5-10.

The head of Capnia nigra is prognathous and somewhat flattened. Its length is about equal to its width which is greatest at the compound eyes. The mandibles, antennae, and eyes are located laterally on the head; the ocelli are dorsally located.

SUTURES OF THE CRANIUM OR HEAD CAPSULE: The principal sutures of the cranium of *Capnia nigra* are the postfrontal, postoccipital, subgenal, epistomal, ocular, and antennal sutures.

The epicranial suture is not completely developed, since frontal sutures rarely if ever occur in Plecoptera (Crampton, 1932); and in *Capnia nigra* with which we are here concerned the coronal suture also is either entirely absent or only very weakly indicated.

Postfrontal sutures (pfsu), which may be confused easily with frontal sutures, are present and are well demarked. From a mesal point on the vertex, where they meet at a very obtuse angle, each postfrontal suture extends along a straight line to the posterior margin of the lateral ocellus and then curves sharply around the outer edge of the ocellus. Within a very short distance anterior to the ocellus it terminates at the posterior end of the tentorial macula.

The postoccipital suture (pocs) closely parallels the dorsal and lateral margins of the foramen magnum.

Near its anterolateral extremities it is weakly marked. There is no occipital suture.

The subgenal sutures each consist of two portions, the pleurostomal and hypostomal sutures. Each of the paired pleurostomal sutures (pls) seem to be identical with the linear exterior edge of the anterior tentorial pits formed by the fan-shaped anterior tentorial arms. Each hypostomal suture (hms) follows closely the cranial margin between the lower mandibular articulatory point and the posterior tentorial pit.

The epistomal suture (es) is a very distinct suture connecting the two anterior tentorial pits across the front part of the cranium. This suture is produced by a deep inflection resulting internally in a strong epistomal ridge (esr) which forms a brace between the upper articulatory points of the mandibles.

Ocular sutures (os), surrounding the compound eyes at their bases, are present.

An antennal suture (as) entirely surrounds each antennal socket close to its edge.

AREAS OF THE HEAD CAPSULE: The principal areas of the cranium are the clypeus, frons, parietals, postocciput, genae, subgenae, and postgenae. Not all of these are demarked by sutures.

The clypeus (cl) is a small, transverse sclerite bounded anteriorly by a membranous region between it and the labrum, and posteriorly by the epistomal suture.

The frons (fr) is a large area bounded anteriorly and posteriorly by the epistomal and postfrontal sutures, respectively. Laterally it is bounded by the antennal sockets and the tentorial maculae.

Immediately anterior to the median ocellus, which is situated near the middle of the frons, a transverse suture extends for a very short distance to either side of the ocellus. In one genus of Capniidae this suture completely divides the frons into two parts. It has been suggested to me by Dr. Crampton that this suture, which in practically all stoneflies is a very short and inconspicuous suture in front of the median ocellus, may be the actual frontal suture. In such a case the true frons would be confined to the region between the clypeus and the median ocellus; the frontal region posterior to the median ocellus would probably have to be considered to be a secondary postfrons. However, since this view is by no means proven, it seems advisable to recognize the entire area from the postfrontal sutures to the clypeus as the frons since it has been interpreted in this manner by Crmapton (1932) and Hoke (1924).

The tentorial maculae (tm) are two slightly concave areas of the dorsal cranial surface corresponding to the points on the internal surface of the cranium where the anterior tentorial arms abut against it. They usually lie within the frontal area. In Capnia they are relatively large oval areas whose long axes coincide with an imaginary line connecting either lateral ocellus with the nearest point of the antennal socket of the same side of the head.

All three ocelli (oc) are borne on the frons. The lateral ocelli are situated close to the lateral angles of the postfrontal sutures. The distance between them is slightly less than three times the distance of either ocellus from the compound eye nearest to it. The median ocellus is slightly closer to the epistomal suture than to the median point of junction of the postfrontal sutures.

The parietals (par), due to the absence of a delimiting coronal suture, merge into a large transverse area in the posterior part of the cranium. On each side of the head this plate extends to meet the gena at the constricted region between the antennal socket and the compound eye. It also extends laterally behind the compound eye to the postgenal region below. The dorsal area of the parietal sclerite is known as the vertex. The latter region usually bears a few longitudinal embossings.

The antennal sclerites (asc) consist of narrow but distinct bands surrounding the antennal sockets. Each has an anterodorsal and an anteroventral antennifer (af) or expanded articulatory point.

The ocular sclerite (osc) is a narrow internal rim or shelf around the margin of the compound eye. It is easily visible through the outer cuticle of the eye in cleared specimens.

The compound eyes (eye) are situated laterally on the head. They are slightly oval or nearly round in outline and protrude conspicuously outward from the cranium. Each compound eye is composed of approximately 200 ommatidia.

The postocciput (poc) forms the posterior rim of the cranium. It is a narrow, roughly horseshoe-shaped or U-shaped sclerite whose ends terminate at the posterior tentorial pits. Ventrolaterally its posterior margin is produced on each side into a small occipital condyle (occ) with which the cephalinger (cep) of the corresponding lateral cervical sclerite articulates.

The subgenae consist of two pairs of tiny, elongate sclerites. Each pleurostoma (pm) is a very tiny plate situated between the base of the mandible and the antennal socket. Each hypostoma (hm) is a narrow band or thickening bordering the foramen magnum between the lower mandibular articulatory point and the posterior tentorial pit.

The genae (ge) are a pair of undifferentiated ventral areas between the hypostoma and the eye on either side of the head.

The postgenae (pge) are a pair of undifferentiated ventral areas below and behind the compound eyes on either side of the head.

TENTORIUM: The tentorium (Fig. 2) consists of a corporotentorium (ct) in the center of the head and three pairs of arms supporting it from different parts of the cranium. The anterior (ata) and posterior (pta) tentorial arms are formed by invaginations of the cranium. The dorsal tentorial arms (dta) are said to arise as outgrowths of the anterior tentorial arms.

The anterior tentorial arms (ata) arise from the anterior tentorial pits which are curved sutures extending from the dorsal antennifer to the ventral antennifer. Thus, each anterior tentorial arm is a scoop-shaped, lamellar structure the outer end of which is continuous with the anterior section of the antennal sclerite. It tapers rapidly to its point of attachment with the corporotentorium.

The posterior tentorial arms (pta) arise from the posterior tentorial pits which are oval openings at the anteroventral extremities of the postocciput. They are shorter, narrower, and stouter than the anterior tentorial arms.

The dorsal tentorial arms (dta) are longer and narrower than those described above. They appear to arise at the region of fusion of the anterior tentorial arms with the corporotentorium. They narrow slightly ectally toward their abruptly expanded peltate apices which abut against the internally concave tentorial maculae (tm) which are situated at the posterolateral angles of the frons.

The corporotentorium (ct) or "body" of the tentorium is the central, somewhat sagittally elongate portion to which all tentorial arms are entally attached.

HEAD APPENDAGES: The movable parts of the head are the following: antennae, labrum, mandibles, maxillae, hypopharynx, and labrum.

The antennae are filiform and are about equal in length to the length of the head and thorax combined. They are composed of a series of segments varying between 25 and 30 in number. The basal segment or scape (s), which is short and thick, articulates basally with the antennal sclerite at two points (with the upper and lower antennifers) and distally with the pedicel (p) at two points in a plane at right angles to the plane of movement of the scape. The combination of these two articulations forms a universal joint allowing movement of the flagellum in all directions. The pedicel is shorter and of only about half the diameter of the scape. The flagellum is nearly immovably articulated with the pedicel at its base. Constricted regions in the apparent first segment of the flagellum indicate that it is a fusion product of the first two and sometimes three original segments. It is thus usually about twice as long as the segments immediately following it. The second flagellar segment is must smaller than the first. From this segment nearly to the end of the antenna the length of the segments increases. The size of a few of the apical ones is slightly smaller than that of the subapical segments.

The labrum (lr) or upper lip, though not a true appendage, is movable and functions as one of the mouthparts. It is a transverse, roughly quadrangular sclerite attached to a membranous region in front of the clypeus. It is slightly convex above and slightly produced along its distal margin. Its lateral tormae extend into the membranous region at its base but do not articulate with the clypeus. .

The mandibles (Figs. 9,10) are well developed and asymmetrical. Curved opposable molar surfaces (mo) crossed by many fine ridges, apparently for grinding food, are located at their inner angles. The molar area of the left mandible is concave while the opposable mola of the right mandible is convex. The left mandible bears four teeth; one submarginal on the dorsal or concave surface near the mola, and three marginal apical ones. The right mandible bears three teeth; one submarginal on the ventral or concave surface near the mola, and two marginal apical ones.

The base of the mandible is triangular in shape.

A strong flexor tendon is attached to the inner angle of the base. To the sharp lateroventral angle a weaker retractor tendon is attached. On the margin between these two tendonal attachments close to the retractor tendon is a conspicuous condyle which articulates with the pleurostomal margin on the lower surface of the cranium. The upper angle of the base bears a smaller condyle that articulates in a socket of the subgena contiguous with the lateral basal angle of the clypeus.

The maxillae (Figs. 5,6) are composed of several distinct parts; namely, cardo, stipes, parastipes, lacinia, galea, and palpus. The axis of the cardo is oriented at about right angles to the sagittal line while the remainder of the maxilla assumes a sagittal position closing the preoral cavity laterally.

The cardo is divided by a distinct suture into two nearly equally sized convex sclerites, the basicardo (bc) and the disticardo (dc). The dividing suture extends from the single proximal articulatory point of the cardo on the anterior margin of the posterior tentorial pit to a distal ventral articulatory point. Another distal articulatory point occurs on the dorsal edge of the disticardo. The resulting dicondylic hinge thus permits of horizontal motion of the outer parts of the maxilla.

The stipes (si) which is the largest sclerite of the maxilla is situated mostly on the ventral surface, but also is reflected slightly onto the dorsal surface of the maxilla.

The parastipes (ps) is a narrow sclerite demarked from the mesal edge of the stipes. It is broadest at about the middle, is very narrow basally, and is pointed distally.

The lacinia (la) is the inner of two lobes borne apically by the stipes. It is a well sclerotized, roughly pyramidal or cone-shaped structure attached on its ventral surface to the stipes by a dicondylic hinge. Dorsally its base is connected with a well sclerotized but very small retractoral plate (rp). Numerous strong muscle fibers extend from this plate to the wall of the stipes near its proximal end. The lacinia is hinged in such a manner that contraction of these muscles obviously must move the lacinia inwardly. Doubtless this mechanism constitutes one of the chief means by which food is manipulated into the preoral and oral cavities. The mesal edge of the lacinia is a sharp ridge bearing a subapical fringe of long setae and a sharp bidentate apex that is well adapted to such a function as that described above.

The galea is the outer lobe borne distally by the stipes. It is divided into a small poorly, defined, poorly sclerotized basigalea (bg) and a large, well defined distigalea (dg) of about the same length as the lacinia. The distigalea is a bluntly pointed structure bearing two longitudinal membranous regions and numerous apparently sensory papillae.

The 5-segmented maxillary palpus (mxp) arises laterally in the membranous region near the base of the galea; there is no differentiated palpifer. Its basal segment is the shortest and its apical segment is the thinnest. In ascending order of size the sequence of segments is as follows: 1,2,3 and 5, and 4.

The hypopharynx (Fig. 7) of Capnia is a large, thick lobe filling the preoral cavity and apparently consisting only of the lingua; superlinguae are not present. Its bulbous anterior end is unsclerotized and is slightly bilobed. Its distal surfaces bear innumerable minutely microscopic spinulae which offer a rough surface for manipulation of food.

The so-called basal plates or bars (bpl) are fused into a single process for most of their length.

The entire process consists of a long, thin, basal section which forks distally into two diverging plates that lie on either side of the hypopharynx and extend nearly to its apex.

The <u>suspensoria</u> (sus) consist of five tiny plates; namely, an unpaired plate and two sets of paired lateral plates lying directly above the apices of the arms of the fused basal plates. Each of the lower pair of suspensoria articulates with an arm of the basal plates and with the unpaired plate above it. The unpaired plate extends around the front of the hypopharynx to articulate with both lower plates and also with the other or most dorsal pair of plates. The latter articulate at their dorsal ends with the mandibles in the region of the attachment of the flexor tendon of each.

The small <u>mouth</u> (mh) opening lies in a groove in the hypopharynx between the upper pair of suspensorial plates. The unpaired suspensorial plate crossing the front of the hypopharynx supports the lower margin of the mouth. The mouth is opened or closed by the action of the mandibles. As the chewing surfaces of the mandibles are adducted the points of attachment of the suspensoria to the two mandibles move farther apart. This movement, which causes the spreading apart of the upper pair of suspensoria and a play of interaction between all the suspensorial plates, opens the mouth. By the reverse of the same mechanism, closure of the jaws closes the mouth.

The labium (Fig. 8) closes the preoral cavity ventrally.

The postlabium or basal section is composed of a large submentum and a small mentum. The submentum (sm) is the largest demarked area of the labium. In shape it is transverse and trapezoidal. Its base merges with the membranous neck region. Its distal margin is completely demarked from the mentum. The mentum (mn) is a much smaller and more transverse sclerite than the submentum from which it is demarked by a straight line. Its distal margin is arcuately emarginate and a small mesal region is fused with the prelabium.

The prelabium is smaller and narrower than the postlabium. However, its length is greater than that of the postlabium. The labiostipites (lbi) is its largest portion. This protrudes basally into the mentum with which, as mentioned above, it is mesally fused. Distally it is constricted in the region of attachment of the palpi to almost one-third of its greatest width. Beyond the bases of the palpi it expands again to accommodate the bases of the glossae and paraglossae. The glossae (gl) are well demarked below from the labiostipites by a darkly sclerotized rim. Each glossa bears a small nipple apically. The paraglossae (pgl) are the same length as the glossae but are slightly broader than the latter. Basally they merge with the labiostipites. Basolaterally each is bounded by a darkly sclerotized rim. Both glossae and paraglossae bear sensory papillae at their apices. The labial palpi are 3-segmented and have no demarked palpiger at their bases. When extended they reach forward about the same distance as do the glossae and paraglossae. The second segment is always the longest, the third segment is very short and usually nearly hemispherical.

CERVIX OR NECK

Fig. 25

The cervix or membranous neck region (Fig. 25) between head and prothorax bears three sclerites, the ventral cervical sclerite and a pair of lateral cervical sclerites.

The ventral cervical sclerite (vc) lies free, immediately anterior to the prothoracic presternum. It is slightly smaller and more oval than the latter.

The lateral cervical sclerites (lc) are roughly hemispherical protrusions that are attached posteriorly to the prothoracic precoxal bridge and which send a stout projection cephalad to articulate with the occipital condyle of the head.

THORAX

Figs. 17,25,31-33,36,37.

THORACIC TERGA (Fig. 37).

Pronotum: The prothoracic tergum consists of a single large sclerite, the pronotum (pn), which is roughly square in shape. The lateral margins are deflected so as to encroach slightly on the pleural region. Near its anterior margin and running parallel to it is a suture delimiting the narrow transverse precosta (pc) (Snodgrass, 1935). Near the posterior border of the pronotum is a similar suture. In some stoneflies these two sutures are continuous with lateral submarginal grooves and collectively constitute the *marginal groove* (Claassen, 1931). A poorly defined mid-dorsal line connects the two above mentioned sutures. The *disc* or dorsal area of the pronotum bears a few irregular embossings on either side of the mid-line.

Mesonotum: The mesothoracic tergum is demarked into four main regions; *prescutum*, *scutum*, *scutellum*, and *postscutellum*; and other minor regions.

The *prescutum* (psc) is the anterior-most mesotergal sclerite. Its broad posterior margin protrudes arcuately into the larger scutum to its rear, and the narrower anterior end projects downward and under the posterior edge of the pronotum. It is divided along the mid-dorsal line by a distinct suture.

The *prealar bridges* (pra) are distinct sclerites broadly joined to either side of the prescutum. Each bridge curves around the wing base and narrows to a blunt end abutting against, but not united with, the epimeron in the pleural region (Fig. 36).

The *scutum* (sct), the largest sclerite of the tergum, is roughly haxagonal in shape. The *anterior notal wing processes* (anp) consist of a pair of tiny projections at the anterior lateral angles of the scutum. The *posterior notal wing processes* (pnp) are larger and better demarked than the former, are triangular in shape, and are supported not only by the scutum but also along a line of union with the postscutellum.

The scutellum (scl) is a partially demarked region in the posterior part of the scutum. It is bounded laterally and posteriorly by a U-shaped suture; its anterior end is undemarked from the scutum. The scutellum of the male of *Capnia nigra* is not demarked from the scutum except in its posterior region where a section of the demarking suture persists. This condition may possibly be correlated with the lack of functional wings in the male sex of this species.

The postscutellum (pscl) is a rectangular and somewhat transverse sclerite united along its anterior border with the posterior notal processes, the scutum, and the scutellum, and to the metathoracic presternum and prealar bridges along its posterior border. In the middle of this sclerite is a slightly raised lighter colored transverse area. On either side and to the rear of this are a pair of larger and more rounded light colored areas.

There is no postalar bridge in the mesothorax of *Capnia*.

Metanotum: The metathoracic tergum is smaller than that of the mesothorax but is otherwise very similar to it. It differs, however, in the following details. The prealar bridge (pra) is much smaller and less sclerotized than that of the mesothorax, and is not united with the prescutum as is the case in the mesothorax. A complete postalar bridge (poa) occurs in the metathorax and appears to be formed by an extension of the dorsal edge of the epimeron which unites with the lateral margin of the postscutellum.

THORACIC PLEURA (Fig. 36).

Propleuron: The prothoracic pleuron is composed of the primitive eupleuron and eutrochantin (Crampton, 1926). Plecoptera are the only pterygotan insects to retain the apterygotan condition in which eupleuron (anapleurite) and eutrochantin (coxopleurite) are distinct sclerites.

The eupleuron, the larger of these two regions, is divided into two main parts by the nearly vertical pleural suture (pls). The small region posterior to the pleural suture corresponds to the upper region of the definitive epimeron. (Crampton, 1926). The larger region anterior to the suture corresponds to the upper region of the definitive episternum. Extending anteriorly and ventrally from the latter, and well demarked from it, is the precoxal bridge (pr) which in this genus and in all other Capniidae is well sclerotized and is united with the basisternum to form a complete precoxal bridge.

The eutrochantin (etn) (Crampton, 1926) is also divided into two regions by the pleural suture. It is thus composed of a very tiny posterior portion which corresponds to the lower region of the definitive epimeron and a larger anterior arm which corresponds to the lower region of the definitive episternum. The latter curves ventrally to articulate with the anterior proximal edge of the coxa.

A postcoxal bridge (po) is present but not quite complete in the pleural region, i.e. there is a small gap separating it from the epimeron.

Mesopleuron: The mesothoracic pleura are more highly evolved than the prothoracic pleura.

A pleural suture (pls) extends obliquely cephalodorsad from the pleural coxal articulation or coxifer to the alifer to the wing, dividing the pleuron into two main regions, the epimeron and the episternum.

The *epimeron* (epm) is the upper, posterior, and smaller of the two main regions of the pleuron. It is bounded above by the articular corium of the wing, and posteroventrally by the coxal articulatory corium. It is broadest posteriorly, and narrows to a pointed anterior apex at the base of the alifer.

The *episternum* is subdivided by a poorly demarked, angular suture into two secondary regions known as *anepisternum* and *katepisternum*.

The *anepisternum* (aes) projects upward to form three wing processes, the *anterior* (ab) and the *posterior basalares* (pb) and the *alifer* (al). The *anterior basalare* (ab) is shorter and broader than the other two pleural wing-base processes and is rounded apically. It is strengthened by a longitudinal ridge near its anterior margin. Its posterior margin is projected internally in a knife-blade-like ridge which lies close to the inner surface of the posterior basalare. The two basalares are connected by only a very thin membrane so that free movement of the anterior basalare in response to the action of muscles attached to its internal ridge is allowed along a vertical sagittal plane. The *posterior basalare* (pb) projects higher than the anterior basalare and expands apically to form two points of articulation with the wing-base. Both basalares merge at their bases with the anepisternum. In the male of *Capnia nigra* which is strongly brachypterous, the two basalares are fused together. The alifer (al) is the smallest of the three pleural wing processes. It is heavily sclerotized and appears to be formed largely of the pleural ridge; but possibly its base is formed partly by a small narrow portion of the anepisternum and also by a portion of the epimeron.

The katepisternum (kes) or lower region of the episternum is smaller than the anepisternum. It lies as a narrow strip between the anepisternum and the basisternum and then extends posteriorly and dorsally to meet the pleural suture along a broad margin.

The trochantin (tn) arises from the lower posterior region of the katepisternum, and its base lies deep within the latter.

There is no postcoxal bridge in this segment.

Metapleuron: The metathoracic pleuron is similar to that of the mesothorax described above. Only the following few minor differences occur. The pleuron as a whole is smaller than that of the mesothorax but the epimeron (epm) is larger having a greater dorsal development resulting in the formation of a complete postalar bridge not present in the mesothorax. The katepisternum (kes) is better demarked from the basisternum in this segment than it is in the mesothorax, and the trochantin (tn) does not encroach upon the katepisternum to the extent that it does in the mesothorax.

THORACIC STERNA (Fig. 25).

Prosternum: The prothoracic presternum (prs) lies just anterior to the arcuately emarginate margin of the basisternum. It is a small, nearly round sclerite.

The basisternum (bs) is the largest prosternal sclerite. To its broad anterior region the precoxal bridges are fused; the postcoxal bridges are fused to its smaller posterior end and to the outer edges of the furcae.

The furcasternum (fs) is a small transverse sclerite situated at the posterior end of the basisternum and demarked from it by a distinct suture that extends from one furcal pit to the other (sternacostal suture).

The postfurcasternum (pfs) is a larger sclerite than the above. In shape, it is transversely oval, exhibiting a tendency toward a division into two parts by membranization along the mid-ventral line. It is entirely isolated from other sclerotized regions by membrane.

The spinasternum (ss) appears to be more closely associated with the mesothorax than with the prothorax. However, since the spinasternum is usually considered to be the posterior-most sclerite of a thoracic segment (Crampton, 1926), I have provisionally adopted this view and am considering the anterior-most spinasternum of the thorax as a prothoracic structure. It is an extremely narrow, transverse, bow-shaped sclerite nearly as wide as the entire segment. It has an abrupt expansion at the middle and is fused at its apices to the anterior lateral angles of the mesothoracic basisternum.

Mesosternum: The presternum (prs) of the mesothorax is a small oval sclerite situated in the space enclosed by the prothoracic spinasternum and the mesothoracic basisternum.

The basisternum (bs) of the mesothorax is much larger than that of the prothorax. As a result of this the mesothoracic coxae are more widely separated from each other than are those of the prothorax. The basisternum is a transverse sclerite with an arcuately emarginate anterior margin and an arcuately protruding posterior region. It is bounded along an extensive lateral margin by the katepisternum of the pleuron. From the latter it is well demarked except posteriorly where for a short distance the demarking suture drops out. As mentioned previously, the anterior lateral angles of the mesobasisternum are fused to the prothoracic spinasternum.

The furcasternum (fs) is a small, slightly transverse sclerite which is strongly united with, but well differentiated from, the basisternum. The furcal pits of this segment are slightly farther apart than are those of the prosternum. A very distinct, semicircular, submarginal suture whose ends terminate near the anterior ends of the furcal pits gives a semicircular appearance to the furcasternum. This submarginal suture demarks a distinct posterior marginal band which is fused mesally with the elongate spinasternum and laterally is continuous with a pair of furcasternal arms. The furcasternal arms (fsa) are a pair of elongate processes extending from the furcal pits toward the coxae. Although they are not articulated with the coxae they appear to be adapted to offer them very strong support in the movement of the legs.

The spinasternum is a small, mesal, sagitally elongate, and well sclerotized plate which is united with the posterior region of the furcasternum and usually extends slightly under the metathoracic presternum at its posterior end.

The postfurcasternum (pfs) is divided into two roughly circular plates lying on either side of the spinasternum.

Metasternum: The presternum (prs) of the metathorax lies close to the strongly arcuate anterior margin of the basisternum and is triangular or rounded in shape. It is at least twice as large as the mesothoracic presternum.

The basisternum (bs) is smaller and more transverse than that of the mesothorax. Finger-like projections occur at its anterior lateral angles at the positions corresponding to the points on the mesothoracic basisternum where fusion with the apices of the spinasternum occurs. The basisternum is often completely differentiated from the katepisternum by the demarking suture.

The *furcasternum* (fs) is an extremely narrow, transverse sclerite strongly united with, but well differentiated from, the basisternum. It is not united with the first abdominal sternite. The *furcal pits* (fsp) are widely separated. The *furcasternal arms* (fsa) are smaller than those of the mesosternum.

There is no metathoracic spinasternum.

WINGS (Figs. 17,36,37).

Articulation with the Thorax.

Fore wing: The axillary sclerites (Figs. 36,37) figure prominently in this most complicated of hinges, the wing articulation of insects.

The *first axillary sclerite* of *Capnia nigra* is an elongate plate situated between the lateral edge of the scutum and the second axillary sclerite. Anteriorly the first axillary is produced into a long "neck" supported on the inner side by the anterior notal process and abutting on the outer surfaces against the base of the radial vein. Apically the "neck" articulates with the base of the subcostal vein. The first axillary sclerite is not visible in the lower wing membrane.

The *second axillary sclerite*, which is roughly quadrangular in shape, lies between the first axillary and the median plate. It is closely articulated above with the base of the radial vein to which it is partly fused. Viewed from the lower surface of the wing it is concave; it articulates with the alifer of the episternum.

The *third axillary sclerite* and the *median plate* are fused into a single, strongly sclerotized, subtriangular plate. The base of this triangle articulates at one end with the posterior notal process and at the other with the base of the anal cell. Between these two points there is a small protruding flange to which strong muscles are attached.

The *humeral plate* (hp) appears to be a sclerotization of the lower wing membrane only, although it is sometimes partly visible from above. It is a tiny triangular plate articulating between the base of the costa and the anterior protuberance of the anterior basalare. The posterior protuberance of this basalare articulates with the base of the subcosta.

Two other secondary axillary sclerites are visible only in the lower wing membrane (Fig. 36); the anterior subalare and the posterior subalare (sub). The anterior subalare which articulates with the second axillary sclerite, is the larger of the two. The posterior subalare is a very small sclerite situated close to the lower tip of the third axillary sclerite.

In the folding of the wing, the straight outer margin on the combination third axillary and median plate forms the major hinging surface. Reference to Figure 37 will make plain the mechanism of this folding process. By the use of muscles extending from attachment points within the body to the margin of the third axillary sclerite the straight outer margin of this sclerite is forced upward and over onto the dorsum of the insect through a wide arc. Since the anterior part of the wing base does not pass through this wide arc of space but pivots at the bases of the subcosta and radius, the wing must of necessity be forced posteriorly inward, and thus it comes to rest over the abdomen as the third axillary is folded back over the dorsum.

Hind wing: The wing base of the hind wing is very similar to that of the fore wing in most details. A few minor modifications occur at the base of the anal veins due to the larger size of the anal area (vannus) in the hind wing.

Wing Venation.

The venation of the genus *Capnia* (Fig. 17) is much reduced both in its longitudinal veins and in its crossveins. Those veins which are present are well developed and of nearly equal strength.

Fore wing: The veins of the fore wing are well sclerotized and are dark brown in color except for the base of the cubitus which is weakly sclerotized.

The costal vein (C) is simple, forming the anterior margin of the wing.

The subcosta (Sc) is a nearly straight vein which curves rather abruptly to enter the radius at the cord or just before reaching it.

The radius (R) branches into R_1 and Rs shortly distad of its junction with media. R_1 is bowed strongly upward from the point of origin; in some cases the bend is as strong as the downward bending of Rs at this same point. R_1 is unbranched; Rs is once forked at or beyond the cord.

Media (M) arises from the radial stem nearly at right angles to it. From a point of junction with the arculus the media extends as a simple vein to the cord where it forks to form M_1 and M_2.*

The basal part of the cubitus (Cu) is very weakly developed. At its point of junction with the arculus or slightly proximad of this point it branches into two nearly straight veins, Cu_1 and Cu_2.

The anal veins (A) are two in number, arising from the tiny anal cell. The first anal vein proceeds outward from the apex of the anal cell for a very short distance. At the cubito-anal crossvein it bends abruptly caudad and within another very short distance bends abruptly outward again. At this angular bend a heavy patch of sclerotization occurs. Most of it occurs above the vein and assumes a roughly triangular shape. A small amount of sclerotization occurs below the vein, however. The region of the anal veins is not developed into a vannus in the fore wing.

Crossveins are few in Capnia nigra. The following primary crossveins are present: humeral, radial,

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*The arculus, as used here, is defined for convenience as the crossvein between the bases of M and Cu in the fore wing and between Rs + M and Cu in the hind wing of Plecoptera.

radio-medial, medio-cubital, arculus, cubito-anal, and anal. Supplementary crossveins are 4 or 5 in number: one or two costal, one oblique crossvein in the marginal cell beyond the subcosta, one median, and one intercubital.

The cord is an obliquely transverse line of bracing at the broadest part of the wing slightly distad of the middle. It is composed of r, r-m, m-cu, cu and the bases of M_1 and M_2.

Hind wing: The veins of the hind wing are well marked but not as darkly sclerotized as those of the fore wing.

The costal vein (C) is unbranched, forming the costal margin of the wing.

The radius (R) branches near its base into R_1 and Rs. R_1 is not bowed at the base as it is in the fore wing. Rs branches from R_1 at a sharp angle. It may branch into R_{2+3} and R_{4+5} either just after passing through the cord or just basad of it. In the latter case basal sections of R_2 and R_3 become part of the cord.

The base of media (M) joins the radius at an acute angle at a point slightly distad of the arculus. It branches into M_{1+2} and M_{3+4} some distance beyond the cord.

The *cubitus* (Cu) branches into Cu_1 and Cu_2 very near its base and shortly beyond *cu-a*.

An *anal fan* (vannus) is present and is of considerable size in the hind wing. It extends distally to a point slightly beyond the cord or about two-thirds the distance to the wing tip.

The *anal veins* (A) are three in number. The *first anal vein* arises from the apex of the anal cell, curves slightly cephalad, and then proceeds along a nearly straight line to the wing margin. The *second anal vein*, which is nearly as long as the first, arises from the base of the anal cell. Arising from the same point is the much shorter *third anal vein*.

Primary *crossveins* are as in the fore wing; secondary or supplementary crossveins are fewer in number than in the fore wing since a secondary median crossvein is never present in the hind wing.

The *cord* of the hind wing is similar to that of the fore wing except that since media forks distad of the cord in the hind wing the bases of M_{1+2} and M_{3+4} do not enter into the composition of the cord.

LEGS (Figs. 31, 32).

The legs (Fig. 31) are long and slender. The fore legs are the smallest, being slightly smaller than the mesothoracic legs which in turn are considerably smaller than the metathoracic legs. The differences in sizes of the legs is accounted for especially by differences in length of the femur, tibia, and tarsus since the coxa and trochanter are practically identical in size in all six legs.

The coxa (cx) or basal leg segment is moderately sized, appearing largest in sternal view. In anterior view the coxa is unmarked except for a narrow prearticular part of the basicoxite which is well delimited by the basicostal suture. No coxal suture is present. On the posterior surface of the coxa, however, is a suture that extends basad from the posterior trochanteral articulation (Fig. 31). Between the basal end of this suture and the trochantinal articulation a moderately large meron is demarked at the base of the coxa.

The trochanter (tr) is a very short segment articulated with the coxa by an anterior and a posterior condyle. The deeply emarginate upper margin of the coxa allows for a wide range of motion of the leg on this dicondylic hinge. A dicondylic hinge is also present at the distal end of the trochanter. It operates in a plate at right angles to the distal coxal hinge, but permits of much less freedom of motion than the latter since nearly the entire distal rim of the trochanter is closely adjacent to the end of the femur.

The *femur* (fe) is approximately twice as long as the coxa and trochanter combined. It is of nearly uniform width throughout its length. The sides of the femur are bounded ventrally by ridges running the length of the segment. These ridges delimit a concave ventral surface of the femur forming a groove for the reception of the tibia when the latter is flexed close against the femur.

The *tibia* (ti) is slightly longer and more slender than the femur. It is slightly compressed and nearly uniform in cross-section throughout its length. It is articulated to the femur by a dicondylic hinge. At its distal, lower margin it bears two diverging spurs.

The *basitarsus* is articulated to the tibia by a dorsal monocondylic hinge. It is a nearly cylindrical segment and is about three times as long as wide.

The *second tarsomere* is of about the same diameter as the first but is very short, being only about one-fourth the length of the first tarsal segment to which it is closely articulated.

The *third tarsomere* or *distitarsus*, which is slightly longer than the first, is the longest of the three tarsal segments (except in the metathoracic legs where the first tarsal segment is the longest). It articulates loosely with the distal end of the second tarsal segment by means of a dorsal monocondylic hinge.

The *pretarsus* (Fig. 32) or terminal region of the leg consists of *claws*, *arolium*, *orbicula*, *basipulvilli*, and the *unguitractor*. The *claws* or *ungues* are the largest parts of the pretarsus. They both articulate with a small dorsal process (*unguifer*) of the last tarsal segment. From this point they diverge and curve downward to their sharply pointed apices. Ventrally their bases are connected with membrane which is also closely attached to the mesally located *unguitractor* (ut). The unguitractor is a ventral sclerite that can be retracted into the distitarsus by the action of muscles in the tibia that are attached to the *unguitractoral tendon* which is also attached to the proximal end of the unguitractor. Retraction of the unguitractor results in flexure of the claws. Located immediately below the claws and very close to the lateral distal angles of the unquitractor is a pair of setiform basipulvilli (bp). These are somewhat curved inward and are not as long as the claws. A median lobe, the arolium (ar), lies between the claws. This structure is largely membranous. Dorsally it is partly covered by a sclerotized plate called the orbicula (or). The orbicula expands distally and is slightly deflected over the sides of the arolium.

ABDOMEN

Figs. 42,48,49,54,55.

The abdomen of Plecoptera is generally considered to consist of eleven segments, although interpretations as to the segmental distribution of the genitalia vary.

The PREGENITAL ABDOMINAL SEGMENTS of the male of *Capnia nigra* are eight in number. The tergal and sternal regions of all pregenital segments are entirely sclerotized. The tergal and sternal plates of the first abdominal segment are relatively small and are widely separated laterally by a pleural membranous region against which the hind coxae lie. The tergal and sternal regions of the remaining pregenital segments are separated by only a narrow strip of membranization which extends along the pleuron.

The female pregenital segments are seven in number. They are similar to those of the male except that a mid-dorsal membranous stripe of about one-third the width of the abdomen traverses all eight segments (Fig. 49).

The MALE TERMINALIA of Capnia nigra involve abdominal segments nine, ten, and eleven. The posterior margin of the ninth tergite is conspicuously elevated to form a large median process (Fig. 54). The tenth tergite is divided into two rounded sclerites fused posteromesally to the basal bulb of the supraanal process. The supraanal process (sa) is a short recurved process.

On the sternum (Fig. 42), the ninth segment and the subanal lobes are involved in genitalic modifications. A narrow basal rim of the ninth sternite is continuous laterally with the tergal sclerite. A small ventral appendage or lobe (va) is borne mesally on the basal rim. The major portion of the ninth sternite consists of a large rounded lobe or subgenital plate which is separated by membrane from all other sclerotized parts of the segment except at its lateral basal angles. Although it is usually not produced beyond the bases of the subanal lobes in the Capniidae, Klapalek (1896) has used the term subgenital plate for this structure. The subanal lobes (sbl) are small, roughly triangular sclerites which are closely adjacent to each other along their mesal edges. They are both joined mesally to an internal fusion plate (fp) which in Capnia nigra is two to three times as long as wide. It is widest near the base and tapers posteriorly to a slender apical region which extends beyond the subanal lobes. Anteriorly it is connected by membrane with a narrow, sclerotized, retractoral plate (rp) to which strong muscles are attached. Klapalek (1896) has figured this entire structure in detail and has called it a titillator. However, since this same term has been applied to a different structure in Leuctra, I prefer to use the term fusion plate (fp). The cerci are borne in the membranous apical abdominal region on either side of the anus. They are 16-segmented in the male specimen studied.

FEMALE TERMINALIA. The female genital opening lies on the mid-ventral line betwenn the margins of the eighth and ninth sternites. There are no external genitalic modifications except in the distal region of the eighth sternite, the hind margin of which has a slightly recessed area with a broadly arcuate margin (Fig. 48). The eighth tergite is membranized medially to form the distal end of the membranous stripe mentioned under the discussion of pregenital segments. The ninth segment is unmodified. The tenth segment is nearly as large as the ninth dorsally, but ventrally is made up chiefly of the subanal lobes. The subanal lobes (sbl) are subtriangular in shape and are slightly larger than those of the male. No median fusion plate, such as that which joins the subanal lobes of the male, is present. The cerci (ce), which lie on either side of the anus, are similar to those of the male and are composed of nineteen segments in the specimen studied. The epiproct (epi), or remnant of the dorsal part of the eleventh abdominal segment, which lies above the anus but below the protruding margin of the tenth tergite, is a very tiny sclerite.

PART II.

COMPARATIVE MORPHOLOGY OF THE CAPNIIDAE

ALLOCAPNIA Claassen

Figs. 18,26,35,38,38A,45,59.

The following discussion concerning Allocapnia is based on a study of the genotype species, Allocapnia granulata (Claassen) and on all but three of our other North American species in this genus.

Several characters indicate that Allocapnia is a very specialized and homogeneous group of Capniidae. All of its species have a very marked tendency toward the atrophy of thoracic sutures. Its wing bases, anal fan, and male genitalia are distinctive also.

Its closest affinities seem to be with Capnia which it resembles somewhat in sternal thoracic characters, in the slight bend at the base of R_1 of the fore wing, in the ninth sternite and in other genitalic features of the male. The supraanal process of one species of Capnia, C. spinulosa Claassen, is identical with that of Allocapnia in its basic plan (elongate, bipartite, lower prong grooved to form a sheath for the upper prong). As in Capnia there is a tendency toward brachypterism especially in the male sex.

Brachyptery is considerably more advanced in some species than in others and often varies markedly in extent within a given species.

HEAD: The head capsule and mouthparts of Allocapnia do not differ noticeably from those of Capnia.

THORAX: All three thoracic segments differ significantly from those of Capnia. The pronotum is similar to that of Capnia but the meso- and metanota (Fig. 38) are considerably specialized by the fusion of most of the tergal plates and by other variations. The prealar bridge (pra), prescutum (psc), and scutum (sct) usually merge with one another to form a single irregularly shaped plate. The anterior notal wing procell is somewhat protrusile and causes the displacement outward of the first axillary sclerite. The lateral edges of the scutum (sct) of both wing-bearing segments are deeply emarginate at a point opposite the third axillary sclerite. This modification is necessary to permit movement of the unusually large bundle of muscles extending from this sclerite to points of attachment within the thorax. The posterior notal wing processes and the postscutellum are poorly demarked from the scutum. The scutellum (scl) is well demarked, however.

The prothoracic pleuron of Allocapnia is like that of Capnia. The meso- and metathoracic pleura (Fig. 35), are different in several respects, however. The anterior basalare (ab) is united with the anterior margin of the posterior basalare (pb) and therefore is not capable of independent motion. Apparently as a compensatory mechanism, a small region of the apex of the posterior basalare is made moveable by the development of two lines of membranization extending inwardly from either side of the basalare. These two converging lines sometimes meet so as to demark completely a tiny apical sclerite. There is no suture demarking the anepisternum (aes) from the katepisternum (kes) in Allocapnia. The trochantin (tn) does not arise within the katepisternum (kes) as it does in Capnia but arises at its lower margin. The spiracular sclerites are considerably larger than those of Capnia. There is no postalar bridge in either the meso- or metathorax.

The prosternum is like that of Capnia (Fig. 26). The mesosternum is also similar to that of Capnia, but it differs in some respects. In Allocapnia the anterior angles of the basisternum do not bear digitate projections and are not joined to the apices of the arms of the spinasternum which lies anterior to it. The furcasternum is like that of *Capnia nigra* except that it is larger and the sternacostal suture demarking its anterior border is sometimes poorly developed. The postfurcasternal plates are never united to the spinasternum. In the metasternum no digitate projections occur at the anterior lateral angles of the basisternum as they do in *Capnia*. The furcal pits are widely separated and the sternacostal suture connecting them is sometimes so indistinct that a postfurcasternal sclerite is virtually undemarked.

WINGS: The *wing bases* of the meso- and metathorax are similar to each other but are considerably different from those of *Capnia*. The differences can be understood best by a comparison of Figures 37 and 38. In *Allocapnia* the tegula is unusually large, the humeral plate is merely a tiny remnant; the first axillary sclerite is displaced outward by the protruding anterior notal process; the third axillary sclerite is notable for the tremendous development of its muscle flange especially in the hind wing; a very tiny accessory sclerite occurs between the base of the anal cell and the posterior angle of the third axillary sclerite in the fore wing but not in the hind wing.

An interesting condition occurs in the males of one species of Allocapnia, A. vivipara (Claassen) (Fig. 38A) in which there are almost no wings at all. The wings are so reduced as to be much smaller even than the wing pads of a normal, full-grown naiad. The axillary sclerites, however, are of nearly normal size, although they have undergone some modifications. The first axillary sclerite of the fore wings is fused at its posterior end with the scutum; and the posterior end of the third axillary is fused to the posterior notal wing process (pnp). In the metathorax the fusion of these sclerites is greater, and in addition, the three axillary sclerites are partially fused together. The tegula (tg) is large, and is fused to the prealar bridge (pra) and to the scutum (sct) in both meso- and metathorax.

Wing venation of both fore and hind wings of Allocapnia is basically similar to that of other Capniidae (Fig. 18). It differs however, in a few very significant details. Even in fully winged specimens the region of the wing beyond the cord is relatively small, and the subcosta ends considerably basad of the cord. R_1 of the fore wing is bent upward slightly at its origin but not to the extent of the arcuation of this vein in *Capnia*; 1st A is straight. In the hind wing, media is usually unbranched and in some species is atrophied basally or absent entirely; Cu is unbranched.

The simple unbranched condition of Cu in the hind wing is due apparently to the complete atrophy of Cu_1 in this genus. Intermediate stages of brachyptery are exhibited in *Paracapnia* where the apical section of Cu_1 beyond m-cu is almost always absent. Okamoto's (1922) figure of the hind wing of *Takagripopteryx* shows a condition of Cu_1 like that of *Paracapnia*. The partial brachyptery of Cu_1 in these two genera is a strong indication that *Allocapnia* (a closely related genus) has acquired its unbranched cubitus by the complete atrophy of Cu_1.

The vannus extends coniserably beyond thecord and is nearly as large as the rest of the wing; its venation, however, is similar to that of *Capnia*.

LEGS: The legs are similar to those of Capnia.

ABDOMEN: Abdominal features of Allocapnia are similar to those of Capnia nigra except as they are involved in specific modifications.

The pregenital segments of the male sex vary in number among the species of Allocapnia from 5 to 7 depending on the number of segments exhibiting genitalic modifications. The tergal and sternal regions are entirely sclerotized and are separated by only a narrow strip of membranization which extends along the pleuron. All pregenital segments of the female sex are traversed mid-dorsally by a membranous stripe of about one-half the width of the abdomen.

The terminalia of the male sex of Allocapnia involve from four to six apical abdominal segments. The sixth, seventh, and eighth or the seventh and eighth or only the eighth tergite may bear sclerotized protuberances. The ninth and tenth tergites are always membranous. The supraanal process is a large, elongate, dorsally recurved, bipartite structure which lies over the membranous portions of the ninth and tenth tergites. The lower branch of this process is grooved and serves as a sheath for the upper portion through which the genital products are discharged.

The basal region of the ninth sternite is continuous laterally with the pleural region (Fig. 45). The ninth sternite bears no ventral appendage. The subgenital plate (sbp) merges with the basal portion of the segment: it is strongly demarked laterally from a relatively broad membranous region. Apically it bears a small nipple. The fusion plate of the subanal lobes in Allocapnia is two or three times as broad as that of Capnia at its base (Figs. 59,60). It tapers only slightly for most of its length; near the apex it narrows abruptly to a small, downwardly hooked, apical process. The retractoral plate (rp) is small and transverse in A. pygmaea and in several other species, while in A. recta it is sagittally elongate.

The genitalia and terminalia of the female sex are basically similar to those of Capnia. In some species the eighth tergite is membranized dorsally and forms the posterior end of the dorsal membranous stripe.

CAPNIA Pictet

Figs. 1-3,5-10,17,25,31-33,36,37,42-44,48,49,54-58.

Since several anatomical features of Capnia exhibit a considerable amount of variation among the numerous species of this genus, further notes concerning the entire genus are necessary to supplement the discussion of Capnia nigra contained in the preceding pages.

The following discussion of Capnia is based on a study of the genotype species, Capnia nigra, and upon another European and nearly all known American species of this genus. A list of the names of all of the species studied is included in a table at the end of this article.

It seems probable that Capnia is still an actively evolving genus since structures that offer excellent and constant generic differences in other genera exhibit wide ranges of variation in Capnia. There appear to be at least three intergrading subgroups within the genus.

HEAD: Neither the cranium nor the mouthparts appear to vary noticeably among the species of Capnia studied.

THORAX: In general, the only thoracic sclerites that exhibit variations within the genus Capnia are those of the mesosternum. As was noted under the discussion of Capnia nigra however, a strongly brachypterous condition of the male is associated with a merging of certain usually well demarked tergal and pleural regions of the pterothorax.

With but one exception known to me the wings of our North American species of Capnia are not atrophied sufficiently to be accompanied by the mergence of thoracic sclerites. The completely wingless male of Capnia fibula Claassen exhibits tergal and pleural modifications of the meso- and metathorax (Fig. 39) that are as remarkable as any that are to be found in the entire genus. The region normally occupied by the axillary sclerites and the tegula is completely and uniformly sclerotized. This region merges with the scutum (sct), the prealar bridge (pra), and the posterior notal wing process (pnp) but not with the anterior notal wing process (anp) which is distinctly visible. That this area contains, and is principally composed of, the three axillary sclerites and the tegula is indicated by the condition existing in Allocapnia vivipara (see discussion under Allocapnia and Fig. 38A) where a less complete fusion of these sclerites has taken place.

Other interesting modifications accompany the brachyptery of the male of Capnia fibula. Only a small section of the suture that demarks the scutellum from the scutum is present. In the pterothoracic pleura also the anterior and posterior basalares and the alifer fuse into a single, apparently nonfunctional process. The mesothoracic furcasternum varies from a roughly semicircular shape in Capnia nigra (Fig. 25) and a few other species of Capnia to the transverse shape shown in Figure 33. In a few species the postfurcasternal plates are united mesally with the spinasternum and also lie closely adjacent to, but are not united with, the furcasternum. This condition is often associated with a bipartite condition of the supraanal process of the male.

WINGS: The wings of all species of Capnia are identical with those of C. nigra (Fig. 17) except for minor variations in numbers of crossveins and in the course of the first anal vein. In one species, Capnia venosa (Banks), there are usually one or more crossveins beyond the cord between R_1

and R_2. In many species the bend at the base of the first anal vein of the fore wing is slight and no patch of sclerotization occurs at this bend. All stages of intergradation between this condition and that of Capnia nigra where both the angular bend of the first anal vein and the triangular patch of sclerotization are well developed occur among the species of Capnia.

ABDOMEN: Abdominal features of Capnia vary considerably since several segments may be involved in genitalic modifications especially in the male sex.

The Pregenital Segments of the male sex vary in number among the species of Capnia from three to eight, depending on the number of segments exhibiting genitalic modifications. As in Capnia nigra the tergal and sternal regions of all pregenital segments are entirely sclerotized. The first five or six tergites are sometimes divided into two laterotergal plates by a moderately broad band of membranization when none of these are modified into genital segments.

The pregenital segments of the female are identical to those of Capnia nigra (Fig. 49) except in a few species of Capnia in which the first one or two abdominal tergites are not membranized mesally.

Male Terminalia: The genitalia of the male sex of *Capnia* involve from three to eight distal abdominal tergites depending on the species concerned. In only one known species do the fourth, fifth, and sixth tergites bear chitinized protuberances. In numerous cases the seventh tergite alone bears protuberances of various shapes and sizes. In such cases the eighth and ninth tergites are usually membranous dorsally. In other species only the eighth tergite bears protuberances. Dorsal processes rarely occur on the ninth segment. Sometimes no tergal genital structures except the supra-anal process is always recurved over the abdomen and may assume various forms varying from a greatly attenuate type to a markedly bulbous type. It is usually unipartite but is sometimes bipartite and variously shaped.

On the sternum, only the ninth sternite and the subanal lobes are involved in genitalic modifications. The basal region of the ninth sternite is continuous laterally with the pleural region, as in *Capnia nigra* (Fig. 42). This basal region varies considerably in size among the species of *Capnia* studied (Figs. 43,44) but is usually at least twice as broad as that of *Capnia nigra*. Some species, particularly the more northern ones such as *C. nearctica* Banks, have a subgenital plate which is very similar to that of *Allocapnia* (Fig. 45). Perhaps the most remarkable difference between *C. nigra* and all other species of *Capnia* is the entire absence of a ventral lobe and the complete fusion of the subgenital plate to the basal region of the segment (Fig. 43,44) in all species except *C. nigra*. The median nipple at the apex of the subgenital plate shows some specific differences of shape.

The fusion plate of the subanal lobes of *Capnia* exhibits a considerable amount of variation. In many species it is much broader than in *Capnia nigra* (Fig. 56). In at least one species of *Capnia*, *C. fubula* (Fig. 57) the fusion plate is narrower than that of *C. nigra* and its retractoral plate is long and subulate.

Female Genitalia and Terminalia: The genitalia and terminalia of the female sex are similar to those of *Capnia nigra* (Figs. 48,49) except for specific variations in the eighth sternite which is rarely if ever protrusile or bipartite.

CAPNIONEURA Ris

Figs. 4,11,19,27,46.

I have had the pleasure of studying the genotype species, Capnioneura nemuroides, at the Museum of Comparative Zoology of Harvard University. The specimens studied were identified by Ris himself, and they agree perfectly with his description and figure of the male (1913) and of the female (1905).

The elongate wings, the long straight veins, the absence of costal crossveins, and the short cerci indicate a closer relationship with Nemocapnia and Eucapnopsis than with other genera of Capniidae. The above-mentioned characters and several features of the male genitalia seem to indicate affinities with the Leuctridae also.

Indeed, certain features exhibited by Capnioneura provoke a considerable amount of doubt as to the advisability of recognizing the Leuctridae and the Capniidae as families distinct from each other. In some features, particularly of the male genitalia, Capnioneura is definitely more similar to Paraleuctra and Megaleuctra (Leuctridae) than to any Capniid genera. However, if the Capniidae and Leuctridae are to be recognized as distinct families, the genus *Capnioneura* must be assigned to the Capniidae because of its numerous affinities with other genera of this family.

HEAD: In certain features of both the head capsule and the mouthparts *Capnioneura* differs very significantly from all other Capniidae. The frons is completely divided into two parts by a suture immediately in front of the median ocellus. As was suggested under the discussion of the frons of *Capnia nigra*, the anterior portion of the head capsule that is delimited by this suture may possibly constitute the entire true frons. The distance between the lateral ocelli is nearly five times the distance of either ocellus from the compound eye nearest to it. Postfrontal sutures are entirely lacking but the coronal suture is distinctly visible in the posterior region of the head.

One of the most interesting modifications of the cranium of *Capnioneura* concerns the anterior tentorial pits (Fig. 4). In all other genera of Capniidae they assume the form and position as described in detail for *Capnia nigra* on a previous page. In *Capnioneura* the anterior tentorial pits are not continuous with the anterior border of the antennal socket. Each anterior tentorial pit is visible externally as a curved suture which is laterally continuous with the hypostomal suture. It passes in front of the antennal socket and meets the antennal suture at a point near the ventral antennifer. The curved plate or region of the head capsule which is bounded by this suture and by the antennal suture merges with the frons.

The labium (Fig. 11) differs from that of Capnia in several important respects. The paraglossae (pgl) are large, and each is demarked at its base by a diagonal sclerotic rim or bar. Nearly the whole distal half of the labiostipites (lbi) is membranous. The lateral distal angles of the submentum (sm) bear sclerotized points that articulate with the mentum (mn).

THORAX: The thorax of Capnioneura (Fig. 27) differs from that of Capnia principally in sternal characters of the meso- and metathorax. Less significant differences also occur in the pronotum and in the meso- and metathoracic pleura.

A precosta is not demarked in the pronotum. In the meso- and metathoracic pleura the demarcation between the anepisternum and the katepisternum is very indistinct but is similar to that of *Capnia* in other respects. The demarcation between the pleuron and the sternum is distinct and the base of the torchantin does not encroach on the katepisternum.

The prothoracic sternum of *Capnioneura* differs from that of *Capnia* principally in the furcasternum which is more transverse in *Capnioneura* than in *Capnia*. The mesothoracic furcasternum is small, strongly transverse and split along the mid-ventral line by a distinct suture. The postfurcasternal plates of the female specimen studied are fused on three sides to the spinasternum, furcasternum, and furcasternal arms. In the male specimen which I studied the furcasternal plates are separated from the furcasternal arms by a narrow intervening membranous region. The furcal pits of the metathorax are about as far apart as are those of the mesothorax. The metathoracic furcasternum is narrow, transverse, and united with the first abdominal sternite.

WINGS: The wing bases and venation (Fig. 19) are similar to those of *Capnia* in most details but differ significantly in some. The subcosta is straight and runs into the costa at the cord. A crossvein extends between R_1 and the apex of Sc. There are no other costal crossveins either before or beyond the tip of the subcosta. R_1 of the fore wing is not bent at its origin. The first anal vein of the fore wing is straight. The anal fan of the hind wing extends beyond the cord but is not as broad as that of *Capnia* and is small in size relative to the size of the rest of the wing. The venation of the anal fan is considerably different from that of *Capnia* in possessing four anal veins two of which arise at separate points at the apex of the anal cell and the other two of which arise from separate points at the base of the anal cell. The first three are long and straight; the fourth is less than one-half the length of the third.

ABDOMEN: The abdomen of *Capnioneura* is very interesting because of its numerous unique features and its affinities with both the Capniidae and the Leuctridae.

The *Pregenital6Segments* of the male sex are eight in number. Both the tergites and the sternites of all segments except the first are completely sclerotized. The first abdominal tergite is mostly membranous.

The pregenital abdominal segments (7 in number) of the female are notable for the lack of sclerotization. The tergites of each of these segments is represented only by a pair of small, pleurally located plates. Each pregenital sternite bears a single median plate which covers only about half of its segment.

Male Terminalia: Several features of the male genitalia are particularly noteworthy (Fig. 46). The ninth tergite is unmodified. The tenth tergite is not divided into two rounded lobes as in other Capniidae but forms a continuous transverse sclerite. The supraanal process is a short, upwardly directed, posteriorly grooved structure strongly resembling that of *Megaleuctra* and *Paraleuctra*. The ninth sternite bears no ventral appendage. Its subgenital plate more strongly resembles that of *Paraleuctra* than that of any Capniid genus. It is produced under the subanal lobes, bears no nipple at its apex, and is not demarked laterally by a distinct suture although it is partially demarked from the rest of the ninth sternite by regions of membranization. The subanal lobes are remarkably different from those of other Capniid genera but are identifiable as being of the Capniid type by their conspicuous fusion plate.

The subanal lobes are of an extremely specialized type. Each consists of two separate, very narrow and elongate sections. The basal section is attached, as usual, at the lateral angles of the tenth tergite. It extends anteriorly for a short distance and then curves mesally to meet at a mid-ventral point with the base of the distal section of the subanal lobe and with the fusion plate. The distal sections of the subanal lobes lie parallel to each other along a sagittal line. In ventral view they appear nearly straight and are of uniform width for most of their length but taper to a pointed apex. In lateral view they appear to curve gently upward. The length of the fusion plate is about half the length of the median sagittal portions of the subanal lobes. From a bulbous region near its base a narrower projection extends posteriorly to an apex which appears blunt in ventral view. In lateral view, the bulbous portion lies dorsad of the lobes. Apically it is deflected at a right angle bend so as to project down between the subanal lobes. Each cercus is composed of a single segment. The first segment bears a flap that curves around the inner surface of the basal segment and partly covers its dorsal surface. What appears to represent the remainder of a second segment occurs as a very tiny button at the apex of the cercus.

Female Terminalia: The eighth and ninth tergites, like the pregenital tergites, are membranous. The eighth tergite bears a small median sclerotized plate similar to that found in some Leuctridae (Paraleuctra). The tenth tergite is completely sclerotized. The seventh and eighth sternites are mesally fused. The eighth sternite is slightly produced and slightly cleft. The ninth sternite is completely sclerotized. The subanal lobes are unmodified. The cerci are 1-segmented and bear a tiny nipple (probably segment two) apically. The eighth sternite of Capnioneura nemuroides Ris, as described above, is similar to that of Paraleuctra, but that of C. brachyptera, as described by Ris (1932), is neither produced nor cleft.

CAPNOPSIS Morton

Figs. 12,20.

I have been very fortunate in obtaining a specimen of this genus for study. Quite by accident, I discovered a single female in the Cornell Collection bearing the label Allocapnia pygmaea. Although it is not a well preserved specimen it is unquestionably a Capnopsis. As might well be suspected from a study of the excellent figures of the wings published by Rostock in 1892 it is a very interesting and specialized genus of Capniidae. In many ways it appears quite unique; but in several of its features it bears resemblances to various other genera of Capniidae.

HEAD: The head capsule is basically similar to that of other Capniidae but resembles Paracapnia in particular in the entire absence of a coronal and of postfrontal sutures. The antennae are short (15-segmented) and appear to be nearly glabrous. The labium (Fig. 12) differs from that of Capnia and other Capniid genera in several respects. When extended forward, the palpi project considerably beyond the glossae and paraglossae. The paraglossae, as well as the glossae, are demarked at their bases by transverse, sclerotic rims. The labiostipites is not distinctly divided into a distal membranous region and a sclerotized basal region. The mentum appears to merge at its lateral angles with the submentum.

THORAX: The proportionate sizes of the thoracic segments is considerably different from other Capniid genera except in the sternum. The pronotum is noticeably more transverse than in other genera, and the metathoracic pleura and terga are also markedly shorter.

The pronotum is not split by a mid-dorsal suture, and, as mentioned above, it is markedly transverse. The postscutellum of the mesothorax is relatively large but otherwise is practically unmodified. The metathoracic tergum is considerably shortened as a result of which its demarked regions are exceptionally transverse.

The thoracic pleuron, except for proportionate sizes in the metathorax is very similar to that of Capnia. There is no postcoxal bridge in the prothorax, however. The mesothoracic trochantin encroaches on the katepisternum slightly more than in Capnia; the trochantin of the metathorax does not encroach on the katepisternum of this segment at all.

The sternum is very similar to that of Capnia but differs in a few important details. In the prosternum a postcoxal bridge is absent and the apices of the arms of the spinasternum are not united with the lateral anterior angles of the mesothoracic basisternum although the latter sclerite and the basisternum of the metathorax bear digitate projections at their lateral anterior angles. The mesothoracic furcasternum is very small, triangular, and free from the furcasternal plates. The metathoracic furcasternum is united with the first abdominal sternite.

WINGS: The wings of Capnopsis (Fig. 29) are extremely interesting and remarkable for the amount of reduction which they exhibit. Most of the principal remigial longitudinal veins are present but the vanal region is extremely reduced.

Fore Wing: R_1 is straight; Rs leaves R at nearly a right angle; it is once forked at the cord. M is two branched. Cu is two or three branched. Rostock (1892) figures Cu as arising from the base of the anal cell. This is true in the hind wing of my specimen but not in the fore wing. 1st A is short and nearly straight. 2nd A is entirely absent. All of the primary crossveins except m-cu are present. No accessory crossveins are present in the costal area. The accessory crossvein between M and Cu_1 and the one which lies opposite it between Cu_1 and Cu_2 are both present.

Hind Wing: The remigium of the hind wing is short and unusually broad. Its venation is similar to that of the fore wing except that Rs is unbranched and an accessory costal crossvein occurs basad of the tip of the subcosta in one of the wings studied. The anal area is remarkably reduced. Nothing remains of its but the anal cell to which, peculiarly enough, the base of Cu is joined. That the vein I am considering to be Cu_2 in this case is correctly identified seems certain since the crossvein that occurs between Cu_1 and Cu_2 is one of the most constant features of the Capniidae.

ABDOMEN: The first abdominal tergite is mostly membranous. Tergites two through eight are traversed by a membranous band which is about one-third the width of the abdomen. The ninth and tenth tergites are completely sclerotized. All abdominal sternites appear to be completely sclerotized. The eighth sternite and the subanal lobes are practically unmodified. According to Morton the cerci are from seven to ten segmented.

EUCAPNOPSIS Okamoto

Figs. 13,21,28,47,63.

My work on this genus is based on specimens of our North American species, *E. brevicauda*, which fit Okamoto's original generic definition so well that there can be hardly any doubt as to the correctness of its generic assignment. I have not seen specimens of the genotype species.

As was previously noted, this genus is closely related to *Capnioneura* and *Nemocapnia* for several reasons.

HEAD: The cranium and all of the mouthparts except the labium of *Eucapnopsis* (Fig. 13) are similar to those of *Capnia*. The labial palpi of this genus are considerably longer than those of *Capnia* and thus when extended anteriorly they project considerably beyond the distal ends of the glossae and paraglossae. The labial palpi of *Eucapnopsis* are interesting also for a sexually dimorphic feature which they exhibit. In the female sex the second and third segments are about equal in length, the second being the thickest one. In the male the apical segment is much longer (often twice as long) and larger than the antepenultimate one, giving to the palpi a club-shaped appearance. In both sexes the third or apical segment is always at least twice as long as wide. The glossae and paraglossae are similar to those of Capnia but a considerably larger distal portion of the labiostipites is membranous than is the case in Capnia. The lateral angles of the submentum merge with the mentum but in the central region the two sclerites are separated by a broad V-shaped suture.

THORAX: The thoracic tergum of Eucapnopsis is virtually identical to that of Capnia but certain significant differences occur in the pleural and sternal regions.

In Eucapnopsis there is a distinct postalar bridge not only in the metathorax but in the mesothorax. In neither wing-bearing segment does the trochantin encroach on the katepisternum.

Thoracic sternal differences are few but very distinct (Fig. 28). In the prothorax the postcoxal bridge is not complete. It lies free as an indistinct curved sclrite not attached either to the epimeron or to the basisternum. The mesothoracic furcasternum is relatively small, narrowly transverse, and slightly curved. The postfurcasternal plates are not united with it or with the spinasternum.

WINGS: The wings of Eucapnopsis (Fig. 21) differ considerably from those of Capnia but are very similar to those of Capnioneura and especially of Nemocapnia. R_1 of the fore wing is not bowed at its base. The number of accessory costal crossveins basad of the tip of the subcosta varies from one to four but is usually two or three. A costal crossvein beyond the tip of the subcosta is nearly as frequently absent as present. The first and second anal veins of the fore wing are straight. The anal fan of the hind wing extends slightly beyond the cord and is relatively small in area. The first and second anal veins of the hind wing are long and straight; the third is an extremely short and inconspicuous vein.

ABDOMEN: The abdomen of Eucapnopsis is generally rounded above and flattened below.

The Pregenital Segments of the male sex are eight in number. The first five tergites are traversed mid-dorsally by a very narrow and indistinct membranous line. The remaining progenital tergites and all of the pregenital sternites are completely sclerotized.

The pregenital tergites of the female are traversed by a mid-dorsal membranous stripe which is about one-third the width of the abdomen. The sternites are completely sclerotized.

Male Terminalia: The tergal sclerites are unmodified except for the tenth tergite, which as in Capnia, is divided into two rounded portions. The supraanal process of the species studied is small and bulbous. The ninth sternite of the male differs considerably from that of other genera of Capniidae (Fig. 47). The subgenital plate is separated from a narrow basal rim except at its lateral angles by a membranous region. The basal rim bears a median appendage which is about one and one-half times as long as wide and is beset with numerous heavy setae. The subgenital plate is about as broad as long; a narrow marginal area is demarked on each side near the apex; a small nipple is borne at the tip. The subanal lobes are subtriangular in shape. Their fusion plate (Fig. 63) is about two and one-half times as long as broad, is broadest at the base, and protrudes beyond the subanal lobes in the form of a very strongly compressed, knife-like process. Anteriorly it terminates in a broadly rounded lobe and it does not possess a retractoral plate. The cerci are very short and are composed of four or five segments.

Female Terminalia: The posterior end of the dorsal membranous stripe is formed by membranization of the eighth tergite. The ninth and tenth tergites are completely sclerotized. The sternites seem to exhibit no generic characters. The cerci, like those of the male, are four to five segmented.

ISOCAPNIA Banks

Figs. 14,22,29,50,64.

The following discussion of the morphology of *Isocapnia* is based on a study of types and other specimens of *I. grandis* and *I. integra*.

It is difficult to determine the generic affinities of Isocapnia since it does not closely resemble any particular Capniid genus but seems to bear a few points of resemblance to the members of almost every genus of Capniidae. In the length of the labial palpus and its third segment it resembles Eucapnopsis. In the basal demarcation of its paraglossae it resembles Capnioneura. In the union of its presternites with the corresponding basisternum and in its pterothoracic epimera it resembles Nemocapnia. In its male genitalia and cerci it resembles Capnia. However, by its usual large size and its peculiar combination of body and wing characters it can be distinguished easily from all other Capniid genera.

HEAD: The cranium is similar to that of other genera of Capniidae except that a coronal suture is usually present and the parietal region is relatively large in Isocapnia, The labium (Fig. 14) resembles Eucapnopsis in that its palpi, when extended anteriorly, projects beyond the ends of the glossae and paraglossae and in that the third segment is about as long as the second. It differs from Eucapnopsis in that the mentum and submentum are completely separated from each other.

THORAX: The thoracic tergum is similar to that of Capnia except in the highly variable suturing and coloration of the postscutellum.

The pterothoracic pleura are similar to those of Capnia in all but the following details. In both segments a postalar bridge is present. The demarcation between pleuron and sternum is complete. The base of the trochantin does not encroach upon the katepisternum. The mesothoracic epimeron bears a transverse, darkly colored, and slightly depressed region. In the corresponding position of the metathoracic epimeron is a dark patch. These areas, as in Nemocapnia, apparently represent the beginnings of a division into anepimeron and katepimeron.

The sternum (Fig. 29) is very distinctive but somewhat resembles that of Nemocapnia from which it differs in the following respects. The prothoracic furcasternum is larger and not so narrow as that of Nemocapnia. Its sternacostal suture is incompletely demarked. In some specimens of I. grandis this furcasternum is produced posteriorly at two points to unite with the postfurcasternum. The mesothoracic presternum is larger than that of Nemocapnia. The furcasternum, spinasternum, and postfurcasternal plates of this segment are united to each other. The furcasternum is transverse; its posterior margin is sometimes only indistinctly demarked from the furcasternal plates. The furcasternal arms are united with the postfurcasternal plates in some specimens but not in others. The metathoracic presternum is large and partially divided secondarily into two transverse sections. The furcasternum of the metathorax is a large, transverse, rectangular sclerite which is only very poorly demarked from the first abdominal sternite with which it is united.

WINGS: The wings (Fig. 22) are large and not as slender as in Nemocapnia or Eucapnopsis. Costal crossveins basad of the tip of subcosta are one to five in number; those beyond the apex of the subcosta vary from none to three in number. R_1 and 1st A of the fore wing are straight at the base. The radial sector of the fore wing may fork in the cord or beyond it and may be two to four branched. The vannus of the hind wing is similar to that of Capnia in both size and venation.

ABDOMEN: The Pregenital Segments of the male are eight in number. Both the tergites and the sternites of all segments are completely sclerotized.

The pregenital sternites of the female are completely sclerotized. The first abdominal tergite has a large, transverse, membranous area. The remaining pregenital segments are traversed by a mid-dorsal membranous stripe which is of only one-fourth to one-fifth the width of the abdomen.

Male Terminalia: The ninth tergite is unmodified. The tenth tergite is divided into two rounded portions which unite posteromesally with the bulbous base of the supraanal process. The supraanal process is a recurved, usually elongate structure. The ninth sternite (Fig. 50) is completely divided into two separate parts. The relatively small, transverse, basal portion articulates laterally with the subgenital plate and the posterior angles of the decurved ninth tergite. Mesally this irregularly shaped plate bears a conspicuous ventral appendage which is very narrow at the base and of nearly one-third the width of the abdomen near its apex. The subgenital plate is well demarked on all sides from surrounding sclerotized regions. It's apex bears no nipple. The subanal lobes are roughly triangular in shape. Their fusion plate (Fig. 64) is extremely elongate. It extends for a considerable distance beyond the apices of the subanal lobes as two very slender, sharply pointed processes which are joined together for most of their length. To its base, which is bulbous, is attached an extremely long, subulate, retractoral plate. The cerci of all the specimens studied are broken. One specimen has a cercus of 13 segments and appears to have had probably 20 or more.

Female Terminalia: The seventh and eighth tergites are split by the posterior end of the dorsal membranous stripe. The ninth and tenth tergites are completely sclerotized. The median posterior region of the eighth sternite is sometimes recessed but is never produced. The ninth sternite is completely sclerotized. The subanal lobes are unmodified. The cerci are most probably many-segmented like those of the male.

NEMOCAPNIA Banks

Figs. 15,23,30,34,51,65.

This discussion and the supplementing figures of Nemocapnia are based on specimens of N. carolina Banks that were carefully checked against the three type specimens of this species at the Museum of Comparative Zoology.

Wing venational features and certain prosternal structures ally this species closely with Eucapnopsis. Certain sternal and pleural features ally it with Capnia. Features of the labium, male genitalia, cerci, and of the thoracic sternum and pleuron easily distinguish Nemocapnia from all other genera of Capniidae.

HEAD: The cranium and all of the mouthparts of Nemocapnia except the labium are similar to those of Capnia. The labium of Nemocapnia (Fig. 15) differs from that of Capnia in the following respects. The labiostipites is unusually large but its distal membranous region is rather small. The mentum is completely separated from the labiostipites and from the submentum. The lateral distal angles of the submentum bear sclerotized points which articulate with the mentum.

THORAX: The thoracic tergum of Nemocapnia is identical to that of Capnia.

The pleuron is also very similar to that of Capnia even as to the incompleteness of the suture demarking the pleuron from the sternum and the encroachment of the bases of the trochantins of both pterothoracic segments upon the katepisternum. It differs from Capnia in having a transverse groove on the epimeron (Fig. 34). This groove is very distinct in the mesothorax and less distinct in the metathorax. It appears to correspond to the line of division of the epimeron into anepimeron and katepimeron. This is particularly noteworthy since, to my knowledge, such a division occurs in no other stonefly except the closely related Isocapnia.

The thoracic sternum (Fig. 30) is considerably different from the sternum of all other Capniidae in its combination of diagnostic characters. The lateral cervical sclerites are fused posteriorly to the precoxal bridge of the prothorax. The presternum is not separated from the basisternum. The furcasternum is a small, narrow, transverse sclerite. The postfurcasternum is an oval sclerite with a tendency toward membranization mesally. The spinasternum is fused at its apices with the anterior lateral angles of the mesothoracic basisternum. The postcoxal bridges of the prothorax are incompletely formed, being composed merely of a small sclerite that lies behind each coxa.

The mesothoracic presternum is not separated from the basisternum. The lateral posterior angles of the basisternum are continuous with the katepisternum. The furcal pits are widely separated. The furcasternum is a well defined, narrowly transverse sclerite. The spinasternum is of an unusually narrow elongate shape and is united with the posterior mesal point of the furcasternum. The postfurcasternal plates are large and are united closely with the spinasternum and furcasternum.

The metathoracic presternum is large and triangular in shape. Its posterior mesal angle merges with the basisternum. The basisternum is considerably shorter than that of the mesothorax. It bears finger-like projections at its anterior lateral angles, and merges at its posterior lateral angles with the katepisternum. The furcal pits of this segment are even more widely separated than those of the mesothorax. The furcasternum is a narrowly transverse, arched sclerite which is not united with the first abdominal sternite.

WINGS: The venation (Fig. 23) of the hind wing is virtually identical to that of Eucapnopsis. The venation of the fore wing is more like that of Capnioneura than that of Eucapnopsis. It resembles Capnioneura in the straight subcosta which runs into the costa and in the absence of supplementary costal crossveins except for the occasional occurrence of one crossvein basad of the tip of the subcosta. It may be distinguished from either of the above-mentioned genera by the anal veins. The first anal vein is slightly bent just beyond cu-a as in Capnia. The second anal vein curves abruptly near its apex to enter the margin of the wing at an angle of nearly 90°.

ABDOMEN: The Pregenital Segments of the male sex are eight in number. Both the tergites and the sternites of all segments are completely sclerotized.

The pregenital segments of the female are similar to those of Eucapnopsis.

Male Terminalia; The ninth tergite of the sin- species known bearstwo slightly raised knobs. The supraanal process is an elongate, recurved prolongation arising from a large basal region which is closely united with the two halves of the tenth tergite. The ninth sternite bears no ventral appendage (Fig. 51). Its undifferentiated basal region is relatively large. A subgenital plate is demarked by a distinct suture but it is not separated laterally from the rest of the sternite by membranization. The subanal lobes are roughly triangular in shape. Their fusion plate (Fig. 65) is pyriform and apically is produced as a strongly depressed, slightly decurved process. It has no anterior extension or retractoral plate. The cerci are composed of six or seven segments.

Female Terminalia are similar to those of Eucapnopsis.

PARACAPNIA gen. nov.

Figs. 16,24,40,41,52,53,66.

This genus includes the species opis (Newman) and curvata n. sp. The erection of a new genus for these two species is necessary since they exhibit numerous features that will not permit of their being assigned to any other Capniid genus.

HEAD: The head capsule and mouthparts are similar to those of Capnia and other Capniidae but differ in at least two important respects. The coronal and postfrontal sutures are entirely lacking, as in Capnopsis; and the paraglossae of the labium (Fig. 16) are usually narrower and never broader than the glossae. A distal membranous region of the labiostipites is not distinctly demarked from the more sclerotized basal region. The palpi, when extended forward, reach about to the tips of the glossae and paraglossae.

THORAX: The thoracic tergum is very similar to that of Capnia. The pronotum differs in having no mid-dorsal pronotal suture and in that the lateral cervical sclerites are not united with the precoxal bridge.

The pterothoracic pleura differ from those of Capnia in some respects. In Paracapnia a demarcation between anepisternum and katepisternum is absent except for a slight indication of it anteriorly. The demarcation between the pleuron and the sternum of these two segments is very weak and incomplete. A postalar bridge is present in both segments.

The prosternum (Fig. 40) is nearly identical to that of Capnia but the pterothoracic sternum is quite distinct from that of any other Capniid genus. The trochantins of the pterothoracic segments encroach upon the katepisternum to an even greater extent than is the case in Capnia. The mesothoracic furcasternum, postfurcasternal plates, and spinasternum are closely united. The furcasternum is relatively large, has an arcuate anterior margin (sternacostal suture) and a straight or slightly arcuate and well defined posterior margin. Frequently a mid-ventral suture partially splits the furcasternum. A similar suture along the mid-ventral line also often extends a short distance into the basisternum from the sternacostal suture. The spinasternum is long and narrow. The postfurcasternal plates are large and united with the spinasternum and furcasternum. The metathoracic furcasternum is similar in shape to that of the mesothorax but is slightly larger. It is not united with the first abdominal sternite.

WINGS: The wing shape and venation of Paracapnia (Fig. 24) is similar to that of Capnia but differs in some very important details. R_1 of the fore wing is slightly curved cephalad at its base and then is bowed strongly caudad at a short distance beyond its point of origin. The first anal vein is straight. The second anal vein is very short and lies on the margin of the wing. The number of costal crossveins before the tip of the subcosta varies from none to three; beyond the subcosta there is only one costal crossvein or none at all in some cases. In the hind wing the first and second anal veins are long, straight, and about equal in length; the third anal vein has nearly disappeared. Cu_1 of the hind wing is practically always completely atrophied beyond m-cu. In a very few cases I have found conditions of partial atrophy of this apical portion of Cu_1.

ABDOMEN: The Pregenital Segments of the male abdomen are eight in number. Both the tergites and the sternites of all segments are completely sclerotized.

The pregenital sternites of the female are completely sclerotized. The first abdominal tergite is mostly membranous. The remaining pregenital segments are traversed by a mid-dorsal membranous stripe which is of one-third the width of the abdomen.

Male Terminalia: The ninth and tenth tergites are membranized mid-dorsally under the supraanal process. Two lateral portionsof the tenth tergites are demarked. The recurved supraanal process is attached to the posterior mesal border of the tenth tergite (Fig. 53); it has no bulbous base. The ninth sternite (Fig. 41) bears no ventral appendage. The subgenital plate merges basally with the anterior region of the ninth sternite. It is demarked laterally from the rest of the ninth sternite by a distinct suture and a narrow region of membranization. Apically it bears a tiny nipple. The subanal lobes are roughly triangular in shape. Their mesal edges diverge posteriorly and are bluntly pointed apically. The fusion plate (Fig. 66) which lies between them is also bluntly pointed and gives to this combination of structures a trilobed apical margin. The fusion plate is parallel-sided and remarkably large. Anteriorly it is connected by membrane to a pair of comma-shaped retractoral plates. The cerci are from 17 to 23 segmented and as long or longer than those of any other Capniid. Some of the subapical segments are as much as nine times as long as broad.

Female Terminalia: The membranous stripe that traverses the pregenital tergites also extends over segment eight and part of nine. The tenth tergite is completely sclerotized. The sternal plates, including the eighth sternite and the subanal lobes, are unmodified. The cerci are like those of the male.

PART III.

TAXONOMY OF THE CAPNIIDAE

Relative to other families of Plecoptera, the Capniidae are in good taxonomic order. It is a family composed of some seventy-five species distributed in twelve genera.

The genus Capnia was proposed by Pictet in 1841. Banks (1900) gave tribal rank to the genus on the basis of the absence of furcation of the radial sector beyond the cord in the fore wing. Klapalek (1905) raised the tribe to family rank on the basis of the following genitalic characters: (1) long cerci, (2) elongate supraanal process, (3) small subanal lobes. Banks (1906) discovered that the group may be characterized by the possession of only a single, unforked vein below the anal cell in the fore wing. Rostock, as early as 1892, was the first to note the sparsity of crossveins in the fore wing (in Capnia and Capnopsis). In their monograph of the Plecoptera (1925) Needham and Claassen used as family characters the many-segmented cerci, and the sparsity of crossveins in the fore wing; there is only one (or rarely two) mediocubital crossveins and one intercubital crossvein.

The abdominal characters (length of cerci, shape of supraanal process, size of subanal lobes) used by Klapalek to characterize the Capniidae are now known to be subject to too much variation to be of any significance. The number of cercal segments varies from many in several genera to only one in the genus Capnioneura. The supraanal process varies even in the single genus Capnia from a bulbous type to a much elongated type and from a unipartite to a bipartite condition; and the subanal lobes are not noticeably different in size from those of other families of stoneflies.

Two commonly used characters are very significant for distinguishing the Capniidae from other Families: (1) the single unforked vein below the anal cell in the fore wing, and (2) the absence of a series of mediocubital and intercubital crossveins in the fore wing. The use of the single, unforked vein below the anal cell (Cu_2) in the fore wing as a family character breaks down in only one instance; in Capnopsis Cu_2 is absent. The presence of a single accessory crossvein between M and Cu_1 is constant for all known genera of Capniidae. This vein is an even more constant feature in the Capniidae than the primary crossvein m-cu which is absent in Capnopsis. Almost invariably a single crossvein also occurs between Cu_1 and Cu_2 opposite the above-mentioned crossvein.

A condition occurs in the male genitalia which is constant for all genera of Capniidae and which occurs in no other family of stoneflies. It is particularly noteworthy since it has not been recognized previously as a family character. The subanal lobes of the males of all Capniidae are joined together mesally by an internally located plate which will be called the fusion plate. As early as 1896 Klapalek drew excellent figures of this structure in the male of Capnia nigra. Since that time it has gone unnoticed by practically all Plecopterologists.

The Capniidae are considerably more closely related to the Leuctridae than to any other family (see especially the discussion under Capnioneura). The parietal region of the head capsule is usually shorter in the Capniidae than in the Leuctridae, but intermediate conditions occur. The mouthparts of the two families are similar, but significant differences do occur, especially in the labium. The submentum of the Capniidae is hardly more than half as long as that of Leuctridae, and the bases of the palpi are separated by a much narrower labiostipital region in the Capniidae than in the Leuctridae. On the basis of features of the labial palpi, head capsule, distance between furcal pits, shape of coxae, and male genitalia the Leuctridae are much more closely related to the Capniidae than to the Nemouridae under which family they are placed by some workers.

GENERIC CHARACTERS

Wing characters have been used extensively for generic distinctions in the Capniidae. Since wing venation offers excellent generic differences in this family a fairly good classification has resulted from their use. However, in the minds of some workers, there has been considerable doubt as to the validity of certain genera of Capniidae and even as to the family placement of some of them. Such misgivings are due to a still incomplete knowledgeof the comparative morphology of numerous body structures. It is hoped that the findings of this present study will dispel some of this doubt.

I have been fortunate in having access to a large percentage of the known species and genera of Capniidae. Of most of them I have had genotypic material. Comparative studies of all external morphological details have been attempted in order to arrive at a basic understanding of generic relationships and characters. For the most part these studies confirm previous generic classifications, but in a few instances there are important contradictions.

I have found that the wings and thoracic sterna offer the best generic characters. The thoracic sterna exhibit a remarkable complexity of variations which are highly diagnostic. The diversity of shape and form that the mesothoracic furcasternum may assume in different genera of Capniidae is particularly noteworthy.* Several features of the thoracic pleural

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*Frison (1935) and Ueno (1938) have already used the mesosternum of Capniidae for generic classification to a limited extent.

and dorsal regions of the labium and particularly of the male genitalia also exhibit significant generic differences. The legs, head capsule, mouthparts other than the labium, and the female genitalia seem to offer no generic characters.

In the citation of references in the following taxonomic discussions no attempt is made at completeness, since such a procedure would be merely a repetition of parts of the recently published Claassen catalogue. Only those papers which bear on the immediate subject are cited. In continually referring to the Capniid literature during this study a few errors existing in the literature in the synonymy of certain genera and species of Capniidae have come to my attention. These are corrected at appropriate points in the following pages.

CAPNIA Pictet, 1841

1841. Capnia Pictet, Perlides, pp. 318-320.
1897. Arsapnia Banks, Trans. Amer. Ent. Soc. 24:22.
1900. Capnura Banks, Trans. Amer. Ent. Soc. 26: 241, 245. New Synonymy.

1906. *Arsapnia*, *Capnura*, Banks, Can. Ent. 38: 224.
1909. Enderlein, Zool. Anz. 34: 391 (*Capnia nigra* designated as genotype).
1924. Claassen, Can. Ent. 56: 43 (*Arsapnia* synonymized under *Capnia*).
1925. Needham & Claassen, Plecop. Amer. North of Mex., pp. 253-254.
1938. *Capnia* (*Arsapnia*), *Capnura*, Banks, Psyche 45: 73.

Containing nearly fifty described species *Capnia* is the largest genus in the Capniidae. Numerous species are known from the western United States and Canada, and a lesser number are distributed from the British Isles through Eurasia to Japan where four species occur. More than half of the known species are restricted to the North American continent.

The genus *Capnia* which was erected by Pictet in 1841 originally contained five species all except one of which have been removed to other genera of stoneflies. The single remaining species, *Capnia nigra* (Pictet) of Europe, was designated as genotype by Enderlein in 1909.

The species *Capnia opis* and another species described in this paper as new do not agree with *Capnia* in generic characters and therefore must be placed in a different genus (*Paracapnia* n.g.).

Capnia nigra, upon casual observation, appears to be generically different from other species of *Capnia* especially in male genitalic features. However, a study of a large percentage of the species in the genus shows, with but one exception, that features that have been accepted as generic or subgeneric characters within *Capnia* are merely extremes of highly variable structures. These extremes are bridged by numerous intermediate conditions except in the case of *Capnia nigra*. In this species the ninth sternite of the male bears a distinct median basal appendage of which there is no trace in any other species of *Capnia*. Although the presence or absence of a ventral lobe or appendage on the ninth sternite of the male has been used as a generic character in the Capniidae, it has not been so used in *Capnia*. This is fortunate because the presence of a ventral lobe in *Capnia nigra* is not supported by other constant characters that could be considered to be of generic or subgeneric value. Since *Capnia* is a large genus, apparently with active evolutionary tendencies, it is probable that conditions of the ninth sternite intermediate between that of *Capnia nigra* and those of other species of *Capnia* will be discovered as additional species are described. Even if such is not the case, one would hesitate to give generic or subgeneric rank to a single species on the basis of secondary sexual characters that are distinctive of only one sex and are unsupported by other characters of generic or subgeneric value.

Although Claassen (1924) had not studied the genotype *Capnia nigra*, his synonymy of *Arsapnia* under *Capnia* is correct. When the genus *Arsapnia* was proposed in 1897 and keyed in 1907 by Banks, the length of the discal cell in proportion to the length of the region beyond the cord was used to distinguish the genus. This criterion cannot be used however, because of the tremendous variations in the extent of brachypterism which affect particularly the distal region of the wing and thus greatly influence the proportionate sizes of the discal cell and region beyond the cord. In 1938 Banks removed *Arsapnia* from synonymy again and placed it as a subgenus of *Capnia* on the basis of the course of the first anal vein of the fore wing. In *Capnia nigra* he noted that the first anal vein is angularly bent near its base and has a conspicuous sclerotized patch within the angle. In Arsapnia decepta Banks found the first anal vein to be only gently curved and without a sclerotized patch. As has been discussed under the morphological treatment of Capnia in this article, numerous intermediate conditions between these two extremes occur within the genus Capnia. Wide variation may occur even within a single species. Therefore these characters are not available for generic or subgeneric distinctions.

The synonymy of the monotypic genus Capnura Banks under Capnia is also asserted here. A study of the type specimens of Capnura venosa Banks demonstrates no significant generic or subgeneric distinctions. The presence of crossveins beyond the cord (between R_1 and R_2) in the fore wing, the only perceivable differentiating character and the one which was used to define Capnura, is highly variable. The number of crossveins varies even between the two fore wings of a single specimen. In the type specimens the number of such crossveins was found to vary from one to four. The highly variable condition of the number of crossveins in the apical region of the wing has recently been recognized to be more the rule than the exception in Plecoptera and must be considered in this case also to be of no value as a generic character. It is very likely that further collecting will disclose specimens in which apical crossveins are entirely lacking. The tendency toward the development of such crossveins is useful however as a secondary specific character.

It now becomes apparent because of variational tendencies within the genus Capnia that only a few characters are distinctive of the genus. The sclerites of the mesosternum can consistently be differentiated from other genera of Capniidae. However, because of greater ease of use for taxonomic purposes, two wing characters that have been pointed out by Banks (1938) supply by far the best criteria for distinguishing the genus: (1) R_1 bent upward at its origin; (2) first anal vein bent abruptly caudad at its junction with cu-a and then curved outwardly again.

Capnia fibula Claassen.

This is a peculiar and interesting species which has been mentioned elsewhere in this paper because of its entire lack of wings and accompanying thoracic modifications. It deserves further mention here because of its remarkable features and the inadequacy of previous descriptions.

Capnia fibula was described by Claassen (1924) from a single male and a female from New Mexico. Both type specimens are bleached nearly to transparency in alcohol. The female is a fully winged and also otherwise normal *Capnia*. The type male and also a male specimen in the Museum of Comparative Zoology at Cambridge which is also of this species are entirely wingless. In the original description of the species Claassen entered the wing-spread as 12 mm?. In the Needham and Claassen monograph (1925) this figure was included without the question mark. Such a measurement is entirely misleading since the male has absolutely no wings at all (Fig. 39). Since the specimen of *Capnia fibula* at the Museum of Comparative Zoology is in far better condition than is the holotype at Cornell, I have included figures of the male genitalia here also (Fig. 57,58).

ALLOCAPNIA Claassen, 1924

1924. Capnella Claassen, Can. Ent. 56: 43-44 (Capnella granulata designated as genotype).

1928. Allocapnia Claassen, Ann. Ent. Soc. Amer. 21: 667 (new name for Capnella preoccupied by Gray in Coelenterata (1896).

1929. Capnella, Ueno, Kontyu 4: 147-150.

1935. Capnellula Strand, Folia zool. et hydrobiol. 7: 304 (new name for Capnella preoc. by Gray).

1935. Frison, Ill. Nat. Hist. Survey Bull. 20(4): 355-356, fig. 287.

1938. Ueno, Kontyu 12(5): 168-172, figs. 7-16.

Genotype: Allocapnia granulata (Claassen).

The genus Allocapnia was erected in 1924 to receive several North American species of Capniidae. Containing theirteen North American species and possibly some Japanese species, it is now the second largest genus in the family.

Our North American species of Allocapnia form a very homogeneous group. Although I have not studied any of Ueno's four Japanese species, I am strongly led to suspect by his publications (1929,1938) that perhaps all four of them must be placed in some other genus or genera, possibly new. If Ueno's (1938) sternal and wing venational drawings of his species sikokuensis are correct, this species certainly is not an Allocapnia but is very probably a Capnia. His species bulba almost certainly belongs in the genus Eucapnopsis (see discussion under Eucapnopsis). Ueno states that his species tikumani and nivalis are entirely wingless in both sexes. Therefore, these two species obviously cannot be generically placed on the basis of wing venation. However, Ueno's drawings of the thoracic sternum of tikumani and of the genitalia of both species are somewhat suggestive of Allocapnia and his assignment of these two species to this genus is possibly correct.

It has been suggested by Ueno that the genus Takagripopteryx Okamoto may be synonymous with Allocapnia (see discussion under Takagripopteryx). If this is eventually found to be true, the genus under discussion here, must take the older name Takagripopteryx.

As has been mentioned in the morphological discussion, Allocapnia is different from other Capniidae in numerous characters. Although almost any of these will serve to identify the genus, a complete listing of them is not desirable here. Any one of the following more easily observed characters will serve to identify Allocapnia: (1) Cu of hind wing unbranched; (2) vannus of hind wing greatly developed, extending beyond cord; (3) subcosta ending before cord; (4) prothoracic spinasternum not fused at its lateral angles with the mesothoracic basisternum; (5) anterior basalare immovably united with the posterior basalare.

APTEROPERLA Matsumura, 1931

1931. Apteroperla Matsumura, 6000 illus. ins. Japan,
p. 1426, fig. 15.
1938. Ueno, Kontyu 12: 168.

Genotype: Apteroperla yazawai Matsumura.

The original description is in Japanese and not understandable by me. Ueno (1938) has removed Apteroperla from Apteroperlidae, where it was originally placed, to the Capniidae. Matsumura's figure of the wingless female could easily be a Capniid and Ueno's judgment on this matter is probably correct. Ueno also suggests that Apteroperla may be synonymous with some other Capniid genus, probably Allocapnia.

CAPNIELLA Klapalek, 1920

1920. Capniella Klapalek, Acta Soc. Ent. Ceck. 17: 5.

1936. Neocapniella Claassen, Ann. Ent. Soc. Amer. 29: 622. New Synonymy.

Genotype: Capniella nodosa Klapalek.

This genus, proposed in 1920 as Capniella, was given the new name Neocapniella by Claassen in 1936. Since the basis of this synonymy is Capniella Sahlberg, a nomen nudum (see discussion under Capnopsis), we must return to the original Capniella of Klapalek.

The genus and its type species (C. nodosa from Siberia) are based on two female specimens which we hope are still in existence somewhere in Europe. Klapalek made no figures, but the description seems well done and points out several peculiarities which seem to justify the erection of a new genus. He noted in the fore wing the fusion of Rs and M at their bases, a character unknown in other Capniid genera. Other peculiarities are the presence of two crossveins in the medial field beyond m-cu and a longitudinally keeled subgenital plate. The verification of these as generic characters must await an eventual more complete anatomical study.

CAPNIONEURA Ris, 1905

1905. *Capnioneura* Ris, Mitt. Schweiz. Ent. Ges. 11: 93-95, figs. 1-2.

Genotype: *Capnioneura* *nemuroides* Ris.

The genus *Capnioneura* was proposed by Ris in 1905 for the reception of a single European species *nemuroides*. Two other species occurring in southern Europe are now known.

Ris found this genus to be distinct from all other Capniidae in that the cerci are reduced to a single segment. This condition of single-segmented cerci would usually be assumed to indicate closer affinity with the Nemouridae or the Leuctridae than with the Capniidae. However, Ris observed that the wing venation and genitalia are similar to those of *Capnia*. Thoracic and head characters also give overwhelming support to his conclusion as to its affinities.

For taxonomic purposes the genus can be characterized best by the following features: (1) a transverse suture extending across the frons immediately in front of the median ocellus; (2) postfrontal sutures absent; (3) both glossae and paraglossae demarked at their bases by sclerotic rims; (4) mesothoracic furcasternum transverse and divided by a suture along the mid-ventral line; (5) mesothoracic postfurcasternal plates united with the spinasternum, furcasternum, and sometimes with the furcasternal arms; (6) male subgenital plate produced posteriorly under the subanal lobes; (7) subanal lobes of male divided into two parts, extremely narrow; (8) cerci one-segmented; (9) wings with no costal crossveins; (10) vannus of hing wing with four longitudinal veins.

CAPNOPSIS Morton, 1896

1840. Perla, Zetterstedt, Insecta Lapponica, p. 1059.
1892. Capnodes Rostock, Berlin Et. Ztschr. 37: 3, figs. 1-10.
1895. Capniella Sahlberg, Meddel, Soc. pro Fauna et Flora Fennica 21: 107. Nomen Nudum.
1896. Capnopsis Morton, Trans. Ent. Soc. London 1896: 61. (Capnodes preoccupied by Guenee 1852 in Lepidoptera).
1902. Kempny, Verh. K.K. Zool.-bot. Ges. 52: 227-229, fig. 1.

1940. *Capniella*, Claassen, Cornell Univ. Mem. 232: 96-97.

Genotype: *Capnodes schilleri* Rostock (=*Capnopsis pygmaea* (Zett.)).

The genus *Capnopsis* contains only one species, but has nevertheless been the object of considerable synonymical confusion. In the recent Claassen catalogue this genus was placed under the name *Capniella* Sahlberg. *Capniella* is actually a *nomen nudem* since it was mentioned in a report as a bare name without definition or designation of any species to be included in it. Morton, in working over some Finnish material, informed Sahlberg of his progress. Sahlberg in reporting this information before a meeting of the Society pro Fauna et Flora Fennica mentioned the manuscript name *Capniella*. It may have been that Morton later discovered his manuscript genus *Capniella* to be the same as Rostock's genus *Capnodes* and thus never published it as a new genus.

The species *Capnopsis schilleri* (Rostock) was apparently justifiably synonymized under *C. pygmaea* (Zetterstedt) by Kempny in 1902, and Claassen's recognition of *C. schilleri* as a distinct species in his catalogue must be considered incorrect. His synonymy of *Capnia tenuis* under *Capnopsis pygmaea* is also obviously incorrect since *C. tenuis* is a true *Capnia* and therefore could not possibly be synonymous with a species of *Capnopsis*.

Capnopsis is a most remarkable genus of Capniidae. It may be characterized by the following combination of characters: (1) coronal and postfrontal sutures of head absent; (2) paraglossae delimited basally by a sclerotic rim; (3) labial palpi, when extended forward, project beyond the glossae and paraglossae; (4) metathorax relatively small; (5) 1st A of fore wing short and straight; 2nd A absent; (6) in hind wing, a vannus and vannal veins are absent; only the anal cell remains; (7) m-cu absent in both fore and hind wings.

EUCAPNOPSIS Okamoto, 1922

1922. *Eucapnopsis* Okamoto, Bull. Agri. Exp. Sta. Chosen 1(1): 8 (*E. stigmatica* n. sp. designated as genotype).

1924. *Capnia*, Claassen, Can. Ent. 56: 55-56 (*C. brevicauda* n. sp.).

1925. *Capnia*, Needham & Claassen, Plecop. Amer. North of Mex., p. 269.

1929. Capnia, Ueno, Mem. Coll. Sci., Kyoto Imp. Univ., Ser. B, 4: 141.

1934. Neave, Can. Ent. 66: 6-5.

1935. Frison, Ill. Nat. Hist. Survey Bull. 20(4): 352, 354.

1937. Frison, Ill. Nat. Hist. Survey Bull. 21(3): 86.

1942. Frison, Ill. Nat. Hist. Survey Bull. 22(2): 237, 238.

Genotype: Eucapnopsis stigmatica Okamoto.

The genus Eucapnopsis was proposed as a genus of Capniidae by Okamoto in 1922 for two Japanese species. A North American species, brevicauda, has also been placed in this genus.

Okamoto based the genus principally on the two following characters: (1) cerci composed of very few segments; (2) ninth sternite of male with a basal median lobe. Needham and Claassen and Ueno have subsequently failed to recognize Eucapnopsis as distinct from the genus Capnia. Frison, however, has recognized it as distinct and, until recently (1942) has even placed it in a different family (Leuctridae). A morphological study of Eucapnopsis leaves no doubt that it is a valid genus and that it belongs in the Capniidae and not in the Leuctridae. In returning

Eucapnopsis to the Capniidae Frison (1942 p. 238) used the number of cercal segments as the primary family character and found it necessary to key Eucapnopsis out at a point different from that of the remaining genera of Capniidae. It is obvious however, that in a family where the number of cercal segments varies from one to twenty-five or thirty, such a character can be of virtually no use as a family criterion. The primary family characters are to be found in the sparsity of supplementary corssveins in the fore wing, in the unbranched condition of the second anal vein of the fore wing, in features of the mouthparts particularly of the labium, and in the fusion plate of the subanal lobes of the male. All known genera of Capniidae conform exactly with this combination of characters with but one minor exception. The highly specialized genus Capnopsis has lost the second anal vein of the fore wing.

Ueno's species Allocapnia bulba must be placed in the genus Eucapnopsis, I believe. On the basis of wing venation and male genitalia it does not agree with the genus Allocapnia in which Ueno has placed it. However, the genitalia of bulba (Ueno 1929, fig. 25C) are so similar to those of our species

E. brevicauda as to appear almost conspecific with it. Its cerci are of the abbreviated *Eucapnopsis* type and the wings (Ueno 1929, fig. 25A) except for slight apical brachyptery are similar to those of our species of *Eucapnopsis*. Ueno does not mention the presence of a lobe on the ninth sternite of the male but he might easily have overlooked such a structure.

Eucapnopsis may be characterized by the following features: (1) R_1 of fore wing not bowed at base; (2) first anal vein of fore wing straight; (3) mesothoracic furcasternum small, narrowly transverse; (4) mesothoracic postfurcasternal plates entirely surrounded by membrane; (5) presternal sclerites of all three thoracic segments free from the basisternum; (6) cerci four to five segmented; (7) ninth sternite of male with a ventral appendage. Some of the above listed characters also occur in other genera but the entire combination never occurs in any other genus. For example, on wing venation it is not possible to separate *Nemocapnia* from *Eucapnopsis* with absolute certainty, but the thoracic sternal patterns of the two genera are entirely distinct as are also the ninth sternites of males of the two genera.

ISOCAPNIA Banks, 1938

1938. Isocapnia Banks, Psyche 45: 73-74 (Arsapnia grandis Banks designated as genotype).

1942. Frison, Pan-Pacific Ent. 18: 68-69.

Genotype: Arsapnia grandis Banks.

The genus Isocapnia was erected by Banks in 1938 with the North American species Arsapnia grandis Banks designated as genotype. Three or four North American species in this genus are known. Banks characterized the species of Isocapnia as follows: R at origin of Rs straight; anal area of hind wing reaching not more than three-fourths of the way to wing tip; one oblique crossvein beyond end of subcosta; setae very long; usually five or six costal crossveins; large species. To this Frison (1942) added: females with very narrow, median, longitudinal, membranous stripe extending across abdominal tergites one through eight; and males with a lobe at the base of the ninth abdominal sternite. Most of the above characters appear to be valid generic distinctions. In addition, several previously unrecognized, and in some cases more basic characters, might be mentioned. I considere the following features to be of significance as generic characters: (1) R_1 and 1st A of fore wing straight at base; (2) paraglossae partially demarked from the labiostipites; (3) postalar bridge present on both pterothoracic segments; (4) mesepimeron with a transverse dark band; (5) mesothoracic furcasternum poorly demarked from the furcasternal plates with which it is united; (6) metathoracic furcasternum united with and poorly demarked from the first abdominal sternite; (7) prothoracic presternum broadly fused with the basisternum; (8) basal region of ninth sternite separate from the subgenital plate and bearing a broadly rounded, median, ventral appendage; (9) female with a narrow, median, longitudinal, membranous stripe extending across abdominal tergites two through eight.

NAPCIA Navas, 1917

1917. Napcia Navas, R. Acad. Cien. y Artes Barcelona, Mem. 13^{26}: 8(398).

Genotype: Capnia libera Navas.

I know nothing of this genus since only a single paper concerning it has been written and this has not been accessible to me.

NEMOCAPNIA Banks, 1938

1938. Nemocapnia Banks, Psyche 45: 73,74.

1942. Frison, Ill. Nat. Hist. Survey Bull. 22(2): 262-264.

Genotype: Nemocapnia carolina Banks

The genus Nemocapnia was proposed by Banks (1938) for a single new North American species carolina. Banks defined the genus as follows: R straight at origin of Rs; anal area of hind wing reaching not more than three-fourths of the way to wing tip; no cross-vein beyond end of subcosta; cerci short (7-8 segments); slender species. Of the characters mentioned above only the number of cercal segments will distinguish the genus from closely related genera.

Nemocapnia can be recognized easily by the following combination of characters: (1) presterna of all thoracic segments merge with the basisternum of the segment concerned; (2) mesothoracic furcasternum narrowly transverse and not divided by a suture along the mid-ventral line; (3) meso-thoracic spinasternum extremely narrow; (4) mesothoracic postfurcasternal plates large and united to the spinasternum and furcasternum;

(5) meso- and metathoracic epimeron partially divided into anepimeron and katepimeron by a groove; (6) in fore wing, R_1 straight at base, 1st A slightly curved just beyond cu-a; (7) no costal crossvein beyond Sc; (8) cerci 6 to 7-segmented; (9) subgenital plate of male distinctly demarked but not separated along lateral margins from remainder of 9th sternite by membrane.

PARACAPNIA gen. nov.

Genotype: Paracapnia curvata n. sp.

This new genus contains two species of Eastern North American Capniidae. One of its species P. opis (Newman) has until this time been assigned to Capnia. Such an assignment is definitely incorrect, however, since numerous features of practically all parts of the body distinguish it from Capnia and from all other Capniidae. I have designated P. curvata as genotype since the identity of P. opis is not yet definitely settled.

For taxonomic purposes the genus can be characterized best by the following features: (1) postfrontal and coronal sutures absent; (2) paraglossae usually narrower than the glossae; (3) furcasternum of meso- and metathorax transverse and nearly rectangular; (4) mesothoracic postfurcasternal plates large and united with the furcasternum and the spinasternum; (5) R_1 of fore wing bent caudally shortly beyond its base; 1st A straight; (6) apical portion of Cu_1 of hind wing atrophied; (7) subgenital plate of male separated laterally from the rest of the 9th sternite by a narrow band of membrane; (8) fusion plate of subanal lobes of male parallel-sided or nearly so and unusually large; with a pair of retractoral plates.

Key to Species of *Paracapnia*

Supraanal process of male angulate at base, projecting forward and tapering toward apex, 0.40 to 0.50 mm. long - - - - - - - - - - - - - -*P. opis*

Supraanal process of male not angulate at base, thinner than that of the above species, projecting forward and tapering slightly toward apex, 0.55 to 0.60 mm. long - - - - - - - *P. curvata*

Paracapnia curvata n. sp. Fig. 53.

As has been pointed out previously (Hanson 1943) the identity of *Paracapnia opis* is not yet definitely established but must for the present be accepted as defined by Ricker (1938) who studied the genitalia of the type.

Several specimens of *Paracapnia* that I have in my collection differ consistently from numerous specimens of *P. opis* that I have studied from several widely separated localities. The females of the two species seem to be indistinguishable but the males can be distinguished easily by the shape and length of the supraanal process (see key).

Agrees in all general morphological details with the description of *Paracapnia* given in the preceding pages. Length to tip of wings, 6 to 7 mm. in male, 6 to 9 mm. in female; length of body, 4 to 5 mm. in male, 6 to 8 mm. in female; length of fore wing, 4 to 5 mm. in male, 6 to 7 mm. in female.

Male: Abdominal tergites without protuberances or other sclerotic modifications. Ninth tergite with a narrow median sagittal band of membrane. Supraanal process recurved, not angulate at base, projecting forward and tapering slightly toward the apex; 0.55 to 0.60 mm. long. The dorsal region of the supraanal process is largely membranous, especially toward the apex. This membranous portion may bulge upward so as to open genital tube within the supraanal process. When in this condition the supraanal process does not appear to taper toward the apex in lateral view but may even expand apically.

Female: Posterior margin of eighth abdominal sternite broadly rounded. A broad median region is indistinctly demarked; it bears a small, mesal light colored or membranous spot on the posterior margin. The ninth sternite is unmodified except for a transverse region of membranization along the posterior border of the segment.

Collection Data: Holotype male, allotype female -- Arietta, Hamilton Co., N.Y., alt. 1800 ft., April 5, 1937 (Alexander). Paratopotypes -- 1♂ 1♀. Paratypes -- Sacandaga River, Wells, N.Y., April 3, 1937 (Alexander) 2♂ 3♀. Cook Co., Minn., April 25, 1940 (Harden) 3♂: April 28, 1940 (Harden) 1♀.

TAKAGRIPOPTERYX Okamoto, 1922

1922. Takagripopteryx Okamoto, Bull. Agr. Exp. Sta. Gov.-Gen. Chosen 1: 3.

1929. Ueno, Mem. Coll. Sci., Kyoto Imp. Univ., Ser. B, 4: 150.

Genotype: *Takagripopteryx nigra* Okamoto.

The genus *Takagripopteryx* was proposed in 1922 by Okamoto for a single Japanese species *T. nigra* Okamoto which he placed in the family Leptoperlidae. Claassen (1924) has transferred the genus to the Capniidae where it obviously belongs. Ueno (1929) has suggested that the genus may be synonymous with *Allocapnia*. However, Okamoto figures the cubitus of the hind wing as being branched while the cubitus of the hind wing of all North American species of *Allocapnia* is unbranched. The atrophy of the apical portion of Cu_1 of the hind wing may also be a significant difference. In addition, Okamoto describes *Takagripopteryx* as having an unipartite supraanal process while all other known species of *Allocapnia* have a bipartite supraanal process. Therefore, I am inclined to believe that *Takagripopteryx* is a valid genus.

No specimens of this genus have been available for study.

List of the Species of Capniidae of the World

Allocapnia Claassen

curiosa Frison
*forbesi Frison
*granulata (Claassen)
*illinoensis Frison
*maria Hanson
*minima (Newport)
*mystica Frison
nivalis (Ueno)
*pygmaea (Burmeister)
*recta (Claassen)
*rickeri Frison
Sikokuensis Ueno
tikumani Ueno
virginiana Frison
*vivipara (Claassen)

Apteroperla Matsumura

yazawai Matsumura

Capnia Pictet

affinis Morton
apicalis Navas
*atra Morton
*bakeri (Banks)
*barberi Claassen
bituberculata Ueno
*californica Claassen
*coloradensis Claassen
*columbiana Claassen
*confusa Claassen
conica Klapalek
*decepta (Banks)
*distincta Frison
dusmeti Navas
elevata Frison
*elongata Claassen
*excavata Claassen
*fibula Claassen
*glabra Claassen

*Species marked with an asterisk have been studied during the preparation of this paper.

Capnia (cont.)

*gracilaria Claassen
*hantzchi Ricker
japonica Okamoto
jewetti Frison
*manitoba Claassen
maynari Navas
melia Frison
*nana Claassen
*nearctica Banks
*nigra (Pictet)
*oenone Neave
oklandi Morton
oregona Frison
praerupta Bengtsson
*projecta Frison
*promota Frison
sparre schneideri Esben-Petersen
*spinulosa Claassen
storkani Samal
takahashii Okamoto
*teresa Claassen
*tumida Claassen
umpqua Frison
variabilis Klapalek

Capnia (cont.)

*venosa (Banks)
vidua Klapalek
zaicevi Klapalek

Capniella Klapalek

nodosa Klapalek

Capnioneura Ris

brachyptera Despax
mitis Despax
*nemuroides Ris

Capnopsis Morton

*pygmaea (Zetterstedt)

Eucapnopsis Okamota

*brevicauda (Claassen)
bulba (Ueno)
stigmatica (Okamoto)
4-segmentata (Okamoto)

Isocapnia Banks

abbreviate Frison
*crinita (Needham & Claassen)
*grandis (Banks)
*integra Hanson

Napcia Navas

libera (Navas)

Nemocapnia Banks

*carolina Banks

Paracapnia Hanson

*curvata Hanson
*opis (Newman)

Takagripopteryx Okamoto

nigra Okamoto

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ABBREVIATIONS

1 - first axillary sclerite
2 - second axillary sclerite
3 - third axillary sclerite
A - anal vein
a - anal crossvein
ab - anterior basalare
aepm - anepimeron
aes - anepisternum
af - antennifer
al - alifer
anp - anterior notal wing process
ar - arolium
arc - arculus
as - antennal suture
asc - antennal sclerite
ata - anterior tentorial arm
bc - basicardo
bg - basigalea
bp - basipulvillus
bpl - basal plate
bs - basisternum
C - costa

ce - cercus
cep - cephalinger
cl - clypeus
co - condyle
ct - corporotentorium
Cu - cubitus
cu - cubital crossvein
cu-a - cubito-anal crossvein
cx - coxa
dc - disticardo
dg - distigalea
dta - dorsal tentorial arm
epi - epiproct
epm - epimeron
eps - episternum
es - epistomal suture
esr - epistomal ridge
etn - eutrochantin
eye - compound eye
fe - femur
fp - fusion plate
fr - frons
fs - furcasternum
fsp - furcal pit

fsa - furcasternal arm

ge - gena

gl - glossa

h - humeral crossvein

hm - hypostoma

hms - hypostomal suture

hp - humeral plate

kepm - katepimeron

kes - katepisternum

la - lacinia

lbi - labiostipites

lc - lateral cervical sclerite

lp - labial palpus

lr - labrum

M - media

m-cu - mediocubital crossvein

md - mandible

me - meron

mh - mouth

mn - mentum

mo - mola

mxp - maxillary palpus

oc - ocellus

occ - occipital condyle

or - orbicula
os - ocular suture
osc - ocular sclerite
p - pedicel
par - parietal sclerite
pb - posterior basalare
pc - precosta
pfs - postfrontal suture (one arm of epicranial suture)
pge - postgena
pgl - paraglossa
pls - pleural suture
pm - pleurostoma
pms - pleurostomal suture
pn - pronotum
pnp - posterior notalwing process
po - postcoxal bridge
poa - postalar bridge
poc - postocciput
pocs - postoccipital suture
pr - precoxal bridge
pra - prealar bridge
prs - presternum
ps - parastipes

psc - prescutum

pscl - postscutellum

pta - posterior tentorial arm

ptar - pretarsus

R - radius

r - radial crossvein

r-m - radiomedial crossvein

rp - retractoral plate

Rs - radial sector

s - scape

sa - supraanal process

sbl - subanal lobe

sbp - subgenital plate

Sc - subcosta

scl - scutellum

sct - scutum

si - stipes

sm - submentum

sp - spiracle

sps - spiracular sclerite

ss - spinasternum

sub - subalar sclerite

sus - suspensoria

st - abdominal sternite
stc - sternacostal suture
t - abdominal tergite
ta - tarsus
tg - tegula
ti - tibia
tm - tentorial macula
tn - trochantin
tr - trochanter
un - ungue
ut - unguitractor
va - ventral appendage or lobe
vc - ventral cervical sclerite

EXPLANATION OF PLATES

Plate I

Fig. 1. Head capsule of *Capnia nigra*, dorsal view.

2. Head capsule and tentorium of *Capnia nigra*, ventral view.

3. Head capsule of *Capnia nigra*, lateral view.

4. Head capsule of *Capnioneura*, lateral view.

5. Left maxilla of *Capnia nigra*, dorsal view.

6. Right maxilla of *Capnia nigra*, ventral view.

7. Hypopharynx of *Capnia nigra*, lateral view.

8. Labium of *Capnia nigra*.

9. Left mandible of *Capnia nigra*, ventral view.

10. Right mandible of *Capnia nigra*, dorsal view.

Plate II

Fig.11. *Capnioneura*, labium.

12. *Capnopsis*, labium.

13. *Eucapnopsis*, labium.

14. *Isocapnia*, labium.

15. *Nemocapnia*, labium.

16. *Paracapnia*, labium.

17. *Capnia nigra*, wings.

18. *Allocapnia*, wings.

Plate III

Fig. 19. Capnioneura, wings.

20. Capnopsis, wings.
21. Eucapnopsis, wings.
22. Isocapnia, wings.
23. Nemocapnia, wings.
24. Paracapnia, wings.

Plate IV

Fig. 25. Capnia nigra, thoracic sternum.

26. Allocapnia, thoracic sternum.
27. Capnioneura, thoracic sternum.
28. Eucapnopsis, thoracic sternum.
29. Isocapnia, thoracic sternum.
30. Nemocapnia, thoracic sternum.
31. Middle leg of Capnia.
32. Pretarsus of Capnia.
33. Furcasternum of Capnia sp.
34. Epimeron of Nemocapnia.
35. Mesopleuron of Allocapnia.

Plate V

Fig. 36. _Capnia nigra_ ♀, thoracic pleuron.

37. _Capnia nigra_ ♀, thoracic tergum.

38. _Allocapnia_, thoracic tergum.

38A _Allocapnia vivipara_, metatergum.

39. _Capnia fibula_ ♂, thoracic tergum.

40. _Paracapnia_, thoracic sternum.

41. _Paracapnia_, male genitalia, ventral view.

Plate VI

Fig. 42. _Capnia nigra_, male genitalia, ventral view.

43. _Capnia glabra_, ninth sternite of male.

44. _Capnia nana_, ninth sternite of male.

45. _Allocapnia_, male genitalia, ventral view.

46. _Capnioneura_, male genitalia, ventral view.

47. _Eucapnopsis_, male genitalia, ventral view.

48. _Capnia nigra_, abdomen of female, ventral view.

49. _Capnia nigra_, abdomen of female, dorsal view.

Plate VII

Fig. 50. *Isocapnia*, male genitalia, ventral view.

51. *Nemocapnia*, male genitalia, ventral view.

52. *Paracapnia opis*, supraanal process, lateral view.

53. *Paracapnia curvata*, male genitalia, lateral view.

54. *Capnia nigra*, male genitalia, lateral view.

55. *Capnia nigra*, fusion plate, internal view.

56. *Capnia nana*, fusion plate, internal view.

57. *Capnia fibula*, fusion plate, internal view.

58. *Capnia fibula*, male genitalia, lateral view.

59. *Allocapnia pygmaea*, fusion plate, internal view.

60. *Allocapnia recta*, fusion plate, internal view.

61. *Capnioneura*, fusion plate, internal view.

62. *Capnioneura*, fusion plate, lateral view.

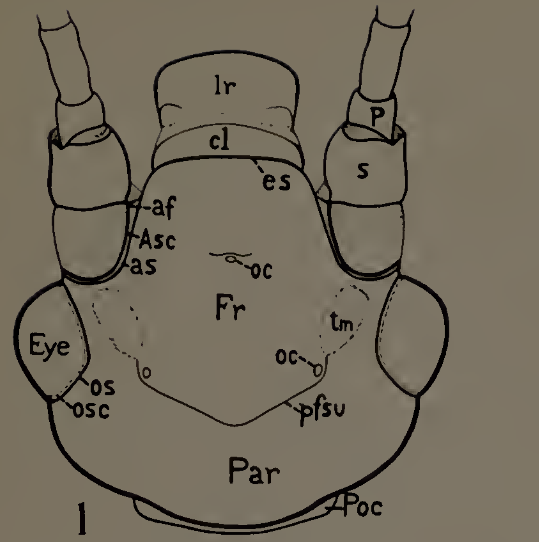
63. *Eucapnopsis*, fusion plate, internal view.

64. *Isocapnia*, fusion plate, internal view.

65. *Nemocapnia*, fusion plate, internal view.

66. *Paracapnia*, fusion plate, internal view.

Plate I



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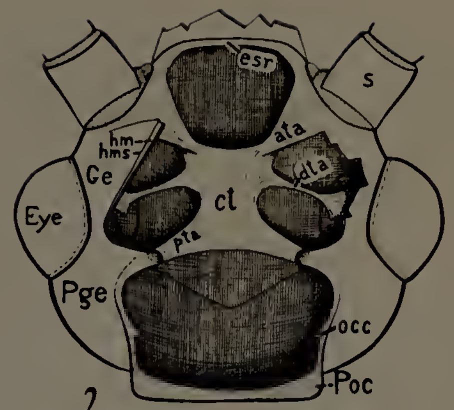

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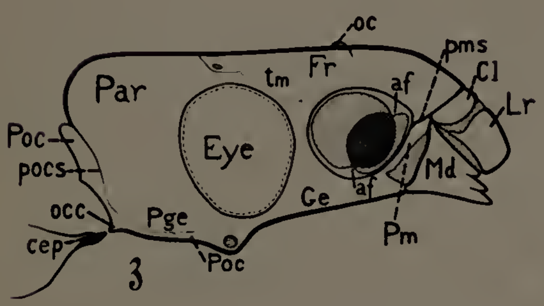

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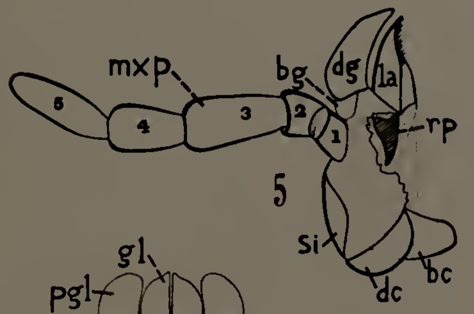
4 CAPNIONEURA



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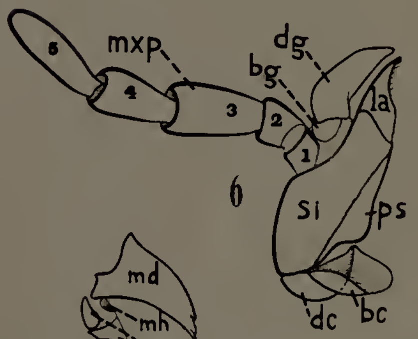

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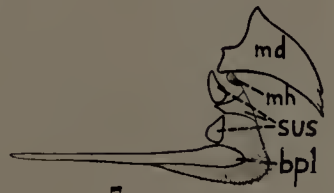

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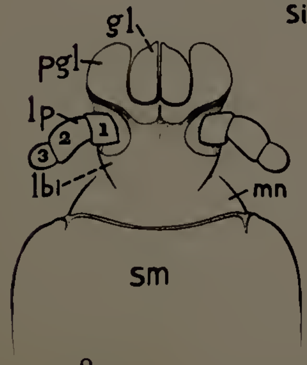

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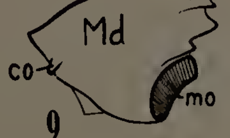

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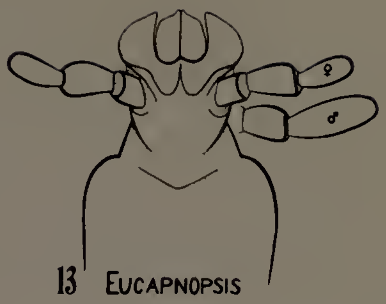
Plate II

11 CAPNIONEURA

12 CAPNOPSIS

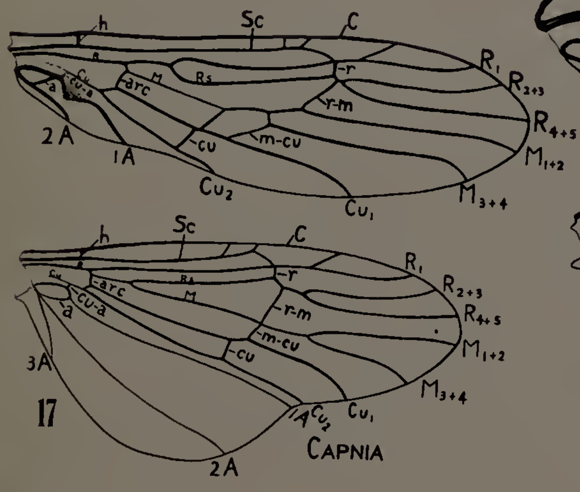


13 EUCAPNOPSIS

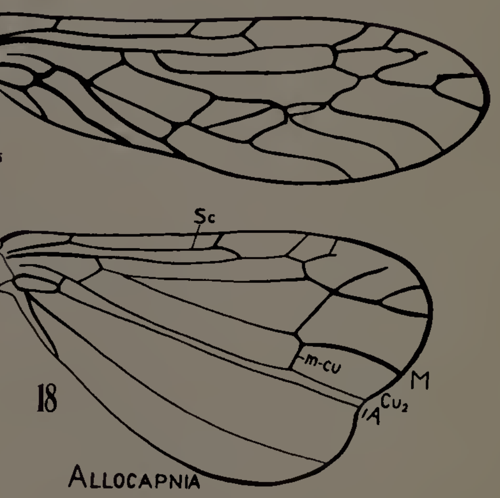
14 ISOCAPNIA

15 NEMOCAPNIA

16 PARACAPNIA

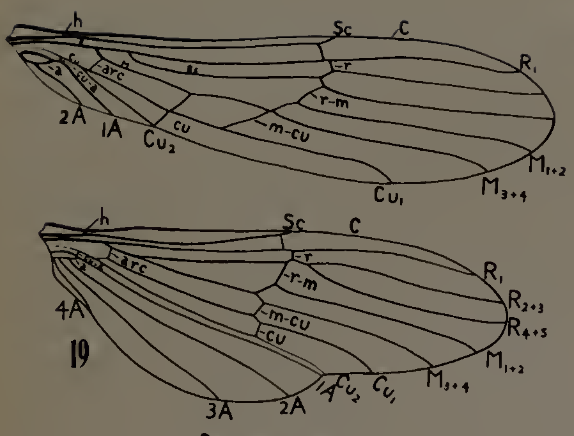


17 CAPNIA



18 ALLOCAPNIA

Plate III



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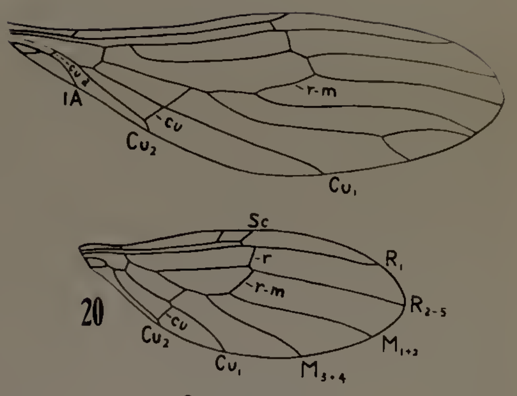
Capnioneura



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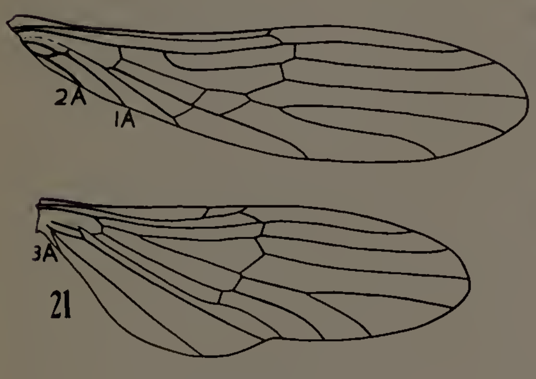
Capnopsis



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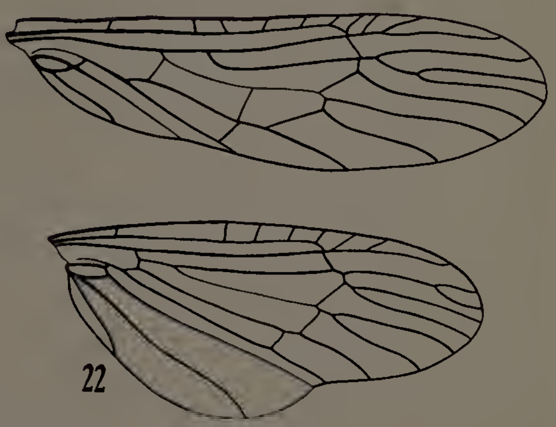
Eucapnopsis



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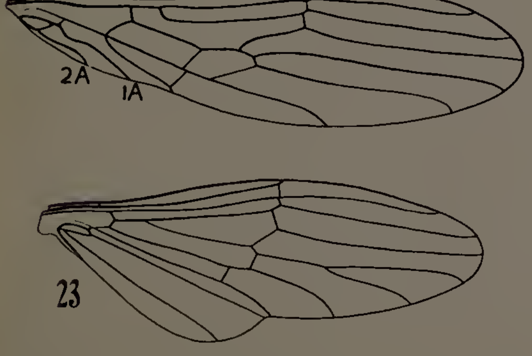
Isocapnia



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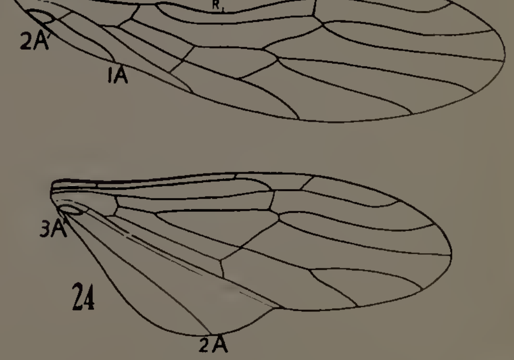
Nemocapnia



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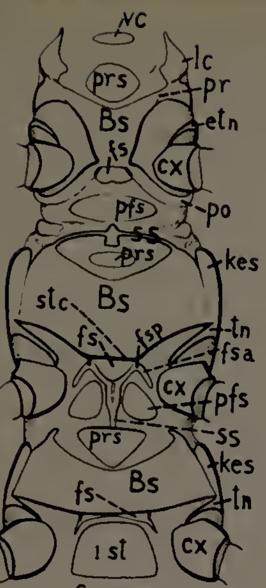
Paracapnia

Plate IV



25 CAPNIA

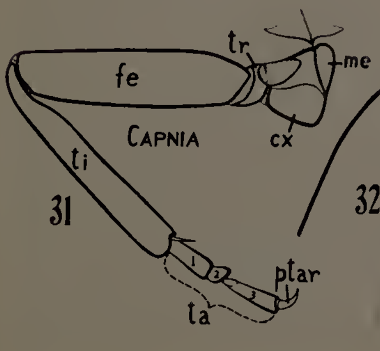
26 ALLOCAPNIA

27 CAPNIONEURA

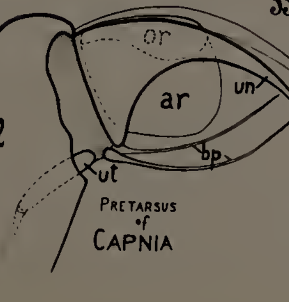
28 EUCAPNOPSIS

29 ISOCAPNIA

30 NEMOCAPNIA

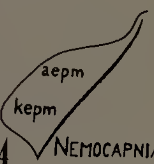


31 CAPNIA

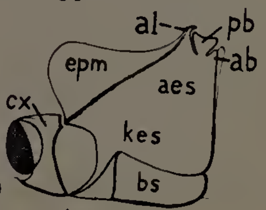


32 PRETARSUS of CAPNIA

33 CAPNIA

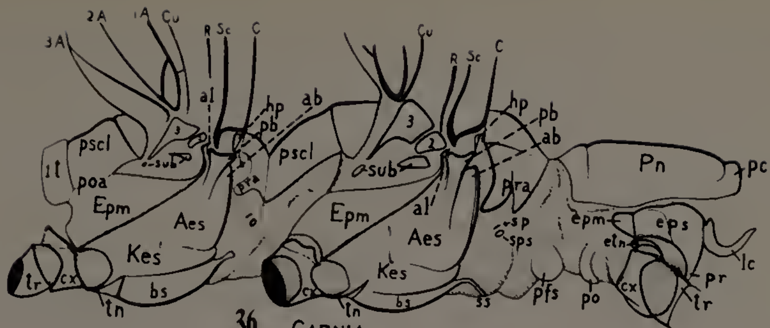


34 NEMOCAPNIA

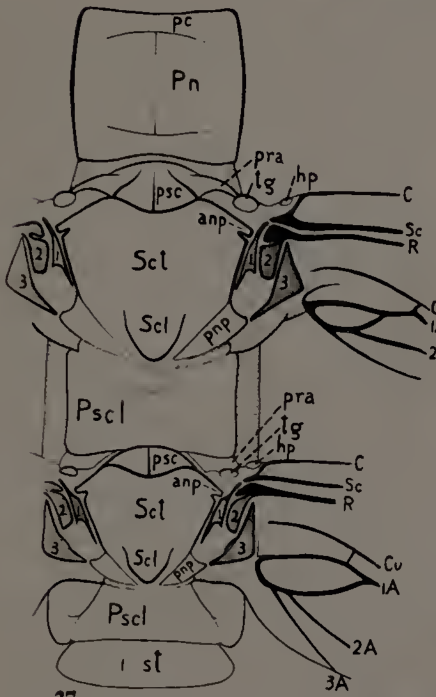


35 ALLOCAPNIA

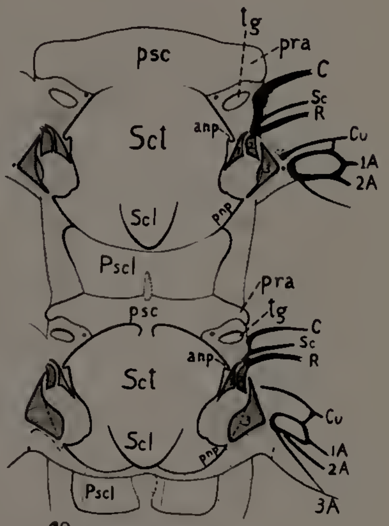
Plate V



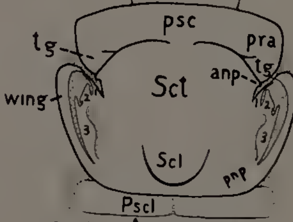
36 CAPNIA



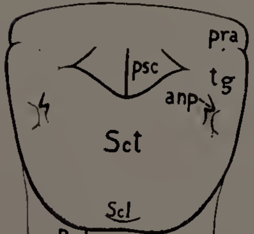
37 CAPNIA



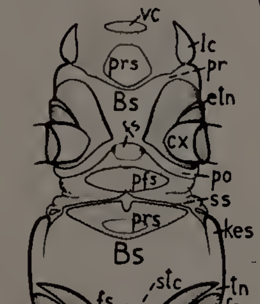
38 ALLOCAPNIA



38 A ALLOCAPNIA VIVIPARA



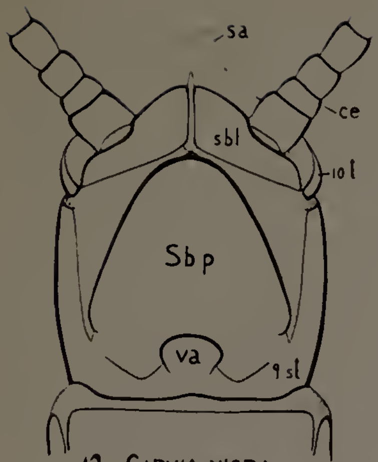
39 CAPNIA FIBULA



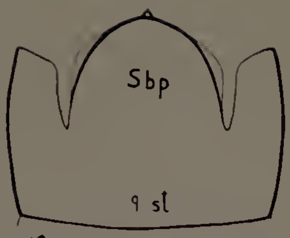
40 PARACAPNIA

41 PARACAPNIA

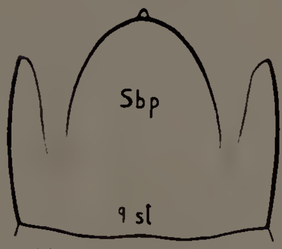
Plate VI



42 Capnia nigra

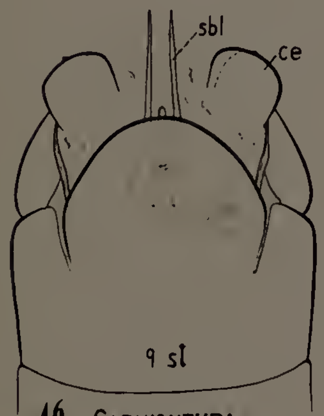


43 Capnia glabra

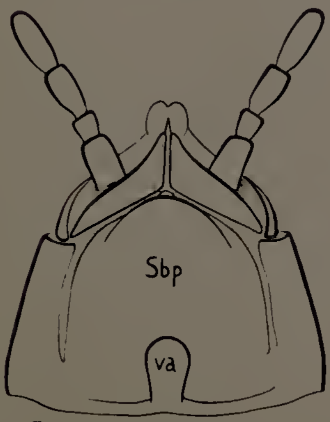


44 Capnia nana

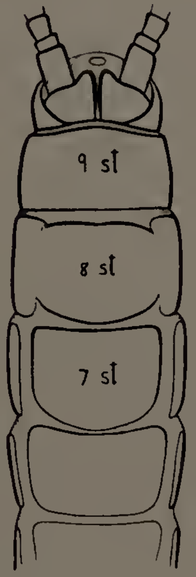
45 Allocapnia



46 Capnioneura



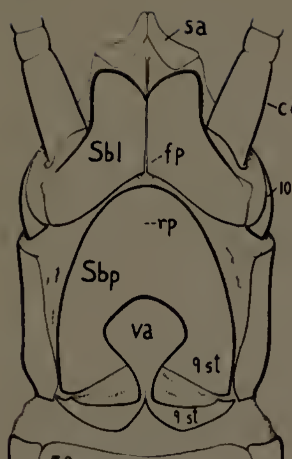
47 Eucapnopsis



48 Capnia

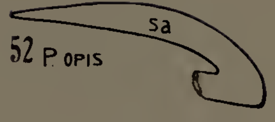
49 Capnia

Plate VII

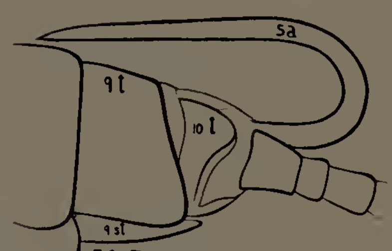


50 ISOCAPNIA

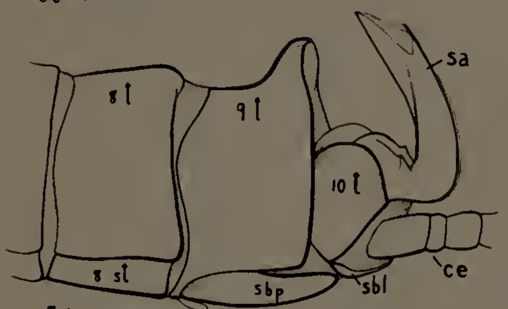
51 NEMOCAPNIA



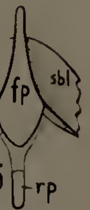
52 P. OPIS



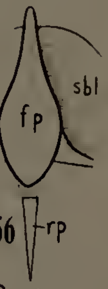
53 P. CURVATA



54 CAPNIA NIGRA

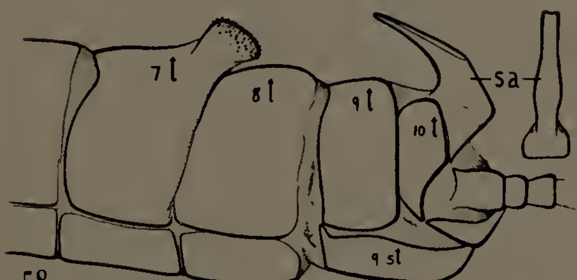


55 C. NIGRA

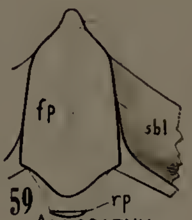


56 C. NANA

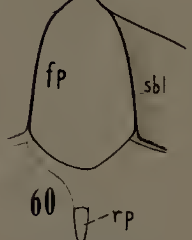
57 C. FIBULA



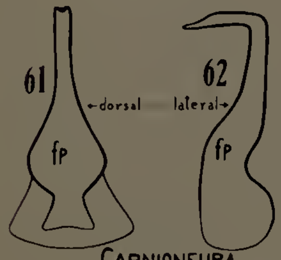
58 CAPNIA FIBULA



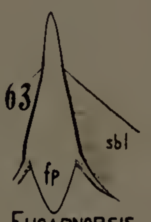
59 ALLOCAPNIA PYGMAEA



60 ALLOCAPNIA RECTA



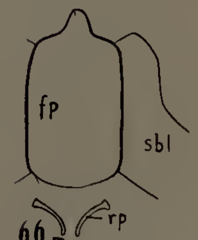
CAPNIONEURA



EUCAPNOPSIS

ISOCAPNIA

NEMOCAPNIA



66 PARACAPNIA

Approved by

Charles P. Alexander

R. E. Torrey

R. A. Van Meter

G. C. Crampton

Graduate Committee

Date March, 1943