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ANATOMY AND TAXONOMY OF THE MATURE NAIADS OF THE DRAGONFLY GENUS PLATHEMIS (FAMILY LIBELLULIDAE)

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ANATOMY AND TAXONOMY OF THE MATURE NAIADS OF THE DRAGONFLY GENUS PLATHEMIS (FAMILY LIBELLULIDAE) [1]

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The interrelationships of a particular group of insects cannot be fixed conclusively until a complete comparative study has been made. Studies of external morphology of various portions of widely differing species of insects have been published, but detailed comparative studies, particularly on the generic and specific levels, are few. Not until one compares all the structures of any given species with all the structures of other species do we begin to understand fully the phylogenetic and taxonomic relationships of the insects in question.

The difficulty with which the immature stages of dragonflies are identified to species is concurrent with a sparsity of morphological work done on these naiads. This paper is intended to provide a detailed morphological study of the last instar naiad of a common dragonfly, *Plathemis lydia* (Drury), that may serve as a foundation for comparative morphological studies, which in turn may reveal some taxonomic characters.

About 25 specimens were used in this study, and most of the features described were checked on the entire series.

Figures of nearly all the external anatomical features of *Plathemis lydia* are included to supplement the discussion. The presentation of the comparative morphology of the mature naiad of the only other known species of this genus, *Plathemis subornata* Hagen, is supplemented by figures wherever characters of taxonomic significance occur.

EXTERNAL ANATOMY OF PLATHEMIS LYDIA (DRURY)

The naiad of *Plathemis lydia* is rather large, robust, and elongate, approximately 23 to 24 mm. in length. Its surface is smooth and

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covered with long light-colored setae, most densely on the legs and lateral margins of the body.

The genus *Plathemis* differs from its closest relative, *Libellula,* in having the head widest behind the eyes and the front margin of the median lobe of the labium crenulate (Needham and Betten, 1901).

THE HEAD

The head of *Plathemis lydia* (figs. 1-13) is essentially hypognathous but is slightly inclined to the horizontal so that the ventral portions are anteriormost. The head is approximately 4.5 mm. in width, widest behind the compound eyes, and somewhat wider than long. The antennae are located on the median portion of the face, above a protuberant transverse ridge, which is provided with numerous long scurfy hairs. The enormous eyes cap the prominent anterolateral angles of the head, while the mandibles and maxillae are lateroventral in position. The prehensile spoon-shaped labium, characteristic of all libelluloid naiads, forms, in its natural position, a mask that completely covers the other mouthparts and the face up to the antennal bases.

SUTURES OF THE CRANIUM

The principal cranial sutures of *Plathemis lydia* are the epicranial, postoccipital, pleurostomal, epistomal, clypeolabral, clypeal, ocular, and antennal sutures.

The EPICRANIAL "SUTURE" or ecdysial sulcus is completely developed and consists of *postfrontal* arms and a *coronal* stem. This "suture" is more or less T-shaped, with the postfrontal arms diverging laterally, a condition that is typical of odonate naiads (Snodgrass, 1947). The *postfrontal sutures* (pfs) or arms of the cleavage line are well developed but extremely short and merge with the ocular sutures at the posteromedial corners of the compound eyes. The *coronal suture* (cos) or stem of the cleavage line is of greater extent and proceeds across the top of the head almost to the cervical margin where it meets the postoccipital suture.

The POSTOCCIPITAL SUTURE (pocs) is not strongly developed and lies very close to and somewhat parallel with the dorsal and lateral margins of the foramen magnum. The greatly elongated exterior edges of the posterior tentorial pits are partially coincident with this suture. There is no *occipital suture.*

The PLEUROSTOMAL SUTURES (pms) are only faintly indicated where they are identical with the exterior edges of the anterior tentorial pits formed by the fan-shaped ends of the anterior tentorial

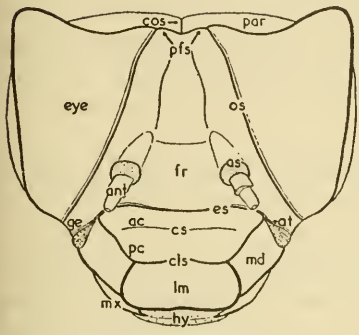

FIG. 1 HEAD, ANTERIOR

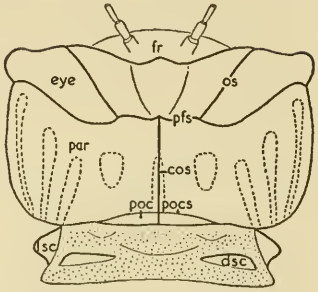

FIG. 2 HEAD and CERVIX, DORSAL

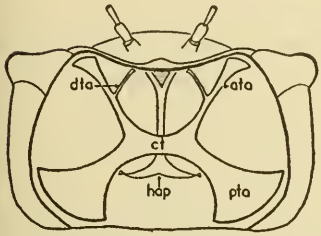

FIG. 3 TENTORIUM, DORSAL

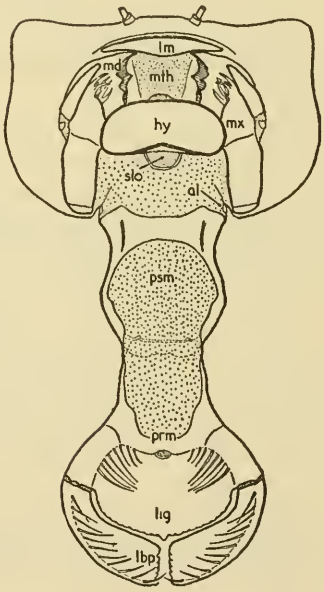

FIG. 6 HEAD, VENTRAL LABIUM, DORSAL

FIG. 4 LABRUM, ANTERIOR

FIG. 5 ANTENNA

Figs. 1-6.—Head capsule of *Plathemis lydia*.

arms. Their posterior counterparts, the *hypostomal sutures,* are absent.

The EPISTOMAL SUTURE (es) is a very distinct suture connecting the two anterior tentorial pits across the face. This suture is the external indication of a deep inflection, which results internally in a strong *epistomal ridge* that forms a brace between the anterior mandibular articulations.

The CLYPEOLABRAL SUTURE (cls) separates the anteclypeus and the labrum. It is well developed and is regarded by Ferris (1942, 1943) as a primary segmental line.

The CLYPEAL SUTURE (cs) is a very shallow fold on the dorsal surface of the clypeus. It divides the clypeus into a ventral anteclypeus (ac) and a dorsal postclypeus (pc). It is often only faintly indicated.

OCULAR SUTURES (os) are present and surround the compound eyes at their bases.

An ANTENNAL SUTURE (as) entirely surrounds each antennal socket.

AREAS OF THE HEAD CAPSULE

The demarked areas of the cranium are the clypeus, frons, antennal and ocular sclerites, parietals, postocciput, genae, subgenae, and postgenae.

The CLYPEUS (cl) is a broad sclerite typically supporting the anterior mandibular articulations at its basal angles and the labrum at its distal margin. A clypeal suture (cs) transversely divides the clypeus into a ventral *anteclypeus* (ac) and a dorsal *postclypeus* (pc). The clypeus bears numerous long inconspicuous setae which are closely appressed to its surface.

The FRONS (fr) is a large area bounded dorsally, laterally, and ventrally by the postfrontal, ocular, and epistomal sutures, respectively. The frons bears the antennal sockets. The facial portion is provided with long setae which lie between the antennal sockets and in two lines on either side of an imaginary vertical midline. There are no ocelli.

The ANTENNAL SCLERITES (asc) are extremely narrow rings surrounding the antennal sockets. They are too faintly indicated to be included in a drawing of this scale.

The OCULAR SCLERITES (osc) are very faintly indicated narrow rings, which surround the enormous compound eyes.

The PARIETALS (par) are a pair of sclerites that encompass most of the dorsal and dorsolateral areas of the cranium, extending laterally to the genae and posterolaterally to the postgenae. The two sclerites are separated on the dorsal surface of the cranium by the median coronal suture.

Seven elongate and two ovoid areas are present on the dorsal surface and are surrounded by numerous medium to long setae and short dark-colored spines. These glabrous spots are the areas of insertion of the gnathal muscles (Asahina, 1954).

The COMPOUND EYES (eye) are situated on the prominent anterolateral angles of the head. They are irregular in shape and, according to Lew (1933), composed of "three sets of distinctly distinguishable tissues." Lew also notes that only the pigmented tissue on the protuberant portion of the eye is functional.

The POSTOCCIPUT (poc) forms the posterior rim of the cranium. It is a narrow U-shaped sclerite, with its ends terminating at the posterior tentorial pits.

Of the SUBGENAE, only the *pleurostomae* (pm) are present. Each pleurostoma is an extremely small, elongate sclerite arising at the base of the mandible and extending to the ventral exterior edge of the anterior tentorial pit.

The GENAE (ge) are a pair of undifferentiated sclerites between the compound eyes and the antennal bases.

The POSTGENAE (pge) are a pair of undifferentiated areas posterolateral to the compound eyes.

THE TENTORIUM

The tentorium consists of a corporotentorium in the center of the head and three pairs of arms supporting it from different parts of the cranium. The anterior and posterior tentorial arms arise as invaginations of the cranial wall, while the small dorsal tentorial arms are outgrowths of the anterior tentorial arms.

The ANTERIOR TENTORIAL ARMS (ata) arise from slits (at) between the compound eyes and the bases of the mandibles. From these points of attachment the anterior arms converge posteriorly to fuse with the corporotentorium in the center of the head.

The POSTERIOR TENTORIAL ARMS (pta) arise from the posterior tentorial pits which are partially coincident with the anterior portions of the postoccipital suture. They are much stouter than the anterior arms.

The DORSAL TENTORIAL ARMS (dta) are shorter and narrower than those described above. Each dorsal arm arises from the mesal margin of the anterior tentorial arm midway between the anterior tentorial pit and the region of fusion of the anterior arm with the corporotentorium. The dorsal tentorial arms are weakly attached to the cranial wall and are easily dislodged.

The CORPOROTENTORIUM (ct) is located in the center of the head and is transverse in shape.

HEAD APPENDAGES

The movable parts of the head are the antennae, labrum, mandibles, maxillae, hypopharynx, and labium.

The ANTENNAE (ant) are setiform and about equal in length to the length of the head. Each antenna is composed of seven segments. The basal segment or *scape* (s) is short and thick and located in the medioventral portion of a circular membrane that is bounded by the antennal sclerite. The second segment or *pedicel* (p) is longer than and about two-thirds the diameter of the scape. It narrows abruptly distally to meet the *flagellum* (f), which is about one-half the diameter of the pedicel. The first, third, fourth, and fifth flagellar segments are subequal in length and each is approximately one and one-half times the length of the second segment. The terminal or fifth flagellar segment tapers apically to a fine point. Each segment of the antenna bears several long light-colored setae.

The LABRUM (lm) or upper lip is movable and, though not a true appendage, complements the other mouthparts. It is a transverse, reniform sclerite suspended from the clypeus by a narrow strip of membrane. The dorsal and ventral margins are parallel, the dorsal margin being produced while the ventral margin is emarginate. The anterolateral *tormae* extend into the membranous region at the base of the labrum but do not articulate with the clypeus. With the exception of a small bare subtriangular dorsomedial area, the anterior surface bears numerous short spiniform setae. In addition, many long setae are present on the distal margin.

The MANDIBLES (md) are well developed and lie horizontally in the space between the labrum and the hypopharynx. Each mandible has its mesal surface differentiated into a distal toothed *incisor area* (in) and a proximal *molar surface* (mo). The right mandible bears three sharp apical teeth on the incisor lobe, apparently for tearing the food, and three heavily sclerotized, blunt teeth on the molar surface. The left mandible is identical in size to the right mandible but differs slightly in dentition. The former has the ventral incisor tooth apically bicuspidate and the proximal molar tooth lacking.

The base of the mandible is triangular in outline. Each mandible articulates dorsally on the base of the clypeus and ventrally, by means of a conspicuous *condyle* (co), on the lower margin of the cranium. A strong *adductor tendon* (adt) is attached to the inner angle of the

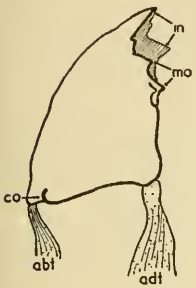

FIG. 7 RIGHT MANDIBLE, VENTRAL

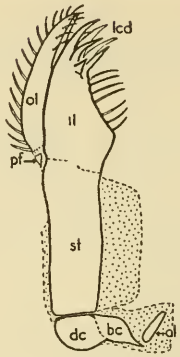

FIG. 8 RIGHT MAXILLA, VENTRAL

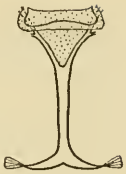

FIG. 9. HYPOPHARYNGEAL APODEME, VENTRAL

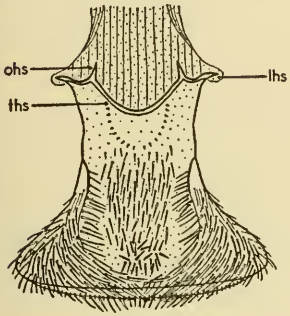

FIG. 10 HYPOPHARYNX, ANTERIOR

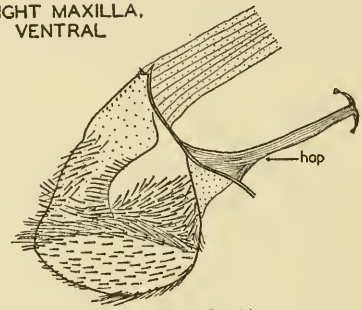

FIG. 11 HYPOPHARYNX, LATERAL

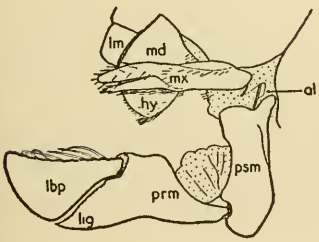

FIG. 12 GNATHAL APPENDAGES, LATERAL

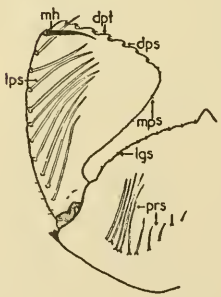

FIG. 13 RIGHT LABIAL PALPUS and LIGULA, DORSAL

FIGS. 7-13.—Gnathal appendages of *Plathemis lydia.*

base of each mandible. In addition, a weaker *abductor tendon* (abt) is attached to the lateral margin of the base, close to the ventral condyle. The muscles inserted on these tendons have their origins on the cranium.

The MAXILLAE (mx) are composed of two distinct portions; a basal part consisting of cardo and stipes, and an apical portion divided into two freely movable processes, here called the inner lobe and the outer lobe. The maxillae assume a position beneath the mandibles and lateral to the hypopharynx and are suspended from the head by a single point of articulation.

The *cardo* is divided by an arcuate suture into two sclerites, the *basicardo* (bc) and the *disticardo* (dc). The dividing suture almost encloses the more proximal and convex disticardo close to the margin of the stipes. In the retracted position the cardo is folded dorsally above the stipes, where it articulates on the anterior margin of the posterior tentorial pit.

The *stipes* (st) is the largest sclerite of the maxilla. The parastipital region is undemarked from the remainder of the stipes.

The *inner lobe* (il) has been generally regarded as representing the fused *lacinia* and *galea* of more typical mandibulate insects (Tillyard, 1917; Chao, 1953; Asahina, 1954), but Snodgrass (1954) has theorized that the galea has been lost and that the inner lobe represents only the lacinia. In *Plathemis lydia* this lobe typically bears, on its mesal margin, a subapical fringe of long setae and several long, sharp apical teeth, called *laciniadentes* (lcd) by Crampton (1923). In protraction of the maxillae the inner lobes are thrust forward beyond the mandibles to grasp the prey and pass it from the labium to the mandibles.

The slender *outer lobe* (ol), arising at the distolateral angle of the stipes, has been interpreted as the galea by Crampton (1923), but numerous other workers regard it as the *palpus* of the maxilla. In the adult dragonfly the outer lobe is provided with two muscles, as shown by Snodgrass (1954). This, according to Snodgrass, identifies it as the maxillary palpus; a galea has but one muscle. The outer margin of this lobe bears many well-developed inwardly curving setae.

A small sclerite, the *palpifer* (pf), is the actual area upon which the outer lobe takes its origin.

The HYPOPHARYNX (hy) of *Plathemis lydia* is a large cushionlike lobe that projects downward between the anterior portions of the maxillae and is separated from the base of the labium by a wide membranous area between the maxillary stipites. It apparently consists only of the lingua; superlinguae are not present. The adoral

surface is mostly unsclerotized. It bears a curious group of eighteen short spines arranged in a semicircle just ventrad of the transverse bar of the hypopharyngeal suspensorium as well as numerous other setae and spinulae scattered over the surface. The lateral, distal, and aboral surfaces are sclerotized. The former two bear many long, curved setae and spines, while the latter is glabrous.

The *hypopharyngeal apodeme* (hap) is a characteristic feature of the dragonfly naiad. Its shaft extends posteriorly through the head below the tentorium and the crossbar is embedded in the posterior edge of the base of the postmentum of the labium where it is held in place by "small apical brushes of fine fibers" (Snodgrass, 1954).

The *suspensorium of the hypopharynx* consists of a transverse bow-shaped bar (ths) on the dorsal margin of the base of the hypopharynx and two pairs of arms, oral (ohs) and lateral (lhs), which are continuous with the former.

The nymphal LABIUM consists of two major parts hinged on each other by an elbowlike joint. Numerous inconsistencies in the terminology of these parts are present in the literature. The present writer has followed the labial nomenclature of Corbet (1953) and Snodgrass (1954) in calling the proximal part the *postmentum* and the distal portions the *prementum* and its distal lobes the *labial palpi* and the *ligula*. In the retracted position the labium is folded so that the aboral surface of the postmentum is pressed against the ventral surface of the head and thorax, and the distal adoral surface, formed by the prementum, the palpi, and the ligula, forms a deep spoonlike mask that covers the face and other mouthparts up to the antennal bases. In protraction, the prementum is thrust out beyond the head by a forward swing of the postmentum. At the same time the distolateral lobes are thrown wide apart with their movable hooks erect (Amans, 1881—from Snodgrass, 1954).

The *labial palpi* (lbp) are curved lamellar structures forming part of the spoonlike mask. In broadest perspective, as in figure 13, each palpus appears more or less triangular in outline because of its greatly expanded distal portion. Each palpus possesses a prominent *movable hook* (mh) on its distolateral angle and 10 long, slender *lateral palpal setae* (lps) lying nearly parallel to its outer margin. In addition, the distal margin of the palpus bears seven or eight teeth (dpt), which are mesally directed and about as broad as long. Each tooth is provided with one to three short, spiniform setae (dps). The mesal margin of each palpus also bears several minute setae (mps).

The *ligula* (lig) lies between the bases of the palpi and is fused with the prementum. The median portion of its distal margin is an-

teriorly produced, forming a small triangular lobe. The remainder of the distal margin is evenly crenulate and possesses 10 or 11 short, spiniform setae (lgs) on each side of the central lobe.

The *prementum* (prm) bears, on each side, eight long, slender setae (prs), of which the five outermost ones are distinctly the longer. In addition, a pair of small secondary setae is present on each side just mesad of the premental setae with which they are often included by many authors.

Of the numerous setae mentioned above, the *lateral palpal setae* (lps) and the *premental setae* (prs) are of the greatest importance in the current taxonomy of immature Odonata.

The *postmentum* (psm) is a hollow stalk that supports the prementum, and the entire labium swings on its base. The lateral margins of the base of the postmentum are thickened and extend laterally in the head membrane as a pair of folding *articular rods* (al) the ends of which lie adjacent to the maxillary cardines. "The true hinge points of the labium on the head are thus at the mesal ends of these rods where the rods join the basal lobes of the postmentum" (Snodgrass, 1954).

CERVIX OR NECK

Since the origin of the cervix (figs. 2, 16) has not been definitely established, it is discussed briefly and separately from both head and thorax. In *Plathemis lydia* this membranous region bears two pairs of sclerites, the lateral cervical sclerites and the dorsal cervical sclerites.

The LATERAL CERVICAL SCLERITES (lsc) are large, laterally protuberant pyramidal sclerites on the anterolateral margin of the neck membrane.

The DORSAL CERVICAL SCLERITES (dsc) lie free in the neck membrane. They are transversely elongate and much smaller than the above.

THORAX

The thorax of *Plathemis lydia* (figs. 14-19) is "characterized by three special features. First is the obliquity of the mesothoracic and metathoracic pleura as indicated by the posterior slant of the pleural sulci from the leg bases to the wings. Second is the almost complete union of the adjoining pleural plates of the wing-bearing segments, resulting in the suppression of an intersegmental groove between the epimeron of the mesothorax and the episternum of the metathorax. Third is the dorsal extension of the upper plates of the mesothoracic

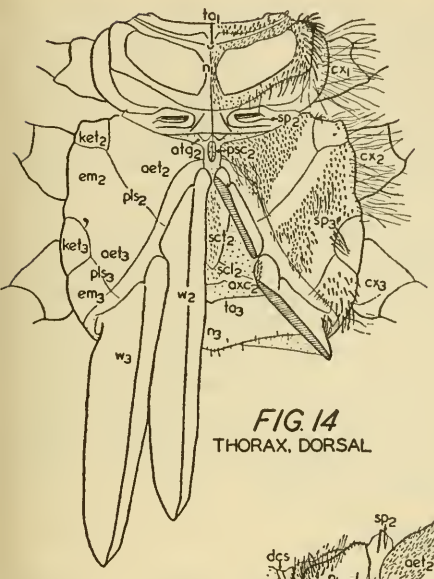

FIG. 14
THORAX, DORSAL

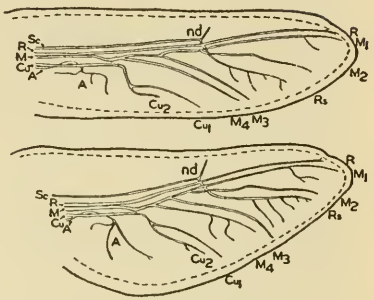

FIG. 15 WING PADS

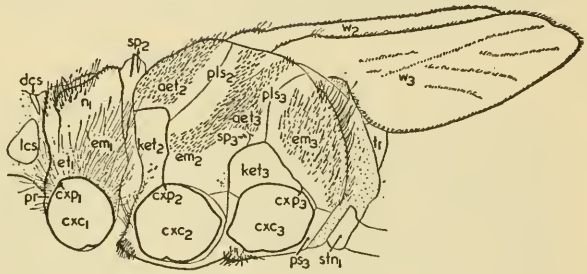

FIG. 16
THORAX, LATERAL

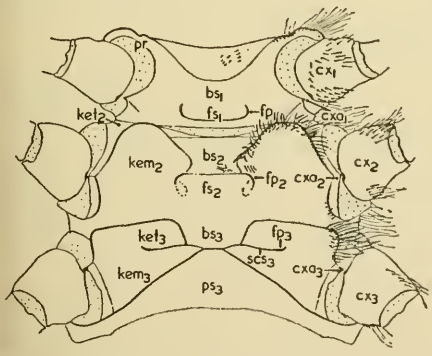

FIG. 17 THORAX, VENTRAL

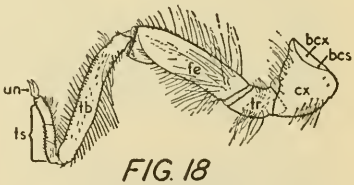

FIG. 18
LEFT MESOTHORACIC LEG

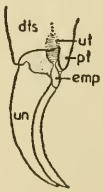

FIG. 19
MESOTHORACIC
PRETARSUS

FIGS. 14-19.—Thorax of *Plathemis lydia*.

episterna until they meet along the midline of the back in front of the wings, and the corresponding downward extension of the metathoracic epimera on the ventral surface behind the legs. These features of the thorax evidently have no particular functional significance for the larva, since the larva uses its legs in the ordinary manner for locomotion, and its wings are entirely passive rudiments of the future organs of flight. On the other hand, the thoracic structure is clearly a functional adaptation for the benefit of the adult; it must have been early impressed upon the larva, and retained by the larva because it had no disadvantage for the larval activities" (Snodgrass, 1954). Sargent (1937), by puncture-scarring the larval cuticle, has shown that the dorsal extension of the mesothoracic episterna takes place by marginal growth, while the metathoracic epimera increase both by general expansion and by growth of the ventral margins. The postcoxal plate of the metasternum, according to Sargent, moves bodily backward from the legs as the epimeral plates intervene.

THORACIC TERGA

PRONOTUM: The prothoracic tergum (fig. 14) consists of a single large sclerite, the *pronotum* (n_1), which is roughly transversely rectangular in shape. The anterodorsal angles are produced as hemispherical lobes each of which bears numerous long setae and short spines. The *disc* or dorsal surface of the pronotum consists of two oblong glabrous areas which are bounded anteriorly and posteriorly by bands of minute inconspicuous setae and separated by a median longitudinal spiniferous band which is enlarged at either end. A conspicuous pit close to the spiniferous anterior margin marks the position of the *prothoracic tergal apophysis* (ta_1) which gives attachment to the dorsal longitudinal muscles (Asahina, 1954).

MESONOTUM: The mesothoracic tergum (fig. 14) is transversely compressed as a result of the upward extension of the pleural sclerites. The mesonotum proper is demarked into four main regions: acrotergite, prescutum, scutum, and scutellum. A portion of the dorsal surface of the intersegmental membrane, lying between the mesothoracic spiracles, has become secondarily sclerotized forming a plate which narrows anteriorly and is roughly trapezoidal in shape.

The *acrotergite* (atg) is the anteriormost mesotergal sclerite. It is secondarily divided into two triangular plates with posteriorly directed apices. It is extremely reduced and separated from the prescutum by membrane.

The *prescutum* (psc_2) is a much-reduced, longitudinally elongate, protuberant sclerite between the dorsally extended portions of the

mesothoracic anepisterna. It is separated from the latter, and also from the wing bases and the scutum, by a membranous area.

The *scutum* (sct_2), the largest sclerite of the tergum, is a longitudinally elongate, posteriorly convergent, weakly sclerotized lobe in the membranous region between the anterior wing bases. Its posterior margin is fused with the scutellum. Numerous tiny posteriorly-directed spines are present on the dorsal surface.

The *scutellum* (scl_2) is a small hemispherical lobe just posterior to the scutum. Its anterior end is undemarked, but its posterior margin is arcuate and continuous laterally with the *axillary cords* (axc_2) of the basal wing membrane. Setae of various sizes are scattered over the scutellar surface.

METANOTUM: The metathoracic tergum (fig. 14) consists of a single transversely elongate sclerite, the *metanotum* (n_3), which is situated between the posterior wing bases. The *metathoracic tergal apophysis* is represented by a shallow pit (ta_3) on its anterior margin. Numerous short setae are borne on the median dorsal surface.

THORACIC PLEURA

The thoracic pleura (figs. 14, 16, 17) are relatively large and greatly modified and consist of propleuron, mesopleuron, and metapleuron.

PROPLEURON: The prothoracic pleuron is composed of two regions, the episternum and the epimeron, which are somewhat separated by a shallow vertical depression lying above the pleural coxal process (cxp_1). The pleural suture is lacking.

The *episternum* (et_1) is a relatively very small area bounded anteroventrally by the precoxal bridge and posteriorly by the epimeron. Neither of the delimiting sutures is entire. The marginally setiferous *precoxal bridge* (pr) is well sclerotized and united ventrally with the basisternum.

The *epimeron* (em_1), the largest portion of the propleuron, is fused with the pronotum. It is posteriorly separated from the mesothoracic katepisternum by the peritremal plate of the mesothoracic spiracle above and a flexible, folded, partially sclerotized area below.

MESOPLEURON: The mesothoracic pleura are much more highly developed than the prothoracic pleura. Each pleuron is divided into two main regions, the episternum and the epimeron, by the *pleural suture* (pls_2), which extends obliquely posterodorsad from the pleural coxal process to the wing base. The episternum is further divided by a well-demarked transverse suture into two secondary regions known as anepisternum and katepisternum.

The *anepisternum* (aet_2) is a large sclerite which is bounded anteriorly by the spiracular peritreme, anterodorsally by a small membranous area which bears the metanotal prescutum, and posterodorsally by the base of the fore wing. This dorsal extension is typical of odonate naiads.

The *katepisternum* (ket_2) extends ventrally in front of the coxal cavity and meets the basisternum on the anterior margin of the mesosternal surface. The katepisternum is bounded anteriorly by a flexible, vertically folded, partially sclerotized area beyond which lies the prothoracic epimeron.

The *epimeron* (em_2) has become fused with the posteriorly adjacent metathoracic anepisternum. This fusion has resulted in the suppression of the mesopleural-metapleural intersegmental suture but the posterior portion is obviously the metanepisternum since it bears the metathoracic spiracle. The resultant large composite sclerite is reflected ventrally and passes behind the coxal cavity to the sternal surface, where it is produced into a large forwardly directed lobe which bears numerous long curved spines and setae.

The *mesothoracic spiracle* (sp_2) lies in the upper part of a long sclerotized peritermal plate between the pronotum and the mesothoracic anepisternum. This is the only spiracle that becomes immediately functional for respiration upon emergence of the naiad from the water prior to transformation. The remaining thoracic and abdominal spiracles are functional in the adult only (Snodgrass, 1954).

METAPLEURON: The metathoracic pleuron is somewhat similar to, but smaller than, that of the mesothorax described above. It is divided into two portions, the episternum and the epimeron, by the *pleural suture* (pls_3), which proceeds obliquely dorsocephalad from the *coxal process* (cxp_3) to the center of the pleuron and then swings posteriorly to the wing base. The episternum is further divided by a distinct arcuate suture into an anepisternum and a katepisternum.

The *anepisternum* (aet_3), which bears the *metathoracic spiracle* (sp_3), is fused with the mesothoracic epimeron, i.e., it is not anteriorly delimited by an intersegmental suture. It extends dorsally to the base of the hind wing.

The *katepisternum* (ket_3) or lower region of the episternum is smaller than the anepisternum. In addition to its normal pleural position, the katepisternum narrows abruptly to pass in front of the coxal cavity and is reflected ventrally where it expands and extends to the basisternum. This sternal portion is fused with the posteriorly adjacent, ventrally isolated katepimeron, from which it is partially de-

marked by the lateral portions of the *sternacostal suture* (scs_3). The resultant composite sclerite is anterolaterally produced into a distinct, large, setiferous lobe close to the anterior margin of the coxal cavity.

The *epimeron* (em_3) is the posteriormost sclerite of the pleuron. It extends from behind the coxal cavity to the posterior portion of the base of the hind wing. The *katepimeron* (kem_3), or ventral portion of the epimeron, has become completely isolated on the sternal surface owing to the intervention of the large poststernum posterior to the coxal cavity. This ventral prolongation of the epimeron extends almost to the midline of the venter.

PLEURAL CHAETOTAXY: The entire pleural surface, with the exception of the portions adjacent to the pleural sutures, is clothed with short setae and spines, whose average length increases slightly posteriorly. In addition, the prothoracic pleura and the areas adjacent to the coxal cavities are provided with numerous light-colored setae, which are unusual in their extreme length.

THORACIC STERNA

PROSTERNUM: The prothoracic sternum (fig. 17) consists of a single broad sclerite which represents the fused basisternum and furcasternum. A large partially sclerotized, spiniferous, hemispherical area anterior to the prosternum is of secondary origin and not part of the definitive prosternum.

The *basisternum* (bs_1), the largest prosternal area, is fused anterolaterally with the *precoxalia* (pr) of the episternum and posteriorly with the small furcasternum. Its lateral margins form the *sternal coxal articulations* (cxa_1).

The *furcasternum* (fs_1) is a small transverse area located between the prosternal *furcal pits* (fp_1), which are the external manifestations of the endoskeletal furcal apophyses.

MESOSTERNUM: The mesothoracic sternal sclerites (fig. 17) are also two in number.

The *basisternum* (bs_2) is a medium-sized roughly anvil-shaped sclerite in the anteromedian portion of the mesosternum. It is bounded anteriorly and laterally by the ventrally prolonged mesothoracic pleura.

The *furcasternum* (fs_2) is a small transverse sclerite situated at the posterior end of the basisternum and demarked from it by a spiniferous ridge that extends between the *furcal pits* (fp_2).

METASTERNUM: The metathoracic sternum (fig. 17) is composed of two sclerites, the basisternum and the poststernum (Asahina, 1954), which are completely separated by the medioventrally con-

vergent metapleura. The anterior margin of the metasternum is undemarked from the posterior portion of the mesosternum.

The *basisternum* (bs_3) is a small transversely elongate area in the anterior portion of the metasternum situated between the ventrally extended portions of the metapleural katepisterna.

The *poststernum* (ps_3), the largest sternal sclerite, is the posteriormost portion of the metasternum. It is roughly triangular in outline, with the blunt apex directed forward and the basal angles reflected upward on the pleuron behind the coxal cavities. The poststernum intervenes between the pleural and ventral portions of the metepimeron.

The *furcal pits* (fp_3) have become isolated and lie in the lateral ends of a deep inflection that partially separates the ventrally reflected episternal and epimeral plates.

WINGS

The wing pads (fig. 15) of a dragonfly naiad are held inverted on the back with the spiniferous costal margin uppermost. One distinct axillary sclerite is present at the base of the adult wing (Snodgrass, 1909) but this sclerite is not demarked in the naiad.

WING TRACHEATION: The veins of the adult wings are preceded by tracheae in the nymphal wing pads. "Springing from a basal tracheal trunk that lies just inside the thorax, there are six tracheae extending out into the wing sac" (Needham, 1951). These tracheae are indicated externally on the wing pad surface by rows of well-developed setae. The tracheae themselves are best observed in freshly killed specimens in which the tracheae are filled with air (Needham, 1903), but the present writer observed the tracheae through the morphologically ventral surface of the left wing pad by rendering dried specimens translucent with the addition of either alcohol or xylene.

In describing the position of these tracheae, the Comstock-Needham system of wing-venation terminology has been used.

The *fore wing* (w_2) of *Plathemis lydia* is rather narrow and elongate. Six tracheae extend out into the wing sac: costa, subcosta, radius, media, cubitus, and anal.

The *costa* or *costal trachea* is almost completely atrophied. The remaining portion is fused into the thickened leading edge of the wing.

The *subcosta* (Sc) is shallowly forked at its terminus, which is approximately two-thirds the distance from the wing base to the apex. It sends a short branch obliquely forward to the nodal region (nd)

of the costal margin and a very minute branch posteriorly to connect with the radius.

The *radius* (R) is of greater extent than the subcosta. It is deeply forked in the region of the nodus (nd) just posterior to the subcostal fork. The main portion of the radial trachea proceeds unbranched to the apex of the wing where it sends a minute branch forward. The *radial sector* (Rs), or posterior branch of the radius, lies across the base of the terminal fork of the median trachea and extends out to occupy the field between M_2 and M_3.

The *media* (M) is 4-branched. At approximately one-third of the distance from base to apex it bends slightly posteriorly and gives off a narrow trachea, M_4, which proceeds almost to the wing margin. Farther along its extent it gives off a second posterior branch, M_3, which lies just above and parallel to M_4 and extends almost to the wing margin. At a point just posterior to the radial fork the median trachea again forks, this time sending one branch, M_2, nearly to the wing margin to occupy the field just above the radial sector and a second branch, M_1, to the wing apex posterior and parallel to the radius.

The *cubitus* (Cu) bends abruptly posteriorly just below the first forking of the median trachea and forks once into Cu_1 and Cu_2, the first of which almost reaches the hind margin of the wing.

The *anal trunk* (A) is crowded forward against the base of the cubital trachea. It loops forward under the cubitus and then returns to its original level via the anal crossing. The anal trachea then descends slightly and forks twice.

In the *hind wing* (w_3) the tracheation is almost identical with that of the fore wing and differs only in the extent of certain tracheae. The hind-wing pad is expanded posteriorly and subsequently the cubital and anal tracheae are of greater extent than in the fore wing, which has not undergone such an expansion.

LEGS

The legs of *Plathemis lydia* (figs. 18, 19) are long and slender. The forelegs are subequal in length to the mesothoracic legs, which in turn are considerably smaller than the metathoracic legs. The differences in sizes of the legs is accounted for primarily by differences in length of the femur, tibia, and tarsus since the coxa and trochanter are almost identical in size in all three pairs of legs.

The coxa (cx) or basal leg segment is of moderate size and more or less conical in shape. It articulates with the pleural coxal process

and with the sternal coxal articulation of the thorax at the basal portion of the outer and inner surfaces, respectively. The basal end of the coxa is girdled by a submarginal *basicostal suture* (bcs), which forms internally a submarginal basicostal ridge and sets off a narrow marginal flange, the *basicoxite* (bcx), which is enlarged on the outer surface posterior to the pleural articulation.

The TROCHANTER (tr) is a rather small segment that is proximally constricted. This gives it a superficially 2-segmented appearance. Its distal end is obliquely truncate with the concave dorsal surface shorter than the convex ventral surface. It is attached proximally to the coxa by a membrane and articulates with the coxa by an anterior and a posterior condyle. The deeply emarginate dorsal margin of the coxa allows for a wide range of motion of the leg on this dicondylic hinge. A dicondylic hinge is present at the distal end of the trochanter also. This operates at a right angle to the coxotrochanteral hinge but permits of much less freedom 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 the second longest segment of the leg. It is nearly cylindrical and armed with numerous spines and setae, especially on its dorsal and ventral surfaces. In addition, the posterior surface of the prothoracic femur, the anterior and posterior surfaces of the mesothoracic femur, and the anterior surface of the hind femur are also provided with numerous setae and spines. This is evidently correlated with the natural position of the legs; forelegs held anteriorly, middle legs held posterolaterally, and hind legs held posteriorly. The distal margin of the femur is crowned with several short spines.

The TIBIA (tb) is the longest segment of the leg, nearly cylindrical, and rather slender. Its proximal end is bent toward the femur, allowing the tibia to be flexed close against the undersurface of the femur. The tibia articulates with the femur by a dicondylic hinge. Numerous medium to long spines and setae are borne on both the dorsal and ventral tibial surfaces, the heaviest spines being present on the ventral surface close to the distal margin. In addition, there are many short spines scattered generally over the entire surface.

The TARSUS (ts) is 3-segmented. The basal segment or *basitarsus* is the second longest tarsal segment. It is slightly bent near its distal end and can be flexed against the tibia. The *second tarsomere* is only slightly shorter than the basitarsus. It is obliquely truncate distally so that its dorsal surface is shorter than the ventral surface. The third tarsomere, or *distitarsus* (dts), is the longest of the three tarsal segments. It bears a ventrodistal projection, the *plantella* (pt), which is

well developed. All three segments of the tarsus bear on their ventral surfaces several heavy spurs which decrease in size distally.

The PRETARSUS (fig. 19) or terminal region of the leg consists of claws, empodium, and unguitractor. The *claws* or *ungues* (un) are the largest parts of the pretarsus, and they articulate with a small dorsal process of the distitarsus. Ventrally, the bases of the claws are connected with membrane which is also closely attached to the mesally located *unguitractor* (ut). The unguitractor is a sclerite that can be retracted into the distitarsus by the action of muscles in the tibia which are attached to the unguitractoral tendon which is in turn attached to the unguitractor. The unguitractor is partially hidden by the plantella. An *empodium* (emp) is attached to the distal end of the unguitractor by a narrow stalk. The remainder of the empodium is more or less paddle-shaped.

ABDOMEN

The abdomen of *Plathemis lydia* (figs. 20-24) is elongate and slightly longer than the head and thorax combined. It is broadest at the fifth segment and tapers gradually posteriorly to the tips of three horny processes enclosing the anus. The abdomen consists of ten complete annular segments and probably rudiments of the eleventh and twelfth segments (Heymons, 1904).

ABDOMINAL TERGA

The abdominal terga (figs. 20, 24) are distinctly transversely elongate in shape. They increase slightly in the transverse dimension from the first to the fifth segment and then shorten to give a markedly tapered appearance to the abdomen. The middorsal line and lateral margins are produced in the form of keels, giving the abdomen a triquetral appearance. Sharp, posteriorly curved *dorsal hooks* (dh) are present on the dorsal midline of segments three to six, but absent on the remaining segments. The dorsal hook on segment five is the longest of the four hooks, all of which are densely covered with sharp, spiniform setae. Long, sharp *lateral spines* (lsp) are present on the posterolateral angles of segments eight and nine, one pair per segment. The spines are approximately one-sixth as long as the segments bearing them. Smaller spines are present in rows on the lateral and posterior tergal margins and scattered generally over the dorsal surface. The spines gradually increase in size and density as they progress posteriorly. The terga are also adorned with a few scattered setae and long lateral hairs.

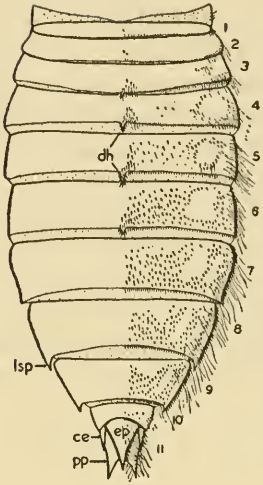

FIG. 20
ABDOMEN, DORSAL

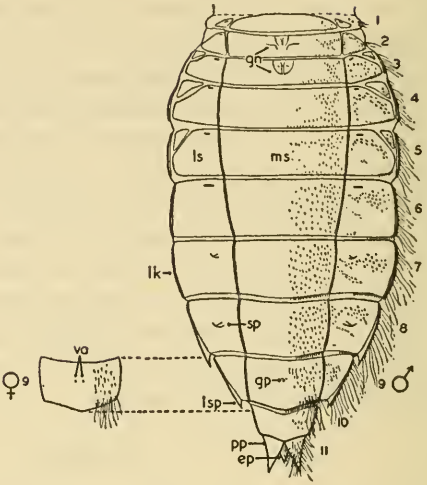

FIG. 21
ABDOMEN, VENTRAL

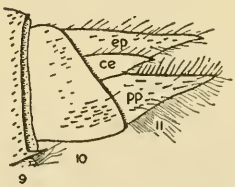

FIG. 22
ANAL APPENDAGES,
LATERAL

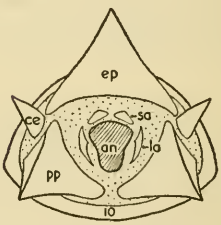

FIG. 23
ANAL APPENDAGES,
POSTERIOR

FIG. 24
DORSAL HOOKS - P. LYDIA

FIG. 25
DORSAL HOOKS - P. SUBORNATA

FIGS. 20-25.—Abdomen of *Plathemis lydia* and *P. subornata* (fig. 25).

ABDOMINAL STERNA

The sterna (fig. 21) are slightly convex and each of the first nine is divided by two longitudinal sutures into "a broad median plate (ms) and two small lateral plates (ls), which latter are movably hinged on the edges of the tergum and on the median sternal plate" (Snodgrass, 1954). The sternum of segment 10 is undivided and unseparated from the tergal surface.

The MEDIAN PLATES (ms) or *median sternites* (Snodgrass, 1954) of abdominal segments 1 and 4-8 of the male and of segments 1-8 in the female are unmodified and devoid of genital processes. The second and third median sternites of the male bear rudiments of the *accessory genitalia* (gn) of the adult, and the ninth median sternite bears the centrally located rudimentary *genital pore* (gp). On the ninth median sternite of the female there are two small, centrally located tubercles (va), which are most probably the rudiments of the *valvulae* of the ovipositor.

The LATERAL PLATES (ls) of the first eight segments bear the abdominal *spiracles* (sp), the largest of which is on segment eight. Numerous authors, including Calvert (1893), Wallengren (1914), Tillyard (1917), and Whedon (1918), have referred to the lateral plates as "pleurites," but Snodgrass (1954) states that the term "pleuron" "has no very definite meaning as applied to the abdomen." He substitutes instead the term *"laterosternites"* for the lateral sternal plates. In *Plathemis lydia* each laterosternite of segments 3, 4, and 5 is secondarily divided into a small anterolateral sclerite (episternite—Wallengren, 1914; triangular sclerite—Schmidt, 1951) and a larger posterior sclerite (epimerite—Wallengren; spiracular sclerite—Schmidt) which bears the spiracle.

Numerous posteriorly directed, short, spiniform setae are borne on the lateral keels, the lateroposterior margins of laterosternites 2-9, and the posterior margins of median sternites 7-9. Numerous other minute spines and setae are present on the entire ventral surface and are generally larger on the laterosternites than on the median sternites.

ANAL APPENDAGES

The anal appendages (figs. 22, 23) of the nymphal abdomen are of interest because of the different interpretations of their homologies. These terminal structures may be divided into two groups on the basis of their segmental relationships. The first group consists of epiproct, paraprocts, and cerci, of which the first two are thought to comprise the modified eleventh abdominal segment (Heymons, 1904)

or anal pyramid (Tillyard, 1917). The cerci are considered to be the appendages of the eleventh segment. The second group is believed by Heymons (1904) to be the remnant of the twelfth abdominal segment. It is composed of the laminae supra-anales and the laminae sub-anales.

The EPIPROCT (ep) is the tergum of the eleventh segment (Heymons, 1904; Crampton, 1918). In *Plathemis lydia* the epiproct is a wide, triangular, horny process that emerges from beneath the posterodorsal margin of the tenth tergum to surround the anus from above.

The PARAPROCTS (pp) complement the epiproct by surrounding the anus laterally and ventrally. Each of these two triangular horny processes resembles the epiproct in appearance but is slightly smaller in size. The paraprocts, according to Heymons (1904), are actually the true cerci. Crampton (1918) contended that the paraprocts and cerci were distinct structures but that they belonged to the tenth segment. The most current theory is that of Snodgrass (1931), who maintains that the paraprocts pertain to the eleventh segment and probably represent the sternal sclerites of that segment.

The CERCI (ce) are paired appendages that arise from the dorsolateral posterior margin of the tenth tergum, immediately laterad of the epiproct. These appendages were termed "cercoids" by Heymons (1904) and Tillyard (1917), both of whom maintained that the true cerci were the lateral anal appendages or paraprocts. In recent papers, both Snodgrass (1954) and Asahina (1954) agree that the "cercoids" of Heymons are the true cerci, as previously maintained by Crampton (1918). Crampton, however, theorized that the cerci arose from the tenth abdominal segment, but more recent authors (Snodgrass; Asahina) place them with the epiproct and paraprocts on the eleventh segment.

If the epiproct and paraprocts are spread apart, as in figure 23, four small sclerites can be seen surrounding the anus (an). According to Heymons (1904), the middorsal pair or *laminae supra-anales* (sa) is the reduced twelfth tergite, while the two lateral ones or *laminae subanales* (la) represent the bipartite sternite. The membranous circumanal fold containing these sclerites has been termed the *periproct* by Snodgrass (1931).

COMPARATIVE ANATOMY OF THE GENUS PLATHEMIS

The present writer has found that the mature naiads of the two known species of the genus *Plathemis* are practically identical as regards external morphology. However, they have been shown by Needham and Westfall (1955) to differ in the relative size and

shape of the dorsal abdominal hooks. Needham states that the dorsal hooks in both species are present on abdominal segments 2–6. Garman (1927), in his description of *Plathemis lydia,* states that the dorsal hooks are present on segments 3 to 5 or 6. The present writer's observations on 25 naiads of *P. lydia* from Amherst, Mass., and 6 exuviae of *P. subornata* from Ana Springs, Oreg., are not in conformity with those of either Needham or Garman. The writer has found that in both species the dorsal hooks occur always and only on segments 3–6.

In *Plathemis lydia* the dorsal hooks are present on abdominal segments 3 to 6, the longest being on segment 5. They are all posteriorly curved, sharp and thornlike, and covered with spiniform setae (fig. 24).

In *P. subornata* the dorsal hooks are also present on abdominal segments 3 to 6, the longest also being on segment 5. In this species, however, the dorsal hooks differ from those of *P. lydia* in being blunt and hairy (fig. 25).

TAXONOMY AND DISTRIBUTION

GENERIC CHARACTERS: The naiads of the genus *Plathemis* Hagen (1861) can be separated from all other odonate naiads by the following characters:

1. Naiads without caudal gills, with small spinose appendages at apex of abdomen .....Suborder Anisoptera—DRAGONFLIES
2. Labium forming a deep spoonlike mask covering face up to antennae; distal edge of labial palpus evenly and regularly toothed; ligula never with two large teeth at middle of distal margin.....Family LIBELLULIDAE
3. Head without frontal horn; lateral spines of abdominal segment 8 shorter than length (along sagittal line) of segment 9; no dorsal hook on abdominal segment 9.....Subfamily LIBELLULINAE
4. Eyes capping anterolateral angles of head, more frontal than lateral; abdomen lanceolate in outline, gradually narrowed to apex.....Tribe LIBELLULINI
5. Ligula of labium crenulate on distal margin; labial palpi each with 10 lateral setae; prementum with 8 setae. Abdomen with dorsal hooks on segments 3–6, and small lateral spines on segments 8 and 9; paraprocts twice as long as cerci.....Genus *Plathemis*

SPECIFIC CHARACTERS: The mature naiads of the two known species of the genus *Plathemis* can be separated as follows:

Dorsal abdominal hooks on segments 3–6, all sharp and thornlike and bearing spiniform setae.....*P. lydia*
Dorsal abdominal hooks on segments 3–6, all blunt and hairy.....*P. subornata*

PREVIOUS SPECIFIC DESCRIPTIONS

Plathemis lydia:

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DISTRIBUTION AND DATES

Plathemis lydia: A very common and widely distributed species, inhabiting mucky ponds. CANADA: British Columbia, New Brunswick, Nova Scotia, Ontario, Quebec. UNITED STATES: 39 States, with the exception of Arizona, Delaware, Maryland, Montana, Nevada, North Dakota, Oregon, South Dakota, Wyoming. April 18 (Miss.) to October 16 (Tenn.).

Plathemis subornata: A western species, inhabiting swales and seepage pools in desert and semidesert areas. CANADA: British Columbia. UNITED STATES: Arizona, California, Colorado, Kansas, Nebraska, Nevada, New Mexico, Oregon, Texas, Utah. MEXICO: Chihuahua, Sonora. April (Calif.) to October 16 (Tex.).

ABBREVIATIONS

A —anal trachea
abt —abductor tendon
ac —anteclypeus
adt —adductor tendon
aet —anepisternum
al —articular rod of labium
an —anus
ant —antenna
as —antennal suture
asc —antennal sclerite
at —anterior tentorial pit
ata —anterior tentorial arm
atg —acrotergite
axc —axillary cord
bc —basicardo
bsc —basicostal suture
bcx —basicoxite
bs —basisternum
ce —cercus
cl —clypeus
cls —clypeolabral suture
co —condyle
cos —coronal suture
cs —clypeal suture
ct —corporotentorium
Cu —cubital trachea
cx —coxa
cxa —coxal articulation
cxc —coxal cavity
cxp —pleural coxal process
dc —disticardo
dh —dorsal hook
dps —distal palpal setae
dpt —distal palpal tooth
dsc —dorsal cervical sclerite
dta —dorsal tentorial arm
dts —distitarsus
em —epimeron
emp —empodium
ep —epiproct
es —epistomal suture
et —episternum
eye —compound eye
f —flagellum
fe —femur
fp —furcal pit
fr —frons
fs —furcasternum
ge —gena
gn —accessory genitalia
gp —genital pore
hap —hypopharyngeal apodeme
hy —hypopharynx
igm —insertions of gnathal muscles
il —inner lobe
in —incisor lobe
kem —katepimeron
ket —katepisternum

la —lamina sub-analis
lbp —labial palpus
lcd —laciniadentes
lgs —ligular seta
lhs —lateral suspensorial arm
lig —ligula
lk —lateral keel
lm —labrum
lps —lateral palpal seta
ls —laterosternite
lsc —lateral cervical sclerite
lsp —lateral spine
M —median trachea
md —mandible
mh —movable hook
mo —molar surface
mps —median palpal seta
ms —median sternite
mth —mouth
mx —maxilla
n —notum
nd —nodal region
ohs —oral suspensorial arm
ol —outer lobe
os —ocular suture
osc —ocular sclerite
p —pedicel
par —parietal lobe
pc —postclypeus
pf —palpifer
pfs —postfrontal suture
pge —postgena
pls —pleural suture
pm —pleurostoma
pms —pleurostomal suture
poc —postocciput
pocs —postoccipital suture
pp —paraproct
pr —precoxale
prm —prementum
prs —premental seta
ps —poststernum
psc —prescutum
psm —postmentum
pt —plantella
pta —posterior tentorial arm
R —radial trachea
Rs —radial sector trachea
s —scape
sa —lamina supra-analis
Sc —subcostal trachea
scl —scutellum
scs —sternacostal suture
sct —scutum
sp —spiracle
st —stipes
stn —sternum
ta —tergal apophysis
tb —tibia
ths —transverse suspensorial bar
tr —trochanter
ts —tarsus
un —ungue
ut —unguitractor plate
va —valvulae
w —wing

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