THE ABDOMINAL NERVOUS SYSTEM OF *PTERONARCYS* (PLECOPTERA: PTERONARCIDAE)[1]

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ABSTRACT

The abdominal nervous system in the nymph of *Pteronarcys proteus* Newman, and in the adult of *P. californica* Newport is described. The ganglia of segments 3 and 4 are coalesced. The transverse nerves of segments 4, 5 and 6 arise from the ganglia of the immediately-following segments. Only the first three segments contain both dorsal and ventral nerves. The muscles and nerves of the genital segments are described.

Although the order Plecoptera is often referred to as an orthopteroid order, various writers (Snodgrass, 1936; Quadri, 1940) have shown that the external genitalia of both the male and the female insects are in no way generalized or orthopteroid. The original purpose of this study was to compare the abdominal nervous system in Plecoptera with the same system in Orthoptera (Schmitt, 1954), and also to determine whether the musculature and nervous system of the genital segments might provide clues helpful in establishing whether the absence of orthopteroid genitalia represents an ancestral condition.

The family Pteronarcide is usually described as one of the more generalized of Plecoptera, and the large size of species of the genus *Pteronarcys* make them especially attractive subjects for detailed studies on the nervous system. Nymphs of *Pteronarcys proteus* Newman were obtained from hillside streams in Warren County, New Jersey, through the courtesy of Dr. Lyle E. Hagmann. Unfortunately, no adults of this species could be found, and studies on adult *Pteronarcys* were made on specimens of *Pteronarcys californica* Newport, obtained from Messrs. Stanley G. Jewett, Jr. and William C. Crothers.

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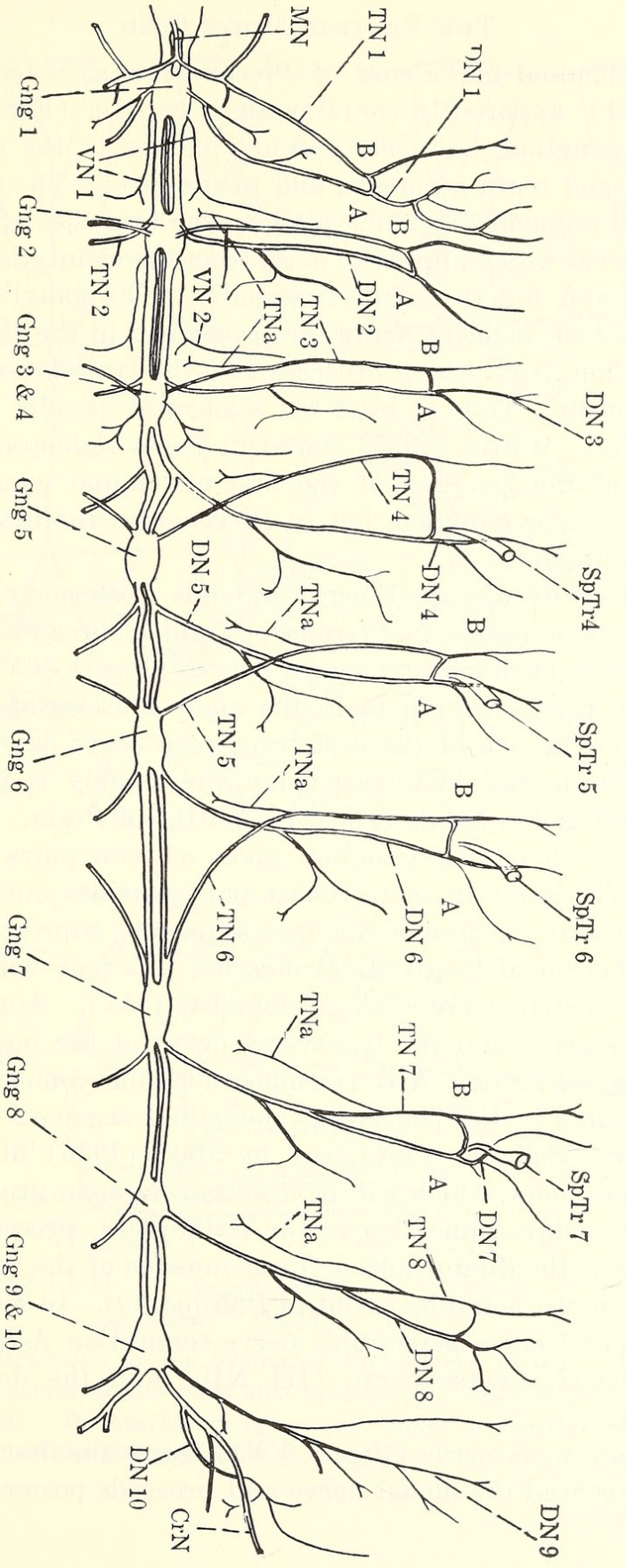

Fig. 1. The central nervous system of the abdomen of a full-grown nymph of *Pteronarcys proteus* Newman, showing the nerves of the right side.

THE VENTRAL NERVE CORD

The abdominal nerve cord of *Pteronarcys*, as noted by Newport (1851), apparently contains eight ganglia (Fig. 1). The terminal ganglion, however, provides nerves to the muscles of the ninth and tenth segments, and to the cerci. The muscles of the fourth segment are innervated by the branches of a pair of lateral nerves which appear to arise from the connection between the third and fourth definitive ganglia. The ganglion centers of these fourth segment nerves are contained in the third definitive ganglion, from which proceeds also the lateral nerves of the third segment. Thus at least ten segmental ganglia can be accounted for. Wittig (1955) found in *Perla abdominalis* Burm. a fusion of the ganglion of the first abdominal ganglion with the metathoracic ganglion, but in *Pteronarcys* the first ganglion remains separate.

A median or unpaired nerve extends posteriorly from the metathoracic ganglion in *Pteronarcys* and bifurcates to provide two lateral branches or tranverse nerves (Fig. 1, *TN1*). These transverse nerves terminate in the alary muscles of the heart. An anterior branch of the first transverse nerve extending into the metathorax was not traced, but presumably is homologous with a similar branch described by Wittig in *Perla*.

The first abdominal ganglion gives off two pairs of lateral nerves. The anterior, more robust pair provides innervation to the muscles of the first abdominal segment. Since they terminate in the dorsal longitudinal muscles, this pair will be designated the dorsal nerve (*DN*), (Schmitt, 1954). A nerve joins the dorsal nerve and the transverse nerve at the position A-B. This nerve connection, A-B, resembles a similar connection found by the writer in the pregenital abdominal segments of certain Orthoptera (Schmitt, 1954), and by Maki (1936) in a neuropteran, *Chauliodes*, which will be discussed later in greater detail. From this nerve connection in the Orthoptera, proceeds the innervation of the dilator and occlusor muscles of the spiracle, but no such muscles could be found in *Pteronarcys*. In *Perla* Wittig (1955) found not a perceptible nerve connection A-B but a union of the transverse nerve (III N10) and the dorsal nerve (III N8).

A second, weak nerve (Fig. 1, *VN1*) leaves the first abdominal ganglion behind the dorsal nerve and proceeds posteriorly along

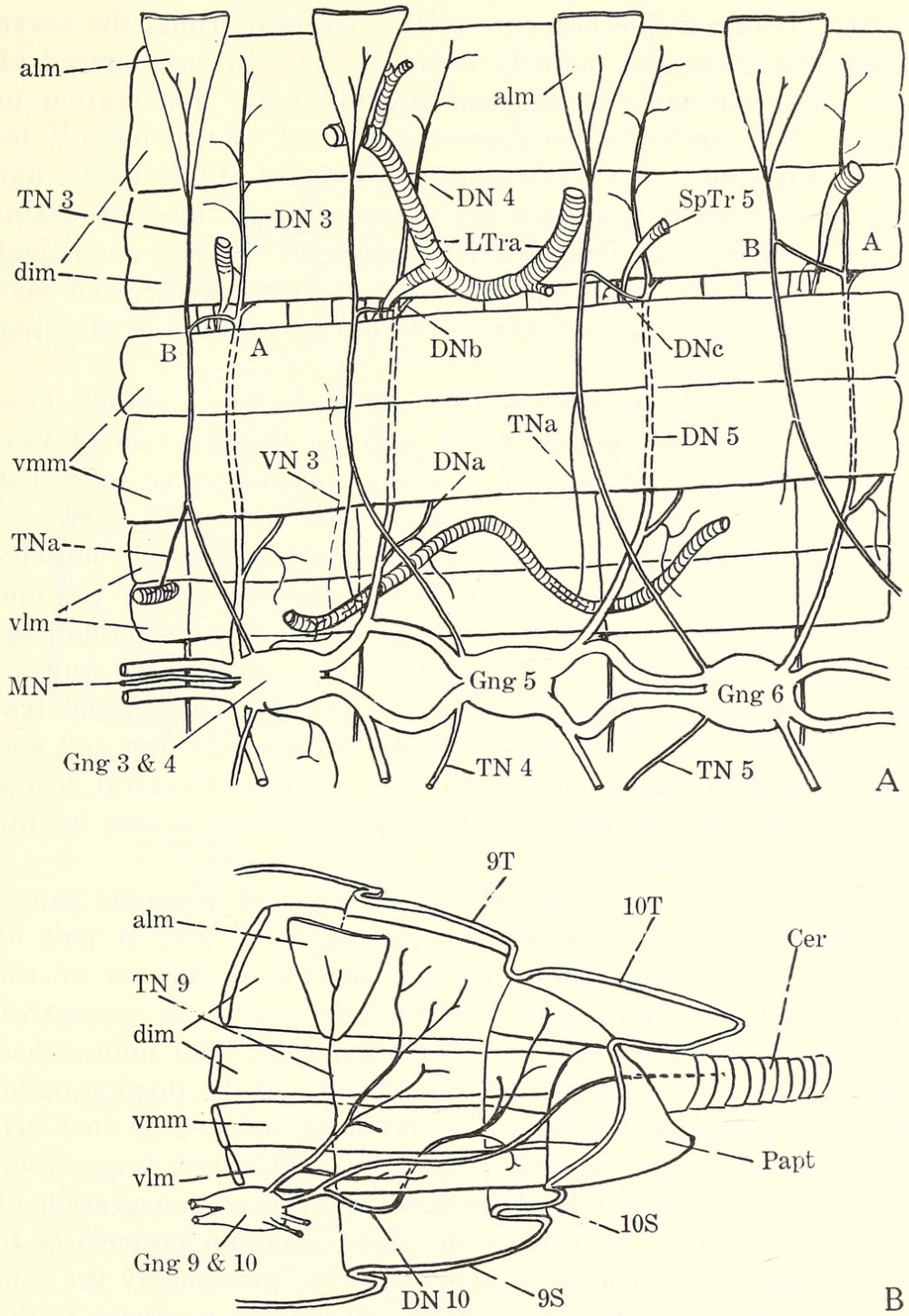

Fig. 2. Structures of the nymph of *Pteronarcys proteus*. A. Muscles, ganglia and nerves of the right side of abdominal segments 3, 4, 5 and 6 viewed mesally. B. Muscles, ganglion and nerves in the right side of the terminal part of the abdomen, viewed mesally.

the ventral tracheal trunk which parallels the ventral nerve cord. After giving off fine branches to this tracheal trunk, the nerve passes laterally and dorsally along the integument, laterad of the segmental muscles, but not providing any innervation to them. It is probably homologous with the "ventral nerve" described by the writer in Orthoptera (Schmitt, 1954, 1962), but the absence of any muscle innervations leaves this uncertain. Wittig (1955) describes in *Perla* a nerve of the first abdominal segment, III N9, which appears to be the same nerve, and says of it that it perhaps innervates the lateral muscles of the first abdominal segment.

The second abdominal ganglion in *Pteronarcys* gives off three pairs of nerves. One pair of these are the dorsal nerves (*DN2*). A second much finer pair, which arises posteriorly and somewhat more medially from the ganglion, are the transverse nerves of the second segment. These nerves terminate in the alary muscles of the heart and are connected to the dorsal nerve by the fine connection (A-B) previously described in the first abdominal segment. A fine branch, *TNa*, leaves the transverse nerve ventrad to the point "B" and innervates the ventral longitudinal tracheal trunk. A median nerve extends between the first and second ganglia, but gives off no branches. A pair of ventral nerves resembling those of the first abdominal ganglion makes up the third pair of nerves.

The nerves of the third abdominal segment resemble superficially at least those of the second. (Figs. 1, 2A) A pair of dorsal nerves arises from the anterior-lateral corners of the ganglion or, less frequently from the interganglionic connective, at a point just anterior to the third ganglion. An unbranched median nerve extends between the second and the third ganglia, but the transverse nerves, which may be recognized by such criteria as the connection A-B with the dorsal nerve, innervation of the ventral longitudinal tracheal trunk, and innervation of the alary muscles, arise from the third ganglion posteriorly to the dorsal nerves. The third pair of nerves, presumably the ventral nerves, is very fine and weak. All ganglia posterior to the third lack the ventral nerves.

As previously noted, the dorsal nerves of the fourth abdominal segment appear to arise from the interganglionic connective, usually at a point somewhere between one quarter and one half

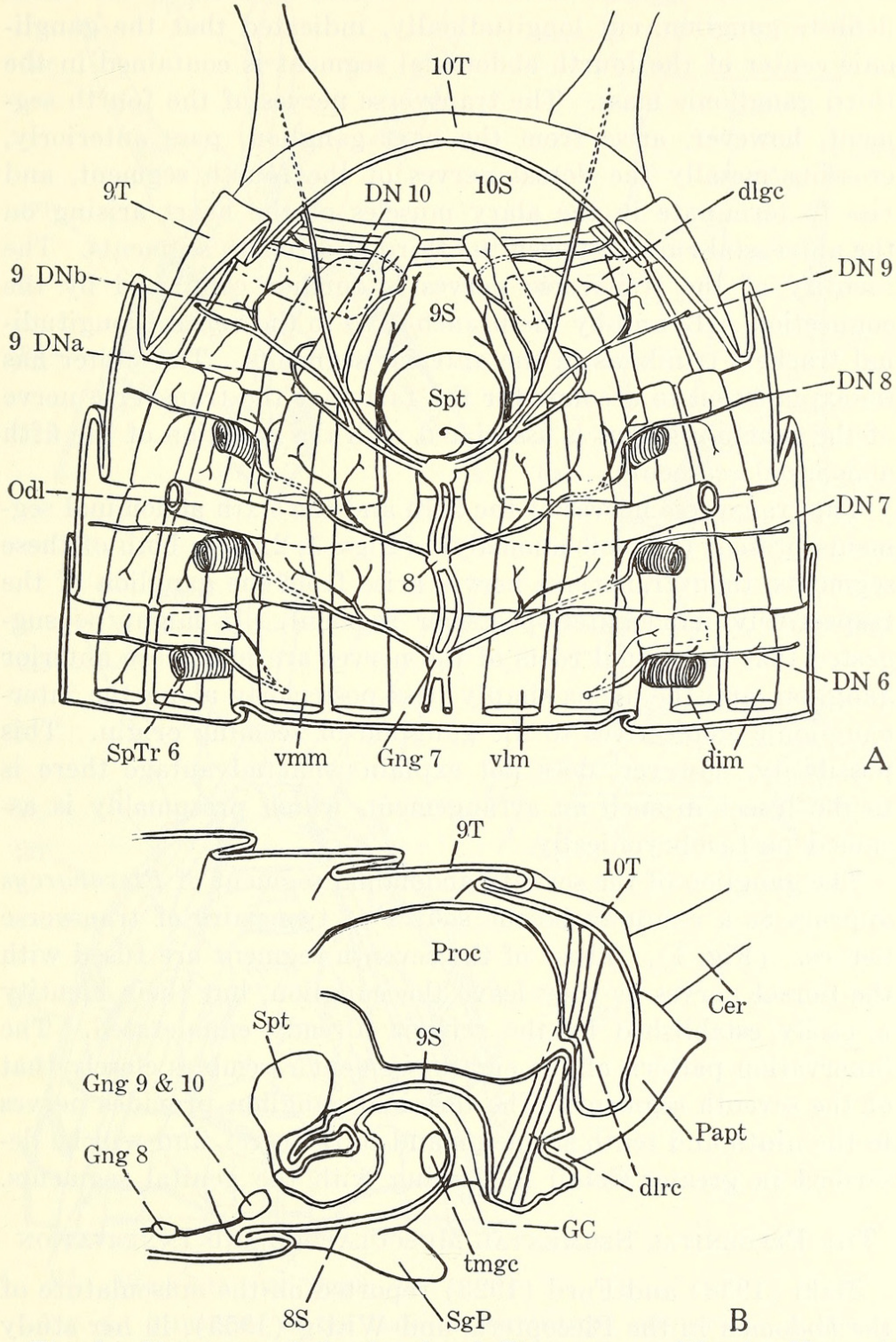

Fig. 3. Structures of the female of *Pteronarcys californica* Newport. A. Internal genitalia, nerves and muscles of the terminal part of the abdomen. B. Right half of the terminal part of the abdomen.

of the interganglionic distance. Paraffin sections of the third definite ganglion, cut longitudinally, indicated that the ganglionic center of the fourth abdominal segment is contained in the third ganglionic mass. The transverse nerves of the fourth segment, however, arise from the next ganglion, pass anteriorly, crossing mesally the dorsal nerves of the fourth segment, and rise to terminate in the alary muscles of the heart arising on the antecostal ridge between the third and fourth segments. The identity of the transverse nerves is further confirmed by the connection A-B, and by the branch *TNa* to the ventral longitudinal tracheal trunk, as in the anterior segments. The writer has no explanation to account for the fact that the transverse nerve of the fourth segment is associated with the ganglion of the fifth abdominal segment.

The transverse nerves of the fifth and the sixth abdominal segments present the same anomaly. (Figs. 1, 2A) In both of these segments, their transverse nerves arise from the ganglion of the respectively immediately-posterior segment. It might be suggested that the actual roots of the nerves are in a more anterior ganglion, and the axons simply pass posteriorly along the interganglionic connectives to the ganglion of seeming origin. This possibility, however, does not explain what advantage there is to the insect in such an arrangement, which presumably is assumed post-embryonically.

The ganglion of the seventh abdominal segment of *Pteronarcys* appears as a result to be the source of two pairs of transverse nerves. (Fig. 1). Those of the seventh segment are fused with the dorsal nerves as they leave the ganglion, but their identity is easily established by the criteria already enumerated. The innervation pattern of the eighth segment resembles closely that of the seventh segment. The terminal ganglion provides nerves to the ninth and tenth segments and to the cerci, and will be described in greater detail in dealing with the genital segments.

THE PREGENITAL SEGMENTAL MUSCULATURE AND INNERVATION

Maki (1938) and Ford (1923) reported on the musculature of the abdomen in the Plecoptera, and Wittig (1955), in her study of the thorax of *Perla*, provides some information on the first abdominal segment. All three papers, however, deal with species in the family Perlidae, and there appear to be no previous reports on the abdominal musculature in the Pteronarcidae.

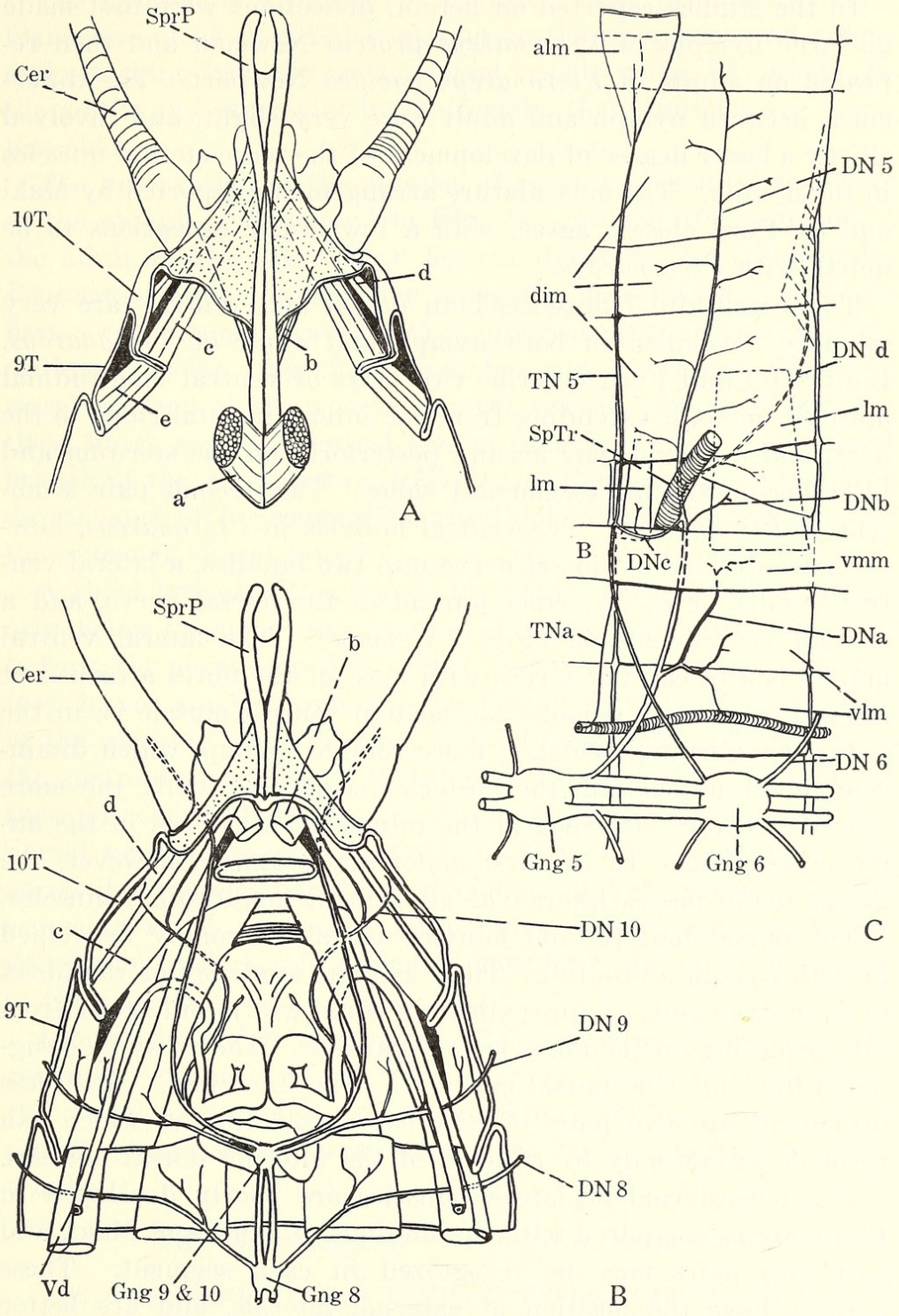

Fig. 4. Structures of the male of *Pteronarcys californica*. A. Dorsal view of supra anal plate, showing muscles and associated structures. B. Internal genitalia, nerves and muscles of the terminal part of the abdomen. C. Nerves and muscles of the right side of segment 5, viewed mesally.

In the studies reported on herein, dissections were first made on large nymphs of *Pteronarcys proteus* Newman and then repeated on adults of *Pteronarcys pacifica* Newport. The differences between nymph and adult were very slight, and involved chiefly a lesser degree of development of the tergo-sternal muscles in the nymph. The musculature arrangements reported by Maki and by Ford closely agree, with a few minor exceptions to be noted, with *Pteronarcys.*

The longitudinal muscles, both dorsal and ventral, are very strongly developed in both nymph and adult of *Pteronarcys.* Both Maki and Ford describe two pairs of ventral longitudinal muscles, one pair extending from one intersegmental ridge to the next, and a second pair arising posteriorly on the sternum and inserting on the intersegmental ridge. This second pair is absent in *Pteronarcys.* The ventral muscles in *Pteronarcys,* however, are divided by dorsal nerve into two bundles, a lateral ventral bundle (Fig. 2A, *vlm*) laterad of the dorsal nerve, and a median ventral muscle (Fig. 2A, *vmm*). The lateral ventral bundle is a broad, flat series, with most of the fibres attached at the intersegmental ridge. The median ventral muscle is, in the anterior segments, a thicker, more rounded group, which diminishes in prominence in the posterior segments. Only the more lateral fibres are attached at the intersegmental lines in the anterior segments. In the first abdominal segment, however, the dorsal nerve passes laterad of all ventral longitudinal muscles.

The dorsal longitudinal muscles are also strongly developed in both nymph and adult. There is some tendency of the fibres to form two bands of approximately equal width, but apart from this, grouping of the fibres is very variable. They may be designated the "internal dorsal muscles" (Fig. 2A, *dim*). Much less prominent are two pairs of external dorsal muscles which can be made visible only by removal of the internal dorsal muscles.

The tergosternal or lateral muscles are poorly developed in *Pteronarcys,* compared with the findings of Ford and Maki, and only two pairs may be recognized in each segment. These muscles have the position of external laterals, and are better developed in the adult than in the nymph. (Fig. 4C, *lm*). No occlusor or dilator muscles of the spiracles could be found in *Pteronarcys,* although both Maki and Ford describe such muscles in the Perlidae.

The nymphs of *Pteronarcys* contain rather prominent dorsal transverse or alary muscles, arising on the intersegmental ridges and attaching laterally on the dorsal vessel. (Fig. 2A, *alm*). In the adult, and especially in the female, these muscles are much less obvious.

The innervation of the muscles of several pregenital segments of the nymph is illustrated in Fig. 2A, and the fifth segment of the adult in Fig. 4C. Both figures show the right side only. Proceeding from the ganglion along the dorsal nerve, one finds first a conspicuous branch, *DNa,* innervating the ventral longitudinal muscles. The finer branches may be traced along the mesal surface of the ventral lateral muscle, *vlm,* and between these fibres and the ventral median muscle, *vmm.* The second branch of the dorsal nerve, *DNb,* leaves the main nerve near the dorsal edge of the ventral longitudinal muscles and innervates the external lateral muscles.

A third branch, *DNc,* leaves the dorsal nerve passing anteriorly, below the spiracular trachea, and joins the transverse nerve to form the nerve loop A-B, which resembles a similarily-situated loop in certain Orthoptera (Marquardt, 1939; Schmitt, 1954), in the cecropia moth (Beckel, 1958; Libby, 1959, 1961), and in the neuropterous insect, *Chauliodes* (Maki, 1936). In all of these insects, the nerves to the spiracular muscles arise from this dorsal nerve-transverse nerve loop, and it is unfortunate that spiracular muscles could not be found in *Pteronarcys.* In the segments which contain a tergosternal muscle anterior to the spiracular trachea, a fine branch from *DNc* provides innervation to those fibres.

Innervation of the external dorsal muscles arises from the remaining branches of the dorsal nerve. An anterior branch of the dorsal nerve enters the integument. The main part of the dorsal nerve passes laterad of the lateral longitudinal tracheal trunk.

The Genital and Postgenital Segments

The muscles and nerves of the posterior segments of the abdomen of the *Pteronarcys* nymph are represented in Fig. 2B. The last alary muscles of the heart arise on the intersegmental ridge between the eighth and the ninth segments and the fine nerves to these muscles are, presumably, the transverse nerves.

The more median of the ventral longitudinal muscles of the ninth segment lacks a posterior attachment and is continuous with the corresponding muscle of the tenth segment. A similar fusion of the ventral internal longitudinal muscles of segments nine and ten has been described in the Orthoptera by Ander (1939) and in other Plecoptera by Brink (1956). Innervation of the fused muscles in *Pteronarcys* is provided by branches from both the ninth and the tenth dorsal nerves. The dorsal nerves of the tenth segment pass laterad of the fused ventral longitudinal muscles, but the nerves which enter the cerci and the paraprocts remain medial in position. Branches from the dorsal nerves of both the ninth and the tenth segments innervate the dilator muscles of the rectum.

THE MALE

The male genitalia of *Pteronarcys* have been described by Smith (1917) and by Snodgrass (1936). Brink (1956) provides an excellent review of the literature on the reproductive system and the genitalia in the Plecoptera. The arrangement of muscles and nerves in the male of *Pteronarcys pacifica* is shown in Figure 4, A,B. The most prominent feature of the male genitalia is the median supra anal plate or process (*SprP*). Three pairs of muscles were found to be inserted on this structure, although Smith (1917) illustrates only a single pair. The precise functions of these muscles probably should be described from observations on live stoneflies but as none were available these muscles will merely be designated by letters. The pair of muscles designated by the letter *a* arise on the ninth tergum and insert on the anterior end of the supra anal process. These muscles are short and very stout. A second pair of muscles, *b*, extend from the supra anal process to the tenth segment, being attached immediately beneath the cerci. The tenth segment is divided in *Pteronarcys pacifica* into a dorsal portion, bearing the genital lobes or tergal processes, and a ventral arch, from which the cerci arise. The ventral arch becomes very narrow medianly, where the ventral longitudinal muscles are inserted. A third pair of large muscles, *c*, arise on the anterior phragma of the tenth segment and insert on the supra and process immediately posterior to muscle *b*. A fourth pair of tergal muscles, *d*, arise on the anterior phragma of the tenth segment, laterad of muscle *c* and

insert on the ventral ring of the tenth segment, just anterior to the cerci. Mention should also be made of a fifth pair of muscles of tergal muscles, *e*, which are aligned with muscle *c*, and extend between the phragma at each end of segment nine.

The ventral musculature of segments nine and ten is also shown in Fig. 4B. The median pair are the fused muscles of segments nine and ten previously described from the nymph. The lateral pair of ventral muscles of the ninth segment show almost no change from the corresponding muscles in the nymph. The median pair of ventral longitudinal muscles in segment eight are broad flat sheets of muscles which serve to retract the subgenital plate or ninth sternum and thus expose more fully the orifice of the genital cavity.

The vasa deferentia (*Vd*) in *Pteronarcys* are much coiled in the posterior segments, but ultimately they may be traced to the positions shown in Fig. 4B. It is interesting to note that to reach a median position they pass beneath the fused ventral longitudinal muscles, as has been described in Orthoptera and Thysanura by Ander (1939) and in other Plecoptera by Brink (1956).

Despite the seeming complexity of the male genital structures, the nervous system in the genital region shows very little change from the nymph. The dorsal nerves of the ninth segment pass beneath or laterad of the vasa deferentia and terminate in the large tergal muscles *a*. The nerves of the tenth segment pass beneath the vasa deferentia and, as in the nymph, beneath the fused ventral longitudinal muscles but above the lateral pair of ventral longitudinals. After innervating the fused muscles, it provides nerves to muscles *c* and *d*, and a branch reaches muscle *b* by a posterior extension. The nerves of the cerci, after leaving their common roots with the tenth segment nerves, pass posteriorly along the dorsal surface of the fused ventral longitudinal muscles, as in the nymph, and in so doing, pass above the vasa deferentia. Brink (1956) has already observed this arrangement in other Plecoptera. As is well known, Snodgrass (1936) has interpreted this nerve-gonoduct relationship as evidence that primitive genital ducts turned downward to the body wall between the nerves of the tenth and the eleventh abdominal segments, and, further, that the cerci are appendages of the eleventh abdominal segment.

THE FEMALE

As in the case of the male, it may be said that the genital structures of the female are developed with surprisingly little change from the fundamental features of the nymph. Fig. 3A presents a ventral view of the genital segments of the female of *Pteronarcys pacifica*. As shown by Quadri (1940), the eighth sternum bears posteriorly a pair of sclerotized processes, the subgenital plates, (Fig. 3B, *SgP*) having no associated musculature. A deeply invaginated transverse genital cleft, involving the remainder of the eighth sternum and a large part of the ninth sternum, immediately follows. A transverse muscle arises on the posterior lateral edges of the eighth sternum and is thus contained within the inflexed part of the eighth sternum (Fig. 3B, *tmgc*). The sclerotized parts of the ninth sternum consist of a narrow transverse piece forming the posterior edge of the genital cleft, and a pair of triangular sclerites on either side of the genital cleft, on each of which is inserted a large tergo-sternal muscle, the dilator of the genital cleft. (Fig. 3A, *dlgc*). The tenth sternum is represented by a narrow sclerite.

The arrangement of nerves, muscles, and certain other internal structures of the female is shown in Fig 3A. The muscles of the seventh segment do not differ significantly from those of the nympth. The lateral oviducts lead to the short median oviduct by passing ventrad of the ventral longitudinal muscles of the seventh segment, as has been described in Orthoptera by Ander (1939) and in Plecoptera by Brink (1956). The eighth segment presents no marked change from the nymph, other than the development of the transverse muscle of the genital cleft. (Fig. 3B, *tmgc*). In the ninth segment, the most conspicuous change is the enlargement of the tergosternal muscles to become the dilators of the genital cleft (*dlgc*). As in the nymph the median pair of ventral longitudinal muscles of the ninth segment is fused with those of the tenth. The dilators of the rectum are well developed and extend as an almost continuous band between the tergum and sternum of the tenth segment. In view of the relatively smaller diameter of the rectum in the area of attachment, it is more likely that the contraction of these muscles serves to draw up the sternum and thereby increase the opening of the genital cleft.

As may be seen in Fig. 3A, the nerves of the seventh seg-

ment of the adult do not differ from those of the nymph. The eighth segment nerves provide a branch which passes ventrally beneath the ventral longitudinal muscles and innervates the transverse muscle of the genital cleft. The nerves of the ninth segment and the last nerves, containing the fused nerves of the tenth segment and the cerci leave the terminal ganglion separately but in close proximity. The first branches of the nerves of the ninth segment (*9DNa*) innervate the median pair of ventral longitudinal muscles, and the second (*9DNb*) innervate the dilators of the genital cleft and the lower bands of the dorsal longitudinal muscles. The last pair of nerves in the female provides first, on each side, a branch to the ninth sternum, which is hardly to be expected if this pair represents nerve elements of the tenth and eleventh segments only. Just beyond the branches to the ninth sternum, the nerves of the tenth segment separate from the cercal nerves, innervate and pass beneath the median pair of ventral longitudinal muscles, and then follow the body contours to reach the very short dorsal muscles. A branch of this nerve provides innervation of the dilators of the rectum.

Discussion

The abdominal musculature of nymphs of *Pteronarcys proteus* Newman serves primarily to produce vigorous sideways movements of the abdomen which propel the insect through the water, and consists almost exclusively of longitudinal muscles. The musculature of the adult insect is inherited directly from the nymph, but without adding any special features for its existence. Thus it is the requirements of the aquatic environment which have governed the plan of musculature in *Pteronarcys*.

The segmental nerve plan in *Pteronarcys* is much reduced, as compared with that of the Orthoptera. The dorsal nerve is highly developed, but the ventral nerve is much reduced and is found only in the first three segments. The most remarkable feature of the abdominal nervous system in *Pteronarcys* is undoubtedly the posterior transposition of the apparent origin of the transverse nerves in segments four, five, and six, to the ganglia of the immediately-posterior segments. Newport's Plate 21, figure 14, reveals that he observed this phenomenon as

regards segments four and five, but apparently failed to note that the transverse nerves cross over rather than fuse with the dorsal nerves. It now becomes of interest to discover how extensively this exists in the Plecoptera, and also how it comes about.

The musculature and nervous system of the genital segments provides nothing to suggest that any ancestor of *Pteronarcys* possessed essentially orthopteroid genitalia. Probably the most interesting feature of the internal anatomy of the genital segments is the absence, in both sexes, of elaborate systems of muscles and nerves, the needs of both sexes being served with surprisingly little modification of the nymphal condition.

Key to figure abbreviations

alm, alary muscle
Cer, cerus
Crn, cercal nerve
dim, dorsal internal muscle
dlge, dilator of the genital cleft
dlrc, dilator of the rectum
DN, dorsal nerve
DN1, DN2, etc., dorsal nerve of the indicated segment
DNa, DNb, etc., branches of the dorsal nerve
GC, genital cleft
Gng 1, Gng 2, etc., ganglion of the indicated segment
lm, lateral muscle
LTra, lateral tracheal trunk
MN, median nerve
Odl, lateral oviduct
Papt, paraproct
Proc, proctodaeum
8S, 9S, etc., sternum of the indicated segment
SgP, subgenital plate
SprP, supra anal plate
Spt, spermatheca
Sp Tr 4, SP Tr 5, etc., spiracular trachea of the indicated segment
8T, 9T, etc., tergum of the indicated segment
tmgc, transverse muscle of the genital cavity
TN 1, TN 2, etc., transverse nerve of the indicated segment

TNa, branch of transverse nerve to the ventral tracheal trunk
Vd, vas deferens
vlm, lateral ventral muscle
vmm, median ventral muscle
VN1, VN2, etc., ventral nerve of the indicated segment

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