

Some Evolutionary Trends in Plecoptera¹

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Structural Evolution

The families and subfamilies of stoneflies recognized by the writer are as follows:

Distribution

- A. Suborder Holognatha
(Setipalpia)
- Eustheniidae
 - Eustheniinae Australia and New Zealand
 - Diamphipnoinae Southern South America
 - Austroperlidae Australia and New Zealand
 - Leptoperlidae
 - Leptoperlinae Australia and New Zealand; Fiji Islands; temperate South America
 - Scopurinae Japan
 - Peltoperlidae North and South America; east Asia and the bordering islands, south to Borneo
 - Nemouridae
 - Notonemourinae Australia and New Zealand
 - Nemourinae Holarctic region
 - Leuctrinae Holarctic region; South Africa; Tierra del Fuego
 - Capniinae Holarctic
 - Taeniopteryginae Holarctic
 - Pteronarcidae North America; eastern Siberia
- B. Suborder Systellognatha
(Filipalpia)
- Perlodidae
 - Isogeninae Holarctic
 - Perlodinae Holarctic
 - Isoperlinae Holarctic
 - Chloroperlidae
 - Paraperlinae Nearctic
 - Chloroperlinae Holarctic
 - Perlidae
 - Perlinae Old-world tropics, and the temperature regions of Africa, Eurasia and eastern North America
 - Acroneuriinae North and South America; eastern and southeastern Asia

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Tillyard places the ancestors of present day stoneflies in the family Lemmatophoridae of the Permian order Protoperlaria. These insects had small wing-like lateral expansions of the prothorax, and a fairly well-developed posterior (concave) median vein in both wings, both of which have been lost in modern stoneflies. Developments in some of the morphological features which have been most studied are as follows:

Nymphal mouth parts: The holoognathous families are characterized by bulky mandibles, by short thick palpi, and by having the paraglossae and glossae of the labium about equal in length. In the adult the mandibles remain large and functional. The systellognathous families have thin nymphal mandibles, more slender palpi, and paraglossae greatly exceeding the glossae. In the adult the mandibles commonly are much reduced, but Dr. Frison has described sclerotized mandibles in adult *Isoperla decepta* and *I. minuta*, and has observed the latter to feed.

Gills: Lateral abdominal gills are distinguishable in Protoperlaria and are a primitive character. Among modern families they occur regularly in Eustheniidae, where they are simple in Eustheniinae and branched in Diamphipnoidae. Other holoognathous families lack lateral abdominal gills, but in many instances other gills have been developed. These are found in rather diverse locations; for example: on the 10th segment surrounding the anus (Leptoperlidae), inside the cloaca (*Leuctra claasseni*), on the ventral side of the thorax and a few of the abdominal segments (Pteronarcidae), on the lateral and ventral sides of the thorax, and on the subanal lobes (Peltoperlidae), on the coxae (*Taeniopteryx*), and even on the mentum (*Nemoura cataractae*). Only one systellognathous stonefly has lateral abdominal gills (*Oroperla*), but it also has a series of thoracic, cervical and submental gills whose homologues occur in varying abundance among other Isogeninae. Among the other subfamilies of Perlodidae all gills have been lost, except for short submental gills in some Perlodinae. Chloroperlidae lack gills entirely. Perlidae are all characterized by profusely branched lateral thoracic gills, and, in many species, by similar gills attached to the subanal lobes.

Cross-veins: A conspicuous evolutionary trend has been toward a reduction of crossveins. In Eustheniidae they are present almost throughout the wing; in Pteronarcidae most of the crossveins of the anal fan of the hind wing are gone, but they are profuse elsewhere; in Leptoperlidae and Austroperlidae they are less profuse but still numerous. Other holoognathous groups have lost all or nearly all crossveins in the distal portion of both wings (except often in the costal space), and proximally retain only the mediocubital and intercubital series in the fore wings, and sometimes a fair series of costals. Even the M-Cu and Cu₁-Cu₂ series are much reduced in number in Capniinae. In Systellognatha two lines of descent start out with numerous crossveins but lose them in later development. Firstly, the isogenine perlids have few to many apical crossveins in *Arcynopteryx* and some *Isogenus*, but these are lost in the more advanced branches of *Isogenus* and in the derived Isoperlinae. Secondly, among the Perlodinae *Perlodes* retains apical crossveins but *Dictyoptyerygella* lacks them. They are likewise absent in Chloroperlidae.

Among the Perlidae, the Acroneuriinae often (but not always) have apical crossveins. Two genera (*Atoperla*, *Perlinella*) have retained (reacquired?) a few crossveins in the anal region of the forewing, but these lack any in the apical portions of the wings. The Perlinae typically lack extra apical crossveins, but one or two may appear sporadically. Finally, the hind wing has a series of intercubital crossveins in the primitive holoognathous families, and also in Perlidae and most Perlodidae (reduced to 1-3 in *Isoperla*). In Nemouridae they are regularly reduced to a single crossvein, as is true also of Chloroperlinae and *Kathroperla*, but not of *Paraperla*.

Posterior portion of the wings: There has been a tendency for the anal area of the hind wing (and to a less extent the fore wing) to be reduced in more advanced forms, this reduction being correlated, in a general way, with small size of the insect as a whole. Thus among the holoognathous families the small *Leuctrae* and *Capniæ* have a small anal fold in the hind wing, while in *Capniella* the folded anal region is completely absent. The same development occurs in Chloroperlinae, where *Alloperla* has a rather small anal area, in *Chloroperla* it is much smaller with A_2 only about half as long as A_1 , and in *Hastaperla* it is very small, with both anal veins vestigial. With the reduction of anal surface, the number of branches of the second anal vein of the hind wing of course also decreases. In Chloroperlinae the second cubital vein is much reduced in size in the fore wing, and the same is true even in the hind wing in *Hastaperla*.

Thoracic structure: The external anatomy of stoneflies has not been extensively studied from a comparative standpoint, an exception being Hanson's excellent monograph of Capniinae. However, the ventral thoracic plates have been used as a partial basis for generic or subgeneric recognition by Banks, Hanson and others. Here we will note only the "Y-ridge" or supporting structure of the mesosternum. I have not examined material of the primitive southern holoognathous families, but such a ridge appears in Pteronarcidiidae and also in the Scopurinae of Japan. In both cases the arms of the ridge are attached to the posterior or inner corners of the furcal pits (elongate depressions marking the site of an inwardly-directed blade of the exoskeleton, used for muscle attachment). In primitive members of Isogeninae and also in all Perlodinae and Isoperlinae the same relationship holds; however in some members of both *Arcynopteryx* and *Isogenus* the arms of the Y become attached to the anterior corners of the furcal pits. This shift apparently occurred independently in the two genera, and there is considerable other variation in these and other ridges, particularly in *Isogenus*. Of the other systellognathous families, Chloroperlidae retain the primitive posterior attachment of the Y-ridge in some genera; in others the arms of the Y are lost. Perlidae have the anterior attachment, with the arms of the Y short and often nearly horizontal, more like a T.

Male genitalia: Nothing is more characteristic of stoneflies than the large supra-anal process which so often constitutes a main part of the male genitalial apparatus. It was already large and well developed

in Protoperlaria, and occurs in much the same form in Eustheniidae, Leptoperlidae and Austroperlidae. In these forms the process is suspended from the tip of a strong, produced tenth tergite. The same point of insertion occurs in many Nemouridae, in particular Notonemourinae, most Capniinae, some Leuctrinae and some Nemourinae; however, except in Notonemourinae, the process is directed upward and/or forward, instead of downward. In other Nemourinae and most Taeniopteryginae the tenth tergite tends to be shortened, and weakened medially. In a few Leuctrinae and Capniinae the supra-anal process is lost, in which event the tergite remains (or again becomes) normally sclerotized.

Another line of development of the supra-anal apparatus consists of a shift of the attachment of the process forward to the front of the tenth tergite, splitting the tergite into two by the groove in which the process lies. At the same time a tough enveloping membrane or cowl is developed around the sides and posterior end of the process, which dorsally may become sclerotized to form the two paragenital plates. This is the condition found in the Pteronarcyidae. The same arrangement occurs among the Isogeninae, with the addition of two lateral styles lying close to the supra-anal process, in most species. In the other two subfamilies of Perlodidae all this apparatus is lost, except that *Calliperla* (Isoperlinae) retains a small poorly-sclerotized process. The supra-anal apparatus still persists in Chloroperlidae: in the Paraperlinae it is fairly close to the typical isogenine form, except that no lateral stylets are present. In *Alloperla* all but the tip of the process is fused to the tenth tergite, in which case the tip is often referred to as the supra-anal process proper. In the subgenera *Sweltsa* and *Alloperla* s.s. there is still a deep groove in which the basal part of the apparatus lies. However, in *Suwallia* and *Neaviperla* this has largely disappeared. The same is true of the genera *Chloroperla* and *Hastaperla*, in some species of which it is difficult or impossible to differentiate the former basal part of the apparatus from the dorsum of the tergite, and only the small erect tip remains.

Finally, the Perlidae have all lost the accessory structures associated with the supra-anal process, but in the Perlinae the tenth tergite remains split and the genital hooks developed from its borders often assume complicated shapes. The process itself is a low, poorly sclerotized region merely filling in the back of the tergite. In Acroneuriinae the tenth tergite is complete posteriorly, though *Claassenia* has genital hooks developed from the sides of its posterior margin. The supra-anal process itself is unrecognizable except in the Japanese genus *Caroperla*, where it is terminal, erect and of moderate size—apparently a survival from pre-perlid ancestors.

The vagaries of the supra-anal process are of course often associated with a development or loss of other genitalial characters, of the most varied nature. No segment of the abdomen, unless it be the most anterior one, has escaped being involved in the male sexual apparatus, nor have its appendages the cerci and the subanal lobes. Many of these developments have little consistency from one genus to the next and have evi-

dently been produced independently, hence are not of much value in tracing familial lineages; but others can be traced quite extensively and are mentioned in a later section.

Systematic List of Genera

The summary table to follow indicates the systematic position of the genera and subgenera to be currently recognized on the basis of the best information at hand. It is far from a definitive arrangement, as in many groups no recent revision has been attempted, and it seems that a considerable consolidation of genera should be effected, especially in Perlidae. In spite of this, the present arrangement should have some value when used in conjunction with Claassen's (1940) very useful world catalogue of Plecoptera. Because of Dr. Claassen's untimely death this catalogue did not receive the careful systematic reviewing which he had planned. The present generic list corrects at least the more obvious anomalies of the arrangement of the Catalogue, but errors doubtless remain, even though some of the more questionable genera have been listed by family only.

Apart from reassignment of a number of genera, the only novelties are the new subfamilies Diamphipnoinae (type genus *Diamphipnoa* Gerstaecker) and Notonemourinae (type *Notonemoura* Tillyard). It is possible that the large southern group Leptoperlinae could also conveniently be subdivided. On the other hand the subfamily Neoperlinae of Klapálek has here been consolidated with Perlinae. It was based solely on the absence of the anterior ocellus and the proximation of the posterior ones—characters found in members of various other groups where they have not evoked subfamilial recognition. It should be noticed that although numerous species of *Neoperla* have been described from the American tropical regions, none has been shown to have genital hooks developed from the tenth tergite, and it is to be presumed that they all belong in *Anacroneturia* or some related genus. No unquestioned Perlinae have been taken, in America, south of the United States.

Family Eustheniidae Tillyard 1921

Subfamily Eustheniinae

Eusthenia Westwood 1832

Eustheniopsis Tillyard 1921

Stenoperla MacLachlan 1866

Thaumatoperla Tillyard 1921

Subfamily Diamphipnoinae new

Diamphipnoa Gerstaecker 1873

Family Austroperlidae Tillyard 1921

Austroperla Needham 1905

Tasmanoperla Tillyard 1921

Family Leptoperlidae Tillyard 1921

Subfamily Leptoperlinae

Antarctoperla Enderlein 1905

Auklandobius Enderlein 1909

- Dinotoperla* Tillyard 1921
- Eunotoperla* Tillyard 1924
- Gripoptera* Sámal 1921
- Gripopteryx* Pictet 1841
- Klapopteryx* Pictet 1841
- Leptoperla* Newman 1839
- Megaleptoperla* Tillyard 1923
- Nesoperla* Tillyard 1923
- Nydyse* Navás 1923
- Paragripopteryx* Enderlein 1909
- Paranotoperla* Enderlein 1909
- Senzilla* Navás 1917
- Trinotoperla* Tillyard 1924
- Zelandobius* Tillyard 1924
- Zelandoperla* Tillyard 1923
- Subfamily Scopurinae Uéno 1938
- Scopura* Uéno 1929
- Family Peltoperlidae Claassen 1931
- Cryptoperla* Needham 1909
- Neopeltoperla* Kohno 1945
- Nogiperla* Okamoto 1912
- Peltoperla* Needham 1905
- Incertae sedis, possibly Peltoperlidae: *Microperla* Chu 1928,
- Styloperla* Wu 1935
- Family Nemouridae Klapálek 1905
- Subfamily Notonemourinae new
- Notonemoura* Tillyard 1923
- Spaniocerca* Tillyard 1923
- Spaniocercoides* Kimmins 1938
- Subfamily Nemourinae Klapálek 1905
- Nemoura* Pictet 1841. Subgenera *Amphinemura* Ris 1902,
- Nemurella* Kempny 1898, *Paranemoura* Needham and Claassen 1925, *Protonemura* Kempny 1898.
- Subfamily Leuctrinae Klapálek 1905
- Aphanicerca* Tillyard 1931. Subgenera *Aphanicercella* Tillyard 1931, *Aphanicercopsis* Barnard 1934.
- Desmonemoura* Tillyard 1931
- Leuctra* Stephens 1835. Subgenera *Despaxia* Ricker 1943,
- Moselia* Ricker 1943, *Pachyleuctra* Despax 1929, *Paraleuctra* Hanson 1941.
- Megaleuctra* Neave 1934
- Perlomyia* Banks 1906
- Rhopalopsale* Klapálek 1903
- Stroblia* Klapálek 1903
- Udamocercia* Enderlein 1909
- Subfamily Capniinae Klapálek 1905
- Allocapnia* Claassen 1928
- Apteroperla* Matsumura 1931

Capnia Pictet 1941. Subgenus *Parcapnia* Hanson 1946

Capniella Klapálek 1920

Capnioneura Ris 1905

Capnopsis Morton 1896

Eucapnopsis Okamoto 1922

Isocapnia Banks 1938

Nemocapnia Banks 1938

Takagripopteryx Okamoto 1922

Subfamily Taeniopteryginae Klapálek 1905

Brachyptera Newport 1848. Subgenera *Doddsia* Needham and Claassen 1925, *Obipteryx* Okamoto 1922, *Oemopteryx* Klapálek 1902, *Rhabdiopteryx* Klapálek 1902, *Strophopteryx* Frison 1929, *Taenionema* Banks 1905.

Kyphopteryx Kimmins 1946

Taeniopteryx Pictet 1841

Nemouridae of uncertain affinity: *Allonuria* Claassen 1936, *Napcia* Navás 1917, *Neofulla* Claassen 1936, *Neonemura* Navás 1919, *Nephopteryx* Navás 1915.

Family Pteronarcidae Enderlein 1909

Pteronarcella Banks 1900

Pteronarcys Newman 1838

Family Perlodidae Klapálek 1912

Subfamily Isogeninae Ricker 1943

Arcynopteryx Klapálek 1904. Subgenera *Filchneria* Klapálek 1907, *Frisonia* Ricker 1943, *Megarcys* Klapálek 1912, *Oroperla* Needham 1933, *Perlinodes* Needham and Claassen 1925, *Protarcys* Klapálek 1912, *Skwala* Ricker 1943.

Isogenus Newman 1833. Subgenera *Dictyogenus* Klapálek 1904, *Diploperla* Needham and Claassen 1925, *Hydroperla* Frison 1935, *Isogenoides* Klapálek 1912, *Pictetia* Banks 1947.

Pseudomegarcys Kohno 1946

Subfamily Perlodinae

Dictyopterygella Klapálek 1904

Perlodes Banks 1903

Perlodinella Klapálek 1912

Skobeleva Klapálek 1912

Subfamily Isoperlinae Frison 1942

Calliperla Banks 1947

Isoperla Banks 1906

Perlodidae of uncertain position: *Diperla* Navás 1936, *Hedinia* Navás 1936, *Suzukia* Okamoto 1912.

Family Chloroperlidae Okamoto 1912

Subfamily Paraperlinae Ricker 1943

Kathroperla Banks 1920

Paraperla Banks 1906

Subfamily Chloroperlinae

Alloperla Banks 1906

Chloroperla Newman 1836

Haploperla Navás 1934

Hastaperla Ricker 1935

Family Perlidae

Subfamily Acroneuriinae Klapálek 1914

Acroneuria Pictet 1941. Subgenera *Beloneuria* Needham and Claassen 1925, *Eccoptura* Klapálek 1921, *Hesperoperla* Banks 1938, *Niponiella* Klapálek 1907.

Anacroneuria Klapálek 1909

Atoperla Banks 1905

Brahmana Klapálek 1914

Caroperla Kohno 1946

Claassenia Wu 1934

Eutactophlebia Klapálek 1914

Gibosia Okamoto 1912

Inconeuria Klapálek 1916

Kalidasia Klapálek 1914

Kempnyia Klapálek 1914

Kiotina Klapálek 1909

Klapalekia Claassen 1936

Macrogynoplax Enderlein 1909

Mesoperla Klapálek 1913

Mesoperlina Klapálek 1921

Neoeuryplax Claassen 1936

Nirvania Klapálek 1914

Onychoplax Klapálek 1914

Perlesta Banks 1906

Perlinella Banks 1900

Schistoperla Banks 1937

Subfamily Perlinae McLachlan 1886

Agnentina Klapálek 1907

Cerconychia Klapálek 1913

Dyaperla Banks 1939

Etrocorema Klapálek 1909

Formosita Klapálek 1914

Hemimelanena Klapálek 1907

Kamimuria Klapálek 1907

Kiotina Klapálek 1907

Marthamea Klapálek 1907

Ncooperla Needham 1905. Subgenera: *Javanita* Klapálek 1909, *Ochthopetina* Enderlein 1909, *Oodeia* Klapálek 1921, *Phanoperla* Banks 1938.

Ncooperlops Banks 1939

Ncophasganophora Lestage 1922

Oyamia Klapálek 1907

Paragnetina Klapálek 1907

Perla Geoffroy 1764. Subgenera: *Dinocras* Klapálek 1907, *Esera* Navás 1909.

Tetropina Klapálek 1909

Togoperla Klapálek 1907

Tylopyge Klapálek 1913

Perlidae of uncertain affinities: *Collampla* Navás 1929, *Colloperla* Navás 1936, *Folga* Navás 1918, *Forca* Navás 1925, *Forquilla* Navás 1924, *Laeissa* Navás 1934, *Nakaharia* Navás 1916, *Nedanta* Navás 1932.

Distribution of the Families and Subfamilies

On zoogeographical grounds various groups of stoneflies can be arranged as follows:

1. Eustheniidae, Leptoperlidae and Austroperlidae are ancient families now confined to the southern periphery of a probable former world-wide range—namely the Australasian region and southern South America—thus paralleling the well-known distribution of the marsupials among mammals. However a wingless leptoperlid has persisted in Japan.

2. The Pteronarcidiidae are to be regarded as a North American family, primarily, which has invaded Asia in relatively recent times, where it is known from eastern Siberia and Sakhalin.

3. Peltoperlidae are rather generally distributed in North America, but are not rich in species. A single species has been described from South America, but it is poorly known. In Asia the family is represented from Japan and the China coast southwestward to India, and on adjacent islands of the Pacific; but again is nowhere abundant.

4. The nemourid holorhynchos stoneflies are represented by a distinct subfamily in Australasia, and by some Leuctrinae in South Africa and in Tierra del Fuego (*Udamocercia*). Like the Eustheniidae *et al.*, these southern forms can be regarded as survivals of types once much more widespread. In the case of *Udamocercia*, the closely-related (?identical) genus *Megaleuctra* still lives in North America, and has also been recognized in the Baltic amber. The more typical Leuctrinae, and also the Nemourinae, Capniinae and Taeniopteryginae have a holarctic distribution, south in Asia to the Himalayan ranges and in America to Mexico City (*Nemoura venusta*).

5. Among Systellognatha two of the families are holarctic while the Perlidae are primarily tropical. Both in Perlodidae and Chloroperlidae the North American fauna seems more varied than the Eurasian—though it is also better known. In any event more interesting primitive forms or “missing links” have turned up in America—for example *Oroperla*, *Calliperla* and the Paraperlinae—but it is scarcely possible to identify the center of origin of either family.

6. The Perlidae divide themselves rather sharply into the two subfamilies Perlinae and Acroneuriinae, characterizing the old and new worlds respectively. Most abundant in the American tropics, Acroneuriinae also have a considerable development in temperate North America. They are fairly numerous in eastern Siberia, Japan and China and also occur in India (*Brahmana*) and the Malayan region (*Kalidasia*), if these two genera are true acroneuriines.

The Perlinae, on the other hand, are *the* stoneflies of the old-world tropics, including Africa, India and the East Indies. A fair number of species range north into Europe, and a much larger number occur through central Asia, China and Japan. Three Oriental genera have invaded North America, presumably not too long ago. These are *Neoperla* (1 species), *Neophasganophora* (1 or 2 species) and *Paragnetina* (5 species). However, it is interesting that none of these species occurs west of the great plains, where they might have been expected to be if the invasion has been really recent.

Evolutionary Sequence

No study of this sort is complete without a family tree, even if only a tentative one. Like most phylogenetic trees, the one shown in figure 1 is simplified in this respect: that, strictly speaking, no living group of organisms is the ancestor of any other living group. This is true even in cases (which are known at the specific and possibly the generic level in some well-studied groups of animals) where a given form X seems likely to have given birth to form Y, and X appears not to have changed appreciably itself since the event. When dealing, as here, with families and subfamilies, such an eventuality becomes most improbable. For example, no modern isogenine is ancestor to any other stonefly family or subfamily; we suggest only that some modern Isogeninae are reasonable facsimiles of the real ancestors of Chloroperlidae, etc., and can stand for them in the family tree. Or in other words, if the actual ancestors were before us, we believe that they would look enough like modern isogenines to be classified in the same subfamily. In figure 1 groups having combinations of characteristics not present in any known species are shown in boxes and are given a letter designation.

The transition from the Permian Protoperlaria to modern stoneflies was marked by the loss of the lateral expansions of the prothorax and the loss of the posterior median vein. The Eustheniinae are possible ancestors of all other living stoneflies. The transition from Eustheniinae to Leptoperlidae was a simplification of venation, loss of lateral gills, and a development of circumanal branched gills.

Concerning the origin of Nemouridae there are two possible hypotheses, between which it is difficult to choose. Taking a leptoperlid as a starting point, a further loss of crossveins and loss of the circumanal gills would yield a primitive nemourid (C). Such a nemourid would have retained long cerci and would have copulatory apparatus somewhat as in Notonemourinae, where the suspension of the supra-anal process and subanal lobes are much akin to some forms of Leptoperlidae, with the exception of the ventral lobe on the ninth sternite—the latter being a very characteristic nemourid structure. It is this lobe, however, which suggests a relationship between Nemouridae and Peltoperlidae, which also have it, and in that event these two families would have branched directly from Eustheniidae and had a short common history before going their separate ways. This is the path illustrated in figure 1. Whatever their origin, a major cleavage soon occurred among the early nemourids,

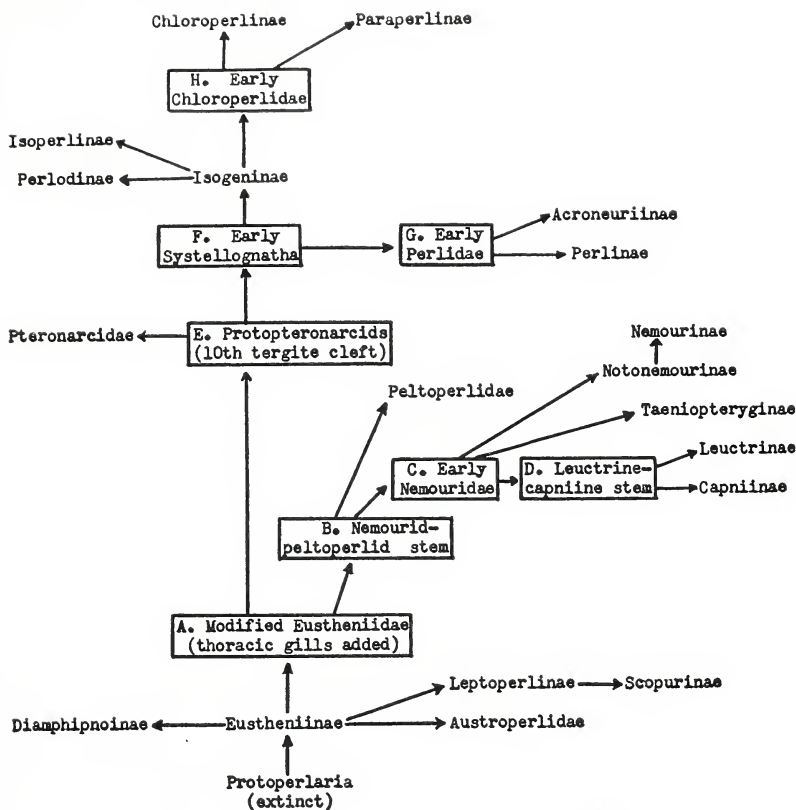


Figure 1. Tentative phylogenetic tree for Plecoptera.

splitting off a group (D), characterized by slender nymphs having wing pads lying parallel to the axis of the body, from the more robust nymphal types having the wing pads set obliquely (the primitive position). Group D became further divided into the modern Capniinae and Leuctrinae, of which the former characteristically have reduced medial and cubital crossveins and long cerci, and the latter have several crossveins and only a single cercal segment—though it is not easy to draw a satisfactory line of demarcation. The more typical nemourine stem gave rise to the Taeniopteryginae on the one hand and the Notonemourinae on the other, the latter being an Australasian subfamily some of whose members are quite plausible ancestors of the widespread northern Nemourinae.

The Peltoperlidae are the most puzzling of stoneflies. Their body form superficially suggests a cockroach, and it is perhaps surprising

that they have not at some time or other been considered as direct descendants of some palaeozoic blattoid ancestor! Venation and gills, of course, would not permit such a phylogeny even if a suitable ancestor were available. The thin posterior projections of their nymphal thoracic sterna are apparently unique in the order. The ventral lobe of *Peltoperlidae* suggests nemourid affinities, while their thoracic gills relate them to the main stem of stonefly evolution. The latter occurrence makes it necessary to place the origin of double thoracic gills far back in the history of the group—probably in a form still recognizable as a eustheniid (A). Such an ancestor also had a pair of cervical gills (found in two surviving isogenines and a few *Peltoperlae*) and possibly also the submental gills characteristic of many isogenines. The supra-anal process of *Peltoperla* is not as prominent as in Eustheniidae or Nemouridae, but the tenth tergite has not been cleft.

The main trunk of stonefly evolution from the Eustheniidae apparently led first to a form (E) in which the tenth tergite became split and the suspension of the supra-anal process moved forward to the segment's anterior border; it probably also had lost some of the crossveins of the anal area of the hind wing. Of such a form the Pteronarcidae are the nearest modern representatives, differing only in the fact that the gills have shifted to a ventral position, have become branched, and, on the abdomen, are gone from all but the two or three most anterior segments. Further "main-line" evolution of Group E involved a major change in nymphal mouth parts from the hognathous to the systelognathous type, corresponding, in general, to a change in feeding habit from herbivorous to carnivorous. The ancestor which made this change (F) still had the lateral abdominal and thoracic gills, and had a fairly profuse supply of crossveins. Both of these characters persist in the more primitive Isogeninae, though abdominal gills occur in only one species today. Evolution within the Isogeninae involves a progressive loss of gills and of crossveins; while the loss of the supra-anal apparatus, on two separate occasions, has produced the Isoperlinae and Perlodinae. A third development from Isogeninae yielded the Chloroperlidae, which retained the supra-anal process. This family is characterized by long slender nymphs usually with short cerci, and with mouth parts somewhat altered from the perlodid form. Surviving genera also have either an unusually elongated head capsule (Paraperlinae), or the anal area much reduced in the hind wing and the second cubital of the forewing very short (Chloroperlinae); but they were doubtless preceded by early forms (H) which lacked these specializations.

Most characteristic of all modern stoneflies are the Perlidae—the only family which has been really successful in adapting itself to tropical conditions; or perhaps we should say, which has driven other families out of the lush tropical zone. Our figure shows it diverging from the primitive systelognathous ancestor (F) which it had in common with the Perlodidae. The abdominal gills of that ancestor do not appear in any modern perlid, but its lateral thoracic gills are a constant feature of the family—they are always finely branched however.

At an early stage the family divided into the two groups which today are characteristic of the two hemispheres. In both divisions the supra-anal process lost all function or disappeared (except that one acroneuriine, *Caroperla*, still has it, quite possibly from primitive times). In Perlinae the "genital hooks", or elongated corners of the cleft of the tergite, are retained and indeed undergo a rather grandiose development, taking complex forms in different genera. At the same time the surplus crossveins of the wing have disappeared. The Acroneuriinae, on the other hand, have lost the genital hooks of the tenth tergite, which latter has become entire (except for hooks developed more laterally in *Claassenia*); however the subanal lobes are almost always produced upward into sharp hooks or similar copulatory organs. Many *Acroneuriae* also retain the numerous apical crossveins which must have characterized the earliest Perlidae.

Literature Cited

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