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Affinity of Ephemeroptera: A Review of the Proposed Phylogenetic Relationships of the Major Pterygote Groups, the Ephemeroptera, Odonata, and Neoptera, Based on Comparative Embryology

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Abstract. The Ephemeroptera, which represent one of the pterygote basal clades, were examined in light of comparative embryology, focusing on the following characters: 1) amnioserosal fold, 2) germ type, 3) cleavage, 4) egg tooth, 5) formation of midgut epithelium, 6) invagination type of embryo, 7) formation of proctodaeum, 8) micropyle, 9) extension of embryonic area, 10) clypeolabral rudiment, 11) superlingua, and 12) caudal filament as an elongation of telson. The embryological and morphological ground plans in insects or pterygotes were discussed as well as their evolutionary transition. The pterygote phylogenies currently proposed were reviewed from the comparative embryological standpoint, and the phylogeny as [Ephemeroptera + (Odonata + Neoptera)] was supported.
Key words. Ephemeroptera, Odonata, Neoptera, Comparative embryology, Ground plan, Affinity, Phylogeny

Introduction

Insects account for three quarters of all animal species. More than 99 percent of them are wing-acquired insects or the Pterygota. The evolution of insects or pterygotes, which have attained a spectacular prosperity and radiation, is an interesting subject. In this article, we focus on the mayflies or Ephemeroptera, one of the closest relatives to the early pterygote ancestors (cf. Hennig, 1953).

The phylogeny of insects particularly on the basal clades of pterygotes remains controversial. Three phylogenies have been proposed concerning the interrelationships of the major pterygote groups, i. e., the Ephemeroptera, the Odonata, and all the remaining pterygote groups, the Neoptera. Hennig (1953, 1969) and Rohdendorf et al. (1962) supported the phylogeny [Paleoptera (= Ephemeroptera + Odonata) + Neoptera] from morphological evidence and based on paleontology, respectively. Kristensen (1975, 1991) and Wheeler and Carpenter (1996) supported the phylogeny [Ephemeroptera + (Odonata + Neoptera)] mainly from morphological evidence and from an overall analysis, respectively. Lemche (1940) and Matsuda (1981), through studies of comparative morphology, and Boudreaux (1979), based on functional morphological evidence and the development of wing buds, supported the phylogeny [Odonata + (Ephemeroptera + Neoptera)]. Thus, the study of Ephemeroptera may be especially significant to attempts to elucidate the evolutionary transition of the basic body plan as well as the ground plan of morphogenesis in insects or pterygotes and to reconstruct their phylogeny.

A comparative embryological approach is useful for elucidating phylogenetic accounts. Despite of a number of studies such as Joly (1876), Heymons (1896a, b, c), Murphy (1922), Ando and Kawana (1956), Wolf (1960), Bohle (1969), and Tsui and Peters (1974), the ephemeropteran embryology is still not well understood.

We have been conducting a comparative embryological study of the Ephemeroptera, using *Ephemera japonica* McLachlan (Ephemeridae) as materials (cf. Tojo and Machida, 1996, 1997a, b, 1998a, b; Tojo, 1999). In previous works, we examined the embryonic development of the species in detail, to extend discussions on the insect or pterygote body plan and embryogenesis in the light of evolution, and referred to the ground plan of body construction and embryogenesis of the insects or pterygotes as well as their evolutionary transition (Tojo and Machida, 1996, 1997a, b, 1998a, b, 2001; Tojo, 1999). In this paper, based on our previous studies, we discuss and illustrate the evolutionary transition of the body plan and ground plan of embryogenesis of insects or pterygotes, so as to re-examine the pterygote phylogeny, with special reference to the affinity of the three major pterygote groups, the Ephemeroptera, Odonata and Neoptera.

Revaluation of embryological characters

For the basal clades of insects, we adopted Hennig's "Entognatha-Ectognatha system" which is currently the most reliable (cf. Hennig, 1969; Kristensen, 1975). However, the Zygentoma are also taken into account: not to do so would be to recognize unconditionally the Ephemeroptera - Odonata - Neoptera as monophyletic: the monophyly or Pterygota should be examined, as a prerequisite to any discussion of their affinities. For determining the state of each character, the Archaeognatha were used as the out-group of Dicondylia (= Zygentoma + Pterygota).

The following twelve characters were used for elucidating the phylogeny: 1) amnioserosal fold, 2) germ type, 3) cleavage, 4) egg tooth, 5) formation of midgut epithelium, 6) invagination type of embryo, 7) formation of proctodaeum, 8) micropyles, 9) extension of embryonic area, 10) clypeolabral rudiment, 11) superlingua, and 12) caudal filament as an elongation of telson. Because this number is too small to illustrate the phylogeny directly and cladistically, we mapped the characters, the state of each of which was determined for the three different phylogenies (cf. Fig. 1A-C). The results supported monophylies of Pterygota, Dicondylia and Ectognatha. In Figure 1A to C, numerals indicate the characters or character states, as designated above (and in the text): transformation of each character is shown by the dashing numeral. Open and solid circles represent plesiomorphic (ancestral) and apomorphic (derived) character states, respectively. Double-headed and single-headed arrows indicate synapomorphic (or symplesiomorphic) relationships and the transformation of character, respectively. The double-headed shaded lines show the parallel acquisition of a character by the groups indicated with arrows. The arrowed numerals in parentheses show that the character was transformed in another form within one or more groups of the lineage conserved.

1) Amnioserosal fold

In myriapods and entognathous insects, the embryonic membrane is represented by the serosa, and neither the amnion nor the amnioserosal fold is developed. These structures first appeared in the Ectognatha (= Archaeognatha + Dicondylia [= Zygentoma + Pterygota]) as an autapomorphy (cf. Machida *et al.*, 1994; Machida and Ando, 1998; Machida *et al.* [2002] newly proposed an idea that the amnion is an apomorphy of the Diplura plus Ectognatha).

In the Dicondylia, the amnioserosal fold is completely fused, forming a closed amniotic cavity system, the amnioserosal fold - amniotic cavity, which had been considered to be an autapomorphy of the group. The amnioserosal fold was inherited into the archaeognathan and dicondylian (including the Ephemeroptera) lineages as a synapomorphy, and in the latter it transformed itself into the amnioserosal fold - amniotic cavity system.

The numerals 1 and 1' are used here to refer to the amnioserosal fold and the amnioserosal fold-amniotic cavity system, respectively.

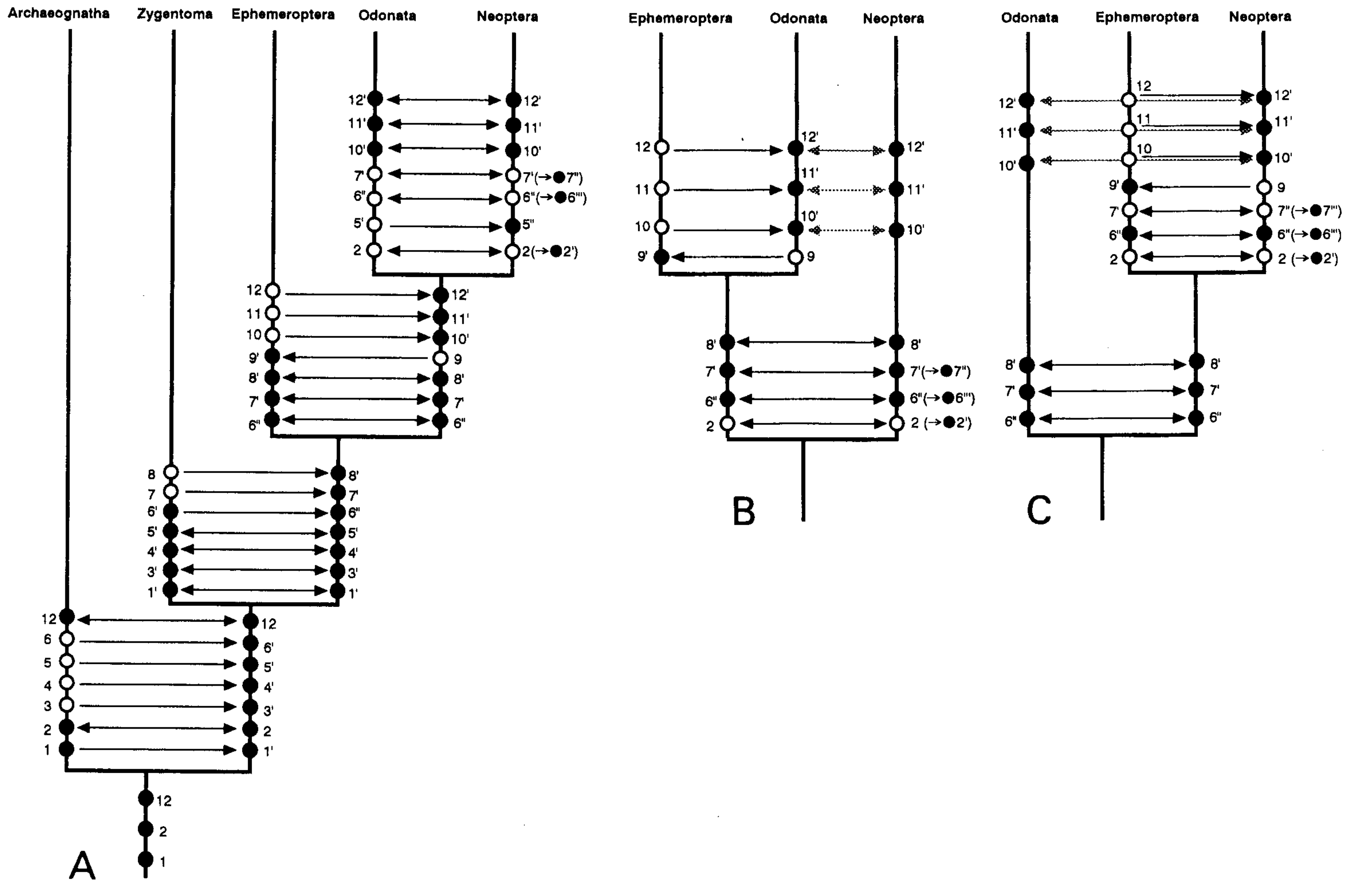

Fig. 1. Map of the embryological characters for the currently proposed phylogenesis of Ectognatha / Pterygota (A - C). See text.

As to the function of this system, certain mechanical advantages, such as protection of the embryo, have been assumed (Sharov, 1966; Ando, 1970, 1988; Zeh et al., 1989), but nothing definite is known (cf. Anderson, 1972a). However, Machida et al. (1994, 2002) and Machida and Ando (1998) have extended discussion on the functional role of the amnioserosal fold, based on the evolutionary transition of functional specialization between the embryo proper and embryonic membranes in the Atelocerata (= Myriapoda + Insecta). They concluded that the fold was acquired during the evolution of insects in order to secrete the serosal cuticle beneath the embryo, a function lost in the course of atelocerate evolution. It has been confirmed that in the ephemeropteran *Ephemera japonica*, the serosal cuticle is not secreted until the completion of anatrepsis; that is, until the embryo is ventrally covered by the amnioserosal fold and the entire egg surface is occupied by serosa (Tojo and Machida, 1997b, 2001). This may support the assumption of Machida et al. (1994, 2002) and Machida and Ando (1998) that the principal functional role of the amnioserosal fold and the amnioserosal fold - amniotic cavity system as its advanced form lies in the secretion of serosal cuticle beneath the embryo.

2) Germ type

The embryo of Ephemeroptera can be categorized as a typical short germ type, characterized by the sequential proliferation of segments anterior to posterior (cf. Krause, 1939) (e. g., baetids *Baetis rhodani* and *Baetis vernus* [Bohle, 1969], ephemerids *Ephemera strigata* [Ando and Kawana, 1956], *Ephemera japonica* [Tojo and Machida, 1997a, b, 1998a, b], and a polymitarcyid *Tortopus incertus* [Tsui and Peters, 1974]).

The germ rudiment of the short germ type first appeared in the Archaeognatha (Machida, 1981) and was inherited by the dicondylian lineage (e. g., the odonaten *Epiophlebia superstes* [Ando, 1962], the plecopteran *Kamimuria tibialis* [Kishimoto and Ando, 1985], and in higher orders such as paraneopterans [Anderson, 1972a]). It may be regarded as an autapomorphy of Ectognatha (cf. Sander, 1984).

The numeral 2 represents the short germ type.

Appendix: In the higher neopterans, germ type is transformed into the long form, which is recognized as an apomorphy (shown by 2'; cf. Krause, 1939).

3) Cleavage

The cleavage is fundamentally holoblastic in the arthropods, whereas in primitive insects including the Archaeognatha, total cleavage is predominant. The fertilized egg of *Ephemera japonica*, however, undergoes a typical superficial cleavage (Tojo and Machida, 1998a, b), which is characteristic of dicondylian insects (Johannsen and Butt, 1941; Sharov, 1966). The superficial cleavage in insects is recognized as an autapomorphy of Dicondylia (cf. Machida et al., 1990).

The numerals 3 and 3' are used to indicate total and superficial cleavages, respectively.

4) Egg tooth

In the final embryonic stage of Ephemeroptera, the larval cuticle is secreted beneath the embryonic cuticle, and a sclerotized egg tooth appears in the frontal region (e. g., a siphlonurid *Siphlonurus lacustris* and heptageniids *Heptagenia sulphurea*, *Heptagenia lateralis* [Degrange, 1960], a polymitarcyid *Tortopus inceratus* [Tsui and Peters, 1974] and an ephemerid *Ephemera japonica* [Tojo, 1999]).

The egg tooth is not found in entognathous insects and archaeognathans (cf. Jura, 1972; Machida, 1981), but is present in the zygentomans (cf. Sharov, 1953). Thus it can be recognized as an autapomorphy of the dicondylian lineage (cf. Sharov, 1966; Ando and Kobayashi, 1996).

The numerals 4 and 4' indicate the absence and presence of egg tooth, respectively.

5) Formation of midgut epithelium

The midgut epithelium is exclusively derived from yolk cells in apterygotes other than the dicondylian apterygote Zygentoma, i. e., the Collembola (Uljanin, 1875; Claypole, 1898; Uzel, 1898; Prowazek, 1900; Jura, 1972; Jura and Krzysztofowicz, 1977), Diplura (Heymons, 1897; Ikeda, 2001) and Archaeognatha (Machida and Ando, 1981). On the other hand, in the pterygotes, more strictly the neopterans, the midgut epithelium is entirely originated from the midgut epithelial rudiments arising from the blind ends of stomodaeum and prctodaeum, and is ectodermal in origin (cf. Johannsen and Butt, 1941; Anderson, 1972a, b; Ando and Kobayashi, 1996).

Our studies revealed that the midgut epithelium in ephemeropteran *Ephemera japonica* has a dual origin: the anterior and posterior parts are respectively stomodaeal and proctodaeal, i. e., ectodermal in origin, and the middle part is of yolk cell in origin (cf. Tojo, 1999). Such a midgut epithelium has been also reported for the Zygentoma (e. g., *Lepisma saccharina*; Sharov, 1953) and Odonata (e. g., *Epiophlebia superstes*; Ando, 1962), that is, the most ancestral dicondylian Zygentoma, and another representative of the most primitive pterygotes, the Odonata.

An anagenetical transition in the formation of the midgut epithelium occurred in insects: the midgut epithelium is formed exclusively by yolk cells in entognathous insects and in archaeognathans, whereas it is ectodermal in origin in neopterans. In the zygentomans, ephemeropterans and odonatans, it is formed by both yolk cells and by ectoderm.

This anagenetical transition can be interpreted in terms of the character states. First, the midgut epithelium formation by yolk cells is recognized as a plesiomorphic event within insects (cf. Machida and Ando, 1981), because it is basic to the myriapods and crustaceans (Johannsen and Butt, 1941; Anderson, 1973; Machida and Ando, 1981). The participation of ectoderm in the formation of midgut epithelium is apomorphic for Dicondylia. In the Neoptera, the midgut epithelium is exclusively ectodermal in origin, implying loss of the ability for differentiation by the yolk cells, a character which can be recognized as being apomorphic to the group.

The numerals 5, 5' and 5" indicate, respectively, that the midgut epithelium was formed exclusively by yolk cells, the ectoderm played a role in the formation, and the midgut epithelium was formed exclusively by the ectoderm, i. e., the yolk cells lost the ability to differentiate into the midgut epithelium.

6) Invagination type of embryo

The invagination of embryo into yolk is considered to have been first acquired by the Dicondylia, because it appears to be closely linked to the acquisition of the amnioserosal fold-amniotic cavity system (cf. Tojo and Machida, 1997b; Machida and Ando, 1998). Thus, the invagination of embryo can be recognized as a synapomorphy of Zygentoma and Pterygota. The Archaeognatha (e. g., *Pedetontus unimaculatus* [Machida et al., 1994, Machida and Ando, 1998]) have an amnioserosal fold, but it does not develop into a cavity system.

The deep invagination in S-shaped embryos of the ephemeropteran *Ephemera japonica* (Tojo and Machida, 1996, 1997a, b) also occurs in representatives of primitive pterygotes (as well as in some higher pterygotes such as the paraneopteran orders), whereas in the Zygentoman (e. g., *Lepisma saccharina*; Sharov, 1966), the invagination is not so extensive. It may be safely assumed that the deep invagination is basic to the pterygotes and apomorphic to their stem.

The numerals 6, 6' and 6" respectively indicate the primitive condition found in Archaeognatha, the invagination of embryo in Zygentoma, and the deep invagination of S-shaped embryos.

Appendix: In some higher neopterans, the invagination-type of embryo is transformed into other forms, which are recognized as apomorphic (shown by 6'''; cf. Johannsen and Butt, 1941).

7) Formation of proctodaeum

In apterygotes, i. e., the entognathans, archaeognathans and zygentomans, the proctodaeum is formed as a simple ectodermal invagination like in myriapods and crustaceans. This feature is recognized as plesiomorphic within insects.

In pterygotes, however, the proctodaeum is formed by the fusion of belt-like proctodaeal rudiments, such as in the Ephemeroptera (e. g., a baetid *Baetis rhodani* [Bohle, 1969], ephemerids *Ephemera danica* [Heymons, 1896a], *Ephemera strigata* [Ando and Kawana 1956] and *Ephemera japonica* [Tojo and Machida, 1996, 1997a, b], a polymitarcyid *Tortopus incertus* [Tsui and Peters, 1974]), Odonata (e. g., *Epiophlebia superstes*; Ando, 1962) and some neopteran groups (e. g., hemipterans *Pyrrhocoris spterus* [Seidel, 1924], *Oncopeltes faciatus* [Butt, 1949], *Pyrilla perpusilla* [Sander, 1956], a mecopteran *Panorpa pryeri* [Suzuki and Ando, 1981], a trichopteran *Stenopsyche griseipennis* [Miyakawa, 1975] and lower lepidopterans *Endoclita signifer* [Kobayashi et al., 1981], *Neomicropteryx nipponensis* [Kobayashi and Ando, 1988]). This manner of proctodaeal formation can be regarded as basic in pterygotes and apomorphic to their stem.

The numerals 7 and 7' represent proctodaeum formed by simple invagination and by the fusion of belt-like rudiments, respectively.

Appendix: In some groups of neopterans, the proctodaeum is formed by simple ectodermal invagination, which may be regarded as a new character of each group (shown by 7''; cf. Johannsen and Butt, 1941).

8) Micropyles

Many ephemeropterans develop micropyles (cf. Degrange, 1960; Koss, 1968; Koss and Edmunds, 1974; Hinton, 1981; Gaino and Mazzini, 1984, 1987, 1988; Gaino et al., 1987, 1989; Tojo and Machida, 1998b, c), as do other pterygote insects (Hinton, 1981; e. g., a plecopteran *Perlodes microphala*; a phasmid *Carausius morosus*; hemipterans *Triatoma infestans*, *Belostoma* sp. and *Lethocerus indius*; a mecopteran *Harpobittacus australis*; lepidoptereans *Crambus pascuellis* and *Lycaena phlaeas*; and dipterans *Psila rosae* and *Fannia canicularis*; etc.).

Micropyles have not been reported in apterygotes or myriapods and are regarded as an autapomorphy of the Pterygota.

The numerals 8 and 8' indicate the absence and presence of micropyles, respectively.

9) Extension of embryonic area

In the Ephemeroptera, a very broad embryonic area is formed, to produce a small germ disc by condensation (e. g., a baetid *Baetis rhodani* [Bohle, 1969]; ephemerids *Ephemera strigata* [Ando and Kawana, 1956] and *Ephemera japonica* [Tojo and Machida, 1997a, b, 1998a, b]). This broad embryonic area, in which condensation results in the formation of germ rudiment, is unique to insects, and is regarded as an autapomorphy to the Ephemeroptera.

The numerals 9 and 9' indicate the embryonic area common to ectognathans and the broad embryonic area found in the Ephemeroptera, respectively.

10) Clypeolabral rudiment

In myriapods and apterygotes, the clypeolabrum arises as a single structure (e. g., a chilopoden *Scolopendra cingulata* [Heymons, 1901]; a symphylan *Hanseniella agilis* [Tiegs, 1940]; a pauropoden *Pauropus silvaticus* [Tiegs, 1947]; a diplopoden *Glomeris marginata* [Dohle, 1964]; a collembolan *Tomocerus ishibashii* [Uemiya and Ando, 1987]; diplurans *Japyx major* [Silvestri, 1933] and *Lepidocampa weberi* [Ikeda and Machida, 1996, 1998]; an archaeognathan *Pedetontus unimaculatus* [Machida, 1981]; and a thysanuran *Lepisma saccharina* [Sharov, 1966]), the same as in the Ephemeroptera (e. g., a ephemerid *Ephemera japonica*; Tojo, 1999), and the clypeolabrum as a single unpaired structure, is regarded as plesiomorphic within the insects. In the Odonata (e. g., *Epiophlebia superstes*; Ando, 1962) and Neoptera (cf. Eastham, 1930; Rempel, 1975; e. g., a lepidopteran *Endoclita sinensis* [Tanaka et al., 1983]; a mecopteran *Panorpa pryeri* [Suzuki, 1990]; and trichopterans *Nemotaulius admorsus* [Kobayashi and Ando, 1990], *Stenopsyche marmorata* [Miyakawa, 1974]), the clypeolabrum is formed by the fusion of paired rudiments, and this is to be regarded as apomorphic to the Odonata and Neoptera.

The numerals 10 and 10' indicate clypeolabral rudiments formed as a single unpaired structure and as a paired structure, respectively.

11) Superlingua

In myriapods, apterygotes and ephemeropterans, the hypopharynx differentiates into the superlinguae and lingua (e. g., a pauropodan *Pauropus silvaticus* [Tiegs, 1947]; a symphylan *Hanseniella agilis* [Tiegs, 1940]; a collembolan *Tomocerus ishibashii* [Uemiya and Ando, 1987]; a dipluran *Lepidocampa weberi* [Ikeda and Machida, 1996, 1998]; an archaeognathan *Pedetontus unimaculatus* [Machida, 1981]; and an ephemeropteran *Ephemera japonica* [Tojo, 1999]), whereas in the odonatans and neopterans, superlinguae do not develop. The differentiation of superlinguae is to be recognized as plesiomorphic within the insects, and the loss of differentiation as synapomorphic to the odonatans and neopterans.

The numerals 11 and 11' indicate the differentiation of superlinguae and the loss of their differentiation, respectively.

12) Caudal filament as an elongation of telson

Our studies have revealed that the caudal filament of the Ephemeroptera is an elongation of telson (Tojo and Machida, 1996, 1997b). Machida (1981) made a similar interpretation for the caudal filament of the archaeognathan *Pedetontus unimaculatus*. Structures closely resembling the caudal filament of Ephemeroptera are present in the Zygentoma and Paleozoic monuran *Dasyleptus* spp., the origin of which could be similar to that in the Ephemeroptera: the Monura is regarded as part of the Dicondylia together with the Zygentoma and Pterygota (Kukalová-Peck, 1987). Structures resembling the caudal filaments in these insects are not found in any other atelocerates, so the caudal filament can be recognized as an autapomorphy of the Ectognatha.

Ectognathans other than the Archaeognatha, Monura, Zygentoma and Ephemeroptera, namely, the Odonata and Neoptera, do not possess the caudal filament, and this character condition, i. e., the loss of caudal filament, may be recognized as a synapomorphy to the Odonata and Neoptera.

The numerals 12 and 12' represent the acquisition and the loss of caudal filaments, respectively.

Affinity of Ephemeroptera evidenced by embryological data

The states of twelve characters were examined and determined. In Figure 1, these characters are mapped on the three phylogenies currently proposed: A) the phylogeny supported by authors such as Kristensen (1975), Wheeler and Carpenter (1996) etc., B) the phylogeny supported by authors such as Hennig (1969) etc., and C) the phylogeny supported by authors such as Boudreaux (1979) etc. The lineages leading to the Archaeognatha, Zygentoma and the stem of Pterygota are shown only in A (Fig. 1A), because these phylogenies support the monophylies of Ectognatha, Dicondylia and Pterygota.

The characters examined here may be too few for us to positively elucidate the phylogeny, and so we examined their distribution. First, it seems that both Dicondylia (= Zygentoma + Pterygota) and Pterygota (= Ephemeroptera + Odonata + Neoptera) are monophyletic, characterized by five (characters 1, 3-6) and three (characters 6-8) autapomorphies, respectively.

Regarding the interrelationships within Pterygota, phylogeny A (Fig. 1A) proves to be the most parsimonious. Phylogenies B (Fig. 1B) and C (Fig. 1C) suppose three parallel acquisitions, characters 10-12, i. e., clypeolabral rudiment, superlingua and caudal filament: no suppositions of parallel acquisition of characters are needed in phylogeny A (Fig. 1A).

Consequently, the comparative embryological examination presented here strongly supports phylogeny A (Fig. 1A), preferred by authors such as Kristensen (1975) and Wheeler and Carpenter (1996) and that is formulated as [Pterygota (= Ephemeroptera + (Odonata + Neoptera))].

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