Early Splitting of Hexapoda Reviewed from the Comparative Embryology*

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Phylogenetic relationships of hexapod basal clades have been greatly debated from multiple sources, but are still not satisfactorily resolved. For example, doubt has been cast on the reality of the Entognatha-Ectognatha system, especially regarding the status of Entognatha. In the past few decades, much embryological knowledge concerning Apterygota has been accumulated. We discuss the early splitting of hexapod basal clades and phylogenetically reconstruct them based on recent progress of apterygote comparative embryology.

Comparison of entognathy formations among three "entognathan" orders reveals a close resemblance between Protura and Collembola but a marked contrast between Diplura and Ellipura. Ellipura is strongly supported, but Entognatha cannot always be substantiated.

Comparative embryological analyses on the basal clades of Hexapoda demonstrate an anagenetical transition of the

functional specialization between embryonic membranes and embryo proper, leading to the acquisition of elaborate structures derived from the embryonic membranes. In this context, the most noticeable is that Diplura and Ectognatha share two significant embryological features. One is the "acquisition of a second embryonic membrane or the amnion", and another is the "loss of ability in serosa for differentiating into the body element or the participation in the definitive dorsal closure". These two can be regarded as being synapomorphic to Diplura and Ectognatha, to strongly suggest the monophyly of their assemblage "Cercophora".

Hereby, the basal splitting of Hexapoda may be formulated as: Ellipura (= Protura + Collembola) + Cercophora (= Diplura + Ectognatha (= Archaeognatha + Dicondylia (= Zygentoma + Pterygota))). Entognatha is dismissed.

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