Cladistic Analysis Reveals Brainless Urbilateria

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Both insects and mammals possess homologous genes and molecular mechanisms that are involved in global body patterning, including the patterning of the central nervous system [reviewed in Hirth and Reichert, 2007]. This has led to the hypothesis that the common ancestor of arthropods and chordates (Urbilateria) possessed a tripartite brain, in which *Otx* was expressed in the anterior part of the developing brain, and *Hox* genes in the posterior part, with a *Pax*-expressing domain positioned between them [Hirth and Reichert, 2007]. Although this hypothesis has been widely cited and has entered textbooks as dogma, it has never been credible, as it is based on an erroneous two-taxon paradigm, in which arthropods and mammals are interpreted as immediate sister groups.

Although some strict cladists insist that two-taxon analyses are never valid, this is clearly not the case. When highly similar features are recognized in two immediate sister groups, a cladistic analysis does dictate that these features be interpreted as homologous. Exceptions must certainly exist (due to parallelism, for example), but at present there is no cladistic methodology for recognizing them. In any case, the important point here is not that arthropods and mammals comprise only two taxa, it is that they are not immediate

sister groups by any stretch of the imagination.

In a very elegant paper, Moroz [2009] reviews the literature, subjects the data to a correct cladistic analysis, and concludes that centralized nervous systems have evolved independently, perhaps as many as seven times. In a particularly striking example, he demonstrates that complex brains have evolved at least three times in molluscs alone. His analysis indicates that Urbilateria did *not* possess a tripartite brain, or any brain at all. Instead, these animals probably possessed an uncentralized nerve net. It is possible, however, that parts of this nerve net were already concentrated into dorsal, lateral and ventral elements, related to sensory, feeding and locomotory functions, respectively.

Moroz appears to pose an evolutionary paradox, however. How can there be homologous genes and molecular mechanisms determining brains that are not homologous? He suggests that modular type molecular mechanisms arose early in metazoan evolution and may be involved in determining many different, complex cellular phenotypes. Hemichordates appear to be a clear example, where many evolutionarily conserved homeodomain-related transcription factors and morphogens determine the main body axes system

and are expressed in distinct non-neural cell populations but not in the widely distributed subepidermal nerve plexus [Lowe et al., 2003, 2006; Lowe, 2008]. Therefore, it appears that evolutionarily conserved molecular modules may have been co-opted many times independently to evolve complex centralized nervous systems.

The revelation that dorsal-ventral patterning in both insects and vertebrates is controlled by homologous morphogens with mutually antagonistic actions [De Robertis and Sasai, 1996] revitalized Geoffroy Saint-Hilaire's 1830 hypothesis that a dorsoventral body axis inversion took place, such that the ventral side of ancestral bilaterians became the dorsal side of chordates [Arendt and Nübler-Jung, 1994, 1997]. The evolutionary model proposed for the supposed inversion is badly flawed, however. The authors took remarkable liberties in reproducing Anderson's 1973 fate map of annelids, and they elected to cite an educational website at the University of Wisconsin for interpreting neurulation in anurans, despite the existence of a detailed primary literature [Vogt, 1929; Keller, 1975; Keller et al., 1992; Beetschen, 2001] demonstrating that neurulation does not occur in the manner they were proposing. Finally, if the nervous system of Urbilateria consisted of an uncentralized nerve

net, as proposed by Moroz and others, the most parsimonious interpretation of a ventral centralized nervous system in arthropods and a dorsal centralized nervous system in chordates is that homologous molecular modules acted independently on different parts of an ancestral uncentralized nerve net.

Perhaps Moroz's most surprising conclusion is that not only centralized nervous systems, but perhaps even neurons themselves, have multiple evolutionary origins. He lists an impressive number of reasons indicating that this might be the case, including the fact that there is no evidence for pan-neuronal genes in all phyla, and the

fact that neurons can arise from different germ layers in different phyla. Although Moroz's conclusion cannot be definitively demonstrated, it does raise important questions regarding how neurons can be recognized, and it points to the need for continued research on nervous system development in as many taxa as possible.

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