

Immunohistochemical localization of neurotransmitters in the nervous system of larval *Limulus polyphemus* (Chelicerata, Xiphosura): evidence for a conserved protocerebral architecture in Euarthropoda

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Abstract

The phylogenetic relationships within the Arthropoda have remained controversial for more than a century. Comparative studies on structure and development of the nervous system have contributed important arguments to this discussion. Earlier studies revealed only few similarities between the brain morphology in representatives of the Chelicerata and the Mandibulata. In the present report, we analysed the brain architecture in larvae of the horseshoe crab *Limulus polyphemus* Linnaeus, 1758 (Chelicerata, Xiphosura) by localizing serotonin-, histamine-, and FMRFamide-like immunoreactivity with special reference to the organization of the protocerebral neuropils. These data are discussed with regard to the brain anatomy in Crustacea, Hexapoda and ‘Myriapoda’ revealing that several protocerebral and other brain structures of horseshoe crab larvae (and other Chelicerata) have homologous counterparts in the brain of these three groups. This suggests an evolutionarily conserved brain design within the different major euarthropod taxa (retained plesiomorphically from the euarthropod ground pattern). These conserved features most likely include (a) a corresponding pattern of brain segmentation with a preoral protocerebrum (associated with the lateral eyes), a deutocerebrum (associated with the first antennae/the chelicerae) with pre- and postoral commissural fibres and a postoral tritocerebrum (associated with the second antennae/the pedipalp); (b) bilateral symmetrically arranged median eyes with histaminergic photoreceptors; (c) the median eye center, which is targeted by the axons of these photoreceptors; (d) interneurons (including serotonergic cells) with somata in an anteriorly located medial cell cluster, that innervate the median eye center; (e) a transverse median unpaired neuropil, the central body, enwrapped by layers of neuronal somata and also innervated by columnar neurons with somata in the anteriorly located median cell cluster; (f) lateral eyes which are composed of subunits comprising several hundreds of cells and histaminergic photoreceptors; (g) these lateral eyes are associated with two optic fibres linked by straight fibers.

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1. Introduction

Morphology and development of the nervous system provide important insights in the discussion on phylogenetic

relationships within the Arthropoda. One of the yet unsettled problems in this field is how the structure of the brain in Chelicerata relates to that of the other euarthropod taxa (‘Myriapoda’, Hexapoda, Crustacea). Neuroanatomical studies have revealed considerable differences in the brain architecture of Chelicerata on the one hand and Crustacea and Hexapoda on the other (Strausfeld and Barth, 1993; Strausfeld et al., 1993; Breidbach, 1995; Strausfeld et al., 1995; Wegerhoff and Breidbach, 1995; Strausfeld, 1998; Strausfeld et al., 1998). Nevertheless, recent reports on the neuromuscular system (Wolf and Harzsch, 2002a,b) and

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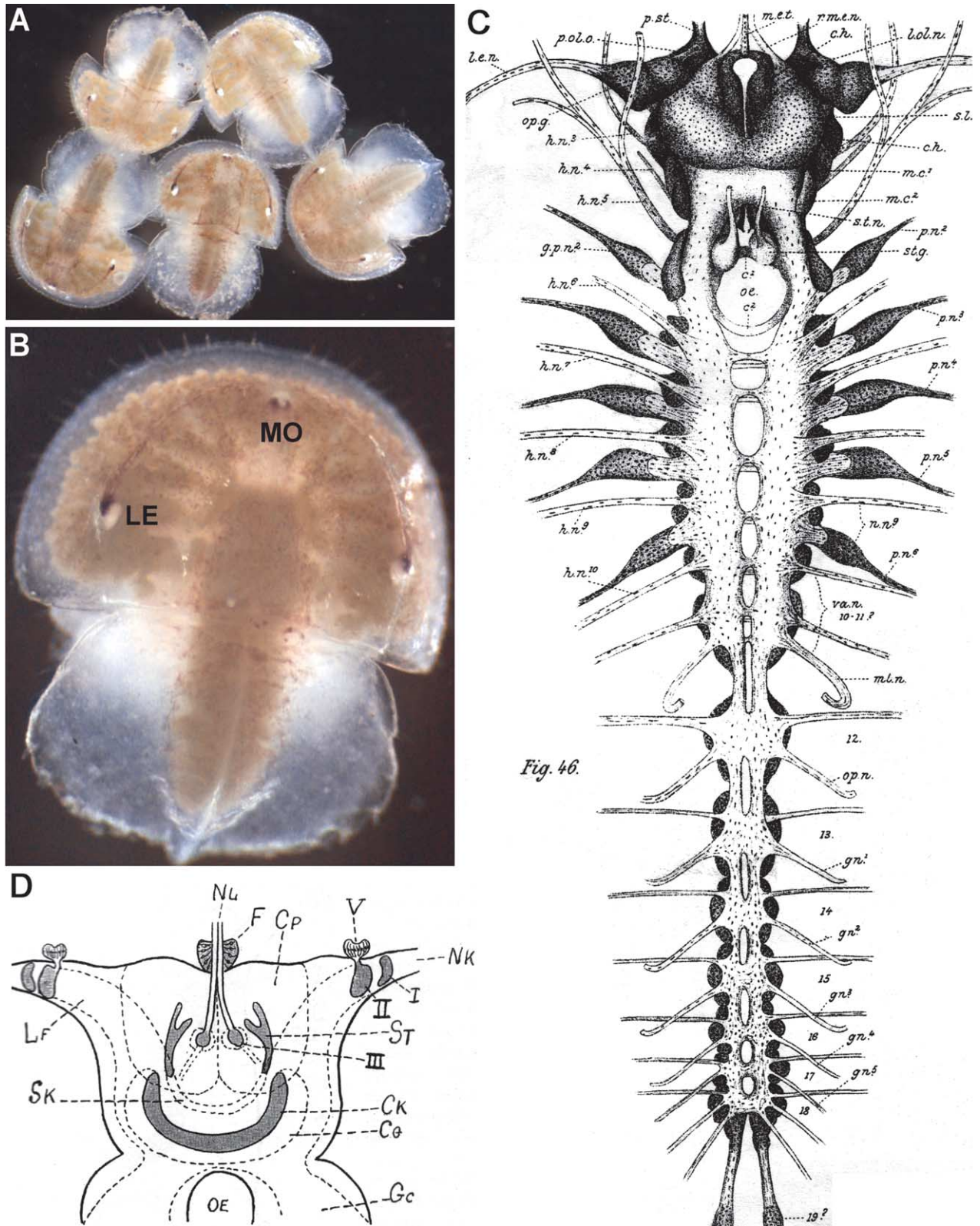


Fig. 1. (A), (B) Second larval stage after hatching of *Limulus polyphemus*. LE lateral eyes, MO median ocelli. (C) The central nervous system of a larva of *L. polyphemus*, from Patten (1894) with his original legends (note that our current understanding of the xiphosuran nervous system is different from Patten's view in several aspects such as the 'primary olfactory organ' or close parallels of the xiphosuran with the vertebrate brain): 'c2. First post-oral commissure, c.h., cerebral hemispheres; g.n. 1–5, gill nerves 1–5; g.p.n., ganglion to pedal nerve = 'neural ganglion' of a vertebrate cranial nerve; h.n. 2–9, Hæmal nerves or peripheral tegumentary nerves; l.e.n., lateral eye-nerve; l.o.l.n., lateral olfactory nerve; m.c. 1–2, two cortical masses of ganglion-cells in front of cheliceral nerves; m.e.t., median eye-tube; mt.n., nerves to chilaria; oe., oesophagus; op.g., optic ganglion; op.n., nerves to operculum; p.n. 1–6, pedal nerves 1–6; p.o.l.o.,

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