The Conserved Bauplan of the Teleostean Telencephalon

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Northcutt [2011] in his commentary on our study ‘The Dorsal Pallium of Zebrafish, *Danio rerio* (Cyprinidae, Teleostei)’ [Mueller et al., 2011] calls our reinterpretation of the pallial eversion in teleosts a ‘piscine Pandora’s box.’ This is an intriguing yet not neutral comparison. The proverbial box of Greek mythology famously stands for an unleashing of evil and bad surprises – a can of worms, so to speak, which once opened cannot be closed and contained again. Which aspects of our paper are surprising and perhaps change the perspective on teleostean brain evolution? We examine the teleostean telencephalon and define the central (Dc) zone as topologically corresponding to the dorsal pallium of other vertebrates. This is important because we locate a brain region in zebrafish that in mammals gives rise to the isocortex. Now, teleosts can be used to trace the evolutionary preconditions of this extraordinary part of the brain. Our study also demonstrates that the posterior (Dp) zone of the zebrafish pallium gets exiled by radial migration and thus topologically corresponds to the lateral pallium [Wullmann and Mueller, 2004]. We call this modified partial eversion an outward-inward folding model to reflect the developmental history of the dorsal pallial division (Dc). Apparently, a disturbing surprise in the eyes of Northcutt is a side aspect of our paper: the argued absence of the dorsal (Dd) pallial zone. Important for the discussion of this region is the circum-

stance that Dd represents an ill-defined region in many studies. What is described as Dd in different teleosts is often either part of the laterodorsal pallial division (Dl) or, at most rostral levels, part of the superficially located Dc zone [Pepels et al., 2002; Harvey-Girard et al., 2007]. In fact, I understand Dd less as a histogenetic unit and more as a piscine Fata Morgana, a nonentity which sprung from the, at times, blurry waters of histological evidence. Dc, in contrast, needs to be recognized as an independent primary pallial division that comprises its own dorsal proliferative zone. This zone of origin is located in the most anterior part of the telencephalon of adult zebrafish and at anterior levels may also include the periventricular stellate zone mentioned by Northcutt. I agree with Northcutt, however, that the dorsal pallium has to be clarified in basal ray-finned fish. Our modified partial eversion model of the teleostean telencephalon might, in fact, open the door for the decipherment of the simple eversion apparently present in basal ray-finned fish. The teleostean pallium develops in a caudorostral direction. For example, the hippocampal sheet (Dl) – a late developing division – overgrows the dorsal pallial sheet (Dc) from a caudolateral to a medio-rostral direction. Thus, reading the telencephala of ray-finned fish from back to front, as we have done, is key for understanding their organization. Future studies in *Polypterus* or *Acipenser* need to con-

sider that a small and perhaps overlooked dorsal pallium (Dc homolog) may be located in a superficial position anterior to the hippocampal sheet (Dl homolog).

To conclude, I wonder if the finding of a dorsal pallium in ray-finned fish can be truly called unexpected? Most comparative anatomists have accepted the existence of a dorsal pallium in sharks (chondrichthyes); likewise its presence has been discussed for lampreys (jawless vertebrates) [Puelles, 2001; Pombal et al., 2009]. Similarly, while the locations of teleostean homologs of the pallial amygdala, hippocampus, and piriform cortex have been debated, their existence has never seriously been questioned [Nieuwenhuys, 2009]. In fact, current research increasingly supports a conserved teleostean telencephalic Bauplan relying on the same basic units found in telencephala of tetrapods. Highly conserved are as well the primordial basal ganglia which display distinct homologs of the mammalian lateral and medial ganglionic eminences [Mueller et al., 2008]. Hence, in my opinion the truly interesting question is not *if* these telencephalic units exist in teleosts but *how* they have been developmentally modified to give rise to the drastic morphological diversification in ray-finned fish. In finding answers to this most intriguing query, teleost models can harbor, instead of Pandora’s wealth of evil, a fountain of good; they can play a pivotal role in identifying molecular and developmental mechanisms of brain evolution at large.

References

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