



Review

New directions in craniofacial morphogenesis

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ABSTRACT

The vertebrate head is an extremely complicated structure: development of the head requires tissue–tissue interactions between derivatives of all the germ layers and coordinated morphogenetic movements in three dimensions. In this review, we highlight a number of recent embryological studies, using chicken, frog, zebrafish and mouse, which have identified crucial signaling centers in the embryonic face. These studies demonstrate how small variations in growth factor signaling can lead to a diversity of phenotypic outcomes. We also discuss novel genetic studies, in human, mouse and zebrafish, which describe cell biological mechanisms fundamental to the growth and morphogenesis of the craniofacial skeleton. Together, these findings underscore the complex interactions leading to species-specific morphology. These and future studies will improve our understanding of the genetic and environmental influences underlying human craniofacial anomalies.

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Introduction

The tissues of the vertebrate head are derived from all the germ layers: ectoderm, mesoderm and endoderm together with the “fourth” tissue layer, the neural crest. The ectoderm forms the epidermis, nervous system and components of the sense organs such as the lens. The endoderm lines the pharynx and contributes to a number of specialized glands. During embryogenesis, both the ectoderm and endoderm signal to the intervening facial mesenchyme. This mesenchyme is composed of mesoderm and neural crest. The mesodermal component later gives rise to the voluntary muscles and endothelial cells while the neural crest-derived mesenchyme forms the majority of the craniofacial skeleton. Given the significant contribution of the neural crest to the craniofacial structures, craniofacial anomalies can often be traced to changes in the neural crest.

In this review, we focus on later events in the morphogenesis of the face, including contributions from the surrounding ectoderm and underlying endoderm. Several recent studies have highlighted specialized signaling centers which control the outgrowth and polarity of the facial structures. These critical anatomical regions have been identified by a combination of experimental approaches,

including analysis of embryonic inductive capabilities, molecular signatures and genetic requirements. Frequently, these anatomical structures express molecules, such as BMPs, FGFs and Wnts, which play multiple roles in facial morphogenesis: first, in specification and growth of tissues and later, during differentiation and skeletogenesis.

We will first review the general development of the head and describe the signaling centers that pattern each region, particularly recent data describing instructive cues from the anterior endoderm and the frontonasal ectodermal zone (FEZ), which control the initial outgrowth of the upper face. Finally, we will discuss new data linking molecular cues to cell movements and cell polarity in craniofacial development.

Development of the face and head

In general, development of the craniofacial structures can be considered in five discrete stages subsequent to the patterning of the germ layers. First, the neural crest is induced at the ectoderm/neuroectoderm border. This is followed by movement of the cranial neural crest into the presumptive facial primordia (Figs. 1A, B; Johnston, 1966; Le Lievre, 1978; Le Lievre and Le Douarin, 1975; Sadaghiani and Thiebaud, 1987) and reviewed in (Creuzet et al., 2005)). Subsequently, regional proliferation of the neural crest leads to the formation of outgrowths called facial prominences (Figs. 1E, F and 3G, H). Next, the facial prominences fuse to presage the mature form of the face (Figs. 2A, B). Finally, the developing face is shaped by

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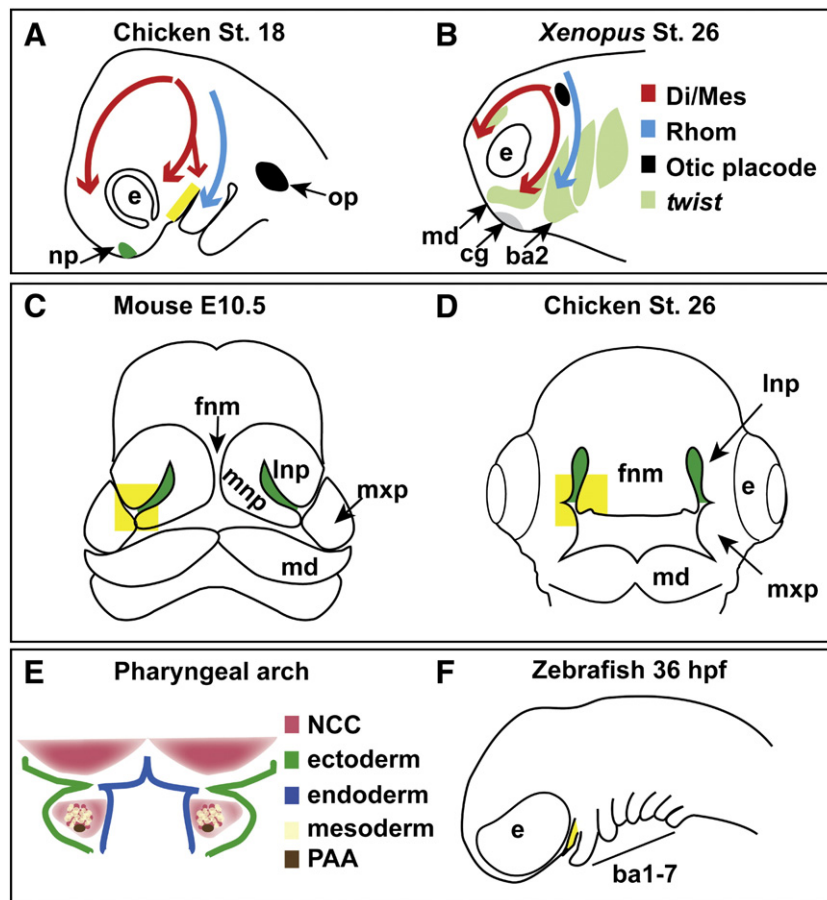


Fig. 1. Craniofacial anatomy. (A, B) Neural crest migration. (A) Lateral view of a stage 18 chicken embryo. Migration of the cephalic neural crest is depicted. Red: diencephalic and mesencephalic crest contributes to the upper face. Blue: rhombencephalic and posterior mesencephalic crest contribute to the mandibular arch. Maxillary prominence highlighted in yellow. (B) The pathways used by the migrating neural crest in the *Xenopus* embryo, superimposed over *twist* expression (green). *Twist* marks the final position of the cranial neural crest. Red: mesencephalic crest; Blue: hyoid crest from the rhombomeres. (C, D) Schematic frontal views of e10.5 mouse and stage 26 chicken embryos. (C) The mouse facial prominences (mnp, md, and mxp) surround the stomodeal opening. Note: the mnp are much more prominent in the mouse than in the chicken face. (D) The midline of the chicken face is much flatter than the mouse. Fusion of the lip will take place at the intersection of the tissues indicated in yellow. Green indicates nasal pits. (E) Frontal section through the first arch depicts tissue organization in the facial prominences. The surface ectoderm (green) encapsulates the neural crest derived mesenchyme (pink), which surrounds and later infiltrates the mesoderm (yellow). The pharyngeal arch arteries (brown) are in the core. The pharyngeal endoderm (blue) lines the pharynx. (F) Lateral view of a zebrafish embryo at 36 hpf, the maxillary prominences (yellow) and branchial arches are present. Key: ba, branchial arch; cg, cement gland; Di/Mes, mandibular stream, from the diencephalon/mesencephalon; e, eye; fmm, frontonasal mass; lmp, lateral nasal prominence; md, mandibular prominence; mnp, medial nasal prominence; mxp, maxillary prominence; NCC, neural crest cells; PAA, pharyngeal arch artery. Rhom, hyoid stream, from rhombencephalon; Fig. 1D modified from Cruetz, 2005; 1E drawn after Sadaghiani and Thiebaud, 1987.

directional growth of the skeleton (Figs. 2E, H, 3F). As many excellent reviews have focused on steps one and two, the initial specification and migration of the neural crest (including (Knecht and Bronner-Fraser, 2002; Le Douarin and Kalcheim, 1999; Sauka-Spengler and Bronner-Fraser, 2008)), we will focus this review on the later stages of facial development.

As the neural crest migrates into the face, the cranial placodes, which are specialized ectodermal thickenings, differentiate. Placodes, with some contributions from the neural crest, give rise to the cranial ganglia and components of the sensory organs such as the lens of the eye, and olfactory glia. Both the otic and olfactory placodes express many growth factors and may influence the formation of the face. For detailed reviews of placodal specification, development and differentiation the reader is referred to the following excellent and extensive reviews (Baker and Bronner-Fraser, 2001; Schlosser, 2006; Streit, 2004).

Development of the viscerocranium during mid-organogenesis

By e9.5 in mice, or week 4 of gestation in humans, the facial primordia consist of five swellings called facial prominences or processes (Figs. 1C, D). The midline of the upper face is composed of the frontonasal mass in the chicken, or the medial nasal prominences

and frontonasal mass in mouse embryos. Compared with the mouse, the chicken has flatter and less distinct medial nasal prominences (Figs. 1C, D). The frontonasal mass and medial nasal processes will develop into the midface and contribute to the forehead, ridge of the nose and the primary palate, which includes the premaxillary segment of the upper jaw. The sides of the nose and cheeks develop from the lateral nasal and maxillary prominences respectively, while the mandibular processes form the lower jaw. These five prominences encircle the stomodeum, or primitive mouth.

During the early pharyngeal arch stages, vertebrate embryos have substantial morphological homology, although the number of arches has changed during evolution (Kuratani, 2005; Meulemans and Bronner-Fraser, 2002). The mandibular primordium, or lower jaw, develops from the first branchial arch (Figs. 1E, F). The branchial, or pharyngeal, arches are metameric structures consisting of an outer ectodermal layer and an inner endodermal layer. Sandwiched between these two layers are mesodermal cores which are initially surrounded by neural crest-derived mesenchyme (Fig. 1E; (Grenier et al., 2009; Kuratani, 2005; Meulemans and Bronner-Fraser, 2002; Noden, 1982; Schilling and Kimmel, 1994). Signals from the first branchial arch ectoderm are required for the osteogenic commitment of the ectomesenchyme (Hall, 1978; Tyler and Hall, 1977).

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