

NII-Electronic Library Service

Tanaka, 1990ab; Kuratani, 1990). This method allowed me to observe fine caliber branches of developing nerves with a resolution that no previous description could have reached and soon I was attracted by the exquisite pattern of developing nerves in embryos. My basic interest had not changed at all - I was struck by the metamorphosis of cranial nerves that, like the skeletal system, were primarily formed segmentally from every other bulges of the hindbrain (rhombomeres), and distributed in each pharyngeal arches.

Besides the nerves, I also visualized the vascular systems and also performed three dimensional reconstruction from the histological sections to observe the distribution of mesodermal elements. Unlike the somitic segmentation that is restricted posterior to the otic vesicle, some of the cranial nerves (cranial nerves V, VII, IX and X, also known as branchiomic nerves) were associated with the pharyngeal arches and seemed to show different pattern of metamerism from that of somites and their derivatives. Thus the embryology for me at that time, was the way to connect developmental biology and gross anatomy. This experience in Tanaka's laboratory (1985-1988) still influences my research, especially in the experiments to elucidate the evolution of the jaw of vertebrates (see below).

I was most fortunate that it was right at that time that Developmental Biology began to deal with the morphological pattern of organisms, from a cell and molecular biology vantage point. Most of all, the neural crest cells, the vertebrate-specific cell lineage, seemed to me particularly important, since these cells are responsible for both branchial arch skeleton and cranial nerves. I also realised that only by studying abroad, was it possible for me to learn the specific experimental embryological techniques that deal with the neural crest.

Experimental embryology

In the Department of Anatomy, Medical College of Georgia, I started first postdoc life. Here, I learnt the construction of chimeras between chick and quail embryos and also neural crest ablation. Combining with my immunohistochemistry and these techniques new to me then, I analyzed the role of neural crest in the differentiation of thymus and morphological patterning of cranial nerves (Kuratani and Bockman, 1990; 1991; 1992; Kuratani *et al.*, 1991). During this period (1988-1991), I also found that the postotic level of the neural crest gives rise to cells that migrate along both the head-specific and trunk-type pathways. I pointed out that each of these pathways prefigured glossopharyngeal-vagus and hypoglossal nerves, respectively, and I called the former (cephalic type) crest cell population the circumpharyngeal crest cells. They first populate the lateral body wall prior to the formation of postotic pharyngeal arches, and become the typical ectomesenchyme only after disappearance of coelomic cavity and subsequent establishment of pharyngeal arches (Kuratani and Kirby, 1991, 1992). I also emphasized that posterior limit of this cell pop-

ulation represents the S-shaped boundary between the head and trunk (Kuratani, 1997).

Another interesting developmental pattern I found was the even-odd-relationships between rhombomeres and cranial nerve roots (Kuratani, 1991). This paper strongly tempted me to expand my research field into molecular developmental biology, which appeared to hold the promise for the future of evolutionary embryology.

Coupling of molecular developmental biology and embryology

As Goethe first described, the most important concepts for animal morphology are metamerism and metamorphosis. In a modern context, both of these concepts are profoundly intertwined with the function of *Hox* genes. All metazoans examined so far contain a set of similar regulatory genes named *Hox*, each showing similar amino acid sequence. They encode transcription factors characteristically containing about 60 amino acids representing the homeobox, that recognizes specific sites on the DNA, regulating the transcription of its target genes. Thus the *Hox* genes can function as 'switches' that determine specific developmental fates for specific cell populations or tissue domains. *Hox* genes are found as clusters, and interesting is that in many organisms, *Hox* genes exhibit nested and coordinated pattern of expression along the anterior posterior axis of the animal embryonic body. Thus more 3' member of *Hox* genes among the cluster tend to be expressed more anteriorly, and those located in 5' region of the cluster are expressed more posteriorly.

In the vertebrates, *Hox* gene expression is often associated with segmental units of the embryos. For examples, in the trunk, somites (primordia of vertebrae and skeletal muscles) express varying sets of *Hox* genes at each axial level, and in the hindbrain, the vertebrate *Hox* genes show anterior expression limit at the boundary of rhombomeres. Moreover, the crest cells attached to these rhombomeres share the same *Hox* expression profiles, implying that *Hox* genes are the key to understand the position-dependent differentiation and evolution of the pharyngeal arches together with rhombomeres. Now the molecular developmental biology had started to use the same terminology that I had used in comparative morphology.

Thus, in June of 1991, I moved to Dr. Gregor Eichele's laboratory in Biochemistry Department, Baylor College of Medicine, where rhombomeres and *Hox* genes were one of the central research projects. Soon I started transplantation experiments of rhombomeres in avian embryos, and observed the behavior of neural crest cells and *Hox* gene expression. As I expected, *Hoxb-1* expression was rather cell autonomous in rhombomere 4 (r4) and it never changed after transplantation of r4 into other levels of the hindbrain. This graft also retained the capacity for neural crest cell production and cranial nerve root formation (Kuratani and Eichele, 1993). In other words, cranial nerve formation is

intrinsic to the rhombomeres, not dependant of the embryonic environment. This finding seemed to show, not only developmental, but also morphological importance, since classically the cranial nerves were thought to have arisen by metamorphoses of spinal nerves in the trunk, which also exhibit metamerism in their morphological pattern. However, it was realized that the spinal nerve was patterned through the mesodermal segments - the somites. Thus vertebrate embryo shows two distinct patterns and mechanisms for peripheral nerve segmentation at the level of molecular and cellular developmental functions, and I concentrated on embryonic expression patterns that might possibly have morphological and evolutionary significance. That research strategy, and using my skills in experimental embryology, were what I was expected to contribute to a future field of study (see Kuratani and Wall, 1992; Lutz *et al.*, 1994ab; Kuratani *et al.*, 1994; Qiu *et al.*, 1994).

Back to the comparative embryology

During postdoc life in the United States, there remained a strong urge towards evolutionary research, which I knew was not easy to promote in that country. It seemed to me it was much easier in Japan and the timing also seemed right. My rhombomere study had come to attention of Shin Aizawa, a mouse molecular geneticist, who was then at RIKEN. He had recently moved to Developmental Biology Institute, Kumamoto University Medical School in 1994 and I joined his lab and started a collaboration on vertebrate head patterning. My first job was the morphological analyses of the skull in *Otx2* haploinsufficiency mouse mutant, and I soon realized that the phenotype was complimentary to that of *Hoxa-2*, the gene expressed in the hyoid arch ectomesenchyme and pattern the stapes and Reichert's cartilage (Matsuo *et al.*, 1995, 1996, 1998; Kuratani *et al.*, 1997b; the mutant mouse was constructed by I. Matsuo). Namely, *Otx2* (another homeobox gene that does not belong to *Hox* genes) is responsible for the rostral part of the mandibular arch derivatives, and its posterior part can be regarded as the Hox-code-default region, the part of the mandibular arch patterned by the absence of *Hox* or *Otx* transcripts. This study still has a great influence on my evolutionary study.

While engaging in some other collaborations, as well as avian experimental embryology (Kuratani and Aizawa, 1995; Shigetani *et al.*, 1995), I finally started research on lamprey embryology, which had been my long-lasting dream. Before going further, I have to mention Dr. Shigeki Hirano in Niigata University School of Medicine. Dr. Hirano helped us greatly to obtain lamprey embryos, at a time when it was not very easy to deal with non-model animal for embryological and developmental studies. I also harboured a strong fear about dealing with this animal; a number of scientists had already accumulated huge amount of descriptive studies by the early 20th century. With less knowledge and an incomplete understanding of this animal, I was more than tentative

about a move into molecular level studies as other scientists used to. I then believed that any new techniques and ideas should be built upon sound bases of morphology and embryology. Thus I decided first to repeat all that I had done in chick embryos; that is, a morphological description of lamprey embryos.

I re-examined all the developmental aspects of the lamprey head histologically and immunohistologically (Kuratani *et al.*, 1997a; 1998; Ueki *et al.*, 1998). This series of work continued even after I moved to Department of Biology, Okayama University in the end of 1997, and our research finally started to look at developmental phenomena such as, patterning of rhombomeres, migration and distribution of the neural crest and *Otx* gene expression (Horigome *et al.*, 1999), segmental patterning of the mesoderm (Kuratani *et al.*, 1999), and expressions of some developmentally important regulatory genes (Ogasawara *et al.*, 2000, 2001; Murakami *et al.*, 2001, 2002).

Looking back now, I realize that my research in Okayama was a struggle, trying several different biological fields, or even different philosophies of zoology. I feel that it is not always easy to integrate and coordinate education and research even if they both deal with the same scientific logic. Students have to be taught the basics. However at the same time science as a business was getting tougher everyday. In my field, nothing was basic and worth teaching, except for some histology and animal taxonomy. Whereas the research theme in my laboratory, Evo-Devo, required the huge amount of knowledge not regularly taught in average national universities in Japan. In my struggle I tried first several possible ways, trying to look for particular research fields suitable for each student and postdoc. It was at that time that I tried to promote the comprehensive description of various vertebrate embryos such as sharks, turtles and sturgeons, for the last time in my career (Kuratani and Horigome, 2000; Kuratani *et al.*, 2000; These two papers were awarded by Zoological Society of that year; Kuratani, 1999). In parallel, experimental embryology continued (Shigetani *et al.*, 1999), and in my impression this field played the most crucial role in the realization of the importance of tissue interactions in the acquisition of evolutionary novelties, especially in the patterning and evolution of the vertebrate jaw. For my lectures in the department, I integrated experimental embryology and molecular developmental biology, and this was finally the most meaningful and exciting to teach.

In Kobe

Based on the experiments performed in Okayama, I could finally explain the jaw evolution as a process of topographical shift of tissue interactions, which is now called the 'heterotopic theory' for the vertebrate jaw (Shigetani *et al.*, 2002, 2005; also see Kuratani *et al.*, 2001; Kuratani, 2003ab, 2004). To complete this theory, it was also necessary for us to show that the lamprey also has the cephalic *Hox* code of the ectomesenchyme, with mandibular arch

defined as the Hox-code-default state as in gnathostomes. We could successfully show that it was actually the case (Takio *et al.*, 2004; Kuratani, 2004). Next, it was also necessary to show that the so called 'lamprey trabecula' was merely a rostral extension of mesodermal neurocranium, unlike in gnathostomes, which I could show by cell labeling studies (Kuratani *et al.*, 2004). In addition, we also found that the heterotopic shift noted above was tightly linked to the evolution of hypophyses, in which changes in spatio-temporal regulation of growth-factor encoding genes was involved (Uchida *et al.*, 2003). The lamprey project that I have been involved for almost 10 years now, has also provided us with new evolutionary theory of the vertebrate brain (Murakami *et al.*, 2004, 2005), and of the skeletal muscles (Kusakabe and Kuratani, 2003; 2004; Kusakabe and Kuratani, 2005). It has been and still is quite fortunate for me that I could work with dynamic young researchers from various backgrounds, such as neurobiology, anatomy, muscle development, evolutionary genomics, cell biology, experimental embryology, molecular biology, and so forth for this animal species, making this project a very exciting one.

As another case of vertebrate novelty, I have also picked up the Chinese soft-shelled turtles, *Pelodiscus sinensis*, as the model for turtles, to describe the developmental changes that allowed them to develop the shells in these animals. Due to the dorsally shifted position of the ribs, topographical relationship between the rib cage and scapula has been reversed in turtles, obliterating the morphological homologies of skeletal elements. Thus the loss of homology is coupled with evolutionary novelties, since the former implies that these animals have cancelled the ancestral developmental constraints that assures the conserved basic architecture of the amniote body. Thus the establishment of novelty requires abrupt changes in developmental process to allow topographical shifts of skeletal elements. So far, we have shown, through the analyses of *Hox* gene expression, that the turtle carapace (dorsal part of the shell) can be regarded as transformed 'thoracic' vertebrae (Ohya *et al.*, 2005), the turtle-specific pattern of muscle differentiation is intrinsic to turtle somites (Nagashima *et al.*, 2005), and that the carapacial ridge (CR: the primordium of the carapace) involves cooption of regulatory genes that are also present in other vertebrate species by differential screening of CR-specific genes (Kuraku *et al.*, 2005). This turtle project has been the major theme of our project since we moved into CDB, RIKEN.

For me, book writing is as important as research. This may even more important than writing original papers or short reviews. This is probably my classical leanings, but I do believe this is the best way for me to express the ideas I have developed. Actually, for the purpose of education as well, I cannot think of any other method more comfortable than writing a book. In the text book of neural crest cells I co-wrote with Dr. Noriko Osumi (Tokyo Medical Dental University at the time; Kuratani and Osumi, 1997), we tried a unification of developmental mechanism and anatomical

patterns of vertebrates. Since then, however, the field of Evo-Devo has become more sophisticated and I felt the necessity of introducing more concepts from various different fields of biology, not only pointing out coincidental patterns between morphology and gene expression patterns. What I needed was not to illuminate the history of morphology, but rather to search for a new way thinking for the future. Particularly, it seemed very important for me to integrate the classical concepts of archetype, homology, recapitulation and the modern theories of genetics, tissue interactions, and gene functions in developmental patterning. My research on lampreys, with which I had not been familiar when I first had a vague idea of book writing in Georgia back in 1990, might have also motivated me to start writing a full-sized book on evolutionary morphology, and this institute (RIKEN CDB) was almost an ideal place for me to concentrate on this task. I finally completed *Evolutionary Morphology* in 2004 (Kuratani, 2004a) and its short and simplified version, *Does the Ontogeny Recapitulate Evolution?* in 2005 (Kuratani, 2005).

Here in Kobe, I am not a typical comparative embryologist, or anatomist, or even developmental biologist. I am basically a zoologist, and would rather be called an evolutionary morphologist, who loves various kinds of animals (particularly moths), and this is the most comfortable way for me to identify myself. Although, in old fashioned papers and text books, I take comfort of the somewhat classical but stuffy atmosphere of Natural History in 19th century, most typically embodied in Victorian London, I would not try to reanimate the dreams of those naturalists back into this century, and I would not wish any to live in that era. I believe that current evolutionary morphology is at its most exciting point ever, and most promising with the knowledge and technology that are available now, not with those back in 19th century. It has taken me quite a long time to formulate my ideas about evolution from a mechanistic point of view, for which I am grateful to all of my mentors and to all of my seniors, and I am grateful to the many friends that I could have through my entire career.

ACKNOWLEDGMENTS

I would like to thank Raj Ladher (Center for Developmental Biology, RIKEN) for his careful reading of the manuscript.

BIBLIOGRAPHY (CITED ABOVE)

- Horigome N, Myojin M, Hirano S, Ueki T, Aizawa S, Kuratani S (1999) Development of cephalic neural crest cells in embryos of *Lampetra japonica*, with special reference to the evolution of the jaw. *Dev Biol* 207: 287–308
- Ishikawa Y, Zukeran C, Kuratani S, Tanaka, S (1986) A staining procedure for nerve fibers in whole mount preparations of the medaka and chick embryos. *Acta Histochem Cytochem* 19: 775–783
- Kuraku S, Usuda R, Kuratani S (2005) Comprehensive survey of carapacial ridge-specific genes in turtle implies co-option of

- some regulatory genes in carapace evolution. *Evol Dev* 7: 3–17
- Kuratani S (1989) Development of the orbital region in the chondrocranium of *Caretta caretta*. Reconsideration of the vertebrate neurocranium configuration. *Anat Anz* 169: 335–349
- Kuratani S (1990) Development of glossopharyngeal nerve branches in the early chick embryo with special reference to morphology of the Jacobson's anastomosis. *Anat Embryol* 181: 253–269
- Kuratani SC (1991) Alternate expression of the HNK-1 epitope in rhombomeres of the chick embryo. *Dev Biol* 144: 215–219
- Kuratani S (1997) Distribution of postotic crest cells in the chick embryo defines the trunk/head interface: embryological interpretation of crest cell distribution and evolution of the vertebrate head. *Anat Embryol* 195: 1–13
- Kuratani S (1999) Development of the chondrocranium in loggerhead turtle, *Caretta caretta*. *Zool Sci* 16: 803–818
- Kuratani S (2003a) Evolutionary developmental biology and vertebrate head segmentation: a perspective from developmental constraint. *Theory Biosci* 122: 230–251
- Kuratani S (2003b) Evolution of the vertebrate jaw: homology and developmental constraints. *Paleontol Res* 7: 89–102
- Kuratani S (2004a) Evolutionary Morphology - Bauplan and embryonic development of vertebrates. Univ Tokyo Press (in Japanese)
- Kuratani S (2004b) Evolution of the vertebrate jaw: comparative embryology reveals the developmental factors behind the evolutionary novelty. *J Anat* 205: 335–347
- Kuratani S (2005) Does Ontogeny Recapitulate Evolution? Iwanami Press (in Japanese)
- Kuratani S, Aizawa S (1995) Patterning of the cranial nerve in the chick embryo is dependent on cranial mesoderm and rhombomeric metamerism. *Dev Growth Differ* 37: 717–731
- Kuratani S, Bockman DE (1990) The participation of neural crest derived mesenchymal cells in development of the epithelial primordium of the thymus. *Arch Histol Cytol* 53: 267–273
- Kuratani S, Bockman DE (1991) Capacity of neural crest from various axial levels to participate in thymic development. *Cell Tiss Res* 263: 99–105
- Kuratani SC, Bockman DE (1992) Inhibition of epibranchial placode-derived ganglia in the developing rat by bisdiamine. *Anat Rec* 233: 617–624
- Kuratani SC, Eichele G (1993) Rhombomere transplantation repatterns the segmental organization of cranial nerves and reveals autonomous expression of a homeodomain protein. *Development* 117: 105–117
- Kuratani S, Horigome N (2000) Development of peripheral nerves in a cat shark, *Scyliorhinus torazame*, with special reference to rhombomeres, cephalic mesoderm, and distribution patterns of crest cells. *Zool Sci* 17: 893–909
- Kuratani SC, Kirby ML (1991) Initial migration and distribution of the cardiac neural crest in the avian embryo: An introduction to the concept of the circumpharyngeal crest. *Am J Anat* 191: 215–227
- Kuratani SC, Kirby ML (1992) Migration and distribution of the circumpharyngeal crest cells in the avian embryo: Formation of the circumpharyngeal ridge and E/C8⁺ crest cells in the vertebrate head region. *Anat Rec* 234: 263–280
- Kuratani S, Osumi N (1997) UP BIOLOGY 97 Neural Crest Cells: Bases of the vertebrate body plan. Univ Tokyo Press (in Japanese)
- Kuratani S, Tanaka S (1990a) Peripheral development of avian trigeminal nerves. *Am J Anat* 187: 65–80
- Kuratani S, Tanaka S (1990b) Peripheral development of the avian vagus nerve with special reference to the morphological innervation of heart and lung. *Anat Embryol* 182: 435–445
- Kuratani SC, Wall NA (1992) Expression of Hox 2.1 protein in a restricted population of neural crest cells and pharyngeal ectoderm. *Dev Dyn* 194: 15–28
- Kuratani S, Tanaka S, Ishikawa Y, Zukeran C (1988a) Early development of the hypoglossal nerve in the chick embryo as observed by the whole-mount staining method. *Am J Anat* 182: 155–168
- Kuratani S, Tanaka S, Ishikawa Y, Zukeran C (1988b) Early development of the facial nerve in the chick embryo with special reference to the development of the chorda tympani. *Am J Anat* 182: 169–182
- Kuratani SC, Miyagawa-Tomita S, Kirby ML (1991) Development of cranial nerves in the chick embryo with special reference to the alterations of cardiac branches after ablation of the cardiac neural crest. *Anat Embryol* 183: 501–514
- Kuratani S, Martin JF, Wawersik S, Lillie B, Eichele G, Olson E (1994) The expression pattern of the chick homeobox gene *gMhox* suggests a role in patterning in the limbs and face and in compartmentalization of somites. *Dev Biol* 161: 357–369
- Kuratani S, Ueki T, Aizawa S, Hirano S (1997a) Peripheral development of the cranial nerves in a cyclostome, *Lampetra japonica*: morphological distribution of nerve branches and the vertebrate body plan. *J Comp Neurol* 384: 483–500
- Kuratani S, Matsuo I, Aizawa S (1997b) Developmental patterning and evolution of the mammalian viscerocranium: Genetic insights into comparative morphology. *Dev Dyn* 209: 139–155
- Kuratani S, Horigome N, Ueki T, Aizawa S, Hirano S (1998) Stereotyped axonal bundle formation and neuromeric patterns in embryos of a cyclostome, *Lampetra japonica*. *J Comp Neurol* 391: 99–114
- Kuratani S, Horigome N, Hirano S (1999) Developmental morphology of the cephalic mesoderm and re-evaluation of segmental theories of the vertebrate head: evidence from embryos of an agnathan vertebrate, *Lampetra japonica*. *Dev Biol* 210: 381–400
- Kuratani S, Nobusada Y, Saito H, Shigetani Y (2000) Morphological development of the cranial nerves and mesodermal head cavities in sturgeon embryos from early pharyngula to mid-larval stages. *Zool Sci* 17: 911–933
- Kuratani S, Nobusada Y, Horigome N, Shigetani Y (2001) Embryology of the lamprey and evolution of the vertebrate jaw: insights from molecular and developmental perspectives. *Phil Trans Roy Soc* 356: 15–32
- Kuratani S, Murakami Y, Nobusada Y, Kusakabe R, Hirano S (2004) Developmental fate of the mandibular mesoderm in the lamprey, *Lethenteron japonicum*: comparative morphology and development of the gnathostome jaw with special reference to the nature of trabecula cranii. *J Exp Zool B Mol Dev Evol* 302B: 458–468
- Kusakabe R, Tochintai S, Kuratani S (2003) Expression of foreign genes in lamprey embryos: an approach to study evolutionary changes in gene regulation. *J Exp Zool B Mol Dev Evol* 296B: 87–97
- Kusakabe R, Takechi M, Tochintai S, Kuratani S (2004) Lamprey contractile protein genes mark different populations of skeletal muscles during development. *J Exp Zool B Mol Dev Evol* 302B: 121–133
- Kusakabe R, Kuratani S (2005) Evolution and developmental patterning of the vertebrate skeletal muscles: perspectives from the lamprey. *Dev Dyn* 234: 824–834
- Lutz B, Kuratani S, Cooney A, Wawersik S, Tsai SY, Eichele G, Tsai M-J (1994a) Developmental regulation of the orphan receptor *COUP-TF II* gene in spinal motor neurons. *Development* 120: 25–36
- Lutz B, Kuratani S, Rugerli EI, Wawersik S, Wong C, Bieber FR, Ballabio A, Eichele G (1994b) Expression of the Kallmann syndrome gene in human brain and in the manipulated chick embryo. *Human Mol Genet* 3: 1717–1723

- Matsuo I, Kuratani S, Kimura C, Takeda N, Aizawa S (1995) Mouse *Otx2* functions in the formation and patterning of rostral head. *Genes Dev* 9: 2646–2658
- Murakami Y, Ogasawara M, Sugahara F, Hirano S, Satoh N, Kuratani S (2001) Identification and expression of the lamprey *Pax-6* gene: Evolutionary origin of segmented brain of vertebrates. *Development* 128: 3521–3531
- Murakami Y, Ogasawara M, Satoh N, Sugahara F, Myojin M, Hirano S, Kuratani S (2002) Compartments in the lamprey embryonic brain as revealed by regulatory gene expression and the distribution of reticulospinal neurons. *Brain Res Bull* 57: 271–275
- Murakami Y, Pasqualetti M, Takio Y, Hirano S, Rijli F, Kuratani S (2004) Segmental development of reticulospinal and branchiomotor neurons in the lamprey: insights into evolution of the vertebrate hindbrain. *Development* 131: 983–995
- Murakami Y, Uchida K, Rijli FM, Kuratani S (2005) Evolution of the brain developmental plan: insights from amphioxus and lamprey. *Dev Biol* 280: 249–259
- Nagashima H, Uchida K, Yamamoto K, Kuraku S, Usuda R, Kuratani S (2005) Turtle-chicken chimera: an experimental approach to understanding evolutionary innovation in the turtle. *Dev Dyn* 232: 149–161
- Ogasawara M, Shigetani Y, Hirano S, Satoh N, Kuratani S (2000) *Pax1/Pax9*-related genes in an agnathan vertebrate, *Lampetra japonica*: expression pattern of *LjPax9* implies sequential evolutionary events towards the gnathostome body plan. *Dev Biol* 223: 399–410
- Ogasawara M, Shigetani Y, Suzuki S, Kuratani S, Sato N (2001) Expression of *thyroid transcription factor-1 (TTF-1)* gene in the ventral forebrain and endostyle of the agnathan vertebrate, *Lampetra japonica*. *Genesis* 30: 51–58
- Ohya YK, Kuraku S, Kuratani S (2005) *Hox* code in embryos of Chinese soft-shelled turtle *Pelodiscus sinensis* correlates with the evolutionary innovation in the turtle. *J Exp Zool B Mol Dev Evol* 304B: 107–118
- Qiu Y, Cooney A, Kuratani S, Tsai SY, Tsai M-J (1994) Spatiotemporal expression patterns of chicken ovalbumin upstream promoter-transcription factors in the developing mouse central nervous system: Evidence for a role in segmental patterning of the diencephalon. *Proc Natl Acad Sci USA* 91: 4451–4455
- Shigetani Y, Aizawa S, Kuratani S (1995) Overlapping origins of pharyngeal arch crest cells on the postotic hindbrain. *Dev Growth Differ* 37: 733–746
- Shigetani Y, Nobusada Y, Kuratani S (2000) Ectodermally-derived FGF8 defines the maxillomandibular region in the early chick embryo: epithelial-mesenchymal interactions in the specification of the craniofacial ectomesenchyme. *Dev Biol* 228: 73–85
- Shigetani Y, Sugahara F, Kawakami Y, Murakami Y, Hirano S, Kuratani S (2002) Heterotopic shift of epithelial-mesenchymal interactions for vertebrate jaw evolution. *Science* 296: 1316–1319
- Shigetani Y, Sugahara F, Kuratani S (2005) Evolutionary scenario of the vertebrate jaw: the heterotopy theory from the perspectives of comparative and molecular embryology. *BioEssays* 27: 331–338
- Takio Y, Pasqualetti M, Kuraku S, Hirano S, Rijli FM, Kuratani S (2004) Lamprey *Hox* genes and the evolution of jaws. *Nature OnLine* 429: 1 p following 262. http://www.nature.com/cgi-taf/DynaPage.taf?file=/nature/journal/v429/n6989/full/nature02616_fs.html
- Uchida K, Murakami Y, Kuraku S, Hirano S, Kuratani S (2003) Development of the adenohipophysis in the lamprey: evolution of the epigenetic patterning programs in organogenesis. *J Exp Zool B Mol Dev Evol* 300B: 32–47
- Ueki T, Kuratani S, Hirano S, Aizawa S (1998) *otd/Otx* cognates in a lamprey, *Lampetra japonica*. *Dev Genes Evol* 208: 223–228