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The Skull Development of Parrots with Special Reference to the Emergence of a Morphologically Unique Cranio-Facial Hinge

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ABSTRACT—The order Psittaciformes (parrots) has unique morphological features in the head that are evolutionarily novel. To better understand the unique evolution of the head in parrots, the developmental pattern of the skull of the budgerigar (*Melopsittacus undulatus*) was initially described on the basis of transparent skeletal specimens. Although the fundamental pattern of the skull development of birds is conserved in parrots, some differences were observed between parrots and other groups of birds. In parrots, the vacuity in the interorbital septum did not emerge throughout ontogeny, in contrast to other lineages of birds, for example Galliformes and Coliiformes. This feature seems to be concerned with the attachment of the unique jaw muscle of parrots, *M. ethmomandibularis*, to the interorbital septum. In spite of a prokinetic skull, the cranio-facial hinge of parrots was brought about by secondary transformation of dermal bones unlike that of birds with a standard prokinetic skull (e.g. *Corvus*) in which the nasal-frontal suture directly becomes a hinge of bending. To further understand the evolution of “pseudoprokinesis” in parrots, the construction of a robust avian phylogeny is desired. The parrot-specific suborbital arch and cranio-facial hinge are not seen until birds leave the nest and can feed themselves. In conclusion, these structures are considered to be essential for eating hard and/or large meals.

Key words: parrots, development, evolutionary novelty, cranio-facial hinge, cranial kinesis

INTRODUCTION

The order Psittaciformes (parrots) is one of the largest groups in birds, including 352 species (Clements, 2000). Although parrots are adapted to various environments ranging from tropical to temperate areas and vary in body size and color pattern, their head morphology is highly conserved across species. The beak is deep and telescoped anteroposteriorly (Beecher, 1962). The upper beak is significantly movable upward, having a distinct cranio-facial hinge (Fig. 1, arrowheads) that is not as developed in other lineages of birds. Also, in some groups of parrots, the lower part of the eye is completely bordered by a unique bony arch, the suborbital arch (Fig. 1, arrows). Such a cranial morphology is thought to serve in cracking hard and/or large nuts that humans cannot break without a hammer. These features have had some authors calling for a “complete recasting of the avian skull” (Beecher, 1962) or claiming “evolutionary novelty” (Zusi, 1993). However, the develop-

ment of such morphological features is not well understood.

To better understand the unique evolution of the head in parrots, the developmental pattern of the skull of the budgerigar (*Melopsittacus undulatus*) was initially described on the basis of transparent skeletal specimens and compared with that of other avian species. Subsequently, the morphogenesis of the unique cranio-facial hinge of parrots was surveyed using histological techniques.

MATERIALS AND METHODS

Animals

Fertilized eggs, chicks and adult birds of *Melopsittacus undulatus* and *Nymphicus hollandicus* were supplied from a private hatchery in Yatomi, Aichi, Japan, during 2002. Embryos were excised with forceps from the surrounding extraembryonic membranes in Petri dishes filled with 0.1 M phosphate-buffered saline (pH 7.4). One group of embryos was fixed with Bouin’s fixative for histological examination. The other group of embryos was fixed with 10% formalin for preparing skeletal specimens.

Transparent skeletal specimens

The embryos fixed with 10% formalin were skinned and eviscerated. Based on the methods of Dingerkus and Uhler (1977) with slight modification, skulls and skeletons were stained. Initially carti-

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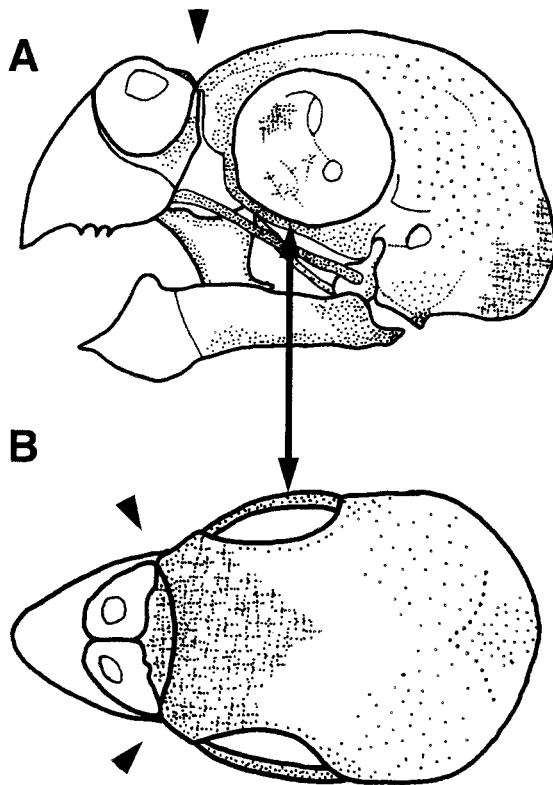


Fig. 1. The skull of adult *Melopsittacus undulatus*. **A**, lateral view; **B**, dorsal view. Two unique structures specific to parrots are shown. Arrowheads: distinct cranio-facial hinge. Arrows: suborbital arch.

lages were stained with alcian blue, which reacts with the mucopolysaccharides. After exposure to a trypsin solution, the bones were stained with alizarin red dissolved in 1.0% KOH. Thereafter, specimens were transferred through a graded series of glycerin/distilled water mixtures (30%, 50%, 70%) and finally stored in 80% glycerin/distilled water. For descriptions, transparent specimens of *Melopsittacus* prepared during 1983–1986 (collections of Kyoto University Museum) were also used. In addition to skeletal specimens of parrots, transparent specimens of the galliform *Coturnix japonica* and several passeriform species were used for comparative analysis.

Histological sections

Following standard procedures, embryos and hatchlings fixed with Bouin's fixative were embedded in paraplast, cut at 8–12 μm , and stained with hematoxylin and eosin (Humason, 1979; Gordon, 1990). The heads of adult specimens fixed with 10% formalin were embedded in celloidin, and cut at 25 μm in transverse sections and 36 μm in sagittal sections.

RESULTS

The skull development of *Melopsittacus undulatus*

The descriptions of skull development were made on the basis of a total of 78 skeletal specimens (Table 1). The development could be divided into the following 7 stages: A–G. The first two stages, the chondrogenic stages, are when cartilaginous elements are formed. The last five stages or osteogenic stages are when replacement of the cartilage by bone occurs and dermal bones are developed. In addition, the development of the lower jaw and hyoid apparatus was

Table 1. The number and skull length of specimens used for descriptions of the skull development. The skull length is given by means and the range between minimum and maximum length is given in parentheses.

Stage	<i>Melopsittacus undulatus</i>		<i>Nymphicus hollandicus</i>	
	Number	Skull length (mm)	Number	Skull length (mm)
A	1	3.5	0	–
B	1	5.0	0	–
C	6	6.6 (6.0–7.0)	0	–
D	39	10.2 (8.0–12.3)	12	13.0 (10.0–16.0)
E	8	16.0 (13.0–20.2)	3	21.6 (18.2–23.7)
F	6	23.8 (22.5–25.1)	3	32.1 (30.8–33.8)
G	17	26.0 (25.3–28.1)	1	36.4

also described. In regard to the external morphology of the embryos (stage A–D), I basically referred to *Gallus* developmental stages (Hamburger and Hamilton, 1951) based on several criteria, represented by shapes of the head structures, limbs and feather germs.

Stage A (Hamburger and Hamilton stage; HH 26–28; Fig. 2)

The neurocranium at this stage consists of the parachordal cartilage, the orbital cartilage, and the trabecula cranii (cartilage). The first two elements fuse to one another and occupy the main part of the neurocranium. The notochord pierces these cartilages forward and reaches the middle of the orbital cartilage. The rostral portion of the orbital cartilage is vertically situated within the cranial cavity and notched on each side for the abducens nerve. The trabecula cranii, the most anteriorly located element, consists of a pair of rods that are separated from one another. These are caudally connected to the orbital cartilage by the polar cartilage like an upward projection. The two visceral elements, the palatoquadrate and Meckel's cartilage are also found ventrally to the orbital cartilage. The proximal end of Meckel's cartilage articulates with the quadrate process of the palatoquadrate. The auditory capsule is situated dorsolateral to the parachordal cartilage. A pair of occipital arches is located on the posterior side of the parachordal cartilage. The hyobranchial apparatus consists of four cartilaginous condensations: the basihyal, a pair of epibranchials, and a centrally located element that is trifurcated and seems to be an urohyal-ceratobranchial complex.

Stage B (HH 34; Fig. 3)

The occipital arch fuses with the parachordal cartilage and auditory capsule rostrally and forms the occipital cartilage where several pairs of the hypoglossal foramina and a pair of vagal foramen are discerned. The trabecular cartilages on either side have fused rostrally to become the trabecular communis. A vertical projection has developed in its mid-line, forming the interorbital septum. As a consequence of the trabecular cartilage fusion, the hypophysial fenestra is open anterior to the orbital cartilage. The rostral tip of the trabecular cartilage elongates ventrally as a prenasal process. The lamina orbitonasalis appears as a small projection

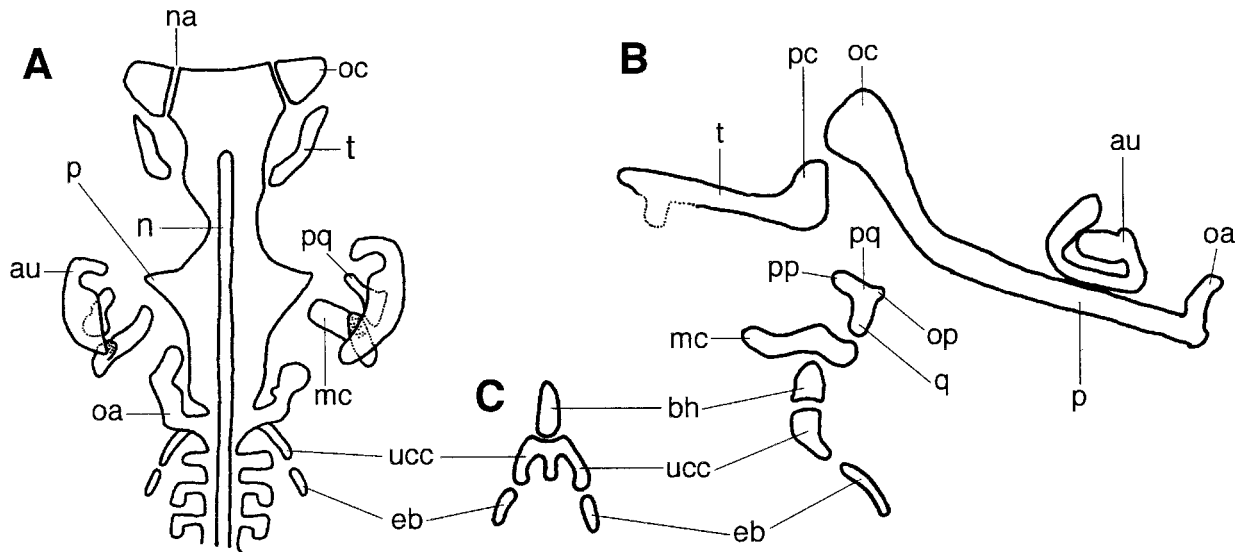


Fig. 2. Neurocranium of *Melopsittacus undulatus* at stage A. **A**, posterodorsal view; **B**, lateral view; **C**, hyoid apparatus. Abbreviations: au, auditory capsule; bh, basihyal; eb, epibranchial; mc, Meckel's cartilage; n, notochord; na, notch for abducens nerve; oa, occipital arch; oc, orbital cartilage; op, otic process of palatoquadrate; p, parachordal cartilage; pc, polar cartilage; pp, pterygoid process of palatoquadrate; pq, palatoquadrate; q, quadrate process of palatoquadrate; t, trabecula cranii; ucc, urohyal-ceratobranchial complex.

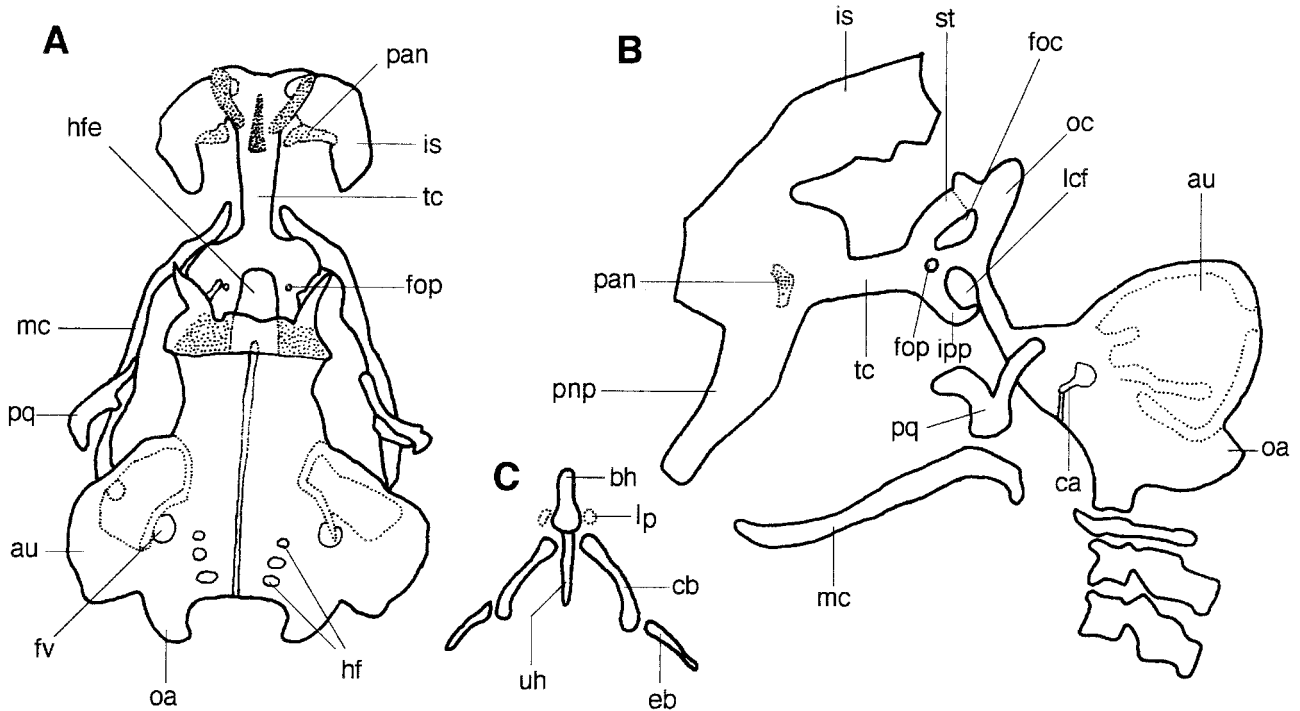


Fig. 3. Neurocranium of *Melopsittacus undulatus* at stage B. **A**, dorsal view; **B**, lateral view; **C**, hyoid apparatus. Abbreviations: au, auditory capsule; bh, basihyal; ca, columella auris; cb, ceratobranchial; eb, epibranchial; foc, foramen for oculomotor nerve; fop, foramen for ophthalmic artery; fv, foramen for vagus nerve; hf, foramina for hypoglossal nerve-roots; hfe, hypophysial fenestra; ipp, infrapolar process; is, interorbital septum; lcf, lateral carotid foramen; lp, lateral process of basihyal; mc, Meckel's cartilage; oa, occipital arch; oc, orbital cartilage; pan, lamina orbitonasalis; pnp, prenasal process; pq, palatoquadrate; st, supratabecular cartilage; tc, trabecula communis; uh, urohyal.

from the lateral side of the interorbital septum. The foramen for the ophthalmic artery penetrates the posterior part of the trabecular communis transversely. The supratabecular cartilage almost attaches to the orbital cartilage, and forms the

foramen for the oculomotor nerve. Meckel's cartilage elongates rostrally and attaches with a counterpart at the distal tip. The pterygoid and otic processes of the quadrate have become notably projected. In the hyobranchial apparatus,

the centrally located complex seen in the previous stage has already differentiated into each element. The medial urohyal attaches to the anterior basihyal.

Stage C (HH 36; Fig. 4)

The neurocranium becomes flatter as compared with the previous stage owing to rostrocaudal elongation. The middle portion of the trabecula communis has been

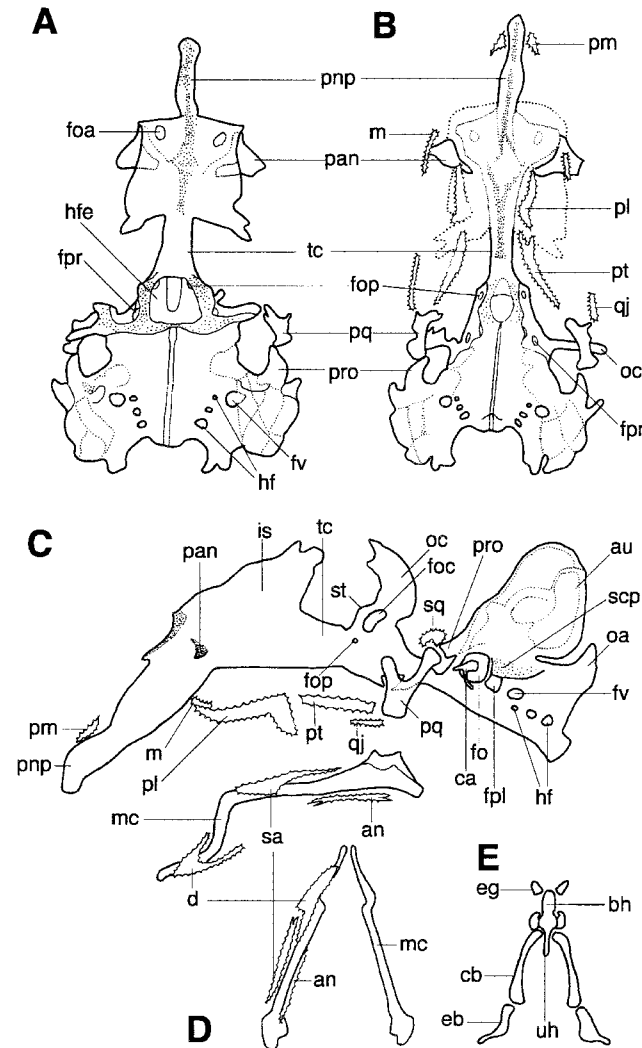


Fig. 4. Head skeleton of *Melopsittacus undulatus* at stage C. **A**, dorsal view; **B**, ventral view; **C**, lateral view; **D**, ventral view of the mandible; **E**, hyoid apparatus. Dermal bones are excluded in **A**. Abbreviations: an, angular; au, auditory capsule; bh, basihyal; ca, columella auris; cb, ceratobranchial; d, dentary; eb, epibranchial; eg, entoglossal; fo, foramen ovale of auditory capsule; foa, fenestra olfactoria advehens; foc, foramen for oculomotor nerve; fop, foramen for ophthalmic artery; fpl, foramen perilymphaticum of auditory capsule; fpr, foramen for profundus branch of trigeminal nerve; fv, foramen for vagus nerve; hf, foramina for hypoglossal nerve-roots; hfe, hypophysial fenestra; is, interorbital septum; m, maxilla; mc, Meckel's cartilage; oa, occipital arch; oc, orbital cartilage; pan, lamina orbitonasalis; pl, palatine; pm, premaxilla; pnp, prenasal process; pq, palatoquadrate; pro, prootic process; pt, pterygoid; qj, quadratojugal; sa, surangular; scp, subcapsular process; sq, squamosal; st, supratrabecular cartilage; tc, trabecula communis; uh, urohyal.

enlarged, forming a primordium of the nasal capsule. The otic process of the quadrate articulates with the prootic process of the metotic cartilage. The columella auris is located in the oval foramen of the auditory capsule that is surrounded caudally by the subcapsular process. Several dermal bones: the premaxilla, maxilla, palatine, pterygoid, quadratojugal, squamosal, dentary, angular, and surangular have emerged as mesenchymal condensations within the dermis.

Stage D (HH 37- hatchlings; Fig. 5)

The nasal capsule has become distinct. The processus tectalis projects upward from the anterior part of the interorbital septum. The posterior part of the interorbital septum has been dilated laterally and forms a flat plate, the planum suprasedale. The supratrabecular process has been separated from the orbital cartilage so that the upper part of the oculomotor foramen is free. At the base of the interorbital septum, a dermal rostrorparasphenoid that is rostrocaudally long has been formed. The primordium of the basi-parasphenoid emerges as a pair of mesenchymal condensation located caudal to the rostrorparasphenoid. The nasal, lacrimal, and jugal are newly formed. The latter organizes the jugal bar, cooperating with the maxilla and quadratojugal. In older specimens, the following states were found: the posterior part of the frontal and that of the parietal are faintly formed, the dermal bones have become pale red due to the uptake of alizarin red, resorption of the cartilage substances occurs in the middle part of the otic process of the quadrate and alizarin uptake is seen there as well as in the ceratobranchials of the hyoid apparatus.

Stage E (Younger nestlings; Fig. 6)

The shape of the neurocranium has not changed as compared with the previous stage. The nasal capsule, interorbital septum, and main part of the metotic cartilage are still cartilaginous. Cartilage resorption occurs at the anterior interorbital septum, making a colorless oval plate. Resorption and replacement with bone are also seen in the lateral portion of the orbital cartilage, prootic region, and occipital region from which the orbitosphenoid, prootic, and three occipital bones originate respectively. Two basi-parasphenoids fuse one another medially and combine with the rostrorparasphenoid anteriorly. Almost all dermal bones are configured into the terminal state, though they are not sutured completely. In older specimens, alizarin uptake is seen at the anterior interorbital septum, showing appearance of the mesethmoid. Moreover, occipital elements including the basioccipital, supraoccipital, and a pair of exoccipital have expanded and fused each other so that the mass of the metotic cartilage is reduced.

Stage F (Older nestlings)

The neurocranium has been almost entirely replaced with bones, with only a part of the interorbital septum and metotic cartilage remaining intact. Although a thin bony plate consisting of a pair of nasals is discerned at the root of the upper beak, the cranio-facial hinge is not seen. The lower jaw becomes stout, forming the mandible symphysis in

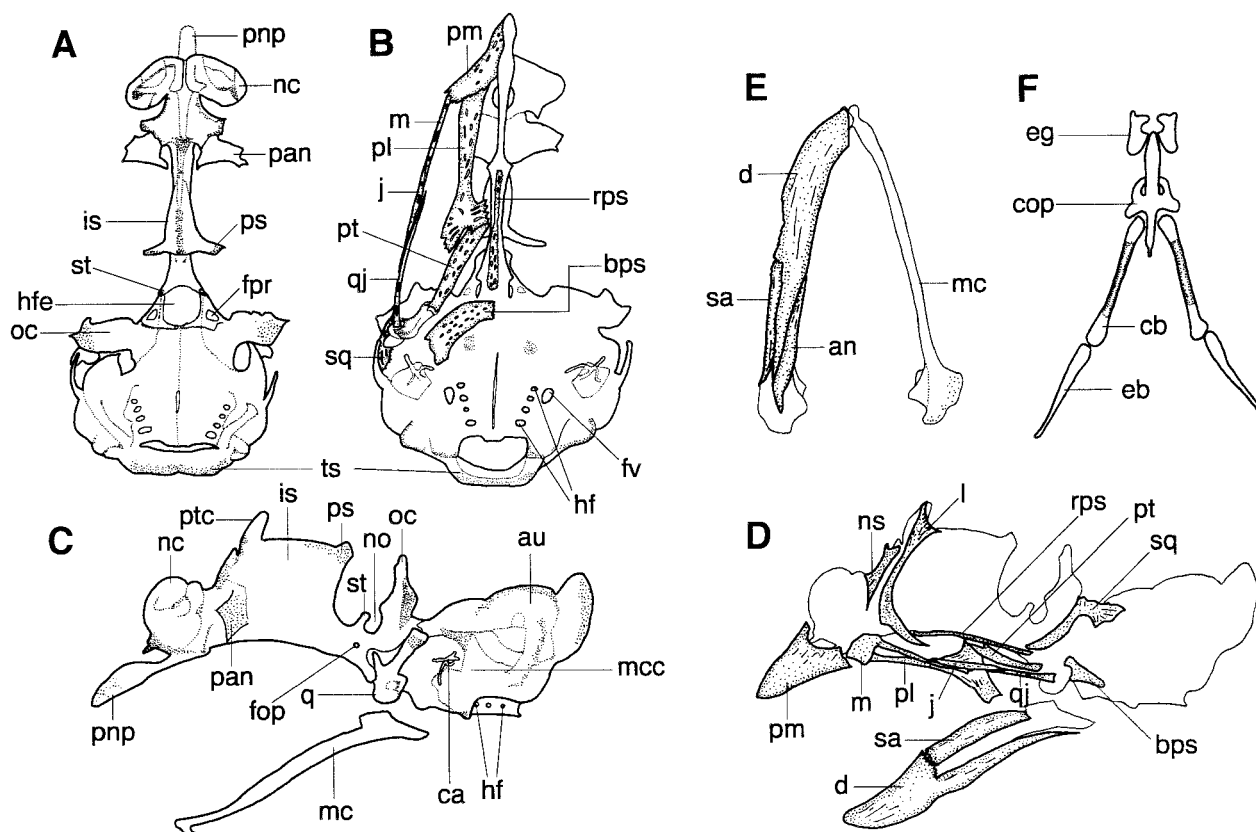


Fig. 5. Head skeleton of *Melopsittacus undulatus* at stage D. **A**, dorsal view of the skull; **B**, ventral view of the skull; **C**, lateral view of the neurocranium; **D**, lateral view of the dermatocranium (the contour of the neurocranium is outlined); **E**, ventral view of the mandible; **F**, hyoid apparatus. Dermal bones are excluded in **A** and the left side of the mandible in **E**. Abbreviations: an, angular; au, auditory capsule; bps, basiparashenoid; ca, columella auris; cb, ceratobranchial; cop, copula; d, dentary; eb, epibranchial; eg, entoglossal; fop, foramen for ophthalmic artery; fv, foramen for vagus nerve; fpr, foramen for profundus branch of trigeminal nerve; hf, foramina for hypoglossal nerve-roots; hfe, hypophysial fenestra; is, interorbital septum; j, jugal; l, lacrimal; m, maxilla; mc, Meckel's cartilage; mcc, metotic cartilage; nc, nasal capsule; no, notch for oculomotor nerve; ns, nasal; oc, orbital cartilage; pan, lamina orbitonasalis; pl, palatine; pm, premaxilla; pnp, prenasal process; ps, planum suprasetale; ptc, processus tectalis; pt, pterygoid; q, quadrate; qj, quadratojugal; rps, rostromparasphenoid; sa, surangular; sq, squamosal; st, supratrabecular cartilage; ts, tectum synoticum.

which sutural boundaries between each dermal element are vague. The dermal bone is firmly sutured. All elements of the hyoid apparatus have been ossified.

Stage G (Independent bird twenty-five days after hatching)

Each element of the dermatocranium is completely fused, and therefore sutural boundaries become inapparent. The suborbital arch is completed. The distinct cranio-facial hinge is seen behind the nasal capsule.

Emergence of the morphologically unique cranio-facial hinge in parrots

To study the morphogenesis of the unique cranio-facial hinge in detail, microscopic examinations were performed by preparing histological sections of *M. undulatus*. In addition, sections and skeletal specimens of the cockatiel, *Nymphicus hollandicus* were also prepared (Table.1). Because the cranio-facial hinge of parrots is seen in the almost same position across species, it is expected that there is little interspecific variation in the developmental pattern. As well as the budgerigar, the cockatiel is available for

embryological studies and has some morphological features that are not seen in the former. Therefore, histological comparisons are effective as a preliminary study of interspecific variation in the developmental pattern of the parrot cranio-facial hinge.

In embryos around hatching, the posterior region of the nasal capsule is occupied by cartilaginous neurocranium and a pair of dermal bones, the nasals, that overlay the neurocranium (Fig. 5). In *M. undulatus*, the pair of nasals is not yet sutured medially at this stage (Fig. 7A). Undifferentiated mesenchymal cells are seen at the boundary of the two dermal bones (Fig. 7B). In *N. hollandicus*, the posteromedial projection (dorsal bar) of the premaxilla remarkably elongates caudally and enters between the two nasal bones. So two pairs of dermal bones are recognized, but they are also separated from each other (Fig. 7D). In younger nestlings, these dermal bones are sutured and construct a thin bony plate above the neurocranium. The thickness of the bony plate is identical rostrocaudally, showing an absence of any hinge-like structure such as a transverse fissure or groove

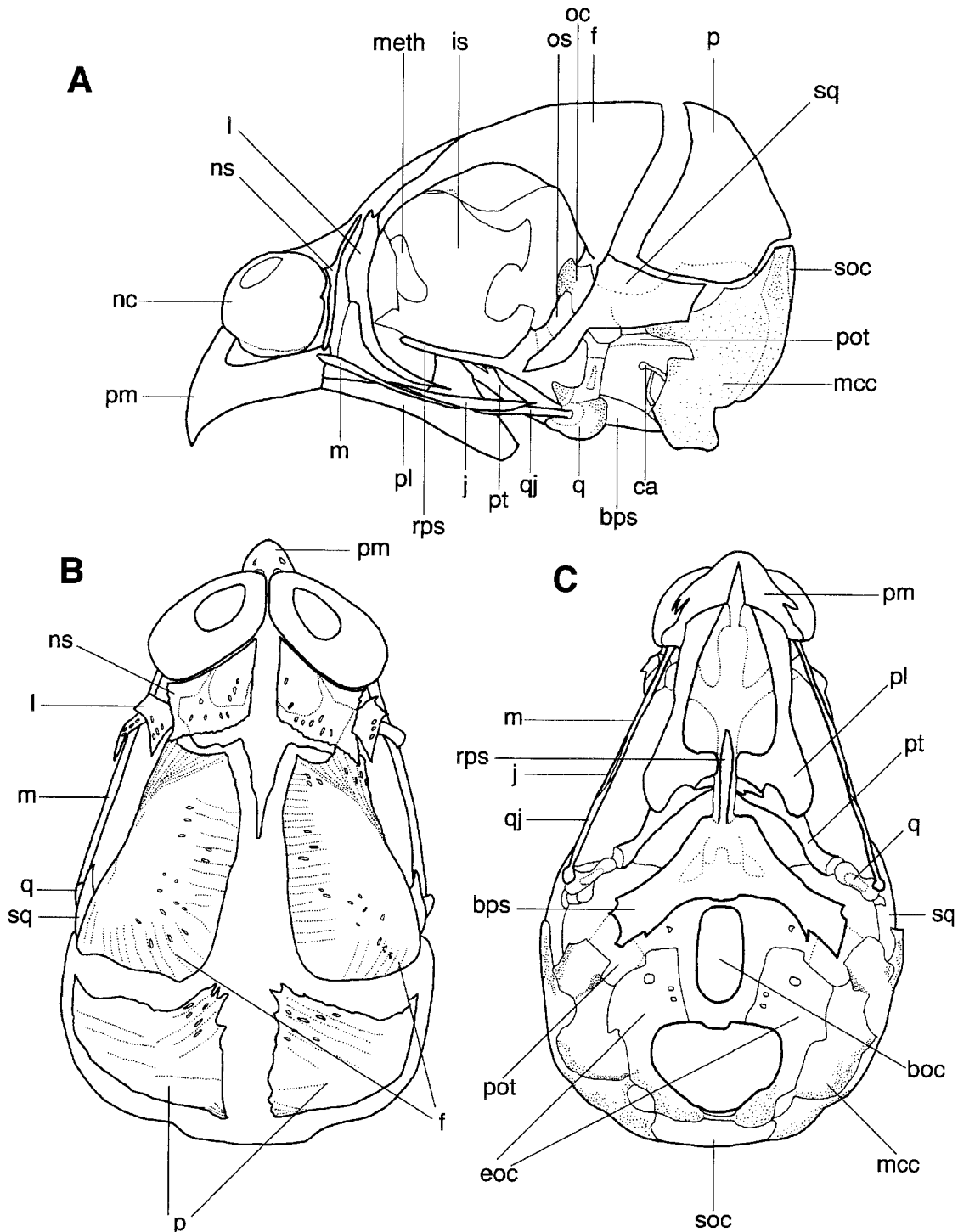


Fig. 6. The skull of *Melopsittacus undulatus* at stage E. **A**, lateral view; **B**, dorsal view; **C**, ventral view. Abbreviations: boc, basioccipital; bps, basiparashenoid; ca, columella auris; eoc, exoccipital; f, frontal; is, interorbital septum; j, jugal; l, lacrimal; m, maxilla; mcc, metotic cartilage; meth, mesethmoid; nc, nasal capsule; ns, nasal; oc, orbital cartilage; os, orbitosphenoid; p, parietal; pl, palatine; pm, premaxilla; pot, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; rps, rostromparashenoid; soc, supraoccipital; sq, squamosal.

in this region (Fig. 7C, E). The first sign of the cranio-facial hinge formation is recognized as a shallow groove above the nasal bones in the oldest nestlings (Fig. 8A). In independent birds that leave the nest and can feed themselves, each element of the skull is completely ossified, fused

together (Fig. 8B) and well pneumatized (Fig. 8C–F). The cranio-facial hinge is obviously recognizable above the skull vault that formerly consisted of a pair of dermal bones in *M. undulatus* and two pairs of dermal bones in *N. hollandicus*. The histological state of the cranio-facial hinge is consider-

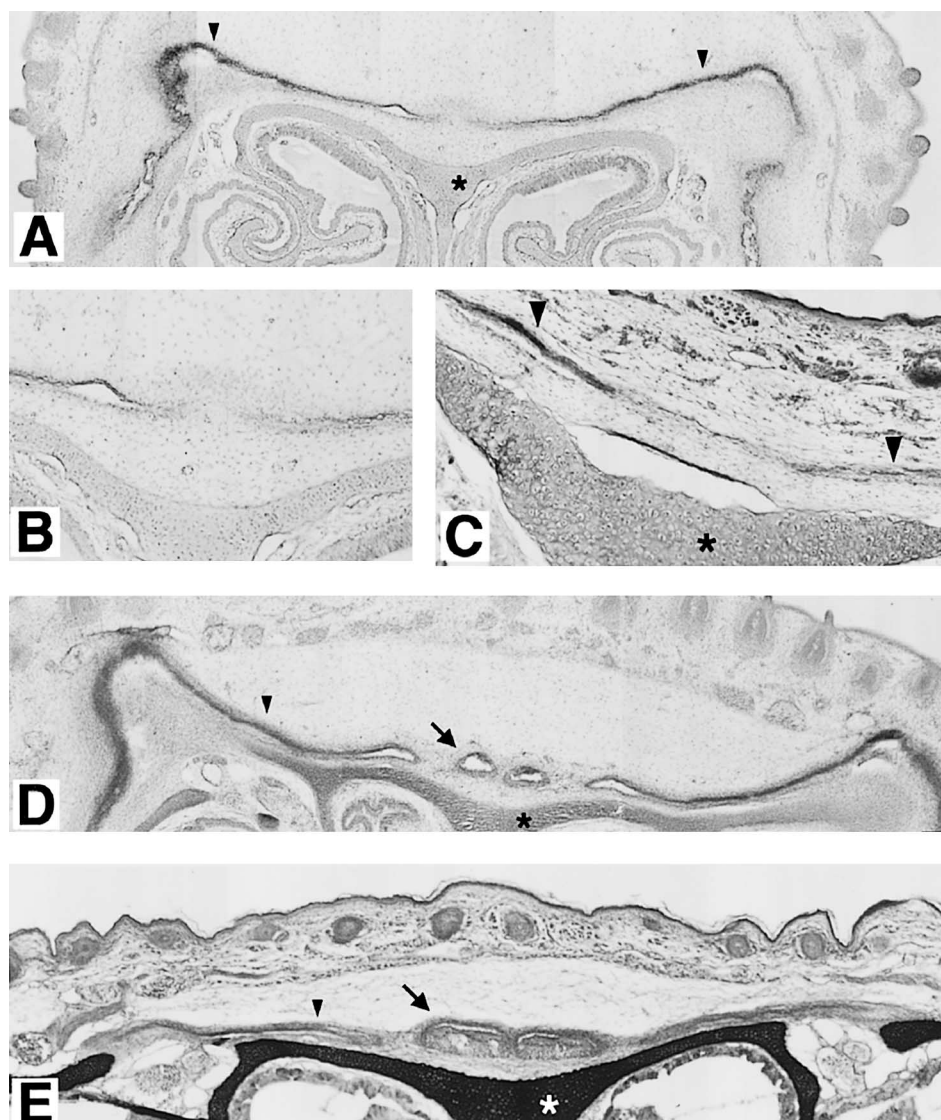


Fig. 7. Transverse sections of the posterior region of the nasal capsule. **A:** A pair of the nasals (arrowheads) that overlay the neurocranium (asterisk) in *M. undulatus* embryo around hatching. **B:** A magnification of **A** showing the boundary between the two nasals. Note undifferentiated mesenchymal cells between the two dermal bones. **C:** In younger nestlings of *M. undulatus*, the nasals begin to suture one another. **D:** The posterior region of the nasal capsule of embryonic *N. hollandicus*. **E:** The posterior region of the nasal capsule of *N. hollandicus* nestlings. The dorsal bar of the premaxilla (arrows) elongates caudally to the anterior border of the frontal and overlays the medial part of the neurocranium. Therefore, two pairs of dermal bones that overlay the neurocranium are recognized in this species.

ably different from that of neighboring parts of the skull vault (Fig. 8C–F). At the hinge, pneumatization of bone is not seen at all and the thickness of bone has become reduced, being constricted like an hourglass. A great deal of fibrous connective tissue like periosteum occupies the upper part of the hinge (Fig. 8F).

DISCUSSION

The skull of vertebrates is composed of two elements: the chondrocranium (neurocranium) which is secondarily replaced by bones and the dermatocranium which is directly formed within the dermis. The developmental pattern of the chondrocranium of *Melopsittacus* was similar to that of other

avian species (de Beer, 1937; Goldschmid, 1972) and so easily comparable. The relative position of the foramina for cranial nerves and general configuration of cartilaginous elements were conserved in the chondrocranium of parrots. One exception is the absence of the vacuity in the interorbital septum. The vacuity is seen in numerous taxa of birds including Coliiformes (Goldschmid, 1972) which is thought to be one of the closest relative of parrots (Espinosa de los Monteros, 2000). In parrots, the vacuity did not emerge throughout ontogeny. This absence may have a relationship with the attachment of the parrot-specific *M. ethmomandibularis* to the interorbital septum and structural reinforcement of the skull against muscle activity for lower jaw movement.

In the development of the dermatocranium, the sequ-

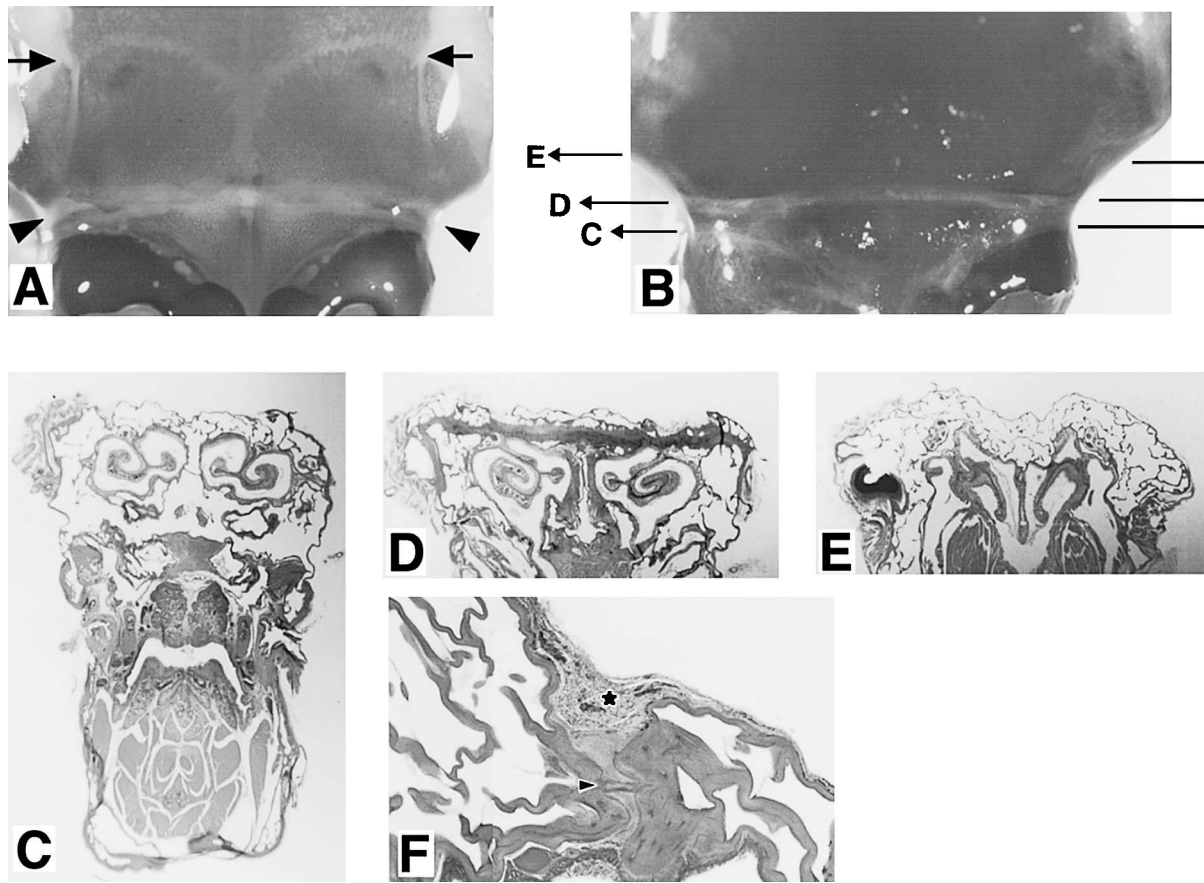


Fig. 8. The emergence of the morphologically unique crano-facial hinge in *M. undulatus*. **A:** A dorsal view of the skull of the oldest nestlings showing the posterior region of the nasal capsule. Arrows indicate the sutural boundaries between the nasal and frontal. Arrowheads show the shallow groove above the nasal bones corresponding to the future crano-facial hinge. **B:** A dorsal view of the skull of an independent bird in which each element of the skull is completely ossified and fused. Each arrow corresponds to lines where the transverse sections given in **C–E** were prepared. **C:** A transverse section of the region somewhat rostral to the crano-facial hinge. **D:** A transverse section at the hinge. **E:** A transverse section of the region somewhat caudal to the hinge. Note the remarkable pneumatization at the skull vault in **C** and **E**, and low level of pneumatization in **D**. **F:** A sagittal section magnifying the crano-facial hinge (arrowhead). At the hinge, the bone has become thinned, but unbroken. A large amount of fibrous connective tissue occupies the upper part of the hinge (asterisk).

ence of appearance of each element was almost identical between altricial parrots and precocial galliform birds (Jollie, 1957). To verify interspecific variations in dermatocranium development, a series of skeletal specimens of Japanese quail, *Coturnix japonica*, was prepared for comparison with parrots. The fertilized egg of the quail is commercially available and so the establishment of a complete series of skeletal specimens is relatively easy. In addition, the small quail skull is more suitable for direct comparisons with small parrot species, rather than the larger chick skull. Consequently, there were few differences between them, except for numbers of ossification centers of the parashenoid. Nonetheless, it has been assumed that some elements of the dermatocranium of parrots contribute to the formation of several unique structures, i.e., the suborbital arch and distinct crano-facial hinge (Fig. 1).

The suborbital arch is a parrot-specific structure surrounding the eye from below. In *Melopsittacus*, the lacrimal, anterior component of the arch, appeared as a slender, dorsoventrally elongated bone at stage D and its foot had

already projected posteriorly (Fig. 5). The squamosal, a posterior component of the arch, appeared earlier than the lacrimal at stage C, as a tiny mesenchymal condensation (Fig. 4). Its zygomatic process was not clearly recognized until the next stage (Fig. 5). The suborbital arch was not completed until the parrots grew large enough to leave the nest. In stages E (Fig. 6) and F, the suborbital process and the zygomatic process have further elongated distally, yet they were still separated from one another without forming a bony arch. Instead, the two processes were tightly connected with a ligamentous sheet, the subocular ligament, located in the dorsomedial part of the already formed *M. pseudomasseter* at these stages. From my observations, the unique suborbital arch may be a secondary structure brought about by ossification of the ligamentous sheet.

The upper beak of parrots shows high movability due to a distinct crano-facial hinge just behind the nasal capsule (Fig. 1). Such cranial kinesis is not unique to parrots but is widespread among birds. Hofer (1949, 1954) intended to divide avian cranial kinesis into two major subcategories,

'prokinesis' and 'rhynchokinesis'. Prokinesis is the common type and thought to be the primitive condition in stem stock of the modern birds (Bock, 1964; Bühler, 1981). In the prokinetic skull as represented by that of crows (*Corvus*), the entire upper jaw moves as a unit around a hinge or region of bending at the junction of the nasal and frontal bones (Fig. 9A). In addition, the posterior border of the nostril ends anterior to the junction (holorhinal nostril). Based on these criteria, the kinetic type in parrots has been regarded as prokinesis (Zusi, 1993).

However, the present study revealed that parrot-type prokinesis was brought about independent of the standard crow-type. Unlike the cranio-facial hinge of birds with a standard prokinetic skull, that of parrots emerged secondarily above the skull vault where several dermal bones are completely fused (Fig. 9B). In oldest nestlings, an indistinct groove corresponding to the future cranio-facial hinge was observed anterior to the sutural boundary between the nasal and frontal bones (Fig. 8A). Therefore, it is hard to conclude that the former nasal-frontal boundary transferred rostrally throughout ontogeny and became the hinge in the adult parrot.

The ancestral stock for all known neornithian birds has been supposed to have a prokinetic skull like that of crows

(Bock, 1964). Subsequently, another type of cranial kinesis, rhynchokinesis, can be derived. Birds with a rhynchokinetic skull (Fig. 9C) have an upper beak that is movable within it and a nostril that extends back beyond the cranio-facial hinge (schizorhinal nostril). Although rhynchokinesis tends to be thought of as a remarkable property of Charadriiformes including plovers and sandpipers (double or distal rhynchokinesis), it is also seen in wide range of avian species belonging to Columbiformes, Gruiformes, and Coraciiformes (proximal rhynchokinesis).

If parrots were directly derived from birds with a standard prokinetic skull, there might have been a need for the "true naso-frontal hinge" to break and a new hinge to develop within the forward skull vault. On the other hand, if parrots were derived from birds with a rhynchokinetic skull and regained the prokinetic skull, it might have been necessary for the nostril to extend forward to the cranio-facial hinge. Unfortunately, the phylogenetic relationship of parrots to other avian groups has been highly controversial (Gadow, 1892; Mayr and Amadon, 1951; Sibly, 1972; Espinosa de los Monteros, 2000; van Tuinen *et al.*, 2000). To verify the above hypotheses and understand the evolution of the "pseudoprokinesis" of parrots, the construction of a robust avian phylogeny is desired.

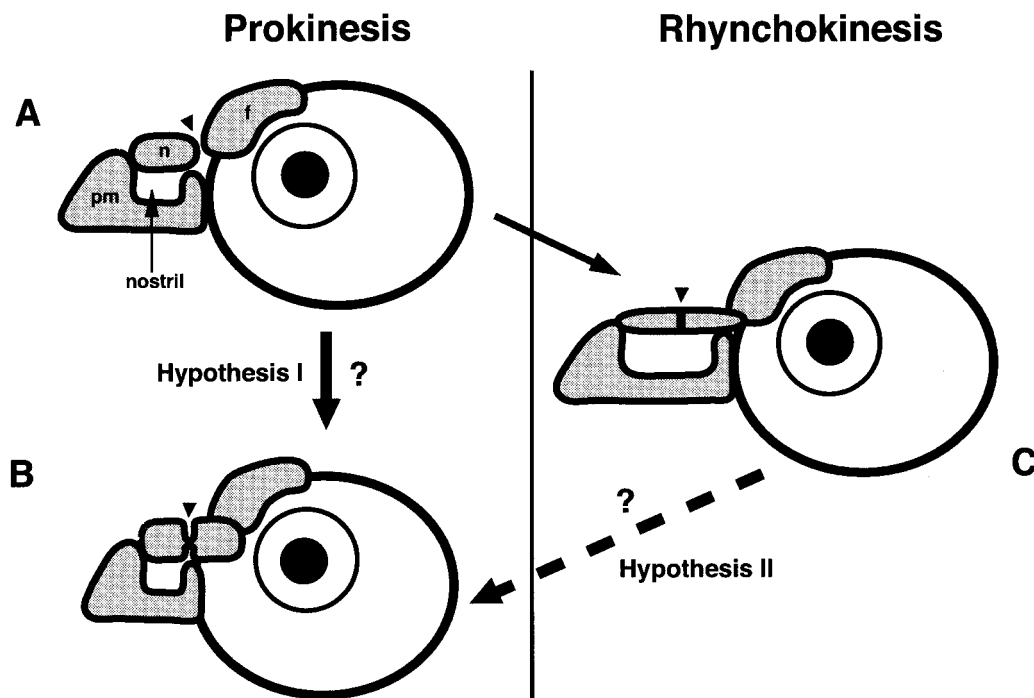


Fig. 9. Two hypotheses explaining the morphological evolution of "pseudoprokinesis" in parrots. **A:** The primitive condition of avian cranial kinesis, standard prokinesis, as seen in crows. The sutural boundary between the nasal and frontal directly becomes the cranio-facial hinge (arrowhead). **B:** Pseudoprokinesis in parrots in which abandonment of the old "naso-frontal hinge" occurs and a new hinge (arrowhead) is reorganized at the base of the upper beak. **C:** Rhynchokinesis probably derived from standard prokinesis, in which some portion of the upper beak (arrowhead) itself changes shape and the nostril extends backward beyond the bending region of the upper beak. Because the prokinesis of parrots was brought about independent of the standard type throughout ontogeny, two hypotheses explaining the evolution of pseudoprokinesis were proposed. Hypothesis I (bold arrow) states that pseudoprokinesis evolved directly from standard prokinesis. Hypothesis II (broken arrow) claims that pseudoprokinesis was derived from rhynchokinesis, with a return to the prokinetic condition. See the text for details about the supposed evolutionary processes for each kinetic type. Which hypothesis is correct is not certain at the present. Abbreviations: f, frontal; n, nasal; pm, premaxilla.

It was unexpected that there would be variations in the developmental pattern of the cranio-facial hinge among parrots. In *M. undulatus*, the cranio-facial hinge ran transversely on the skull vault which formerly consisted of a pair of nasal bones (Fig. 7A–C). On the other hand, two pairs of dermal bones formed the hinge in *N. hollandicus* (Fig. 7D, E). Therefore, it is assumed that 'position' is more critical than 'element' in the organization of the hinge.

As well as the suborbital arch, the cranio-facial hinge of parrots was not formed until birds left the nest. As seen above, the posterior part of the nasal capsule of nestlings is covered with a thin bony plate composed of dermal bones. Such a state of the skull was very similar to that of nestlings or young birds of a wide range of avian species. Histologically, the thickness of the bony plate was identical in the anteroposterior direction. Therefore, the kinematic ability of the upper beak at this stage is thought to be remarkably less than that at the adult stage, no matter that the nasal-frontal suture is more or less movable.

Nestlings of parrots eat meals supplied by their parents. Because these meals are grinded into flour by the parents, the nestlings do not need a wide jaw opening provided by the cranio-facial hinge for taking food. In contrast, adult parrots, except for some lineages specialized in nectar-eating (e.g. *Trichoglossus*), have adapted to eat relatively large meals ranging from plant seeds to ivory nuts. The *M. ethmomandibularis* and *M. pseudomasseter*, unique jaw muscles of parrots, bring much power to adduct lower beak. The suborbital arch seems to reinforce the skull against the power provided by these jaw muscles. Cooperating with them, the cranio-facial hinge seems to work efficiently in cracking large seeds or nuts. In conclusion, these unique structures of parrots are considered to be essential for eating hard and/or large meals.

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