

A Functional and Evolutionary
Analysis of Rhynchokinesis
in Birds

RICHARD L. ZUSI

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ABSTRACT

Zusi, Richard L. A Functional and Evolutionary Analysis of Rhynchokinesis in Birds. *Smithsonian Contributions to Zoology*, number 395, 40 pages, 20 figures, 2 tables 1984.—In this paper avian cranial kinesis is analysed in terms of the configuration of bony hinges found in the upper jaw. Three basic forms of kinesis are recognized: prokinesis, amphikinesis, and rhynchokinesis; rhynchokinesis is subdivided into double, distal, proximal, central, and extensive rhynchokinesis. Schizorhiny is discussed and is regarded as a partial synonym of rhynchokinesis. In distally rhynchokinetic birds, neither the term "holorhinal" nor "schizorhinal" is applicable.

In schizorhinal birds and most rhynchokinetic birds the presence of two hinge axes at the base of the upper jaw imposes a requirement of bending within the jaw during kinesis. Bending takes different forms according to the number of hinges and their geometric configuration within the upper jaw. Proximal rhynchokinesis and distal rhynchokinesis apparently evolved from double rhynchokinesis by loss of different hinges. Extensive rhynchokinesis is an unusual and probably specialized variant. Kinesis in hummingbirds is still little understood.

Downbending of the symphysis of the upper jaw during retraction is a property of amphikinesis and of double and distal rhynchokinesis, and is judged to play an important role in grasping prey, particularly in slender-billed birds that probe. The adaptive significance of rhynchokinesis in certain non-probing birds is not yet known. It is hypothesized that the schizorhinal skull in proximally rhynchokinetic birds reflects ancestry, but has no adaptive explanation, in many living species.

Either prokinesis or some form of rhynchokinesis could be primitive for birds. Rhynchokinesis is not compatible with the presence of teeth in the bending zone of the ventral bar of the upper jaw, and it probably evolved after their loss. Neognathous rhynchokinesis, however, probably evolved from prokinesis. The evolutionary origin of rhynchokinesis from prokinesis required selection for morphological changes that produced two hinge axes at the base of the upper jaw. Once evolved, the properties of these axes were subject to selection in relation to their effects on kinesis. The various forms of kinesis are hypothesized to have evolved by simple steps, and pathways to each kind of kinesis are suggested. In neognathous birds, prokinesis was probably ancestral to amphikinesis, and amphikinesis to rhynchokinesis in most cases, but prokinesis has also evolved secondarily from proximal rhynchokinesis. Rhynchokinesis in paleognathous birds differs from neognathous rhynchokinesis, and it probably evolved by a different pathway.

The use of simple models is valuable in formulating hypotheses about the functional properties and evolutionary history of different forms of kinesis. The functional analysis of kinesis provides a rationale for adaptive radiation and convergence in avian orders that include rhynchokinetic members, and suggests polarities and evolutionary directions that may be useful in phylogenetic analysis.

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A Functional and Evolutionary Analysis of Rhynchokinesis in Birds

Richard L. Zusi

Introduction

All modern birds have the capacity to move the upper jaw, or some portion of the upper jaw, with respect to the brain case. This functional property is known as cranial kinesis (kinetics, or kinematics), and its mechanism includes, in addition to the upper jaw, various portions of the cranium, the lower jaw, the quadrate and bony palate, the jugal bars, certain jaw muscles, ligaments, and various articulations and bony hinges. Thus, much of the morphology of the avian head relates to cranial kinesis. This paper is concerned mainly with the upper jaw and the effects of forces acting on it through the kinetic mechanism. Emphasis is placed on rhynchokinesis, in which bending within the upper jaw accompanies kinetic motion of the jaw as a whole.

The literature on avian cranial kinesis is extensive, beginning, perhaps, with Hérissant (1752) and continuing to the present. Many of the morphological and functional properties of kinesis are understood, but others, even some of the basic ones common to many birds, are not. In addition, certain aspects of the diversity of jaw structure in birds are unexplained. For example,

a variety of forms of kinesis that fall under the current term "rhynchokinesis" has been known for many years (Nitzsch, 1816, 1817), but detailed functional analysis has been largely restricted to the particular form of rhynchokinesis found in woodcock and snipe (Marinelli, 1928; Schumacher, 1929). Only recently has a set of terms for the variants of rhynchokinesis been proposed (Bühler, 1981). Another source of confusion has been the extent and nature of the interaction between schizorhiny and holorhiny on the one hand, and cranial kinesis on the other. The present paper seeks to clarify the terminology and interrelationships of cranial kinesis and schizorhiny, to analyse functional properties of the various forms of kinesis, and to offer clues to the origin and evolution of rhynchokinesis.

METHODS AND MATERIALS.—The data for this paper pertain primarily to variations in the pattern of bending zones or hinges in the upper jaw of birds. I determined the presence and location of bending zones by direct examination of cleaned skulls in the collection of the Smithsonian Institution and from radiographs of the skulls of selected species. The presence of a hinge was usually manifested by flattening of bone that produced a more or less restricted bending axis. A hypothesis of flexibility was tested by manipulation of water-soaked skulls whenever skull

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structure did not permit a clear interpretation. In a few cases, noted in the text, manipulation of fresh birds provided evidence of hinges. Spatial relationships of the bony hinges in skulls of 26 species were plotted on paper by means of a camera lucida. I determined patterns of bending in a hypothetical upper jaw with different configurations of hinges by assuming a jaw structure of two-dimensional, inflexible bars connected by pin hinges, and by laying out the required shapes of the jaw under different degrees of protraction or retraction with a ruler, protractor, and compass. These patterns were confirmed by manipulation of a simple, two-dimensional cardboard model of the upper jaw. The chief sources of possible error in my methods were in distinguishing among several forms of kinesis in borderline cases, and in characterizing flexibility of the ventral hinge of the lateral nasal bar of the upper jaw in a few species. The hypotheses concerning kinetic configurations presented in this paper should be tested against accurate description of bill movement in living birds.

I made the original drawings of skulls with the aid of a microscope and camera lucida, or by tracing projected photographic transparencies. Relative sizes of illustrations were adjusted in some instances to make all skulls more readily comparable.

Anatomical terminology generally follows that of Baumel et al. (1979). I followed the nomenclature of Morony et al. (1975) for scientific names of birds. The Index identifies to family or subfamily all English and generic names used in this paper. The species and number of specimens of the skeletons examined for this study are shown in the Appendix.

ACKNOWLEDGMENTS.—This paper developed from an earlier and still unfinished study of cranial kinesis in the Charadrii begun by me at the University of Michigan Museum of Zoology. Permission to use the collections and radiographic facilities at UMMZ is gratefully acknowledged. I also thank the curators of the British Museum (Natural History) for making their collections available and for the loan of specimens. The late

Leon Kelso generously undertook a major translation from Russian for minimal compensation. Carolyn Cox Lyons rendered the skull drawings in ink and Ellen Paige drew the diagrams and labelled the figures, except for figures 7 and 17, which were done by the author. I benefited from an early discussion of terminology with Walter Bock, and, more recently, from his criticisms and those of Storrs Olson on one or more drafts of the manuscript. Their suggestions were generally followed, but those that were not nevertheless stimulated further study that greatly improved the paper. This research was partially supported by Smithsonian Research Awards Sg 0663049 and Sg 3374156. Finally I thank my wife, Luvia, for typing parts of the manuscript, and for her patience and understanding during its preparation.

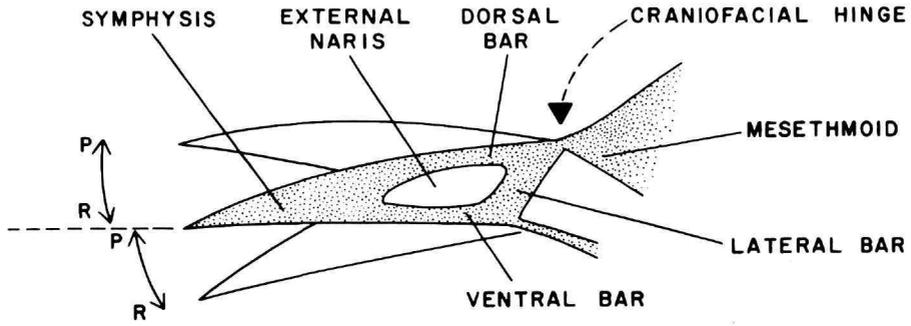
Terminology

AVIAN CRANIAL KINESIS

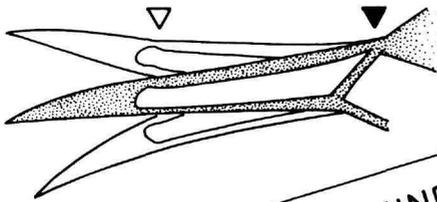
Cranial kinesis in various groups of vertebrates has been described by Frazzetta (1962), Bock (1964), Bühler (1977), and others. Here I recognize prokinesis, rhynchokinesis, and amphikinesis as basic forms of avian kinesis (Figure 1). Although the term "amphikinesis" has been applied within other vertebrate classes in other ways, confusion may be avoided by adding the adjective "avian" as proposed by Bock (1964:3). I follow Bühler (1981) in subdividing rhynchokinesis into five categories that are here called "proximal," "central," "distal," "double," and "extensive" rhynchokinesis (Figure 1) according to the position or extent of bending zones in the dorsal bar of the upper jaw. I have substituted the term "central" for Bühler's "intermediate," and "extensive" for "extended," only because these adjectives form more familiar adverbs when modifying "rhynchokinetic."

Throughout this paper I refer to flexible or inflexible bones. While recognizing that all bones are somewhat flexible, I use inflexible to mean that bending is not readily noticeable under nor-

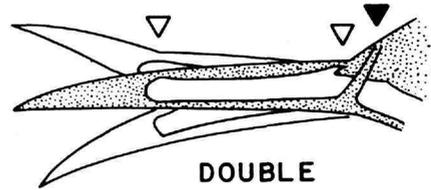
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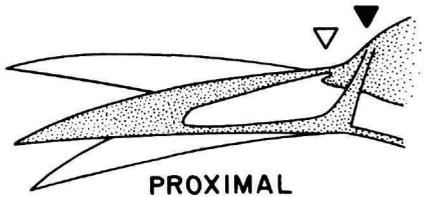
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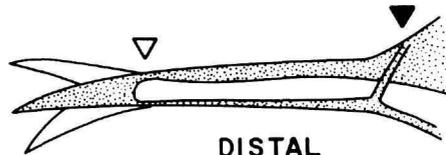
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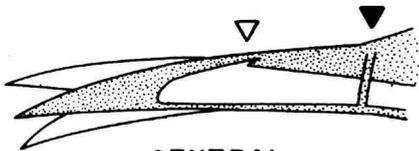
DOUBLE



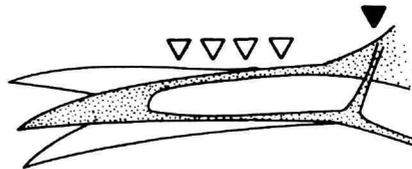
PROXIMAL



DISTAL



CENTRAL



EXTENSIVE

FIGURE 1.—The forms of avian kinesis (stippled figures show upper jaw in closed position; P = protraction, R = retraction; solid pointer indicates craniofacial hinge; open pointers indicate additional bending axes on dorsal bar).

mal stresses. Bones that bend are usually notably flattened, and I use the term "hinge" to mean a localized region of flexibility—not an articulation.

The upper jaw of birds is not easily defined. It could be stated to consist of the nasal, premaxillary, and maxillary bones as defined by most authors, but the homologies of some of these bones have been questioned (McDowell, 1978), and the limits of the bones are lost by fusion in adult birds. A functional definition is more practical. In this paper I draw the caudal limits of the upper jaw dorsally at the craniofacial hinge and ventrally at the hinges of the jugal bars and palatines. Thus, the upper jaw consists of a dorsal bar, two lateral bars, two ventral bars (sometimes fused into one), and a symphysis (Figure 1). In some birds the medial portion of the craniofacial hinge has shifted forward, and in them I regard the caudal limit of the upper jaw to lie at the level of the cranial attachments of the lateral bars. The lateral bar maintains a roughly constant relationship with the ectethmoid, prefrontal, frontal, and orbit in related birds, whereas the mesethmoid and overlying medial portion of the craniofacial hinge may vary considerably in their position relative to the above features, even in closely related birds.

Cranial kinesis includes upward and downward rotation of the upper jaw relative to the brain case. These motions are usually referred to as protraction and retraction of the upper jaw, although the terms apply better to associated motions of the palate with respect to the sphenoidal rostrum. Both protraction and retraction can occur either above or below the closed position of the upper jaw (Figure 1). The ability to protract the upper jaw is related to a variety of avian adaptations (Beecher, 1962; Bock, 1964; Yudin, 1965; Zusi, 1967), but the increase in manipulative versatility of the avian jaw that is afforded by retraction of the upper jaw beyond its closed position is probably most important for an understanding of rhynchokinesis and amphikinesis (see also Zusi, 1967). The phenomenon of coupled kinesis (Bock, 1964) is not directly pertinent

to this paper except for one point. Bock stated that "in a majority of birds, those having a coupled kinetic skull, depression of the upper jaw beyond the normal closed position does not seem possible" (Bock, 1964:24), but he acknowledged that mechanisms to effect depression beyond the closed position might exist. Zusi (1967) proposed two such mechanisms and cited evidence that retraction beyond the closed position occurs in living birds with coupled kinesis. This fact is important for an understanding of the significance of rhynchokinesis.

PROKINESIS (Figure 1).—In a prokinetic skull the upper jaw itself is inflexible and it pivots up and down around the craniofacial hinge. Bending occurs in a flattened region of the nasal processes of the premaxillary bones and in the adjacent premaxillary processes of the nasal bones just rostral to, or dorsal to, the mesethmoid bone (Figure 2). The premaxillary and nasal bones continue backward from the bending axis to fuse with the frontal and mesethmoid bones in adult birds. In rare cases the craniofacial "hinge" is a true articulation. Typically the bony nasal openings end rostral to the craniofacial hinge and the nasal bones provide a firm base for the distribution of protraction and retraction forces to the entire upper jaw.

AMPHIKINESIS (Figure 1).—This form of kinesis differs from prokinesis in that the nasal openings extend back almost to the level of the craniofacial hinge, and the dorsal and ventral bars are flexible near the symphysis. In addition, the lateral bar is flexible near its junction with the dorsal bar. As a result, protraction and retraction forces are transmitted primarily to the symphysis via the lateral and ventral bars. Between the craniofacial and rostral hinges the dorsal bar may be thickened and inflexible, or only slightly flexible. During protraction the entire upper jaw is raised and the tip of the jaw is bent up in addition; in retraction the tip bends down with respect to the rest of the upper jaw.

RHYNCHOKINESIS (Figure 1).—In all forms of rhynchokinesis, bending of the dorsal bar occurs rostral to the base of the upper jaw as delimited

by the cranial attachments of the lateral bars. Different forms of rhynchokinesis are characterized by the location, number, and extent of the hinges on the dorsal bar. Unlike prokinetic birds, rhynchokinetic birds never have a single craniofacial bending zone that includes the nasal bones and the nasal processes of the premaxillae. Instead they have one bending axis passing through the dorsal ends of the lateral bars, and one or more others farther rostral on the dorsal bar. The nasal openings either terminate at the level of, or rarely caudal to, the cranial attachments of the lateral bars, and thus they extend caudally beyond the bending zone(s) of the dorsal bar.

The description of five kinds of rhynchokinesis is somewhat arbitrary because hinges may shift position in the course of evolution, as well as appearing *de novo*. However, I shall argue later that hinges generally have not made extensive evolutionary "migrations" along the bill, and I find that most rhynchokinetic birds can be classified as one of the five kinds.

Double Rhynchokinesis (Figure 1): In this form of rhynchokinesis there are two hinges on the dorsal bar—one near its base and one near the symphysis. Double rhynchokinesis differs from amphikinesis in having two bending axes rather than one at the base of the upper jaw—the basal hinge of the dorsal bar, and the dorsal hinges of the lateral bars. Other workers have described this form of kinesis without naming it (Nitzsch, 1816; Kripp, 1935; Hofer, 1955; Beecher, 1962; Yudin, 1965). Most workers have regarded double rhynchokinesis as an unusual form of avian kinesis and have not dealt with it in their functional analyses. Yudin (1965:69–70) thought that it represented a transitional phylogenetic stage between "little-differentiated rhynchokinesis" and "secondary prokinesis." My examination of skulls, radiographs of skulls, and manipulation of soaked skulls from all schizorhinal groups of birds strongly suggests that double rhynchokinesis is much more common than previously supposed (Table 1). A brief discussion of the mechanics of double rhynchokinesis is given by Zusi (1962:36–38).

Distal Rhynchokinesis (Figure 1): Distal rhynchokinesis differs from double rhynchokinesis in that flexibility of the basal hinge of the dorsal bar is absent. Bending occurs on the dorsal bar only behind the symphysis in a restricted or extended portion of flattened bone. Only the symphysis of the upper jaw is raised or lowered. Characteristically the mesethmoid is expanded forward and fused with the base of the dorsal bar, and the entire dorsal bar is stiffened caudal to its hinge. The lateral bar has a well-defined hinge near its attachment on the cranium, except in kiwis (*Apteryx*).

Proximal Rhynchokinesis (Figure 1): This form of kinesis differs from double rhynchokinesis in that flexibility of the dorsal bar near the symphysis is absent and flexibility of the dorsal bar is limited to its basal portion. There are two axes of bending at the base of the upper jaw as in double rhynchokinesis, one on the dorsal bar and one on the lateral bars. The dorsal bar may be strongly constructed but the ventral bar is always flexible at some point.

Central or Paleognathous Rhynchokinesis (Figure 1): This is the "intermediate rhynchokinesis" of Bühler (1981). The single bending zone of the dorsal bar is located approximately midway between the symphysis and the lateral bars and the nares extend back to the cranial attachments of the lateral bars. Central rhynchokinesis is characteristic of most ratites and most tinamous, and it includes a variety of distinctive characteristics other than the central location of the bending zone.

Extensive Rhynchokinesis (Figure 1): A few birds have an extended zone of bending along the dorsal bar between its cranial attachment and the symphysis. The bar is generally flattened throughout with no evidence of localized hinges. The term "bone spring kinetics" was used by Beecher (1962:28–29) in describing this form of the upper jaw in a tinamou (*Tinamus major*). He stated that some plovers and sandpipers (*Charadrii*) display a combination of a basal hinge and bone spring kinesis, whereas I regard most plovers as doubly rhynchokinetic. Yudin (1958,

1965), Marinelli (1928), Möller (1970), and others refer to extended flexibility of the dorsal bar between the symphysis and its base as an unspecialized or little-differentiated form of rynchokinesis. In almost every case I regard the examples they cite as proximally, doubly, or distally rynchokinetic. It is not always easy to know whether a skull is extensively kinetic, but I have classified as doubly rynchokinetic any skull with a dorsal bar that, no matter how slender, shows greater flexibility near its base and near the symphysis than between those points. Similarly, proximal and distal rynchokinesis are recognized in slender-billed birds by the differentiation of a hinge only near the base of the dorsal bar, or only behind the symphysis.

HOLORHINY AND SCHIZORHINY

Many years ago, Garrod (1873) described two kinds of avian skulls, which he termed "schizorhinal" and "holorhinal." By his definition, the holorhinal skull is characterized by bony external nares whose concave caudal borders lie rostral to the caudal ends of the nasal processes of the premaxillae (Figure 2a). Referring to the premaxillary and maxillary processes of the nasal bone, he stated, "These two processes become continuous behind with the body of the bone, and with one another, there being no interruption of any kind between them" (Garrod, 1873:33). In the schizorhinal skull, the caudal borders of the external nares form an angular space or slit that usually terminates behind the ends of the nasal processes of the premaxillae (Figure 2b). As a result, the maxillary process of the nasal bone is "free" and "almost detached" from the premaxillary process (Garrod, 1873:36). Garrod (1873, 1877) used holorhiny and schizorhiny as a taxonomic character, with limited success.

Because the shape of the caudal border of the nares does not necessarily correlate with its position relative to the nasal processes of the premaxillae, both Hofer (1955) and Yudin (1965) used the terms "atypical" and "typical" to modify

"schizorhinal" and "holorhinal." For example, Hofer described *Cursorius* (Glareolidae) as atypically holorhinal, by which he meant that it was holorhinal in the shape of its nares but functionally schizorhinal in having the lateral bars of the bill independent of the dorsal bar (Figure 2c). Yudin also used "secondary" to indicate ontogenetic change in these features and, by implication, phylogenetic change, whereas by "primary" he meant no such change. In addition, he used "secondary" to indicate a phylogenetic trend inferred from comparison of a series of living species. Thus in describing *Fratercula* as a bird with "secondary atypical schizorhinal" nasal openings, he meant that the caudal borders of the nares were slit-like (schizorhinal), that the borders did not extend caudally as far as the border of the nasal processes of the premaxillaries (atypical), and that the atypical features represented an evolutionary trend away from typical schizorhiny (secondary) as seen in a graded series of the Alcidae from *Cepphus*, *Uria*, and *Alca* through *Cerorhinca* and *Lunda* to *Fratercula*.

The shape of the caudal border of the nares in birds varies from truncate to rounded to slit-like, reflecting the relative width of the bill or the intrusion of bony elements into the nasal opening, and probably other variables (Figure 3). Anatomical relationships such as the position of the nares relative to the caudal end of the nasal process of the premaxillary differ within orders or families, or from young to adult stages. However, most birds that are schizorhinal by the original anatomical definition share certain functional properties that differentiate them from most holorhinal birds. These properties are directly related neither to the shape of the posterior borders of the nares, nor to their position relative to the nasal processes of the premaxillae. Bock and McEvey (1969) therefore recommended that "the distinction between the holorhinal and the schizorhinal nostril be based upon whether the posterior end of the nostril stops anterior to, or projects behind, the nasal-frontal hinge (i.e., separates the hinge of the medial dorsal bar from the hinge of the lateral nasal

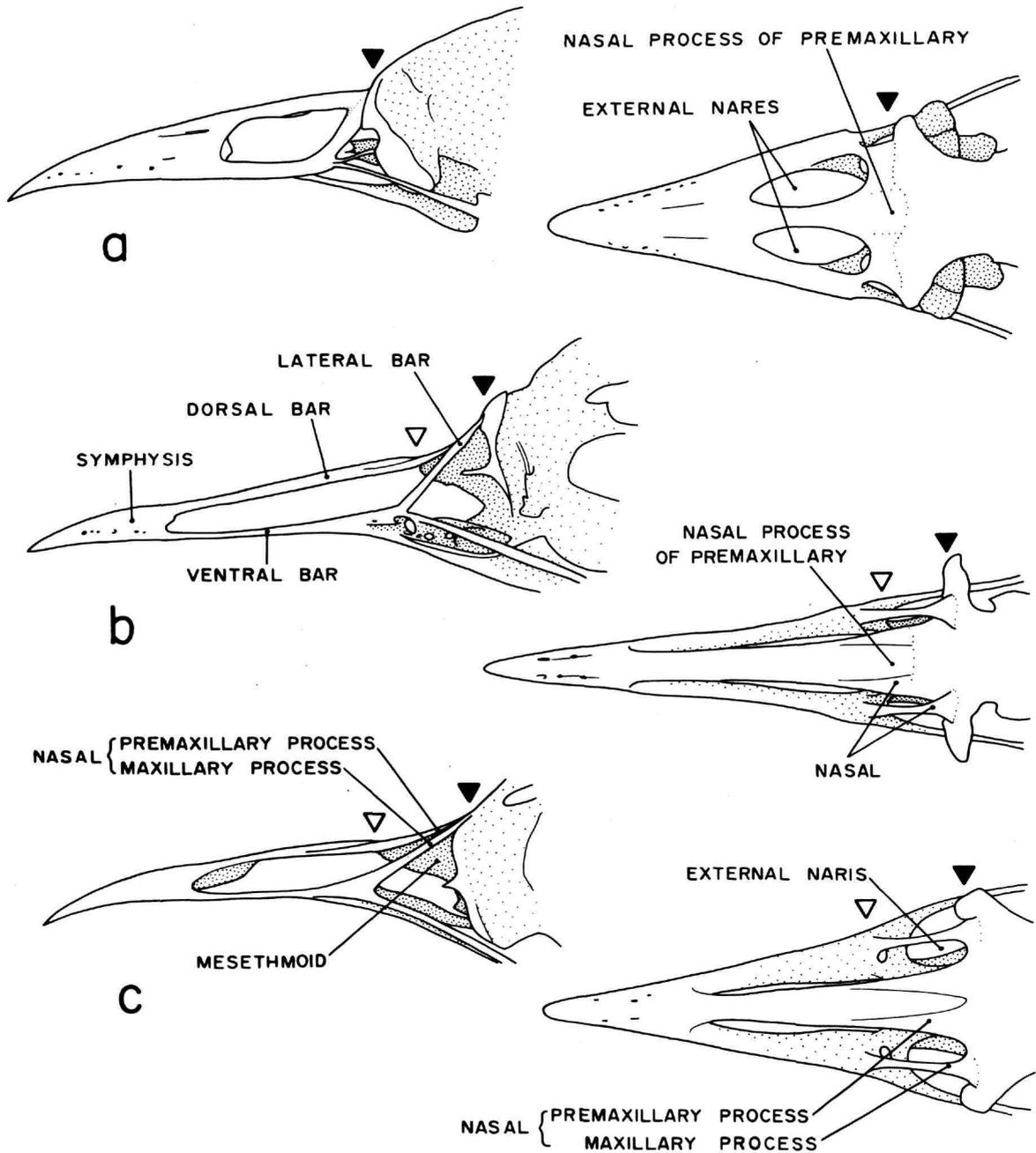


FIGURE 2.—Features of holorhinal and schizorhinal skulls: *a*, holorhinal skull (*Cyanocitta stelleri*); *b*, schizorhinal skull (*Pluvialis squatarola*); *c*, "atypical holorhinal" (=schizorhinal) skull (*Cursorius coromandelicus*). (Left, lateral view; right, dorsal view; solid pointer indicates craniofacial hinge; open pointer indicates additional hinge axis on dorsal bar.)

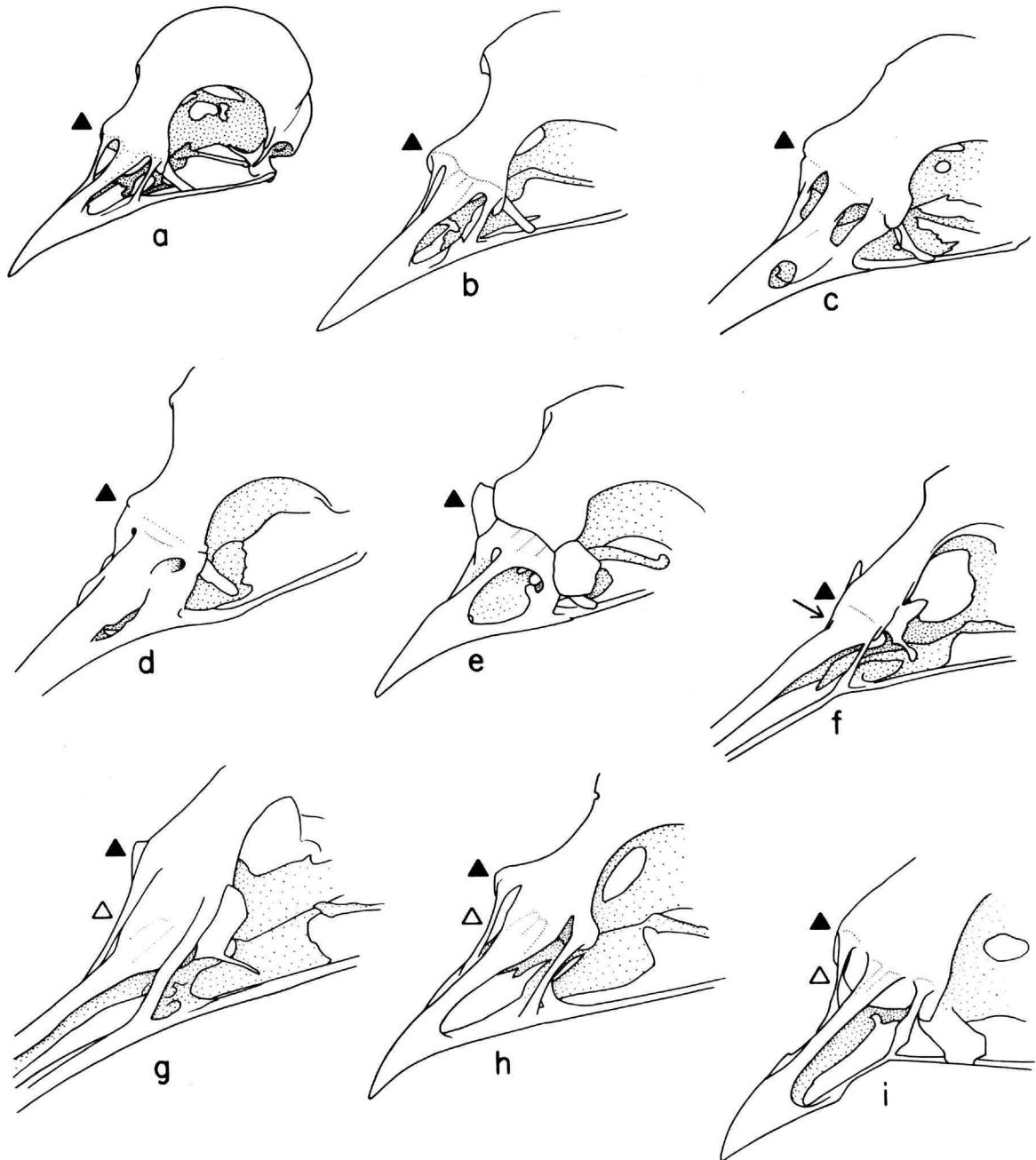


FIGURE 3.—Configurations of external nares openings in holorhinal and schizorhinal birds: a, *Sittasomus griseicapillus*; b, *Philydor guttulatus*; c, *Upupa epops*; d, *Phoeniculus purpureus*; e, *Chelidoptera tenebrosa*; f, *Rallus aquaticus*; g, *Eurypyga helias*; h, *Glareola nordmanni*; i, *Pterocles orientalis*. (Solid pointer indicates craniofacial hinge; open pointer indicates additional bending axis on dorsal bar; arrow shows additional hinge on lateral bar; a-f, holorhinal; g-i, schizorhinal.)

bars)." By "nasal-frontal hinge" they meant the basal hinge of the dorsal bar. Their definition emphasizes the functional differences between the two skull types, but it fails to cover those species in which the nostril terminates near or precisely at the level of the craniofacial hinge, as in some woodcreepers (*Dendrocolaptidae*), ovenbirds (*Furnariidae*), Hoopoes (*Upupidae*), and rails (*Rallidae*) (Figure 3*a-c,f*). The omission is not trivial because one must deal with skulls of this type to explain the origin of schizorhiny or rhynchokinesis. More importantly, their definition does not indicate the relative positions of the basal hinge of the dorsal bar and the dorsal hinge of the lateral bars (original craniofacial hinge), i.e., whether they lie along a single transverse axis or on different axes.

For reasons already presented (page 4), I regard the schizorhinal skull as one in which the medial portion of the craniofacial hinge has shifted forward. If this condition evolved from a holorhinal bird in which the nasal openings reached back to, or nearly to, the craniofacial hinge, the medial hinge of the dorsal bar in the schizorhinal bird would always lie rostral to the cranial attachment and hinge of the lateral bar, and be separated from it by the nares. The location of the original craniofacial hinge, or base of the upper jaw, would be represented by the attachments of the lateral bars, as already explained. Regardless of the precise evolutionary pathways to schizorhiny, the result is that all schizorhinal birds have two hinge axes at the base of the upper jaw. Examples of their diversified form, and of holorhinal birds, are shown in Figure 3.

All schizorhinal birds are rhynchokinetic but some rhynchokinetic birds are not schizorhinal. By my definitions "schizorhiny" is a partial synonym of "rhynchokinesis." As a result, the terms "schizorhinal" and "rhynchokinetic" can be used separately, but they may be redundant when used together, and no bird is both rhynchokinetic and holorhinal.

Paleognathous birds (the ratites and tinamous among living birds) are rhynchokinetic (Figure 4), but Bock (1963) considered them to be ho-

lorhinal. However, they meet my criteria for schizorhiny in that the hinge of the dorsal bar lies rostral to the lateral bar and is therefore functionally separated from the lateral and ventral bars. The ratites are unusual in having an interrupted lateral bar, the parts of which are connected by a ligament. Bending occurs mainly at the ligament, which may be in the position of the dorsal hinge (rheas) or farther ventrally (other ratites). In tinamous the lateral bar is complete and it has a dorsal hinge; it may represent the ancestral condition for the ratites. In any case, the hinge of the dorsal bar lies rostral to the base of the upper jaw, and it probably represents the displaced medial portion of an ancestral craniofacial hinge. Paleognathous birds differ from other schizorhinal birds in that the hinge of the dorsal bar appears to have migrated farther forward from the base of the upper jaw, perhaps even to the extreme level found in kiwis.

A few rhynchokinetic birds have evolved specializations such that the term "schizorhiny" does not apply. In most distally rhynchokinetic birds the medial part of the craniofacial hinge has disappeared (not shifted far forward as often stated). These birds are therefore no longer strictly schizorhinal although their schizorhinal ancestry is clear. They have only a single hinge axis at the base of the upper jaw, but that hinge is interrupted and restricted to the upper ends of the lateral bars. By my definitions neither "holorhinal" nor "schizorhinal" can be applied usefully to these birds.

Bock (1964) stressed the isolation of the lateral and ventral bars from the dorsal bar as the most important functional attribute of the schizorhinal skull and he regarded that isolation as essential for rhynchokinesis. He distinguished "paleognathous rhynchokinesis," in which the ventral bar is isolated from the dorsal bar by an interrupted lateral bar, from "charadriiform rhynchokinesis," in which the ventral bar is isolated by the external nares. I distinguish "paleognathous rhynchokinesis" from all other forms of rhynchokinesis, which I lump under "neognathous rhynchokinesis."

Functional independence of the lateral bars of

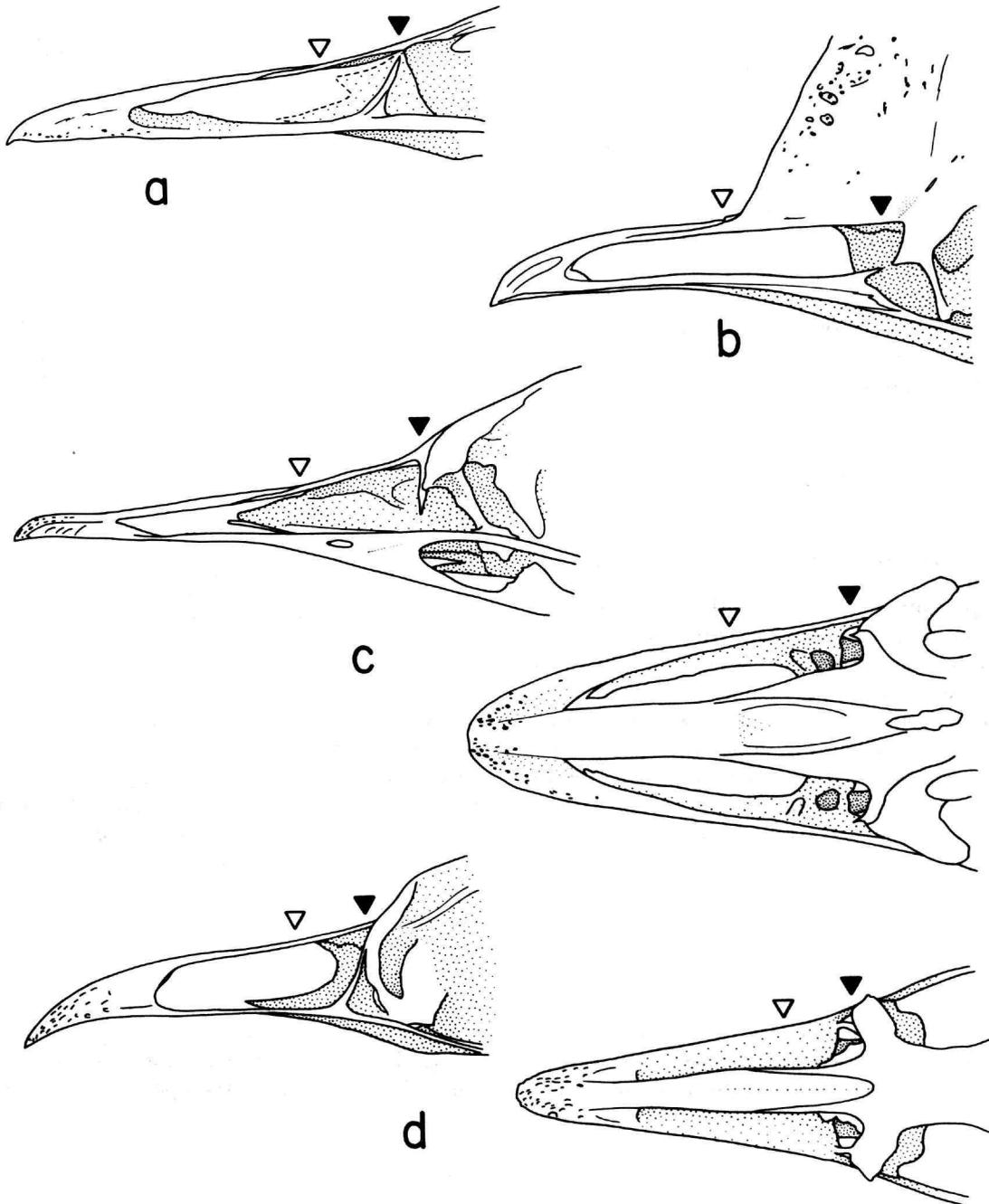


FIGURE 4.—Upper jaws of some paleognathous birds: *a*, *Rhea americana*, immature, lateral view (dashed line = unossified nasal septum); *b*, *Casuarius casuarius*, lateral view; *c*, *Struthio camelus*: lateral view (left), dorsal view (right); *d*, *Eudromia elegans*: lateral view (left), dorsal view (right). (Solid pointer indicates craniofacial hinge or break in lateral bar; open pointer shows rynchokinetic hinge.)

the jaw from the dorsal bar in some birds was known to Nitzsch (1816) and has been much discussed in relation to rhynchokinesis since that time. I agree that isolation of the lateral and ventral bars is essential for rhynchokinesis (and it is a corollary of my definition of rhynchokinesis), but it is not limited to schizorhinal or rhynchokinetic forms and is thus not diagnostic of them. In amphikinetic birds and some prokinetic ones, the lateral and ventral bars are isolated from the dorsal bar without a forward shift of the medial portion of the craniofacial hinge. The craniofacial hinge is essentially complete and limited to a single hinge axis at the base of the upper jaw, whereas that of a schizorhinal bird and most rhynchokinetic birds is separated into two hinge axes. The importance of the double hinge will be evident in the analysis of kinesis that follows.

Functional Analysis of Cranial Kinesis

In prokinetic birds, bones that form the craniofacial hinge are relatively thin and flattened in the frontal plane. The craniofacial hinge in a dried skull may or may not be clearly differentiated anatomically in dorsal view (Figure 3*e,d*, respectively). When the upper jaw rotates, any given point on the jaw travels an arc whose radius centers at the bending axis; as the arcs of all points in the jaw are concentric, the points can maintain constant spatial relationships with each other during kinesis (Figure 5). As a result, construction of the bill may be rigid and bulky without restricting kinesis.

In rhynchokinetic and amphikinetic birds the lateral and ventral bars of the upper jaw are functionally independent of the dorsal bar at its base. Because the conjoined lateral and ventral bars of the bill are connected to the cranium and symphysis respectively, none of the force applied to these bars by the palate and jugal bars is transmitted directly to the base of the dorsal bar as it is in a typical holorrhinal bill.

Assuming for the moment that the lateral bars, the ventral bar, the dorsal bar, and the symphysis form an inflexible unit hinged to the cranium,

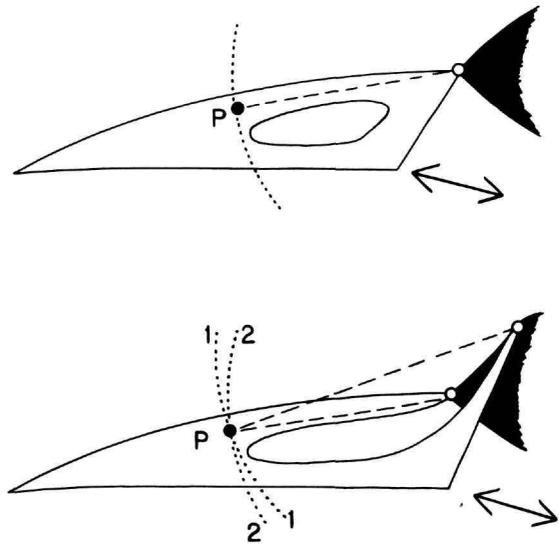


FIGURE 5.—Effects of basal hinge axes on kinetic upper jaw: *upper*, single axis, all points (P) on jaw follow concentric arcs with no constraint; *lower*, two axes, constrained because point P must follow two arcs (1 and 2), preventing kinesis in hypothetical jaw illustrated. (Arrows indicate direction of forces from palate.)

kinesis of a schizorhinal upper jaw would not be possible because each point on the jaw would be required to follow two diverging paths simultaneously. As shown in Figure 5, point P would have to follow arc 1, whose radius centers at the cranial hinge of the lateral bar, and at the same time arc 2, centering on the cranial hinge of the dorsal bar. All other points on the jaw would also have to follow two arcs, and the jaw would break if moved. Whereas flexibility within the upper jaw of the amphikinetic skull is not controlled in any way by its single basal hinge, the presence of two basal hinge axes in the rhynchokinetic skull *requires* flexibility within the upper jaw if kinesis is to occur at all. Flexibility within the upper jaws of schizorhinal birds almost always occurs at comparable locations in the upper jaw and palate, which is to say that certain hinge locations can be identified and predicted. These hinges are in part the basis for the five kinds of rhynchokinesis, and the letters that I will use to designate them

are as follows (see Figure 6a): A, lateral bar near junction with cranium; B, dorsal bar near junction with cranium or mesethmoid extension; C, dorsal bar near junction with symphysis; D, ventral bar near junction with symphysis; E, lateral bar near junction with ventral bar. (Flexible portions of the jugal bars and palatine bones are not pertinent to this paper.) All five hinges (A–E) are present in only a few species of rhynchokinetic birds. In most species, flexibility is lacking at one or more of the designated hinge locations.

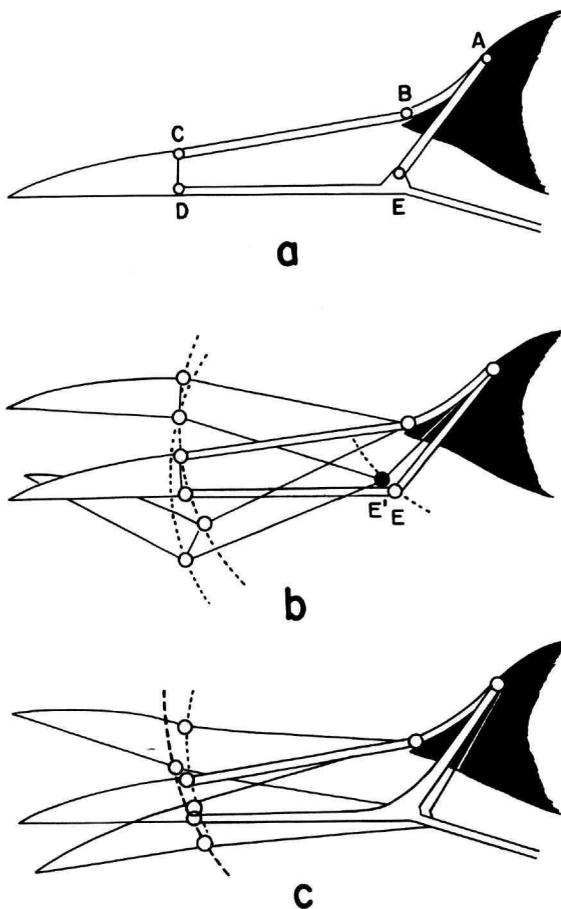


FIGURE 6.—Kinetic hinges and kinesis: a, full complement of hinges (A–E); b, two of many possible bill shapes after protraction from E to E'; c, loss of E stabilizes bill during protraction and retraction.

Most authors assume that many rhynchokinetic birds have an extensively flexible dorsal bar. Such birds are said to represent the generalized state of “rhynchokinesis,” an intermediate stage in the shift of a hinge from the base of the bill toward the tip (Hofer, 1945), or a shift from the tip toward the base (Möller, 1970). As explained below, hinge B is probably limited in the extent to which it has shifted forward from the ancestral condition in most schizorhinal birds, and with few exceptions, the various forms of rhynchokinesis have been derived through loss of either hinge B or C, or both, from a doubly rhynchokinetic ancestor. The taxonomic distributions of amphikinesis and the five forms of rhynchokinesis are summarized in Table 1.

An inflexible and complete lateral bar immovably attached to the cranium would block kinesis, and hinge A is therefore present in all rhynchokinetic birds except those with an incomplete lateral bar. Assuming that each of the hinges (B through E) may be either present or absent, there are 16 possible combinations of their presence or absence with hinge A. Of these, 11 combinations would theoretically block kinesis (e.g., AB shown in Figure 5b). All of the remaining five combinations would permit kinesis, and four of them are found in living birds (ABCE is not found). Each of these four combinations corresponds to a named form of rhynchokinesis, as follows:

- ABCDE double rhynchokinesis
- ABCD double rhynchokinesis
- ACDE distal rhynchokinesis
- ABDE proximal rhynchokinesis

If the central hinge of tinamous corresponds to hinge B, then ABDE would also describe central rhynchokinesis. One of the combinations (ABD) that would theoretically block kinesis is found in the Tooth-billed Pigeon (*Didunculus strigirostris*), but in fact it does not prevent kinesis in that species for reasons given on pages 18, 19.

When all hinges are present (e.g., *Actitis*: Scolopacidae) the bill is weak and easily bent by external forces applied to it, whether or not the

palate is stabilized (Figure 6*b*). In many doubly rhynchokinetic species the bill is strengthened by the absence of hinge E; in this prevalent form of rhynchokinesis (Table 1) the lateral and ventral bars act as a rigid unit connecting hinges A and D, and the dorsal bar connects hinges B and C. The following discussion applies to this form of rhynchokinesis (i.e., ABCD), in which bending of the upper jaw during protraction and retraction is determined by the arcs of radii AD and BC, centering on axes A and B respectively (Figure 6*c*). The configuration of the arcs of AD and BC prescribes the degree and direction of rotation of the symphysis with respect to the dorsal and ventral bars during motions of the upper jaw. The paths of the two arcs depend upon the positions of hinges A, B, C, and D relative to each other. When referring to horizontal or vertical distances between hinges A and B, horizontal distance is measured along the long axis of the base of the dorsal bar and vertical distance is measured on a line 90° to the horizontal axis.

The effects on kinesis of a change in position of hinges A, B, C, or D are demonstrated in Table 2, in which degrees of rotation of the symphysis at hinge C are indicated for specified degrees of protraction and retraction of the upper jaw around hinge B. The data were determined graphically, using compass, protractor, and ruler, from a basic hinge configuration and from variations on that pattern (Figure 7). Data from each pattern are shown in the rows of Table 2, and the pattern of hinges (from Figure 7) that corresponds to each row is listed in the table. Effects of change can be appreciated by comparing various rows with the pattern in row 1 and by comparing other rows that show sequential change of hinge position.

In these hypothetical examples, when other relations are constant, the degree of protraction and retraction of the symphysis during protraction and retraction of the upper jaw is increased by: (1) increased vertical distance of hinge A above hinge B (compare rows 2 and 1 of Table 2); (2) caudal shift of hinge B toward a position directly ventral to hinge axis A (compare rows 6,

1, and 5); (3) a more dorsoventrally depressed or slender bill (i.e., dorsal and ventral bars, and therefore hinges C and D, closer together, compare rows 1 and 15); (4) a rostral shift of hinge D relative to hinge C (compare rows 9, 1, and 10); (5) rostral shift of both hinges C and D (compare rows 11, 12, 1, and 12).

For an understanding of kinesis in some species it will be important to note that rotation of the symphysis during kinetic motions of the upper jaw is minimal or absent when hinge B lies directly between hinges A and D, that is, on a line joining A and D in lateral view (Figure 7). This configuration applies to row 7 of Table 2, and it is approximated in row 13. In these examples it is clear that there is little or no bending at hinge C, and that that hinge could be lost, producing proximal rhynchokinesis, without detriment to kinesis.

Certain configurations of A, B, C, and D would cause antagonistic motion of the bill tip—downward rotation during protraction of the upper jaw, upward rotation during retraction, or both. These detrimental motions would occur during kinesis if hinge B lay dorsal to a line passing through hinge axes A and D during kinesis. This configuration applies to row 8 of Table 2. Reference to Figure 7 will show that such a dorsal position of B would result from rostral migration of hinge B along the dorsal bar until B passed line AD. Hinge A lies dorsal to the level of hinge B in doubly rhynchokinetic birds, and the amount of hypothetical forward shifting of hinge B that is possible before the hinge crosses line AD is proportional to the vertical distance between hinges A and B. The position of line AD relative to hinge B changes during kinetic motions of the upper jaw in a given species, but line AD probably does not normally cross hinge B in the hinge configurations of living birds, as it does at maximum retraction in the example in row 7 of Table 2. It is clear that any location of hinge B rostral to A but ventral to line AD produces a complementary effect on bill tip bending during kinesis (Figure 8*a*; Table 2, rows 1, 5, 6) but that a more rostral location of hinge B produces the

TABLE 2.—Hypothetical effects of different configurations of hinges A, B, C, and D on bending at the symphysis during protraction and retraction of upper jaw. Rows show degrees of protraction or retraction around hinge C at given degrees of kinetic rotation around hinge B (hinge configurations correspond to Figure 7; italicized numbers = degrees of reversed rotation around hinge C)

Hinge configuration*	Protraction		Retraction			
	8°	4°	2°	4°	6°	8°
1	6.5	3.0	1.0	2.5	3.5	4.5
2	4.0	1.0	0.5	1.5	2.0	2.0
3	0.5	0	0.5	0.5	1.0	1.5
4	2.5	2.0	0.5	1.5	2.5	4.0
5	9.0	4.5	2.0	4.0	6.0	7.0
6	4.0	2.0	0.5	1.0	1.5	2.0
7	1.0	0	0	0	0	0.5
8	1.5	1.0	1.0	1.5	2.5	4.0
9	5.0	2.5	1.0	2.0	2.5	3.0
10	10.5	5.0	1.5	2.5	4.0	5.0
11	3.5	1.0	1.0	2.0	2.5	3.0
12	7.0	3.0	2.0	3.5	5.0	6.5
13	2.0	1.0	0	0.5	1.0	1.0
14	4.0	2.0	0.5	1.0	2.0	2.5
15	17.0	7.5	3.0	7.0	9.0	11.0
16	9.0	3.5	1.5	3.0	4.0	5.0

* Hinge configuration:

- | | | | |
|------------------------|------------------------|--------------------------------------|--------------------------------------|
| 1 A B C D | 5 A B ¹ C D | 9 A B C D ¹ | 13 A ⁴ B C D |
| 2 A ¹ B C D | 6 A B ² C D | 10 A B C D ² | 14 A ⁵ B C D |
| 3 A ² B C D | 7 A B ³ C D | 11 A B C ¹ D ⁵ | 15 A B C D ⁵ |
| 4 A ³ B C D | 8 A B ⁴ C D | 12 A B C ² D ⁴ | 16 A ¹ B C D ⁵ |

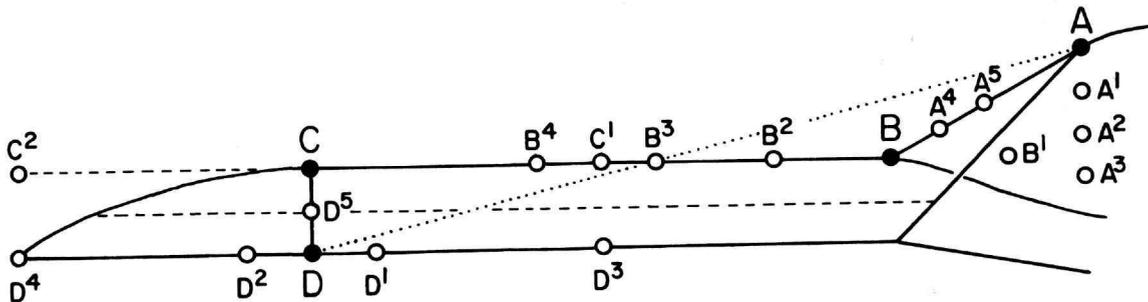


FIGURE 7.—Hinge positions in hypothetical, doubly rynchokinetic upper jaw lacking hinge E (alternate positions of hinges A, B, C, and D are numbered; solid lines show jaw in closed position; dotted line connects hinges A and D; dashed lines show other bill shapes; see Table 2 for kinetic effects).

opposite effect (Table 2, row 8). In addition, as hinge B approaches hinge C, an increasingly sharp kink in the dorsal bar between the two hinges would appear during retraction of the

upper jaw (Figure 8b). I think it is for these reasons that hinge B typically lies only a short distance rostral to hinge A in doubly rynchokinetic birds.

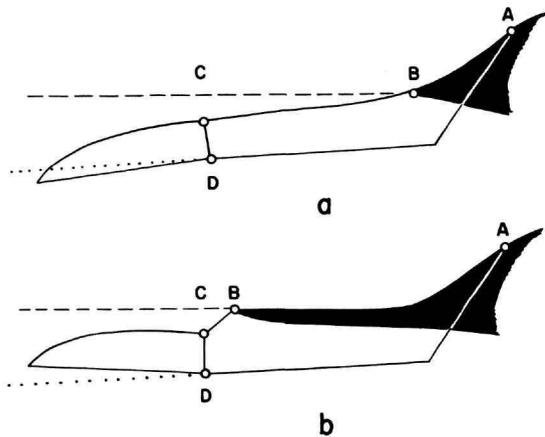


FIGURE 8.—Kinetic effects of rostral shift of hinge B: *a*, in normal position of B, retraction of symphysis complements retraction of jaw; *b*, with hypothetical rostral shift of B, symphysis protracts during retraction of jaw. (Dashed line shows long axis of dorsal bar in closed position; dotted lines show long axis of retracted ventral bar.)

Complementary bending of the symphysis also decreases and eventually gives way to reverse bending as the vertical distance between hinges A and B is reduced and hinge B lies dorsal rather than ventral to line AD (see Table 2, rows 3 and 4). In rhynchokinetic birds, differences in the relative positions of hinges A and B are typically as shown at A, A¹, A⁴, or A⁵ rather than at A² or A³ in Figure 7, and the likelihood of reversed bending of the symphysis as a result of line AD falling below hinge B is therefore slight.

The preceding discussion of particular hinge configurations is based on hypothetical patterns, but the patterns were chosen to approximate configurations found in a variety of species of rhynchokinetic birds. For example, in 12 doubly rhynchokinetic species of nine families for which I plotted the pattern of hinges on paper, all had configurations in which complementary motion of the symphysis would be comparable to those shown in Table 2 (rows 1, 2, 6, 9, 10, 12, 14–16). The species included were *Eudocimus albus*, *Grus canadensis*, *Eurypyga helias*, *Pluvialis squatarola*, *Vanellus indicus*, *Himantopus mexicanus*, *Jacana spinosa*, *Nycticryphes semicollaris*, *Tringa flavipes*,

Ducula bicolor, *Columba speciosa*, and *Goura scheepmakeri*.

PROKINESIS, AMPHIKINESIS, AND DOUBLE RHYNCHOKINESIS.—During retraction of the upper jaw the backward pull of jaw muscles on the palate applies tension forces to the ventral bar, and during protraction of the jaw, compression forces are applied. The upper jaw resists deformation under these forces on the ventral bar in varying degree depending upon the flexibility of the bars and the amount of ossification around the nares. Birds with relatively small nasal openings have correspondingly rigid bills, and are prokinetic. The prokinetic upper jaw is commonly constructed to withstand bending under the forces of grasping or biting along the tomium, or breakage under compression forces (as in woodpeckers). This type of bill is also easily modified for ornamental purposes without impairing its other functions (Hofer, 1955).

In some prokinetic birds the nasal openings reach back to the level of the craniofacial hinge (see Figure 3). This feature appears to have evolved under different circumstances. It is found in certain philydorine ovenbirds (Furnariidae, e.g., *Philydor guttulatus*) and woodcreepers (Dendrocolaptidae, e.g., *Sittasomus griseicapillus*)—groups that have apparently evolved from proximally rhynchokinetic furnariids (Feduccia, 1973). These prokinetic birds exhibit a flattened ventral bar and caudally extended nares that probably reflect their rhynchokinetic ancestry. By contrast, in Hoopoes (Upupidae) the nares reach the craniofacial hinge, but the upper jaw is extensively ossified and the ventral bar strongly constructed; their nearest relatives, the wood hoopoes (Phoeniculidae) and other Coraciiformes are prokinetic, with nares that do not reach the craniofacial hinge. The backward extension of the nares in the Upupidae is thus derived from prokinetic ancestors and probably has nothing to do with kinesis.

Some rails (Rallidae) are amphikinetic, with jaws constructed of slender bars and with large nasal openings. In them the dorsal and ventral bars are flexible caudal to the symphysis and the

nasal openings extend caudally almost to the craniofacial hinge. I found the amphikinetic upper jaw only in the genus *Rallus* and in the late Quaternary rail, *Capellirallus*, of New Zealand shown in Figure 9 (also see Olson, 1975; 1977). In these genera, the lateral and ventral bars are relatively independent of the dorsal bar, even though the nasal opening does not reach caudally as far as the craniofacial hinge. The lateral bar is flexible at its juncture with the dorsal bar just rostromedial to the craniofacial hinge (Figure 3f). As a result, forces applied to the ventral bar during protraction or retraction of the palate produce rotation of the symphysis relative to the dorsal and ventral bars, and in addition, rotation of the upper jaw around the craniofacial hinge (demonstrated in soaked skulls). During protraction and retraction the angle between the lateral and dorsal bars (from lateral view) decreases or increases, respectively, reflecting independent motion of the ventral and lateral bars and motion of the bill tip. Rotation of the bill tip reduces the effect of forces from the palate on rotation of the dorsal bar around the craniofacial hinge. The presence of a dorsal hinge on the lateral bar within the upper jaw, separate from the complete craniofacial hinge, suggests that amphikinesis in rails was derived from prokinesis.

Amphikinesis may be more widespread among birds with large nasal openings and slender dorsal and ventral bars, but it would be difficult to identify unless hinges C and D were morphologically distinct. Hofer (1955:114) stated that the dorsal bar was flexible in *Gavia* (loon) and *Podiceps* (grebe), but I could not verify that in water-soaked skulls.

As a consequence of the flexibility of the upper jaw in amphikinetic and doubly rhynchokinetic birds with hinge E, their jaws are less suited for strong biting along the tomium than those of most prokinetic birds. However, as I demonstrated with a simple model of the upper jaw, they are capable of several different forms of grasping with the bill tip that make even slender bills unusually versatile. In the model, the symphysis can bend down around a simulated prey item to meet the partially depressed lower jaw, with or without depression of the dorsal bar. The symphysis can also bend down to meet the closed lower jaw even when the dorsal bar is raised. When prey is grasped, the response of these weak upper jaws is apparently to "wrap around" the prey (Figure 10). It is of interest to compare the hypothetical consequence of the loss of hinge E in an amphikinetic jaw with that in a doubly rhynchokinetic one (see Figure 11). If the upper jaw were strengthened by loss of E, an amphikinetic jaw would then become prokinetic. By contrast, loss of hinge E in a doubly rhynchokinetic jaw would strengthen the jaw without removing mobility of the symphysis; however, the "wrap around" action would no longer be possible because it would require shortening of radius AD.

PROXIMAL RHYNCHOKINESIS.—Many proximally rhynchokinetic birds probably evolved from doubly rhynchokinetic ancestors, that is, from birds with at least hinges A, B, C, and D, by loss of hinge C (Figure 12, compare *d* and *e*). The ventral bar in most rhynchokinetic forms, unlike that of most prokinetic birds, is flattened and flexible, either as a localized hinge at D or as a more extensive zone of flexibility (Figure 12,

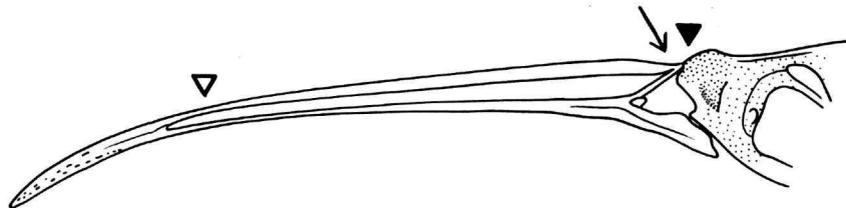


FIGURE 9.—Amphikinetic upper jaw of *Capellirallus* (solid pointer indicates craniofacial hinge; open pointer indicates hinge near bill tip; arrow shows bending point on lateral bar).

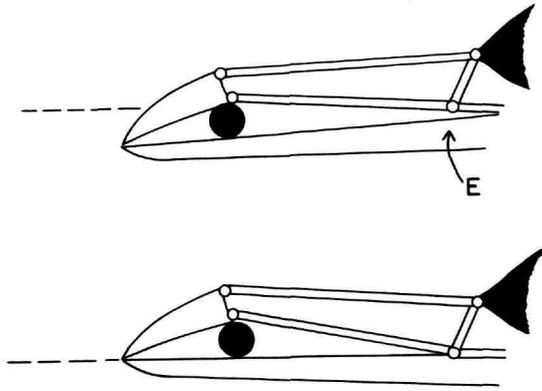


FIGURE 10.—Versatility of kinesis in amphikinetic jaw with hinge E; bill tip can “wrap around” prey with lower jaw open (above) or closed (below) (dashed line shows long axis of closed jaws).

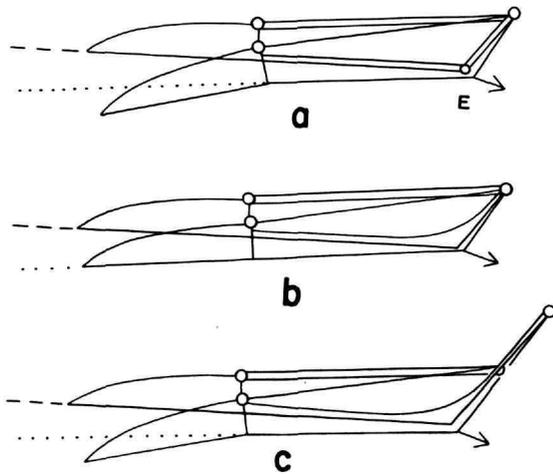


FIGURE 11.—Effect of loss of hinge E on retraction of amphikinetic and rhynchokinetic jaws: *a*, amphikinetic jaw with E; *b*, amphikinetic jaw lacking E; *c*, doubly rhynchokinetic jaw lacking E. (Dashed line shows position of closed upper jaw; dotted line shows long axis of retracted ventral bar; arrow shows retraction force.)

compare *b* and *f* with *a* and *e*). Loss of hinges C and E would cause akinesis if hinge D were represented by a narrowly restricted bending zone because of divergence between arcs AD and BD. Instead, the flexibility of the ventral bar is usually more extensive and it probably bends as

if there were multiple hinges along its length. Stresses that would arise within the upper jaw during kinesis from the double hinges A and B in the absence of hinge E would be partially alleviated by the presence of extensive flexibility in the ventral bar. An example of this configuration is the Limpkin (*Aramus*: Figure 12*e*).

The effect of extensive flexibility of the ventral bar can be simulated most simply by a model with two hinges along the bar as shown in Figure 13. Protraction is probably weakened by the potential for buckling of the ventral bar under compression (Figure 13*b*), but retraction is not necessarily weakened because a flexible bar may be capable of transmitting strong tension forces (Figure 13*c*). During retraction, however, the ventral bar could bend in a complicated way depending upon the configuration of the hinges and the amount of retraction. Such bending is apparently negligible in proximally rhynchokinetic birds for a variety of reasons: hinges A and B are often in close apposition, hinge B may lie close to a line joining hinges A and D' (Figure 13*a*), or the flexible portion of the ventral bar may extend caudally such that hinge D' becomes a functional analog of hinge E. Furthermore, the extent of retraction in living birds is probably not great. In a hypothetical model, an awkward bowing of the ventral bar becomes more pronounced as the vertical distance of hinge A above B is reduced, or as hinge B shifts rostrally away from hinge A. In paleognathous birds, hinge A lies on or below the long axis of the dorsal bar, and B lies farther rostral along the dorsal bar than in other birds. Downward bowing of the ventral bar during retraction (as shown in Figure 13*d*) and separation of the palate from the sphenoidal rostrum would therefore occur in paleognathous birds during retraction of the upper jaw were it not for the presence of an interrupted lateral bar or hinge E. (Figure 13 shows a hypothetical situation in which hinge E is absent.)

The Tooth-billed Pigeon (Figure 12*b*) is proximally rhynchokinetic, lacks hinge E, and has a narrowly restricted hinge at D. It is thus theoretically akinetic, as mentioned on page 13. How-

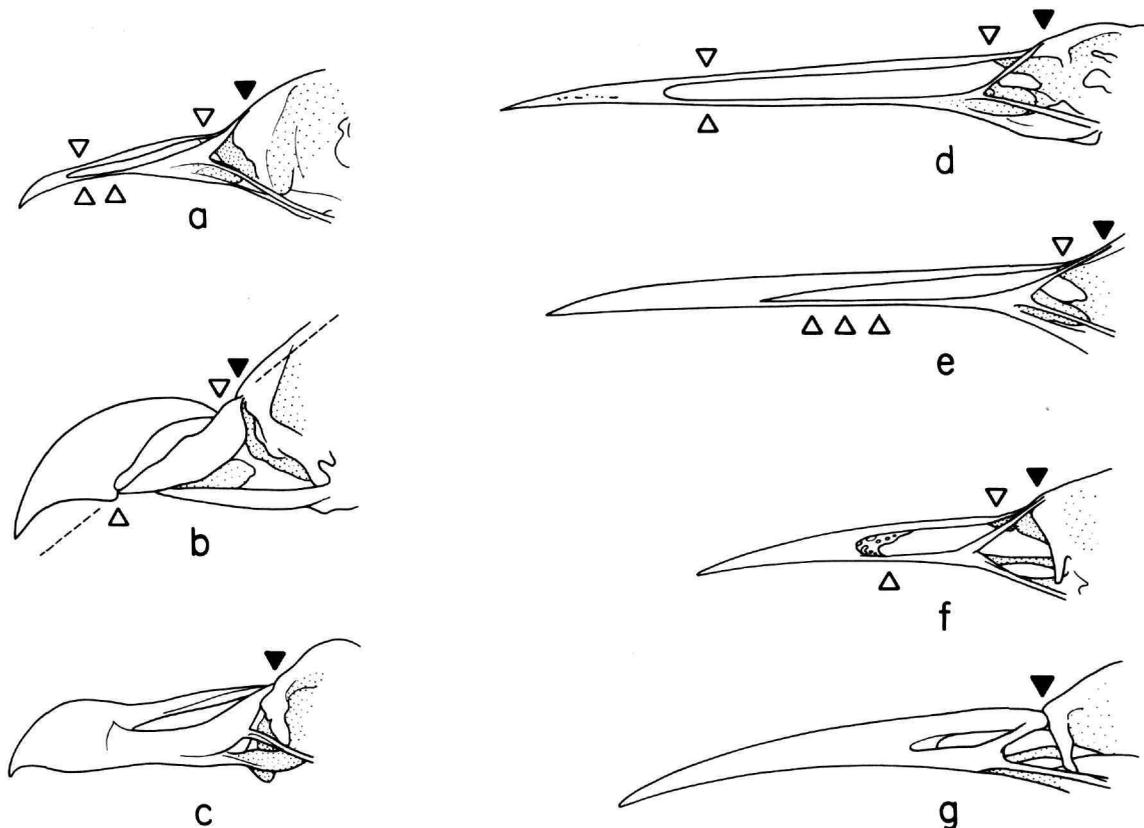


FIGURE 12.—Jaws of some rhynchokinetic and prokinetic birds: *a*, *Ducula bicolor*; *b*, *Didunculus strigirostris*; *c*, *Raphus cucullatus*; *d*, *Grus leucogeranus*; *e*, *Aramus guarauna*; *f*, *Furnarius leucopus*; *g*, *Xiphorhynchus guttatus*. (Solid pointer indicates craniofacial hinge; open pointers indicate other bending points or zones.)

ever, in this species hinges A and B are not widely separated, and hinge B lies on a line connecting hinges A and D when the bill is closed; divergence of arcs AD and BD during protraction or retraction is therefore minimal (Table 2, row 7). Thus, the theoretical restrictions on kinesis are essentially removed within the normal range of kinetic rotation of the dorsal bar by the special configuration of hinges A, B, and D.

In the proximally rhynchokinetic Black Skimmer (*Rynchops niger*), hinges A and B are widely separated, but the ventral bar is extensively flex-

ible, hinge E is well developed, and line AD passes through hinge B. These combined features maximize kinetic mobility in skimmers (see Zusi, 1962) by removing the opposition to protraction inherent in the proximally rhynchokinetic upper jaw.

Proximally rhynchokinetic species commonly exhibit a configuration in which line AD passes through, or nearly through, hinge B, minimizing the tendency for internal bending of the upper jaw during kinesis. Such was the case in eight species of seven families for which I plotted the

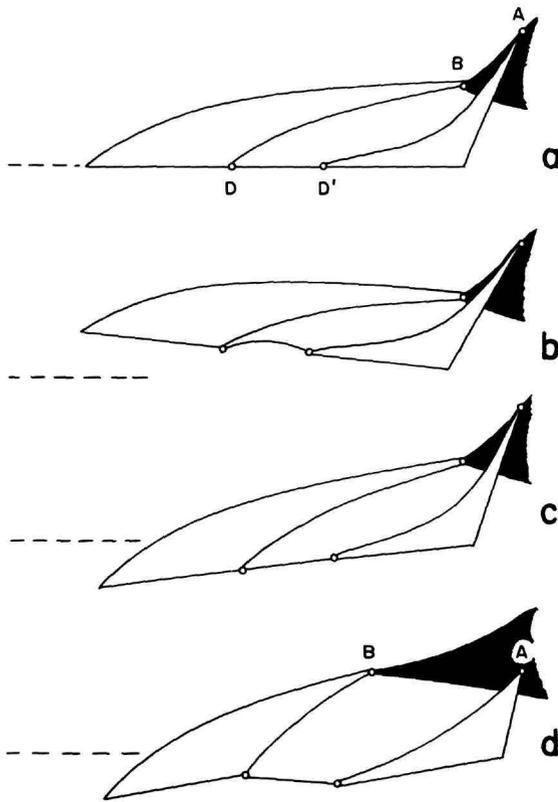


FIGURE 13.—Kinetic properties of proximal and central rhynchokinesis (hinge E lacking; extensive flexibility of ventral bar (D-D')); a-c, proximal rhynchokinesis: a, upper jaw in closed position; b, upper jaw protracted; c, upper jaw retracted; d, hypothetical centrally rhynchokinetic jaw retracted; rostral position of B and ventral position of A produce kink in ventral bar. (Dashed line shows closed position.)

hinge positions on paper (*Turnix sylvatica*, *Dromas ardeola*, *Attagis malouinus*, *Rynchops niger*, *Pterocles bicinctus*, *Didunculus strigirostris*, *Furnarius leucopus*, *Margarornis rubiginosus*). Six species (*Chionus alba*, *Cursorius coromandelicus*, *Alle alle*, *Aramus guarauna*, *Sterna hirundo*, *Larus philadelphia*) from five additional families more closely approached the configurations typical of doubly rhynchokinetic species.

DISTAL RHYNCHOKINESIS.—This form of ki-

nesis occurs only in certain charadriiform birds, in kiwis (*Apteryx*), and possibly in some hummingbirds. The dorsal bar bends just caudal to the symphysis rather than at or near its juncture with the cranium. The distally rhynchokinetic upper jaw of charadriiform birds and kiwis is usually rigid because the dorsal bar is strengthened and hinge B is lost. At the same time the jaw remains capable of powerful gaping or grasping at the tip.

Loss of hinge B imposes certain requirements on a kinetic jaw: the ventral bar must be flexible caudal to the symphysis and the base of the lateral bar (hinge E) must be flexible, or the bar incomplete. Should hinge E be lacking, then point D would have to follow an arc of radius AD, moving essentially perpendicular to the long axis of the rigid dorsal bar (Figure 14). However, point D would also have to follow an arc of short radius, CD, and move in a direction that is initially almost parallel to the long axis of the dorsal bar. Only through the flexibility of hinge E can this conflict be resolved such that the ventral bar (and point D) follows the arc of radius CD.

EXTENSIVE RHYNCHOKINESIS.—This form of kinesis is characterized by a lack of hinges B and C in the dorsal bar. Instead the bar is dorsoventrally flattened throughout its length and bends evenly between the symphysis and mesethmoid. This is an uncommon form of kinesis; I found it only in some tinamous, some specimens of oystercatchers (*Haematopus*), some specimens of turnstones (*Arenaria*), and in the Banded Stilt (*Cladorhynchus*) and avocets (*Recurvirostra*). Other species with gracile construction of the dorsal bar

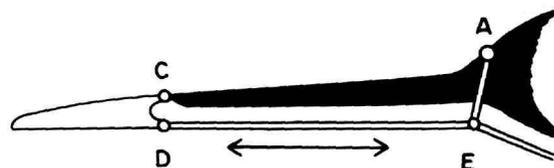


FIGURE 14.—Diagram of distally rhynchokinetic jaw (hinge E allows D to move along arc of radius CD rather than AD; arrows show motions of ventral bar).

closely approach extensive rhynchokinesis and they may show slight bending along that bar, but I include them with other kinetic types according to the pattern of their localized hinges. Examples of species that approach extensive rhynchokinesis may be found among the following kinetic types: central or proximal rhynchokinesis (some tinamous, the White-breasted Mesite (*Mesitornis variegata*), the Lesser Painted Snipe (*Nycticryphes semicollaris*), some Furnariidae); double rhynchokinesis (some tringine sandpipers (e.g., Spotted Sandpiper, *Actitis macularia*), some plovers (Charadriidae), some pigeons (Columbidae)); and distal rhynchokinesis (some specimens of oystercatchers and turnstones, and the Buff-breasted Sandpiper, *Tryngites subruficollis*).

Extensively rhynchokinetic species differ from each other in their patterns of jaw structure. In tinamous the ventral bar is extremely flattened in the frontal plane throughout its length, and the lateral bars are flexible at both ends and weakly connected to the cranium and ventral bars. In oystercatchers and turnstones some specimens are extensively rhynchokinetic but others show a hinge near the symphysis and are distally rhynchokinetic. Hinge E is present and the ventral bar is flexible within its rostral half. In the Banded Stilt (*Cladorhynchus*) and avocets (*Recurvirostra*), E is absent and the ventral bar is flexible in its rostral half (*Cladorhynchus*) or only near the symphysis (*Recurvirostra*). Thus we see that extensive rhynchokinesis occurs in association with four different hinge patterns and is present in only four families. I anticipate that extensive rhynchokinesis will be shown to have different adaptive explanations among the four families, and will prove to represent a specialized, rather than an unspecialized, form of rhynchokinesis.

CENTRAL RHYNCHOKINESIS.—This form of kinesis is characteristic of the paleognathous birds, including at least the Struthionidae, Rheidae, Casuariidae, some Tinamidae, and probably the moas (Dinornithiformes) and elephantbirds (Aepyornithiformes) (see illustrations in Archey, 1941; Parker, 1895; Lamberton, 1930). Some authors have regarded the ratites as akinetic and

others have postulated limited or passive kinesis. By manipulating the jaws of fresh specimens of *Struthio camelus*, *Rhea americana*, and *Casuarus casuarius*, I found that the upper jaw can bend upward and slightly downward at the axes shown in Figure 4. Whether or not ratites actively protract the upper jaw above the closed position, the flexibility of their upper jaws indicates kinesis. A fully developed kinetic mechanism is necessary to counteract upward forces on the flexible upper jaw, to effect a strong grasp, and to achieve some downbending of the upper jaw during grasping.

Most tinamous possess hinges A and B; the complete lateral bar meets the ventral bar by a weak syndesmosis and bending occurs near the junction of the two bars (hinge E). In ratites, the lateral bar is incomplete and partially ligamentous. The ligament of the Ostrich (*Struthio*) lies at the base of the lateral bar; in rheas (*Rhea*, *Pterocnemia*) the ligament is near the cranial at-

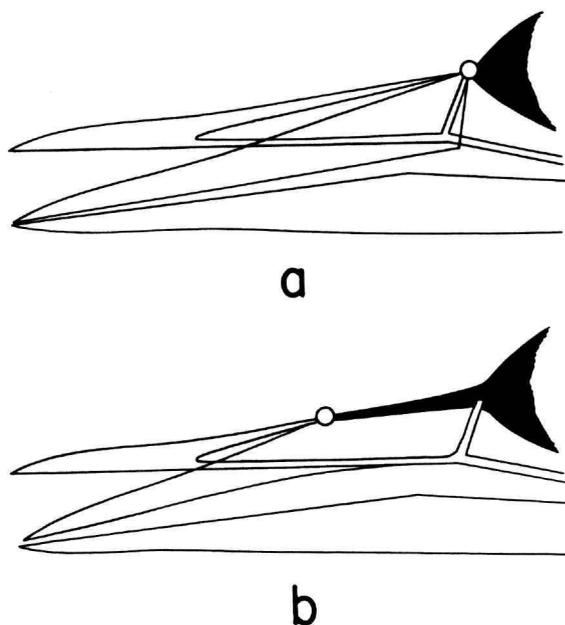


FIGURE 15.—Retraction of jaw in prokinetic and centrally rhynchokinetic birds: a, prokinetic; b, centrally rhynchokinetic. (Note difference in angle of upper to lower jaw.)

tachment of the lateral bar; in cassowaries (*Casuarius*) it is near the middle of the bar; in Emus (*Dromaius*) the bar is largely ligamentous; and in kiwis (*Apteryx*) the lateral bar may closely approach the ventral bar, but there is no ligamentous connection. Thus, as explained by Bock (1963), all ratites have flexibility in the interrupted lateral bar that permits craniocaudal motion of the ventral bar, independent of the dorsal bar. The long, straight, rostral extension of the sphenoidal rostrum characteristic of paleognaths forms a gliding plane for the vomers, which in turn are attached to the maxillary bones; the basal portion of the ventral bar of the lower jaw is therefore restricted to rostrocaudal motion. If a complete lateral bar lacking hinge E were present in ratites, the basal portion of the ventral bar would be forced to rotate upward or downward

around hinge A, compressing the vomers against the rostrum during protraction and separating the palate from the rostrum during retraction. Such inefficient motions do not occur because the lateral bars of ratites are incomplete. The lateral bar in tinamous is complete but it meets the ventral bar almost vertically and the direction of motion of its distal end is thus primarily rostrocaudal.

In paleognathous birds, the rostral location of hinge B, accompanied by extension of the mesethmoid or partial ossification of the nasal septum, provides a greater angle between upper and lower jaws during a given retraction of the upper jaw than would obtain in a comparable prokinetic bird (Figure 15). This configuration may increase the efficiency of grasping by the flexible upper jaw.

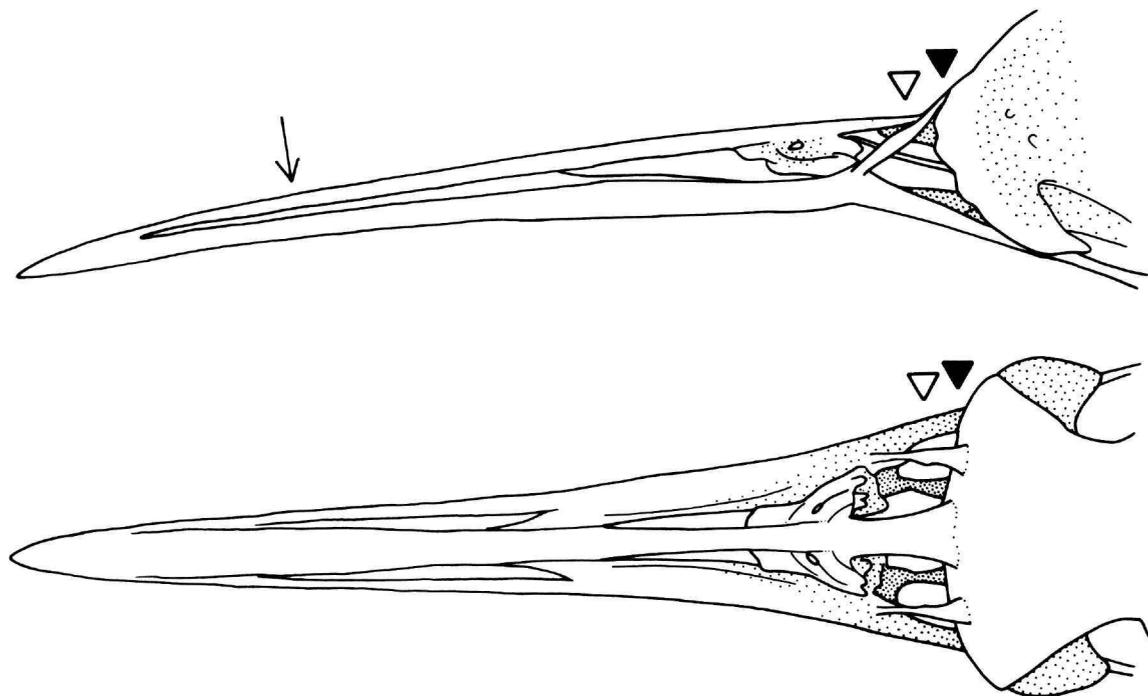


FIGURE 16.—Upper jaw of schizorhinal hummingbird (*Campylopterus largipennis*): above, lateral view; below, dorsal view. (Solid pointer indicates craniofacial hinge; open pointer shows rhychokinetic hinge; arrow indicates equivocal bending.)

HUMMINGBIRDS.—Hummingbirds of a few genera are apparently prokinetic (e.g., Phaethornithinae: *Glaucis*, *Threnetes*, *Ramphodon*, *Phaethornis*, *Eutoxeres*), but most are proximally rhynchokinetic. Hinge axes A and B, however, are not widely separated relative to the length of the bill, and hinge A is not elevated markedly above B (Figure 16). It is thus doubtful that, during kinesis, the double hinges of most hummingbirds produce enough stress within the upper jaw to require distal bending. Immediately rostral to the craniofacial hinge, the dorsal bar is thickened and it supports bony flanges on either side that are associated with the nasal passages. Farther rostrad the dorsal bar becomes dorsoventrally flattened, and, with the two laterally compressed ventral bars, forms an inverted trough that contains the tongue and most of the closed lower jaw. Extensive flattening of the rostral portion of the dorsal bar suggests flexibility in the distal portion of the jaw in all hummingbirds. A few genera (e.g., *Coeligena*, *Ensifera*) have lost hinge B and thus resemble the configuration of distal rhynchokinesis, with an extended anterior hinge (C). However, hummingbirds differ from all doubly or distally rhynchokinetic birds in having the flattened surface of the ventral bars oriented vertically in opposition to the direction of bending, rather than horizontally. Thus the osteological evidence does not point clearly to a particular kind of kinesis. I noted no bending within the upper jaw while manipulating fresh specimens of *Calypte* and *Mellisuga*, and in hummingbirds there is no line of softer rhamphotheca between the dorsal and ventral bars comparable to that found in all other rhynchokinetic birds in relation to the independent motion of the ventral bar. I tentatively conclude that most hummingbirds are proximally rhynchokinetic.

In living hummingbirds an illusion of bill-tip motion in the upper jaw occurs during a slight depression of the largely ensheathed lower jaw because only the tips of the mandibles separate. The problem of hummingbird kinesis might best be solved from photographs of opened and closed bills of live birds taken in lateral view.

Evolution of Rhynchokinesis

ADAPTIVE ASPECTS OF RHYNCHOKINESIS

Up to now I have dealt mainly with anatomical and functional properties of kinesis in the upper jaw. The functional property common to rhynchokinetic skulls is obligatory bending within the jaw during kinesis. How this relates to the diverse feeding adaptations found among rhynchokinetic birds is largely unknown and can only be touched on here. Many rhynchokinetic and amphikinetic birds probably have a special need for downbending of the distal part of the upper jaw as a consequence of the shape and use of their bills. Many of them employ probing in soft substrates as part of their feeding patterns. Their bills are consequently slender, without a hook or abrupt curvature at the tip, and are capable of strong grasping only through retraction of the symphysis of the upper jaw. Bending at the tip permits withdrawal of animals or plants from mud or sand. In addition, the flexible tip may be used to push food into the mouth as described by Burton (1974) for snipe.

The importance of probing as a feeding method in many distally rhynchokinetic birds is well known (e.g., woodcock, snipe, godwits, dowitcher, calidridines, oystercatchers, kiwi). Probing is also an important element in the feeding patterns of the amphikinetic rails (*Rallus*: Meanly, 1969; Bent, 1926), and in the doubly rhynchokinetic ibises (Threskiornithidae: Kushlan, 1977; Raseroka, 1975), cranes (Gruidae: Walkinshaw, 1949; Allen, 1952; Walkinshaw, 1973), kagus (Rhynochetidae: Steinbacher, 1962), plovers (Charadriidae: Burton, 1974), and tringine sandpipers (Scolopacidae: Burton, 1974).

Although I have emphasized downbending of the bill tip, the possible importance of upbending of the symphysis during protraction of the upper jaw in all forms of rhynchokinesis, except proximal rhynchokinesis, should not be overlooked. Bending of the upper jaw allows a bird to grasp a larger food item with the tip of the bill than it

could without such bending—a feature of possible importance to fruit-eating pigeons.

Proximally rhynchokinetic birds generally have feeding patterns that include little, if any, probing, but that require a stronger bill or sharper tomia for biting or grasping. Limpkins (Aramidae) deliver blows to mussel shells and large snail opercula (Snyder and Snyder, 1969); coursers and pratincoles (Glareolidae) take many large, hard-bodied insects (Maclean, 1976); Crab Plovers (Dromadidae) grasp crabs in the bill and batter them to death or insensibility before swallowing (Gilliard, 1958); Sheathbills (Chionidae) rip open the skin from carcasses of penguin chicks and adults (Burger, 1981); seedsnipe (*Thinocorus*) bite pieces off succulent leaves and graze other forms of vegetation (Maclean, 1969); gulls, skuas, jaegers, terns, skimmers, and alcids often take large prey that require a strong grasp, and terns, skimmers, and alcids carry slippery prey in the bill from feeding sites to the nesting colony. In all of these birds rhynchokinesis may have more phylogenetic than adaptive significance.

The adaptive significance of rhynchokinetic jaw structure is essentially unknown for the mesites (Mesitornithidae), button quails and hemipodes (Turnicidae), sunbitterns (Eurypygidae), ibisbills (Ibitorhynchidae), jacanas (Jacanidae), painted snipe (Rostratulidae), plains wanderer (Pedionomidae), sandgrouse (Pteroclididae), pigeons and doves (Columbidae), ovenbirds (Furnariidae), New Zealand wrens (Xenicidae), and the paleognathous birds.

ORIGIN OF RHYNCHOKINESIS

The origin of birds and the evolution of avian cranial kinesis are still matters of controversy and speculation. Walker (1972) presented evidence for the common origin of birds and crocodylians from a thecodont ancestor, and he argued that the structure of the skull in modern and fossil crocodiles suggested a former prokinesis, similar to that of birds, that was subsequently lost in crocodiles. By contrast, Ostrom (1973, 1976)

regarded *Archaeopteryx* as a derivative of a coelurosaurian dinosaur, and Colbert and Russell (1969) thought that *Dromaeosaurus albertensis*, a coelurosaurian, was mesokinetic. Versluys (1910), Bock (1964), and Wellnhofer (1974) thought it most likely that *Archaeopteryx* was mesokinetic, but Whetstone (1983) studied a new preparation of *Archaeopteryx* and concluded that it was not metakinetic, mesokinetic, prokinetic, or rhynchokinetic, without precluding the presence of some form of kinesis. Disagreements among these authors regarding kinesis stem from the equivocal interpretation of the presence of articulations or flexibility at several critical points in the somewhat crushed or incomplete fossils.

Unlike *Archaeopteryx*, coelurosaurs, or thecodonts, all modern birds and the Cretaceous toothed birds lack bony connections of the preorbital and postorbital bars with the jugal bar, and the external naris has enlarged or shifted caudally at the expense of the antorbital fenestra. Freedom of motion of the jugal bars is essential for all of the known forms of avian kinesis and for the peculiar maxillary kinesis hypothesized for *Hesperornis* by Gingerich (1976). Bending of the dorsal and ventral bars in the region of the external nares of both reptiles and birds would constitute rhynchokinesis; bending in the region of the antorbital fenestrae would constitute prokinesis. There is nothing to prevent the development of prokinesis when teeth are extensively distributed along the ventral bar. However, the necessity for a thin and flexible ventral bar in the upper jaw of rhynchokinetic and amphikinetic birds implies that these forms of kinesis evolved after the loss of teeth from the flexible portion of the premaxillary and maxillary bones of the ventral bar, at least in the region of the external nares. Various dinosaurs (e.g., *Ornithomimus*; see Romer, 1956:153) and *Hesperornis* lacked teeth in the rostral portion of the upper jaw. In *Hesperornis* the only changes necessary to produce rhynchokinesis would be interruption of the lateral bar and flexibility in the dorsal and ventral bars. Thus, both prokinesis and some form of rhynchokinesis could have been among the first forms of avian kinesis.

The schizorhinal skull of neognathous birds exhibits a complicated configuration of bending zones near the base of the upper jaw in which two hinge axes are separated from each other in three dimensions—rostrocaudally, dorsoventrally, and mesiolaterally. Neognathous rhynchokinesis is absent from most living birds, from all fossil birds, and *Archaeopteryx*, and from crocodylians and coelurosaurian dinosaurs, and it is thus probably a derived state within birds. In the discussion that follows I shall assume that neognathous rhynchokinesis evolved from holorhinal ancestors. To understand the evolutionary origin of schizorhiny and rhynchokinesis we must therefore explain the rostral shift of the medial portion of the craniofacial hinge. In a hypothetical model, a rostral shift is incompatible with kinesis unless the nasal opening extends back to, or nearly to, the original craniofacial hinge. For this reason the ancestor from which neognathous rhynchokinesis evolved was most likely prokinetic with large nasal openings, or amphikinetic.

Two anatomical changes would serve to separate the craniofacial hinge into two hinge axes. One is a forward extension of the mesethmoid under the dorsal bar. The flexible zone of the dorsal bar would also shift rostrally from the original craniofacial hinge with extension of the mesethmoid; otherwise retraction of the upper jaw would be blocked. The other change is a shift of the dorsal bar ventrally toward the ventral bars. The first change would separate the craniofacial hinge horizontally and the second would separate it vertically. In many neognathous, schizorhinal birds both changes have apparently occurred, with the result that the hinge of the dorsal bar lies rostroventrad from the original craniofacial hinge axis.

Several possible explanations for extension of the mesethmoid come to mind: (1) to increase the bony support for the olfactory membranes and conchae; (2) to act as a retractor stop by limiting downward rotation of the dorsal bar rostral to the hinge; (3) to increase the effect of retraction of the palate on downbending of the symphysis in flexible-billed birds by limiting downbending at the craniofacial hinge; (4) to

increase the angle of the retracted upper jaw by shifting the dorsal bending zone toward the symphysis, as in central rhynchokinesis (see Figure 15).

The prokinetic bustards (Otididae) may serve as a model for an early stage of evolution of schizorhiny or rhynchokinesis by rostral extension of the mesethmoid. (Bustards do not necessarily represent such a stage; they may, in fact, be secondarily prokinetic.) In them the mesethmoid protrudes rostrally beyond the cranial attachment and bending axis of the lateral portion of the nasal bone. The external naris is large, but it does not reach the craniofacial hinge (Figure 17). To judge from manipulation of water-soaked skulls of *Neotis cafra* and *Choriotis kori*, the craniofacial hinge does not form a single transverse axis; rather, the medial portion lies somewhat rostral to the lateral portion. The thin sheet of bone constituting the caudal border of the naris bends during protraction or retraction, contrary to a hypothetical model in which bending is not possible and kinesis is blocked. This bending and some flexibility of the flattened ventral bar allows a change in shape of the external nares during kinetic rotation of the upper jaw; the change is caused by motion of the lateral and ventral bars relative to the dorsal bar. Such bending at the narial border might lead to physiological adaptation, and eventually evolutionary adaptation, that would block the development of ossification in the region of bending and thereby extend the external naris caudally to produce schizorhiny. These changes might occur rapidly in an evolutionary sense, leaving few, if any, examples of the intermediate stage among living birds. I hypothesize that the development of schizorhiny in the manner just described most likely would occur in birds preadapted for rhynchokinesis by flexibility of the distal portion of the dorsal and ventral bars (hinges C and D), such that independent motion of the lateral and dorsal bars and bending at the narial border would be increased. In this way prokinesis could lead to double rhynchokinesis through an amphikinetic stage. The amphikinetic skull as it occurs in *Rallus* is less likely to lead to schizorhiny

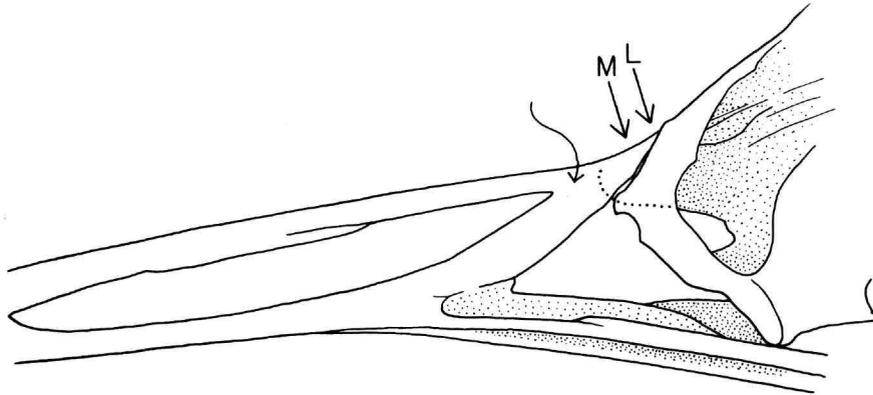


FIGURE 17.—Skull of *Choriotis kori*, left lateral view (arrows L and M indicate regions of bending of lateral and medial portions of craniofacial hinge; curved arrow shows bending region of narial border; dotted outline represents mesethmoid).

because independent motion of the lateral bar can be fully developed within that configuration without modifying the caudal narial border.

The second change leading to schizorhiny and rhynchokinesis—an evolutionary ventrad shift of the dorsal bar—would produce a more slender bill that might be advantageous for penetrating crevices or flowers, or probing vegetation or mud. Comparison of the two ibises in Figure 18 shows how shifts of the dorsal bar and changes in the mesethmoid relate to increased separation of the basal hinge axes. These shifts undoubtedly can be reversed under selection for a stouter bill. For example, in adult spoonbills (Figure 18a) the solid, paddle-like construction of the prokinetic upper jaw is adapted for side-to-side sweeping through the water (Allen, 1942; Vestjens, 1975). The skeleton of a 54-day chick of the Roseate Spoonbill (*Ajaia ajaja*; USNM 554780) has external nares that extend caudally beyond the craniofacial hinge; its dorsal and ventral bars are unfused almost to the paddle-like symphysis, and the dorsal bar is flattened and flexible caudal to the symphysis (see also Hofer, 1955, fig. 14). The young spoonbill has a single craniofacial hinge axis, but the structure of the juvenile jaw suggests that spoonbills evolved from an ibis-like form by fusion of the dorsal and ventral bars and

melding of hinges A and B into a single bending axis.

Once the rhynchokinetic jaw had evolved, its further development would probably be guided by selection for more efficient bending of the bill tip, although such bending is not unique to rhynchokinetic birds. Bill tip motion in a bird lacking hinge E requires the presence of a second hinge axis at the base of the bill (Figure 11). A few doubly rhynchokinetic birds have flexibility at E, but most apparently need the added strength and stability afforded by thickening of the lateral bar at its junction with the ventral bar. The presence of a second basal hinge axis thus appears to be a necessity for any bird that needs the temporary grasping capacity afforded by bill-tip motion as well as the stability afforded by the loss of hinge E. Natural selection would maintain or modify the double hinge, once evolved, because of its functional relation to rhynchokinesis.

PATHWAYS OF EVOLUTION

In the absence of a fossil record of skull structure in most rhynchokinetic orders we must rely on inferences about the evolution of morphological features from living species. Such inferences require a knowledge of the mechanics of kinesis.

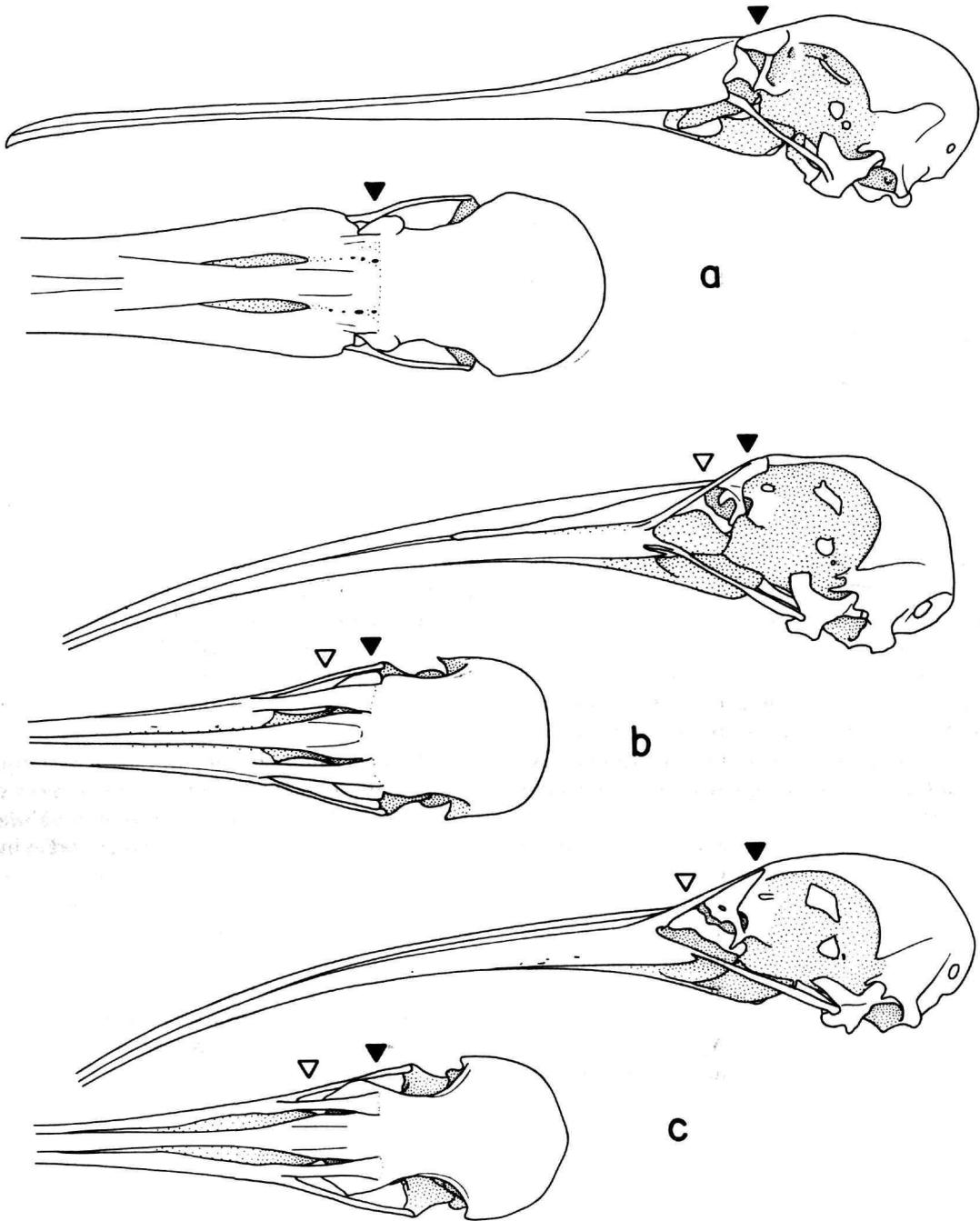


FIGURE 18.—Bending zones at base of upper jaw in spoonbill (*a*) and ibises (*b,c*): *a*, *Ajaia ajaja*; *b*, *Hagedashia hagedash*; *c*, *Eudocimus albus*. (Solid pointer indicates craniofacial hinge; open pointer indicates rhynchokinetic hinge; see text for explanation.)

Before presenting a hypothetical scheme for the evolution of different jaw morphologies I will discuss the key questions: how did distal rhynchokinesis evolve?; how did proximal rhynchokinesis evolve?; how often did prokinesis re-evolve from rhynchokinesis?

DISTAL RHYNCHOKINESIS.—There is no mechanical reason why distal rhynchokinesis could not evolve by forward migration of the medial part of the craniofacial hinge (B) from a prokinetic ancestor with large external nares, if certain combinations and configurations of hinges were already present in the upper jaw. As noted earlier, kinesis would be blocked by the presence of two hinge axes at the base of the upper jaw unless one of the following hinge combinations were present: hinge D in the form of extended flexibility of the ventral bar; hinges D and E (or an interrupted lateral bar); hinges C, D, and E; or hinges C and D. I have already discussed the effects on kinesis of a forward shift of hinge B in a jaw with hinges C and D (see Table 2); the hypothesized reversal of bill tip motion after hinge B passed dorsal to line AD makes this pathway to distal rhynchokinesis extremely unlikely. We can also discard the first alternative, because kinesis would become increasingly awkward and inefficient as hinge B moved forward (Figure 13*d*).

I know of no way to choose between the other two possibilities by examination of any single distally rhynchokinetic species, because the specialized end-products of each alternative pathway could be the same. Comparison of related species, however, suggests that both pathways are unlikely. Assuming forward migration of hinge B from an ancestor with hinges D and E, one would expect to find relatives of the distally rhynchokinetic forms in different stages of migration of hinge B. As a corollary, one would not expect to find double rhynchokinesis to be the prevalent form of kinesis in relatives of distally rhynchokinetic forms. By these criteria this pathway is virtually eliminated as a possibility for the Scolopacidae and Haematopodidae, but it remains a viable explanation for the Apterygidae.

If the ancestor had hinges C, D, and E, we would expect to find birds in which hinge B approached hinge C to varying degrees, with the dorsal bar stiffened caudal to hinge B. There is no support among the relatives of Scolopacidae, Haematopodidae, or Apterygidae for this explanation.

Another route to distal rhynchokinesis would be *limited* forward migration of hinge B (producing schizorhiny) from an ancestor with hinges C and D, followed by loss of hinge B. In this case, we would expect to find gradations of flexibility at hinge B in different species, and many doubly rhynchokinetic relatives of the distally rhynchokinetic forms, with E present or absent. This is what we find for the Scolopacidae and Haematopodidae, but not for the Apterygidae. The probable evolutionary route to distal rhynchokinesis in the Charadrii can be simulated by arranging various species of the Scolopacidae in a morphocline from double rhynchokinesis to strongly developed distal rhynchokinesis (Figure 19*a-d*). An extensive forward migration of hinge B is not indicated; instead, the dorsal bar becomes progressively thickened and distal rhynchokinesis arises by obliteration of hinge B. Thus I conclude that there is strong evidence for the evolution of distal rhynchokinesis from double rhynchokinesis in the Charadrii, and weaker evidence, for lack of close relatives, of the evolution of distal rhynchokinesis in the Apterygidae by a simple forward migration of hinge B.

It is worth noting that only one change would be necessary to produce distal rhynchokinesis from an amphikinetic bird—loss of flexibility of the medial portion of the craniofacial hinge. The result would be a transfer of all protraction and retraction forces from the palate to the tip of the jaw via the lateral and ventral bars. However, I have found no amphikinetic birds among the close relatives of distally rhynchokinetic ones.

PROXIMAL RHYNCHOKINESIS.—Evolution of proximal rhynchokinesis by a limited forward shift of the medial portion of the craniofacial hinge from an ancestor with no other hinges or with only hinge D is unlikely because these combinations would block kinesis (see page 12). Only

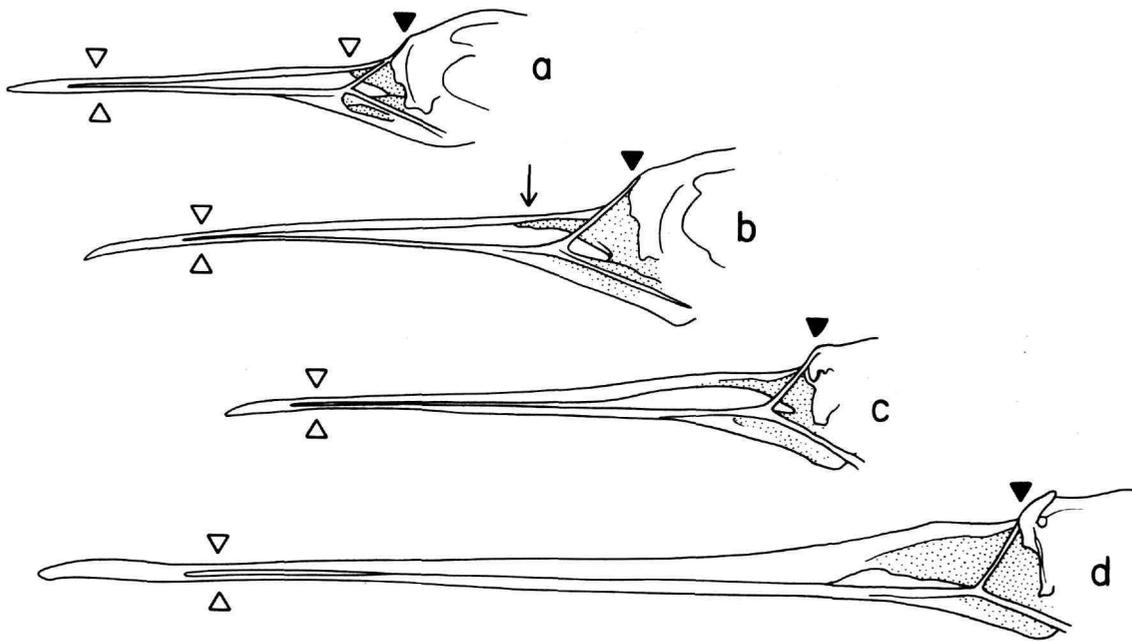


FIGURE 19.—Morphocline from double to distal rhynchokinesis: a, *Actitis macularia*; b, *Philomachus pugnax*; c, *Calidris alpina*; d, *Limnodromus griseus*. (Solid pointer indicates craniofacial hinge; open pointers show additional hinges; arrow shows reduced hinge.)

in the event that hinge B shifted forward along the path of a line joining hinges A and D would kinesis remain effective. However, kinesis would not be blocked if hinge D were extensively flexible or if hinges D and E were present. Similarly, a doubly rhynchokinetic bird could become proximally rhynchokinetic through loss of hinge C, without blocking kinesis, if hinge D were extensively flexible or if hinges D and E were both present. A flattened and extensively flexible ventral bar is a feature commonly found in rhynchokinetic birds, but in prokinetic birds, other than certain Passeriformes, it is found mainly in groups that may be secondarily evolved from rhynchokinetic ancestors. Hinge E is also rare in prokinetic forms. Thus the evolution of proximal rhynchokinesis directly from a prokinetic form is unlikely because of mechanical restrictions, and there is no clear example of it among birds. Derivation of proximal rhynchokinesis from a doubly rhynchokinetic ancestor by a subsequent

loss of hinge C is therefore the most likely pathway because these birds already have a flexible ventral bar, and sometimes hinge E as well.

Proximal rhynchokinesis occurs in three families of Gruiformes, many Charadrii, the Lari and Alcae, the Columbiformes, the Trochilidae, and the Furnariidae (Table 1, page 6). The prevalence of doubly rhynchokinetic forms in the Gruiformes, Charadriiformes, and Columbiformes further supports a hypothesis of the derivation of proximal rhynchokinesis from double rhynchokinesis in those orders. The Furnariidae remain equivocal because, to judge from osteology alone, they appear to lack doubly rhynchokinetic species. However, some have slender bills that may in fact be doubly rhynchokinetic. Though many have hinge E, in some it is poorly defined and some lack it.

A return to prokinesis does not necessarily follow the secondary evolution of proximal rhynchokinesis. As long as there is no need for strong

biting along the ventral bar, the bar can remain flexible. There is also no need to reduce hinges A and B to a single axis if their effects on kinesis are essentially neutralized by appropriate configurations of hinges A, B, and D. On the other hand, if the bill were regularly stressed by pounding, prying, strong maxillary biting, or some other use, the ventral bar would probably be heavily ossified and the upper jaw would be an inflexible unit. A return to a single craniofacial hinge axis would then be the most efficient means of maintaining kinesis (see Figure 12*c,g*).

PROKINESIS.—Prokinetic birds have apparently evolved from rhynchokinetic ancestors in some instances. The following taxa are especially pertinent to this problem because of their association with rhynchokinetic forms in current classification: Plataleinae (spoonbills), Heliornithidae (sun grebes and finfoots), Otididae (bustards), Cariamidae (seriamas), Psophiidae (trumpeters), Rallidae (rails and allies), Burhinidae (thick-knees), *Pluvianus* (Egyptian Plover), Phoenicopteridae (flamingos—if included in Charadriiformes), *Raphus* (Dodo), Phaethornithinae (hermits), Dendrocolaptidae (woodcreepers), and *Xenicus* (Bush Wren, Rock Wren). An evolutionary return to prokinesis could be virtually unrecognizable, as pointed out by Bock (1964), but one or more of the following features might be retained in a prokinetic bird of rhynchokinetic ancestry: (1) a flattened, flexible ventral bar; (2) an osteological gap or any other suggestion of former separation of the lateral bar from the base of the dorsal bar; (3) a rostral extension of the mesethmoid beyond the cranial attachment of the lateral portion of the craniofacial hinge.

The first feature is developed to varying degrees in the Otididae, Psophiidae, Rallidae, Burhinidae, *Pluvianus*, and *Xenicus longipes*, but it is not necessarily evidence of former rhynchokinesis because it also occurs in some prokinetic passeriform birds (e.g., some Troglodytidae (wrens), Mimidae (mockingbirds and allies), Turdinae (thrushes)) for which there is no other evidence of rhynchokinetic ancestry. The second feature is seen only in the Plataleinae and in *Raphus*. In them the slit-like gap typically terminates at the

craniofacial hinge and it apparently indicates former rhynchokinesis in *Raphus* because the craniofacial hinge is still slightly separated into two axes, and in Plataleinae for reasons given on page 26. The third feature is pronounced only in the Otididae and Phaethornithinae. Prokinesis in the Otididae could be interpreted either as a preadaptation for rhynchokinesis or as a modification from rhynchokinetic ancestry. In hummingbirds, lack of dorsoventral flexibility in the ventral bar suggests that the protruding mesethmoid is not a sign of former rhynchokinesis. It may simply serve as a support or retraction stop for the long bill in all hummingbirds.

DIRECTIONS OF EVOLUTION

The most probable sequence of evolutionary steps to each form of kinesis is shown in Figure 20, based on hypothetical mechanical consequences of a change from one form to the next as presented in this paper. In general, I think that evolutionary reversal, that is, direct return to an immediately ancestral form of kinesis, occurred infrequently because a reversal of the initial changes in morphology and function is not likely to be advantageous. For example, if used for probing, a slender, prokinetic upper jaw with large nares might become amphikinetic and then evolve toward double rhynchokinesis by forward extension of the mesethmoid and hinge B, because these changes would improve its function as a probing and grasping instrument. A return to amphikinesis or prokinesis would provide no advantage in a probing bill. Proximal rhynchokinesis can evolve from double rhynchokinesis only because of the presence of hinges associated with double rhynchokinesis. Specializations for uses other than probing reduce the chance of a return to probing and double rhynchokinesis. In the evolution of distal rhynchokinesis, any lessening of flexibility in hinge B and strengthening of the base of the dorsal bar of a doubly rhynchokinetic bird would increase its effectiveness in probing, while reducing its efficiency in forceps feeding. Subsequent weakening of the dorsal bar of a distally rhynchokinetic form, however, would not improve probing, and forceps feeding

would not improve until hinge B were reconstituted.

Paleognathous rynchokinesis in birds could have evolved directly from some form of kinesis in reptilian ancestors, or it could have developed from avian prokinesis through a proximally rynchokinetic stage. Hinge C is absent from adult paleognathous birds and from juvenile skeletal specimens of *Rhynchotus*, *Struthio*, *Rhea*, *Dromaius*, and *Casuarius* that I have examined; thus the hinge on the dorsal bar in paleognaths probably represents part of an original craniofacial hinge that shifted forward through evolution, accompanied by ossification of the underlying septum. There is no evidence that double rynchokinesis was involved in the evolution of paleognathous rynchokinesis, as it was in many neognaths. Furthermore, the paleognathous birds differ from rynchokinetic neognaths in that the dorsal bar did not shift toward the ventral bar and away from the level of the original craniofacial hinge in the course of evolution. For these reasons and others presented by Bock (1974), rynchokinesis in paleognaths and neognaths probably evolved by different pathways.

Discussion

This paper serves to introduce the complexities of the rynchokinetic, amphikinetic, and prokinetic skulls of birds without exploring their morphology in detail. It is intended to clarify concepts and terminology related to kinesis, to focus attention on the unsolved problems in this field, and to stimulate new research.

I have shown that the double hinge axes of the rynchokinetic skull impose certain restrictions on kinesis of the upper jaw. The double hinge axis is a significant feature in the analysis of function of both schizorhiny and rynchokinesis. By my definitions schizorhiny and holorhiny are reduced to partial synonyms of rynchokinesis and prokinesis, respectively.

Much of the analysis of kinesis in this paper is based on the mechanical properties of hypothetical models that assume inflexible bars connected by pin hinges. The application of this method is

particularly successful within the Charadrii, many of which have well-defined and restricted hinges and in which some of the functional properties are easily understood and often clearly related to specific feeding methods (Zusi, in preparation). In some other rynchokinetic groups the theoretical conditions of the model are less closely approximated by the birds—hinges are not well-defined, the inflexibility of “inflexible” bars is open to question, the adaptations involved are not evident, and the configurations of hinges are theoretically detrimental to kinesis. I have nevertheless applied a consistent method of analysis throughout the rynchokinetic birds because the significance of morphological configurations in difficult groups was clarified first by the models. For example, the structure of the upper jaw in proximally rynchokinetic birds was most probably derived from a doubly rynchokinetic ancestor. This conclusion came from hypothetical models that demonstrated the following: first, a simple step-wise derivation of double rynchokinesis from prokinesis; second, a simple derivation of proximal rynchokinesis from double rynchokinesis; third, the kinetic conflicts associated with proximal rynchokinesis; and fourth, the different hinge configurations that would serve to overcome the conflicts. The presence of such configurations in proximally rynchokinetic birds was thus explained. It was not possible to understand the structure of the proximally rynchokinetic skull, even with a full appreciation of its functional properties and adaptive value, without reconstructing its probable morphological history. These conclusions could not have come only from manipulation of skulls or observations of kinesis in living birds. The functional implications of models have been essential for their formulation.

Reference to Table 1 (page 6) reveals a high frequency of probable evolutionary shifts from double rynchokinesis to proximal rynchokinesis. This change is usually associated with stronger biting or pounding or with the taking of larger prey, and its prevalence is related to a wide diversity of feeding habits among these birds. By contrast, the evolution of distal rynch-

chokinesis from double rhynchokinesis is a rare event outside the Charadrii and appears to be almost exclusively associated with deep probing and the support of a long, slender bill. Food resources that are obtainable by deep probing and that are also sufficiently concentrated and constant to support the specialization of distal rhynchokinesis may be restricted to invertebrates in moist or wet soil, and nectar in long tubular flowers. The Charadrii have largely monopolized the former food source except in New Zealand, where the kiwi replaces the woodcock. Feeding on nectar in tubular flowers requires neither a stiffened upper jaw nor bill-tip grasping. Thus distal rhynchokinesis is not found in passerine nectar feeders and is poorly developed, if present at all, in hummingbirds.

The analysis of kinesis has taxonomic applications of several kinds. Through functional-morphological analysis this paper demonstrates the probable directions of evolution in a complex morphocline (Figure 20) and suggests polarities among morphological states that could serve for phylogenetic analysis. Interpretation of polarity is somewhat clouded by the circular configuration of part of the morphocline, which makes the determination of the most primitive state difficult and implies that convergence to that state has occurred. Nevertheless, I have presented evidence that, within neognathous birds, amphikinesis is an evolutionary derivative of prokinesis, that double rhynchokinesis is derived relative to prokinesis, and that distal rhynchokinesis and most or all cases of proximal rhynchokinesis are derived relative to double rhynchokinesis. Paleognathous rhynchokinesis may be derived relative to avian prokinesis, or it may represent a primitive state from an early radiation of paleognathous birds.

I have found that the origin and subsequent modification of each of the forms of neognathous rhynchokinesis can be traced and explained by simple steps. The probable evolutionary transformations of even the most specialized morphologies, such as those of the skimmers (*Rynchops*) and woodcock (*Scolopax*), can be readily

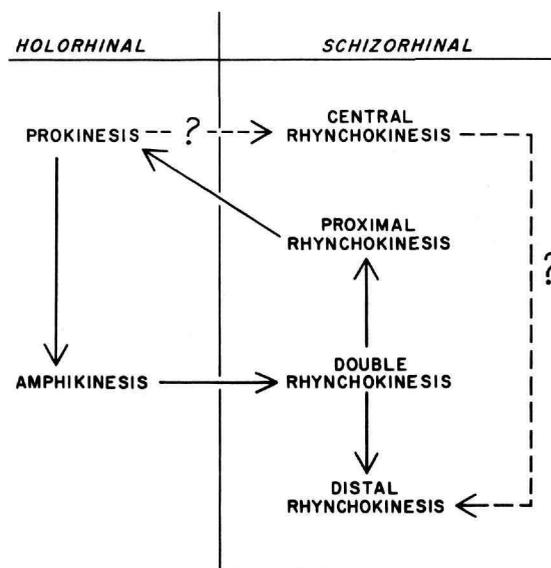


FIGURE 20.—Hypothetical evolutionary routes to different kinds of cranial kinesis (dashed arrows refer to paleognathous birds; solid arrows refer to neognathous birds).

visualized. In this way, functional analysis is beginning to provide a rationale for the remarkable diversity in bill structure found in such orders as the Gruiformes, Charadriiformes, and Columbiiformes. Still unexplained is the evolutionary process by which the morphological diversity of these and other orders arose. This problem will require different approaches and methods. But many questions concerning the pattern of structure and function of the upper jaw in birds also remain to be answered. These problems could best be solved in the immediate future by study of the nasal region and its relation to bill structure and function, by detailed comparative studies of jaw structure within and among many orders of birds, by accurate mapping of kinetic motions in a wide variety of species, by obtaining new information on developmental anatomy of the jaws, by studies of kinesis in live birds, by comparing detailed accounts of foraging behavior of rhynchokinetic birds and their prokinetic and amphikinetic relatives, and by the discovery of enlightening fossils.

Appendix

Species and Numbers of Skeletons of Rhynchokinetic Birds Examined

In addition to studies on the rhynchokinetic species listed below, comparisons were made with a variety of prokinetic and amphikinetic birds, with emphasis on the following: Plataleinae, Psophiidae, Rallidae, Heliornithidae, Cariamidae, Otididae, Burhinidae, Glareolidae (*Pluvianus*), Raphidae, Trochilidae (Phaethornithinae), Dendrocolaptidae, Xenicidae (*Xenicus*).

- TINAMIDAE:** *Tinamus tao* 2, *T. solitarius* 1, *T. major* 3; *Crypturellus cinereus* 1, *C. soui* 4, *C. undulatus* 1, *C. idoneus* 1, *C. cinnamomeus* 2, *C. boucardi* 1, *C. parvirostris* 1, *C. tataupa* 3; *Rhynchotus rufescens* 4, *Nothoprocta perdicaria* 1, *Nothura maculosa* 11, *Eudromia elegans* 13.
- STRUTHIONIDAE:** *Struthio camelus* 3.
- RHEIDAE:** *Rhea americana* 2, *Pterocnemia pennata* 2.
- CASUARIIDAE:** *Casuarius casuarius* 2, *C. unappendiculatus* 2.
- DROMADIDAE:** *Dromaius novaehollandiae* 4.
- APTERYGIDAE:** *Apteryx australis* 3.
- THRESKIORNITHIDAE:** *Threskiornis aethiopicus* 8, *T. melanocephalus* 1; *Carpodacus spinicollis* 2, *Nipponia nippon* 1, *Hagedashia hagedash* 1, *Harpiprion caerulescens* 2, *Theristicus caudatus* 2, *T. branickii* 1, *T. melanopsis* 1; *Mesembrinibis cayennensis* 2, *Eudocimus albus* 7, *E. ruber* 3; *Plegadis falcinellus* 6, *P. chihi* 6, *P. ridgwayi* 1.
- MESITORNITHIDAE:** *Mesitornis variegata* 1, *Monias benschi* 1.
- TURNICIDAE:** *Turnix tanki* 3, *T. suscitator* 1, *T. varia* 2.
- RHYNOCHETIDAE:** *Rhynchotus jubatus* 1.
- EURYPYGIDAE:** *Eurypyga helias* 5.
- GRUIDAE:** *Grus grus* 5, *G. monacha* 1, *G. canadensis* 10, *G. japonensis* 2, *G. americana* 4, *G. vipio* 1, *G. antigone* 4, *G. rubicunda* 1, *G. leucogeranus* 4; *Bugeranus carunculatus* 1, *Anthropoides virgo* 5, *A. paradisea* 4; *Balearica pavonina* 5, *B. rugulorum* 1.
- ARAMIDAE:** *Aramus guarauna* 6.
- CHARADRIIDAE:** *Vanellus vanellus* 6, *V. armatus* 4, *V. spinosus* 2, *V. duvaucelii* 1, *V. tectus* 3, *V. albiceps* 2, *V. coronatus* 1, *V. senegallus* 3, *V. cayanus* 2, *V. chilensis* 5, *V. indicus* 2, *V. tricolor* 1, *V. miles* 1; *Pluvialis dominica* 7, *P. squatarola* 5; *Charadrius hiaticula* 2, *C. semipalmatus* 7, *C. placidus* 5, *C. dubius* 2, *C. wilsonia* 5, *C. vociferus* 5, *C. melodus* 2, *C. pecuarius* 2, *C. sanctaehelenae* 4, *C. tricoloris* 1, *C. alexandrinus* 5, *C. collaris* 2, *C. falklandicus* 3, *C. mongolus* 5, *C. asiaticus* 2, *C. modestus* 4, *C. montanus* 4; *Anarhynchus frontalis* 2, *Eudromias ruficollis* 1.
- GLAREOLIDAE:** *Rhinoptilus cinctus* 1, *R. chalconotus* 1, *Cursorius coromandelicus* 1, *C. temminckii* 1; *Glareola pratincola* 1, *G. maldivarum* 2, *G. nordmanni* 1, *G. nuchalis* 4, *G. lactea* 3.
- DROMADIDAE:** *Dromas ardeola* 3.
- CHIONIDIDAE:** *Chionis alba* 5, *C. minor* 3.
- HAEMATOPODIDAE:** *Haematopus ostralegus* 10, *H. bachmani* 3, *H. leucopodus* 5, *H. ater* 7.
- RECURVIROSTRIDAE:** *Himantopus himantopus* 5, *H. mexicanus* 5; *Cladorhynchus leucocephalus* 1, *Recurvirostra avosetta* 4, *R. americana* 4.
- IBIDORHYNCHIDAE:** *Ibidorhynchus struthersii* 3.
- JACANIDAE:** *Actophilornis africana* 5, *Hydrophasianus chirurgus* 5, *Metopidius indicus* 2, *Jacana spinosa* 11, *J. jacana* 5.
- ROSTRATULIDAE:** *Rostratula benghalensis* 5, *Nycticryphes semicollaris* 1.
- PEDIONOMIDAE:** *Pedionomus torquatus* 1.
- THINOCORIDAE:** *Attagis malouinus* 1, *Thinocorus orbignyianus* 2, *T. rumicivorus* 5.
- SCOLOPACIDAE**
- TRINGINAE:** *Limosa limosa* 2, *L. haemastica* 5, *L. lapponica* 1, *L. fedoa* 5; *Numenius minutus* 1, *N. borealis* 5, *N. phaeopus* 5, *N. tahitiensis* 5, *N. arquata* 2, *N. madagascariensis* 2, *N. americanus* 5; *Bartramia longicauda* 7, *Tringa totanus* 1, *T. nebularia* 1, *T. melanoleuca* 8, *T. flavipes* 8, *T. ochropus* 2, *T. solitaria* 4, *T. glareola* 3; *Catoptrophorus semipalmatus* 8, *Xenus cinereus* 1, *Actitis hypoleucos* 3, *A. macularia* 7; *Heteroscelus brevipes* 2, *H. incanus* 3, *Prosobonia cancellata* 1.
- ARENARIIDAE:** *Arenaria interpres* 5, *A. melanocephala* 1.
- PHALAROPODINAE:** *Phalaropus tricolor* 2, *P. lobatus* 1, *P. fulcarius* 1.
- SCOLOPACINAE:** *Scolopax rusticola* 5, *S. minor* 5.

- GALLINAGONINAE:** *Gallinago stenura* 3, *G. megala* 1, *G. gallinago* 5, *G. paraguayae* 3, *G. nobilis* 4, *G. jamesoni* 1; *Lymnocyrtus minimus* 1, *Limnodromus griseus* 5, *L. scolopaceus* 5.
- CALIDRIDINAE:** *Aphriza virgata* 1, *Calidris canutus* 5, *C. alba* 5, *C. pusilla* 5, *C. mauri* 5, *C. ruficollis* 4, *C. minuta* 1, *C. temminckii* 1, *C. subminuta* 1, *C. minutilla* 5, *C. fuscicollis* 5, *C. bairdii* 5, *C. melanotos* 5, *C. acuminata* 1, *C. maritima* 3, *C. ptilocnemis* 5, *C. alpina* 5, *C. ferruginea* 4; *Eurynorhynchus pygmeus* 1, *Limicola falcinellus* 1, *Micropalama himantopus* 5, *Tryngites sub-ruficollis* 2, *Philomachus pugnax* 9.
- STERCORARIIDAE:** *Catharacta skua* 3, *C. maccormicki* 3; *Stercorarius pomarinus* 3, *S. parasiticus* 5, *S. longicaudus* 5.
- LARIDAE**
- LARINAE:** *Gabianus scoresbii* 4, *Pagophila alba* 4, *Larus fuliginosus* 3, *L. crassirostris* 2, *L. audouinii* 1, *L. canus* 9, *L. argentatus* 4, *L. californicus* 4, *L. occidentalis* 4, *L. dominicanus* 3, *L. schistisagus* 3, *L. marinus* 3, *L. glaucescens* 3, *L. hyperboreus* 5, *L. ichthyaetus* 1, *L. atricilla* 5, *L. cirrocephalus* 3, *L. pipixcan* 2, *L. novaehollandiae* 3, *L. bulleri* 1, *L. maculipennis* 1, *L. ridibundus* 3, *L. genei* 1, *L. philadelphia* 5, *L. saundersi* 1; *Rhodostethia rosea* 3, *Rissa tridactyla* 4, *R. brevirostris* 3; *Creagrurus furcatus* 2, *Xema sabini* 4.
- STERNINAE:** *Chlidonias hybrida* 1, *C. leucoptera* 2, *C. nigra* 4; *Phaetusa simplex* 2, *Gelochelidon nilotica* 2, *Hydroprogne caspia* 4, *Sterna hirundinacea* 4, *S. hirundo* 5, *S. paradisaea* 7, *S. vittata* 5, *S. forsteri* 4, *S. dougallii* 4, *S. striata* 2, *S. sumatrana* 2, *S. aleutica* 2, *S. lunata* 3, *S. anaethetus* 2, *S. fuscata* 5, *S. superciliaris* 2, *S. albifrons* 6; *Thalasseus bergii* 3, *T. maximus* 5, *T. sandvicensis* 4; *Larosterna inca* 4, *Procelsterna cerulea* 5, *Anous stolidus* 5, *A. minutus* 5; *Gygis alba* 5.
- RYNCHOPIDAE:** *Rynchops niger* 5, *R. flavirostris* 2.
- ALCIDAE:** *Alle alle* 3, *Pinguinus impennis* 2, *Alca torda* 5, *Uria lomvia* 5, *U. aalge* 5; *Cepphus grylle* 6, *C. columba* 5, *C. carbo* 3; *Brachyramphus marmoratus* 1, *B. brevirostris* 1, *B. hypoleucus* 1; *Synthliboramphus antiquus* 5, *Ptychoramphus aleuticus* 3, *Cyclorhynchus psittacula* 5, *Aethia cristatella* 4, *A. pusilla* 4, *A. pygmaea* 1; *Cerorhinca monocerata* 4, *Fratercula arctica* 4, *F. corniculata* 4; *Lunda cirrhata* 4.
- PTEROCLIDIDAE:** *Syrnhaptes paradoxus* 2, *Pterocles alchata* 1, *P. orientalis* 1, *P. gutturalis* 2, *P. burchelli* 3, *P. bicinctus* 4.
- COLUMBIDAE:** *Columba livia* 4, *C. rupestris* 1, *C. guinea* 4, *C. palumbus* 4, *C. hodgsonii* 2, *C. leucocephala* 3, *C. squamosa* 2, *C. speciosa* 4, *C. fasciata* 3, *C. araucana* 1, *C. cayennensis* 2, *C. inornata* 3, *C. plumbea* 2, *C. subvinacea* 1; *Streptopelia orientalis* 1, *S. decaocto* 2, *S. semitorquata* 3, *S. capicola* 3, *S. vinacea* 1, *S. tranquebarica* 2, *S. chinensis* 3, *S. senegalensis* 3; *Macropygia unchall* 3, *Turacoena manadensis* 1, *Turtur chalcophilus* 3, *T. afer* 3, *T. brehmeri* 2; *Oena capensis* 2, *Chalcophaps indica* 2, *Phaps chalcoptera* 1, *Ocyphaps lophotes* 2, *Petrophassa plumifera* 2, *P. ferruginea* 1, *P. smithii* 2; *Geopelia cuneata* 1, *G. striata* 3, *G. humeralis* 2; *Leucosarcia melanoleuca* 3, *Ectopistes migratorius* 3, *Zenaida macroura* 5, *Z. auriculata* 3, *Z. aurita* 4, *Z. asiatica* 3; *Columbina passerina* 5, *C. buckleyi* 2, *C. talpacoti* 3, *C. picui* 3; *Claravis pretiosa* 2, *Scardafella inca* 3, *Leptotila verreauxi* 4, *L. rufaxilla* 2, *L. plumbeiceps* 3, *L. jamaicensis* 3, *L. cassini* 1; *Geotrygon chrysis* 3, *G. montana* 3; *Starnoenas cyanocephala* 2, *Caloenas nicobarica* 3, *Gallinolumba tristigmata* 1, *Goura cristata* 4, *G. scheepmakeri* 1, *G. victoria* 2; *Didunculus strigirostris* 1, *Phapitreron leucotis* 1, *P. amethystina* 1; *Treron vernans* 5, *T. pompadora* 2, *T. curvirostra* 1, *T. phoenicoptera* 1, *T. calva* 2; *Ptilinopus occipitalis* 1, *P. leclancheri* 1, *P. roseicapilla* 1, *P. purpuratus* 1, *P. dupetithouarsii* 2, *P. iozonus* 1, *P. melanospila* 1; *Ducula radiata* 1, *D. aenea* 5, *D. pacifica* 1, *D. oceanica* 1, *D. aurorae* 1, *D. badia* 2, *D. bicolor* 1, *D. luctuosa* 1, *D. spilorrhhoa* 1; *Hemiphaga novaeseelandiae* 1.
- TROCHILIDAE**
- TROCHILINAE:** *Dorifera ludovicae* 1, *Androdon aequatorialis* 1, *Phaeochroa cuvierii* 1; *Campylopterus curvipennis* 1, *C. largipennis* 1, *C. ensipennis* 1, *C. villaviscensio* 1; *Eupetomena macroura* 1, *Florisuga mellivora* 1, *Colibri delphinae* 1, *C. coruscans* 1; *Anthracothorax viridigula* 1, *A. dominicus* 1; *Eulampis jugularis* 2, *Sericotes holosericeus* 2, *Chrysolampis mosquitus* 1, *Orthorhynchus cristatus* 1, *Klais guimeti* 1, *Abeillia abeillei* 1, *Stephanoxis lalandi* 1, *Popelairia conversii* 1, *Chlorestes notatus* 1, *Chlorostilbon maugaeus* 1, *C. gibsoni* 1; *Cyananthus latirostris* 1, *Cyanophaea bicolor* 1, *Thalurania furcata* 2, *T. glaucopsis* 1; *Panterpe insignis* 1, *Damophila julie* 1, *Lepidopyga coeruleogularis* 1, *Hylocharis leucotis* 1, *H. cyanus* 1; *Chrysuronia oenone* 1, *Trochilus polytmus* 1, *Polytmus guainumbi* 1, *Leucippus taczanoskii* 1, *Amazilia chionogaster* 1, *A. candida* 1, *A. amabilis* 1, *A. beryllina* 1, *A. saucerrottei* 1, *A. tzacatl* 1, *A. violiceps* 1; *Eupherusa eximia* 1, *Chalybura urochrysis* 1, *Lampornis clemenciae* 1, *Adelomyia melanogenys* 1, *Phlogophilus hemileucurus* 1, *Polyplancta aurescens* 1, *Heliodoxa gularis* 1, *Eugenes fulgens* 1, *Sternoclyta cyanopectus* 1, *Topaza pella* 1, *Oreotrochilus estella* 1, *Urochroa bougueri* 1, *Patagona gigas* 1, *Aglaeactis cupripennis* 1, *Lafresnaya lafresnaya* 1, *Pterophanes cyanopterus* 1, *Coeligena coeligena* 1, *C. wilsoni* 1, *C. torquata* 2, *C. lutetiae* 1, *C. iris* 1; *Ensifera ensifera* 2, *Sephanoides sephanoides* 1, *Boissonneaua matthewsii* 1, *Heliangelus amethysticollis* 1, *H. exortis* 1; *Eriocnemis luciani* 1, *Haplophoedia aureliae* 1, *Ocreatus underwoodii* 1, *Lesbia victoriae* 1, *Sappho sparganura* 1, *Polyonymus caroli* 1, *Ramphomicron microrhynchum* 1, *Metallura theresiae* 1, *M. williamsi* 1; *Chalcostigma ruficeps* 1, *C. stanleyi* 1, *Oxyopogon guerinii* 1, *Aglaiocercus kingi* 1, *Oreonympha nobilis* 1, *Augastes*

lumachellus 1, *Schistes geoffroyi* 1, *Heliothryx aurita* 1, *Heliomaster constantii* 1, *Rhodopsis vesper* 1, *Philodice evelynae* 1, *Archilochus colubris* 2, *A. alexandri* 1; *Calypte anna* 2, *Myrtis fanny* 1, *Chaetocercus jourdanii* 1.

FURNARIIDAE: *Geositta cunicularia* 6, *Upucerthia certhioides* 1, *U. dumetria* 2; *Cinclodes patagonicus* 3, *Chilia melanura* 1, *Furnarius leucopus* 5, *F. rufus* 3; *Aphrastura spinicauda* 5, *Leptasthenura platensis* 1, *L. aegithaloides* 3; *Schizoeaca fuliginosa* 1, *Synallaxis phryganophila* 1, *S. azarae* 1, *S. albescens* 3, *S. spixi* 1, *S. brachyura* 4, *S. gujanensis* 2, *S. rutilans* 1, *S. castanea* 1, *S. erythrothorax* 1, *S. cinnamomea* 4; *Certhiaxis erythroptis* 1, *C. obsoleta* 1, *C. subcristata* 2, *C. pyrrhophia* 1, *C. sulphurifera* 1,

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XENICIDAE: *Acanthisitta chloris* 1.

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