Biomechanics of the jaw apparatus of the gigantic Eocene bird *Diatryma*: implications for diet and mode of life

Lawrence M. Witmer and Kenneth D. Rose

Abstract.—Discovery of several new specimens of the gigantic Eocene ground bird *Diatryma gigantea* from the Willwood Formation of northwestern Wyoming, has prompted an analysis of its feeding apparatus and an assessment of the mode of life of this unusual bird. *Diatryma* exhibits many of the features predicted by biomechanical models to occur in animals delivering large dorsoventral bite forces. Similarly, the mandible of *Diatryma*, which was modeled as a curved beam, appears well equipped to withstand such forces, especially if they were applied asymmetrically. Interpretation of these size-independent biomechanical properties in light of the large absolute skull size of *Diatryma* suggests a formidable feeding apparatus. The absence of modern analogues complicates the determination of just how this unique skull morphology correlates with diet. Suggestions that *Diatryma* was an herbivore seem improbable in that they require the postulation of excessively high safety factors in the construction of the skull. The traditional hypothesis of *Diatryma* as a carnivorous bird accords as well or better with the data at hand. Carnivory raises the probability of "accidental" encounter with bones, thus explaining the high safety factors. In fact, the skull and mandible of *Diatryma* are so massive that bone crushing may have been an important behavior. *Diatryma* could have been a scavenger. However, limb allometry and phylogenetic interpretation of limb proportions call into question the picture of *Diatryma* as a slow, plodding graviportal animal, suggesting that active predation was within its behavioral repertoire.

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Introduction

Gigantic animals of the past are sure to capture the imagination and quickly find their way into the public consciousness. In many cases, popular accounts are well supported by scientific evidence. However, claims about some extinct animals remain virtually unsubstantiated to this day. Such is the case with the flightless early Eocene bird *Diatryma gigantea* (Fig. 1). *Diatryma* is widely characterized as a 2-m tall, huge-headed predator that fed upon the small mammals of its time (Feduccia 1980; Carroll 1988; Alexander 1989; Gould 1989a; Martin 1989). Despite its prevalence, this predatory hypothesis has never been documented formally. Because we cannot directly observe *Diatryma* feeding, hypotheses of this sort are difficult to falsify. If a modern analogue of *Diatryma* were available, it would be easier to postulate a mode of life for *Diatryma* through morphological and functional comparisons ("form-function

correlation;" see Radinsky 1987). However, no bird even remotely similar to *Diatryma* exists in modern avifaunas. Without modern analogues, the form-function correlation is empty, and an alternative approach is "biomechanical design analysis" (Radinsky 1987). Ideally both methods should be employed together, and neither is complete without some knowledge of phylogenetic history (Lauder 1981).

By any avian measure, *Diatryma* was a giant. Thus, when making comparisons with other birds, we are faced with the classic problems of size and scaling (Schmidt-Nielsen 1984; Alexander 1989). Perhaps *Diatryma* approximates a "scaled up" version of some modern bird. Tempting as such an allometric explanation may be, however, it may well be spurious if it involves "a distant extrapolation into a size range not only unrepresented in the data, but also biologically absurd" (Gould 1966: p. 596; see also Schmidt-Nielsen 1984),

A

B
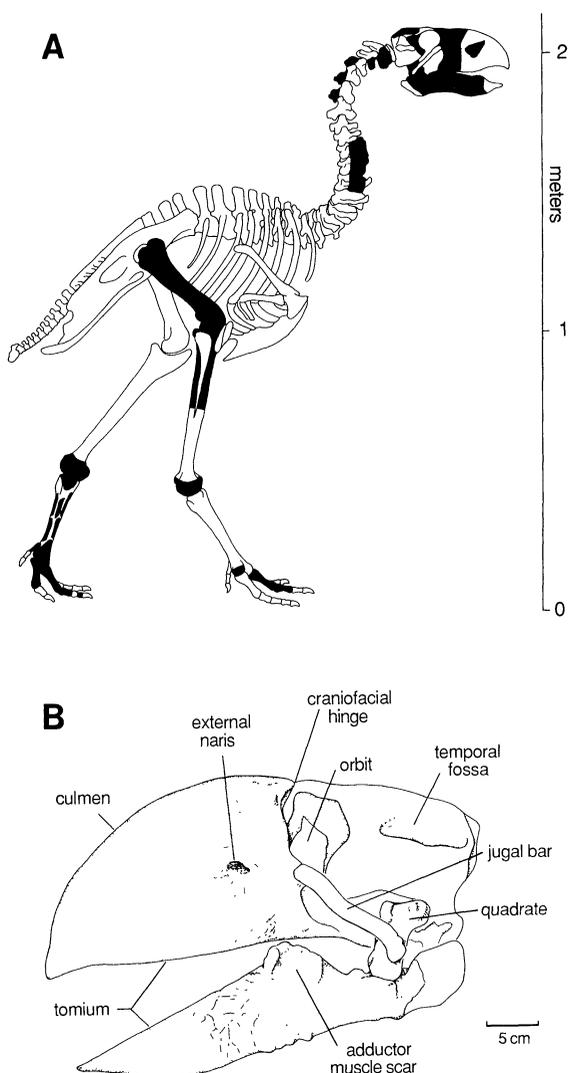
FIGURE 1. A, Restoration of the skeleton of *Diatryma gigantea* (redrawn from Matthew and Granger 1917). Shaded elements are bones preserved in the new specimens. See Table 1 and the text for description and measurements. B, Restoration of skull of *D. gigantea* in left lateral view based on the new material, a cast of AMNH 6169 (USNM 8885), and photographs published by Matthew and Granger (1917).

Basic physical properties (such as area-volume relationships) prevent the maintenance of geometrical similarity over large changes in linear dimension. Furthermore, even if the shapes of skulls of different size are generally similar, we cannot assume functional equivalence: size changes can open up new functional possibilities (Gould 1966). Thus, even if *Diatryma* ate insects, its bill would not necessarily resemble a warbler's; conversely, if *Diatryma* had a bill shaped like a warbler's, it would not necessarily have been insectivorous. In effect, size changes may create new morphologies that are permissive of new biological roles (Gans 1986; Wainwright 1988); hence, even if the small-skulled ancestors of *Diatryma* ate plants, its apomorphically large skull may have permitted different functional opportunities, such as carnivory.

The discovery of several new specimens of *Diatryma* (including portions of a skull and mandible), the rarity of such material, and the paucity of primary literature on the functional morphology of this famous bird, have prompted the present study. Here we record the new material, present static biomechanical analyses of aspects of the jaw mechanism based on this material, and propose potential feeding behaviors and preferences. Although *Diatryma* figures prominently in many "animals of the past" books, the scientific literature devoted to *Diatryma* is meager, the most important papers being Matthew and Granger (1917), Sinclair (1928), Troxell (1931), K.-H. Fischer (1978), and, most recently, Andors (1988) who provided an excellent revision and review of virtually all aspects of the biology of *Diatryma*.

Material

Specimens described herein (Table 1) were collected by a joint United States Geological Survey (USGS)–Johns Hopkins University project in the Early Eocene Willwood Formation of the Bighorn Basin, northwestern Wyoming, and are part of the USGS collection (Paleontology and Stratigraphy Branch, Denver, Colorado). Following Andors (1988), all specimens are considered to represent *Diatryma gigantea* rather than *D. steini* (the species erected by Matthew and Granger [1917]). Detailed descriptions of individual elements

as would be a regression of, for example, finchlike birds (body mass of about 50 g) extrapolated to *Diatryma* (about 10^5 g).

Another approach would be to ignore the large size of *Diatryma*, and look among the seemingly endless variety of avian skulls for one otherwise morphologically similar. If a match were found with warblers, for instance, we could hypothesize that *Diatryma* ate primarily insects. Size is critical, however.

TABLE 1. New material of *Diatryma gigantea* with pertinent measurements (mm) of some of the elements.

USGS 21862: Partial skull and cervical series	
Consists of: Partial mandible, right quadrate, ventral half of left quadrate, skull-roof fragment, right postorbital process, partial upper jaw, five cervical centra, and several cervical neural-arch fragments	
Greatest height of the mandible at the coronoid process	103.5
Thickness of ramus at point halfway between apex of coronoid process and caudal margin of symphysis	~22
Average transverse dimension from lateral side of jaw articulation to tip of medial process of mandible	80.7
Estimated length of restored mandible	~385
Estimated length of restored mandibular symphysis	~185
Greatest height of right quadrate	80.7
Average greatest breadth across mandibular process of quadrate	61.4
Greatest height of upper jaw from culmen to tomium	165
USGS 25008: Partial proximal right hind limb	
Consists of: right femur and proximal half of right tibiotarsus	
Greatest femoral length from trochanter to lateral condyle	330
Greatest proximal transverse width of femur	146
Craniocaudal diameter of femoral midshaft	40
Mediolateral diameter of femoral midshaft	58
Circumference of femoral midshaft	158
Preserved length of tibiotarsus	239
Circumference of tibiotarsal midshaft	120
USGS 25031: Partial right hind limb	
Consists of: Proximal right femur and partial right tarsometatarsus	
Tarsometatarsal midshaft breadth	47.1
USGS 16497: Distal elements of both hind limbs	
Consists of: distal fragments of both tibiotarsi, fragmentary left tarsometatarsus, and several complete or fragmentary phalanges	
Preserved width of distal end of left tibiotarsus	~102
Average length of phalanx 1 of digit III measured along axis	96.5
USGS 25024: Distal trochlea of tarsometatarsus (probably digit IV from right side)	
USGS 21915: Proximal end of phalanx 1 of digits II or IV	
USGS 21916: Phalanx (probably phalanx 1 of digit IV)	

FIGURE 2. Mandible of *Diatryma gigantea* (USGS 21862) in (A) left lateral view, (B) dorsal view, and (C) ventral view. D, Caudal view of the left articular region of the same specimen. Hatching designates unrestored broken areas. Outlines of the retroarticular processes have been added based on photographs of AMNH 6169 published by Matthew and Granger (1917).

were presented by Matthew and Granger (1917), K.-H. Fischer (1978), and especially Andors (1988). The new remains belong to at least seven individuals (Fig. 1A). Terminology of morphological structures follows Baumel et al. (1979).

The most significant new specimen is USGS 21862, collected in 1987 by A. Aslan (from USGS Locality D-1532, at about the 485-m level in the Willwood Formation). It includes portions of a skull and fragments of several cervical vertebrae. The mandible is nearly complete (Fig. 2), lacking only the tip of the symphysis, the right tomium (i.e., triturating surface; Fig. 1B), and small parts of the retroarticular processes. No sutures between the bones can be identified with certainty. The lengths of the restored mandible and restored symphysis (Table 1) are conservative estimates.

The right quadrate is virtually complete; only the tip of the orbital process is missing.

Only the ventral half of the left quadrate is preserved. This specimen also includes a skull roof fragment that measures about 100 mm by 115 mm and is about 24 mm at its thickest. It must be comprised of portions of the parietals and frontals, although no sutures are visible. Part of the rim of the right temporal fossa is preserved. The endocranial surface bone has been abraded, revealing a rather dense network of greatly disrupted and deformed bony trabeculae. USGS 21862 also includes the right postorbital process. This well-preserved fragment shows a broken caudal edge, suggesting that it was fused to the zygomatic process and enclosed a temporal fenestra as in American Museum of Natural History (AMNH) 6169 (Matthew and Granger 1917; Andors 1988).

USGS 21862 preserves a large caudal portion of the upper jaw. All sutures are obliterated, and the specimen is crushed laterally (much like AMNH 6169; Matthew and Granger 1917). About 125 mm of the culmen is present, extending almost to the craniofacial articulation. About 75 mm of the left tomium is preserved. It is about 22 mm at its thickest and is somewhat "infolded" as noted by Troxell (1931); presumably it was more bladelike rostrally, as in other specimens (Matthew and Granger 1917; Troxell 1931; K.-H. Fischer 1978; Andors 1988). The caudal portions of the external nares are preserved on both sides. A small part of the sulcus that runs rostroventrally from each naris is present on the left side. On both sides there is evidence of the diarthrodial articulation with the jugal bar (Andrews 1917; Matthew and Granger 1917; Andors 1988). The lateral bar of the upper jaw unit (in the sense of Zusi 1984) is quite thick (about 18–19 mm) in the transverse plane.

Associated with the skull were numerous fragments of cervical vertebrae. Preserved are centra of the axis, C3, and three consecutive centra from a more caudal part of the cervical series. There are numerous neural-arch fragments, none of which seem to fit the centra at hand. By comparison with the photographs in Matthew and Granger (1917), it seems likely that most of the neural-arch fragments pertain to cranial cervicals.

USGS 25008 comprises a right femur and the proximal half of the right tibiotarsus, collected by G. Winterfeld in 1988 (USGS Locality D-1792, about 385 m). The femur is almost complete, lacking only the medial condyle, but is slightly crushed in a few places. The distal portions of both cnemial crests are missing on the tibiotarsus. However, the proximal articulations and fibular crest are relatively well preserved.

USGS 25031 is a damaged proximal right femur and partial right tarsometatarsus collected in 1990 by M. Shekelle (USGS Locality D-1873). The proximal end and trochlea IV are missing from the tarsometatarsus.

USGS 16497 (USGS Locality D-1429, 446 m) includes distal elements of both hind limbs. Distal fragments of both tibiotarsi are present. The left is the better of the two, preserving a portion of the supratendinal bridge. The left tarsometatarsus is fragmented into many pieces that do not fit together well. One of its proximal articular facets is preserved. Trochlea of metatarsals II and III are present, but IV is missing. The distal half of metatarsal I is preserved. Phalanx 1 of digit II lacks the distal end. Phalanx 1 of digit III is preserved virtually complete in both feet. Phalanx 2 of digit III is missing its proximal end. There are a number of other phalangeal fragments, not all of which can be reliably identified.

The remaining specimens consist of isolated foot bones. USGS 25024 (USGS Locality D-1826) is a distal trochlea of a tarsometatarsus, probably digit IV from the right side. USGS 21915 (USGS Locality D-1772, 566 m) is the proximal end of what may be phalanx 1 of digits II or IV, judging from the photographs in Matthew and Granger (1917). USGS 21916 (USGS Locality D-1411, 412 m) is also an isolated phalanx, probably phalanx 1 of digit IV.

Biomechanical Analysis

General Remarks.—Biomechanical studies of form cannot be viewed in isolation. Morphology is influenced by a number of constraints such as those arising from historical, functional, and architectural (formal) factors (Seilacher 1970; Raup 1972; Reif et al. 1985; Gould 1989b). Complete understanding of the

fossils of *Diatryma* cannot be attained without an analysis of each of these factors. Andors (1988, 1989) provided information on historical constraint with his phylogenetic hypothesis of the relationships of *Diatryma*; he considered Anseriformes to be the sister group of *Diatryma* with Galliformes being the sister group of these two. Because both of these orders are primarily herbivorous, phylogenetic inference argues for an herbivorous mode of life for the ancestor of the *Diatryma* clade. However, so many features of *Diatryma* are clearly highly derived relative to these taxa, especially regarding body mass and feeding apparatus, that it is difficult to assess the influence of historical factors. Clearly, dietary shifts occur throughout phylogeny. The second factor, functional constraint, involves the ahistorical influence of the exigencies of current utility on form and is one of the issues at question in this paper. Architectural constraints are considered throughout, implicitly if not explicitly; these involve the material properties of bone and other connective tissues and their adherence to ahistorical laws of physics in their associations with each other and the environment.

~ *Modeling the External Forces of the Upper and Lower Jaws.*—Any static mechanical analysis of bird skulls must start with the work of Bock (1966, 1974). Indeed, Andors (1988) applied aspects of Bock's (1966) analysis to *Diatryma*; his general conclusions agree with ours. Bock (1966) applied free-body analysis to the skulls of birds in his study of the external and internal forces acting on the upper jaw and mandible. Contrary to mammals, in which apposition of triturating surfaces takes place through adduction of the lower jaw only, birds, by virtue of their cranial kinesis, adduct both the upper and the lower jaws. As a result, the upper jaw of many birds can be modeled as a beam operating as a third-class lever (Fig. 3). The craniofacial hinge (or joint) acts as the fulcrum (resulting in a joint reaction force), the pterygoideus musculature acts as a caudoventrally directed force, and the bite point results in a force (the bite force) acting normal to the tomial surface.

There are several assumptions that must be made in such a model (Bock 1966). The most
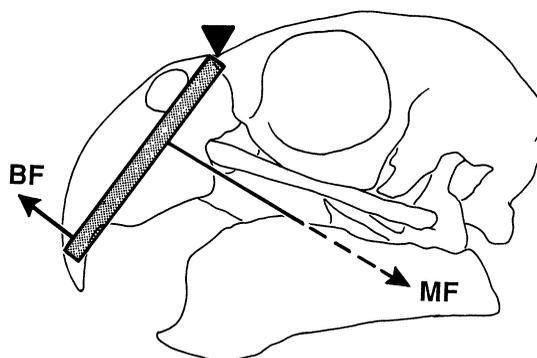
FIGURE 3. Skull of a yellowhead Amazon parrot (*Amazona ochrocephala*, USNM 226872) to demonstrate the avian upper jaw modeled as a third-class lever. The craniofacial articulation (triangle) acts as the fulcrum. A food item (not shown) acts as the resistance, here designated as the bite force (**BF**). The pterygoideus musculature provides the force (**MF**) acting to move the beam against the resistance.

important assumption is that the beam is a rigid unit. That is, the upper jaw must not undergo significant deformation under typical loadings. Bock restricted his analysis to birds with prokinetic skulls and excluded birds with rhynchokinetic skulls. In the former, the rigid upper jaw acts as a unit, whereas in the latter, the upper jaw has flexion zones within it. The skull of *Diatryma* is clearly prokinetic (see Andors [1988] for a discussion of the kinetic system), and the upper jaw must have acted as a rigid unit. It is also assumed that "the mechanical system is completely determined, [and] all force vectors and all movements of parts are known exactly" (Bock 1966: p. 16). This assumption is rarely (if ever) valid in biological systems, and the researcher must make some reasonable estimates (Bock 1966). Another assumption is that the craniofacial hinge should act as a frictionless pin hinge that stores no energy (Bock 1966). Bock regarded the amount of energy stored as negligible.

When a bird—*Diatryma* in this case (Fig. 4)—adducts its upper jaw as in biting, there are two major forces involved: an adductor muscle force (**MF**) and the bite force (**BF**). In birds, the adductor muscle force comes from the pterygoideus musculature, which attaches to the mandible and basicranium caudally and the palatal skeleton rostrally. Contraction of M. pterygoideus retracts the palatal
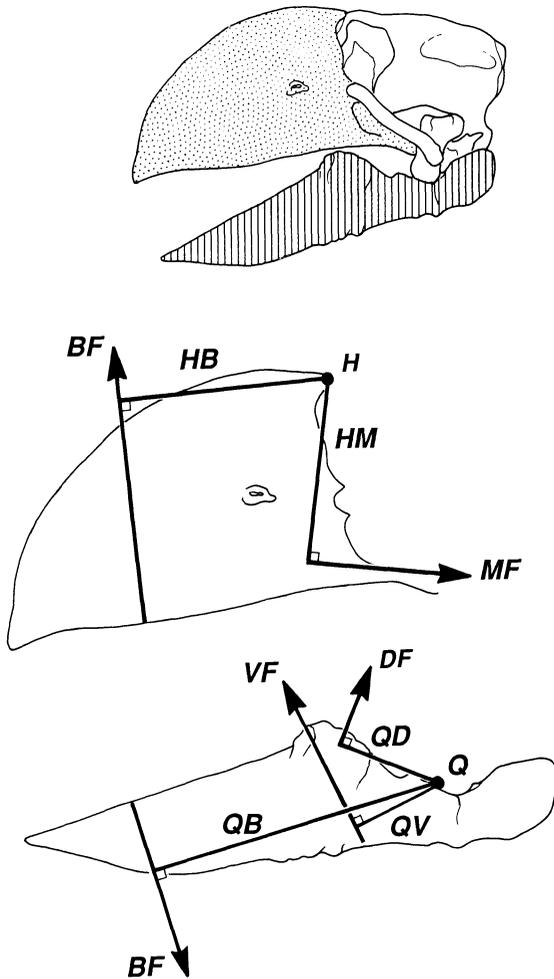
FIGURE 4. Analysis of external forces acting on the jaws of *Diatryma gigantea*. Top, Reference drawing of the entire skull with shaded portions representing the functional units selected for free-body analysis. Middle, Free-body diagram of upper jaw. Bottom, Free-body diagram of lower jaw. Potential mechanisms of increasing bite force are (1) to increase the muscle force exerted by the adductor muscles, (2) to increase the distance over which the adductors act (i.e., increase their moment arms), and (3) to inititate the bite more caudally (i.e., decrease the moment arm of the bite force). Abbreviations: **BF**, bite force; **DF**, muscle force of dorsal (external) adductors; H, craniofacial articulation (axis of rotation for upper jaw); *HB*, moment arm of bite force in upper jaw; *HM*, moment arm of pterygoideus muscle force; **MF**, muscle force of pterygoideus musculature; Q, quadratomandibular joint (axis of rotation for lower jaw); *QB*, moment arm of bite force in lower jaw, *QD*, moment arm of dorsal adductor muscle force; *QV*, moment arm of ventral adductor muscle force; **VF**, muscle force of ventral adductors (pterygoideus).

skeleton, depressing the upper jaw, which rotates about the craniofacial hinge (H). The moment arm (*HM*) of the pterygoideus muscle force is the perpendicular distance from

the axis of rotation (H) to the muscle force vector (**MF**). Thus, the pterygoideus muscles generate a moment, which is the product of the force (**MF**) and the distance (*HM*) over which it acts. Adduction of the upper jaw produces a bite force on a food item held in the jaws. Again following Bock (1966), we view this as the equal and opposite reaction force (**BF**) of the food on the jaw acting perpendicular to the tomial edge. The corresponding moment is the product of **BF** and *HB*. When the jaw apparatus is not moving, we assume static rotational equilibrium. As a convention, counterclockwise moments are considered positive in sign, and clockwise moments negative. If a system is in static equilibrium, then the sum of all moments about the axis of rotation must be zero (Eqs. 1, 2).

$$(\mathbf{MF})(HM) - (\mathbf{BF})(HB) = 0 \qquad (1)$$

or

$$\mathbf{BF} = (\mathbf{MF})(HM)/HB \qquad (2)$$

The analysis presented here seeks to characterize qualitatively the major design elements of the feeding apparatus, and we have simplified the muscle vectors (following Bock 1966) to enhance clarity. Although this model runs the risk of being too simple, it is unlikely that oversimplification unduly influences our major conclusions and offers the advantages of being easy to grasp and carrying few additional assumptions.

Inspection of Eqs. (1) and (2) shows three clear ways to increase bite force (**BF**): (1) increase the pterygoideus muscle force (**MF**), (2) increase the moment arm of the pterygoideus (*HM*), and (3) decrease the moment arm at which the bite force is applied. Pterygoideus muscles force (**MF**) could be increased by changing muscle architecture (see Gans and Bock 1965; Gans and de Vree 1987; Gans 1988) or by increasing muscle mass. The moment arm of the pterygoideus (*HM*) can be increased by increasing the height of the upper jaw. Finally, the moment arm of the bite force (*HB*) can be decreased by initiating the bite in a more caudal position.

Although we cannot accurately estimate the

muscle force (**MF**) of the pterygoideus of *Diatryma* or know its architecture, bony morphology suggests that it was massive. The palatine bones (the rostral attachment of the pterygoideus) are "large, stout bones with a heavy inferior border" (Matthew and Granger 1917: p. 312). Likewise, the caudal attachments of the muscle, the mandible and braincase, are robustly constructed. Being a simple linear quantity, the moment arm of the pterygoideus (*HM*) is much easier to determine. The upper jaw is very high and deep, especially caudally (Fig. 4). Thus, *HM* is a large number.

The actual length of the moment arm of the bite force (*HB*) depends mostly on the behavior of the animal (i.e., where it chooses to initiate the bite) and thus remains unknown. The bite force is least at the rostral tip and increases in the caudal direction as *HB* decreases. It is therefore of some interest that the tomium (of the mandible [Fig. 2B] as well as the upper jaw) is sharp and bladelike rostrally but transversely expanded caudally (see also Troxell 1931), a morphological differentiation that also reflects a functional differentiation: cutting rostrally and crushing caudally (Andors 1988). Thus, the crushing portion of the tomia corresponds to the point along the tomium where biomechanics predicts the bite force to be maximal. However, the transverse expansion of the caudal tomium must represent a compromise. The bite *stress* (force per unit of area) would be higher if the tomium remained bladelike, but a bladelike edge would be in greater danger of failing in transverse shear or bending. The expanded tomial surface distributes the force over a greater area and thus resists failure during heavy biting by reducing those bite stresses that can be generated.

A critical element of Bock's (1966) analysis involves the forces at the craniofacial hinge. In the birds he modeled (crows, woodpeckers, and cardinals), the craniofacial hinge is composed of a very thin, flattened strip of bone. Consequently, this hinge is perhaps the weakest element of the jaw apparatus. Based on the material properties of bones and calculated cross-sectional areas, Bock (1966) concluded that the hinge of his crow would fail

at remarkably low stresses. In fact, his analysis suggests that crows and cardinals cannot exert large bite forces at the very caudal part of the bill, because the craniofacial hinge would fail in shear. Thus, there is an apparent compromise between bite force and hinge shear stress.

Given the huge bite forces that *Diatryma* could generate, how did its craniofacial hinge resist catastrophic failure? It is unlikely that a bird so large could join the heavy upper jaw unit to the cranial unit with bone as thin as that found in the birds that Bock (1966) studied. Shear could be resisted by increased cross-sectional area of bone at the hinge, but there are constraints on how thick a sheet of bone can get before it will no longer bend like a hinge. Some large birds such as ostriches and the Cretaceous diving bird *Hesperornis* exhibit one solution to this problem in that their hinges consist of two (or rarely three) layers of thin bone, separated by a layer of connective tissue, resulting in a plywoodlike construction (Bühler 1981; Bühler et al. 1988). Although the shear strength of such a biological material has not been tested, it is likely to be much higher than the single lamina of crows and cardinals. Another solution appears to be found in the larger parrots. In these birds, many of the flexion zones seen in other birds—including the craniofacial hinge—have become syndesmoses or even diarthroses (Fig. 9A; Bühler 1981). It is not clear if these changes are responses to jaw forces, a consequence of large size, or some combination of these two. It is clear, however, that these large skulled forms can produce tremendous forces: W. J. Beecher (1962: p. 21) reported that the "black cockatoo, *Calyptorhynchus*, easily cracks ivory nuts with its massive bill—a task which humans may accomplish only with a hammer and anvil!"

Although the craniofacial hinge is not completely preserved in any known specimen, we suggest that *Diatryma*, like large parrots, probably had a diarthrodial craniofacial articulation. It is difficult to imagine that even the multilayered hinge system of ostriches and *Hesperornis* could be functional at such a great size. *Diatryma* also resembles large parrots in exhibiting a diarthrodial articulation

between the upper jaw and the jugal bar (Fig. 1; see also Andrews 1917; Matthew and Granger 1917; Andors 1988). Perhaps, as noted, transformation of flexion zones to syndesmoses or diarthroses is a size-scaling phenomenon, and resistance to shear stress is a beneficial byproduct. The *in vivo* response of a diarthrodial craniofacial hinge to shear stress is unknown, but the connective tissue support of a joint capsule likely confers additional stability.

Bock (1966) modeled the mandible in much the same way as the upper jaw, and we apply this model here to *Diatryma* (Fig. 4). Whereas in the upper jaw only one major muscle adducted the jaw, two complex sets of muscles adduct the lower jaw: the pterygoideus musculature (**VF**) and a suite of muscles termed the "dorsal adductors" (**DF**) by Bock (1966). The bite force (**BF**) is as before. The axis of rotation (Q) is the quadratomandibular articulation. The moment arms to the various force vectors (*QV*, *QD*, *QB*) again are perpendicular distances drawn from the jaw joint (Q). If the jaw is in static equilibrium, the sum of the moments equals zero (Eqs. 3, 4).

$$(\mathbf{DF})(QD) + (\mathbf{VF})(QV) - (\mathbf{BF})(QB) = 0 \qquad (3)$$

or

$$\mathbf{BF} = [(\mathbf{DF})(QD) + (\mathbf{VF})(QV)]/QB \qquad (4)$$

The implications of Eq. (4) are similar to those of Eq. (2). Increasing the force of the adductor muscles (**DF** and **VF**), increasing the length of their moment arms (*QD* and *QV*, respectively), and/or decreasing the moment arm of the bite force (i.e., initiate the bite at a more caudal position on the mandible) all have the effect of increasing bite force (**BF**).

As with the upper jaw, *Diatryma* manifests the mandibular characteristics expected in an animal emphasizing large bite forces. Because part of the caudal attachment of the pterygoideus muscles is to the braincase, their ability to adduct the lower jaw (**VF**) may have been somewhat less than to adduct the upper jaw (**MF**). However, the development of the "dorsal adductors" (**DF**), in particular M. adductor mandibulae externus, is extraordinary,

as remarked upon by Matthew and Granger (1917), Troxell (1931), and Andors (1988). The external adductors extended far up onto the skull roof, excavating a temporal fossa. The postorbital and zygomatic processes were fused, enclosing a temporal fenestra and serving as additional area for muscle attachment (Figs. 1, 4). Furthermore, the external adductor muscle scars on the mandible are very rugose and extensive, extending from almost as caudal as the quadrate articulation all the way rostrally to the caudal border of the mandibular symphysis on the ventral surface of the mandible (Figs. 2, 4).

The moment arm of the pterygoideus musculature (*QV*) can be lengthened by deepening the mandible. By relative or absolute measures, the lower jaw of *Diatryma* is very deep. Furthermore, shifting or extending the dorsal adductor force vector (**DF**) rostrally along the mandible increases the moment arm of the dorsal adductors (*QD*) and hence its mechanical advantage (Greaves 1988b). As mentioned, the adductor mandibulae externus muscle scar extends rostrally up to the mandibular symphysis of USGS 21862, a point that is actually rostral to portions of the tomium. Finally, as in the upper jaw, it seems likely that the thickened caudal portion of the tomium (Fig. 2B) was a site of great force application, with bite force decreasing rostrally as its moment arm increases.

Unlike the craniofacial hinge, which was the "weak link" in the upper jaw adduction system, the quadratomandibular joint is a very complex and heavily reinforced diarthrosis. The quadrate is a stout, pillarlike element (Fig. 1) capable of withstanding considerable compressional loading. Bock's (1966) analysis suggested that shear stress at the joint was not significant.

Structures acting to prevent dislocation of the balancing-side jaw articulation are found in many animals that engage in heavy biting (Bramble 1978; Druzinsky and Greaves 1979; Greaves 1988b). In *Diatryma* there is evidence for hypertrophy of the ligamentous stabilization of the jaw joint. In most modern birds, the medial jugomandibular ligament is a thick ligament associated with the articular capsule

(Bühler 1981) that runs from the lateral surface of the jugal bar around the caudal aspect of the quadrate to attach to the caudodorsal surface of the medial process of the mandible (Lebedinsky 1921; Bock 1964). Goodman and Fisher (1962) noted that this ligament is larger in anseriforms that emphasize biting than in those that do not. In *Diatryma* the mandibular attachment of the medial jugomandibular ligament is a large oval pit on the caudal surface of the medial process of the mandible resembling the fovea capitis femoris (Fig. 2D). Formation of a pit is unusual, and the ligament attaching to this pit must have been very stout. The dorsomedial lip of the pit is also expanded for ligamentous attachment. A dorsal crest running medially from the articulare pneumatic foramen to the tip of the medial process is probably for the occipitomandibular ligament, another stabilizer of the jaw joint. These ligaments, in conjunction with the muscles stabilizing the joint, suggest that *Diatryma* had soft-tissue mechanisms to resist dislocation of the jaw articulation. It is also possible that *Diatryma* decreased stress at the balancing-side jaw joint by having asymmetrical adductor recruitment (i.e., decreased balancing-side adductor activity) as suggested by Dessem (1989) for dogs.

In summary, a biomechanical model of bird skulls based on beam theory makes certain predictions about the structure of a skull "designed" to optimize bite force (Bock 1966). *Diatryma* exhibits virtually all of those predicted features. Combined with the huge absolute size of the head, these findings suggest the application of enormous bite forces, especially in the caudal part of the bill.

The Mandibular Symphysis. —Besides its overall massiveness, the most distinctive characteristic of the mandible of *Diatryma* is its elongate, thick, and fused symphysis comprising about half the total mandibular length (Fig. 2). Such a long symphysis is unusual in birds, and is apomorphic with respect to any proposed outgroups. Despite the remarkable diversity of symphyseal morphology, there has been very little functional analysis of this structure in birds. Mandibular symphyseal biomechanics, however, has been a subject of

great interest to mammalogists (e.g., Beecher 1977, 1979; Hylander 1984, 1985; Greaves 1988a). Although developed for mammals, the models are based on physical principles of general applicability and can be applied to birds as well.

All neornithine birds have a fused mandibular symphysis. Although it is often argued that a fused symphysis evolved to improve force transmission from one side (the balancing side) to the other (the working side), Greaves (1988a) cautioned that force transmission occurs with little attenuation across the patent symphyses of many mammals (because of particular ligaments, etc.; see Scapino 1981). In fact, Greaves (1988a) noted that a fused symphysis is something of an expensive liability that, once present, requires structural modification (e.g., buttressing) to resist failure. *Diatryma* inherited its fused symphysis; thus, its unusual symphyseal morphology may reflect attempts to buttress it against the stresses encountered during use of the massive feeding apparatus.

Six major types of mandibular symphyseal stresses can be hypothesized (Beecher 1979; Hylander 1984, 1985). These include three kinds of symphyseal bending caused by (1) medial transverse bending of the rami, (2) lateral transverse bending of the rami, and (3) twisting of the rami around their longitudinal axes; two kinds of shear: (4) dorsoventral shear and (5) rostrocaudal shear; and (6) transverse symphyseal torsion.

The first three symphyseal stresses result from stresses in the mandibular rami (corpora). If the mandible is modeled as a U-shaped curved beam (see below), loading of the rami translates into stress at the symphysis. Symphyseal stress resulting from medial transverse bending of the rami is easy to envision in birds (Fig. 5) because of the fiber direction of the portions of the pterygoideus musculature that originate medially from the palatine bones and insert on the rami. Contraction of this portion would tend to bend the ramus medially. At the symphysis, such bending would cause compression along the lingual part of the symphysis and tension along the labial part. Medial transverse bend-
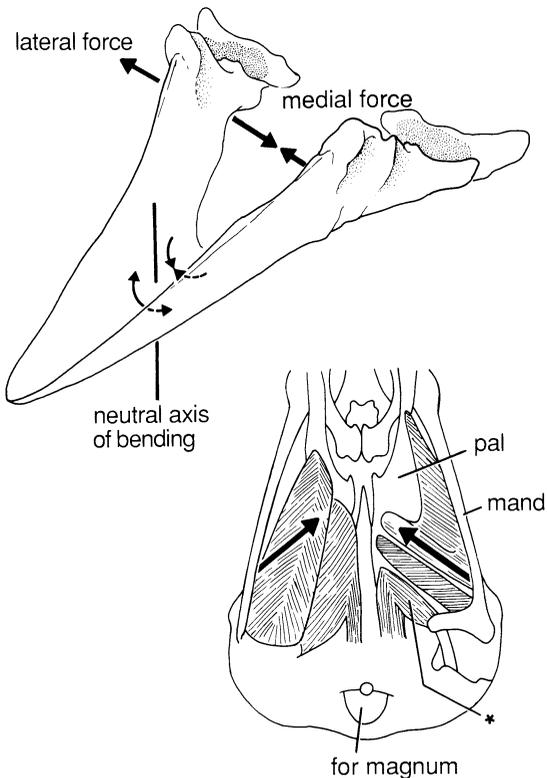
FIGURE 5. Top, Symphyseal stresses in the mandible of *Diatryma gigantea* resulting from medial and lateral transverse bending of the rami. The mandible is in left rostrodorsolateral view. The articular surfaces are stippled. The rostrocaudal location of the neutral axis is arbitrary. The arrows flanking the neutral axis pertain to symphyseal stresses under medial transverse bending: tension labial to the axis, compression lingual to the axis. The direction of the stresses reverse under lateral bending: compression labially, tension lingually. Bottom, Ventral view of skull of a common crow, *Corvus brachyrhynchos*, with pterygoideus musculature added (simplified from Bock 1964) to show one of the sources of medial transverse bending of the rami. The arrows show the rostromedial pull of the pterygoideus on the mandibular rami. The asterisk designates the portion of M. pterygoideus that attaches to the medial process of the mandible and can effect lateral ramal bending. Abbreviations: *for magnum*, foramen magnum; *mand*, mandible; *pal*, palatine bone.

ing probably is important in potentially all birds.

Lateral transverse bending in birds (Fig. 5) can result from a number of different stress regimes. Ironically, the pterygoideus can effect lateral as well as medial bending. In some birds, when the part of the pterygoideus that attaches to the medial process of the mandible (* in Fig. 5) contracts, it tends to act like a bowstring in bending the ramus laterally (Burton 1977; Bühler 1981). Lateral transverse bending also may result from a regime similar to that in monkeys (Hylander 1984): when the working side is fixed during biting, the lateral component of the balancing-side external adductors pulls the balancing-side ramus laterally. Although most if not all birds are isognathous, Ziswiler (1965) reported that in at least some cardueline finches the mandible undergoes pronounced mediolateral movements when husking seeds; such movements could cause lateral transverse bending. Lateral bending also could result if the animal moved its head and jaws laterally against resistance, as when tugging against a food item held stationary by its feet. The principal symphyseal stresses in lateral transverse bending are lingual tension and labial compression.

Symphyseal bending caused by twisting of the rami results from the tendency of the external adductors to evert the ventral borders of the rami, especially during biting at the rostral extremity of the jaws (Hylander 1984); such bending causes tension ventrally and compression dorsally (Fig. 6A).

Dorsoventral symphyseal shear results from bilateral contraction of the adductor muscles during unilateral biting, which tends to move the balancing-side ramus dorsally relative to the working-side ramus (Fig. 6B). In this type of shear, the principal tensile stresses are oriented dorsally and laterally about 45° toward the balancing side, and compressive stresses are 90° to this (Hylander 1984). Transverse symphyseal torsion is a little more complex. The symphysis can be twisted under the same loading regime as for dorsoventral shear (Fig. 6B). Because during bilateral contraction the balancing-side adductors do not encounter the food item, they attempt to adduct the ramus past the equivalent point, thus setting up twisting moments in the symphysis. The principal stresses are oriented as in dorsoventral shear on the lingual side but oppositely on the labial side (Hylander 1984). In rostrocaudal shear, the balancing-side ramus moves caudally relative to the working side (Fig. 6C), with the principal tensile stress being angled about 45° caudally and toward the

balancing side. Rostrocaudal shear is probably important in birds that engage in tugging or tearing behaviors.

Hylander (1984) reported that transverse bending and dorsoventral shear and/or transverse torsion were the most important stresses at the symphysis during mastication in macaques. During incision, dorsoventral shear and bending caused by longitudinal twisting of the rami were most important. Birds do not masticate and do not have incisors. Nevertheless, mastication is an acceptable analogue for birds that repeatedly develop large bite forces at the caudal portions of their bills such as many seed-eaters and perhaps *Diatryma*. Incision is probably a good analogue for bill use in birds that manipulate food items with the tips of their bills. In fact, Greaves (1988a) regarded the application of large incisal bite forces to small food items as a potentially important factor in the development of symphyseal fusion in mammals.

Hylander (1984, 1985) discussed the potential responses to these stresses. As mentioned above, mandibles subjected to transverse bending loads (either medial or lateral) can be modeled as curved beams (Hylander 1984, 1985). The flexure formula for bending stress (σ) in straight beams must be modified for curved beams (Eq. [5]; see Hylander 1984, 1985):

$$\sigma = (K)(\mathbf{M})(c)/I \qquad (5)$$

where $\mathbf{M}$ is the bending moment, c is the distance from the outer fiber of the beam to the neutral axis of bending (which is where tension and compression are both zero and which coincides with the centroid of the section), and I is the second moment of area (moment of inertia). K is the correction factor for the curved beam and relates to the radius of curvature of the beam and the distance from the surface closest to the center of curvature to the neutral axis. In straight beams, the stress concentrations are linearly distributed from one side of a beam to the other. However, in curved beams, because of K, the stress concentrations are not rectilinear, with
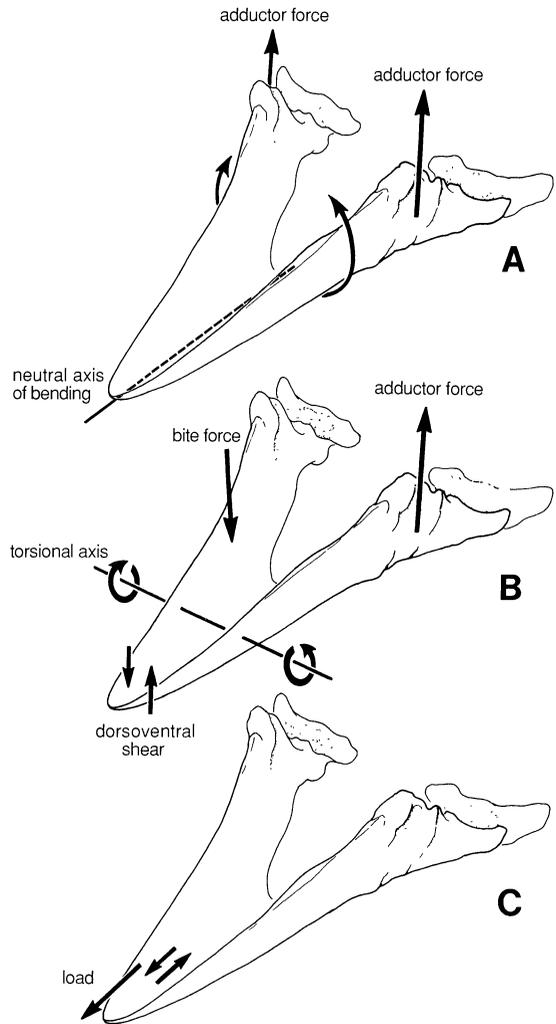
FIGURE 6. Symphyseal stresses in the mandible of *Diatryma gigantea* resulting from bending due to eversion (longitudinal twisting) of the rami (A), transverse symphyseal torsion and dorsoventral shear (B), and rostrocaudal shear (C). Same view as in Fig. 5. A, Contraction of the external adductors, which wrap around the ventral surface of rami, tend to evert the rami, thus setting up tension ventral to the neutral axis and compression dorsal to it. B, Asymmetrical biting produces a loading regime tending to twist the symphysis transversely and cause the working side of the symphysis to shear dorsoventrally past the balancing side. C, Asymmetrical tensional loads or perhaps forces resulting from streptostyly (not shown) tend to cause one side of the symphysis to shear rostrocaudally past the other.

stress along the concave surface being greater than that along the convex surface. Thus, one would expect mechanisms to reduce the bending stress (σ) along the concave (lingual) surface. This may be accomplished by de-

creasing the moment (**M**) or *c* or by increasing the second moment of area (*I*).

Lateral and medial transverse bending is countered by increasing the labiolingual thickness of the symphysis (Hylander 1984, 1985). Labiolingual thickening has the effect of increasing the cross-sectional area of bone in the plane of bending, thus increasing the second moment of area (*I*). Furthermore, increasing the labiolingual thickness of the symphysis (which also can be envisioned as extending the symphysis caudally) shifts the neutral axis caudally, reducing the moment arm of the adductor musculature and hence its bending moment (**M**). However, it also increases the distance from the outer surface to the neutral axis and hence increases *c*. Thus, large *I* clearly reduces bending stress, but there is a tradeoff between reducing **M** and increasing *c*. The balance of this tradeoff is unknown in *Diatryma*.

In symphyseal bending caused by twisting of the mandibular rami, eversion of the ventral borders of the rami tends to cause the ventral surface of the symphysis to fail in tension. The simplest way to resist such failure is to increase *I* by deepening the symphysis dorsoventrally. Hylander (1984, 1985), however, noted that the most efficient way (in terms of use of materials) to increase *I* is by adding bone to the lingual surface of the ventral border, thus creating an asymmetrical cross section. An asymmetrical section reduces tension more than compression because such a distribution of bone shifts the neutral axis ventrally (stress is proportional to the distance of the outer surface to the neutral axis). This reduction is critical because bone is weaker in tension than compression.

Whereas shape is important in responding to bending stresses, shear stresses require simply an increase in the cross-sectional area of bone in the plane of shear (Hylander 1984, 1985). Thus, increasing vertical symphyseal depth should be important in countering dorsoventral shear, and increasing the symphyseal length should be important for rostrocaudal shear.

In transverse symphyseal torsion, the cross section of an elliptical beam such as a mandibular symphysis is maximally stressed at the outer surface of the ellipse's minor axis. In most birds, the symphysis is rostrocaudally longer than dorsoventrally deep such that the minor axis is approximately vertical. Ideally, the best response to torsion is a circular cross section, but a cylindrical symphysis may not be biologically possible because of other constraints (apposition of upper and lower tomia, movement of the tongue, etc.). Beams loaded in torsion tend to fail in shear, with the orientation of the principal shear stresses being 45° to the axis of the beam (Shigley 1976). If a mandibular symphysis is modeled as a transverse beam, then the following relation (Eq. [6]) for torsional shear stress pertains (Shigley 1976):

$$\tau = \mathbf{T}\, r/J, \qquad (6)$$

where torsional shear (τ) is equal to the product of the external twisting moment (**T**) and the distance from the neutral axis to the surface (*r*, the radius if the beam has a circular section) divided by the polar moment of inertia (*J*). This equation obviously is similar to the flexure formula (Eq. [5]). *J* is the second moment of area with respect to an axis perpendicular to the plane of section and is thus a measure of the torsional properties (e.g., stiffness) of a beam. *J* is an overestimate for noncircular sections such as a mandibular symphysis (Piziali et al. 1976; Miller and Purkey 1980), but the following relationship remains true: $J \propto I_x + I_y$, where I_y is the second moment of area of the major axis of an ellipse (the rostrocaudal dimension of an avian mandibular symphysis) and I_x is the second moment of area of the minor axis (the dorsoventral dimension). Torsional shear (τ) may be reduced by increasing the polar moment of inertia (*J*). Extending the symphysis caudally between the rami increases *J* by increasing the second moment of area in the rostrocaudal direction (I_x). Within constraints, increasing I_y also increases *J* and helps produce a more circular cross section. As with the flexure formula, lengthening the symphysis results in a compromise between the beneficial effects of decreasing **T** (be decreasing the moment arm) and the detrimental effects of increasing *r*.

In summary, the problems posed by differ-

ent stresses may be solved by developing similar morphologies. For example, increasing the length of the symphysis (adding bone to the ventrolingual border) is the predicted response to (1) medial and lateral transverse bending, (2) bending caused by twisting of the rami, (3) rostrocaudal shear, and (4) transverse symphyseal torsion. Increasing the depth of the symphysis is the predicted response to dorsoventral shear and transverse symphyseal torsion.

The mandible of *Diatryma* conforms well to a model of a symphysis that is subjected to large bending moments. Its symphysis is remarkably long, and virtually all of the symphyseal bone is located on the lingual aspect. This situation is probably a response to medial and lateral transverse bending. The large pterygoideus musculature of *Diatryma*, involved as it is in powerful adduction of both upper and lower jaws, must have imparted considerable medial bending stress to the rami. Lateral transverse bending is not hard to envision in *Diatryma*, especially if it employed lateral ripping movements of the head. Furthermore, unilateral biting loads the skull asymmetrically and produces the lateral bending moments described above. Transverse bending was virtually ubiquitous in macaques, as Hylander (1984) had some difficulty in experimentally isolating it from other loading regimes. Transverse bending (medial and/or lateral) may be among the more important stresses on avian symphyses as well.

The symphyseal morphology of *Diatryma* is also consistent with bending caused by twisting (eversion) of the mandibular rami resulting from the pull of the external adductors. In *Diatryma*, eversion of the rami was accentuated by the insertion of the external adductors, which wrapped around the ventral margin all the way to the midline (manifested by the prominent muscle scars; Fig. 2). The great ventrolingual extension of its symphysis may be a response to this stress.

Another factor that may have contributed to the long symphysis in *Diatryma* is rostrocaudal shear. Although Hylander (1984, 1985) did not regard this as important in macaques, it may be more important in birds. Quadrate

streptostyly, which involves rostrocaudal movements of the mandibular processes of the quadrates, may impart significant moments (Zusi 1967). More importantly, birds that engage in tearing behaviors with the tips of their bills, such as raptors (and perhaps *Diatryma*), may exert asymmetrical tensile forces on the bill tip when pulling the head and neck caudally against resistance. The asymmetrical nature of these forces could produce rostrocaudal shear at the symphysis.

Most birds appear poorly prepared to handle large forces that would tend to shear the symphysis dorsoventrally. Their symphyses are generally long and low, with little cross-sectional area disposed to resist vertical shear. Some birds, however, do demonstrate some dorsoventral depth to the symphysis. Among these are the larger seed-eating birds, which probably develop vertical shearing stresses during nut cracking. *Diatryma* also shows considerable dorsoventral symphyseal thickness, attaining dimensions of at least 32 mm. Furthermore, the great length of the symphysis over which the shear would be distributed would tend to reduce the chance of failure.

The symphyses of few birds approximate the circular cross section that would tend to resist pure transverse torsion. However, many birds, especially those delivering large bite forces (granivores, some folivores, some raptors) have the relatively thick, long symphyses that promote large polar moments of inertia. *Diatryma* clearly fits in this class, and would have been able to withstand the large torsional moments imposed by heavy biting.

The Mandibular Rami.—Bock and Kummer (1968) modeled the mandibles of birds (specifically crows) as an I-beam. They concluded that the very elliptical cross section of avian mandibular rami (a long, vertical major axis and a short, horizontal minor axis), combined with the concentration of cortical bone dorsally and ventrally, suggest considerable resistance to sagittal bending of the rami. Resistance to mediolateral bending depends on the thickness of the walls and on the presence of an intramandibular hinge.

Diatryma clearly displays the features Bock and Kummer (1968) predicted for a rigid man-
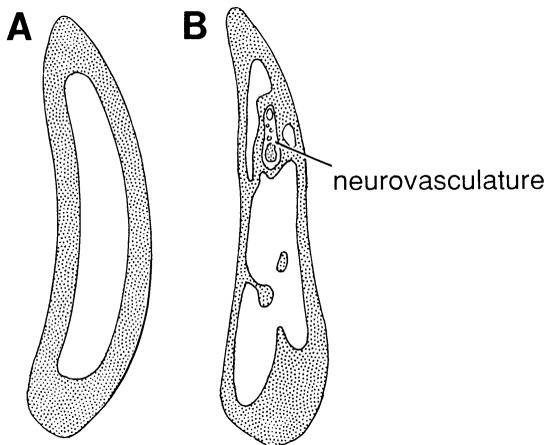
FIGURE 7. Cross sections through the left mandibular rami of (A) *Diatryma gigantea* and (B) a common crow, *Corvus brachyrhynchos* (B), viewed rostally (drawn to unit height). Note that the sections are dorsoventrally tall with thick dorsal and ventral cortices, suggesting considerable sagittal bending strength. The lateral and medial cortices of *D. gigantea* are also thick, indicating strength against transverse bending loads. Furthermore, the trabecular bone of *Diatryma* (not shown) is relatively much more extensive, conferring additional strength. (B redrawn from Bock and Kummer 1968.)

dibular ramus (Fig. 7; see also Andors 1988). The dorsal and ventral cortices are thickened relative to the compact bone in the walls. In agreement with the conclusions reached above regarding the symphysis, the ramus was not likely to bend dorsoventrally under large bite forces. The rami of USGS 21862 are also thick mediolaterally, and there is clearly no intramandibular hinge (a bending zone found in some birds that enhances transverse bending; see Bühler 1981). Thus, the rami appear rigid with respect to transverse bending loads. In fact, the substance of the bone of USGS 21862 is a remarkably dense lattice of trabecular bone, far from the largely open space bridged by a few trabeculae observed in other birds. It should be noted that despite the great overall length of the mandible, the ramus itself is quite short, principally because of the elongate symphysis. There is no appreciable length of the ramus between external adductor muscles and symphysis.

Summary of Biomechanical Analyses.—The results of the above analyses, adapted largely from models developed by Bock (1966) and Hylander (1984), all point to the presence of a very powerful feeding apparatus in *Diatry-*

ma. The upper jaw was massively constructed, as were the pterygoideus muscles that brought it into apposition with the lower jaw. The tall profile of the upper jaw assured a long moment arm of these muscles and thus increased the moment of the adductors. The tomia at the caudal portion of both jaws were expanded into crushing surfaces, precisely where biomechanics predicts the largest bite forces. The mandible itself was adducted by an extensive and rostrally situated adductor mandibulae muscle, both of which suggest large bite forces. The large pterygoideus, by virtue of the deep mandible, exerted its force via a long moment arm.

The mandibular symphysis of *Diatryma* is remarkable for both its thickness and its length. By deposition of bone in the plane of the principal stresses, the mandible was capable of resisting failure because of medial and lateral transverse bending, bending caused by twisting of the rami, and rostrocaudal shear. The symphysis was thickened vertically, perhaps in response to the dorsoventral shear engendered by hard biting. Such biting forces also would have tended to shear the symphysis in transverse torsion, a stress that was resisted by the large polar moments of inertia of the long, thick symphysis. Finally, the mandibular rami were rigid members, constructed to resist both vertical and transverse bending loads.

Discussion

The foregoing analysis clearly demonstrates that *Diatryma* possessed a formidable jaw apparatus capable of delivering and withstanding large bite forces. How did *Diatryma* use this structure? Assuming that the massive, heavy skull of *Diatryma* was more than a display organ for behavioral interactions, one safely can conclude that it was primarily adapted for use in feeding. Potential resources known to have occurred during the Willwood Eocene include molluscs, fruit, seeds, foliage, vertebrates.

Diatryma may have fed on a variety of invertebrates such as molluscs or large crustaceans. Its huge jaws easily would have crushed the shells or exoskeletons of these invertebrates. However, most of the known early

Eocene molluscs are relatively small (Hanley 1976), and it is unlikely that they composed a large part of the diet of *Diatryma*. *Diatryma* could have easily taken fruit. Large frugivorous birds such as cassowaries and emus, however, swallow the fruits whole. Assuming *Diatryma*, with its huge gape, also swallowed fruits whole, then the powerful jaw apparatus could not be an adaptation for frugivory.

However, fruits contain seeds. Morse (1975) and Welty and Baptista (1988) discussed a number of different strategies for eating seeds, such as swallowing them whole (seeds are then subdivided in the muscular gizzard) as in many galliforms and small gruiforms, opening them with blows delivered by the beak as in corvids and some other passeriforms, and husking or cracking the seeds with the bill as in many fringillids, ploceids, estrildids, and psittacids. The morphology of the last group, parrots and finches (Fig. 8), is similar to that of *Diatryma*. Nut-cracking has received considerable attention (e.g., Ziswiler 1965), particularly in hawfinches and grosbeaks of the genus *Coccothraustes* (Fig. 8B; Sims 1955; Mountfort 1957). The skulls of these birds exhibit many of the same features found in *Diatryma*: hypertrophied musculature; massive, rigid, and dorsoventrally deep upper and lower jaws; vertically and especially caudally expanded mandibular symphysis; and the replacement of flexion zones with syndesmoses and diarthroses. These birds, which generate large bite forces and load their skulls asymmetrically, provide empirical confirmation of the biomechanical model.

Diatryma could have been a gigantic nut-cracker, using its immense bill to open gigantic seeds. If a 55-g hawfinch with a 35-mm skull can crack olive pits that materials-testing machines required forces of 470 N–700 N (100 lb—160 lb) to crush (Sims 1955), then the forces delivered by *Diatryma* must have been sufficient to crack any nut in the flora. Recall also the statement from W. J. Beecher (1962) quoted above regarding nut-cracking in cockatoos. On the basis of the diversity of the flora, seeds were probably abundant and encompassed a size range comparable to that seen in modern floras (Wing 1980, pers.
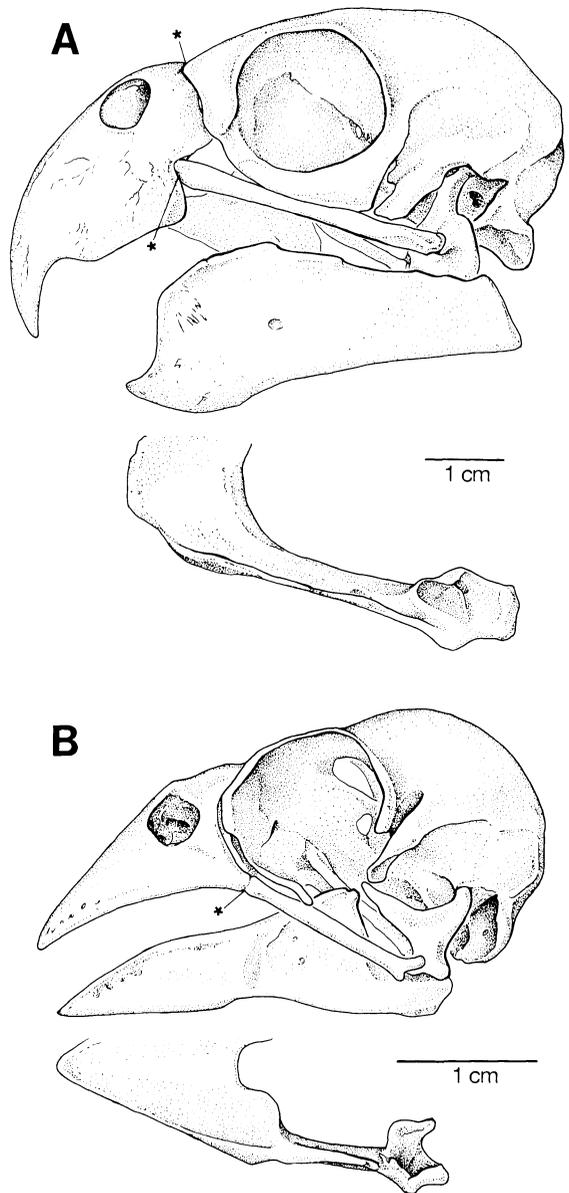
FIGURE 8. Skulls of birds that crack seeds, in left lateral view and their lower jaws in dorsal view. A, Yellowhead Amazon parrot, Psittacidae, *Amazona ochrocephala* (USNM 226872). B, Evening grosbeak, *Coccothraustes vespertinus* (USNM 561107). These birds generate large dorsoventral bite forces and show many of the skull features observed in *Diatryma*. The asterisks denote diarthrodial or syndesmotic articulations that are typically flexion zones in other birds. Scale bars equal 1 cm.

comm.). However, unless *Diatryma* was routinely cracking coconut-sized seeds, the immense size of the heavy skull seems excessive; birds that crack large seeds today (e.g., large parrots) do so with much smaller skulls. Thus,

the skull appears "too large" for Diatryma to have been principally a seed eater. A better strategy for a large-bodied seed eater would be to swallow whole as many seeds as possible and transfer the role of seed-cracking from skull to gizzard, which is the strategy taken by turkeys and many other birds (Welty and Baptista 1988).

Watson (1976) and especially Andors (1988, 1989) proposed that Diatryma was predominantly a folivore. Folivory (including the consumption of leaves, grass, buds, and other "green foliage") is very unusual among birds (Morse 1975). Among the birds that include foliage as part of their diet, screamers (Anseriformes, Anhimidae; Fig. 9A), hoatzins (Opisthocomus hoazin, Cuculiformes; Fig. 9B), and owl parrots (Strigops habroptilus, Psittaciformes, Psittacidae) are primarily folivorous (Morse 1975; Morton 1978). Other important folivores are some ratites, some geese (Anseriformes, Anatidae; Fig. 9C; see Goodman and Fisher 1962), various galliform birds, plantcutters (Passeriformes, Phytotomidae), and several rails (Morse 1975). Many of these species (Fig. 9) show some of the features that in Diatryma were correlated with large bite forces. In most cases, the upper jaw is deep caudally, and the naris is small and occupies little space in the rigid upper jaw. The adductor muscles of both jaws are enlarged in at least folivorous geese (Goodman and Fisher 1962) and also some rails (e.g., Porphyrio spp.). The mandible is quite deep in some folivores such as the anatid folivores (Fig. 9C), Porphyrio (Fig. 10A), and Strigops, but not markedly so in the others. In fact, the deep mandible of at least the geese and Strigops may result more from plesiomorphy than from adaptation (i.e., they inherited their deep mandibles from nonfolivorous ancestors). In many of the folivores (e.g., hoatzins, plantcutters, screamers, geese), portions of their tomia display a transverse expansion, as in Diatryma. Thus, avian folivores present a few of the characteristics associated with large bite forces. These results agree well with those of Beecher (1979) who, after surveying mammalian mandibular symphyses, concluded that chewing leaves demands larger bite forces than frugivory or insectivory.

Mammals and birds, however, approach herbivory in different ways. Mammalian folivores masticate, whereas birds do not. Mammals store plant material in their muscular cheeks and often spend great amounts of time in oral processing. Mastication involves large stresses. Hence the skulls of herbivorous mammals are heavily buttressed. Birds, however, lack muscular cheeks, and much (perhaps most) of the food would shear off and fall on the ground. Consequently, birds have transferred the grinding function from mouth to gut where the muscular gizzard breaks down resistant food items. The skulls of herbivorous birds tend to be cropping organs. Goodman and Fisher (1962) showed that among anseriforms, herbivores have somewhat more robust skulls than nonherbivores, suggesting that cropping vegetation does entail relatively large stresses.

Folivory in birds has been studied most extensively in hoatzins, which are clearly the most specialized for eating green foliage (e.g., they possess foregut fermentation; Grajal et al. 1989). Hoatzins crop vegetation and swallow the leaves whole, with little or no oral subdivision, instead subdividing food items in a very muscular crop rather than the gizzard (S. D. Strahl pers. comm.; Grajal et al. 1989). Consequently, their skulls are not highly modified or heavily buttressed against stresses encountered in biting (Fig. 9B). Their mandibles are relatively lightly built with a rostrocaudally very short symphysis. The mandibles of anhimids (Fig. 9A) and plantcutters, other primarily folivorous groups, also are not particularly robust, and have short symphyses like hoatzins. Although the upper jaws of anhimids are somewhat tall caudally, they are remarkably open structures that do not seem well suited to developing large bite forces (Fig. 9A).

The skull of the folivorous New Zealand flightless rail or takahe, Porphyrio (=Notornis) mantelli, provides a better comparison with Diatryma (cf. Fig. 10A and 10B) and has been used to suggest that Diatryma was a grass and leaf eater (Watson 1976; Andors 1988). Takahes eat especially tough plants (grass and leaves) and, perhaps more importantly, engage in behaviors that stress the feeding ap-

paratus, such as stripping grass stems (Greenway 1958; Williams 1960). Species of *Porphyrio* (Fig. 10A) all tend to have deep mandibles with prominent adductor muscle scars, relatively long symphyses, and tomia with rostral cutting and caudal crushing surfaces (Andors 1988). Likewise, they have rigid, deep upper jaws. In this case these features are apomorphic (having evolved from ancestors with lightly built, schizorhinal, rhynchokinetic ancestors) and may represent adaptation.

Takahes are also large for rails (Greenway 1958). However, they are not gigantic, and are diminutive (about 45 cm tall) when compared to *Diatryma* (about 215 cm tall). Furthermore, their skulls are similar only if size is divorced from shape. *Diatryma* has a skull five times longer than that of a takahe; hence, a similar diet may not be indicated. One obvious observation is of critical importance: the material properties of the food items (grass and leaves) are independent of the body mass of the animals consuming them. At a certain point—perhaps represented by takahes—the skull becomes massive and powerful enough to take tough foliage; extending such trends further to the size of *Diatryma* results in a considerable waste of energy to maintain the metabolically expensive bone with no added benefit if similar foliage is taken. If *Diatryma* ate grass or leaves, then its skull was constructed with extraordinarily high safety factors (Alexander 1981; Biewener 1982; Currey 1984).

All of the huge birds of the past several hundred years have been partly, if not strictly, herbivorous (Morse 1975; Davies 1976; Feduccia 1980). Ratites, including the extinct moas and elephant birds, encompass a body size range that includes *Diatryma* (Fig. 11), but compared to them, *Diatryma* had an enormous head (Fig. 12). Although *Diatryma* is only intermediate in height between the smaller (rheas and cassowaries) and larger (ostriches, moas, and elephant birds) ratites, its head is 50% longer and twice as tall as that of the largest elephant bird (Fig. 11), which is typically viewed as a grazer or browser (Wetmore 1967; Feduccia 1980) and dwarfs that of ostriches, the largest living bird. The feeding apparatus of ratites (other than kiwis) is rath-
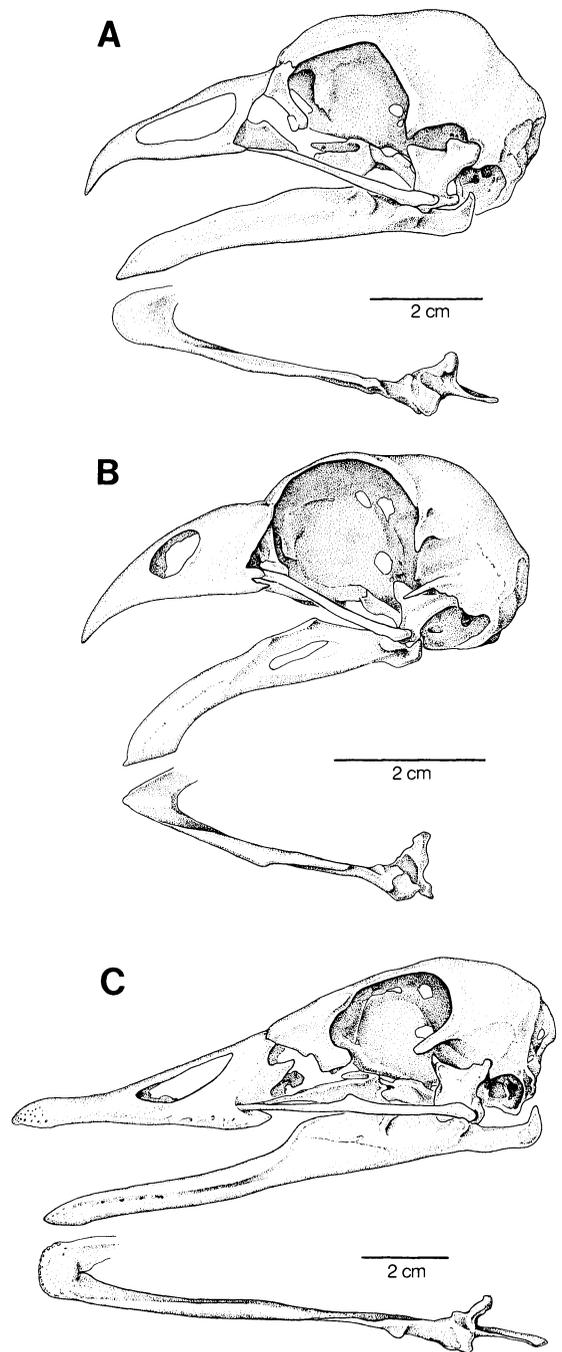
FIGURE 9. Skulls of folivorous birds in left lateral view and their lower jaws in dorsal view. A, Southern crested screamer, Anhimidae, *Chauna torquata* (USNM 430022). B, Hoatzin, Opisthocomidae, *Opisthocomus hoazin* (USNM 612024). C, Canada goose, Anatidae, *Branta canadensis*. These birds share a few features with *Diatryma* that have been associated with generating large bite forces, but they have more lightly built mandibles with short symphyses. Scale bars equal 2 cm.

A

B

C
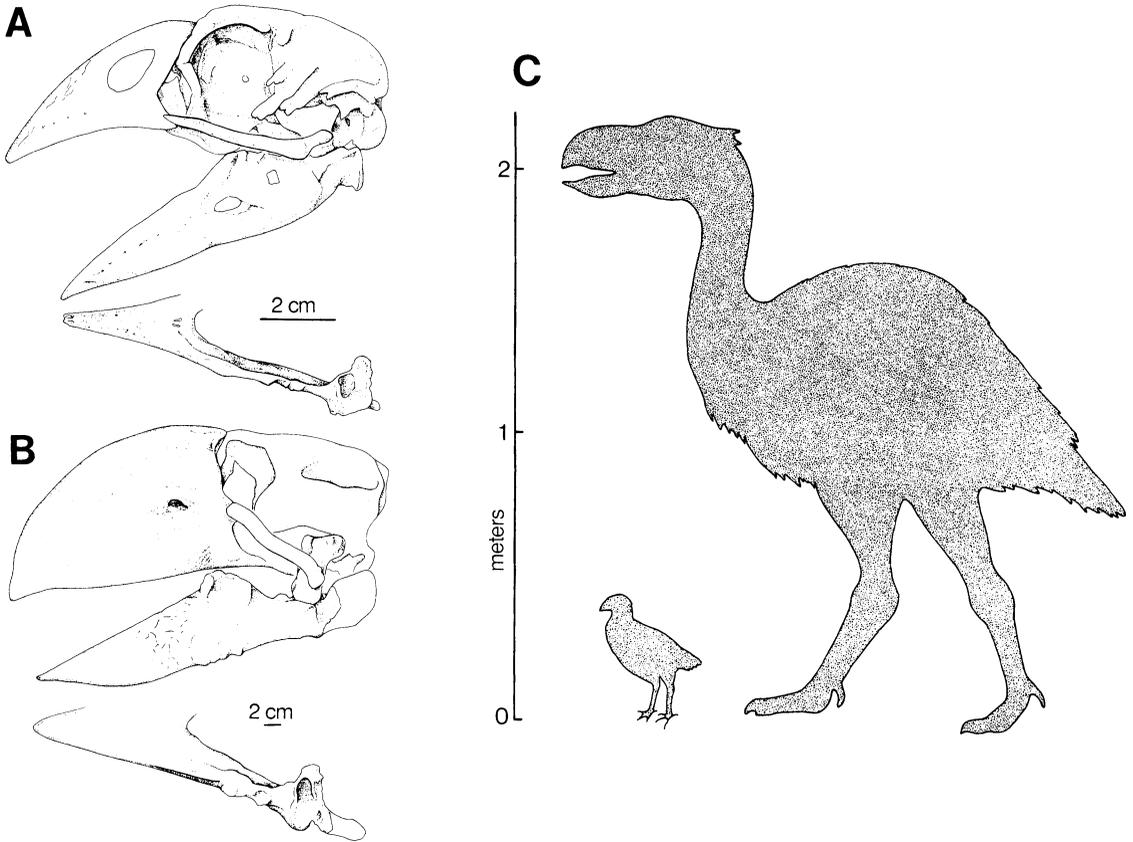
FIGURE 10.   Comparison of *Diatryma* with a takahe, a folivorous rail that has been advanced as a modern analogue for *Diatryma* by Watson (1976) and Andors (1988). Skulls in left lateral view and lower jaws in dorsal view. A, Takahe, Rallidae, *Porphyrio* (=*Notornis*) *mantelli* (USNM 619797); B, *Diatryma gigantea*. Scale bars equal 2 cm. Although these skulls show numerous similarities when enlarged to unit length, the skull of *Diatryma* is about five times as large as a takahe's. C, Silhouettes of body shapes of *Diatryma* and a takahe to the same scale.

| *Aepyornis* | *Dinornis* | *Struthio* | *Diatryma* | phorusrhacid | *Casuarius* | *Rhea* |
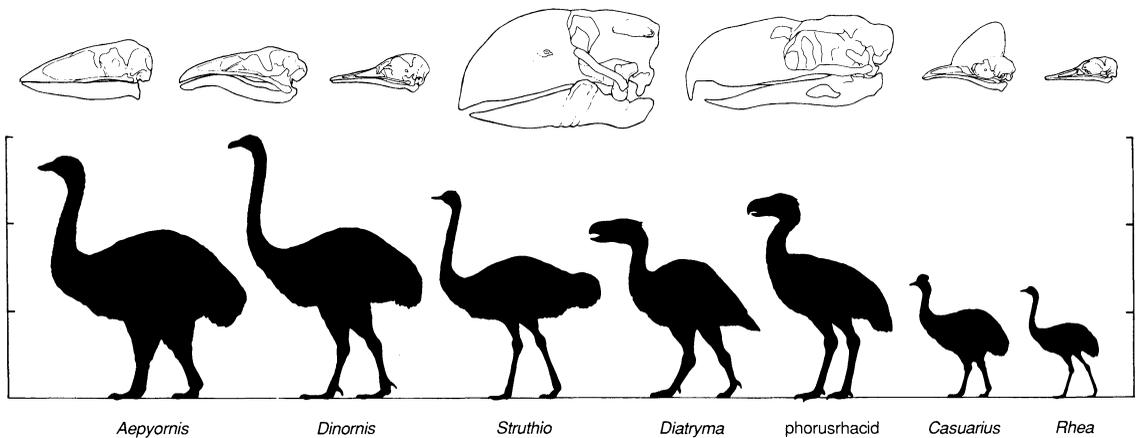
FIGURE 11.   Body silhouettes (below) and skulls (above) of several Recent, subfossil, and fossil large ground birds. Each row is to the same scale. Elephant birds (*Aepyornis*), moas (*Dinornis*), ostriches (*Struthio*), cassowaries (*Casuarius*), and rheas (*Rhea*) are ratites. All are mostly to completely herbivorous, and all have relatively small, lightly built skulls. *Diatryma* and phorusrhacids have decidedly larger, more robust skulls. Phorusrhacids are widely considered to have been carnivorous and predatory in habits. Gradations on scale equal 1 m. Silhouettes of ratites after Wetmore (1967); skulls of *Aepyornis*, *Struthio*, *Casuarius*, and *Rhea* partially after Simonetta (1960); *Aepyornis* partly after Monnier (1913); *Dinornis* skull after Archey (1941); phorusrhacid skull after Andrews (1899).

er homogeneous (Simonetta 1960; Bock 1963). Their skulls tend to be long and low, with lightly built, flexible jaws, and short mandibular symphyses (Fig. 11). They are not constructed to generate and withstand large bite forces, but instead are efficient cropping organs. *Diatryma* has a very different skull morphology, but this fact does not preclude the possibility that it was herbivorous. However, if *Diatryma* did eat leaves or grass, then the seeming "excessive construction" of the jaws and concomitant extremely high safety factors require explanation.

The traditional hypothesis of *Diatryma* as a carnivore better accounts for the available data. Matthew and Granger (1917: p. 319) made no direct presentation of the predatory hypothesis, but noted that *Diatryma* "was probably of similar habits" to *Phorusrhacos*, a member of a group of gigantic predatory birds (Phorusrhacidae) that radiated in South America during the Tertiary (Ameghino 1894; Andrews 1899). Although the predatory hypothesis was never explicitly stated, it became dogma, presumably because of the superficial resemblance of phorusrhacids and *Diatryma*.

Although it should be remembered that the life habits of phorusrhacids also are unknown, these birds provide the closest analogue to *Diatryma* and, within limits, permit form-function correlation. Phorusrhacids universally have been regarded as predators (see, e.g., Ameghino 1894; Andrews 1899; Marshall 1978; Feduccia 1980; Tonni 1980; Olson 1985) because of their large body size, large head size, raptorial (i.e., hooked) bill, and paleoecology (in particular, the absence of large mammalian predators in South America during most of the Tertiary). Figure 11 shows some of the obvious similarities between phorusrhacids and *Diatryma*, such as the deep, rigid upper jaw and small external naris. They are also similar in having relatively huge heads in comparison to the herbivorous ratites (Fig. 12). The mandibles of phorusrhacids are not quite as massive as in *Diatryma*, but the symphyses are quite long (about 30% of total mandibular length versus about 45%–50% in *Diatryma*).

It is not difficult to envision *Diatryma* as a predator, hence the popularity of the idea. Its
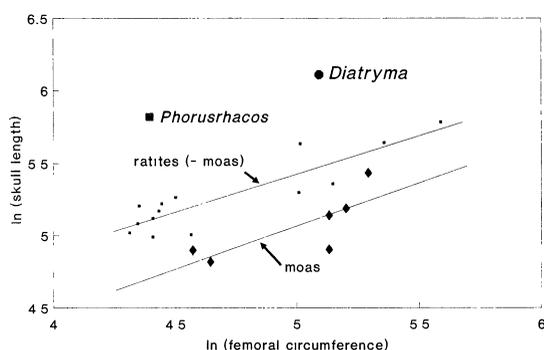
FIGURE 12. Least-squares regression of total skull length and femoral circumference for some large-bodied birds. Femoral circumference correlates highly with body mass in birds and other vertebrates (Anderson et al. 1985; Ruff and Heinrich MS) and is used here as a surrogate for body mass. Separate regression lines for ratites other than moas (small squares, $r = 0.89$) and for moas (diamonds, $r = 0.78$) were calculated; moas have relatively small skulls for their body mass. *Diatryma* (circle; based on a cast of AMNH 6169, see also Andors 1988) and *Phorusrhacos* (large square; from Andrews 1899) fall well above the lines, indicating that their skulls are relatively very large in comparison to ratites of similar size. Data for moas from Oliver (1949) and Cracraft (1976b); for elephant birds from Burckhardt (1893), Monnier (1913), and Wiman (1935). Other ratites consist of specimens of *Rhea*, *Pterocnemia*, *Struthio*, *Casuarius*, and *Dromaius*, USNM collection.

huge head had a gape of about 12 cm in diameter. It probably could have swallowed whole many of the smaller mammals in the early Eocene fauna (Martin 1983, 1989) such as *Cantius*, *Hyopsodus*, and *Diacodexis*, and juveniles of many of the larger mammals such as *Hyracotherium* and *Phenacodus* (Fig. 13). Among Willwood mammals, only adult *Coryphodon*, *Ectoganus*, and perhaps *Pachyaena* exceeded *Diatryma* in body size. However, this mode of life—swallowing prey whole—would not explain the massively constructed skull, especially if *Diatryma* could get the prey down its gullet without a struggle. Struggling prey, however, provide for the possibility of encountering bone as the jaws were adducted. Modern diurnal raptors and vultures often break the bones of the small rodents that constitute the bulk of their diet (Hoffman 1988). *Diatryma* inevitably would have encountered bones when manipulating prey in preparation for swallowing.

Bones are highly resistant food items. If *Diatryma* bit on a foreleg of a *Hyracotherium*, for instance, the radius would provide an
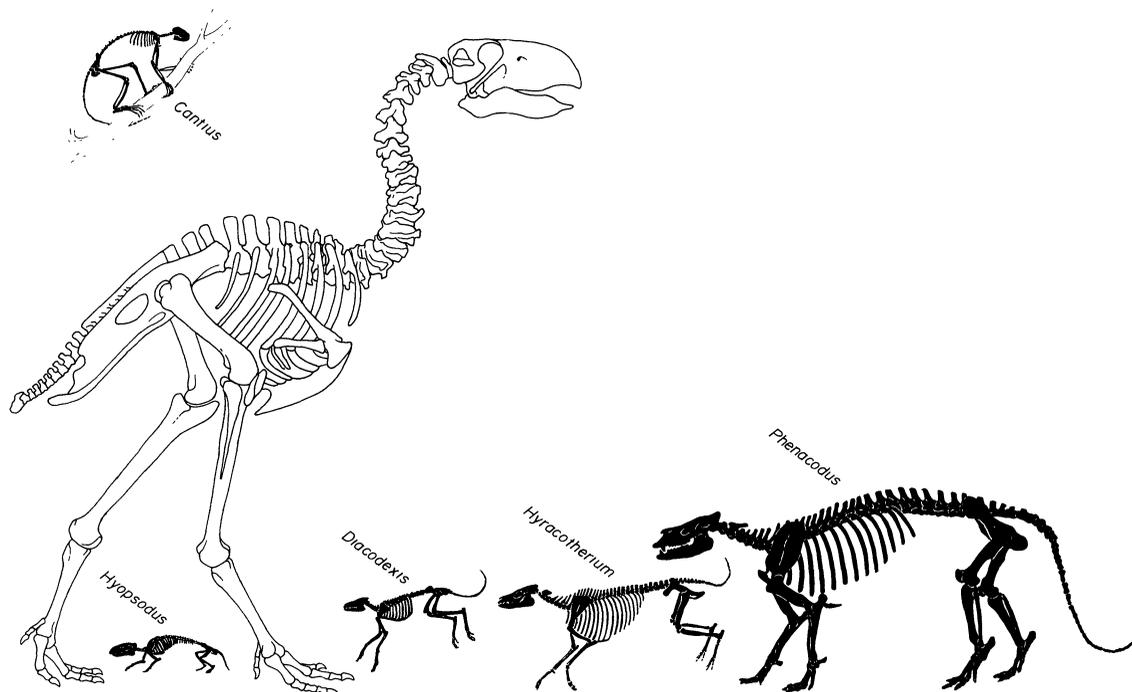
FIGURE 13. Skeletons of *Diatryma gigantea* (redrawn from Matthew and Granger 1917) and potential mammalian prey items from the Willwood fauna, drawn to the same scale.

"unexpected" large point force; if the feeding apparatus is not sufficiently strong, it would fail catastrophically and fracture. Furthermore, such a scenario loads the skull asymmetrically and results in many of the mandibular symphyseal stresses outlined above. Thus, the safety factors that appeared inordinately high under the herbivory hypothesis become much more reasonable under the carnivory hypothesis. The buttressing and thickness of the jaws could well be a protective response against the "accidental" biting of bones.

An extension of this hypothesis is that *Diatryma* actually sought bones. That is, in addition to active predation, *Diatryma* may have scavenged carcasses in search of carrion and the marrow enclosed within the bones, much as hyenas do today. In fact, *Diatryma* exhibits many of the same features (e.g., tall, thick mandibular rami, massive adductor musculature, etc.) associated with bone crushing in hyenas (Biknevicius 1990). Bone crushing as a mode of life is unknown among modern birds. The same result, however, is attained by lammergeiers (accipitrid vultures, *Gypaetus barbatus*), which not only swallow whole bones but drop ungulate bones from great heights to break them open for their marrow, which they scoop out with their specialized tongues (W. Fischer 1968). Furthermore, one group of heavy-bodied phorusrhacids (Brontornithinae) have been described as being primarily scavengers (Tonni 1980). *Diatryma* was well equipped to scavenge the larger mammalian carcasses for carrion as well as bones. As mentioned above, the rostral portions of the tomial surfaces were bladelike and easily could have sheared off hunks of flesh which would then be bolted down the gullet. If bones were encountered, either accidentally or intentionally, they could be shifted caudally in the mouth to where the tomial surfaces were transversely expanded and bite forces were maximal.

Whereas complex tomial surfaces and the development of large bite forces are expected in a predatory or scavenging bird, the shape of the upper jaw of *Diatryma*—in particular, the lack of a raptorial hook on the premax-
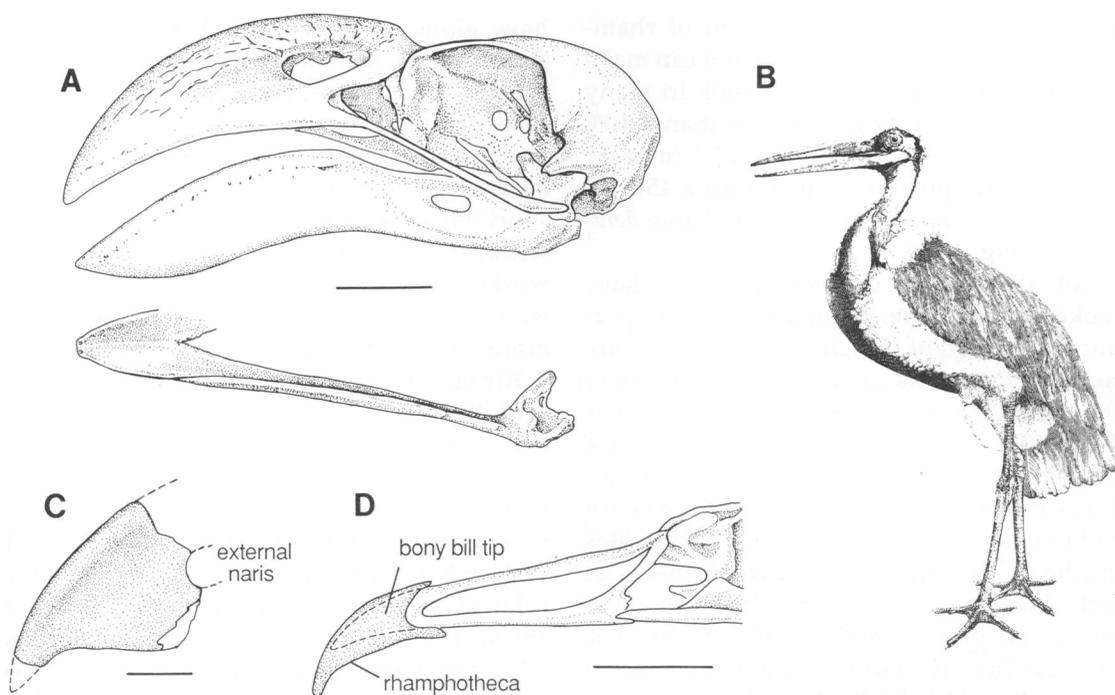
FIGURE 14. A, African carrion crow (thick-billed raven), Corvidae, *Corvus crassirostris* (USNM 288186), a scavenger lacking a hooked bill; regarded by K.-H. Fischer (1978) as a modern analogue of *Diatryma*. Scale bar equals 2 cm. B, Marabou stork, Ciconiidae, *Leptoptilus crumeniferus*, another important scavenger lacking a raptorially hooked premaxilla. C, Premaxillary fragment of juvenile specimen of *D. gigantea* (=*Omorhamphus storchii*) in left lateral view, showing a marked hook to the upper jaw. Scale bar equals about 2 cm. Redrawn from a photograph in Sinclair (1928). D, Rostral half of a skull of a ring-billed gull (*Larus delawarensis*) with the horny rhamphotheca attached. The bony premaxillary tip is about as down-turned as is commonly reconstructed for *Diatryma*, but the horny covering contributes significantly to the functional hook. Scale bar equals 2 cm.

illa—seems inconsistent with a flesh-eating hypothesis (Watson 1976; Andors 1988). Virtually all modern raptorial birds (falcons, hawks, eagles, both New and Old World vultures, owls, etc.) have a sharply down-turned tip to the upper jaw. Phorusrhacids also have a similar hook. The hooked premaxilla is oriented 90° to both the long axis of the skull and the pull of the neck musculature, and is thus well disposed to holding the flesh in the jaws as the neck muscles retract the skull and rip a piece of flesh off a carcass. Furthermore, the sharp tip of the hook aids in opening carcasses. Two questions are relevant here: first, are we certain that *Diatryma* actually lacked a hooked bill, and second, is a hook absolutely necessary for a raptorial mode of life?

Although most authors state that *Diatryma* lacks a hooked premaxilla (Andrews 1917; Matthew and Granger 1917; Troxell 1931; An-

dors 1988), it is not clear if the available specimens are sufficient to answer this question unequivocally. Neither the USGS specimens nor the German specimen described by K.-H. Fischer (1978) provide the necessary information. The best North American rostrum, AMNH 6169, is distorted but reasonably complete, and the tip is turned only slightly ventrally. However, a juvenile specimen of *Diatryma* (originally named *Omorhamphus storchii* by Sinclair [1928] but synonymized with *Diatryma* by Brodkorb [1967]; see also Andors [1988]) preserves the rostral portion of the upper jaw (Fig. 14C), which is clearly hooked. Thus, these fossils provide conflicting information as to whether or not the premaxilla of *Diatryma* was hooked. *Diatryma* almost certainly did not have the very strongly hooked bill of most modern raptors, but, with its rhamphothecal covering, it probably projected ventrally at about 90° to provide the ben-

efits discussed above. The amount of rhamphothecal covering is unknown but can make dramatic contributions to the hook in many modern birds, ranging from less than a 10% increase in some owls, a 20% to 25% increase in various accipitriforms, to almost a 45% increase in one specimen of gull (*Larus delawarensis*; Fig. 14D).

Not all modern carnivorous birds have hooked premaxillae. Among the most important scavengers of the Old World tropics are the adjutant storks of the genus *Leptoptilus*. The marabou stork, *Leptoptilus crumeniferus* (Fig. 14B), is one of the first to arrive at a carcass on the east African savannah. Like all storks, the bills of these birds are straight with no hook. These birds quickly open carcasses and have little trouble ripping off pieces of flesh. Like most scavengers, they also catch and eat live prey. Corvids (crows, ravens, jays, etc.) also are efficient scavengers and lack a premaxillary hook. In fact, K.-H. Fischer (1978), who characterized *Diatryma* as a predator and scavenger, suggested that among modern birds, the African carrion crow (*Corvus crassirostris*; Fig. 14A) most resembles *Diatryma* in skull shape. Thus, while a hooked bill is indeed efficient at tearing flesh, it is not absolutely necessary. The point is that the absence of a raptorial hook in known adult specimens of *Diatryma* cannot be advanced as evidence against the predatory hypothesis. The hook may well have been present, and, in any event, it is not a requisite feature of a predaceous mode of life.

It is clear from the analysis of the skull presented above that *Diatryma* was well equipped for a carnivorous mode of life, probably as an active predator and scavenger. A valid question is whether or not *Diatryma* could actually capture its prey. Steadman (1987) accurately reflected a long-held view of *Diatryma* as a fleet-footed predator. This popular view was countered by Watson (1976) and K.-H. Fischer (1978), among others, who portrayed *Diatryma* as a graviportal animal, more like a moa or an elephant bird than an ostrich. The main basis for this assertion is the short tarsometatarsus of *Diatryma*. Graviportal animals tend to have short distal limb segments, whereas cursorial animals tend to

have elongate ones (Gray 1968). This relationship certainly holds for birds such as ostriches, rheas, emus, and secretary birds that have greatly elongate tarsometatarsi and are rapid runners. In contrast, the large moas, even larger elephant birds, and *Diatryma* have short tarsometatarsi which, in conjunction with their large body masses, have led most workers to consider them as relatively slow walkers if not graviportal (Archey 1941; Wetmore 1967; Feduccia 1980; Andors 1988).

Alexander's (1983a,b, 1985; see also Maloiy et al. 1979) studies of allometric scaling of the legs of birds (especially ground birds and moas in particular) provide for different interpretation of locomotion in *Diatryma*. His regression of a functionally and taxonomically broad sample of birds shows that moas indeed have relatively short tarsometatarsi (Alexander 1983a, 1985). However, Alexander (1985: p. 170) noted that "there is nothing very extraordinary about the proportions of moa leg bones," with many groups of birds falling even further off the regression line. Moas, and by extension *Diatryma*, are not as unusual as they may seem at first.

Just as important as constraints imposed by scaling phenomena are those imposed by phylogenetic history. Table 2 shows a comparison of the limb proportions of *Diatryma* and other birds. Based on a limb described by Troxell (1931), the limb proportions of *Diatryma* are roughly 1:1.6:0.9 (femur : tibiotarsus : tarsometatarsus). These are very similar to those of the Mesozoic birds *Archaeopteryx* (de Beer 1954) and *Ichthyornis* (Marsh 1880) and virtually identical to the early Tertiary palaeognaths *Lithornis*, *Pseudocrypturus*, and *Paracathartes* (Houde 1988) and the early phorusrhacid *Aenigmavis* (Peters 1987). Thus, rather than postulating apomorphic reduction of the tarsometatarsus of *Diatryma* in connection with graviportal locomotion, it is better to regard these limb proportions as being simply plesiomorphic.

Another simple analysis also suggests that *Diatryma* was not necessarily graviportal. In general, the thicknesses of limb bones increase out of proportion to body weight such that heavier animals have disproportionately thick bones for a given length (Schmidt-Niel-

TABLE 2. Limb proportions (femur: tibiotarsus: tarso-metatarsus). Comparison of *Diatryma* with other early or primitive birds shows that the limb proportions of *Diatryma* are best viewed as primitive rather than apomorphically graviportal. Elongate distal limb segments in *Rhea*, *Struthio*, and *Sagittarius* are apomorphic features associated with cursoriality.

Taxon	Source	Ratio
Archaeopteryx	de Beer 1954	1:1.4:0.8
Ichthyornis	Marsh 1880	1:1.9:1
Palaeognathae		
Lithornis plebius	Houde 1988	1:1.5:0.9
L. promiscuus	Houde 1988	1:1.6:0.9
Pseudocrypturus	Houde 1988	1:1.4:0.8
Paracathartes	Houde 1988	1:1.6:1
Anomalopteryx (moa)	Alexander 1983a	1:1.6:1
Rhea	pers. obs.	1:1.5:1.4
Struthio	Alexander 1983a	1:1.8:1.7
Neognathae		
Meleagris	Alexander 1983a	1:1.5:1.1
Aenigmavis	Peters 1987	1:1.5:0.9
Diatryma	Troxell 1931	1:1.6:0.9
Sagittarius	Alexander 1983a	1:2.6:2.6

FIGURE 15. Least-squares regression of femoral length and femoral circumference for ratites and *Diatryma*, intended as a rough measure of relative body weight. The regression line ($r = 0.91$) pertains to ratite data only. Anomalopterygid moas and aepyornithids (large squares) are widely regarded as graviportal and mostly fall below the line, indicating a relatively stout femur. Dinornithid moas were probably apomorphically cursorial and exhibit gracile femora. *Diatryma* (circles) clearly lies above the line, separate from the graviportal group, suggesting a relatively lightly built femur. These data do not support the view of *Diatryma* as necessarily a slow, graviportal walker. Data for *Diatryma* are (from top to bottom) from AMNH 6169 (Andors 1988), USNM 15118 (cast, see also Andors 1988), and USGS 25008; other data come from the same sources as in Fig. 12.

sen 1984). Graviportal animals, by definition, are heavy and should be expected to have bones of relatively large circumference relative to length. A regression of large bodied ratites (Fig. 15) shows that, as predicted, most of the birds that commonly have been regarded as graviportal (anomalopterygine moas and elephant birds) fall below the line, indicating disproportionately thick femora. Of some interest are the dinornithine moas which, despite large body size, have relatively thin femora, supporting Cracraft's (1976a,b) suggestion that these moas are apomorphically cursorial. Likewise, *Diatryma* has relatively gracile femora (i.e., relatively long), which plot well above the regression line and far from the graviportal taxa.

Diatryma was no speedster. Nevertheless, it is equally inaccurate to portray it as a plodding, graviportal giant. Alexander (1983b, 1985) concluded that moas could run, perhaps as fast as human Olympic sprinters. *Diatryma* probably could run fast enough to catch most of the contemporary mammals, especially young, old, or sick individuals. It is unfair to judge the running ability of *Diatryma* by modern standards in that the Eocene mammalian fauna as a whole was much less cursorial (i.e., slower) than later faunas (Bakker 1983; Rose 1990). Like most living carnivorous mammals, *Diatryma* probably scavenged when it

could and actively sought prey when it had to (Fig. 16).

Summary

Biomechanical analysis of the feeding apparatus suggests that the massive, deep jaws and powerful muscles of *Diatryma* enabled it to develop large dorsoventral bite forces. The massiveness of the upper jaw, the length and shape of the mandibular symphysis, and the form of the mandibular rami reflect the buttressing of the feeding apparatus that permitted such forces to be withstood. Whatever *Diatryma* ate, it could bite it hard. Our analysis of potential food items suggests that most forms of herbivory (frugivory, granivory, and folivory) are inconsistent with the skull morphology and would result in large amounts of metabolic energy being wasted on maintaining the unnecessarily huge bony bill. Conclusions drawn from the similarities of modern folivorous birds to *Diatryma* (Watson 1976; Andors 1988) have neglected scaling phenomena. We suggest that *Diatryma* was carnivorous. It probably could pursue and kill live prey, could have scavenged carcasses, and may have been specialized as a bone crusher.
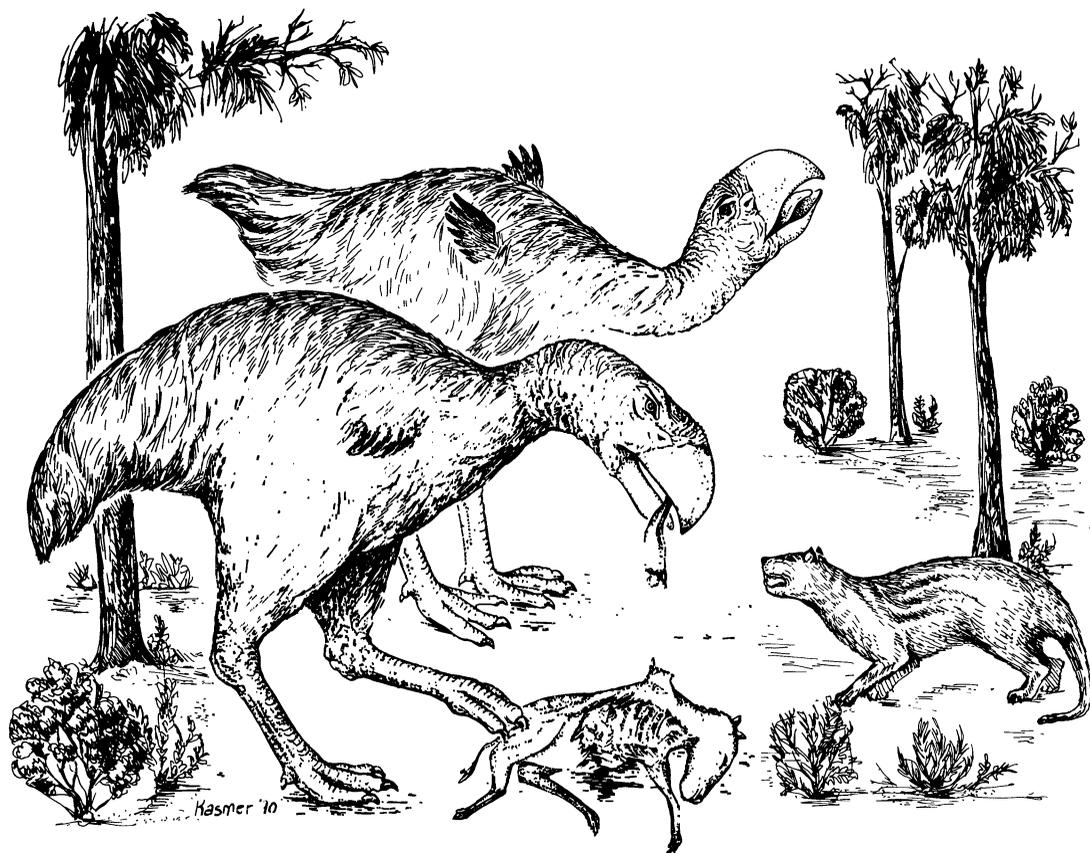
FIGURE 16.   Life restoration of the *Diatryma gigantea* feeding on a carcass of the early horse *Hyracotherium* as an oxyaenid creodont looks on. *Diatryma* was probably capable of both active predation and scavenging (see the text).

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