A FEEDING ADAPTATION OF THE JAW ARTICULATION IN NEW WORLD JAYS (CORVIDAE)

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ABSTRACT.—The jaw articulation of most endemic New World jays (Corvidae) has a condyle of the quadrate and an opposing cotyla of the lower jaw not found in other birds. They also have well-developed meatic articular facets of the quadrate and cranium. The tip of the rhamphotheca of the lower mandible is chisel shaped. These and other features constitute a functional unit, the buttress complex, that braces the partially opened lower jaw and enhances its use as a chisel. The buttress complex stabilizes the lower jaw by anchoring the jaw on the quadrate and reducing torque on the quadrate during pounding. A hypothesis of pounding with the lower mandible was confirmed by field observations of *Aphelocoma coerulescens coerulescens*, which stabs acorns with the lower mandible and then tears off the shell using both mandibles. This may be an unusually effective method of peeling acorns, and it differs from the techniques used by *Garrulus* and *Pica*. The origin of the complex may not be associated with acorn eating. A slight modification of the jaw articulation in *Cyanolyca* probably represents the evolutionary precursor of the buttress complex. The distribution of the complex in the Corvidae suggests that *Cyanolyca* is the sister group of other endemic New World jays. *Gymnorhinus* is related to the New World jays, not to *Nucifraga*. An example of convergent evolution is provided by *Hemignathus wilsoni* (Drepanidinae). *Received 15 August 1986, accepted 22 April 1987.*

MANY members of the Corvidae pound hard food items with the tip of the bill while holding the food against a firm substrate with one or both feet. Most birds that pound with their bills on a hard substrate (e.g. woodpeckers) use both mandibles or primarily the upper for the transmission of force (Spring 1965). Because of its unstable suspension from the cranium, the lower jaw alone appears not to be an effective implement for strong pounding. For this reason my curiosity was aroused by an unusual configuration in the lower jaw and quadrate of a New World jay that implied use of only the lower mandible in pounding. I studied modifications of the lower jaw and its articulation as a functionally integrated character complex. The variation and taxonomic distribution of this apomorphous complex have some phylogenetic implications within the Corvidae (*sensu* Blake and Vaurie 1962).

Although acorns and other nuts are important food items for many species of Corvidae, the only well-defined modification of the bill for cracking nuts is the rhamphothecal bulge in the lower jaw of the nutcrackers (*Nucifraga*; references in Turcek and Kelso 1968). Most corvids have stout bills capable of a variety of manipulations. The modifications I describe are found only in certain New World jays and are clearly associated in some species with a special technique for opening nuts, especially acorns. Within the Corvidae, however, the occurrence of this character complex does not correlate well with the occurrence of acorn eating; it appears to represent an evolutionary novelty of broader ecological significance within the family.

MATERIALS AND METHODS

I examined skulls of 76 species from all genera of the Corvidae except *Temnurus* and *Zavattariornis*. The jaw articulations of 2 additional species were observed in skin specimens by softening and reflecting a flap of skin. I also examined 13 species from 4 families allied to the Corvidae. To determine the action of the jaw articulation and its ligaments, I manipulated a freshly killed Blue Jay (*Cyanocitta cristata*) and American Crow (*Corvus brachyrhynchos*). Information about ontogenetic stages of the features under study was obtained by clearing and staining (Taylor 1967) two nestlings of the Florida Scrub Jay (*Aphelocoma coerulescens coerulescens*) and by dissection of a hatchling Fish Crow (*Corvus ossifragus*). Jaw muscles of an adult Eurasian Jay (*Garrulus glandarius*) and one adult Blue Jay were dissected. I drew the original illustrations in pencil, using a dissecting microscope and drawing tube for all anatomical figures; final figures were inked by an illustrator. Field observations, pho-

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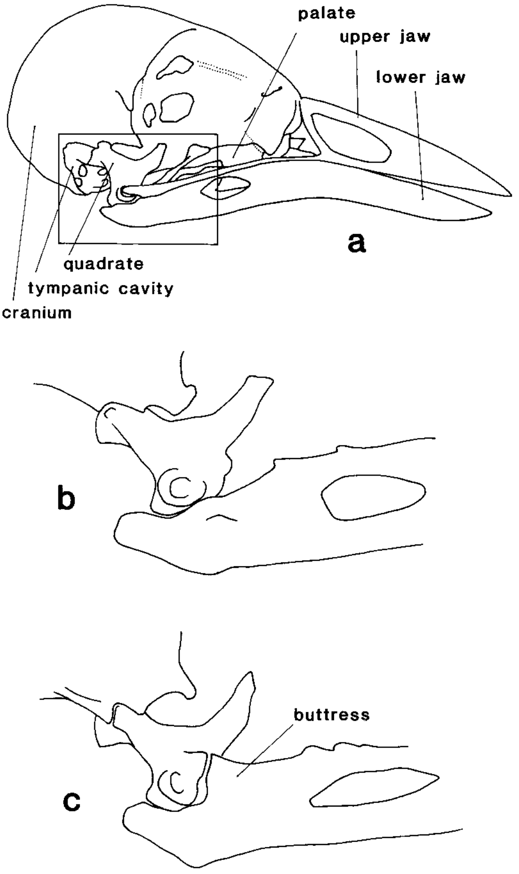

Fig. 1. Osteology of the jaw articulation in corvids. (a) Skull of *Garrulus glandarius,* lateral view. Box includes major features discussed in this paper. (b) Lower jaw and quadrate of *Pica nuttalli.* (c) *Aphelocoma coerulescens.* Note buttress in *Aphelocoma.*

tographs, and motion pictures (8 mm, 36 frames/s) of the feeding behavior of the Florida Scrub Jay were obtained at the Archbold Biological Station in Lake Placid, Florida, during 10-18 September 1983, and brief observations of a captive American Crow were made in Maryland.

An analysis of hypothetical forces on the jaw articulation during mandibular pounding was undertaken [see Bock (1966, 1968) for similar analyses pertinent to birds]. The analysis is not intended to reflect actual forces in the living bird because the muscles acting on the system are unknown, the exact direction and magnitude of each force are unknown, and the planes of rotation of the lower jaw and quadrate are neither constant nor precisely known. Nevertheless, the analysis produced a set of hypothetical, relative values by which functional properties of the jaw articulations of different species could be compared. The system was assumed to remain in static equilibrium. Magnitudes and directions of some force vectors were set arbitrarily; magnitudes and directions of all others were determined graphically by assuming that the sum of all torques equaled zero and that the sum of all force components on the x- and y-axes of each bone equaled zero. Slight discrepancies from zero resulted from errors in graphing. Gravity was ignored because its effect on the system in a living bird would be highly variable. All numerical values for vectors represent indices that are proportional to vector lengths. These indices are useful for comparison, but units of force or torque are unspecified.

I use the term "jaw" when referring to the entire lower jaw or only to its articulation. "Upper mandible" and "lower mandible" refer to the rostral portions of the jaws covered by rhamphotheca. "Bill" refers to both mandibles. Anatomical terminology generally follows Baumel et al. (1979), but 5 new terms are proposed: *cotyla prootica* (prootic cotyla) and *cotyla squamosa* (squamosal cotyla) of the cranium for the articular depressions that receive the prootic and squamosal condyles of the quadrate; *processus meaticus* (meatic process) for the process of the quadrate that articulates with the suprameatic process of the squamosal; *condylus rostralis* (rostral condyle) of the quadrate and *cotyla rostralis* (rostral cotyla) for new structures of the quadratomandibular articulation.

For uniformity throughout the family Corvidae and convenience in referring to groups of species by a generic name, I use the scientific nomenclature of Blake and Vaurie (1962); for Drepanidinae I follow Greenway (1968). Common names are from the A.O.U. Check-list (A.O.U. 1983) and Goodwin (1986).

RESULTS

MORPHOLOGY

Osteology.—This paper is concerned with the suspension system of the lower jaw, including the jaw, quadrate, and cranium (Fig. 1a, b). Although the upper jaw and palate are linked to the suspension system, they are peripheral to this discussion. In certain jays the suspension system, hereafter called the jaw articulation, differs from that of other corvids by the presence of a prominent buttress on the lower jaw (Fig. 1c).

In most corvids [illustrated by the Yellow-billed Magpie (*Pica nuttalli*) in Fig. 2] the quadrate articulates with the lower jaw by a rounded medial condyle and an elongate, obliquely transverse surface formed by the confluence of the lateral and caudal condyles. In the closed position the latter condyles abut on the elon-

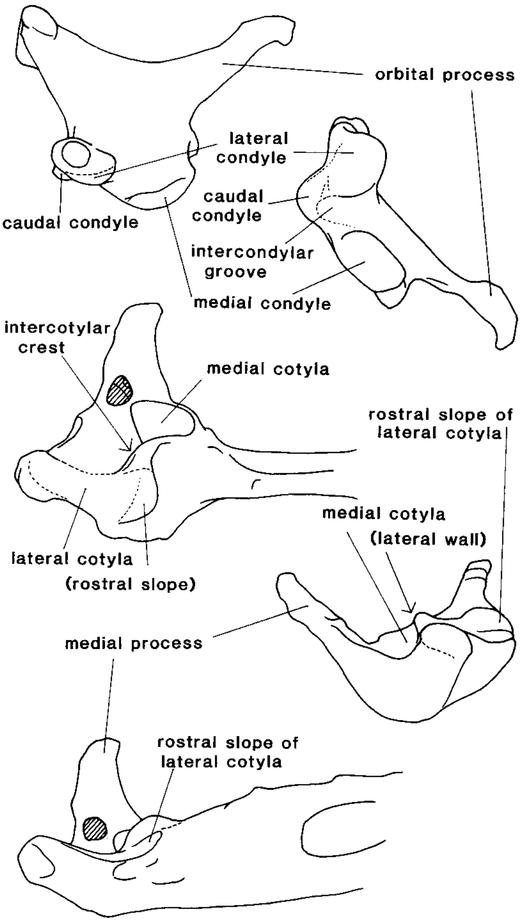

Fig. 2. Quadrate and lower jaw of *Pica nuttalli,* showing right quadrate (upper two figures) and right ramus of lower jaw (lower three figures). Top to bottom: lateral, ventral, dorsal, caudal, and caudodorsolateral views.

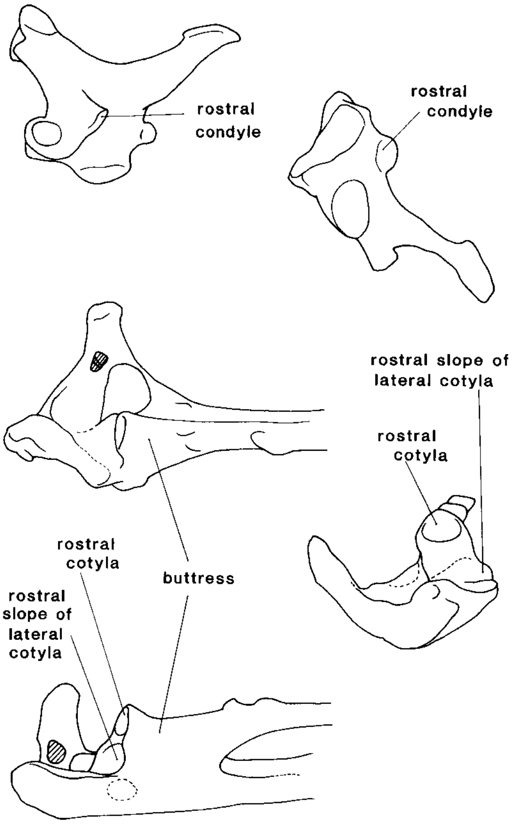

Fig. 3. Quadrate and lower jaw of *Aphelocoma coerulescens,* showing right quadrate (upper two figures) and right ramus of lower jaw (lower three figures). Top to bottom: lateral, ventral, dorsal, caudal, and caudodorsolateral views.

gate, lateral cotyla of the lower jaw, and the medial condyle rests on the caudal end of a well-defined medial cotyla of the lower jaw. Upon opening, the lower jaw slides caudolaterally with respect to the quadrate, which itself rotates rostromedially about its cranial articulation. The medial condyle of the quadrate slides rostrally along the medial cotyla, guided by its prominent lateral wall. Backward sliding of the partially opened lower jaw is resisted weakly when the lateral condyle of the quadrate abuts the rostral slope of the lateral cotyla. Backward dislocation of the mandible from the quadrate is resisted firmly at the articulation only when the lower jaw is opened wide and the intercotylar crest abuts the intercondylar groove of the quadrate. Most corvids conform to this description.

Some jays (illustrated by *Aphelocoma coerulescens* in Fig. 3) possess an additional condyle of the quadratomandibular articulation, the rostral condyle, and an additional cotyla of the articular fossa of the lower jaw, the rostral cotyla. The rostral condyle consists of a convex articular surface oriented rostroventrally on a pedicel of the quadrate, located rostrodorsal to the lateral condyle. Facing it is the articular surface of the rostral cotyla of the lower jaw, located rostral and dorsal to the lateral cotyla on a prominent, vertical buttress of the mandibular ramus (Figs. 1 and 3). The base of the buttress is formed by an unusually steep rostral slope of the lateral cotyla. Adjacent and dorsal

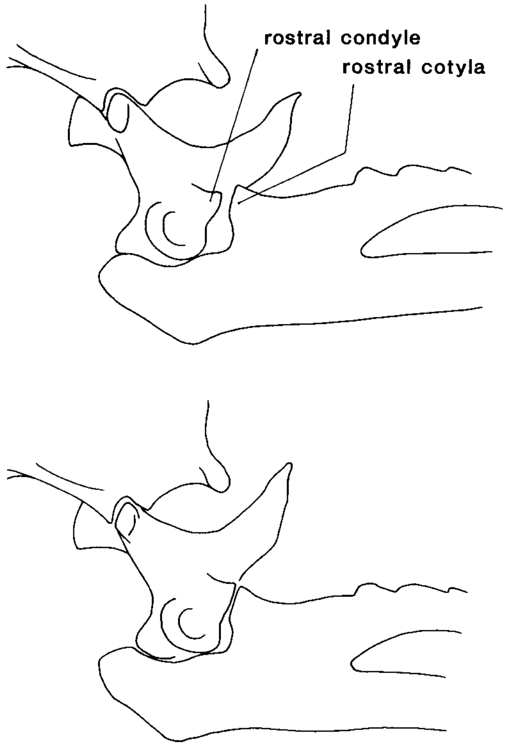

Fig. 4. Lower jaw and quadrate of *Aphelocoma coerulescens*, showing jaws closed (top) and partially open (bottom). Note change in fit of rostral cotyla and rostral condyle.

to this slope is the vertical face of the rostral cotyla. The rostral slope of the lateral cotyla is homologous with the more gentle slope found in other corvids, but the rostral cotyla is a new structure. The articular surface of the rostral cotyla is usually circular and concave. When the jaws are closed, the rostral cotyla faces the rostral condyle, but the former lies somewhat dorsal to the latter. As the lower jaw opens and the quadrate slides along the rostral slope of the lateral cotyla, the rostral cotyla and the rostral condyle approach each other and eventually meet (Fig. 4). The best fit of these articular surfaces occurs when the lower jaw is only partially opened and shifted backward on the quadrate. With further opening of the jaw, these articular surfaces lose contact, and the lateral and medial cotylas and condyles provide the major support.

In corvids, as in most birds, the otic process of the quadrate articulates with the cranium (quadrato-squamoso-otic articulation) by two well-defined rounded condyles: the squamosal condyle laterally and the prootic condyle medially (Fig. 5). These condyles fit into separate concavities of the cranium: the squamosal cotyla and the prootic cotyla. In some species (e.g. *Pica*, *Corvus*) a small bony projection, the meatic process, occurs on the otic process of the quadrate adjacent and caudal to the squamosal condyle. The meatic process meets the cranial surface of the suprameatic process on the dorsal rim of the tympanic cavity as a rudimentary articulation. Some species lack the meatic process (e.g. *Garrulus*); others have the meatic articular facets moderately well developed (e.g. *Corvus*). Those species of jay that possess the mandibular buttress and rostral condyle of the quadrate, however, have the meatic and suprameatic processes markedly enlarged (Fig. 6). In them the meatic process projects caudolateral to the squamosal condyle and forms the lateral extremity of the cranial articulation of the quadrate. The meatic process has a flat articular surface that opposes a well-developed articular facet of the suprameatic process. The meatic articular facets are enclosed in the articular capsule of the quadrato-squamoso-otic articulation.

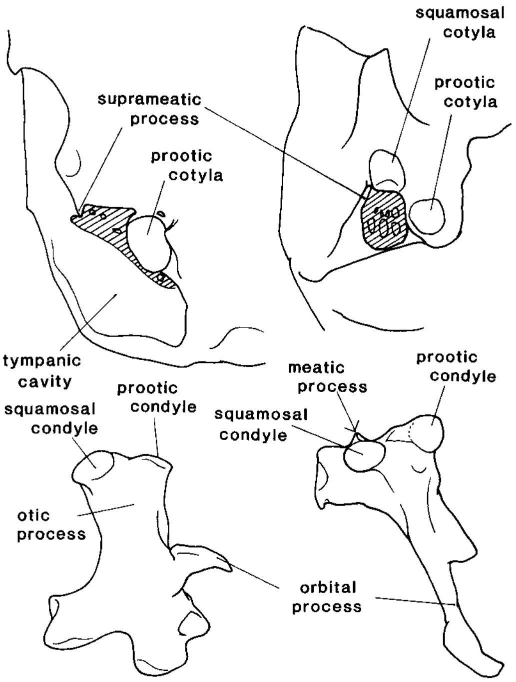

Fig. 5. Cranium and quadrate of *Pica nuttalli*. (Top) Otic region of cranium, right side: left, anteroventral view; right, ventral view. (Bottom) Right quadrate: left, anterior view; right, dorsal view.

Variation.—The mandibular buttress is found

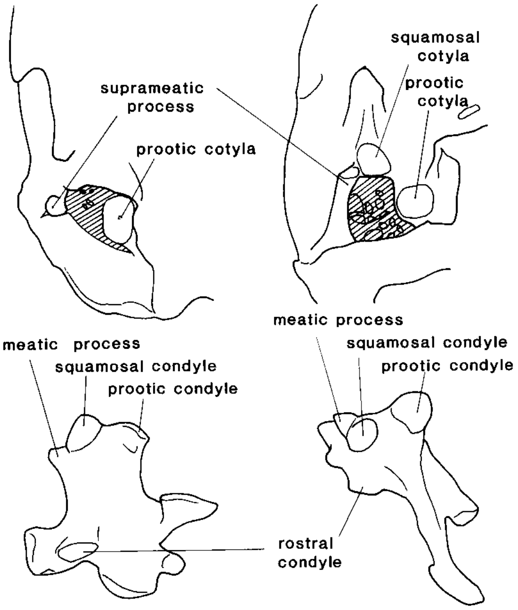

Fig. 6. Cranium and quadrate of *Aphelocoma coerulescens.* (Top) Otic region of cranium, right side: left, anteroventral view; right, ventral view. (Bottom) Right quadrate: left, anterior view; right, dorsal view.

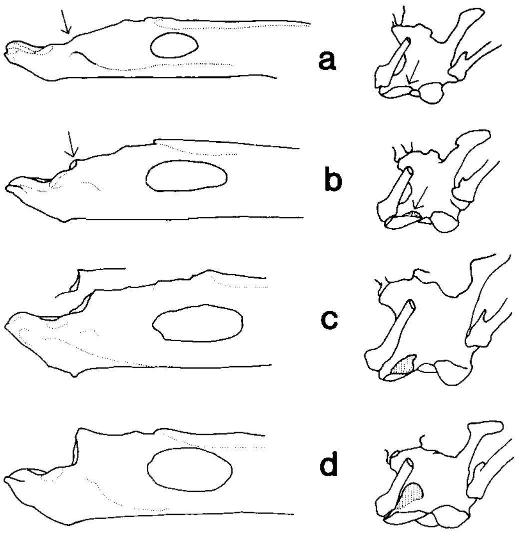

Fig. 7. Variation in the jaw articulation within *Cyanolyca* and *Cyanocorax.* Left, lateral view of right ramus of lower jaw; right, anteroventrolateral view of right quadrate. Arrows indicate absence or rudimentary condition of rostral condyle of quadrate (right, shaded) or rostral cotyla of mandible (left). (a) *Cyanolyca viridicyana jolyaea;* (b) *Cyanolyca cucullata mitrata;* (c) *Cyanocorax violaceus violaceus,* showing variation; (d) *Cyanocorax dickeyi.*

in all genera of jays endemic to the New World except *Cyanolyca,* in which it is absent or poorly developed. It is absent from endemic Old World genera (*Temnurus* not examined; *Zavattariornis* from figures in Ripley 1955) and from the widely distributed genera *Garrulus, Perisoreus, Nucifraga, Pica,* and *Corvus.* Varying degrees of development of the buttress are seen among the species of *Cyanolyca* and within *Cyanocorax* (Figs. 7 and 8, Appendix). The degree to which the rostral slope of the lateral cotyla of the lower jaw is raised and ridged in *Cyanolyca* shows individual variation and apparently taxonomic variation at the specific and subspecific levels (Appendix). In a specimen of *Cyanolyca cucullata mitrata* (Azure-hooded Jay; UMMZ 209292) a rudimentary rostral condyle of the quadrate is present (Fig. 7). In all *Cyanolyca* the lateral condyle of the quadrate and rostral slope of the lateral cotyla are separated by a wide gap when the jaws are closed (Fig. 8). Neither the meatic process of the quadrate nor the suprameatic process of the squamosal is enlarged.

Within *Cyanocorax,* the buttress is always present. The Violaceous Jay (*Cyanocorax violaceus*), Purplish Jay (*C. cyanomelas*), Azure Jay (*C. caeruleus*), Curl-crested Jay (*C. cristatellus*), and Azure-naped Jay (*C. heilprini*) differ from more highly developed species in that the mandibular buttress is lower, less vertical, and more widely separated from the rostral condyle of the quadrate when the jaws are closed. Both the rostral cotyla and the rostral condyle are smaller, and the latter is adjacent to the lateral condyle (Figs. 7 and 8). The meatic processes are well developed in these species, however (Fig. 8; not verified in *C. heilprini*). *Calocitta* and *Psilorhinus* also fit this description.

Ontogeny.—The nestling of *Aphelocoma coerulescens* shows a marked development of the mandibular buttress at the time of hatching (Fig. 9). The membrane bones of the lower jaw are mainly ossified, but Meckel's cartilage is well developed and its expanded caudal end, the articular, is entirely cartilagenous. The quadrate is also formed of cartilage, with only a small center of ossification on its body. The rostral portion of the cartilagenous articular is much expanded dorsally (rostral cotyla) and lies in close proximity to a moderately developed rostral condyle on the quadrate. Dorsal expansion of the articular is accompanied by (and may

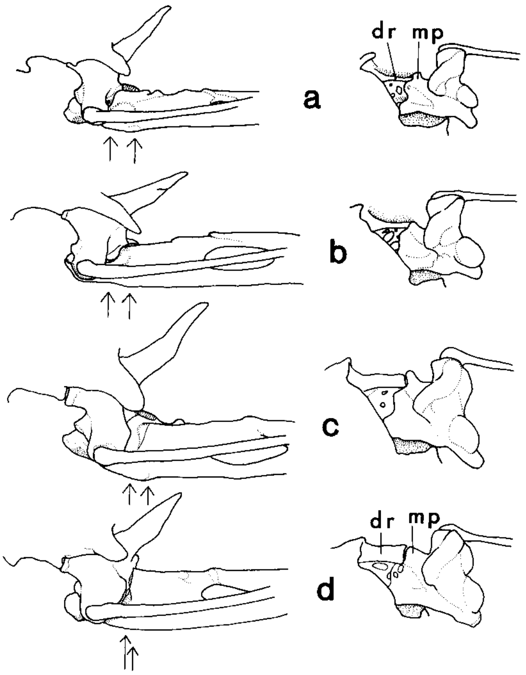

Fig. 8. Variation in the jaw articulation within *Cyanolyca* and *Cyanocorax.* Left, dorsolateral view of right quadrate and mandibular ramus with jaws closed; arrows show approximate distance between contact surfaces of rostral condyle and rostral cotyla (c, d) or their precursors (a, b). Right, ventral view of right quadrate. Note relative development of dorsal rim of tympanic cavity (dr) and meatic process (mp). (a) *Cyanolyca viridicyana jolyaea,* (b) *Cyanolyca cucullata mitrata,* (c) *Cyanocorax violaceus violaceus,* (d) *Cyanocorax dickeyi.*

result from) an unusual deepening and broadening of the caudal end of the supraangular bone. The meatic process of the quadrate and the suprameatic process of the squamosal are also well developed. Thus, the major innovations are in place at hatching. In a 10-day-old chick, however, ossification of the jaw-quadrate articulation and of the meatic articulation is not yet completed.

The hatchling of *Corvus ossifragus* (which lacks a buttress) lacks a caudal deepening of the supraangular bone, and the quadrate is separated from the rostral portion of the articular cartilage by a wide gap. The conformation of the jaw articulation is thus not markedly different from that of an adult.

Other features.—Jaw muscles are not much affected by the presence of a buttress. In adult *Garrulus glandarius,* a species lacking the buttress, M. adductor mandibulae posterior inserts on the broad, dorsal surface of the ramus just rostral to the jaw articulation. *Cyanocitta cristata* has a well-developed buttress and a correspondingly narrower dorsal surface of the ramus. In the adult of that species the muscle is of comparable size, but it inserts instead on the medial surface of the ramus.

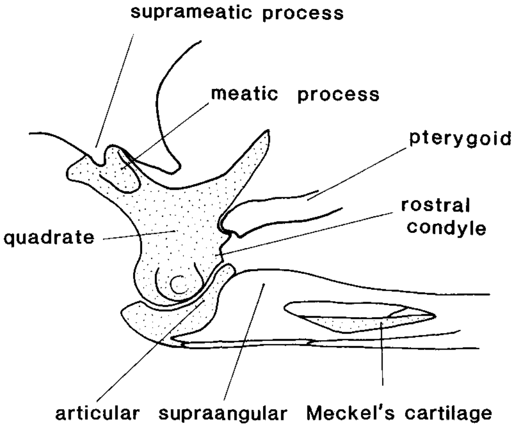

Fig. 9. Jaw articulation of hatchling *Aphelocoma coerulescens coerulescens,* right lateral view. Stipple indicates cartilage; jugal bar removed.

The rostral cotyla and rostral condyle are enclosed in the articular capsule of the quadratomandibular articulation. Neither the ligaments nor the articular capsule of the lower jaw appears to play an important role in stabilization of the partially opened lower jaw. The capsule is loose enough to permit sliding of the lower jaw on the quadrate. The medial jugomandibular ligament extends from the caudoventral edge of the jugal bar caudad and then mediad around the jaw articulation to its attachment on the caudal edge of the articular. It does not restrain the lower jaw from sliding caudally against the quadrate until the jaw is widely opened.

The tip of the rhamphotheca of the lower mandible of *Aphelocoma* and other jays with a buttress is wedge shaped and lacks a recurved tip. By contrast, the upper mandible typically has a pronounced, decurved tip (Fig. 10). Corvids that lack the buttress may also have a wedge-shaped lower mandible, but these species have little if any decurved hook on the upper mandible (e.g. *Pica, Cyanopica*). Others have a recurved tip on the lower mandible and a hook on the upper (e.g. *Garrulus, Cyanolyca, Platylophus, Urocissa*). These details of form of the rhamphotheca are already present in nestlings bearing an egg tooth and thus are not the result of wear; however, wear may change rhamphothecal conformation in adult birds to some degree (worn tips and jagged tomial edges in many specimens). The implications of rhamphothecal morphology are that jays with a buttress have a lower mandible that is suitable, and an upper mandible that is unsuitable, for strong pounding. By contrast, corvids that lack the buttress either have both mandibles suitable, or both unsuitable, for pounding.

I consider the combination of modifications of the lower jaw, quadrate, and cranium as the "buttress complex." The entire dorsal rim of the tympanic cavity may also be modified in various ways as part of this complex, but I have not studied its morphology in detail. In jays with a buttress complex the new and modified articulations of the lower jaw, quadrate, and cranium make their best fit when the lower jaw is partially opened (Fig. 4). Their conformation suggests that they serve to resist compression in that position rather than to facilitate movement. The implication is that the chisel-like lower jaw is used for pounding in jays with a buttress complex. To test this hypothesis I made field observations on the use of the bill in opening acorns by the Florida Scrub Jay, a species in which the buttress complex is well developed.

FEEDING BEHAVIOR

Aphelocoma c. coerulescens.—According to Amadon (1944) and Woolfenden and Fitzpatrick (1984), the Florida Scrub Jay feeds mainly on animal matter and acorns. Many acorns are eaten during autumn, but others are buried and eaten during other seasons. I observed that birds carried one or two acorns in the bill and possibly a third in the throat while moving to a caching site. Typically, a bird carried an acorn in the tip of the bill to a sandy spot. The acorn was moved back into the throat and the closed, or nearly closed, bill was pushed into the sand to its base. The bill was then opened, widening the hole, and the acorn brought forward from the throat and dropped into the hole. The bird tapped the acorn five or six times with both mandibles of the open bill, driving the acorn into the sand. The force of a blow used to bury an acorn was apparently less than that used to open an acorn because the skin of the acorn was scratched but not broken during caching. Sand was flicked over the buried acorn with sideswipes of the bill, and one or two leaves or pieces of wood were placed on top of the spot. Alternatively, a bird sometimes pushed an acorn directly into the sand while it was held in the bill, using rapid butting motions of the head.

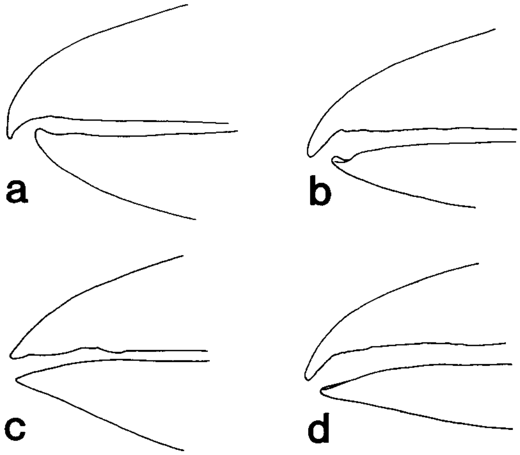

Fig. 10. Bill tips of various corvids, left lateral view. Sizes adjusted variously for ease of comparison. (a) *Garrulus lanceolatus,* (b) *Cyanolyca viridicyana,* (c) *Pica nuttalli,* (d) *Aphelocoma coerulescens coerulescens.*

To open an unshelled peanut held vertically between the fingers, a jay perched on the hand, raised its head and neck high with the bill pointed downward, and directed blows downward and sometimes inward using motion of the whole body. The bill was opened slightly, and the upper mandible appeared to be raised slightly (Fig. 11). Blows were directed tangentially toward the outer edge of the peanut, sometimes glancing off so that the bill hit one's finger. When the lower jaw penetrated the shell, more blows were directed toward adjacent portions of the shell, or the shell was grasped and a piece twisted off. The shell was thus peeled until the upper peanut was largely exposed, at which time the bird hammered the nut with the lower mandible or both mandibles to remove pieces, or grasped and removed the entire nut. The nut typically was moved back into the throat while the bird continued to remove shell to obtain the second nut.

Acorns offered by hand were carried intact to a tree branch or to a piece of wood on the ground. The acorn was held against the surface of a roughly horizontal branch with its central axis parallel to the branch. It was secured by

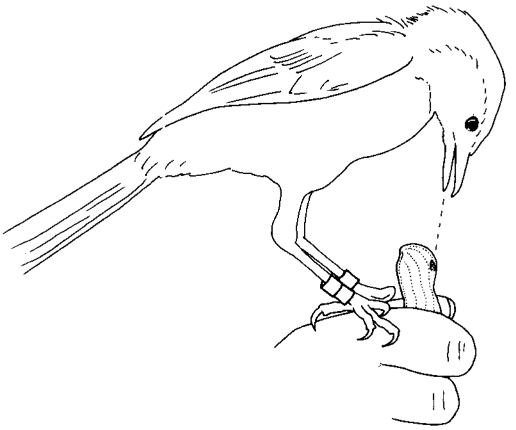

Fig. 11. *Aphelocoma coerulescens coerulescens* pounding peanut held in hand. Drawn from 35-mm transparency taken at 1/1,000 s. Note partially opened bill during downward strike and peripheral puncture of peanut from first blow.

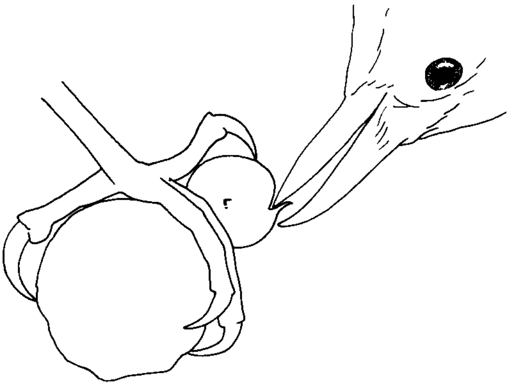

Fig. 12. *Aphelocoma coerulescens coerulescens* opening acorn. Right foot clings to branch and supports acorn. Only lower jaw penetrates shell; upper jaw is in position for grasping.

the inner front toe of one foot or held between the feet (Fig. 12). The inner toe rested on the acorn with the claw angled downward against the shell. Most acorns plucked from trees or picked from the ground lacked cups, but if a cup were present, several blows at the edge of the cup removed it. Powerful blows of the slightly opened bill, involving motion of the whole body, were directed roughly tangential to the surface of the acorn. Only the lower mandible struck the acorn; upon breaking the shell it penetrated between the shell and the meat (Fig. 12). The shell was then struck again, or a portion was grasped between the mandibles and torn off by a twist of the head. Further blows and twists removed more shell, and the acorn was turned periodically so that the same pounding motion enlarged the opening in its wall. [After making these observations, I found that Brown (1964) noted similar behavior in Steller's Jay (*Cyanocitta stelleri*).] When about two-thirds of the shell on the exposed half of the acorn had been removed, the birds repeatedly drove both mandibles into the exposed nut, removing pieces and storing them in the throat until about half of the meat had been removed. Acorns were usually dropped and discarded with considerable portions uneaten.

Use of the lower mandible as a chisel apparently is related to the process of peeling the tough, seamless shell of acorns before extracting the meat. Blows directed somewhat tangentially to any curved object would be especially effective for peeling because the mandibles would be in position to grasp and remove pieces of shell. A blow from the lower mandible would push the acorn against the branch and against the bracing toe. Rotation of the acorn about its axis at the moment of impact is apparently limited by the toe and claw, and by friction with the bark. If the upper mandible alone were to strike a roughly tangential blow such that both mandibles could grasp a portion of the shell, it could strike only the inner surface of the acorn and drive the nut off the branch.

Comparison with other species.—Many corvids that lack the buttress complex pound their food, and some that lack the buttress eat acorns (*Garrulus glandarius*; Lanceolated Jay, *G. lanceolatus*; Lidth's Jay, *G. lidthi*; Black-billed Magpie, *Pica pica*; *P. nuttalli*; Azure-winged Magpie, *Cyanopica cyana*; Eurasian Jackdaw, *Corvus monedula*; Eurasian Rook, *C. frugilegus*; and Common Raven, *C. corax*; Goodwin 1986). *Garrulus* opens acorns by biting and prying rather than by hammering, according to Goodwin (1951). He did not state whether the hooked tips of the mandibles, the tomial edges, or both, are used for biting. Biting an acorn rather than stabbing it may be feasible only for a large, powerful bird such as *Garrulus glandarius* (approximately twice the body mass of *Aphelocoma coerulescens*) because penetration of the shell depends solely on forces applied through the lever system of the jaws by the jaw muscles. Bossema (1979) noted that *G. glandarius* readily dehusked the thin-shelled acorns of the native Eurasian oak, *Quercus robur*, but usually did not succeed in opening the thicker shells of the introduced New World oak, *Q. rubra.*

The Yellow-billed Magpie lacks the buttress complex. It pounds acorns, and leverage of the entire body is applied to the blows. Sometimes hundreds of blows, in series of about 20, are required to open the shell. A bird commonly discards any acorn that proves difficult to open (Bent 1946). It is not clear from the description by Bent (1946) whether both mandibles, or only one, are used in pounding, but the wedge-shaped tips of both mandibles imply that both are used.

Florida Scrub Jays that I observed usually penetrated the wall of the acorn on the third or fourth blow, tore off pieces of shell by about the tenth blow, and removed meat after 15–20 blows. In the Mexican Jay (*Aphelocoma ultramarina*) "a few strong pecks usually open most nuts or break up large insects" (Westcott 1969).

These scant observations suggest that stabbing with a lower jaw supported by a buttress complex is an unusually effective and rapid method of shelling an acorn, even for a small bird; biting may be effective only on thin-shelled acorns and by a large bird. Pounding, perhaps with both mandibles, is relatively ineffective even in some large corvids.

It is important to know whether sole use of the lower mandible in pounding occurs in corvids such as the American Crow that are generalized feeders and that lack the buttress complex. On two occasions I observed feeding behavior of a captive American Crow that was offered unshelled peanuts and chicken bones held in the hand. Its method of removing soft tissue from bones, attacking the cartilagenous end of a long bone, or breaching a peanut shell held in the hand was to peck with the bill tip or to grasp with the tomial edges of one side of the bill. Pieces were pulled or twisted off. Exploratory biting or pecking with the bill tip sometimes was done with the bill opened wide. The edge of any hole made in compact bone or in the peanut shell by these means was pecked more vigorously with the bill nearly closed. The blows were not perpendicular to the surface but at a shallow angle, so that only the lower mandible penetrated the bone. The compact bone of a long chicken bone was then grasped with both mandibles, and pieces were pulled or twisted off. After a sufficient hole was made in the end of the bone, the bird inserted its lower mandible into the marrow cavity and scraped it backward against the inner surface of the compact bone, extracting marrow. When given a peanut the crow held it against a branch and pecked it tentatively with both mandibles. It then pecked more vigorously with the bill slightly open, penetrating with the lower mandible at an acute angle to the surface. These motions were much like those used by the Florida Scrub Jay in peeling an acorn, but the crow's approach to hard foods was more exploratory and less stereotyped than that of the jay.

FUNCTIONAL ANALYSIS

The following discussion of *Pica nuttalli* and *Aphelocoma coerulescens* is based on the known pounding behavior of *Aphelocoma; Pica* is analyzed as if it pounded in the same way. I consider only the minimum number of force components that could maintain stability of the lower jaw at the moment of impact while pounding. In life, additional forces from other jaw muscles probably are involved. The positions and directions of forces were estimated on skulls with the jaws partially open—the position in which the rostral condyle and cotyla of *Aphelocoma* fit together most closely (Fig. 13). The y-axis of the quadrate is positioned to intersect both articulations of the quadrate.

The lower jaw articulates with the quadrate, which in turn articulates with the cranium, the palate, and the jugal bars. When the lower jaw is moderately depressed, the force of a blow by the lower mandible could be transferred to the quadrate, causing caudal rotation of the quadrate and retraction of the palate and upper jaw. Such motions and the resistance of the kinetic mechanism would absorb the shock of the blow and dissipate its force at the jaw articulation. Concomitantly, the force of the blow on the food item would be reduced. For this analysis I assumed that stability of the lower jaw and quadrate relative to the cranium is most advantageous for pounding [see also Spring (1965) regarding woodpeckers], and that shock absorbing would be accomplished with little or no movement of the kinetic mechanism. The discussion of forces therefore is based on an assumption of static equilibrium. Forces on the lower jaw, quadrate, and cranium are analyzed separately.

Species without a buttress complex.—Before pounding, the partially opened lower jaw probably is shifted caudally and held in position by

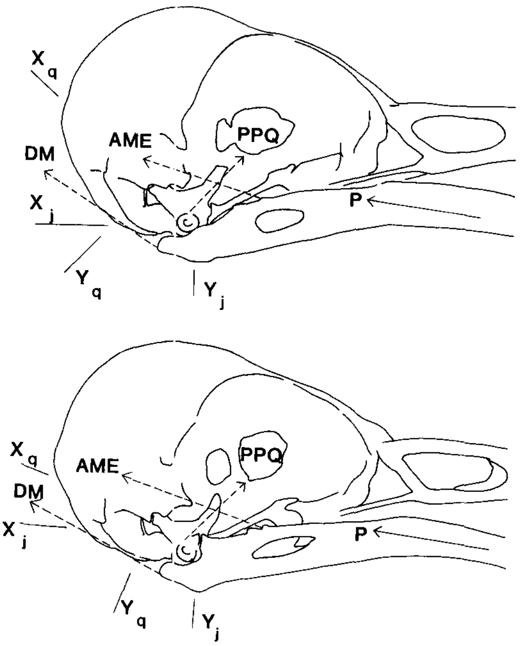

Fig. 13. Skulls of *Pica nuttalli* (top) and *Aphelocoma coerulescens* showing basis for force diagrams in Figs. 14–16. Skulls drawn at comparable size and oriented with the lateral surface of the lower jaw on the horizontal plane. Dashed arrows indicate estimates of directions of muscle forces; solid arrow is force of pounding by tip of lower mandible, set parallel to long axis of distal portion of ramus. Axes of lower jaw (x_j, y_j) and quadrate (x_q, y_q) are indicated outside of skull. AME = M. adductor mandibulae externus, DM = M. depressor mandibulae, P = force of pounding, PPQ = M. protractor pterygoidei et quadrati.

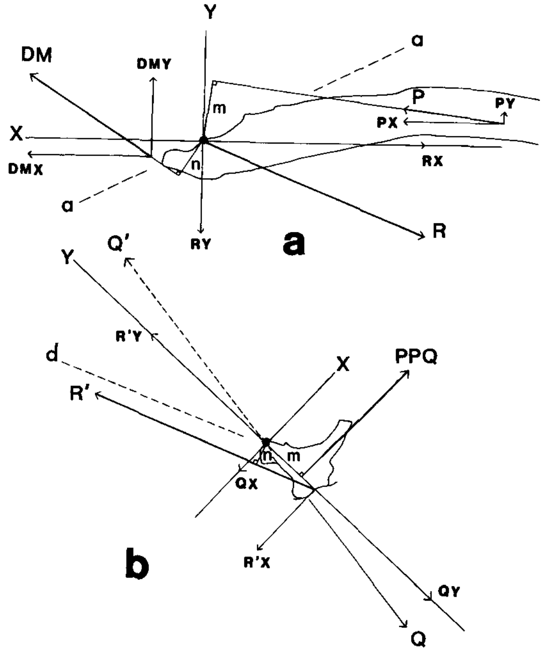

Fig. 14. Force diagram for lower jaw (a) and quadrate (b) of *Pica nuttalli*, right lateral view. Force vectors on lower jaw are P (pounding force, set at 10), DM (M. depressor mandibulae), and R (force from quadrate equal and opposite to resultant of forces P and DM). Lengths of force arrows proportional to amount of force, determined graphically by assuming sum of torques = 0, and sum of forces on x- and y-axes = 0. Components of all force vectors parallel to x- and y-axes shown (e.g. PX and PY of P); m and n are moment arms. Dashed line **a** parallels plane of articular surface; solid circle is point of rotation.

Forces on quadrate are R′ (resultant of P and DM from lower jaw), PPQ (M. protractor pterygoidei et quadrati), and Q (force from cranium at point of rotation equal and opposite to resultant of R′ and PPQ). Dashed line **d** parallels dorsal rim of tympanic cavity; dotted arrow **Q**′ is force on cranium equal and opposite to Q; solid circle is point of rotation; m and n are moment arms.

muscle antagonists such as the depressor mandibulae and mandibular adductors. Although the adductors may continue to contract during pounding, I will describe only the simplest possible case. The forces that act on the lower jaw are P (pounding force), DM (force of M. depressor mandibulae), and R (force from quadrate equal and opposite to resultant of P and DM) (Fig. 14a). The force vector (P), arbitrarily set at 10, exerts a negative torque (counterclockwise in right lateral view) on the lower jaw about its articulation on the quadrate ($P \cdot m$), and the depressor (DM) exerts a positive (clockwise) torque ($DM \cdot n$). The sum of these torques in a stable state would be zero [$(DM \cdot n) - (P \cdot m) = 0$]. Force vectors P and DM can be resolved into positive (dorsal) vectors parallel to the y-axis of the lower jaw (PY, DMY) and negative vectors (caudal) parallel to the x-axis (PX, DMX); vector R has a positive component (RX) on x and a negative component on y. Again, the sum of the forces on the x- and y-axes of the lower jaw would be zero ($RX - DMX - PX = 0$, $DMY + PY - RY = 0$).

Forces on the quadrate are R′ (resultant of P and DM from the lower jaw; Fig. 14a), PPQ (force of M. protractor pterygoidei et quadrati, parallel to the x-axis), and Q (force from cranium equal and opposite to resultant of R′ and PPQ; Fig. 14b). Force R′ would produce positive

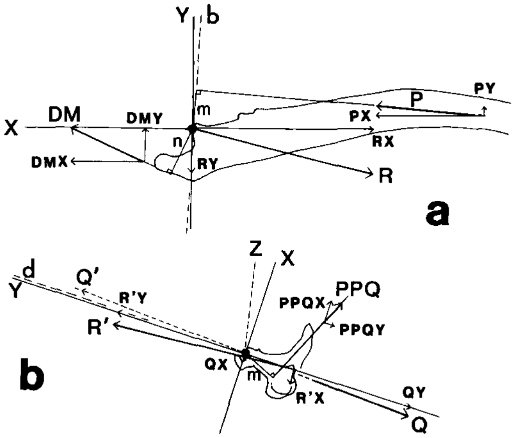

Fig. 15. Force diagram for lower jaw (a) and quadrate (b) of *Aphelocoma coerulescens coerulescens*, right lateral view. Forces calculated as in Fig. 14 (see text), but center of rotation shifted to rostral cotyla. Dashed line **b** parallels plane of articular surface of buttress, and **z** parallels plane of facet of meatic process.

Analysis of quadrate and symbols as in Fig. 14, but PPQ has components parallel to x- and y-axes. Moment arm n too short to be labeled.

(clockwise) torque on the quadrate about its cranial articulation ($R' \cdot n$), which in turn could be neutralized by negative torque from the protractor pterygoidei et quadrati muscle ($PPQ \cdot m$); $(R' \cdot n) - (PPQ \cdot m) = 0$. The force from the lower jaw (R') has a positive (caudodorsal) component on the y-axis of the quadrate (R'Y); in addition, it has a negative (caudoventral) component (R'X), and the protractor muscle a positive component (PPQ), parallel to the x-axis. Force Q has a negative component on the y-axis (QY) and a negative one on the x-axis (QX). The sum of all force vectors on the x- and y-axes would equal zero ($R'Y - QY = 0$, $PPQ - QX - R'X = 0$).

The cranium receives a force (Q') from the quadrate equal to the resultant of R' and PPQ (Fig. 14b). This force acts at an angle of about 30° to the dorsal rim of the tympanic cavity (d). Forces on the cranium would be neutralized by equal and opposite forces from the neck.

In the case just described, the equal and opposite force (R and R') at the jaw articulation do not act perpendicular to the articular surface (a) but at an angle of 49° to it. The lower jaw would slide caudally on the quadrate unless stabilized by another force. I think that the articular capsule is incapable of resisting strong forces and that isometric contraction of other jaw muscles, especially M. pterygoideus, would be needed.

Species with a buttress complex (Fig. 15).—In birds with a buttress, the point of rotation of the lower jaw is at the rostral cotyla, not at the usual articular surface, when the jaw is partially opened and shifted caudally. The analysis of forces (Fig. 15a) is the same as for *Pica* (Fig. 14). The resultant R' of forces P and DM on the lower jaw acts on the quadrate, which exerts an equal and opposite force (R) at an angle of 79° to the articular surfaces of the buttress (b). Sliding of the lower jaw on the quadrate would be prevented by the combined resistance of the buttress and the other articular surfaces, and contraction of M. pterygoideus would be unnecessary.

Analysis of forces on the quadrate (Fig. 15) is the same as for *Pica* (Fig. 14b), but PPQ does not parallel the x- or y-axis and therefore has a component parallel to each axis. Force from the lower jaw (R') imparts a weak positive torque to the quadrate; both the force and its moment arm are less than in *Pica.* The force of the protractor pterygoidei et quadrati necessary to neutralize torque on the quadrate is correspondingly reduced. The sum of the torques is zero [$(R' \cdot n) - (PPQ \cdot m) = 0$; n is too short to be labeled in Fig. 15b]. A force (Q) equal and opposite to the resultant of R' and PPQ acts on the quadrate at its cranial articulation. At static equilibrium, forces on the x- and y-axes are: $PPQX - QX - R'X = 0$ and $PPQY + QY - R'Y = 0$. The effect of forces on the quadrate during pounding is almost exclusively one of compression along the y-axis of the quadrate.

As shown in Fig. 15b, the quadrate exerts a force (Q') on the cranium nearly parallel (2°) to the dorsal rim of the tympanic cavity (d) and approximately perpendicular (76°) to the articular facets of the meatic and suprameatic processes (z). Thus, compression forces are probably dispersed through these articular surfaces to the thickened dorsal rim of the tympanic cavity. The dorsal rim (d) lies along the line of force (Q' in Fig. 15), unlike the case for species without a buttress (Fig. 14).

Effective pounding by the lower jaw requires stability of the partially opened jaw. Stability would be maximal if the force (R) from the quadrate on the lower jaw acted at 90° to its articular surface and if the equal and opposite force (R') on the quadrate imparted no torque to the quadrate. Maximum stability is achieved in neither of the cases analyzed above; stability

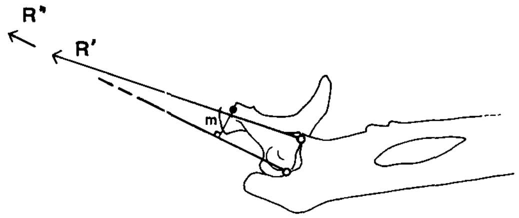

Fig. 16. Force diagram for lower jaw and quadrate of *Aphelocoma coerulescens coerulescens*, left lateral view. R′ is force on quadrate from lower jaw as in Fig. 15b. R″ is force (shortened to save space) from lower jaw recalculated after hypothetical shift of point of rotation from rostral cotyla to lateral cotyla (open circles). Torque on quadrate about point of rotation (solid circle) equals force × moment arm (m; moment arm of R′ too short to label): for R′ index of torque = 7 (17.4 × 0.4), for R″ torque = 67 (31.9 × 2.1).

therefore would benefit by reduction of the force transmitted through the jaw articulation in both cases. Figures for some of these parameters in the hypothetical situations I described are given in Table 1. Note that *Aphelocoma* exceeds *Pica* in these measures of stability. The magnitude of torque on the quadrate is size related, and comparisons between *Pica* and *Aphelocoma* are therefore not meaningful. However, in *Aphelocoma* torque is much increased if the buttress is assumed to be absent and the point of rotation shifted to the lateral condyle as in *Pica* (Fig. 16: see legend).

The total amount of muscle force required to maintain stability of the lower jaw during pounding would be one measure of efficiency of the system; the total muscle force in *Aphelocoma* is about one-third that of *Pica* (Table 1).

Although we do not know all of the forces and muscles involved in pounding by live birds, the results presented above are not peculiar to the simplified example chosen. I have also analyzed forces in the system with the addition of the pseudotemporalis superficialis or adductor mandibulae externus muscles, with different amounts of force by various muscles and with different forces of pounding. The exact amounts differ from those shown in Table 1, but all of the conclusions remain the same.

I hypothesize that the presence of a buttress complex increases efficiency by reducing the muscle force necessary to stabilize the lower jaw while pounding. Resistance to compression of the quadrate contributes more to stabilization than it does in birds without a buttress. This effect is achieved by a change in the position of the point of rotation of the lower jaw on the quadrate such that torque on the quadrate is reduced, and by an approach toward perpendicular orientation of the rostral and meatic articular surfaces to the forces acting on them. Stability in birds without a buttress might be achieved by isometric contraction of the pterygoideus muscle and other jaw muscles.

TABLE 1. Hypothetical force analysis of *Pica* and *Aphelocoma* during pounding with the lower jaw. See Figs. 14 and 15 for diagrams of species.

Measure	*Pica nuttalli*	*Aphelocoma coerulescens*
Angle of resultant vector of forces on jaw to plane of articular surface[a]	49°	79°
Index to amount of force on quadrate from lower jaw[b]	24	17
Index to total muscle force on jaw and quadrate[c]	32	10

[a] Angle of R′ to a (= R to a).
[b] Length of vector R′.
[c] Length of vectors DM + PPQ.

DISCUSSION

Systematic implications.—Published evidence for monophyly of the New World jays is weak and based on poorly defined similarities without evidence for polarities of the characters. The similarities include plumage features (Amadon 1944, Hardy 1969), vocalizations (Hardy 1969), and pterylosis (Clench 1985). One aspect of the jaw articulation, however, strongly suggests that the buttress had a common origin within the Corvidae and is synapomorphous at that level. The medial portion of the lateral cotyla of the mandible and the medial portion of the lateral condyle of the quadrate meet and brace the lower jaw when it is partially open and shifted caudad in some species of *Cyanolyca.* This contrasts with other corvids and with related families (Artamidae, Cracticidae, Paradisaeidae, and Oriolidae; see Appendix) in which the entire lateral condyle or its lateral portion braces the lower jaw. It is precisely from the medial sectors of the lateral cotyla and lateral condyle that the rostral cotyla and rostral condyle of the buttress complex are formed (Fig. 7). Evolutionary development of the buttress complex probably occurred by a dorsal migration and enlargement of the medial contact point, and by strengthening the cranial articulation of the quadrate. Absence of the buttress in some species and individuals of *Cyanolyca* may reflect either evolutionary reversal or unexpressed genetic potential within the genus.

The several stages of development of the buttress complex within *Cyanolyca* and *Cyanocorax* can be arranged in a stepped morphocline (Figs. 7 and 8, Appendix), but it is not known whether the intermediate stages found in *Cyanocorax* represent progressive or retrogressive steps in evolution. Whether the buttress complex developed only once within New World jays or more than once from a rudimentary state cannot be determined without a robust phylogeny of the group. The most parsimonious interpretation of this character complex implies that *Cyanolyca* represents the sister group of the remaining genera of New World blue jays: *Cyanocorax, Psilorhinus, Calocitta, Cissilopha, Aphelocoma, Cyanocitta,* and *Gymnorhinus.*

The presence of the buttress complex in the Pinyon Jay (*Gymnorhinus cyanocephala,* Fig. 17) supports other evidence that *Gymnorhinus* is a member of the New World jay group (Amadon 1944, Ligon 1974) and counters the evidence for relationship with Old World corvines such as *Nucifraga* (Hardy 1969). *Gymnorhinus* and *Nucifraga* appear to be evolving within similar environmental parameters, and they have converged in many aspects of morphology and behavior. The relatively long, slender, and pointed bills of Clark's Nutcracker (*Nucifraga columbiana*) and the Pinyon Jay, both of which feed extensively on pine nuts, are used for stabbing into unripe cones, hammering on bark, probing into the ground, and reaching into ripe cones and crevices in bark (Balda et al. 1972, Tomback 1977). Nutcrackers open pine nuts at their seams by applying pressure with both mandibles or by blows directed at the seam of a nut held by the toes (Bunch et al. 1983). It is not known whether Pinyon Jays and nutcrackers use the lower jaw differently in pounding.

Specialization on acorns.—Acorns are an important food in *Aphelocoma coerulescens* (Woolfenden and Fitzpatrick 1984), *A. ultramarina, Cyanocitta stelleri, C. cristata,* and probably *Cyanocorax yncas* (Green Jay; Goodwin 1986) and *C. dickeyi* (Tufted Jay; Crossin 1967). All of these species have the buttress complex well developed; foods and feeding behavior of other species in these genera are not well known. Although the buttress complex is used effectively in opening acorns, one cannot safely assume that its origins were related to acorn eating or that its use in all species is associated with opening nuts. Many species with a buttress complex are not known to eat acorns (*Cissilopha, Calocitta, Psilorhinus*). However, feeding habits of most of those species are poorly known (Goodwin 1986), and they may eventually be shown to do so. Probably only one species of oak occurs southward into the Andes of Colombia (Muller 1942), yet 10 of the 11 species of *Cyanocorax,* all of which have the buttress complex, occur in South America beyond the range of oaks. Tropical New World jays are known to eat a variety of tough, spherical foods (palm fruits, snails, beetles, shelled eggs) that could be opened effectively by piercing with the lower mandible.

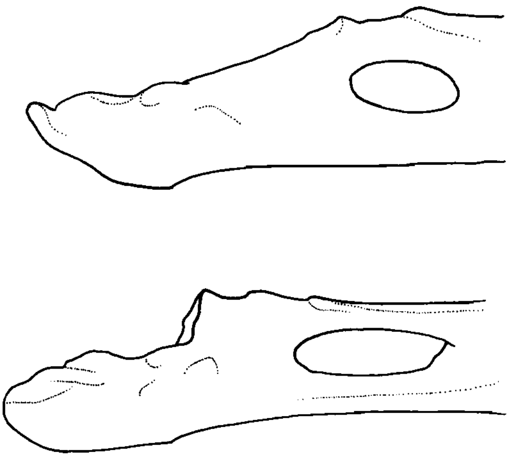

Fig. 17. Lateral view of right mandibular ramus of *Nucifraga columbiana* (top) and *Gymnorhinus cyanocephala* (bottom).

Acorn eating has not been recorded for the genus *Cyanolyca* (Goodwin 1986). Skutch (1967) described foraging of the Black-throated Jay (*Cyanolyca pumilo*) in humid forest, largely of oaks and pines with many epiphytes, as a thorough and methodical search for insects and spiders on the foliage, branches, curled leaves, and epiphytes of trees, undergrowth, and vine tangles. Curled leaves were plucked, held against a branch with one foot, and pulled apart with the bill. The Dwarf Jay (*Cyanolyca nana*) was studied by Hardy (1971) in Mexican forests where oaks were dominant, but he found no evidence of acorn eating. The birds commonly removed oak galls from the backs of oak leaves, however, and hammered them open "in typical corvid fashion." Whether the blows were essentially tangential to the gall and struck with the lower mandible alone was not noted. Early development of the buttress probably was associated with breaking and peeling of a variety of foods. With greater development it became effective in opening hard nuts, which then assumed great importance in the diet of some species.

Many species of the Corvidae are omnivorous and without obvious specializations for feeding. The discovery of a buttress system related to opening shelled foods suggests that diversified feeding behavior may be based in part on the presence of special adaptations. Such adaptations are not characteristic of the entire family, but have evolved independently in different phyletic lines. For example, at least three methods for opening acorns occur in the Corvidae: biting in *Garrulus*, pounding with both (?) mandibles in *Pica*, and pounding with the lower mandible in *Aphelocoma*, *Cyanocitta*, and probably other New World jays. Associated structural modifications in *Aphelocoma* are described here; the first two examples have not been studied. Much information on feeding behavior and morphology is presently lacking.

Adaptation.—I regard the buttress complex as an adaptation. Although it is not necessary or even desirable to link natural selection to the definition of adaptation (Greene 1986), most definitions of adaptation include natural selection as its explanation: "... unless a feature that is now fixed in the population can be proven to have arisen by a series of changes, each associated with increasing reproductive superiority over the previous, the adaptive nature of its origin and its present status as an adaptation remains in the realm of probability" (Stern 1970: 46). Regrettably, reproductive superiority over that of an ancestor can never be demonstrated, and reproductive superiority over a living relative, if demonstrable, is difficult to relate causally to a particular "adaptation." Nevertheless, the buttress complex represents an apomorphy with several performance advantages that may have improved the fitness of the populations in which it developed. First, field studies reveal a new biological role—opening of hard foods—related to use of the lower jaw in feeding in at least some of the endemic New World jays that have full development of the buttress complex. Second, a hypothetical analysis of forces acting to stabilize the lower jaw in species with and without a buttress complex suggests that less energy is required to stabilize the jaw while pounding if a buttress is present. Third, preliminary observations suggest that acorns are opened more effectively in corvids that pound with the lower jaw, supported by a buttress complex, than in those that use other methods in the absence of the complex. (A better test, however, would be a comparison of acorn eating within New World jays with, and without, a buttress.) The ability to eat and cache acorns or other nuts provides a source of food throughout the year (Woolfenden and Fitzpatrick 1984: 44), which in turn may influence reproductive patterns (Balda and Bateman 1973, Tomback 1977). Development of these capabilities in New World jays apparently was independent of similar trends in other corvids.

It is tempting to regard the buttress complex as a key adaptation, or a key innovation, that led to the diversification of New World jays. To do so, however, would require evidence that the innovation was linked to increased speciation rates (Lauder 1981) and diversification at the generic level. Such evidence is presently lacking.

Pounding with the lower jaw occurs in at least one corvid that lacks the buttress. Stabilization of the lower jaw probably could be effected in that species by isometric contraction of jaw muscles. As suggested above, strong and frequent pounding may require a more efficient means of stabilization, such as the buttress complex. This conclusion is supported by an example of convergent evolution. The Akiapolaau (*Hemignathus wilsoni*), a Hawaiian honeycreeper, exposes hidden insects by pounding into wood with its short, straight lower mandible, while raising the long, decurved upper mandible out of the way (Berger 1981). Its congener, the Nukupuu (*H. lucidus*), does not use the curved lower mandible for pounding. The Akiapolaau has a buttress on the lower jaw, whereas the Nukupuu does not. The mandibular buttress of *H. wilsoni* is formed by dorsal curvature of the rostral surface of the medial cotyla. There is no new condyle on the quadrate; instead, the medial condyle is much enlarged and its surface is oriented rostroventrally. Upon protraction of the quadrates to raise the upper jaw, this surface faces more directly rostrad and firmly abuts the medial mandibular cotyla. The force of pounding presumably is transmitted directly through the articulation of the quadrate and cranium. A meatic process of the quadrate does not exist;

instead, the otic and squamosal articular facets are broad and reinforced by a descending rostral process from the cranium. The buttress of *Hemignathus wilsoni* shares several functional and morphological similarities with that of jays, but the system is built on the medial cotyla and condyle rather than on the lateral ones, and the specific feeding method is entirely different.

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APPENDIX. Species and number of specimens examined, grouped by degree of development of buttress complex characterized in Figs. 7 and 8 (a-d). Specimens of *Cyanolyca* identified individually: LSU (Louisiana State University Museum of Natural Science), ML (Occidental College, Moore Laboratory of Zoology), MVZ (Museum of Vertebrate Zoology), UMMZ (University of Michigan Museum of Zoology), USNM (National Museum of Natural History).

a[a]

Artamidae

Artamus fuscus (2), *A. leucorhynchus* (2).

Cracticidae

Cracticus nigrogularis (1), *Gymnorhina tibicen* (2), *Strepera graculina* (2), *S. versicolor* (1).

Paradisaeidae

Loboparadisea sericea (2), *Lyocorax pyrrhopterus* (10), *Lophorina superba* (1), *Diphyllodes magnificus* (2), *Paradisea raggiana* (1).

Oriolidae

Oriolus chinensis (2), *O. oriolus* (10).

Corvidae

Platylophus galericulatus (2), *Platysmurus leucopterus* (1), *Garrulus glandarius* (2), *Perisoreus canadensis* (5), *P. infaustus* (1), *Urocissa caerulea* (2), *U. erythrorhyncha* (10), *Cissa chinensis* (9), *Cyanopica cyana* (4), *Dendrocitta vagabunda* (3), *D. occipitalis* (1), *D. formosae* (1), *Crypsirina temia* (3), *Pica pica* (10), *P. nuttalli* (4), *Podoces hendersoni* (3), *Pseudopodoces humilis* (3), *Nucifraga columbiana* (10), *N. caryocatactes* (3), *Pyrrhocorax pyrrhocorax* (3), *P. graculus* (2), *Ptilostomus afer* (3), *Corvus monedula* (5), *C. dauricus* (5), *C. splendens* (4), *C. enca* (2), *C. validus* (3), *C. tristus* (1), *C. capensis* (2), *C. frugilegus* (5), *C. brachyrhynchos* (10), *C. caurinus* (2), *C. ossifragus* (5), *C. palmarum* (5), *C. jamaicensis* (2), *C. nasicus* (5), *C. leucognaphalus* (5), *C. corone* (5), *C. macrorhynchus* (5), *C. orru* (3), *C. coronoides* (1), *C. torquatus* (5), *C. albus* (5), *C. tropicus* (1), *C. cryptoleucus* (5), *C. corax* (5), *C. rhipidurus* (1), *C. albicollis* (4), *C. crassirostris* (1).

Cyanolyca argentigula argentigula (USNM 429795, 429796), *C. viridicyana jolyaea* (LSU 65043, 90158, 114283), *C. pumilo* (ML S-265).

a > b[b]

Cyanolyca pumilo (UMMZ 209295, ML S-111, S-251, S-746, S-983), *C. mirabilis* (ML S-654), *C. nana* (ML S-1046), *C. viridicyana quindiuna* (USNM 428792, 428794), *C. cucullata cucullata* (UMMZ 133985), *C. pulchra* (USNM 371385—skin).

b[c]

Cyanolyca cucullata mitrata (UMMZ 209292), *C. viridicyana turcosa* (LSU 81314), *C. nana* (UMMZ 209298, ML S-674, S-705, S-873).

c

Cyanocorax caeruleus (3), *C. cyanomelas* (8), *C. violaceus* (5), *C. cristatellus* (2), *C. heilprini* (USNM 329484, skin), *Psilorhinus morio* (10), *Calocitta formosa* (4).

d

Cyanocorax cayanus (1), *C. affinis* (8), *C. chrysops* (9), *C. mystacalis* (2), *C. dickeyi* (1), *C. yncas* (10), *Cissilopha melanocyanea* (3), *C. sanblasiana* (9), *C. beecheii* (1), *Aphelocoma coerulescens* (10), *A. ultramarina* (10), *A. unicolor* (2), *Cyanocitta cristata* (10), *C. stelleri* (10), *Gymnorhinus cyanocephala* (10).

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[a] Rostral slope of lateral cotyla of lower jaw may have slightly raised ridge; if so, contact is with entire lateral condyle of quadrate or only its lateral portion in partially opened lower jaw.

[b] Rostral slope of lateral cotyla of lower jaw steeper than in most species of category a; contact is with medial portion of lateral condyle of quadrate in partially opened lower jaw.

[c] Rostral slope of lateral cotyla steeper and more sharply ridged than above; contact with medial portion as above.