RELATIONSHIPS BETWEEN THE BIRDS OF PARADISE AND THE BOWER BIRDS

By WALTER J. BOCK

INTRODUCTION

Ever since their discovery in the early days of world exploration, the birds of paradise and the bower birds have held the interest of ornithologists. The colorful plumage and strange courtship habits of these birds lured expedition after expedition to their homeland, until now they are among the best known groups within the passerines. Yet the possible relationships of the birds of paradise to the bower birds and the affinities of both groups to the other perching birds are, even today, as little known as they were a hundred years ago. Their colorful plumage, bizarre courtship habits, and restriction to the Australian-Papuan region are usually cited as evidence for close affinities between these groups; indeed, until recently, the birds of paradise and the bower birds were usually placed in the same family or subfamily, the belief being that a sharp dividing line could not be drawn between typical birds of paradise, such as *Paradisaea*, and typical bower birds, such as *Ptilonorhynchus*.

The starlings, crows, honeyeaters and even other passerine families have been suggested as the closest relatives of the bird of paradise-bower bird assemblage, with the crows being the choice of most recent workers. This choice is based largely on the plain black plumage, bill shape, and normal courtship habits of the presumably primitive manucodes and crow-bird of paradise (*Lycocorax*). Most of the earlier taxonomic opinions have relied on plumage and other external characters and on a very rudimentary knowledge of the morphology and life history. It is, thus, not surprising that many doubts were entertained about the validity of these conclusions since the necessary supporting evidence was lacking. Our knowledge of the life history of these birds has been greatly advanced only in the past several years (Gilliard, MS). Gathering of the anatomical data has been equally slow. Most of the past morphological studies have dealt with the structure of one or a few genera, as, for example, Berger's excellent description of the musculature of *Paradisaea* (1956; see this paper for a listing of the earlier works), but they were not of primary importance to the general systematic problems.

A major clarification of the affinities of the birds of paradise and bower birds came with the publication of Stonor's (1937) comparative investigation of their skull morphology; the other characters studied by Stonor (1936; 1938) are of lesser value and deal with the affinities between paradisaeine genera. In his work of 1937 Stonor amassed extensive data showing that the bower birds constitute a distinct group which is sharply separated morphologically from the birds of paradise. He advocated placing the birds of paradise and the bower birds in separate families, as concluded earlier by Pycraft (1907:375), and contended that the bower birds (Ptilonorhynchidae) represent an isolated family of oscine birds showing no special relationship to the Paradisaeidae or to any other oscine family. Since the publication of Stonor's paper, the bower birds have been placed in a separate family by most workers, but they are still generally regarded to be closely related to the birds of paradise (for example, Mayr and Amadon, 1951:32). This partial acceptance of Stonor's conclusions reflects the fact that some problems were left unsolved by him and still others arose from his work largely because several important genera were unavailable for examination. The main question is whether these families are absolutely and sharply distinct morphologically. Related to this is the further question of whether the birds of paradise and the bower birds are related to one another in spite of the great differences in their cranial morphology.

It was my good fortune to be able to re-examine these problems through the interest of Ernst Mayr who has long been concerned with these birds and has gathered a wealth of new anatomical material. Dr. Mayr examined the skulls of a few genera not seen by Stonor (*Ailuroedus, Cnemophilus*), but he felt that the relationships should be restudied, and in particular, that efforts should be made to uncover the functional significances and the evolutionary meaning of the morphological differences discovered by Stonor. The new material available includes genera not seen by Stonor which are most important for the new light they throw upon the problem. A preliminary study indicated that the most significant osteological differences between the two groups are the cranial features, and that these differences could be fully understood only after comparisons with related families. Hence the morphological scope of this study was restricted to the head while the taxonomic scope was extended to include the "crow-like" and the "shrike-like" oscines. This latter aspect will be covered in a separate paper. I would like at this time to declare my debt to Stonor for his work which has formed the foundation for the present study. His paper represents the initial and most important step toward clarifying the relationships of the birds of paradise and the bower birds, and although some of my conclusions differ from his, the present report may be thought of as a continuation of the research that he started.

MATERIAL AND ACKNOWLEDGMENTS

Skulls of most genera, and in many cases, several skulls of each genus, were available. Only the skulls of a few important genera, such as *Lycocorax, Macgregoria,* and *Loboparadisea,* were lacking. However, for these genera, I was able to extract the remnant of the skull from a study skin which in every case showed the important features and, in many instances, was as good as a specially prepared skull. Thus the following skeletal material was examined: Of the Paradisaeidae, the genera *Astrapia,* 3 specimens; *Cicinnurus,* 8; *Craspedophora,* 2; *Diphyllodes,* 8; *Drepanornis,* 1, from skin; *Epimachus,* 4; *Loboparadisea,* 1, from skin; *Lophorina,* 5; *Loria,* 1; *Lycocorax,* 1, from skin; *Macgregoria,* 1, from skin; *Manucodia,* 8; *Paradisaea,* 25+; *Paradigalla,* 1, from skin; *Parotia,* 5; *Phonygammus,* 2; *Pteridophora,* 1; *Ptiloris,* 2; *Seleucidis,* 7; and *Semioptera,* 4; of the Ptilonorhynchidae, the genera *Ailuroedus,* 3; *Archboldia,* 1, from skin; *Chlamydera,* 5; *Prionodura,* 1, from skin; *Ptilonorhynchus,* 15+; *Scenopoeetes,* 1, from skin; and *Sericulus* (including *Xanthomelus*), 3, plus *S. bakeri,* 1, from skin. In addition, the following alcoholic specimens were available for examination of the skull and/or dissection of the jaw muscles: *Cnemophilus*; *Loria,* 2; *Paradisaea,* 4; *Pteridophora*; *Ailuroedus*; *Amblyornis*; *Chlamydera*; and *Ptilonorhynchus.*

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In addition, I wish to thank Prof. D. Starck for making available the facilities of the Anatomisches Institut der Universität, Frankfurt a.M. where my study was completed, Mr. Poike, the institute artist, for the many excellent figures of the skull, Miss Alice Boatright for the figures of the jaw muscles, and my wife, Kitty, for checking the manuscript for errors and aiding in countless other ways.

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SKULL STRUCTURE

The Ptilonorhynchidae

The skull of *Ptilonorhynchus* is typical for the bower birds and shall form the basis of description. As seen from the side (fig. 1A), it is stout and bulbous with a short heavy bill that curves only very slightly downward. The upper jaw is typically passerine with

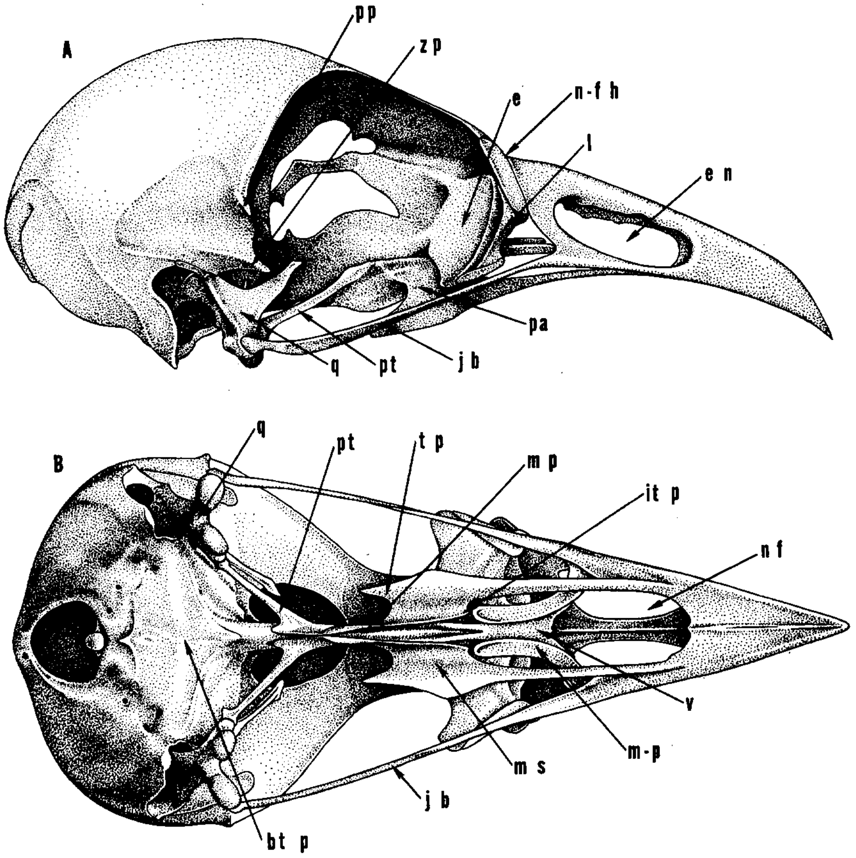

Fig. 1. Side view (A) and ventral view (B) of skull of *Ptilonorhynchus*. Abbreviations are as follows: bt p, basitemporal plate; e, ectethmoid; e n, external naris; it p, interpalatine process; j b, jugal bar; l, lacrymal; m p, mediopalatine process; m-p, maxillopalatine; m s, medial shelf of the palatine; n f, nasal floor; n-f h, nasal-frontal hinge; pa, palatine; p p, postorbital process; pt, pterygoid; q, quadrate; t p, transpalatine process; v, vomer; z p, zygomatic process.

a large oblong external naris and an unossified nasal septum, hence the naris is perforate; nevertheless the general appearance of the bill is that of strength. The nasal-frontal hinge is normally developed, that is, the bone at the junction of the nasal and frontal bones is thin and flexible, but the frontals do not curve forward over the nasal bones nor is a transverse groove present in the bone on the dorsal surface of the hinge. The ectethmoid is small and does not touch the frontal or nasal bones dorsally or the jugal bar ventrally. The lacrymal is large and abuts dorsally with the frontal and nasal bones and approaches the jugal bar ventrally; its structure is unique for the Oscines and is paralleled in size and shape only by the lacrymal of the lyrebird (*Menura*) in the Passeres. The orbital region is typically passerine with the orbit comprising slightly more than one-third of the total skull length. Both the postorbital and the zygomatic processes are present with the zygomatic process ending forward of the ventral tip of the postorbital process; both processes are of medium length and only moderately separated by the temporal fossa. The rest of the brain case is typically passerine. The quadrate is well developed with a long, thin orbital process (fig. 2A) that ends in a small expansion, one that is smaller than the distal expansion seen in *Paradisaea*. The posterior articular condyle of the quadrate is lacking. The pterygoid is of medium length and approaches the palatine at a moderate angle (about 30°); it lies at an angle to the jugal bar, not parallel to it. The jugal bar is relatively straight and thin.

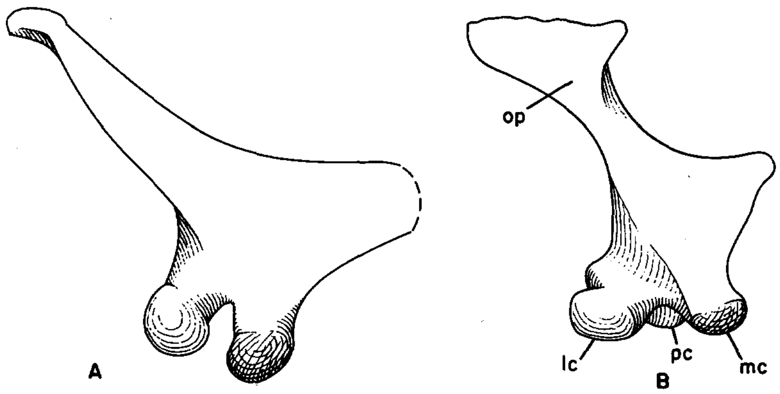

Fig. 2. The quadrate of *Ptilonorhynchus* (A) and of *Paradisaea* (B), redrawn from Stonor (1937). Note the absence of the posterior condyle and the deep groove between the medial and lateral condyles in *Ptilonorhynchus*. lc, lateral condyle of the quadrate; mc, medial condyle of the quadrate; op, orbital process of the quadrate; pc, posterior condyle of the quadrate.

The ventral aspect of the skull of *Ptilonorhynchus* (fig. 1B) is characterized by the short, heavy upper jaw whose lateral edges taper relatively evenly from its base to its tip, and by the lack of ossification of the nasal septum and floor. The palatines are set widely apart at their junction with the premaxilla and they run parallel to one another throughout their entire length. Their outer edge is not thickened, and the transpalatine process is expanded at its base but comes to a point posteriorly. Together, the palatine shelf and the transpalatine process form a diamond-shaped shelf of bone. The interpalatine process is short and blunt; it is almost absent, a condition which is related to the large maxillopalatine. The pterygoids are normal and have a low, blunt dorsal process near their quadrate articulation. The vomer is typically passerine with a long posterior diastema and a broad anterior plate of bone which is notched anteriorly. The maxillopalatines are large and cover a large part of the vomer; their expanded distal ends almost reach the interpalatine process. The thin jugal bars converge gradually as they run from the quadrates to the upper jaw. Only the lateral and medial condyles of the quadrate are present; they are both well developed and are separated from one another by a sharp, deep groove (see fig. 2A). The body of the quadrate is braced medially by the outer wall of the eustachian tube. All other features of the skull base and occipital plate are typically passerine and need not be described separately.

The lower jaw of *Ptilonorhynchus* when seen from the side is bent ventrally at its midpoint, thereby reflecting the curvature of the upper jaw. Anteriorly, the two rami are fused together for about one-fifth of their length to form a short, heavy plate of bone. The rami are deep and heavy. At the midpoint of the mandibular foramen, the dorsal edge of the mandible bends sharply downward toward the articular region. Two sharply defined bony knobs, which serve as points of insertion for parts of the M. adductor mandibulae externus, are present on the dorsal edge of the mandible at the point where it begins to slope downward. Both the retroarticular and the internal processes of the mandible are long (fig. 3A); the latter is very elongate and curves forward, a quite unusual condition for passerine birds. There is no connecting plate of bone between these processes and therefore there is no posterior wall for the articular cavity of the mandible as is found in *Paradisaea*. Near the base of the internal process is a small bony knob which serves as the point of insertion for the occipitomandibular ligament. On the medial side of the mandibular ramus is a small, but rather distinct knob which is the point of insertion for the M. pseudotemporalis superficialis. Although this process is present in many birds, it has apparently never been named. Because it is not definitely known exactly which bone of the lower jaw forms this process and because the process always serves as the point of insertion for the M. pseudotemporalis superficialis, I would suggest that it be called the pseudotemporal process of the mandible. In many

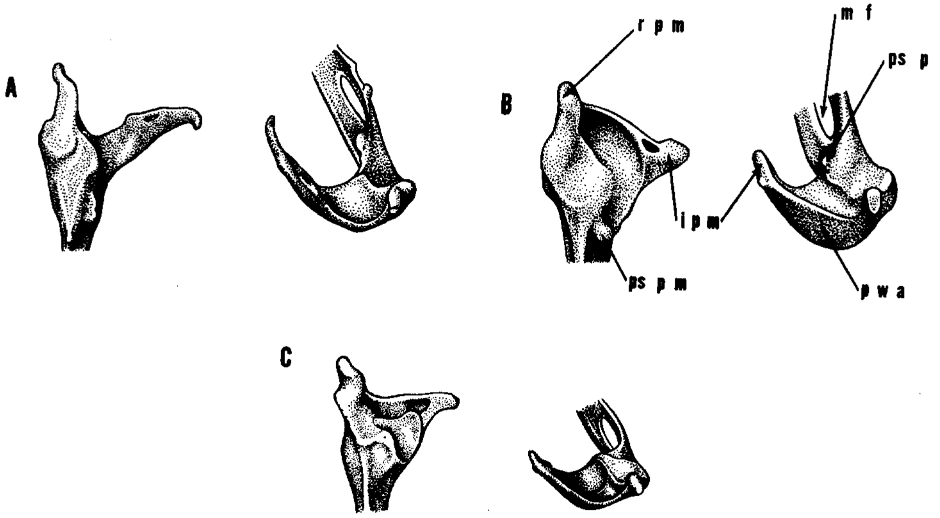

Fig. 3. The mandible of *Ptilonorhynchus* (A), *Paradisaea* (B), and *Loria* (C), showing the articular region seen from above and from behind and above. i p m, internal process of the mandible; m f, mandibular fossa; ps p m, pseudotemporal process of the mandible; p w a, posterior wall of the articular cavity; r p m, retroarticular process of the mandible.

birds, this process apparently develops directly from the ossified Meckel's cartilage, as for example in *Rhea, Otis* and *Rynchops*. In the ploceid finch, *Pyromelana,* Engelbrecht (1958:153, 157, 194) states that a cartilaginous nodule is closely applied to the dorsal surface of Meckel's cartilage and presumably ossifies with the Meckel's cartilage in still later stages (Engelbrecht did not describe the ossification of the chondrocranium). Engelbrecht did not name this nodule or the resulting process of the mandible, but simply referred to it as a "cartilaginous nodule." (I wish to thank Dr. J. Müller of the Anatomisches Institut, Frankfurt, for calling this fact to my attention and for showing me Engelbrecht's paper.) The pseudotemporal process of *Ptilonorhynchus* is much better developed than that seen in *Paradisaea.*

The bower birds form a highly uniform group in regard to their bill shape and skull morphology. The preceding description of the skull of *Ptilonorhynchus* can well serve generally for other genera of bower birds; I shall note only the major points of difference.

The genera *Amblyornis* (alcoholic specimen examined), *Archboldia* (only the lacrymal was exposed and examined in a study skin), *Chlamydera,* and *Sericulus* (including *Xanthomelus*) are very similar to *Ptilonorhynchus* in all details. Of special interest is *Sericulus bakeri* a brightly colored bird that does not build a bower (Gilliard, personal communication). A study skin of this form was available from which I could determine the presence of the lacrymal of the typical bower bird configuration. The nasal septum of *Ailuroedus* is partly ossified, but there is no hint of ossification of the nasal floor. The outer edge of the palatine is somewhat thicker than the rest of the bone, and the transpalatine process is narrower and ends in more of an elongated point than in *Ptilonorhynchus,* but its shape is still different from that in *Paradisaea.* In *Prionodura,* the ectethmoid is bulbous and much larger than that in *Ptilonorhynchus* with the lacrymal being much smaller. Nevertheless, the lacrymal has the same shape as seen in the other bower birds and it separates the ectethmoid from the frontal and nasal bones. The bulbous ectethmoid reaches the palatine and appears to be in contact with the lateral edge of that bone. Possibly the ectethmoid may support the palatine from above, but the exact position of the bones cannot be determined with certainty in this specimen which was extracted from a study skin and was somewhat damaged; better prepared skulls are needed before this point can be established. The ectethmoids of the short, heavy-billed *Scenopoeetes* are larger than those in *Ptilonorhynchus* but not as bulbous as in *Prionodura.* The lacrymal is the same as in other bower birds, separating the ectethmoid from the frontal and the nasal bones, but the ventral part of the bone is smaller and its foot does not reach the jugal bar. Instead the ectethmoid rests upon the jugal bar and seems to support it from above.

THE PARADISAEIDAE

One of the conclusions reached in this study is that the birds of paradise are divisible into two subgroups which are quite different from one another in skull morphology. Consequently detailed descriptions are presented at the subfamilial level and only the main characteristics distinguishing the Paradisaeidae from the Ptilonorhynchidae are given here. These main features include: a small or absent lacrymal with a subsequently enlarged ectethmoid plate which is solidly fused with the frontal bone; shorter orbital process of the quadrate with an expanded distal tip; the structure of the quadrate-mandibular hinge, especially the presence of the posterior condyle of the quadrate; and the shorter, straighter retroarticular and internal processes of the mandible. The Paradisaeinae possess many other features that separate them from the Ptilonorhynchidae, but the somewhat intermediate position of the "more primitive" Cnemophilinae between the true birds of paradise and the bower birds precludes a sharper separation between the two families.

The Paradisaeinae

The Paradisaeinae includes those genera which may be considered as typical birds of paradise and its present limits are defined for the first time in this paper. The skull of *Paradisaea* is typical for this group and forms the basis for description. Seen from the side (fig. 4A), it is of medium length and elongated in shape, not blunt or bulbous. The upper jaw, which accounts for half of the total length of the skull, is of medium build and curves slightly ventrally. It is a quite solid structure because of the extensive ossification of the nasal septum and of the external naris which is reduced to less than one-fourth of the total length of the bill; in outline, the external naris is almost circular as opposed to the oval shape usually found in passerine birds. The ossified nasal septum can be clearly seen through the external nares; hence the bill is imperforate. Its posterior wall is indented ventrally to admit the anterior tip of the vomer which approaches the nasal septum very closely, but the two bones are apparently not fused to one another. The nasal-frontal hinge is well developed as can be appreciated even in a side view. The frontal bones curve over and then inward over the nasals to form a sharply defined hinge, somewhat similar to that found in the more advanced woodpeckers or some of the starlings (for example, *Mino*). The ectethmoid plate is large and articulates with the frontal and nasal bones dorsally and reaches the jugal bar ventrally. At its midpoint, it is indented, that is, the ectethmoid is "winged." Corresponding to the large size

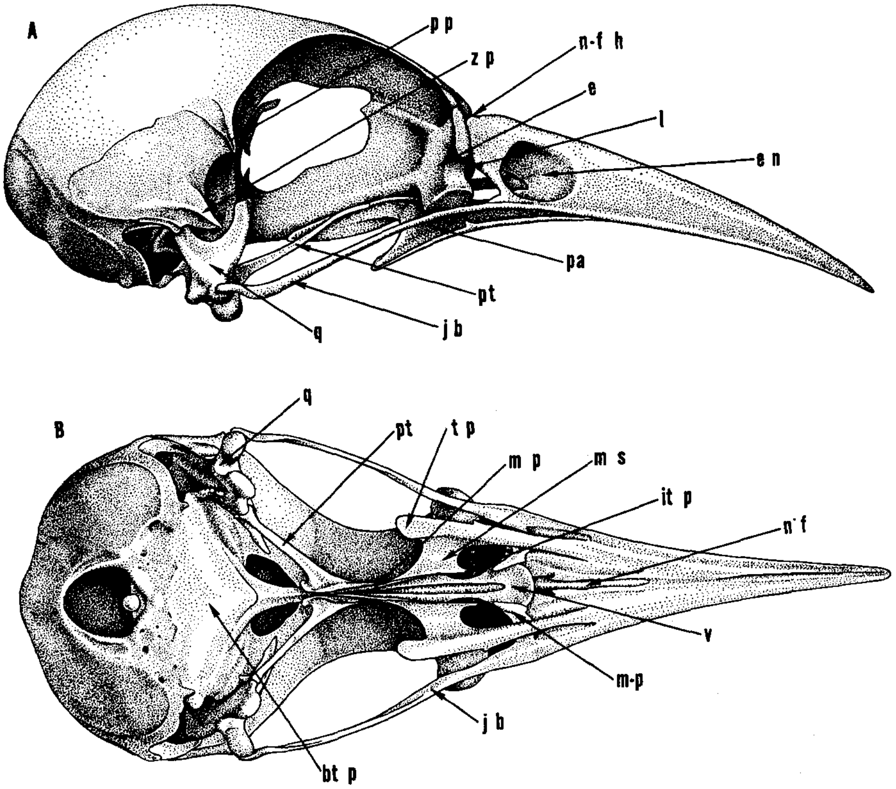

Fig. 4. Side view (A) and ventral view (B) of skull of *Paradisaea*. For explanation of abbrevations see figure 1.

of the ectethmoid, the lacrymal bone is small and fits into the space between the ectethmoid plate and the nasal bone; it has no connection with the frontal. In many specimens of *Paradisaea,* the lacrymal is not present, but it is not possible to determine whether it has become totally reduced, fused with the ectethmoid, or lost during preparation of these specimens.

The orbital region is typically passerine, although the orbit may be a bit small in comparison with other passerine birds as its length is only one-fourth of the total length of the skull. Both the postorbital and the zygomatic processes are present; these are of medium length and are widely separated by the temporal fossa. The anterior tip of the zygomatic process ends posterior to the ventral tip of the postorbital process. Except for being slightly elongated and projecting posteriorly, the brain case is typically passerine. The quadrate is well developed with a short, heavy orbital process that ends in an expanded tip (see fig. 2B). The posterior condyle of the quadrate can be seen clearly as a backward projecting knob just behind the lateral condyle. Beneath the lateral condyle is seen the large prominent medial condyle. The pterygoid is long and approaches the palatine at a shallow angle (about 10°); in fact, the pterygoid lies parallel to the jugal bars when viewed from the side. The pterygoid meets the palatine by means of a long suture, but it can be readily seen that the hemipterygoid has separated from the rest of the pterygoid and has fused onto the dorsal edge of the palatine. On the lateral edge of the palatine, just under the anterior edge of the ectethmoid plate, is a small tooth-like projection. This structure had passed unnoticed until near the end of the study when, unfortunately, I was not able to ascertain its variation in *Paradisaea* or its presence in the other genera of birds of paradise. The presence and function of this tooth-like spur is probably associated with the anterior border of the M. pterygoideus dorsalis lateralis at its origin from the palatine. As this process is most likely an ossified tendon, I would doubt that its presence or absence is of any taxonomic importance. The jugal bar has the shape of a very shallow "S"; its bend near the quadrate is probably involved with the origin of the jugal-articular ligament.

The ventral aspect of the skull (fig. 4B) is characterized by the narrow triangular bill which tapers rapidly at its base. The solid structure of the upper jaw is reflected in the completely ossified floor of the nasal cavity; this ossification is continuous with the ossified nasal septum and reaches as far posteriorly as the vomer. The palatines lie close to one another at their junction with the premaxilla but diverge rapidly as they run backward. The outer edge of the palatine, including the prepalatine and the transpalatine processes, appears as a thickened rod. The transpalatine process projects beyond the rest of the palatine as a heavy, blunt, short process. The interpalatine process is thin and pointed, whereas the mediopalatine process is long as in most passerine birds. Seen from below, the pterygoid shows no special features. It does possess, however, a strong dorsal process (the orbital process of the pterygoid) close to its quadrate articulation which can be seen on the left side of the figure just posterior to the articulation between the pterygoid and the quadrate.

The vomer is typically passerine with a medial diastema extending as far forward as the maxillopalatines. Its expanded anterior end abuts against the ossified nasal floor, but the two bones are probably not fused together. It seems probable, nevertheless, that the vomer is tightly bound to the nasal floor by ligamentous tissue. The small maxillopalatines and the posterior edge of ossified nasal floor, which is fused to the anterior edge of the maxillopalatines, cover the lateral expansions of the anterior tip of the vomer when the skull is viewed from below. The maxillopalatines are short, pointed and lack the expanded distal tip that is characteristic of so many passerine birds. The jugal bars flare out as they pass from the upper jaw to the quadrates. They are slightly expanded anteriorly but become thinner as they approach the quadrate.

Of the condyles of the quadrate, the medial is the largest, most ventral and most prominent. The articular surfaces of the lateral and posterior condyles are continuous with one another. The body of the quadrate is braced medially by the outer corner of the basitemporal plate and the outer walls of the eustachian tube. All other features of the skull base and the occipital region are typically passerine and need not be described.

The lower jaw of *Paradisaea* when seen from the side is bent ventrally at its midpoint, thereby reflecting the downward curvature of the upper jaw. The two rami are fused together anteriorly for about one-third of their total length to form a solid anterior wedge which again reflects the construction of the upper jaw. However, it is the posterior end of the mandible that is most interesting (fig. 3B). On the medial side of the mandible is a small but rather distinct pseudotemporal process which is smaller than that seen in *Ptilonorhynchus*. The short, broad retroarticular process and the relatively blunt, straight internal process of the mandible should be noted as well as the connecting plate of bone between them which forms a posterior wall for the articular cavity of the mandible. Near the distal end of the internal process is a small bump that serves as the point of insertion for the occipitomandibular ligament which runs from the ventral tip of the exoccipital process to the internal process of the mandible.

One of the most interesting, and one of the least discussed features, of the birds of paradise is the relatively great variation in the size and shape of the bill in the different

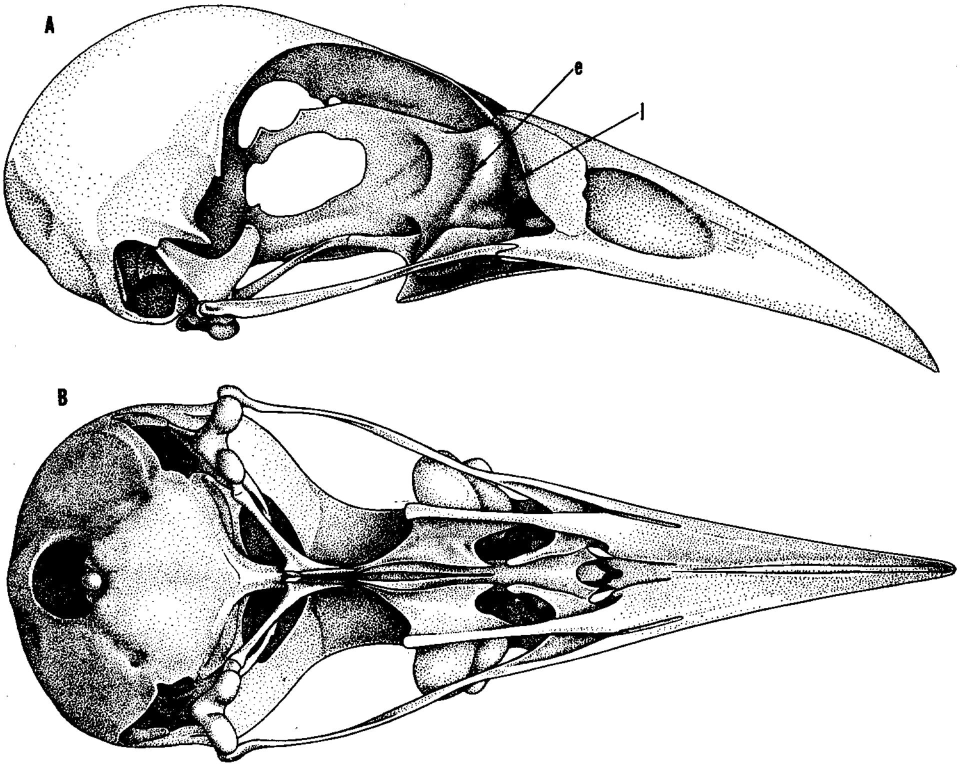

Fig. 5. Side view (A) and ventral view (B) of skull of *Manucodia*. For explanation of abbreviations see figure 1.

genera. Although this variation in bill shape is far less than that seen in the Vangidae or the Drepaniidae, it is greater than that usually found within a well-defined family of passerine birds and could provide an excellent example of adaptive radiation in feeding habits. The bill varies from the short to medium-sized and thin bill of *Cicinnurus* and *Paradisaea,* to the heavy, crow-like bill of *Manucodia* and *Lycocorax,* to the long thin decurved bill of *Epimachus* and *Drepanornis* and to the short, wider and weaker bill of *Loria* and *Loboparadisea.* It would be interesting to correlate the bill shape with the feeding habits of these birds, but not enough is known about their food and methods of obtaining it to do this. Nevertheless, it is possible and necessary to ascertain whether or not the variation in bill shape is reflected in the structure of the skull. Only after this is done, will it be possible to determine which cranial features are characteristic of the group and to ascertain the course of evolution. The following descriptions of the bill and associated cranial structure are limited to the significant points of difference between the genus under consideration and *Paradisaea.*

Lycocorax.—The bill of *Lycocorax* is of medium length for a bird of paradise but wider and heavier than normal; it is very similar to that of *Manucodia.* Still, the structure of the *Lycocorax* skull is very similar to that of *Paradisaea.* The ectethmoid is larger and more bulbous with the remnant of the lacrymal wedged into the dorsal corner between the ectethmoid and the nasal. The palate is similar to that in *Paradisaea,* except that it is a bit sturdier. It is difficult to ascertain whether the vomer is actually fused with the maxillopalatines plus the ossified nasal floor or only joined to these bones by means of heavy ligaments.

Manucodia and *Phonygammus.*—The bills of these genera are of medium length, wide and heavy as in *Lycocorax,* and as would be expected, the skulls of the three genera (fig. 5A, 5B) are very similar to one another and to that of *Paradisaea.* The ectethmoid of *Manucodia* and *Phonygammus* is a bit larger than in *Lycocorax* with its expanded foot resting on the jugal bar. The lacrymal is small and wedged into the dorsal corner between the ectethmoid and the nasal, or it may be lacking altogether.

Ptiloris.—The bill of *Ptiloris* is of medium length, somewhat thin and slightly depressed; it is much like that of *Paradisaea,* but it is a bit longer. The skull does not show any special features, being much the same as in *Paradisaea* except that the lacrymal is larger with its expanded foot resting on the jugal bar.

Craspedophora.—The bill of this genus is long, heavy and only slightly decurved; it appears much like an elongated bill of *Paradisaea.* Again the tapering of the lateral edges of the bill is rapid at the nasal region, after which the sides are almost parallel to one another up to the rounded tip of the bill. The skull is similar to that of *Paradisaea* in most details with the major difference being the ectethmoid-lacrymal mass. The ectethmoid is much the same as in *Paradisaea,* but the lacrymal is much larger and fills most of the space between the ectethmoid and nasal bones, reaching almost to the frontal dorsally and to the jugal bar ventrally. Together, the two bones form a bulbous mass which is as large as the heavy ectethmoid of *Manucodia.* The bones of the palate in *Craspedophora* are more elongate than in *Paradisaea* but are otherwise similar.

Semioptera.—The bill of *Semioptera* is of medium length and rather heavy, although not as heavy as in *Manucodia,* and curves slightly ventrally. The skull is typical of birds of paradise and is especially similar to the skull of *Seleucidis,* including the large lacrymal with its expanded base.

Seleucidis.—The bill of *Seleucidis* is long and thin, and slightly depressed, much like that in *Ptiloris* but longer. Its skull is typical of the birds of paradise in all respects and shows little difference from that of *Paradisaea.* The lacrymal is larger with its expanded base resting on the jugal bar, as in *Ptiloris.* Ventrally, the floor of the nasal cavity is sometimes not completely ossified, but this may be due to variation in age of the specimens or it may be a result of preparation.

Paradigalla.—The bill of *Paradigalla* is of medium length, straight and thin; it is somewhat like that of *Paradisaea,* but a bit longer and thinner. The only specimen of this genus available is the remnant of a skull extracted from a study skin; unfortunately, the skull behind the ectethmoid region of this specimen was completely destroyed. The preserved part is very much like the skull of *Astrapia.* The lacrymal is of medium size with its expanded foot resting on the jugal bar. The external naris is more oblong in shape. Most of the palate anterior to the palatine-pterygoid articulation is preserved and it exhibits all of the typical features of birds of paradise.

Drepanornis.—The bill of *Drepanornis,* as the generic name implies, is long, slender and greatly decurved to form a "sickle-bill" which is very similar to that in *Epimachus.* As in all long-billed birds of paradise, the sides of the bill taper rapidly at the nasal region and then run almost parallel to one another up to the rounded tip. Still, the skull is very similar to that of *Paradisaea* in most respects. The major difference is that the lacrymal in *Drepanornis* is larger, with its expanded foot resting on the jugal bar. It is of interest to note that the skull of *Drepanornis* examined was removed from a study skin, but nevertheless it was in perfect condition except for the occipital region which was badly damaged while removing the brain.

Epimachus.—The bill of *Epimachus* is long, thin and greatly decurved or sickle-shaped as in *Drepanornis.* The skull of *Epimachus* is virtually identical in all respects to that of *Drepanornis* except for the lacrymal ectethmoid region. The lacrymal of *Epimachus* is even larger than that of *Drepanornis* and fills most of the space between the ectethmoid and nasal bones, so that the combined ectethmoid-lacrymal complex forms a bulbous mass which is very similar to that seen in *Craspedophora.*

Astrapia.—The bill of *Astrapia* differs from that in *Paradisaea* only by being slightly more slender, and correspondingly the skull is almost identical in most details in the two genera. The most significant difference is the ectethmoid plate which is thicker than that in *Paradisaea* and approaches the bulbous ectethmoid of *Manucodia*; the lacrymal is completely lacking. The external naris is larger and more oval, the anterior end being expanded toward the tip of the bill.

Cicinnurus.—The bill of *Cicinnurus* is slender and much the same as in *Paradisaea,* but it is shorter. It does not exhibit a marked narrowing at the nasal region as in *Paradisaea* or *Astrapia*; instead the sides of the bill taper evenly from its base to its tip. Although the skull of this bird (fig. 6A, 6B) resembles that of *Paradisaea* in most details there are some points of difference, notably in the palate, that are of significance. In *Cicinnurus,* the lacrymal is much larger, filling the angle between the ectethmoid and the nasal bones and resting on the jugal bar with its expanded foot. The shape of the external naris resembles that of *Astrapia,* as does the nasal-frontal hinge in which the frontals are not folded over the hinge as in *Paradisaea.* The palate in *Cicinnurus* is lighter in its entire construction with the palatines being further separated from one another especially at their junction

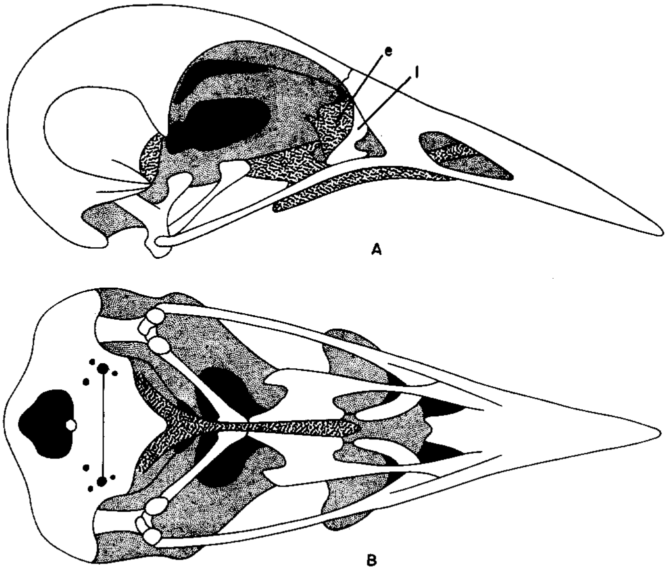

Fig. 6. Side view (A) and ventral view (B) of skull of *Cicinnurus.* For explanation of abbreviations see figure 1.

with the premaxilla. The lateral edge of the palatine is not noticeably thicker than the rest of the bone, the transpalatine process is a bit expanded mediolaterally and is rounded posteriorly, and the distal tip of the maxillopalatine is larger and more expanded. Still these differences are relatively minor as compared to the overall similarity between the skull of *Cicinnurus* and that of *Paradisaea.*

Diphyllodes.—The bill of *Diphyllodes* is slender and short, much like that in *Cicinnurus,* but straighter, not curved slightly downward as in the latter genus. Again the sides of the bill taper evenly from its base to its tip. In most respects, the skulls of these genera are very similar to one another, except for the lacrymal which is much smaller in *Diphyllodes.*

Parotia.—The bill of *Parotia* is somewhat short and wide for a bird of paradise and in many ways it is like that found in *Cicinnurus* or *Diphyllodes.* Notably its bill does not taper rapidly at the nasal region, but the lateral edges converge gradually from the base of the bill to its tip. And, although the skull of *Parotia* is larger than that of either *Diphyllodes* or *Cicinnurus*, it is very similar in structure to them. The external naris is oval in outline; the nasal bone is rather peculiar, being considerably wider dorsally, then tapering to a narrow isthmus and then widening again at the ventral edge of the upper jaw where it fuses to the maxilla. This condition of the nasal bone is a further development over that seen in *Cicinnurus* or *Diphyllodes.* The lacrymal is large, with a slightly expanded foot; consequently, it is more like that in *Cicinnurus* than that in *Diphyllodes.* As already described by Stoner, the roof of the skull between the raised orbital rims is flattened to make space for the large muscles that elevate the crest plumes of these birds. Ventrally, the palate is of greatest interest for it is also much the same as in the small sickle-tails, *Cicinnurus* and *Diphyllodes.* The palatines are rather slightly built for a bird of paradise; they are widely separated, their lateral edge is not noticeably thickened and the transpalatine process is a bit expanded and quite similar in shape to that in the sickle-tails. The maxillopalatines are slightly larger than those in *Paradisaea* but a bit smaller than those in the sickle-tails.

Lophorina.—The bill of *Lophorina* is of medium length, somewhat thin and slightly decurved; the tapering of the lateral edges at the nasal region is somewhat more gradual than in most birds of paradise, but it is not as uniform as in *Cicinnurus* or *Parotia.* Thus, the general shape of the *Lophorina* bill is intermediate between that of *Paradisaea* and *Parotia.* The lacrymal is rather large with its expanded base resting on the jugal bar as in *Cicinnurus* or *Parotia.* The palatine is somewhat like that in *Cicinnurus*, but the lateral edge of the bone is slightly thicker than the rest of the bone, although not noticeably as in *Paradisaea.*

Pteridophora.—The bill of *Pteridophora* is short and straight. Ventrally, it is very much like that in *Cicinnurus* or *Diphyllodes* as the lateral sides of the bill converge quite evenly from its base to its tip. The external naris is oval, with the nasal bone broad and shaped much like that in *Cicinnurus.* The lacrymal is medium-sized with its slightly expanded foot resting on the jugal bar, again rather similar to that in *Cicinnurus.* The palate is of lighter construction and similar in all respects to that in the sickle-tails. Indeed the skull of *Pteridophora* is very like that seen in the sickle-tails or *Parotia.* Of interest is the depressed area in the side wall of the brain case just behind the orbit and just above the postorbital process. Presumably, the muscles which move the long multi-flagged head plumes of this genus take origin from this area and these muscles require a larger area of origin, hence the depression in the outer wall of the brain case.

THE CNEMOPHILINAE

The skulls of several genera were found to be radically different from those seen in *Paradisaea* and the other typical birds of paradise although they possessed some of the basic paradisaeid cranial features and lacked the basic ptilonorhynchid features. Some of these genera, *Loria, Loboparadisea,* and *Cnemophilus* were previously assigned to the bower birds but were placed in the birds of paradise by Stonor and by Mayr and Gilliard (1954:362, footnote). These birds do show their greatest affinities to the true birds of paradise, but they also show degrees of relationship to the bower birds and to the starlings (Sturnidae) from which they probably evolved. Hence this group is assigned to the Paradisaeidae, but it is placed in a separate subfamily—the Cnemophilinae—proposed for the first time in this paper. The reasons for these taxonomic conclusions are presented later (p. 118). Because a well prepared skull was available, the genus *Loria* was chosen as the basis for description of the aberrant birds of paradise. The specimen of *Loria* used is the same one prepared and described by Stonor in his paper of 1937.

The general shape of the skull of *Loria* is short and bulbous; indeed, one could safely say that it is a typically generalized passerine skull (fig. 7A). In overall appearance, it is closer to the skull of a thrush or a starling than to that of *Paradisaea*. The upper jaw comprises about half of the total length of the skull and is straight except for a slight downward curving at its tip. The nasal septum and external naris show no signs of ossification; hence the bill is quite weak in appearance. The external naris is long, slightly more than half of the total length of the bill, and is oblong in shape. The nasal-frontal hinge is normally developed as a thinning and increased flexibility of the bone at the point where the upper jaw meets the brain case; a sharp depression as seen in *Paradisaea* is not present. The ectethmoid plate is large and entire, that is, it lacks the medial depression along the lateral edge which forms the "winged" condition seen in *Paradisaea*. The ventral edge of the ectethmoid closely approaches the dorsal surface of the palatine and the jugal bar. At the dorsolateral corner, where the ectethmoid merges into the frontal bone, is a small foramen which is unique for the birds of paradise. This foramen is most unusual in the passerine birds; I have seen it only in several genera of the Sturnidae and it may have an important bearing on the affinities of the birds of paradise. Another small foramen is present on the posterior face of the ectethmoid plate near the ventral edge of the bone (not visible in figure). Neither of these foramina correspond to the ectethmoid foramen described by Beecher (1953:275), nor does the dorsal foramen of the ectethmoid correspond to the outer foramen in the double condition of the ectethmoid foramen. These foramina are found on the ectethmoid in addition to the ectethmoid foramen which, in *Loria*, is present as the single condition. The lacrymal

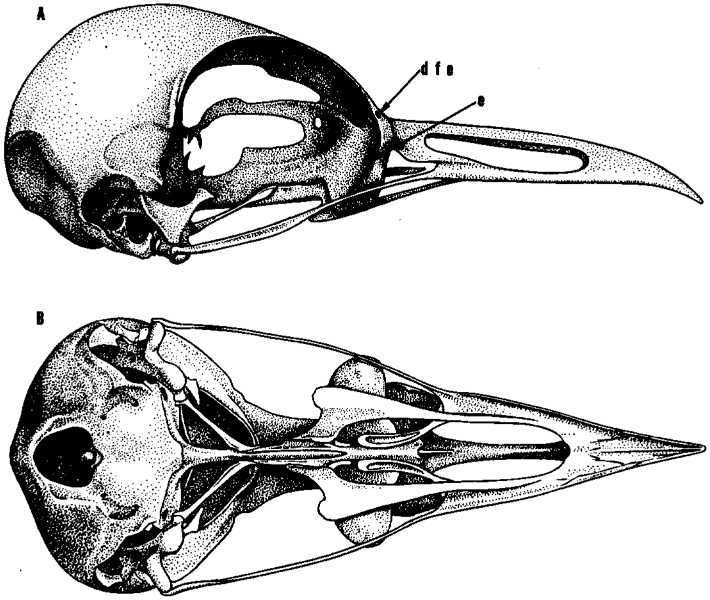

Fig. 7. Side view (A) and ventral view (B) of skull of *Loria*. d f e, dorsolateral foramen of the ectethmoid; e, ectethmoid.

is completely lacking. This is not an artifact of preparation but must be the true condition because Stonor prepared the skull from an alcoholic specimen and did not find a lacrymal even though he was looking especially for it. I was also unable to find a lacrymal when dissecting alcoholic material of *Loria.*

The orbit is normal-sized for a song bird, comprising slightly less than one-third of the total length of the skull. Both the postorbital and zygomatic processes are present but are very poorly developed, being little more than nubbins of bone. The rest of the brain case is typically passerine. The quadrate is rather similar to that in *Paradisaea,* including the expanded distal tip of the orbital process and the backward projection of the posterior condyle. The jugal bar has a shallow "S" shape as in *Paradisaea.*

The ventral aspect of the *Loria* skull is characterized by the wide bill and the lack of nasal ossification (fig. 7B). The bill is broad and tapers slowly and evenly to its tip with only the anterior third of the upper jaw being ossified across the midline. The nasal floor and the nasal septum are completely unossified. The palatines lie near the lateral edge of the bill; they arise far anterior and run parallel to one another. Their lateral edges are not thickened. The interpalatine processes have most likely broken off in this specimen as have the maxillopalatines. I have, however, taken the liberty of drawing the maxillopalatines of *Loboparadisea* in the figure; these are long and are slightly expanded distally. The vomer has the normally expanded anterior tip which is smaller than that in *Paradisaea.* The jugal bars are thin and diverge slightly as they pass from the base of the upper jaw to the quadrates. The pterygoid is much like that in *Paradisaea.* Of the quadrate condyles, the medial one is the largest and the most ventral. The lateral and posterior condyles are continuous with one another, but as in *Paradisaea,* they are smaller than the medial one. The quadrate is most likely supported medially, but the tissue between the quadrate and the basitemporal plate has been cleared away. All other features of the basitemporal plate and the occipital region are typically passerine and need not be described separately.

The weak construction of the bill of *Loria* is reflected in the lower jaw. Instead of the heavy wedge seen in *Paradisaea,* the two rami are fused together only at the very tip of the bill after which they diverge rapidly. The main body of the mandible shows no features of special interest (fig. 3C). The pseudotemporal process is absent. Both the retroarticular and the internal processes of the mandible are short as in *Paradisaea,* but, contrary to the straight condition in *Paradisaea,* the internal process curves slightly forward. The connecting plate between the retroarticular and internal processes is only slightly developed along the medial side of the retroarticular process; hence the articular cavity lacks a posterior wall. Near the distal end of the internal process is a small bump for the attachment of the occipito-mandibular ligament.

Loboparadisea.—A partly damaged skull of this genus was extracted from a study skin, but fortunately all the important characters could be examined. The bill of *Loboparadisea* is somewhat shorter and broader than that of *Loria,* but otherwise they are nearly identical. The ectethmoid is broad and reaches the palatine and jugal bar; the small foramen at the dorsolateral corner is present. The lacrymal is absent. The orbit and brain case are as in *Loria,* as are the short postorbital and zygomatic processes. The orbital process of the quadrate has an expanded distal tip. The palatine is as in *Loria* except that the transpalatine process is broader. The interpalatine process, which is broken in *Loria,* is long and extends forward almost to the large elongate maxillopalatine. The quadrate is supported medially by the basitemporal plate. The lower jaw is similar to that of *Loria* in all respects.

Cnemophilus.—The bill of *Cnemophilus* is similar to that of *Loria* and *Loboparadisea,* and the features of the skull seen in an alcoholic specimen are the same as in these genera. The ectethmoid, including the dorsolateral foramen, is clearly of the *Loria*-type as shown in figure 8. The lacrymal is absent.

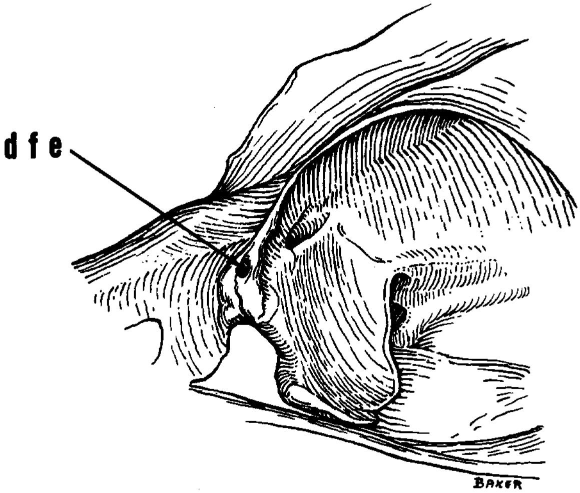

Fig. 8. Side view of skull of *Cnemophilus* showing the ectethmoid with its small dorsolateral foramen. For explanation of abbreviations see figure 7.

Macgregoria.—The skull of *Macgregoria* is of great interest because, while it shows many features of the *Loria*-type, it possesses a few characteristics of *Paradisaea* and a few unique features; hence it is described in detail. The only specimen available is a skull removed from a study skin, but this is in excellent condition except for the occipital region.

The bill of *Macgregoria* (fig. 9A) is of medium length and is slightly depressed at its tip, but it is deeper than that of *Loria*. The general appearance is that of a strong bill even though the nasal septum is completely unossified and the external naris is large and oblong. The nasal-frontal hinge is as in *Loria*, but the brain case slopes up more gradually from the hinge than in *Loria*. The ectethmoid plate is quite different and looks more like that in *Paradisaea*, although the dorsal part of the ectethmoid and its junction with the frontal are unique for the birds of paradise. Ventrally, the ectethmoid does not approach the dorsal surface of the palate closely, although the expanded foot does rest on the jugal bar. A slight indentation at the midpoint of the lateral edge makes the ectethmoid "semi-winged" and hence somewhat like that in *Paradisaea*. The small foramen at the dorsolateral corner of the ectethmoid is absent. A small foramen exists on the posterior face of the ectethmoid near its ventral edge. The lacrymal is lacking. The shape of the orbit and the somewhat elongated brain case are closer to the condition in *Paradisaea* than in *Loria* as are the longer postorbital and zygomatic processes, although the tip of the zygomatic process ends forward of the ventral tip of the postorbital process. The orbital process of the quadrate has an expanded tip (not shown in the figure) and the posterior condyle of the quadrate projects backward as in *Paradisaea*.

The ventral aspect of the skull is characterized by the lack of ossification of the nasal floor and the lightly constructed palate (fig. 9B). The bill tapers evenly from its base to its tip, but it is more pointed than that of *Loria*. The palatine starts to approach the condition of *Paradisaea* in as much as the lateral edge of that bone is a bit thicker than the rest of the bone, the transpalatine process is narrow and the interpalatine process is short. The maxillopalatine is long and slightly expanded as in *Loboparadisea*. The quadrate is supported medially by the lateral edge of the basitemporal plate. All other features of the skull base and occipital region are typically passerine as far as could be observed.

The lower jaw of *Macgregoria* is much more like that of *Paradisaea* in which the bend is quite abrupt. The two mandibular rami are fused together for slightly less than one-third of the length of the lower jaw, forming an anterior wedge but one that is weaker than that found in *Paradisaea*, and the rami do not diverge as much as they pass backward toward the quadrate. The pseudotemporal process is lacking. The retroarticular and internal processes of the mandible are about the same as in

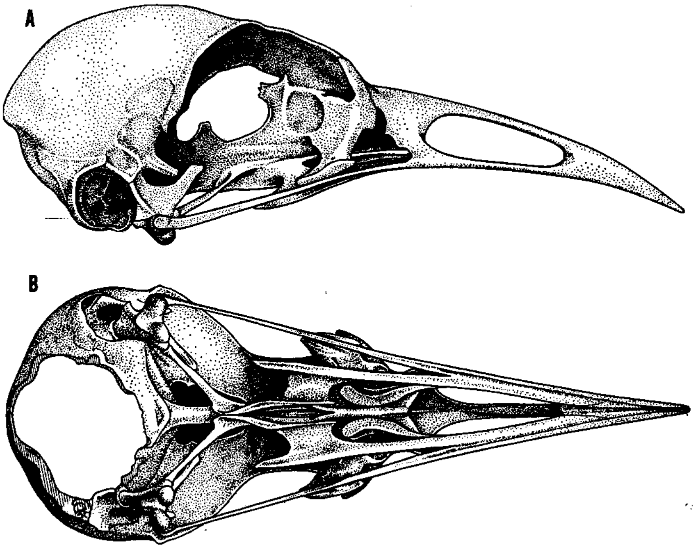

Fig. 9. Side view (A) and ventral view (B) of skull of *Macgregoria.*

Paradisaea except that the internal process of *Macgregoria* may be curved slightly more forward. The connecting plate between these processes is only a bit less developed in *Macgregoria*, if any, than that in *Paradisaea.*

SUMMARY OF THE SKULL TYPES

From the preceding descriptions, it is obvious that several rather distinct skull forms exist in the bird of paradise-bower bird complex. This observation is scarcely new or surprising for Pycraft stated many years ago (1907) that the bower birds are quite distinct in their skull structure and are readily separated from the birds of paradise—a conclusion confirmed by Stonor in recent years with the aid of much more data. Pycraft and Stonor distinguished only two types of skulls, those of *Paradisaea* and *Ptilonorhynchus*; *Loria* was considered by Stonor to be of the skull type of *Paradisaea.* The present descriptions indicate the existence of three major and sharply separated skull forms, those of *Paradisaea, Ptilonorhynchus* and *Loria,* with the latter being divisible into the types characterized by *Loria* and *Macgregoria.* To compare and contrast these types the information was condensed into table 1. I would like to caution the reader against using this table without referring to the descriptions; the simplification necessary may at times either reduce or enlarge the actual difference between some groups in certain of the characters.

Up to this point, the observations and results of Stonor's work have been purposely omitted, not because of a lack of agreement between his work and mine, but in an attempt to avoid bias and confusion in the descriptions and in establishment of the different conditions in the skull structure. Stonor listed differences between the birds of paradise and bower birds in the maxillopalatines, the ossification of the nasal floor and septum, the thickening of the lateral edge of the palatine and the shape of the transpalatine process, the lacrymal-ectethmoid complex, and the orbital process of the quadrate, all of which have been confirmed in this study. Stonor did mention another difference which I was not able to substantiate, this being the presence of a medial notch or concavity in the anterior edge of the vomer in the birds of paradise (1937:476) and its lack in the bower birds (p. 477) in which the anterior edge of the vomer is straight. I found the medial concavity in the bower birds as well as in the birds of paradise and must conclude that the two groups agree in this character. This region of the skull of the bird of paradise is difficult to examine as the ossified nasal floor covers the anterior tip of the vomer from below, and it may be that Stonor was referring to this feature when describing the medial notch in the anterior border of the vomer. However, in any case, the shape of the anterior edge of the vomer is a minor character and this lack of agreement between Stonor's work and the present one is of no importance.

Several differences in the cranial features between the bower birds and birds of paradise found in this study were not mentioned by Stonor, but these were most likely omitted purposely as Stonor may have chosen not to describe all of the observed differences since the major purpose of his paper was to show that the skulls of the two groups are different, and he had sufficient characters to prove this beyond any doubt. A comparison of the differences mentioned by Stonor between *Loria* and *Paradisaea* on the one hand and *Ptilonorhynchus* on the other with those reported in this paper would not be fair because Stonor was only able to examine *Loria* and did not know that several

TABLE 1

SUMMARY OF THE SKULL CHARACTERS

Character	Paradisaeinae	*Macgregoria*	Cnemophilinae	Ptilonorhynchidae
Nasal region	Ossified	Not ossified	Not ossified	Not ossified
Maxillopalatines	Short, blunt	Long, expanded	Long, expanded	Long, expanded
Ectethmoid	Larger, "winged"	Large, "semiwinged"	Large, "entire"	Smaller, "entire"
Lacrymal	Medium—absent	Absent	Absent	Very large
Lateral edge of palatine	Thickened	Somewhat thickened	Not thickened	Not thickened
Transpalatine process	Short, blunt	Long, pointed	Short, expanded	Short, expanded
Orbital process of quadrate	Tip expanded	Tip expanded	Tip expanded	Longer, tip not expanded
Postorbital and zygomatic processes	Well developed	Well developed	Poorly developed	Well developed
Posterior quadrate condyle	Present	Present	Present	Absent
Mandibular rami	Fused into a strong wedge	Fused into a weak wedge	Meet only at a narrow symphysis	Fused into a broad plate
Pseudotemporal process	Moderately developed	Absent	Absent	Well developed
Retroarticular process	Short	Short	Short	Long
Internal process of mandible	Short, straight	Short, straight	Short, straight	Long, curved forward
Posterior wall of articular cavity	Well developed	Moderately developed	Slightly developed	Absent

genera possessed this skull form; hence he did not describe and compare *Loria* in detail. He did show that the skull of *Loria* agreed more closely with that of *Paradisaea* than with that of *Ptilonorhynchus* in spite of the apparent greater similarity with the latter genus in other respects, which situation is in complete accordance with the results of the present study. Thus, the comparison between the major skull conditions in Stonor's work and in the present study are in close agreement, with the existing disagreements stemming largely from the new data resulting from the more abundant material subsequently available.

JAW MUSCLES

The jaw muscles of *Ptilonorhynchus, Paradisaea,* and *Loria* were dissected in the hope that a knowledge of these structures would permit a better understanding of the skull features. Only two specimens of each form were examined, but these were sufficient to present an accurate picture of the jaw muscles. It does not seem necessary to record all minor variations for the systematic problems at hand. The following descriptions are based on the discussion of the jaw apparatus and its function in passerine birds to be published elsewhere (Bock, MS). Consequently the descriptions in the present paper are brief. Only the major deviations from the "typical" passerine condition of the muscles and specializations in both structure and function will be covered. The figures were made by drawing the muscle on a tracing of the skull taken from a photograph. It is hoped that by this method a more accurate representation of the muscles was obtained. The method is, unfortunately, not perfect, for some errors still exist in the size and perspective of the muscles.

My dissections agree in general with the figures presented by Beecher (1953:287) but only within rather wide limits. Some rather striking differences exist as, for example, in the M. adductor mandibulae complex, and the M. pseudotemporalis profundus, both of which Beecher shows to be larger in the Ptilonorhynchidae. I found these muscles to be better developed in the Paradisaeidae. Our figures also differ from one another in the arrangement of the muscle fibers in the M. adductor mandibulae externus and in the M. pseudotemporalis superficialis, but I could not be absolutely sure of the exact orientation of the fibers in my dissections because of inadequate preservation of the specimens. The arrangement of the muscle fibers in the figures represents what I was able to observe, but they should not be accepted as being absolutely correct until they can be checked by dissection of better material.

JAW MUSCLES OF PTILONORHYNCHUS

In general, the jaw muscles of *Ptilonorhynchus* (fig. 10) conform very closely to the typical passerine condition; they are, however, larger and better developed than those present in most insect-eating passerines. All parts of the dorsal adductors of the upper jaw are relatively smaller than those of *Paradisaea,* although the difference is not striking. The M. depressor mandibulae inserts only along the basal half of the internal process of the mandible, its distal limit coinciding with the insertion of the L. occipitomandibulare on the internal process.

The medial parts of the M. pterygoideus are of most interest as they are greatly increased in size, but this is not apparent in the figures because the increase is a result of a deepening of the muscles, not an enlargement in width. The M. pt. ventralis medialis inserts by means of a strong tendon upon the tip of the elongated internal process. It is apparently the change in these muscles that is correlated with the lengthening of the internal process. Usually an increase in the medial parts of the M. pterygoideus means that the upper jaw is depressed more forcibly, but I do not believe that this is its complete action in *Ptilonorhynchus*. The peculiar forward curving of the long internal process of the mandible suggests that the medial portions of the M. pterygoideus may have a special function. The usual action of these medial fibers is to depress the upper jaw and raise the mandible. Yet in the bower birds, it appears that those medial fibers

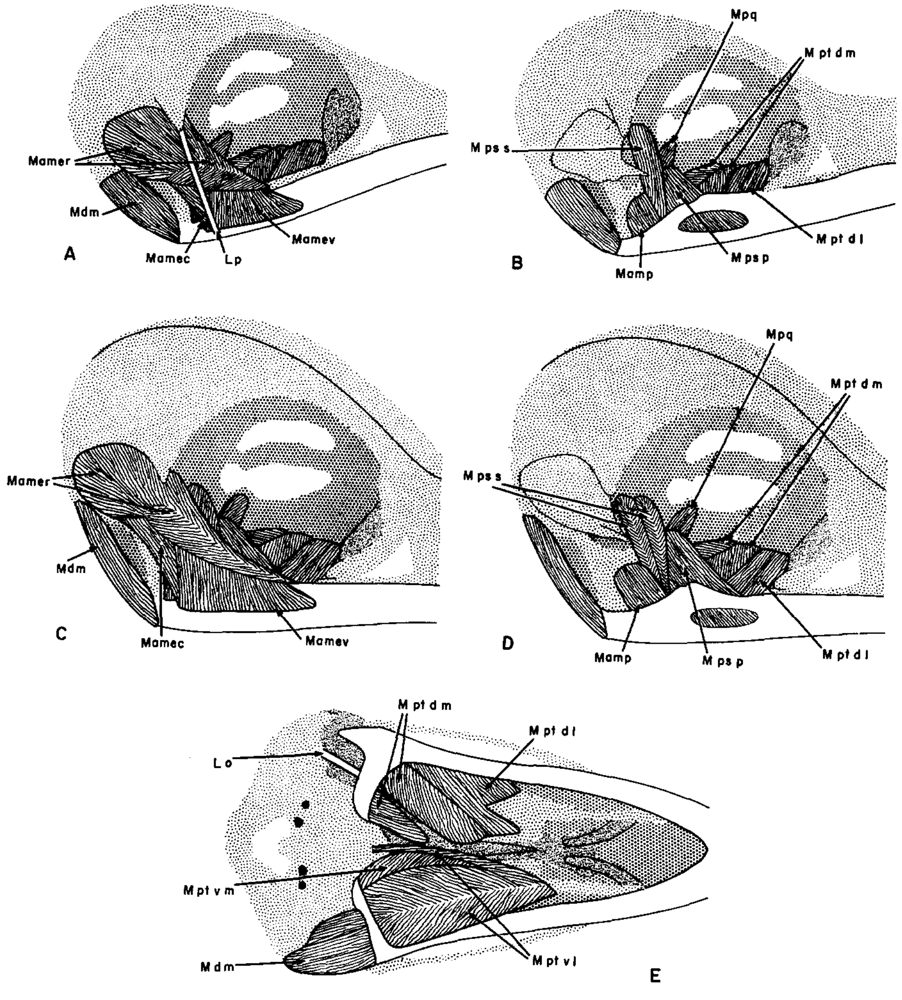

Fig. 10. Jaw muscles of *Ptilonorhynchus*. A, side view; B, view from side after removal of the M. adductor mandibulae externus; C, oblique view into the orbit; D, oblique view into the orbit after removal of the M. adductor mandibulae externus; E, view from beneath showing the M. pterygoideus in which the ventral layer has been removed on the right side of the head. The sets of muscles in the figures are not drawn to the same scale, nor are the jaw muscles in figures 11 and 12 drawn to the same scale as those in this figure. Abbreviations are as follows: Lo, L. occipitomandibulare; Lp, L. postorbitalis; M a m e c, M. adductor mandibulae externus caudalis; M a m e r, M. adductor mandibulae externus rostralis; M a m e v, M. adductor mandibulae externus ventralis; M a m p, M. adductor mandibulae posterior; M d m, M. depressor mandibulae; M p q, M. protractor quadrati; M ps p, M. pseudotemporalis profundus; M ps s, M. pseudotemporalis superficialis; M pt d l, M. pterygoideus dorsalis lateralis; M pt d m, M. pterygoideus dorsalis medialis; M pt v l, M. pterygoideus ventralis lateralis; M pt v m, M. pterygoideus ventralis medialis.

inserting upon the distal end of the curved internal process pull forward and slightly upward on this process and thereby lower the mandible. I am not at all sure that this functional interpretation is correct or even reasonable; direct observations or experiments are needed. Another hypothesis is that the medial parts of the M. pterygoideus serve to steady the mandible when the bill is opened or when the bird is holding an object in its bill. Sims (1955:382) has suggested a similar function for the medial parts of the M. pterygoideus in the Hawfinch (*Coccothraustes*).

JAW MUSCLES OF PARADISAEA

The overall impression given by the jaw muscles of *Paradisaea* (fig. 11) is one of considerable biting power with both the adductors of the mandible and the retractors of the palate being well developed. All the dorsal adductors of *Paradisaea* are better developed than those of *Ptilonorhynchus*. This can be especially well seen in the temporal

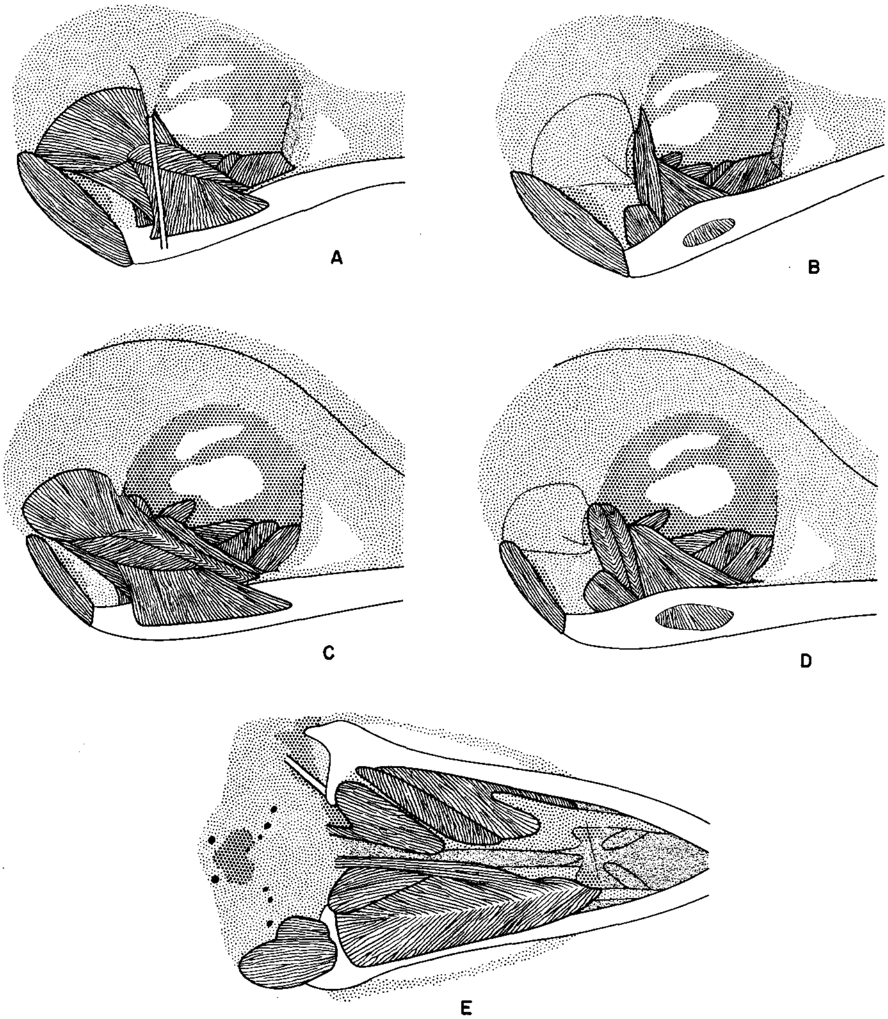

Fig. 11. The jaw muscles of *Paradisaea*. The views are the same as in figure 10.

part and lateral muscle mass of the M. adductor mandibulae externus rostralis, the M. pseudotemporalis superficialis and the M. ps. profundus. The enlargement of the M. ps. profundus is reflected in the enlarged head of the orbital process of the quadrate. The lateral parts of the M. pterygoideus are especially well developed. In particular, the large M. pt. ventralis lateralis can be correlated with the thickened lateral edge and transpalatine process of the palatine. The muscles opening the bill, the M. depressor mandibulae and the M. protractor mandibulae, and the depressors of the upper jaw, the M. pseudotemporalis profundus and the medial parts of the M. pterygoideus, are well developed but show no specializations. Their structure indicates that probing and grasping are relatively important in the feeding mechanism of the true birds of paradise.

JAW MUSCLES OF LORIA

The development of the jaw muscles of *Loria* (fig. 12) closely parallels the structure of the skull. They are, in general, weakly developed and may be best compared to those of a generalized insect eater. Only the M. pseudotemporalis profundus is well developed, being very similar to that seen in *Paradisaea,* which is correlated with the large

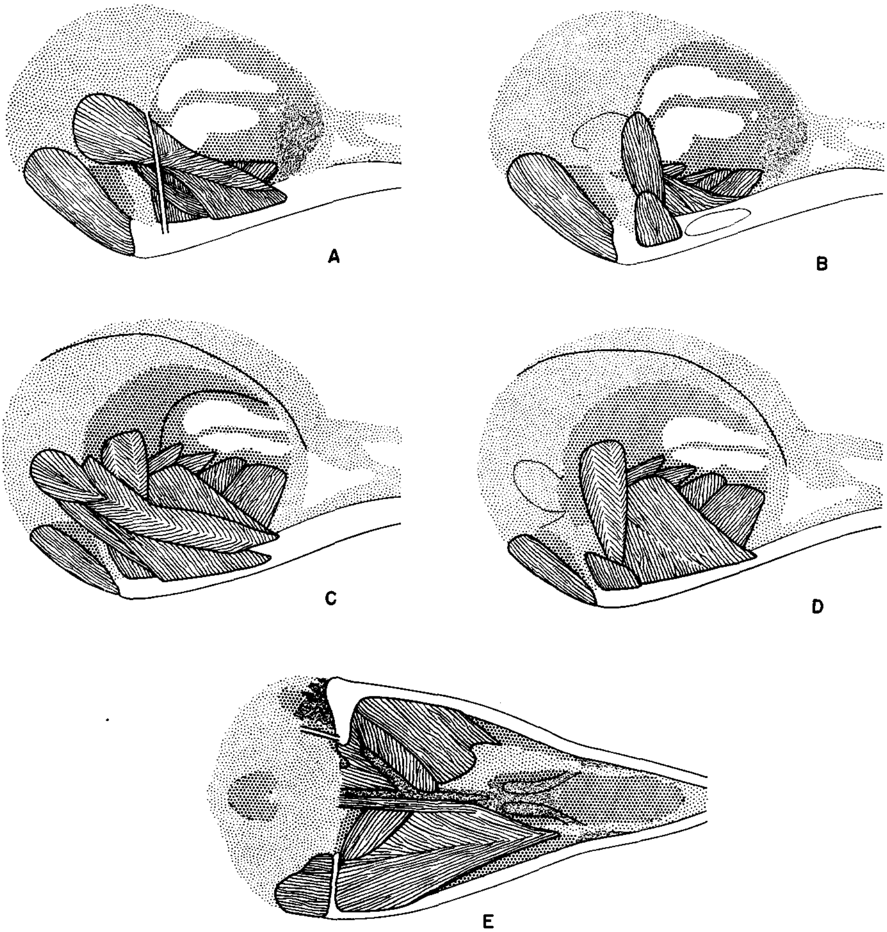

Fig. 12. The jaw muscles of *Loria*. The views are the same as in figure 10.

distal head of the orbital process of the quadrate. In many respects, the jaw muscles of *Loria* are very similar to those of ***Ptilonorhynchus***, but this resemblance is most likely because both groups show only minor deviations from the typical insect-eating passerine condition of the jaw muscles, the existing deviations being largely some increase in size.

FUNCTIONAL ANALYSIS OF THE SKULL TYPES

The skulls of the true birds of paradise and the bower birds are interesting, not only because they are strikingly different from each other, but because they are strikingly different from the skull seen in the typical passerine birds. This is especially true of the bower birds which possess some of the most peculiar and unique cranial features in the entire order of perching birds. Yet the skull of *Loria* is typically passerine in almost all of its features, and even the peculiar foramen at the dorsolateral corner of the ectethmoid plate is paralleled in some of the starlings.

Grouping of the individual cranial features into character complexes (functional groups of characters) and a functional analysis of these character complexes is essential before proceeding to an evaluation of the evolutionary and taxonomic significance of the morphological features. The functional analysis is greatly limited, as I have been able to observe individuals of only a few genera in zoos; these birds for the most part just sat and watched me. Description in the literature of the feeding methods employed by the bower birds and the birds of paradise in sufficient detail to be useful in a functional analysis is completely lacking. Such observations are needed badly and must be made in the field so that natural food and foraging methods may be ascertained. The following analysis is, therefore, limited to a mechanical extrapolation from the skull structure and is consequently strictly hypothetical. It cannot be emphasized too strongly that the results of this investigation are only unproven deductions and are hence subject to error; therefore, the evolutionary and taxonomic conclusions which are based, in part, on these functional deductions may also be wrong.

Loria with its broad weak bill and its lack of specializations presents the least number of problems. Most of the features seen in its skull are similar to those seen in other passerine birds, such as the thrushes or the starlings, so that it may be concluded that *Loria* is a generalized insect and fruit eater. The lack of nasal ossification, weak palatines, small postorbital and zygomatic processes, weak unspecialized mandible, and "normal passerine" jaw muscles all support this conclusion. Why the palatines and the jugal bars are supported from above by the ectethmoid plate is not entirely clear, but this condition is also seen in many unspecialized insect eaters. The answer may lie in the fact that the broadened foot of the ectethmoid lies at the corner of the mouth where insects or fruits to be crushed would be held; hence the greatest stress on the skull would be at this point. The upward force on the palatines and jugals may be large enough to bend or otherwise disrupt these bones if they were not supported from above. The expanded anterior plate of the vomer and the long maxillopalatines are, as in other passerine birds, associated with forming part of the floor of the nasal cavity and with maintaining the opening of the internal naris. The small foramen at the dorsolateral corner of the ectethmoid is apparently not associated with the feeding character complex and may be considered to be an independent character. Its function is not known.

Some problems still exist concerning the expanded head of the orbital process of the mandible and the enlarged M. pseudotemporalis profundus. These features are clearly correlated with one another functionally; they act to close the mouth more forcibly either by depressing the upper jaw or raising the mandible. It is not clear why *Loria* possesses this increased power of adduction, and whether it serves a definite and particular functional need or happened to be the feature that evolved to meet a general need for increased closing power of the beak. Clarification of this point is needed before the evolution of this functional complex in the Cnemophilinae-Paradisaeinae line can be elucidated.

Macgregoria, with its strengthened and pointed bill, must in all probability have different feeding habits than other members of the Cnemophilinae possessing a skull similar to that of *Loria*. This is a bird living in the high-altitude subalpine forests of the New Guinea mountains; indeed, it lives higher on the mountain slopes than almost all other birds of paradise and certainly higher than birds having the *Loria* skull condition. Rand (1940:3) reports that these birds feed by hopping about the ends of branches, searching for fruit among the leaves. They also poked among the moss on tree trunks, pulling off the moss and bark as though they were looking for insects; however, the stomachs of these birds only contained fruit, exclusively the fruit of *Podocarpus* in regions where this plant occurred. It may be that *Macgregoria* pokes its bill into the fruit and then gapes which would serve to break the fruit into smaller pieces; its bill is very similar in structure to that of many icterids such as the orioles (*Icterus*) which feed in this manner. *Macgregoria* may also feed on insects, using its bill as a probe and pincer to obtain insects from crevices. The strong, pointed bill, the anterior wedge of the mandible, the strengthened palatines with the short stout transpalatine processes, the well developed zygomatic, and postorbital process all support this functional conclusion. The last three characters mentioned suggest strongly that *Macgregoria* possesses a stronger set of jaw muscles than is found in *Loria*. This also would be in agreement with the suggestion that *Macgregoria* uses its bill as a probe and pincer. The vomer and maxillopalatines have the same function as in *Loria*. The peculiar structure of the ectethmoid plate, especially the dorsal portion, is most likely not associated with the feeding character complex and may be considered to be a separate character whose function is still unknown.

The skull of the true birds of paradise is one of great strength and solidness, being second in these properties only to some of the shrike-like birds and the finches among the oscines. These birds feed on insects and fruits, and there are reports of them using their bills as probes. It is, therefore, suggested that the birds of paradise use their bills as probes and powerful graspers to obtain insects and other food from crevices. Some of the insects may be large and may have to be crushed between the jaws before being swallowed. The sides of the bills in many genera taper rapidly at the base to produce a narrower anterior portion which would permit these birds to probe into smaller cavities.

In some genera, such as *Manucodia*, the bill is heavier and wider; these birds are probably not probers but apparently still use their bills as strong pincers by which they could feed upon larger animals. In some other genera, such as the *Cicinnurus*-group, the bills taper evenly from base to tip which may limit the probing ability of these forms to some degree. Most of the cranial features seen in the true birds of paradise support the suggestion that the bill is employed as a probe and powerful pincer. These include the completely ossified nasal region with the vomer abutting against the nasal floor, the anterior wedge of the mandible, the heavy palatines with their thickened lateral edges and short, heavy transpalatine processes, the bulbous ectethmoid-lacrymal mass, the expanded head of the orbital process of the quadrate, the well developed zygomatic and postorbital processes, and the jaw muscles. Of the last, the adductors of the mandible and retractors of the palate are strongly developed, indicating that these birds have a powerful bite. That they are not specialized gapers is shown by the normal development of the depressor of the mandible and protractor of the palate; these muscles are enlarged in gapers. However, it does seem likely that in probing, a definite use is made of the kinetic property of the upper jaw—perhaps when the bird must open its bill to grasp its prey—as indicated by the well developed nasal-frontal hinge.

The structure of the quadrate-mandibular hinge, which is rather typical for a song bird, agrees with the preceding functional assumption. The small maxillopalatines are associated with the main feeding complex, as the complete fusion of the nasal floor has reduced the need for large maxillopalatines; only a relatively short portion of the internal nares remains to be protected by these bones. Short, blunt maxillopalatines are seen in many finches and shrikes which also possess a completely ossified nasal floor. The several genera with evenly tapered sides of the bill have a somewhat weaker palate. Perhaps these birds do not have as strong a pincer action and are as well poorer probers. Nevertheless, in any case, it seems probable that all the characteristic features of the skull of *Paradisaea* belong to a single character complex associated with the basic feeding mechanism of these birds. It should be noted that probing and strong pincer action would permit an adaptive radiation into several different types of feeding methods and the evolution of the wide assortment of bills seen in the true birds of paradise.

The skull of the bower birds, with its series of unusual features, such as the lacrymal, presents the greatest problem of this functional analysis. Bower birds are reported to live largely on insects and fruits with no mention of special feeding habits. Thus one would expect their skull to be much like that of *Loria.* And to some degree, the skulls of these two groups are similar, namely in the lack of ossification of the nasal region, the shape of the maxillopalatines, and structure of the vomer. But most of the really peculiar cranial features are still left to be explained functionally. In the absence of any unusual feeding habits, the best working hypothesis is to assume that these peculiar features of the skull of the bower bird are correlated with the bower building habits and courtship displays. The building of bowers, decorating them by "painting" and other means, constructing patios of stones, berries, snail shells and other objects, and displaying with a snail shell or other object held in the bill (see Marshall, 1954, for a description of these habits) requires the joint possession of strong clasping power of the jaws and delicate control of their movements. The combination of these particular functional properties is difficult to achieve as delicate control requires more finely constructed structures, including more muscles operating on the bony system, but these structures are more liable to damage if great stress is placed upon them.

The main drawback to the suggestion that bower building and courtship displays underlie the evolution of the peculiar cranial features of the bower birds is the fact that not all bower birds build bowers and display with objects held in their bill. *Archboldia* and *Scenopoeetes* clear a small area on the forest floor and decorate it in a simple manner, while *Ailuroedus* does not even clear a space on the forest floor. Nevertheless, these genera do have a special feeding habit (see Marshall, 1954:142, 154, 168). *Archboldia* and *Scenopoeetes* feed on snails which they break open on a special stone near the bower, and *Ailuroedus* feeds on small, soft-shelled snails. Handling of the snails probably requires the same functional properties of the skull and jaw muscles as would the bower building and associated displays, especially when one considers the fact that most bower birds display while holding a snail shell in their bill. Hence I suggest that the bower birds must have a good clasping bill that is also capable of fine delicate action, and I shall endeavor to show how the observed structures function to allow these actions.

Holding and shaking heavy objects in the tip of the bill requires a strong connection between the two halves of the jaws which is accomplished by the firm fusion between the premaxillae of the upper jaw and between the rami of the mandible. Both jaws are strengthened, but they are not ossified into solid structures, indicating that a degree of flexibility may be necessary. The well developed postorbital, zygomatic and pseudotemporal processes and the well developed jaw muscles testify to the strong grasping power of the mandibles in the bower birds. Lack of an expanded tip on the orbital process of the quadrate is correlated with the smaller M. pseudotemporalis profundus; the greater length of the process may be associated with quicker action of this muscle. Protection of the brain case and the sense organs seems to be accomplished by isolating the shocks and forces resulting from closing the bill and shaking heavy objects within the jaw apparatus by means of the kinetic property of the upper jaw, the flexible nasal-frontal hinge acting as a shock absorber. The lacrymal may also act as a shock absorber to take up some of the forces.

Next is the question of delicate control of the jaw action; this seems to be correlated with most of the peculiar cranial features. The lack of a posterior quadrate condyle, lack of a connecting plate between the retroarticular and internal processes of the mandible, and the long retroarticular process form a quadrato-articular hinge difficult to understand. The retroarticular process fits into the deep groove between the lateral and medial condyles of the quadrate; hence lateral shifting of the mandible is reduced without infringing upon the swinging of the mandible on the quadrate. This seems to be a strong hinge, but one that allows a greater freedom of rotation than is usually found in passerine birds.

The structure of the quadrate hinge seems to be functionally correlated with the long, forwardly curving internal process of the mandible, the expanded transpalatine process, and the muscle passing between them. The medial portion and a relatively large part of the lateral division of the M. pterygoideus ventralis insert by means of a tendon on the tip of the internal process of the mandible. This part of the M. pterygoideus is not only responsible for the shape of the transpalatine process from which it takes origin, but also for the length and shape of the internal process, as it inserts along the entire internal process up to its distal tip. The M. depressor mandibulae inserts only along the basal half of the internal process; thus it cannot influence the entire shape of this process. The forward curving of the internal process and the large segment of the M. pterygoideus inserting on its distal tip is most unusual for passerine birds. This muscle-bone complex normally acts during the closing of the bill by elevating the mandible and lowering the upper jaw by retracting the palate. Yet its action in the bower birds appears to be somewhat different. The palate is still retracted when the medial parts of the M. pterygoideus contract, but the mandible may be depressed, not raised. If the mandible is held in place on the quadrates of a cleaned skull and then depressed, the distal tip of the internal process moves forward and slightly upward toward the transpalatine process, contrary to the movement in other passerine birds, which is away from the transpalatine process when the mandible is being depressed. The forward movement of the internal process results from its great length and forward curving. Thus, when the medial parts of the M. pterygoideus contract, they may act to draw the tip of the internal process toward the mandible and thereby depress the mandible. This functional suggestion is most difficult to believe; I find it somewhat incredible in spite of the fact that I cannot deduce another explanation for the action of this muscle-bone complex. Needless to say, this suggestion must be carefully checked by additional dissections and by direct observations before it is accepted.

One interesting conclusion that may be derived from this functional suggestion, although it is only a side issue to the discussion, is that a simple osteological change, a lengthening and a forward curving of the internal process, could have brought about a radical change in the action of a muscle without any change in the structure of the muscle. Assuming that the M. pterygoideus-palatine-mandible complex does function in this way, the next step is to inquire into its role in the total bill action. I would doubt that this muscle-bone complex actually aids in depressing the mandible, as the bower birls do not appear to need a powerful depression of the mandible; and if they did, this could be accomplished simply by increasing the mass of the M. depressor mandibulae. It is more likely that it serves in some other manner, as for example, to brace the mandible or to protect the quadrate-mandibular hinge. Another suggestion is that the medial part of the M. pterygoideus serves as an antagonist to the adductors of the mandible and thereby allows a more delicate movement of the jaws. Fine, precise action requires not only more muscles but also action of these muscles against one another as is seen in the human hand or in the tip of the avian wing. The M. depressor mandibulae is not suitable as an antagonist to the dorsal adductors. It has the action of pulling the mandible backward as do the dorsal adductors; hence the action of the M. depressor mandibulae is not fully antagonistic to these muscles. It may be that a forward pull on the mandible is needed simultaneously with its depression which would be provided by the medial portions of the M. pterygoideus. The medial portions of the M. pterygoideus included in this bone-muscle system would also be antagonistic to the rest of the M. pterygoideus which act to raise the mandible as in other passerine birds.

The last feature of the skull to be considered is the large lacrymal. Normally in passerines, the ectethmoid plate abuts against the frontal and nasal bones and serves as a stop, preventing the upper jaw from being depressed excessively. In the bower birds, the lacrymal abuts against the frontal and nasal bones and serves as a stop for the upper jaw. But instead of being a solid, rigid stop as is the ectethmoid, the lacrymal is an elastic one—a shock absorber—which would move slightly before preventing the upper jaw from being depressed further; the lacrymal could thus allow smoother action of the jaws. It is also possible that the lacrymal is more directly correlated with the action of the medial parts of M. pterygoideus. Contraction of this muscle would depress the upper jaw in addition to its action on the mandible; perhaps it is necessary to prevent excessive depression of the upper jaw.

If these functional suggestions are correct, the lacrymal, the shape of the transpalatine process, the long and forwardly curving internal process of the mandible, and the structure of the quadrate-mandibular hinge form an extensive character complex whose function is to allow a more delicate control of the jaw actions. However, it must be strongly emphasized that these suggestions are highly speculative without a hint of direct evidence supporting them. Their only asset is that they seem to fit together to form a reasonable picture agreeing with the use of the bill by these birds in building bowers and eating snails. Direct observations and experiments are needed to prove or disprove these speculations. We need to know whether only members of the non-bower-building genera eat snails, or if this habit is more widespread throughout the family, and we need to learn exactly how the birds break the shells of the snails. The exact use of the bill in bower building is still not known, nor is it known if any special action is needed which is not employed by other birds in nest building. Possibly building of bowers has nothing to do with the structure of the skull. Possibly the skull structure is only associated with the courtship display habits; that is, for the skull structure, the important factor is displaying with a heavy object held in the bill. It is necessary to ascertain whether all members of bower-building genera always display with heavy objects held in their bills. This function is in closer agreement with snail-eating habits suggested for members of non-bower-building genera. Finally, it should be emphasized that possibly none of these habits may be associated with the suggested function for the peculiar skull features of the bower birds and that the correct answer to this problem must be looked for elsewhere.

One strong objection may be raised against the suggestion that the skull structure may be correlated with snail eating in several genera of bower birds. It can be pointed out that other passerine birds eat snails, breaking the shell by hitting the snail on a stone, but do not have any apparent cranial specialization for this feeding habit. An outstanding example of this is seen in the several European thrushes of the genus *Turdus* (for example, *Turdus merula*) which feed regularly on snails but are identical to the other thrushes in their skull structure. Possibly an answer may lie in the size of the snails. The European thrushes eat small snails while the bower birds apparently feed upon larger snails with thicker shells. Possibly the other snail-eating passerines have adaptations for this feeding method which are still unknown. Or possibly the bower birds may have been the only group in which the necessary genetic modifications occurred leading to the anatomical specializations for snail eating. The other perching birds feeding on snails may be limited to smaller snails because the necessary mutations and genetic recombinations for these anatomical specializations never appeared.

Just because an animal acquires a new feeding habit or other habit allowed by its present anatomical structure does not mean, *ipso facto,* that there will appear any structural adaptations permitting the animal to carry out the new habit better and more effectively. The necessary selection forces are present, but the necessary genetic modifications must also appear (see Mayr, 1961, for a fuller discussion of this point). Possibly in the perching birds, the essential genetical modifications for perfecting the snail-eating adaptations appeared by chance only in the bower birds and hence this is the only passerine group having anatomical specializations for snail eating.

Thus, to summarize the main points of the tentative functional analysis: *Loria* is a generalized insect- and fruit-eater as is shown by the unspecialized structure of its skull; only *Macgregoria* of the Cnemophilinae is a prober and grasper, or a gaper, and it is somewhat specialized in the same direction as are the true birds of paradise. *Paradisaea* is a prober and a powerful grasper as is shown by the narrowed bill, the complete ossification of the upper jaw, and the powerful jaw muscles. Some genera, such as *Manucodia,* in this group do not seem to probe, but they are still powerful graspers. A few genera, such as *Cicinnurus,* appear to be less specialized in their skull structure and presumably also in probing and grasping. *Ptilonorhynchus* does not seem to have any special feeding habits, but it is unusual in using its bill in building bowers and in displaying with heavy objects held in its bill. Other bower birds, such as *Ailuroedus,* do not build bowers, but they do have the unusual feeding habit of eating land snails which imposes the same functional demands on the skull as do the bower building and the displaying habits of *Ptilonorhynchus.* The simultaneous functional demand of a strong grasp plus delicate control of the bill action is suggested as being responsible for the peculiar features of the bower bird skull which distinguish it so sharply from the skull of the bird of paradise.

EVOLUTIONARY AND TAXONOMIC CONCLUSIONS

The evolutionary and taxonomic implications of the observed variations in the skull morphology of the birds of paradise and the bower birds can now be evaluated with the help of the functional conclusions tentatively reached in the previous section. This discussion is limited almost entirely to the cranial anatomy, with only a few other anatomical features included; all behavioral and life history evidence have been excluded as these shall be discussed by Gilliard (MS in press). I shall make the assumption, as a point of departure for this discussion, that the birds of paradise and the bower birds are closely related, that is, that they have both evolved from the same immediate common ancestor, and are, hence, more closely allied to one another than to any other group of passerine birds. Much behavioral, life history and distributional evidence supports this assumption, as does much anatomical data. Although all the cranial evidence agrees with this conclusion, the close relationship between the birds of paradise and the bower birds cannot be accepted as absolutely conclusive; additional evidence, other than that supplied by the cranial anatomy, is needed.

The major conclusions are shown in the dendrogram (fig. 13). Even though the birds of paradise and the bower birds apparently are closely related, they should be maintained as separate families because their morphological differences are sufficient to justify familial status under the present concepts of passerine classification. These differences are summarized in table 1 (p. 107).

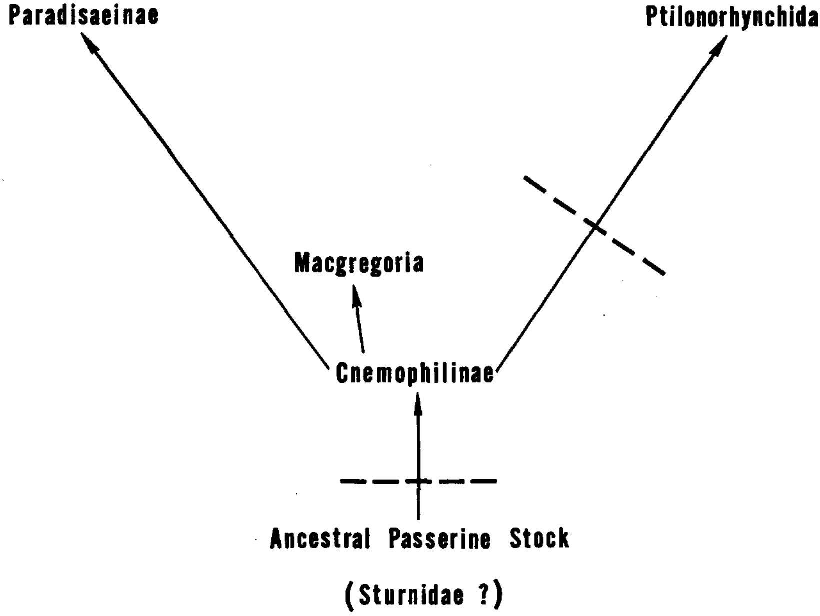

Fig. 13. Dendrogram showing the suggested relationships between the Paradisaeidae and the Ptilonorhynchidae. The boundaries between families are shown by the heavy dashed lines.

The bower birds are very uniform in their cranial anatomy and cannot be subdivided on the basis of these features. The separation of the catbirds (*Ailuroedus* and *Scenopoeetes*) from the other bower birds and the placing of them in a separate family, the Ailuroedidae (Marshall, 1954:184), is not justified in view of very similar skull structure in all bower birds. It may be noted that Marshall's suggestion was made before the structure of the skulls of *Ailuroedus* and *Scenopoeetes* was known.

The birds of paradise may be subdivided into two subfamilies, the Cnemophilinae and the Paradisaeinae. The Cnemophilinae, or "aberrant birds of paradise," represent the primitive group within this complex showing affinities to other passerine birds such as the starlings (Bock, MS). Both the bower birds and the true birds of paradise (Paradisaeinae) seem to have evolved from the Cnemophilinae; however, this group shows greater affinities to the true birds of paradise than to the bower birds and is, therefore, included within the Paradisaeidae. The true birds of paradise cannot be further subdivided on the basis of their skull morphology although it may be pointed out that the *Manucodia* group is not "primitive" in its skull structure.

The aberrant and colorful genus *Lamprolia* of Fiji has been considered at times to be possibly allied to the birds of paradise (see Mayr, 1945:137). Beecher (1953:294) concluded on the basis of its jaw muscles that *Lamprolia* is definitely not related to the birds of paradise and included it with the Malurini of his Cisticolinae. I have examined the skull remnant of this genus, taken from a study skin, and agree with Beecher that *Lamprolia* is not a paradisaeid. The ectethmoid region is definitely not bower bird-like, as the lacrymal is lacking, nor is it *Loria*-like, as the dorsolateral foramen is absent. The entire nasal region is unossified and the jaw muscles are weak which rules out the Paradisaeinae. *Lamprolia* has a very sharply defined nasal-frontal hinge which is formed by a distinct transverse groove across the base of the upper jaw where it merges into the dorsal roof of the skull. This nasal-frontal hinge is similar to that seen in some Old World warblers or flycatchers.

The contention of Iredale (1950:163) that some genera, such as *Pteridophora, Loria, Loboparadisea* and *Semioptera,* are not related to the other birds of paradise is not supported by the skull morphology of these birds. *Pteridophora* and *Semioptera* are typical members of the Paradisaeinae, whereas the skulls of *Loria* and of *Loboparadisea* are identical to that of *Cnemophilus.*

Cnemophilinae, new subfamily.—It is here proposed that the genera *Loria, Loboparadisea, Cnemophilus* and *Macgregoria* be separated from the other genera of the Paradisaeidae as the subfamily Cnemophilinae based on the type genus *Cnemophilus.* None of the other genera included in this group has ever been used as the basis for a formal suprageneric taxon.

Stonor (1937) was the first to show that *Loria* does not belong with the Ptilonorhynchidae where it was previously placed, and he transferred it to the Paradisaeidae on the basis of its skull structure. He also removed *Loboparadisea* from the bower birds and placed it with the Paradisaeidae because of its close external similarity to *Loria*; he was not, however, able to examine the skull of *Loboparadisea.* More recently, Mayr and Gilliard (1954:362, footnote) included *Cnemophilus,* also previously placed with the bower birds, in the Paradisaeidae on the basis of its lack of a free lacrymal in the adult. The affinities of these genera with the birds of paradise have been confirmed in this study, but of greater interest is the fact that they form a distinct group within the Paradisaeidae. *Macgregoria* resembles these genera in many aspects of cranial morphology although it is different in several important features in which it resembles the true birds of paradise. The morphological similarity of these four genera to one another and their distinction from the true birds of paradise is great enough to justify subfamilial recognition. The typical members of the Cnemophilinae, *Loria, Loboparadisea* and *Cnemophilus,* are essentially identical in their skull structure. *Macgregoria* is somewhat aberrant and makes an anatomical definition of this group almost impossible; hence it shall be considered separately.

The typical cnemophiline genera are characterized by their weak, broad bill, unossified nasal region, lack of a lacrymal, large ectethmoid plate with a small dorsolateral foramen, large maxillopalatine, palatines without a thickened lateral edge, broad transpalatine process, and a weak mandible in which the two rami are not fused into a strong anterior wedge. They agree with the true birds of paradise in their lack of a lacrymal, expanded tip of the orbital process of the quadrate, and presence of the posterior condyle of the quadrate, and with some paradisaeine genera, such as *Cicinnurus,* in the structure of the palatines and the maxillopalatines. On the other hand, they agree with the bower birds in the unossified nasal region, large external naris, and large maxillopalatines, and in some aspects of the palatine structure and of the quadrate-mandibular hinge. Lastly, the aberrant birds of paradise agree closely with some other passerine birds in their skull structure. They are, for example, rather similar to the starlings of the genus *Mino* in all important cranial features, including the small foramen at the dorsolateral corner of the ectethmoid plate (these groups do differ, of course, in proportions and strength of some bony elements, but these differences are of minor importance).

Evolution of the cranial features of the Cnemophilinae from those present in the presumed ancestral group involves only minor changes that need not be considered in detail. In fact, the presumed changes are about the same degree of magnitude as are generic changes within many passerine families and would be difficult to understand before a thorough study of the skull throughout the Sturnidae has been done. Indeed the cnemophilines are so little modified from their ancestral group that they could be included within the Sturnidae without even subfamilial distinction if the true birds of paradise and the bower birds had not evolved. Examples of similar situations among the passerines are rare, but some exist. One of the best cases is the genus *Fringilla* which is ancestral to the cardueline finches and hence placed in the same family as the carduelines, but had this more advanced group not evolved, then *Fringilla* would be placed with the emberizine finches from which it had evolved (Bock, 1960:475–477). Another example may be the vireos (Vireonidae) which appear to represent the ancestral stock of the New World nine-primaried oscines and are consequently included within this complex; but had the nine-primaried group not proliferated, the vireos would be placed with the group of Old World insect eaters from which they arose. The Cnemophilinae may, therefore, be considered to represent the ancestral group from which the more derived true birds of paradise and the bower birds have evolved, and hence they serve as the connecting link between these two quite specialized and morphologically different groups.

The genus *Macgregoria* is most puzzling as it does not easily fit into any of the major groups of birds of paradise. Externally, it seems to be quite different from the typical cnemophilines and resembles the genus *Paradigalla* of the Paradisaeinae most closely. I was able to examine only one skull that was removed from a study skin of *Macgregoria.* Luckily only the occipital region of this specimen was destroyed, and as the skull and skin exhibited all signs of full maturity, I believe that the structures seen in this specimen are typical for the genus. It may be noted that almost no significant individual variation was seen in the important cranial features when a large series of skulls from the same paradisaeine genus was examined. *Macgregoria* agrees with the cnemophilines and differs from the true birds of paradise in the complete lack of ossification in the nasal region, the large oblong external nares, and the presence of large maxillopalatines. The lacrymals are lacking in *Macgregoria,* but the shape of the ectethmoid is different from the *Loria* group as well as from *Paradisaea.* The small foramen at the dorsolateral corner of the ectethmoid plate is lacking, although the small foramen is present on the posterior face of the ectethmoid near its ventral edge. The dorsal part of the ectethmoid abuts against the frontal in a peculiar manner; it almost appears as if the dorsal part of the adult ectethmoid is actually the lacrymal which has fused completely to the ectethmoid and to the frontals. The lateral edge of the palatine is somewhat thickened and the transpalatine process is blunt much the same as in *Paradisaea.* The quadrate-mandibular hinge is *Paradisaea*-like as is the fusion of the anterior end of the mandibular rami to form a wedge. The postorbital and zygomatic processes are well developed in *Macgregoria*, but the anterior tip of the latter process is forward of the ventral tip of the former, not behind it as in *Paradisaea*.

This combination of somewhat contradictive characters leads to the problem of whether *Macgregoria* really belongs to the Cnemophilinae or whether it is a primitive member of the Paradisaeinae. Although *Macgregoria* is intermediate between these groups in many cranial features, I do not feel that the true birds of paradise evolved from the cnemophilines by means of *Macgregoria*. This genus has sufficient peculiar features and lacks some important characters of the true birds of paradise, such as the ossification of the nasal region, that I believe it has only paralleled the true birds of paradise in some of its cranial features. Thus I would suggest that several lines of probers and more powerful graspers (and/or gapers) arose from the Cnemophilinae—one leading to *Macgregoria* and the other, being more successful, blossomed out to become the present-day Paradisaeinae. It is possible that *Macgregoria* is truly intermediate between the two subfamilies or even that *Macgregoria* is an offshoot of the Paradisaeinae. As mentioned above, *Macgregoria* is very similar externally to *Paradigalla* and could have possibly evolved from a *Paradigalla*-like ancestor as a fruit-eating bird of paradise. The cranial features, especially the lack of nasal ossifications, could be explained as adaptations for fruit-eating and can easily be derived from the typical cranial condition of the birds of paradise. A definite answer to this problem cannot be given at this time as bits of evidence support each possibility. I feel that there is somewhat better evidence for placing *Macgregoria* in the Cnemophilinae and have so indicated it in the dendrogram (fig. 13) but show it slightly separated from the main body of the aberrant birds of paradise.

PARADISAEINAE.— With the establishment of the Cnemophilinae, the true birds of paradise, comprising all other genera of the Paradisaeidae, must be placed in another subfamily, the Paradisaeinae. This group is characterized by a completely ossified nasal region, short maxillopalatines, strong palatines with (usually) thickened lateral edges, short transpalatine processes and a stout mandible with an anterior wedge formed by the fused rami. The evolution of this group from the Cnemophilinae involves relatively few and simple morphological changes in spite of the great difference between the skulls of typical genera such as *Loria* and *Paradisaea*. Part of the morphological gap between these genera is bridged by the condition in *Cicinnurus*.

Evolution of unspecialized true birds of paradise, such as *Cicinnurus,* from the Cnemophilinae involved a general strengthening of the bill and the jaw muscles with the acquisition of a new feeding habit—powerful grasping with perhaps some probing. This led to the ossification of the nasal region to solidify the upper jaw and the fusion of the mandibular rami to form an anterior wedge and hence to strengthen the mandible. Ossification of the nasal region resulted in a reduction of the maxillopalatines and changes in the shape of the vomer. Enlargement of the jaw muscles affected the size of the postorbital and zygomatic processes and led to a strengthening of the palatines. The most radical of these changes is in the structure of the upper jaw, but this is only ossification of the nasal septum and nasal floor. Ossification within already existing membranes is one of the simplest evolutionary changes in the skeleton and may occur even as a phenotypic alteration.

Evolution of the *Paradisaea* condition from the *Cicinnurus* condition involves continued specialization of characters already present in *Cicinnurus* and apparently resulted from further specialization of probing. The main morphological change is the narrowing of the bill at its base so that the anterior part is relatively thin with almost parallel edges. The lateral edges of the palatines became much thicker, most likely as a result of increase in size of the M. pterygoideus. And the maxillopalatines are still smaller than in *Cicinnurus* as a result of the further ossification of the nasal floor. The jaw muscles have apparently increased in strength. By comparing the palatines, maxillopalatines and nasal floor in the series of *Loria, Cicinnurus,* and *Paradisaea,* one can easily understand how the very specialized palate in the last genus evolved from the rather generalized passerine palate found in the cnemophilines.

The Paradisaeinae cannot be subdivided on the basis of the skull structure with any certainty, but the following comments may be offered. Seven generic groups may be suggested on the basis of a few subtle similarities in the cranial features; these are: (a) *Lycocorax*; (b) *Manucodia* and *Phonygammus*; (c) *Ptiloris, Craspedophora, Semioptera,* and *Seleucidis*; (d) *Paradigalla*; (e) *Drepanornis* and *Epimachus*; (f) *Astrapia*; (g) *Lophorina, Parotia, Pteridophora, Cicinnurus,* and *Diphyllodes*; and (h) *Paradisaea.* However, these groups should not be taken seriously unless they are supported by other data. The least specialized skull is found in the *Lophorina-Diphyllodes* group, as discussed previously. Whether these genera are truly primitive within the Paradisaeinae is another question that cannot be answered at this time.

The paradise crows (*Lycocorax*) and the manucodes (*Manucodia* and *Phonygammus*), which are usually considered to be the most primitive members of the birds of paradise, and the reason for suggesting close affinity of this family with the crows, do not have a generalized skull. Indeed the skulls of these genera possess all the features of *Paradisaea* and are even specialized in the structure of the bulbous ectethmoid mass. These genera may be specialized offshoots of the primitive ancestral stock of the Paradisaeinae, having split off the main line of evolution leading to the true birds of paradise before the development of the specialized courtship habits, but I am very doubtful of this suggestion. These genera were usually considered representative of the ancestral stock of the entire family of birds of paradise because of their plain plumage and normal courtship and breeding haibts. Since the typical members of the Cnemophilinae have dissimilar male and female plumages, and the male plumage is very colorful, the plain coloration in the manucodes and paradise crows is most likely secondary. Perhaps the normal courtship and breeding habits are also secondarily primitive in these genera. If the birds of paradise have evolved from the starlings as is suggested by the similarity of the skulls of the Cnemophilinae and the Sturnidae, then the similarities between the paradise crow-manucode group and the Corvidae is due to convergence and there is no reason to assume that any of the features seen in these genera are primitive. Moreover, these genera are not closely related but seem to have acquired their "primitive" features independently. *Manucodia* and *Phonygammus* have long, coiled tracheae lying between the flight muscles and the skin; this structure has never been reported for *Lycocorax.* I have not had the opportunity to examine an alcoholic specimen of *Lycocorax,* but doubt that this genus possesses an elongated trachea. If *Lycocorax* has such a trachea, then in all probability it would have been observed by some collector and reported in the literature. The fact that *Lycocorax* is not related to the manucodes is not very strong evidence for either side of the argument. Lastly, the members of group "g" possess some generalized cranial features of the Paradisaeinae although they have specialized courtship habits. This combination of characters may be taken as an indication that the highly specialized courtship habits may have evolved before the skull has acquired all of the characteristics of *Paradisaea.*

PTILONORHYNCHIDAE.—Although the bower birds are morphologically quite distinct from the true birds of paradise, they are related to them through the cnemophilines. The main cranial features characterizing the bower birds are the large lacrymal, the shape of the transpalatine process, the structure of the quadrate-articular hinge, the long, forwardly curving internal process of the mandible and the lack of an expanded tip on the orbital process of the quadrate. The evolution of these cranial features from the cnemophiline skull seems to be associated with a general increase in strength of the jaw apparatus and the development of a fine control of the jaw actions. The first has led to the increase in size of the skull and the general thickening of the bones, partial fusion of the mandibular rami to form an anterior wedge, the increase in mass of the jaw muscles with the associated enlargement of the postorbital and zygomatic processes, and changes in the palatine. The second change has resulted in the structure of the quadrate-articular hinge, the structure of the internal process of the mandible, and the large size of the lacrymal.

Most of these differences are relatively simple changes in the size and shape of the bones and muscles and really need not be considered further. The difference in the lacrymal in the bower birds and Cnemophilinae is considerable and must be considered in detail. In the adult skull of the Cnemophilinae, the lacrymal is completely lacking while this bone is large and well developed in the Ptilonorhynchidae, which leads to the question: How can the aberrant birds of paradise be ancestral to the bower birds if the lacrymal is lacking in the former group while present and well developed in the latter? It is usually assumed that the absence of a structure in a group excludes this group as the ancestral stock of a group which possesses this structure. It is always possible to assume that the Cnemophilinae have lost the lacrymal after they gave rise to the bower birds, yet this assumption is not needed even if there were not indications that the skull structure of the present-day cnemophilines is very similar to that of the ancestral stock. The major question is whether the lacrymal is really completely absent in the present-day Cnemophilinae. It could be present in the embryo and become indistinguishably fused with the ectethmoid plate during later ontogeny. Unfortunately, no young specimens of this group were available for examination so that this problem cannot be solved directly. Yet there are some indications that the lacrymal in *Loria* has become fused to the anterior surface of the ectethmoid plate. There is a faint hint of a suture from the dorsolateral foramen to the small foramen on the posterior face of the ectethmoid near its ventral edge (not visible in figure). This suture, if it really exists, may be between the fused lacrymal and ectethmoid bones. In *Mino*, there are also hints that the dorsolateral foramen lies between the ectethmoid and the seemingly absent lacrymal. Berger (1957:240) states that the lacrymal has fused to the anterior surface of the ectethmoid plate in *Aplonis* which also possesses the small dorsolateral foramen.

Therefore it may be suggested that the lacrymal is present in the young of the Cnemophilinae and becomes completely fused with the ectethmoid during the course of ontogeny. Hence the apparent absence of the lacrymal in the aberrant birds of paradise cannot be regarded as proof that the Cnemophilinae cannot represent the ancestral stock of the Ptilonorhynchidae. If the ancestral stock of the bower birds possessed a fused lacrymal in the adult, suppression of its fusion with the ectethmoid and increase in its size could easily take place in the evolution of the bower birds if these changes were functionally advantageous.

The skull of the Ptilonorhynchidae is so uniform that it is not possible to suggest generic groups on the basis of the cranial features (for a listing of the genera included in this family, see p. 92). Nor is it possible from the evidence of the cranial features to deduce anything about the possible course of evolution within this group. One problem does remain from the preceding discussion of function, namely, what were the reasons for the evolution of the bower bird skull? If the skull evolved in connection with the acquisition of a new feeding habit, such as eating snails which are broken by cracking them on a rock, then the non-bower-building genera, for example, *Ailuroedus,* would be primitive. The skull would have acquired all of the specialized features of this family as adaptations for snail eating and would be preadapted for whatever purposes it was employed in bower building and display in the advanced bower-building genera. If, however, the cranial features evolved as adaptations for bower building and associated displays, then the non-bower-building genera would be specialized within the group, having lost their specialized courtship habits. The first possibility seems to be the more reasonable and the one that I favor at present, but certain bits of evidence support the second.

One very curious fact is the rather close similarity between the plumage, including the color, of the typical cnemophilines and some advanced bower birds such as *Sericulus*. This problem cannot be solved by the use of the available cranial evidence and must be left for workers using other types of information. One such type of evidence would be field observations of the feeding habits and uses of the bill in bower building and displays; such data would allow us to ascertain the functional significance of the cranial features with far greater certainty and with this, perhaps to reconstruct the evolution of the skull with greater assurance.

SUMMARY

The skulls of all genera of the Paradisaeidae and the Ptilonorhynchidae are described and compared. The jaw muscles of *Paradisaea, Ptilonorhynchus,* and *Loria* are figured and briefly described.

Three major groups can be characterized by their skull morphology. The Ptilonorhynchidae possess large lacrymals, large maxillopalatines, no nasal ossification, expanded transpalatine processes, long and forwardly curving internal processes of the mandible and a small distal tip of the orbital processes of the quadrate. The Paradisaeinae have a completely ossified upper jaw, smaller lacrymal, short maxillopalatines, thickened lateral edges of the palatine, short blunt transpalatine processes, short straight internal processes of the mandible and a greatly expanded head of the orbital processes of the quadrate. The Cnemophilinae, except *Macgregoria,* are characterized by a weak bill, unossified nasal region, absence of the lacrymal, a small foramen at the dorsolateral corner of the ectethmoid plate, large maxillopalatines, a generalized passerine palate, short straight internal processes of the mandible, and an expanded head of the orbital processes of the quadrate. *Macgregoria* possesses some of the cnemophiline features but tends toward the Paradisaeinae in others. The jaw muscles in each group parallel the skull structure.

The cnemophiline skull seems to be that of a generalized insect and fruit eater; *Macgregoria* may be more specialized as a prober for insects or gaper in eating fruit. The paradisaeine skull is adapted for probing into crevices and grasping insects by a powerful pincer action of the bill as shown by the ossification of the nasal region and the fusion of the mandibular rami to form an anterior wedge. The ptilonorhynchid skull has many peculiar features which seem to combine strong grasping with delicate control of the jaw movements; these functional properties appear to be associated with snail eating and with the bower building habits and courtship displays.

The Paradisaeidae and the Ptilonorhynchidae are assumed to be closely related, which is supported, although not fully proven, by the cranial evidence. Within the Paradisaeidae are two quite distinct groups which are given subfamilial status. The Cnemophilinae, proposed for the first time in this study, contains the genera *Loria, Loboparadisea, Cnemophilus,* and *Macgregoria.* This group represents the ancestral stock of the entire complex and bridges the great morphological gap between the Paradisaeinae and the Ptilonorhynchidae. The Paradisaeinae contains the remaining genera of the birds of paradise, but these genera cannot be further arranged on the basis of skull morphol-

ogy. The Ptilonorhynchidae, consisting of all bower bird genera, shows no further subdivisions on the basis of cranial structure. It may be noted that all genera usually placed in the Paradisaeidae and the Ptilonorhynchidae do belong to these families on the strength of the cranial anatomy; there are no unrelated genera mistakenly included in these families as has been suspected by some recent workers. Furthermore, it may be noted that *Macgregoria* is the only genus whose position within this complex is somewhat doubtful; it is definitely a bird of paradise, but there is question as to which subfamily it should be allocated.

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