RESEARCH ARTICLE

Why the long beak? Phylogeny, convergence, feeding ecology, and evolutionary allometry shaped the skull of the Giant Cowbird *Molothrus oryzivorus* (Icteridae)

Raúl O. Gómez¹ | Jimena Lois-Milevicich²

¹CONICET-Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, Buenos Aires, Argentina

²Departamento de Ecología, Genética y Evolución and Instituto de Ecología, Genética y Evolución (IEGEBA-CONICET), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, Buenos Aires, Argentina

Correspondence

Raúl O. Gómez, CONICET-Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, Buenos Aires, Argentina. Email: raulorenciogomez@gmail.com

Abstract

Cowbirds are a successful group of obligate brood parasites in the Neotropical passerine family Icteridae that offer an interesting model to explore the factors behind the evolution of the bird craniomandibular complex. The Giant Cowbird, Molothrus oryzivorus, stands out from its congeners, among other features, in diet (feeds mostly on fruit, nectar, and arthropods, instead on seeds), its larger body size, and longer, more robust beak with a much broader bony casque than in other cowbirds. In turn, Giant Cowbirds show a remarkable resemblance in these features to the distantly related caciques and oropendolas (some are its breeding hosts). However, the causes behind the latter resemblance and the distinctiveness among cowbirds have not yet been elucidated. We aim to explore the factors involved in the diverging morphology of the Giant Cowbird from its congeners and the convergence with caciques and oropendolas, surveying their skull and lower jaw under an explicit evolutionary framework. Using geometric morphometrics and comparative methods, we assessed the signal of phylogeny, convergence, feeding ecology, and size in skull shape. Our results indicated that evolution of the craniomandibular complex of icterids in general, and of the beak morphology in the Giant Cowbird in particular, are shaped by multiple factors, with phylogeny being largely overridden by changes in size (evolutionary allometry), primarily, and feeding ecology, secondarily. However, the evolution of a broad bony casque in the Giant Cowbird, otherwise a hallmark of caciques and oropendolas, does not appear to have primarily been ruled by evolutionary allometry. Instead, taking into account the unique extreme convergence between Giant Cowbirds and some of its caciques hosts, it might be consequence of selective regimes associated with parasite-host interactions acting on top of other evolutionary processes. This suggests chick mimicry as a reasonable explanation for this peculiar morphology that would require further investigation.

KEYWORDS

ecomorphology, geometric morphometrics, New World blackbirds, passerine birds, skeletal morphology

1 | INTRODUCTION

WILEY_ morphology

The craniomandibular complex of birds, especially the beak, constitutes an all-in-one tool used for multiple tasks, including preening (Bush & Clayton, 2018), vocal modulation (Mejías et al., 2020), nest building (Hansell, 2000), thermoregulation (Tattersall et al., 2009), displaying behaviors (Murphy et al., 2009), intra- or interspecific fighting (Rico-Guevara et al., 2019), and, most obviously, foraging and feeding (Beecher, 1951; Demmel Ferreira et al., 2019; Tokita et al., 2017). As such, ecomorphological variation and evolution of the skull and lower jaw are expected to be multifactorial in nature, being the outcome of several adaptive trade-offs, as well as phylogenetic and/or developmental constraints (Bright et al., 2019; Navalón et al., 2019). However, disentangling the causes behind a particular morphology is challenging. It requires that there be ecomorphological within-group variation (i.e., species show different morphologies, but also diverse diets, habitats, or habits), but also an explicit phylogenetic hypothesis indicating that such variation is not completely tied to evolutionary diversification (Feilich & López-Fernández, 2019; Losos & Miles, 1994), namely, there must be some homoplasy (e.g., due to convergent evolution). The Giant Cowbird Molothrus oryzivorus and its allies fulfill these requirements (Gómez & Lois-Milevicich, 2020; Webster, 2003), providing an interesting model (see below).

Cowbirds (Molothrus) constitute a successful group of New World Blackbirds (Icteridae; Figure 1), extensively studied for being the only Neotropical passerines that are obligated brood parasites (i.e., cowbirds lay eggs in the nest of other bird species [hosts], which provide care for the cowbird's eggs and chicks; Mann, 2017; Reboreda et al., 2019). However, significant aspects of their musculoskeletal system remain understudied (e.g., evolutionary morphology of their skeleton; phylogenetic signal of musculoskeletal traits; morphofunctional properties of gaping) and have received only limited attention during this century (e.g., Gómez & Lois-Milevicich, 2020; Steadman & Oswald, 2020; Webster, 2003), despite their study would help to fill gaps in our knowledge on diverse ecomorphological and evolutionary topics in icterids and other passerines. Such studies would contribute, for instance, to clarify the ancestral condition of icterids regarding skull morphology and gaping behavior (Beecher, 1951), to explore if the functional morphological mechanisms of gaping of other passerines (Zusi, 1993) also apply to icterids, or to test the phylogenetic relationships of extinct icterids (Steadman & Oswald, 2020), among other issues. As most other icterids, cowbirds are chiefly omnivorous, feeding variously on arthropods, seeds, nectar, and fruits, yet most Molothrus species feed mainly on seeds and secondarily on arthropods, the latter of which are mostly consumed during the breeding season (Winkler et al., 2020). The craniomandibular complex of these cowbirds is reminiscent of that of



FIGURE 1 Phylogenetic tree used in the analyses with branch lengths as time, obtained by pruning the time-calibrated tree of Barker et al. (2015). Subfamily names are from Remsen Jr. et al. (2016), but "Cacicinae" is used following Schodde and Remsen Jr. (2016). Giant Cowbird (*Molothrus oryzivorus*) marked in bold. Digital drawings (by ROG) depict representative species (from top to bottom: Grayish Baywing; great-tailed grackle: Giant Cowbird: Orange-backed Troupial: Yellow-rumped cacique: Long-tailed Meadowlark: Rufous-collared sparrow)

seed-eater finches from other families (Beecher, 1951; Webster, 2003) and, particularly their beak and temporal muscle arrangement, has been considered one of the most adapted for consuming seeds among icterids (Beecher, 1951; Webster, 2003), while their skull has shown to carry substantial phylogenetic signal (Gómez & Lois-Milevicich, 2020).

It is noteworthy that the Giant Cowbird stands out from its congeners of the genus Molothrus in many ways (see below), yet it is perhaps the less studied of the currently recognized species of cowbirds and many aspects of its biology and morphology remain poorly known, including most of its reproductive biology, development, and musculoskeletal morphology (Fiorini et al., 2019; Fraga, 2011; Gómez & Lois-Milevicich, 2020; Remsen Jr. et al., 2020). Marked dissimilarities with other Molothrus species include diet preferences, its large body size, and other morphological features including its beak (Ortega, 1998), which have formerly led to consider it in a separate genus (Blake, 1968; Hellmayr, 1938) and even as distantly related to cowbirds (Beecher, 1951; Webster, 2003). This large species (females: 28-33 cm body length; males: 33-38 cm; Ortega, 1998) is also broadly omnivorous, but, unlike other cowbirds, feeds mostly on fruit, nectar, and arthropods (Beecher, 1951; Lowther, 2020), preferring the soft fruits of several fig-related species (McCrary & Gates, 2007; Robinson, 1988). Part of the time it forages on the ground as it is most typical of other cowbirds, but also on the trees and on the back of mammals, such as tapirs and especially capybaras, picking off horseflies and ticks (Mesquita et al., 2020; Robinson, 1988). The long beak of the Giant Cowbird is unlike that of other cowbirds including differences in relative and absolute size and shape of the narial region and the bony casque, but resembles in these features that of distantly related caciques and oropendolas (Webster, 2003), some of which are regularly parasitized by this cowbird (Lowther, 2016; Ortega, 1998). Various authors have speculated on the meaning of such intriguing resemblance, interpreting Giant Cowbird morphology as transitional between other cowbirds and caciques (Beecher, 1951) or, under our current understanding of icterid phylogeny (Figure 1), the result of allometry, coevolution with hosts, and/or mimicry (Fraga, 2011; Mann, 2017; Redondo, 1993; Rothstein et al., 2002). However, this issue has not yet been addressed under a comparative framework.

Extensive current knowledge on icterid evolutionary relationships based on molecular data indicates a nested position of the Giant Cowbird within *Molothrus* and a distant relation between the latter (which are part of Agelaiinae) and caciques and oropendolas (Lanyon, 1992; Johnson & Lanyon, 1999; Powell et al., 2014; Remsen, Powell, Schodde, Barker, & Lanyon, 2016). This allows us to explore the divergent ecology and morphology of this species with respect to its cowbird congeners and its resemblance to caciques and oropendolas, under an explicit phylogenetic framework. Within this main goal, we survey the craniomandibular complex of the Giant Cowbird and its allies, seeking for ecomorphological correlates. Using geometric morphometrics and a phylomorphospace approach, we assess the signal of phylogeny, convergence, feeding ecology, and evolutionary allometry in the dorsal aspect of skull shape. We discuss our results in the context of previous hypotheses and propose explanations for morphology -WILEY

the peculiar skull morphology of the Giant Cowbird and its close resemblance to caciques and oropendolas.

2 | MATERIALS AND METHODS

2.1 | Study sample

We sampled crania of the Giant Cowbird Molothrus oryzivorus (Gmelin, 1788) and the four remaining species of Molothrus Swainson, 1832 in Swainson & Richardson, 1831 that are currently recognized in the Clements Checklist (Clements et al., 2019) and by the South and North American Classification committees of the American Ornithological Society (Remsen Jr. et al., 2020). Other agelaiines (9/20 genera, several monotypic) and species from all major icterid clades with different diets and feeding ecologies, as well as three other nine-primaried oscines (emberizoids) as outgroup taxa, were also sampled. Systematic breadth and representation was guided by recent phylogenetic hypotheses (Powell et al., 2014; Barker et al., 2015; Figure 1). When sampling caciques and oropendolas (i.e., Cacicinae; Schodde & Remsen Jr., 2016) we included species that are regular breeding hosts of giant cowbirds (Mann, 2017). The complete sample consists of 46 dry skulls and lower jaws from adult individuals representing 27 species and 16/30 extant icterid genera (Table S1). Since our preliminary observations consider cranial sexual dimorphism as negligible in comparison to the interspecific variation at the macroevolutionary scale here studied and the limited availability of dry skulls of sexed individuals, we sample both males and females indistinctly. We did not quantitatively examine the lower jaw because several specimens lack adequately preserved mandibles (either broken or incompletely prepared). Specimens examined are from the ornithological collections of the following institutions: AMNH (American Museum of Natural History, New York); FMNH (Field Museum of Natural History, Chicago); MACN (Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina); UF (Florida Museum of Natural History, University of Florida, Gainesville).

2.2 | Cranial qualitative data

When describing craniomandibular morphology we followed the nomenclature of the Nomina Anatomica Avium (Baumel et al., 1993), translating most Latin terms into English vernacular following previous usage (Gómez & Lois-Milevicich, 2020). In addition, we used some additional anatomical terms that have been widely used in icterids and other passerine birds (e.g., Beecher, 1951; Webster, 2003). Within the craniomandibular complex, we focused on the anatomy of the upper jaw, since the Giant Cowbird is at a glance highly distinctive from its congeners in its morphology (Mann, 2017; Ortega, 1998). In addition, they represent a functional morphological complex of undeniable ecological significance (e.g., Beecher, 1962; Pestoni et al., 2018; Richards & Bock, 1973) that is amenable to study from skeletal data

4____WILEY___morpholog

under a comparative framework. Particular attention was given to upper jaw proportions and the morphology of the distinctive bony casque of icterids, which is greatly developed in the Giant Cowbird and in caciques and oropendolas, as has previously been emphasized (Beecher, 1951; Webster, 2003). Osteological correlates of major jaw muscles were also explored, including adductor and depressor jaw muscles as well as pterygoid muscles. Their main variations in birds are known to be at least partially linked to different diets and feeding strategies (Bhattacharyya, 2013; Navalón et al., 2019). Taking into account the feeding habits of giant cowbirds (see Section 2.4), we centered on those described as related to whole-fruit intake (Herrera, 1984; Kalyakin, 2015; Korzun et al., 2001; Moermond & Denslow, 1985: Zubkova & Korzun, 2014).

2.3 Geometric morphometric data

In order to quantitatively assess differences and similarities in the skull of cowbirds and allies, as well as their ecomorphological correlates, we also took a geometric morphometric approach. Dorsal cranial shape was captured using 2D landmark-based geometric morphometrics. We chose the dorsal aspect of the skull since it exhibits the complete outline of the bony casque, which is particularly relevant in the context of previous hypotheses that aimed to explain the similarity of the Giant Cowbird and caciques (Fraga, 2011; Mann, 2017; Redondo, 1993; Rothstein et al., 2002). Fifteen landmarks and eight sliding semilandmarks (Figure 2; Table 1, for landmark definitions) were digitized on both sides of the skull based on digital photographs of the 46 specimens using ImageJ v. 1.52p (Schindelin et al., 2012). We used a single scale bar in the photographs to scale each specimen during image processing. To reduce the effects of parallax, photographs were taken in a standardize way, with the rostral point of the premaxilla slightly elevated, and landmarks and semilandmarks were chosen in such a way that all could lie nearly on the same plane. To minimize acquisition error, one of us (JLM) took all the photographs and the other (ROG) landmarked all images. Landmark and semilandmark coordinates for each specimen were subjected to a



FIGURE 2 Landmarks used to characterize skull shape in dorsal view. 2D landmarks (large circles) and semilandmarks (small circles) are depicted in the skull of the screaming cowbird (MACN 71191). Scale: 5 mm

Generalized Procrustes alignment (GPA), which removed spurious differences in position and orientation, but also in absolute size, leaving shape variation. The alignment was performed using the "bilat.symmetry" function of the R package geomorph (Adams & Otárola-Castillo, 2013) to extracted coordinates for the symmetric component of shape (Klingenberg et al., 2002), which we used subsequently as shape variables, and semilandmarks were slid to minimize bending energy. Centroid size (CS; the square root of the sum of the square distances of each landmark before performing GPA) was used as a proxy for skull size in downstream analyses.

Diet and feeding data 2.4

Data associated with the diet and feeding ecology of the Giant Cowbird and other species were primarily gathered from Winkler et al. (2020) and references cited therein, but supplemented with other studies (Alessio et al., 2005; De la Peña, 2020; McCrary & Gates, 2007; Mesquita et al., 2020). Since most icterids are chiefly omnivorous and almost invariably feed mostly on arthropods during the breeding season (Winkler et al., 2020), we focused whenever possible on major dietary items consumed during the winter periods, when the diets differ the most between species in order to fulfill the prerequisite of within-group variation aforementioned (Feilich & López-Fernández, 2019: Losos & Miles, 1994). This information was translated from descriptions and tabulated in order to assess the relative importance of five main food items in each species diet: invertebrates (mostly arthropods), seeds, fruit, nectar, and vertebrates. Although some diets appear to be quite unique among our sample (e.g., that of some monotypic agelaiines), we clumped together similar diets in order to minimize the number of dietary categories for downstream analyses. We took a categorical approach of diet characterization because data for several relevant species are still sparse to allow

Definitions of skull landmarks used herein (see Figure 2) TABLE 1

Landmark	Definition
1	Tip of premaxilla
2	Caudal end of neurocranium
3	Latero-caudal corner of premaxilla (left side)
4	Latero-caudal corner of premaxilla (right side)
5	Maximal constriction of narial dorsal bar (left side)
6	Maximal constriction of narial dorsal bar (right side)
7	Latero-caudal corner of nasal (left side)
8	Latero-caudal corner of nasal (right side)
9	Maximal interorbital constriction (left side)
10	Maximal interorbital constriction (right side)
11	Caudal end of orbit (left side)
12	Caudal end of orbit (right side)
13	Caudal end of temporal fossa (left side)
14	Caudal end of temporal fossa (right side)
15	Caudal end of bony casque

morphology WILEY

a quantitative approach. This procedure arrived to five broad diet categories to which each species was classified (Table S1): (1) invertebrates, typically insectivorous, plant material is minimal (Inv); (2) omnivorous with invertebrates as main item, but also some plant material (typically seeds) and often vertebrates (InvSF); (3) omnivorous, mostly fruit and invertebrates, often include nectar and vertebrates, but rarely seeds (InvFN); (4) mostly fruit and nectar, invertebrates as a secondary item, might include vertebrates but almost never seeds (FN); (5) mostly seeds, invertebrates as a secondary item, other items are negligible (SInv).

The feeding and foraging behaviors were also taken into account, since icterids use their beaks during feeding in a variety of ways that might include pecking, gleaning, sawing, husking, probing, and most notably, gaping (i.e., opening the beak against resistance within a substrate), implying different mechanical challenges for the skull (Beecher, 1950, 1951, 1962; Winkler et al., 2020). The gaping behavior is a hallmark of icterids, as well as of some other distantly related passerines such as hoopoes and some starlings (Mayr. 2005), and its musculoskeletal basis has been relatively well studied (Beecher, 1951; Zusi, 1967, 1993). However, gaping is not ubiquitous among icterids and it is absent or insignificant during feeding in some species including cowbirds (Beecher, 1951; Winkler et al., 2020). This condition in cowbirds has been formerly considered as plesiomorphic (i.e., derived from the icterid ancestor) based on the then perceived relationships of cowbirds within Icteridae (Beecher, 1951). We therefore considered if a species performs gaping during feeding (referred as gaper) as an ecological variable in our analyses (Table S1).

2.5 | Phylogenetic framework

In order to analyze cranial and ecological data under an explicit evolutionary framework, a phylogenetic tree with branch lengths that include all sampled species was needed (Figure 1). This tree was obtained by pruning the time-calibrated tree of Barker et al. (2015) using the "drop.tip" function of the R package *ape* (Paradis et al., 2004). The study of Barker et al. (2015) encompasses all clades of nine-primaried oscines and its icterid partition is based on data from the comprehensive molecular phylogenetic analysis of Powell et al. (2014). As most previous phylogenetic analyses based on molecular data (see Remsen Jr. et al., 2016 for a review), these studies also recovered four major clades within Icteridae, which have long been referred as: (1) meadowlarks and allies; (2) caciques and oropendolas; (3) troupials and orioles; (4) grackles and allies (i.e., agelaiines, which include cowbirds). We also considered these major clades when exploring and discussing our results (Table S1; Figure 1).

2.6 | Phylomorphospace approach

Visualization methods and statistical analyses to test the effect of phylogeny, feeding ecology, and evolutionary allometry on skull shape were performed in R version 3.6.1 (Team, 2019) using the R packages

geomorph version 3.1.0 (Adams & Otárola-Castillo, 2013), except otherwise noted. We first performed a principal component analysis (PCA) on the Procrustes shape data of the dorsal aspect of the skull to explore the main sources of variation among species. To better visualize how shape variation among species is related to evolutionary history we took a phylomorphospace approach (Sidlauskas, 2008). We projected the phylogeny onto the morphospaces defined by PCs 1-3 based on shape data averaged by species, with ancestors (i.e., internal nodes) estimated using maximum likelihood as implemented in "gm. prcomp" function. We particularly explored the position of the Giant Cowbird in PCs 1-3 relative to the occupation of cowbirds and different major clades, particularly caciques and oropendolas. In this phylomorphospace, Procrustes distances between nodes, terminal (species) or internal (ancestors), represent morphological branch lengths. We therefore computed these Procrustes distances on PCs 1-3 to explore the amount of evolutionary change in skull shape along branches. In order to ponder the amount of change on the branches conducting to the Giant Cowbird and to caciques and oropendolas. we fitted a Gamma distribution to branch length data and estimate the median and its 95% confidence interval (Cl₉₅) of the distribution. This was done using the "eggamma" function of the R package EnvStats (Millard, 2013) and visualized through a density plot using the R package ggplot2 (Wickham, 2009).

To visualize shape changes associated with the main axes of variation we used thin-plate spline deformation grids (Bookstein, 1992). These grids were produced using a wireframe linking the landmarks of the skull and a magnification of 1.5 to depict shape differences between minimum and maximum values for PCs 1-3 and the consensus (mean) shape. We also used these grids to explore shape differences and similarities between the Giant Cowbird and the consensus of other species of Molothrus, the fruit-eating Red-bellied Grackle Hypopyrrhus pyrohypogaster (De Tarragon, 1847), the most recent ancestor of caciques and oropendolas (node Cacicinae), and the Yellow-rumped Cacique Cacicus cela (Linnaeus, 1758), to which a particular resemblance has already been noticed (e.g., Ortega, 1998). Transformation grids between the Giant Cowbird and its direct (i.e., most recent) ancestor, as well as between the node Cacicinae and its direct ancestor, were also computed in order to compare shape changes that occurred on these two branches.

The independently evolved similarity (i.e., pattern convergence) in skull shape between the Giant Cowbird and caciques and oropendolas was quantitatively assessed using a morphospace distance-based approach (Stayton, 2015), based on the PCs 1–3 of the phylomorphospace. Comparisons were made with respect to each of the four sampled species separately. To better contextualize these estimates, we also compare the Giant Cowbird with the only other agelaiine with a presumably similar feeding ecology, the Red-bellied Grackle, the largest agelaiine in our sample, the Great-tailed Grackle *Quiscalus mexicanus* (Gmelin, 1788), and with other cowbirds as well. We calculated four convergence indices (C1, C2, C3, C4) using the function "convrat" of the R package *convevol* version 1.3 (Stayton, 2015). The rationale behind these indices is that the more disparate the ancestors, and the more alike the descendants, the

• WILEY morphology

greater the convergence (see Stayton, 2015 for a full explanation of the indices). To test the statistical significance of each convergence estimate we used the function "convratsig" of convevol, which compares the observed value to the outcomes of 1000 simulated data sets under a Brownian motion model of evolution. To assess the overall strength of phylogenetic signal in skull shape we calculated K_{mult} (Adams, 2014) using all PCs with the "physignal" function, which is a multivariate generalization of the K-statistic (Blomberg et al., 2003). To examine how phylogenetic signal is distributed among main axes of shape variation, we also calculated K_{mult} using only PCs 1-3. The statistical significance of K_{mult} values was then evaluated through permutation tests (1000 iterations) that randomized the data across the tips of the reference phylogeny.

Morphospace occupation of species with different feeding ecologies (i.e., diet; gaping) was also explored. We then evaluated whether shape data show an ecomorphological signal (i.e., species with different feeding ecologies occupy distinct regions of morphospace) and/or its variation is evolutionary linked to variation in size (evolutionary allometry; Klingenberg, 2016). We do so while accounting for phylogeny performing an analysis of variance (ANOVA), using a residual randomization permutation procedure (RRPP), and phylogenetic generalized least squares (PGLS) on shape data and CS averaged by species, using the "procD.pgls" function of geomorph. Statistical significance was assessed comparing observed values to estimates from 1000 permutations of shape data across the tips of the tree (Adams & Collyer, 2018). Evolutionary allometry was visualized by plotting the first principal component of the predicted shape scores from the multivariate regression against log-transformed CS using the "plotAllometry" function, with points identified by diet and clade.

3 RESULTS

3.1 Comparative cranial osteology

Qualitative comparisons of the anatomy of the skulls and lower jaws of the Giant Cowbird to that of its congeners (e.g., Screaming Cowbird Molothrus rufoaxillaris) readily show some marked differences. The upper jaw of the Giant Cowbird is proportionally longer, flatter, and has a more robust complexion (Figure 3a), showing a configuration that markedly contrasts to other cowbirds (Figure 3b). All specimens of Giant Cowbird examined by us have a nasal "bony strut" of uncertain developmental origin (Webster, 2003). This crosspiece of bone appears to link maxillary and premaxillary processes of the nasal on each side of the skull, forming the dorsocaudal margin of the external narial opening while delimiting a foramen caudal to it (Figure 3a). This configuration does not appear to be homologous to the so-called "amphirhinal condition" of many other passerines (see Feduccia, 1967), where nasal and alinasal cartilages ossify delimiting rostral and caudal narial openings. Whatever its developmental origin may be, this "bony strut" is also present (as well as the foramen) in the fruit-eating Red-bellied Grackle (Figure 3c) and in caciques and oropendolas (Figure 3d), yet in those taxa various nasal cartilages (i.e., nasal wall,

alinasal turbinal) also ossify. The robust appearance of the upper jaw in the Giant Cowbird and those taxa with this "bony strut" is also associated to a stouter lateral bar (maxillary process of nasal). Conversely, the maxillary process of the premaxilla (ventral bar) is more slender in the Giant Cowbird than in most other sampled icterids, including cowbirds. Its condition somewhat resembles that of the Red-bellied Grackle and troupials and orioles (Icterus spp.). As is typical of icterids, the narial dorsal bar (premaxillary process of nasal plus frontal process of premaxilla) forms a relatively flat, angled expansion termed bony casque. However, in the Giant Cowbird this casque is greatly enlarged and has rounded lateral and caudal margins, which concealed narial openings in dorsal view (Figure 3a). This configuration markedly contrasts to that in all other icterids but caciques and oropendolas, closely resembling the bony casque of the Yellowrumped Cacique (Figure 3d). In addition, in the Giant Cowbird this bony casque extends farther caudally than in other cowbirds, getting nearer to the level of the craniofacial hinge, which in turn is covered by the extended ossification of nasals and premaxilla spreading over the prokinetic area (Figure 3a).

The distinctiveness of the Giant Cowbird within Molothrus is less obvious in the cranium (i.e., neurocranium), but some differences still exist. The cranial dome (calvaria) is proportionally smaller and narrower than in other cowbirds (Figure 3a,b). The temporal fossa, where originates adductor musculature of the lower jaw, is delimited by a sharp temporal crest and is relatively well developed as in other cowbirds (Figure 3a,b). The temporal fossa is somewhat smaller than in the Red-bellied Grackle (Figure 3c), but it is proportionally larger than in caciques and oropendolas (Figure 3d). The parasphenoidal rostrum is narrower than in other cowbirds, but is wider than in the Redbellied Grackle or the caciques (Figure 3). In addition, in the Giant Cowbird the parasphenoidal rostrum bears a slight keel, which is consequence of the attachment of enlarged retractor muscles of the palatines (part of the pterygoid muscles). A keeled neurocranium is also observed in caciques and oropendolas (Figure 3d) and various other icterids, including troupials and orioles, and contrasts with the flat or slightly convex surface in other cowbirds.

As in other cowbirds and several other agelaiines and nonicterid emberizoids, the retroarticular process of the lower jaw of the Giant Cowbird is poorly developed (Figure 3a), particularly so when compared to the usually well-developed process of most nonagelaiine icterids (the Bobolink Dolichonyx oryzivorus is a notable exception). It should be noted, though, that the retroarticular process in the Giant Cowbird is visibly better developed than in other cowbirds (Figure 3b) and, among the species examined, is most similar in shape and size to that of Red-bellied Grackle (Figure 3c), which might be related to their similar feeding habits. However, the functional significance of such similarity remains to be tested. The poor development of the retroarticular process is associated with reduced depressor muscles of the lower jaw relative to the adductor musculature. Conversely, when it is well developed, such as in caciques and oropendolas (Figure 3d), provides site for the attachment of depressor muscles that are in charge of depressing the mandible against resistance during gaping. Gaping behavior is common in

(a)

orphology

WILEY 7



FIGURE 3 Cranio-mandibular complex of the Giant Cowbird and allies. Skull (lateral view) and, from left to right, details of bony casque (dorsal view), parasphenoidal rostrum (ventral view), and posterior part of right lower jaw (dorsal view) of (a) Giant Cowbird (FMNH 105554), (b) Screaming Cowbird (MACN 71191), (c) Red-bellied Grackle (AMNH 5171), and (d) Yellow-rumped Cacique (FMNH 324084). The pterygoids are missing from AMNH 5171. All elements are oriented with rostral to the right. bc, bony casque; bs, bony strut; ca, calvaria; Fr, frontal bone; Na, nasal; Nmp, maxillary process of nasal; Npp, premaxillary process of nasal; Pfp, frontal process of premaxilla; pka, prokinetic area; Pmp, maxillary process of premaxilla; Psr, parasphenoidal rostrum; Pt, pterygoid; rp, retroarticular process; tf, temporal fossa. Scales: 5 mm

icterids, but it is not known to occur or is unimportant in cowbirds, several other agelaiines, and the Bobolink.

3.2 | Phylomorphospace approach

The PCA of skull shape data averaged by species (Figure 4) shows that shape variation is largely concentrated in the first three PCs (cumulative proportion = 90.46%), with subsequent PCs each contributing little (< 5%; see Table S2 for summary of variance in the first six PCs, Table S3 for PC scores for the first six PCs, and Table S4 for loadings). The PC1 describes 77.91% of total shape variation, largely accounting for changes in the length of the upper jaw and overall bony casque and skull proportions. Moving from PC1 positive to PC1 negative, there is a trend for the beak to become longer, the bony casque larger and more caudally extended, and the neurocranium proportionally smaller. Together with these changes, toward PC1 negative the narial dorsal bar and the interorbital area become wider. The PC2 (6.64% of total shape variation) also depicts changes in proportions of the skull, and the relative position of the maximal constrictions of the narial dorsal bar and interorbital area, which appear more close to each other toward positive values. This axis also describes variation in the craniocaudal extension of the temporal region, where jaw adductor muscles attach, becoming more restricted towards PC2 negative. The PC3 (5.90% of total shape variation) represents increasing stoutness of the beak relative to the neurocranium and broadening of the bony towards positive values.

Qualitative inspection of this phylomorphospace shows that major clades of icterids occupy more or less distinct domains, but most of them broadly overlapping along the PCs 1–3 (Figure 4). Notably, caciques and oropendolas occupy a region of morphospace unexplored by other species but the Giant Cowbird. The striking similarity between these distantly related species is readily apparent on the transformational grids that compare the Giant Cowbird relative to



FIGURE 4 Phylomorphospace of the skull shape of cowbirds, other icterids, and outgroup taxa. Main three axes of variation derived from PCA of Procrustes skull shape in dorsal view, with species colored by phylogenetic group (see Figure 1). Grids representing changes of maxima and minima of each PC relative to the consensus are shown on each axis. gc, Giant Cowbird; gtg, Great-Tailed Grackle; rbg, Red-bellied Grackle; rcs, Rufous-collared Sparrow; yrc, Yellow-rumped Cacique

the common ancestor of caciques and oropendolas (Figure 5a) and to the Yellow-rumped cacique (Figure 5b). These species share similar skull proportions and a long beak, but more notably a broad bony casque, which is even broader in the Giant Cowbird than in the latter. Some other agelaiines, such as the large Great-Tailed Grackle, which approximates these species in the morphospace defined by PCs 1-2, are clearly divergent on PC3. The Red-bellied Grackle, which shares some osteological peculiarities with the Giant Cowbird, is relatively close to the latter, but much closer to the consensus shape. Differences between these two species are clearly depicted in the transformational grid (Figure 5c), which shows that the Giant Cowbird has much wider beak and bony casque and a shorter temporal region. It is remarkable that other cowbirds are at the antipodes of the Giant Cowbird in the morphospace. The transformational grid comparing the Giant Cowbird with the mean of other cowbirds clearly stressed that the former is clearly divergent, having a longer beak with a much broader bony casque and a proportionally smaller neurocranium with a much less developed temporal region (Figure 5d). The phylomorphospace therefore indicates that the Giant Cowbird and caciques and oropendolas converge in skull shape, showing quite similar shape changes occurring from their respective ancestors (Figure 5e,f). These two morphological branches are the longest morphological branches within our icterid sample (Figure 6; Table S5), with values far from the estimated median (0.026) of the fitted Gamma distribution and outside its estimated Cl₉₅ (0.000-0.031), emphasizing that the Giant Cowbird and caciques and oropendolas are also among the most divergent icterids. The only other long branches in our sample lead to outgroup taxa, the Ovenbird (Seiurus aurocapilla) and the Rufous-collared Sparrow (Zonotrichia capensis).

Convergence estimates (C1–C4) based on PCs 1–3 and *p-values* for individual comparisons of the Giant Cowbird with caciques and oropendolas, the Red-bellied Grackle, the Great-Tailed Grackle,

and other cowbirds are shown in Table 2. Convergence was strongest between the Giant Cowbird and the Yellow-rumped cacique, showing 78.5% of convergence (C1), which represents 41% of the total evolution of these lineages (C3) and 15.8% of the total evolution in the clade containing these species (C4). These values are significantly higher than would be expected by chance (all $p \leq .011$). Convergence with the remaining caciques and oropendolas as estimated by C1 was around 50%, but not statistically significant. The Giant Cowbird is also highly convergent with the more closely related Red-bellied Grackle (71.7%), to which we also find other similarities in skull morphology as aforementioned. Index values were also moderately high for comparisons with the largest agelaiine in our sample, the Great-Tailed Grackle (58.1%), likely related to convergence in the long beak and skull proportions, which might be related to allometric changes (see below). Noteworthy, our osteological comparisons failed to find any special (convergent) similarity with this species. Estimates also showed that the Giant Cowbird is completely divergent in skull shape when compared with any other species of cowbird, since all indices equal to zero (p > .999). Phylogenetic signal in skull shape, as estimated by the K_{mult} statistic, was significantly high (> 1), both using all PCs ($K_{mult} = 1$. 2394, p = .001) or only PCs 1–3 (K_{mult} = 1.3787, p = .001). This indicates that the phylogenetic signal in the data is greater relative to expectations of random association of phenotypes and species under a Brownian motion model of evolution, despite the notable cases of convergence outlined above.

Exploration of the morphospace also shows a differential occupation of species with different feeding ecologies (Figure 7). The Giant Cowbird, the Red-bellied Grackle, and caciques and oropendolas, all classified here as having the same diet (InvFN), are mostly restricted to negative values of PC1 negative values or around zero of PC2, and positive values of PC3. Noteworthy, no other species sampled by us occupies this region of morphospace. Similarly, almost all species



FIGURE 5 Transformational grids of skull shape. Grids depicting changes in Procrustes shape between the following pairs of configurations: (a) Giant Cowbird versus consensus of other species of *Molothrus*; (b) Giant cowbird versus Red-bellied Grackle; (c) Giant Cowbird versus node Cacicinae; (d) Giant Cowbird versus Yellow-rumped Cacique; (e) Giant Cowbird versus its direct ancestor; (f) node Cacicinae versus its direct ancestor

feeding mostly on seeds (SInv), such as other cowbirds, the Bobolink, or the Rufous-collared Sparrow, occupy a region defined by positive values of PC1 and PC3, which is otherwise unexplored by other dietary groups. The only exception might be the Red-winged Blackbird (*Agelaius phoeniceus*), which, is the only gaper among the seed-eaters sampled and occupies a region of morphospace that is almost exclusively populated by omnivorous gapers that feed mostly on invertebrates and secondarily on seeds (InvSF). Gaper and non-gaper species also occupy distinct regions of the morphospace, with the Giant Cowbird and the Red-bellied Grackle as the most divergent within the latter, occupying regions that are otherwise reserved to gapers.

The PGLS models performed to assess the influence of size and two aspects of feeding ecology (diet and gaping) on skull shape (Tables 3 and 4) found that variation in size accounted for near 45% of the total variance of shape, whereas diet was associated with 14% of shape variance (Table 3), with no significant interaction between size and diet, and gaping explained 6% of shape variance in the respective model (Table 4), with no significant interaction between



FIGURE 6 Density plot of morphological branch lengths. Indicated are the median (solid line) of the gamma distribution with its Cl₉₅ (darker shaded area) and the branch lengths leading to the Giant Cowbird (black solid arrow) and to the node Cacicinae (open arrow)

TABLE 2Convergence in skull shape

Focal species	C1	C2	C3	C4
Yellow-rumped Cacique	0.785	0.217	0.410	0.158
	(.011)	(<.001)	(.005)	(<.001)
Red-rumped Cacique	0.530	0.146	0.295	0.107
	(.105)	(.001)	(.072)	(.001)
Crested Oropendola	0.416	0.137	0.199	0.100
	(.182)	(.002)	(.215)	(.001)
Russet-backed Oropendola	0.380	0.125	0.234	0.091
	(.240)	(.002)	(.172)	(.007)
Red-bellied Grackle	0.717	0.276	0.638	0.398
	(.018)	(<.001)	(<.001)	(<.001)
Great-tailed Grackle	0.581	0.217	0.494	0.313
	(.053)	(<.001)	(<.001)	(<.001)
Brown-headed Cowbird	0.00	0.00	0.00	0.00
	0.999	0.999	0.999	0.999
Shiny Cowbird	0.00	0.00	0.00	0.00
	0.999	0.999	0.999	0.999
Screaming Cowbird	0.00	0.00	0.00	0.00
	0.999	0.999	0.999	0.999
Bronzed Cowbird	0.00	0.00	0.00	0.00
	0.999	0.999	0.999	0.999

Note: Estimates (C1–C4) based on PCs 1–3 and p-values (in brackets) for individual comparisons of the Giant Cowbird with different focal species. Bold indicates significant p-values (<.05).

size and gaping. The strong association of skull shape and size (i.e., evolutionary allometry) is clearly shown in the allometry plot of regression scores on log-transformed CS (Figure 8). Omnivorous species feeding mostly on arthropods and fruits (InvFN), including the Giant Cowbird and caciques, tended to have larger skulls and higher regression scores, whereas seed-eaters (SInv), insectivorous (Inv), and frugivorous/nectarivorous (FN) species tended to have smaller skulls and lower regression scores. Omnivorous species (gapers) feeding mostly on arthropods (InvSF) tended to have mid-to-large skulls and averaged regression scores.

4 | DISCUSSION

Differences in body size, plumage, diet (preference for fruit over seeds), and beak and skeletal morphology, particularly of the upper jaw and its bony casque, between the Giant Cowbird and other cowbirds, as well as similarities in these features between the former and caciques and oropendolas, have long been noted (Beecher, 1951; Mann, 2017; Ortega, 1998; Webster, 2003). The factors underlying such morphological pattern have intrigued ornithologists for an equally long time. The few previous works mainly relying on skeletal data, such as ours, have interpreted the morphology of the Giant Cowbird as transitional to that of caciques and oropendolas, advocating for a close relationship with the latter (Beecher, 1951; Webster, 2003). These interpretations are clearly contradicted by current understanding of the icterid phylogeny that is largely grounded on comprehensive analyses of molecular data and indicates that the Giant Cowbird is only distantly related to caciques (Figure 1), which had led to underestimate skeletal and other morphological data in icterid systematics (e.g., Powell et al., 2014; but see Gómez & Lois-Milevicich, 2020). Nevertheless, it should be noted that these pioneering morphological approaches either lacked a formal methodology (e.g., Beecher, 1951) or simply were not circumscribed within the epistemological framework of modern phylogenetic systematics (Hennig, 1965). Based on quantitative analyses of both discrete and continuous characters, it has been demonstrated that the craniomandibular complex of cowbirds and allies indeed carries significant phylogenetic signal (Gómez & Lois-Milevicich, 2020). This is further endorsed by our present study, which finds K_{mult} estimates for skull shape data significantly higher than what is expected by chance under a Brownian model of evolution. Present values of K_{mult} for skull shape are smaller than that obtained previously based on a different craniomandibular data set of icterids (Gómez & Lois-Milevicich, 2020), but are still considerably higher when compared with the mean (0.65) of over 330 estimates on multivariate phenotypic data across different taxonomic groups (Adams & Collyer, 2019).

Despite high phylogenetic signal in skull shape data, we also find that the Giant Cowbird markedly differs from its congeners in several aspects of its cranial morphology (Steadman & Oswald, 2020; this study), showing significant similarities with caciques and oropendolas, and, to a lesser degree, the Red-bellied Grackle, some of which have already been noticed (Beecher, 1951; Webster, 2003). Moreover, our results also echo those of Webster (2003), who found caciques and oropendolas to have the most distinct skeleton within Icteridae, with the Giant Cowbird and the Red-bellied Grackle partially bridging the morphological gap with other blackbirds. The unique nature of the skull shape of the Giant Cowbird and caciques and oropendolas is easily visualized in the phylomorphospace (Figure 4), where the Redbellied Grackle appears far less divergent from other icterids than the Giant Cowbird does. The current framework of icterid interrelationships provided by molecular phylogenetics (Johnson & Lanyon, 1999; Powell et al., 2014; Remsen Jr. et al., 2016) clearly indicates that the Giant Cowbird is nested within other cowbirds (Molothrus) and only distantly related to caciques and oropendolas (Figure 1). This scenario

TABLE 3

TABLE 4 Phylogenetic generalized the least squares of skull shape against

gaping and centroid size (CS)



FIGURE 7 Relationship between feeding ecology and skull shape. Morphospace based on PCA of dorsal skull shape with species colored according their diet preferences (see Section 2.4 for an explanation of diet categories). Stroke weight depicts gaping behavior: Gapers (thick) and non-gapers (thin). Symbol shapes depict phylogenetic groups. Cowbirds as well as caciques and oropendolas are depicted by convex hulls. bo, Bobolink; cac, caciques and oropendolas; cow, cowbirds; gc, Giant Cowbird; gtg, Great-Tailed Grackle; rbg, Red-bellied Grackle; rcs, Rufouscollared Sparrow; rwb, Red-winged Blackbird

TABLE 3 Phylogenetic generalized the least squares of skull shape against		Df	SS	MS	Rsq	F	Z	Pr(>F)
diet category and centroid size (CS)	Log (CS)	1	0.0204	0.0204	0.4450	23.5303	3.7788	0.001
	Diet	4	0.0064	0.0016	0.1403	1.8542	1.7157	0.047
	Log (CS): diet	4	0.0043	0.0011	0.0933	1.2329	0.6127	0.269
	Residuals	17	0.0147	0.0009	0.3215			
	Total	26	0.0458					

Note: Statistical significance assessed through 1000 permutations. Bold indicates significant pvalues (<.025).

	df	SS	MS	Rsq	F	Z	Pr(>F)
Log (CS)	1	0.0204	0.0204	0.4498	22.3017	3.6682	0.001
Gaping	1	0.0028	0.0028	0.0609	3.0528	2.1098	0.013
Log (CS): gaping	1	0.0016	0.0016	0.0352	1.7635	1.0727	0.146
Residuals	23	0.0210	0.0009	0.4589			
Total	26	0.0458					

Note: Statistical significance assessed through 1000 permutations. Bold indicates significant pvalues (<.025).

dictates that the similarity between the latter and the Giant Cowbird must be the result of convergence (i.e., evolved independently; see Stayton, 2015), demanding alternative explanations other than inheritance from a common ancestor. According to our estimates with the indices of Stayton (2015), the Giant Cowbird is highly convergent with sampled caciques and oropendolas in skull shape, particularly with the Yellow-rumped Cacique (host of the Giant Cowbird; Lowther, 2016). In the latter case, evolution brings them closer a 78.5% of their maximum ancestral distance, an extremely high amount of convergence when compared to estimates in different groups of birds (Johnson et al., 2017), lizards (Gray et al., 2019), and mammals (Grossnickle et al., 2020). This extreme convergence is further stressed by the unique nature of their skulls among icterids, which is reflected by their

occupation of an otherwise unexplored region of the morphospace, but also by the long branches leading to them (Figure 6). This convergence, however, is 'incomplete' (see Stayton, 2006 for a definition), since the Giant Cowbird closely resembles caciques in overall skull shape and its bony casque, while maintaining morphologies typical of non-gapers (e.g., in the temporal region and lower jaw; Figure 3), which is also depicted in the imperfect match in morphospace occupation.

From Darwin's famous finches (Grant & Grant, 1993; Tokita et al., 2017) to waterfowls (Olsen, 2017), convergence in skull and beak shape in birds has often been explained as adaptation to similar dietary habits (Navalón et al., 2019). In his seminal works, Beecher (1950, 1951) stated that icterids show craniomandibular



FIGURE 8 Evolutionary allometry in skull shape. Predicted shape scores against log-transformed centroid size (CS). Colors depict species diet preferences (see Section 2.4 for an explanation of diet categories), stroke weight depicts gaping behavior, and symbol shapes depict phylogenetic groups (see Section 2.5). Black silhouettes depict the skulls in dorsal view of the Rufous-collared Sparrow (outgroup taxon), the Giant Cowbird, and the Crested Oropendola

adaptations that allow them to exploit almost every food resource available to passerine birds. Despite marked differences in the evolutionary framework, our results agree with his observations, showing that there is an ecomorphological signal in the skull of cowbirds and allies associated with their feeding ecology. This is reflected in the differential occupation of the skull shape morphospace by species according to their diet and gaping behavior (Figure 7), as well as in the Phylogenetic Generalized Least Squares (PGLS) results, which show feeding ecology to be an important, yet barely statistically significant, factor underlying skull shape variation in icterids (Tables 3 and 4). The relatively small proportion of total variance of skull shape associated with feeding ecology seems to be at odds with the observed pattern of differential morphospace occupation of species with different diets and gaping behavior. However, this could be explained by the interaction that exists between the latter and phylogeny in our sample, regarding some feeding groupings as not entirely independent of evolutionary history and therefore much of the variation remained unexplained by size or feeding variables in the PGLS models. This is exemplified by our category including species that feed mostly on fruit and nectar (FN), which is restricted to troupials and orioles and therefore results dependent of phylogeny for this comparative method. The strong association of skull shape and size (i.e., evolutionary allometry) is clearly shown in the allometry plot of regression scores on logtransformed CS (Figure 8). The Giant Cowbird, the Red-bellied Grackle, and caciques and oropendolas, all of which have a diet largely

based on arthropods and fruits (Beecher, 1951; Lowther, 2020; Winkler et al., 2020), also share various features of their skulls (Beecher, 1951; Webster, 2003; Figures 3a,c,d, and 7). Mining the literature, we find that several features have been linked to frugivory in birds (Bhattacharyya, 2013; Herrera, 1984; Kalyakin, 2015; Korzun et al., 2001; Moermond & Denslow, 1985; Zubkova & Korzun, 2014), most of which are also present in the Giant Cowbird and other large fruit-eating icterids but not in other Molothrus, as revealed by our osteological observations. The Giant Cowbird differs from other cowbirds in having a much larger size, an enlarged and more robust, flatter beak (Beecher, 1951; Steadman & Oswald, 2020; Webster, 2003) with strengthened narial lateral bar and prokinetic area, and a keeled neurocranium that indicate greater development of retractor muscles (Figure 3a,b), all of which have been considered characteristic traits of birds that eat whole fruits direct from the tree (Bhattacharyya, 2013; Herrera, 1984; Kalyakin, 2015; Moermond & Denslow, 1985; Zubkova & Korzun, 2014). A robust narial lateral bar aids in transmitting and disseminating the forces imposed on the tomial margin towards the skull roof, and thus protecting the prokinetic area, as has been proposed for frugivorous birds tearing fruits from the branches (Zubkova & Korzun, 2014). It is possible that the spreading of facial ossifications over the craniofacial hinge observed in the Giant Cowbird further strengthen this area.

As aforementioned, the Giant Cowbird and caciques and oropendolas have an extremely wide narial dorsal bar forming a bony casque much broader than in other icterids (Figure 3). Beecher (1951) considered the broad casque of caciques and oropendolas as an evident adaptation for gaping in large fruits. However, the Giant Cowbird does not exhibit gaping behavior neither it has the musculoskeletal traits needed for that task (Beecher, 1951; Webster, 2003; Figure 3a). It is noteworthy that a broad casque caudally extended over the frontal, reminiscent to that of oropendolas, is also present in some large touracos (Korzun et al., 2001). The latter are specialized fruit-eating birds endemic to Africa that either consumed fruit whole from the tree or cut it with their scissors-like beak, but do not gape into it (Korzun et al., 2001). Although the particular functional morphological significance of this casque is uncertain, undoubtedly it does not constitute an adaptation to gaping fruit in the Giant Cowbird, or in the touracos. It is possible that coupled with other osteological features as those described above, a broad casque may also contribute to strengthen the beak in these large-sized species, but this remains speculative.

Interestingly, our PGLS results show a strong association of size and shape variation in skull shape data (Table 3). This indicates that evolutionary allometry has played a major role in shaping the skull of icterids, which produces a trend for the upper jaw to elongate with increasing size (a trend also recovered in mammals and linked to heterochronic processes; Cardini & Polly, 2013), agreeing with previous studies on different avian groups that also recovered a similar pattern, such as raptors (Bright et al., 2016), parrots (Bright et al., 2017), Darwin's finches and Hawaiian honeycreepers (Tokita et al., 2017). This pattern is clearly depicted in the bivariate plot of predicted shape scores against size (Figure 8), which show that both shape and size spaces are somewhat partitioned according to dietary preferences. This suggests that size variation might constitute an effective route by which icterids modified their feeding ecology. Therefore, the incomplete convergence in size and shape of the Giant Cowbird with caciques and oropendolas might be partially explained by evolutionary allometry linked to changes toward a similar feeding ecology, yet important differences in foraging and feeding behavior remain. It is worth mentioning, however, that none of the other large icterids in our sample (all agelaiines; see Figure 8) converge with the Giant Cowbird and caciques and oropendolas in their broad bony casque, disregarding of their diet or feeding behavior. Hence, the evolution of a broad bony casque does not appear to have been ruled by evolutionary allometry.

A possible explanation accounting for this convergence pattern that is often invoked for brood parasitic birds (including cowbirds) and their hosts is coevolution (Redondo, 1993; Rothstein et al., 2002; Smith, 1968; Soler, 2017). Under this scenario, hosts are thought to evolve fine-tuned adaptations as defenses for parasitism, whereas brood parasites evolve corresponding counter-defenses that in turn select for host defenses, thus leading to a coevolutionary arms race (Rothstein, 1990; Soler, 2017). Understanding coevolution as reciprocal evolutionary change in two or more interacting species (e.g., Thompson, 1994), it has to be noted that for coevolution to occur there must be co-occurrence of species in space and time. It is obvious that nowadays the Giant Cowbird co-occurs with caciques and oropendolas that are regular hosts, some of which have largely overlapping geographic distributions (Winkler et al., 2020), but this has not needed to be the case during past times. Evidence indicates that the most recent common ancestor of caciques and oropendolas (node Cacicinae) has already evolved the characteristic skull shape with a long beak and a broad bony casque more than 4.5 million years ago, whereas the Giant Cowbird diverged from other extant cowbirds only recently in evolutionary terms (around 2 million years ago; Barker et al., 2015; Figure 1). According to the skull morphology of other icterids and our ancestor reconstructions, the peculiar skull shape of the Giant Cowbird likely evolved from a condition closer to that of other cowbirds (Figure 4). Therefore, it appears that the long beak and broad casque of the Giant Cowbird and caciques and oropendolas have not evolved jointly. In other words, the changes leading to this particular skull shape in the Giant Cowbird (Figure 5e) and those in the lineage of caciques and oropendolas (Figure 5f) were not reciprocal, since skull shape of the latter evolved even earlier than the most recent ancestor of all extant cowbirds did (Barker et al., 2015; Figure 1).

This does not inhibit, though, that these features of the Giant Cowbird evolved in response to selective regimes associated with parasite-host interactions. In this regard, the resemblance between the Giant Cowbird and its caciques/oropendolas hosts is yet more notable when considering nestling and fledging stages, which has been considered a possible case of host chick mimicry (Mann, 2017; Redondo, 1993). The beak of young giant cowbirds has been described as white (Crandall, 1914; Ortega, 1998), yellow (Redondo, 1993), pinkish-ivory (Fraga, 2011), horn colored (Lowther, 2020), or, morphology WILEY

simply, pale, instead of black as in adults. This pale beak coloration is similar to that of some of its host nestlings and adults (Fraga, 2011; Ortega, 1998), yet it has been noted that nestlings of the Screaming Cowbird, sister group of all other cowbirds, also have an overall pale beak (Fraga, 1979). This withdraws support to the mimicry hypothesis, since it would regard beak coloration as a feature that has been phylogenetically retained from an ancestor (Fraga, 2011). However, chicks of the Giant Cowbird also have a long beak with a broad, pale frontal casque, further exaggerated by white bare parts of the face (Lowther, 2020), enhancing the resemblance to host chicks (Fraga, 2011). To note, the horny casque of giant cowbirds has been described as becoming partially covered with feathers and smaller as the chicks grow into adults, (Fraga, 2011; Lowther, 2020). We could not examine skulls of early ontogenetic stages of the Giant Cowbird, but the adult bony casque appears to be broader than the bare horny casque (i.e., not covered by feathers) and it is as broad as that of some caciques (Figure 3a,d). This suggests that the bony casque does not shrink ontogenetically, but that instead is only the horny casque that changes its appearance with age. Skull ontogenetic series of the Giant Cowbird and caciques and oropendolas would be necessary to settle this issue.

Considering all the above, we agree with previous authors in regarding mimicry as a likely explanation for the resemblance in the frontal casque between chicks of the Giant Cowbird and caciques and oropendolas (Fraga, 2011: Redondo, 1993). This interpretation would also gain some support from two other lines of evidence. One is related to the fact that this close resemblance in beak color and horny casque shape between giant cowbirds and their hosts disappears after chicks have attained nutritional independence from their hosts (Redondo, 1993). This is also the case in the Screaming Cowbird. which nestlings closely mimics those of its preferred host (De Mársico et al., 2012; Fraga, 1979); the latter, in turn, is known to refuse to feed non-mimetic fledglings of other cowbird species (Fiorini et al., 2019; Fraga, 1998). Under such a scenario where the host discriminates against parasitic chicks, mimetic nestlings and fledglings would be clearly adaptive for the parasite survival. The other line of evidence relates to the apparent lack of mimicry at the egg stage between giant cowbirds and their hosts (Fiorini et al., 2019; Fraga, 2011; Ortega, 1998), suggesting that the latter are egg acceptors (Fraga, 2011). This, coupled with the emerging pattern that shows that most host species that discriminate against parasite chicks are acceptors of natural parasite eggs (Grim, 2017), also point to chick mimicry as a reasonable explanation. Ideally, this should be tested experimentally in the field, but the pending nests of the latter, which are located high in the trees and often surrounded by wasps and botflies (Ortega, 1998; Robinson, 1988; Smith, 1968), impose challenges that make this unlikely to occur in the near future.

5 | CONCLUSIONS

Our results indicate that evolution of the craniomandibular complex of icterids in general, and of a long, robust beak and broad bony casque in the Giant Cowbird in particular, are shaped by multiple factors. Hence, the explanations behind the diverging morphology of the Giant Cowbird from its congeners and the remarkable, yet incomplete, convergence with caciques and oropendolas appear to be multifactorial. Several aspects of the skull and lower jaw of the Giant Cowbird are the result of inheritance from cowbird ancestors (phylogeny), such as a relatively broad temporal fossa and a reduced retroarticular process. However, some skull features convergent with caciques and oropendolas (e.g., long, robust beak) show that this phylogenetic signal is largely overprinted by changes in size (evolutionary allometry) linked to ecomorphological changes towards similar diet preferences (feeding ecology). Conversely, the evolution in the Giant Cowbird of a broad bony casque, otherwise a hallmark of caciques and oropendolas, does not appear to have been ruled by evolutionary allometry. Instead, it might be the result of selective regimes associated with parasite-host interactions acting on top of other evolutionary processes, suggesting chick mimicry as a reasonable explanation for this peculiar morphology.

ACKNOWLEDGMENTS

We are grateful to B. Bird and P. Sweet (AMNH), B. Marks (FMNH), Y. Davies and D. Litjmaer (MACN) for access to materials under their care and for their kind assistance. Thanks are extended to T. Webber (UF), who kindly provided photos of the Yellow-breasted Chat. We thank anonymous reviewers for their careful reading and valuable suggestions, which certainly improved this study, and the Editor-in-Chief M. Starck for his proficient work. We also thank CONICET and the University of Buenos Aires for continuous support.

AUTHOR CONTRIBUTIONS

Raúl O. Gómez: Conceptualization (lead); data curation (equal); formal analysis (lead); investigation (lead); methodology (lead); validation (lead); visualization (lead); writing - original draft (lead). Jimena Lois-Milevicich: Data curation (equal); writing-review & editing (supporting).

PEER REVIEW

The peer review history for this article is available at https://publons. com/publon/10.1002/jmor.21408.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Raúl O. Gómez bttps://orcid.org/0000-0002-6600-3787 Jimena Lois-Milevicich bttps://orcid.org/0000-0003-0558-4415

REFERENCES

Adams, D. C. (2014). A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. Systematic Biology, 63, 685–697. https://doi.org/10.1093/sysbio/syu030

- Adams, D. C., & Collyer, M. L. (2018). Multivariate phylogenetic comparative methods: Evaluations, comparisons, and recommendations. *Systematic Biology*, 67, 14–31. https://doi.org/10.1093/sysbio/syx055
- Adams, D. C., & Collyer, M. L. (2019). Phylogenetic comparative methods and the evolution of multivariate phenotypes. *Annual Review of Ecol*ogy, Evolution, and Systematics, 50, 405–425. https://doi.org/10.1146/ annurev-ecolsys-110218-024555
- Adams, D. C., & Otárola-Castillo, E. (2013). Geomorph: An R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution*, 4, 393–399. https://doi.org/10. 1111/2041-210X.12035
- Alessio, V. G., Beltzer, A. H., Lajmanovich, R. C., & Quiroga, M. (2005). Ecología alimentaria de algunas especies de Passeriformes (Furnariidae, Tyrannidae, Icteridae y Emberizidae): Consideraciones sobre algunos aspectos del nicho ecológico. In F. G. Aceñolaza (Ed.), *Temas de la biodiversidad del Litoral Fluvial Argentino II, INSUGEO, Miscelánea* 14 (pp. 441–482). Magna.
- Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., & Lovette, I. J. (2015). New insights into New World biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *Auk*, 132, 333–348. https://doi.org/10.1642/AUK-14-110.1
- Baumel, J. J., King, J. E., Breazile, H. E., & Vanden Berge, J. C. (Eds.). (1993). Handbook of avian anatomy: Nomina anatomica avium (2nd ed.). Publications of the Nuttall Ornithological Club.
- Beecher, W. J. (1950). Convergent evolution in the American orioles. The Wilson Bulletin, 62, 50–86. http://www.jstor.org/stable/4157845
- Beecher, W. J. (1951). Adaptations for food-getting in the American blackbirds. Auk, 68, 411–440. https://doi.org/10.2307/4080840
- Beecher, W. J. (1962). The bio-mechanics of the bird skull. Bulletin of the Chicago Academy of Sciences, 11, 10–33.
- Bhattacharyya, B. N. (2013). Avian jaw function: Adaptation of the sevenmuscle system and a review. Proceedings of the Zoological Society, 66, 75–85. https://doi.org/10.1007/s12595-012-0056-x
- Blake, E. R. (1968). Family Icteridae. In R. A. Paynter, Jr. (Ed.), Check-list of birds of the world (Vol. 14, pp. 138–202). Museum of Comparative Zoology.
- Blomberg, S. P., Garland, T., Jr., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717–745. https://doi.org/10.1111/j.0014-3820.2003. tb00285.x
- Bookstein, F. (1992). Morphometric tools for landmark data: Geometry and biology. Cambridge University Press. https://doi.org/10.1017/ CBO9780511573064
- Bright, J. A., Marugán-Lobón, J., Cobb, S. N., & Rayfield, E. J. (2016). The shapes of bird beaks are highly controlled by nondietary factors. Proceedings of the National Academy of Sciences of the United States of America, 113, 5352–5357. https://doi.org/10.1073/pnas.1602683113
- Bright, J. A., Marugán-Lobón, J., Rayfield, E. J., & Cobb, S. N. (2019). The multifactorial nature of beak and skull shape evolution in parrots and cockatoos (Psittaciformes). BMC Evolutionary Biology, 19, 104. https:// doi.org/10.1186/s12862-019-1432-1
- Bush, S. E., & Clayton, D. H. (2018). Anti-parasite behaviour of birds. Philosophical Transactions of the Royal Society B, 373, 20170196. https:// doi.org/10.1098/rstb.2017.0196
- Cardini, A., & Polly, P. D. (2013). Larger mammals have longer faces because of size-related constraints on skull form. *Nature Communications*, 4, 2458. https://doi.org/10.1038/ncomms3458
- Clements, J. F., Schulenberg, T. S., Iliff, M. J., Billerman, S. M., Fredericks, T. A., Sullivan, B. L., & Wood C. L. (2019). The eBird/Clements Checklist of Birds of the World: v2019. Retrieved from https://www.birds.cornell.edu/clementschecklist/download
- Crandall, L. S. (1914). Notes on costa Rican birds. Zoologica, 47, 39–58. https://doi.org/10.2307/1365741

- De la Peña, M. R. (2020). Aves Argentinas: Descripción, Comportamiento, Reproducción y Distribución (Actualización). Emberizidae, Cardinalidae, Parulidae, Icteridae, Fringillidae, Passeridae. *Comunicaciones del Museo Provincial de Ciencias Naturales 'Florentino Ameghino'*, 12, 1–243.
- De Mársico, M. C., Gantchoff, M. G., & Reboreda, J. C. (2012). Hostparasite coevolution beyond the nest-ling stage? Mimicry of host fledglings by the specialist screaming cowbird. *Proceedings of the Royal Society of London, Series B: Biological Sciences, 279, 3401–3408.* https://doi.org/10.1098/rspb.2012.0612
- De Tarragon, M. (1847). Description d'une nouvelle espèce de Cassique, et note sur le Macronix Ameliœ. *Revue Zoologique*, 10, 252–253.
- Demmel Ferreira, M. M., Tambussi, C. P., Degrange, F. J., Pestoni, S., & Tirao, G. A. (2019). The cranio-mandibular complex of the nightjar Systellura longirostris (Aves, Caprimulgiformes): Functional relationship between osteology, myology and feeding. Zoology, 132, 6–16. https:// doi.org/10.1016/j.zool.2018.11.001
- Feduccia, J. A. (1967). The Amphirhinal condition in the Passeriformes. The Wilson Bulletin, 79, 453–455. http://www.jstor.org/stable/4159665
- Feilich, K. L., & López-Fernández, H. (2019). When does form reflect function? Acknowledging and supporting ecomorphological assumptions. *Integrative and Comparative Biology*, 59, 358–370. https://doi.org/10. 1093/icb/icz070
- Fiorini, V. D., De Mársico, M. C., Ursino, C. A., & Reboreda, J. C. (2019). Obligate brood parasitism on Neotropical birds. In J. Reboreda, V. D. Fiorini, & D. Tuero (Eds.), *Behavioral ecology of Neotropical birds* (pp. 103–131). Springer. https://doi.org/10.1007/978-3-030-14280-3_6
- Fraga, R. M. (1979). Differences between nestlings and fledglings of screaming and bay-winged cowbirds. *The Wilson Bulletin*, 91, 151–154. https://www.jstor.org/stable/4161189
- Fraga, R. M. (1998). Interactions of the parasitic screaming and shiny cowbirds (Molothrus rufoaxillaris and M. bonariensis) with a shared host, the bay-winged cowbird (M. badius). In S. I. Rothstein & S. K. Robinson (Eds.), Parasitic birds and their hosts: Studies in coevolution pp (pp. 173– 193). Oxford University Press.
- Fraga, R. M. (2011). Giant cowbird (Molothrus oryzivorus) parasitism of redrumped caciques (Cacicus haemorrhous) in the Atlantic forest, northeastern Argentina. The Wilson Journal of Ornithology, 123, 277–282. https://doi.org/10.1676/10-103.1
- Gmelin, J. F. (1788). Caroli a Linné [...] Systema Naturae, per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis (13th ed., Aucta, Reformata). Lipsiae [Leipzig, Germany]: Impensis G. E. Beer.
- Gómez, R. O., & Lois-Milevicich, J. (2020). Phylogenetic signal in the skull of cowbirds (Icteridae) assessed by multivariate and cladistic approaches. *Zoologischer Anzeiger - A Journal of Comparative Zoology*, 286, 52–57. https://doi.org/10.1016/j.jcz.2020.03.005
- Grant, B. R., & Grant, P. R. (1993). Evolution of Darwin's finches caused by a rare climatic event. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 251, 111–117. https://doi.org/10.1098/rspb. 1993.0016
- Gray, J. A., Sherratt, E., Hutchinson, M. N., & Jones, M. E. (2019). Evolution of cranial shape in a continental-scale evolutionary radiation of Australian lizards. *Evolution*, 73, 2216–2229. https://doi.org/10.1111/ evo.13851
- Grim, T. (2017). Host Defences against brood parasite nestlings: Theoretical expectations and empirical evidence. In M. Soler (Ed.), Avian brood parasitism: Behaviour, ecology, evolution and coevolution (pp. 539–556). Springer. https://doi.org/10.1007/978-3-319-73138-4_29
- Grossnickle, D. M., Chen, M., Wauer, J. G., Pevsner, S. K., Weaver, L. N., Meng, Q. J., Liu, D., Zhang, Y. G., & Luo, Z. X. (2020). Incomplete convergence of gliding mammal skeletons. *Evolution*, 74, 2662–2680. https://doi.org/10.1111/evo.14094

Hansell, M. (2000). *Bird nests and construction behaviour*. Cambridge University Press.

morphology -WILEY

- Hellmayr, C. E. (1938). Catalogue of birds of the Americas and the adjacent islands in Field Museum of natural history (Vol. 13, Part 10, Zoological Series). Field Museum Natural History Publications.
- Hennig, W. (1965). Phylogenetic systematics. Annual Review of Entomology, 10, 97–116. https://doi.org/10.1146/annurev.en.10.010165.000525
- Herrera, C. (1984). A study of avian frugivores, bird dispersed plants, and their interaction in Mediterranean scrublands. *Ecological Monographs*, 54, 1–23. https://doi.org/10.2307/1942454
- Johnson, A. E., Mitchell, J. S., & Brown, M. B. (2017). Convergent evolution in social swallows (Aves: Hirundinidae). *Ecology and Evolution*, 7, 550– 560. https://doi.org/10.1002/ece3.2641
- Johnson, K. P., & Lanyon, S. M. (1999). Molecular systematics of the grackles and allies, and the effect of additional sequence (cyt b and ND2). Auk, 116, 759–768. https://doi.org/10.2307/4089336
- Kalyakin, M. V. (2015). Morpho-functional analysis of the jaw apparatus of Vietnamese passerine birds (Passeriformes): Inferences on their trophic adaptations, ecology, and systematic position. *Journal für Ornithologie*, 156, 307–315. https://doi.org/10.1007/s10336-015-1246-x
- Klingenberg, C. P. (2016). Size, shape, and form: Concepts of allometry in geometric morphometrics. *Development Genes and Evolution*, 226, 113–137. https://doi.org/10.1007/s00427-016-0539-2
- Klingenberg, C. P., Barluenga, M., & Meyer, A. (2002). Shape analysis of symmetric structures: Quantifying variation among individuals and asymmetry. *Evolution*, 56, 1909–1920. https://doi.org/10.1111/j. 0014-3820.2002.tb00117.x
- Korzun, L. P., Erard, C., & Gasc, J. -P. (2001). Les particularités morphofonctionnelles des appareils du bec et hyoïdien chez les touracos (Aves, Musophagidae): Relations avec la frugivorie. *Comptes rendus de l'Académie des Sciences, Paris, Série III, 324*, 965–977. https://doi.org/ 10.1016/S0764-4469(01)01363-4
- Lanyon, S. M. (1992). Interspecific brood parasitism in blackbirds (Icterinae): A phylogenetic perspective. *Science*, 255, 77–79. https:// doi.org/10.1126/science.1553533
- Linnaeus, C. (1758). Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis (10th ed., Reformata). Laurentius Salvius Holmiae.
- Losos, J. B., & Miles, D. B. (1994). Adaptation, constraint, and the comparative method: Phylogenetic issues and methods. In P. C. Wainwright & S. M. Reilly (Eds.), *Ecological morphology* (pp. 60–98). The University of Chicago Press.
- Lowther, P. E. (2016). Host list of victims and hosts of the parasitic cowbirds (Molothrus). Retrieved from https://www.fieldmuseum.org/sites/ default/files/plowther/2017/01/27/molothrus-hosts-03may2016.pdf
- Lowther, P. E. (2020). Giant cowbird (*Molothrus oryzivorus*), version 1.0. In S. M. Billerman, B. K. Keeney, P. G. Rodewald, & T. S. Schulenberg (Eds.), *Birds of the world*. Ithaca, NY. https://doi.org/10.2173/bow. giacow.01. Retrieved from, https://birdsoftheworld.org/bow/home
- Mann, C. F. (2017). A taxonomic review of obligate and facultative interspecific avian brood parasitism. In M. Soler (Ed.), Avian brood parasitism: Behaviour, ecology, evolution and coevolution (pp. 61–92). Springer. https://doi.org/10.1007/978-3-319-73138-4_4
- Mayr, G. (2005). A new Eocene Chascacocolius-like mousebird (Aves: Coliiformes) with a remarkable gaping adaptation. Organisms, Diversity and Evolution, 5, 167–171. https://doi.org/10.1016/j.ode.2004. 10.013
- McCrary, J., & Gates, E. (2007). Evidence of brood parasitism of giant cowbird (*Molothrus oryzivorus*) on spotbreasted (*Icterus pectoralis*) and streak-backed (*I. pustulatus*) orioles. Ornitología Neotropical, 18, 111–115.
- Mejías, M. A., Roncal, J., Imfeld, T. S., Boisen, S., & Wilson, D. R. (2020). Relationships of song structure to phylogenetic history, habitat, and

¹⁶ WILEY morphology

morphology in the vireos, greenlets, and allies (Passeriformes: Vireonidae). Evolution, 74, 2494-2511. https://doi.org/10.1111/evo. 14099

- Mesquita, G. B., Silva, W. L., Fecchio, A., Martins, T. F., Labruna, M. B., & Dias, R. I. (2020). Amblyomma ticks consumed by a giant cowbird, Molothrus oryzivorus. Ticks and Tick-borne Diseases, 11, 101424. https://doi.org/10.1016/j.ttbdis.2020.101424
- Millard, S. P. (2013). EnvStats: An R package for environments statistics. Springer. https://doi.org/10.1007/978-1-4614-8456-1
- Moermond, T. C., & Denslow, J. S. (1985). Neotropical avian frugivores: Patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Ornithological Monographs, 36, 865-897. https:// doi.org/10.2307/40168322
- Murphy, T. G., Rosenthal, M. F., Montgomerie, R., & Tarvin, K. A. (2009). Female American goldfinches use carotenoid-based bill coloration to signal status. Behavioral Ecology, 20, 1348-1135. https://doi.org/10. 1093/beheco/arp140
- Navalón, G., Bright, J. A., Marugán-Lobón, J., & Rayfield, E. J. (2019). The evolutionary relationship among beak shape, mechanical advantage, and feeding ecology in modern birds. Evolution, 73, 422-435. https:// doi.org/10.1111/evo.13655
- Olsen, A. M. (2017). Feeding ecology is the primary driver of beak shape diversification in waterfowl. Functional Ecology, 31, 1985-1995. https://doi.org/10.1111/1365-2435.12890
- Ortega, C. (1998). Cowbirds and other brood parasites. The University of Arizona Press.
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. Bioinformatics, 20, 289-290. https://doi.org/10.1093/bioinformatics/btg412
- Pestoni, S., Degrange, F. J., Tambussi, C. P., Demmel Ferreira, M. M., & Tirao, G. A. (2018). Functional morphology of the cranio-mandibular complex of the Guira cuckoo (Aves). Journal of Morphology, 279, 780-791. https://doi.org/10.1002/jmor.20810
- Powell, A. F. L. A., Barker, F. K., Lanyon, S. M., Burns, K. J., Klicka, J., & Lovette, I. J. (2014). A comprehensive species-level molecular phylogeny of the New World blackbirds (Icteridae). Molecular Phylogenetics and Evolution, 71, 94-112. https://doi.org/10.1016/j.ympev.2013. 11.009
- Reboreda, J. C., Fiorini, V. D., & Tuero, D. T. (Eds.). (2019). Behavioral ecology of Neotropical birds. Springer Nature.
- Redondo, T. (1993). Exploitation of host mechanisms for parental care by avian brood parasites. Etología, 3, 235-297.
- Remsen, J. V., Jr., Areta, J. I., Cadena, C. D., Claramunt, S., Jaramillo, A., Pacheco, J. F., Robbins, M. B., Stiles, F. G., Stotz, D. F. & Zimmer, K. J. (2020). A classification of the bird species of South America. American Ornithologists' Union. Retrieved from http://www.museum.lsu.edu/ ~Remsen/SACCBaseline.htm
- Remsen, J. V., Jr., Powell, A. F. L. A., Schodde, R., Barker, F. K., & Lanyon, S. M. (2016). A revised classification of the Icteridae (Aves) based on DNA sequence data. Zootaxa, 4093, 285-292. https://doi. org/10.11646/zootaxa.4093.2
- Richards, L. P., & Bock, W. J. (1973). Functional anatomy and adaptive evolution of the feeding apparatus in the Hawaiian honeycreeper genus Loxops (Drepanididae). Ornithological Monographs, 15, i-x, 1-173. https://doi.org/10.2307/40166695
- Rico-Guevara, A., Rubega, M. A., Hurme, K. J., & Dudley, R. (2019). Shifting paradigms in the mechanics of nectar extraction and hummingbird bill morphology. Integrative Organismal Biology, 1, oby006. https://doi. org/10.1093/iob/oby006
- Robinson, S. K. (1988). Foraging ecology and host relationships of giant cowbirds in southeastern Peru. The Wilson Bulletin, 100, 224-235. https://www.jstor.org/stable/4162562
- Rothstein, S. I. (1990). A model system for coevolution: Avian brood parasitism. Annual Review of Ecology and Systematics, 21, 481–508. https:// doi.org/10.1146/annurev.es.21.110190.002405

- Rothstein, S. I., Patten, M. A., & Fleischer, R. C. (2002). Phylogeny, specialization, and brood parasite-Host coevolution: Some possible pitfalls of parsimony. Behavioral Ecology, 13, 1-10. https://doi.org/10.1093/ beheco/13.1.1
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J. Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak, P., & Cardona, A. (2012). Fiji: An open-source platform for biological-image analysis. Nature Methods, 9, 676-682. https://doi.org/10.1038/nmeth. 2019
- Schodde, R., & Remsen, J. V., Jr. (2016). Correction of Cassicinae Bonaparte, 1853 (Aves, Icteridae) to Cacicinae Bonaparte, 1853. Zootaxa, 4162, 188. https://doi.org/10.11646/zootaxa.4162.1.1
- Sidlauskas, B. (2008). Continuous and arrested morphological diversification in sister clades of characiform fishes: A phylomorphospace approach. Evolution, 62, 3135-3156. https://doi.org/10.1111/j.1558-5646.2008.00519.x
- Smith, N. G. (1968). The advantage of being parasitized. Nature, 219, 690-694. https://doi.org/10.1038/219690a0
- Soler, M. (2017). Brood parasitism in birds: A coevolutionary point of view. In M. Soler (Ed.), Avian brood parasitism: Behaviour, ecology, evolution and coevolution (pp. 1-19). Springer. https://doi.org/10.1007/978-3-319-73138-4 1
- Stayton, C. T. (2006). Testing hypotheses of convergence with multivariate data: Morphological and functional convergence among herbivorous lizards. Evolution, 60, 824-841. https://doi.org/10.1111/j.0014-3820. 2006.tb01160.x
- Stayton, C. T. (2015). The definition, recognition, and interpretation of convergent evolution, and two new measures for quantifying and assessing the significance of convergence. Evolution, 69, 2140-2153. https://doi.org/10.1111/evo.12729
- Steadman, D. W., & Oswald, J. A. (2020). New species of troupial (icterus) and cowbird (Molothrus) from ice-age Peru. Wilson Journal of Ornithology, 132, 91-103. https://doi.org/10.1676/1559-4491-132.1.91
- Swainson, W., & Richardson, J. (1831) [1832]). Fauna Boreali-Americana or the zoology of the northern parts of British America: Part second, the birds. John Murrav.
- Tattersall, G. J., Andrade, D. V., & Abe, A. S. (2009). Heat exchange from the toucan bill reveals a controllable vascular thermal radiator. Science, 325, 468-470. https://doi.org/10.1126/science.1175553
- Team, R. C. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved from. https://www. R-project.org/
- Thompson, J. N. (1994). The coevolutionary process. University of Chicago Press.
- Tokita, M., Yano, W., James, H. F., & Abzhanov, A. (2017). Cranial shape evolution in adaptive radiations of birds: Comparative morphometrics of Darwin's finches and Hawaiian honeycreepers. Philosophical Transactions of the Royal Society B, 372, 20150481. https://doi.org/10. 1098/rstb.2015.0481
- Webster, J. D. (2003). Skeletal characters and the genera of blackbirds (Icteridae). Condor, 105, 239-257. https://doi.org/10.1093/condor/ 105.2.239
- Wickham, H. (2009). ggplot2: Elegant graphics for data analysis. Springer-Verlag. https://doi.org/10.1007/978-0-387-98141-3
- Winkler, D. W., Billerman, S. M., & Lovette, I. J. (2020). Troupials and allies (Icteridae), version 1.0. In S. M. Billerman, B. K. Keeney, P. G. Rodewald, & T. S. Schulenberg (Eds.), Birds of the world. Ithaca, NY. https://doi.org/10.2173/bow.icteri1.01
- Zubkova, E. N., & Korzun, L. P. (2014). Morphofunctional aspects of the trophic specialization of the frugivorous green broadbill Calyptomena viridis (Passeriformes, Eurylaimidae): A comparative analysis. Biology Bulletin, 41, 788-800. https://doi.org/10.1134/S1062359014090118
- Zusi, R. L. (1967). The role of the depressor mandibulae muscle in kinesis of the avian skull. Proceedings of the United States National Museum, 123, 1-28.

Zusi, R. L. (1993). Patterns of diversity in the avian skull. In J. Hanken &
B. K. Hall (Eds.), *The skull. Volume 2: Patterns of structural and systematic diversity* (pp. 391–437). The University of Chicago Press.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Gómez, R. O., & Lois-Milevicich, J. (2021). Why the long beak? Phylogeny, convergence, feeding ecology, and evolutionary allometry shaped the skull of the Giant Cowbird *Molothrus oryzivorus* (Icteridae). *Journal of Morphology*, 1–17. https://doi.org/10.1002/jmor.21408