


## RESEARCH ARTICLE

# Redefining the simplicity of the craniomandibular complex of nightjars: The case of *Systellura longirostris* (Aves: Caprimulgidae) by means of anatomical network analysis

Ricardo S. De Mendoza<sup>1</sup>  | Julieta Carril<sup>1</sup>  | Federico J. Degrange<sup>2</sup>  |  
 María M. Demmel Ferreira<sup>2</sup>  | Mauro N. Nieto<sup>2</sup>  | Claudia P. Tambussi<sup>2</sup> 

<sup>1</sup>Laboratorio de Histología y Embriología Descriptiva, Experimental y Comparada (LHYEDEC), Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

<sup>2</sup>Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Universidad Nacional de Córdoba, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Córdoba, Argentina

## Correspondence

Ricardo S. De Mendoza, Laboratorio de Histología y Embriología Descriptiva, Experimental y Comparada (LHYEDEC), Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina.  
 Email: [rsdemendoza@gmail.com](mailto:rsdemendoza@gmail.com)

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## Abstract

To study morphological evolution, it is necessary to combine information from multiple intersecting research fields. Here, we report on the structure of the bony and muscular elements of the craniomandibular complex of birds, highlighting its morphological architecture and complexity (or simplification) in the context of anatomical networks of the Band-winged Nightjar *Systellura longirostris* (Caprimulgi-formes, Caprimulgidae). This species has skull osteology and jaw myology that departs from the general structural plan of the craniomandibular complex of Neornithes and is considered morphologically simple. Our goal is to test if its simplification is also reflected in its anatomical network, particularly in those parameters that measure complexity and to explore if the distribution of the networks in a phylomorphospace is conditioned by their evolutionary history or by convergence. Our results show that *S. longirostris* clusters with other Strisores and momotids and is segregated from the other bird species analyzed when plotted in the phylomorphospace, as a consequence of convergence in the network parameters. *Systellura* has a craniomandibular complex consisting of fewer muscles connecting more bones than the model species (e.g., the rock pigeon or the guira cuckoo). In this sense, *Systellura* is actually more complex regarding the number of integrative bony parts, while its craniomandibular complex is simpler. According to its anatomical network, *Systellura* also can be interpreted as less complex, particularly compared with other Strisores and taxa that reflect the general structure of the craniomandibular complex in Neornithes.

## KEYWORDS

Caprimulgi-formes, complexity, myology, phylomorphospace, Strisores

## 1 | INTRODUCTION

How a new morphology arises is one of the most recurring questions for those who are interested in establishing evolutionary patterns. To study morphological evolution, it is necessary to combine information from multiple intersecting research fields. Undoubtedly, the

morphological information that is obtained isolated and without a comparative context can offer little for our understanding of evolutionary patterns. Here, we aim to compare the structural designs of the bony and muscular elements of the craniomandibular complex (CMC) of birds with different morphologies and feeding habits, in an attempt to evaluate how the connectivity patterns are

reorganized when there is a loss of elements. Specifically, we are interested in investigating the morphological architecture and complexity (or simplification) in the context of anatomical networks of the Band-winged Nightjar *Systellura longirostris* (Caprimulgiformes, Caprimulgidae). The Caprimulgidae (nightjars), Aegothelidae (owllet-nightjars), Apodiformes (swifts and hummingbirds), Nyctibiidae (potoos), Podargidae (frogmouths), and Steatornithidae (oilbirds) are grouped within early radiation of Neoaves called Strisores (Prum et al., 2015) whose relationships with other neoavian subclades are still debated (Nesbitt et al., 2011). *S. longirostris* is known for having skull osteology and jaw myology that departs from the general structural plan of the CMC of birds. For example, they present a thin interorbital septum, reduction of the orbital process of the quadrate bone, a distinct syndesmotic joint in each mandible ramus, and a medially rotated caudal part of the mandible (Bühler, 1970; Demmel Ferreira et al., 2019). They lack two of the seven jaw muscles, which are commonly found in birds (i.e., *m. pseudotemporalis profundus*, and *m. adductor mandibulae externus superficialis*), and also lack some of the typical muscular origins and insertions (i.e., the pterygoid origin of the *m. pterygoideus dorsalis*, the palatine origin of the *m. pterygoideus ventralis*, and the pterygoid insertion of the *m. protractor pterygoidei et quadrati*; Demmel Ferreira et al., 2019). *Systellura* has the ability to open its mouth wide despite having a short beak and, even in the absence of some adductor muscles, it can close its beak quickly thanks to an energy accumulation process related to alternating bending and torsion of the different mandibular portions (named by Smith et al., 2011 as “mechanical instability model”). This particularity in the closing mechanism is shared with hummingbirds, a group with which it is also closely related.

Given the absence of some muscles and some of the muscular origins and insertions, the CMC of *Systellura* has been considered simplified (Demmel Ferreira et al., 2019). *Systellura* shares this simplification with other Caprimulgidae, such as *Setopagis parvula* (Bühler, 1970) or Nyctibiidae (Vieira da Costa & Donatelli, 2009). Consequently, a simplified CMC moves away from the classic avian model represented, for example, by the rock pigeon *Columba livia* (Columbiformes, Columbidae; Bhattacharyya, 1994, 2013; Jones et al., 2019) or the guira cuckoo *Guira guira* (Cuculiformes, Cuculidae; Pestoni et al., 2018).

Here, we characterize the anatomical and functional singularities of *S. longirostris* by means of the connectivity patterns between bones and muscles using anatomical network analysis (AnNA) (Rasskin-Gutman & Esteve-Altava, 2014). This conceptual and methodological approach analyzes the connectivity patterns among different anatomical parts, instead of their morphology or size. Anatomical network analysis allows measuring the topological organization of anatomical systems by using tools of the network theory (Esteve-Altava et al., 2011; Rasskin-Gutman & Buscalioni, 2001; Rasskin-Gutman & Esteve-Altava, 2014). This allows a novel quantitative approach to questions about complexity understood as the degree of integration between parts (Rasskin-Gutman & Esteve-Altava, 2014), as well as the disparity between the degrees of integration of these parts (Lee et al., 2020). It also inquires about

modularity (Esteve-Altava, 2017a, 2017b, 2020) and burden rank, which are the relationships that a morphological character develops with other characters as it evolves (Carril et al., 2020; Rasskin-Gutman & Esteve-Altava, 2018).

The main question we are seeking to answer is whether a system with fewer objects (nodes) would be more or less simple according to its connections. To answer this, we propose two main objectives. First, we test if the simplification of the CMC of *S. longirostris* is also reflected in its anatomical network (particularly on those parameters that measure complexity). Second, we explore if the phylomorphospace distribution of the CMC networks is conditioned by their evolutionary history or by convergence.

## 2 | MATERIALS AND METHODS

### 2.1 | Data acquisition

We collected gross anatomical data about the origin and insertions of jaw muscles, and contact between bones of *S. longirostris* and compared it with the other 17 selected bird taxa (Table 1), by performing our own dissections and carefully reviewing the literature. The muscles were identified with the assistance of a binocular stereoscopic lens and carefully removed from their origin and insertion sites, beginning with the most superficial. The results of the dissections are published elsewhere (Demmel Ferreira et al., 2019; Pestoni et al., 2018). Our approach considers the CMC of the rock pigeon *C. livia* and the guira cuckoo *G. guira* as the basic morphological model. Osteological nomenclature follows (Baumel et al., 1993), meanwhile, myological terminology follows the proposal of Holliday and Witmer (2007). Although the *m. tensor periorbitae* and the *m. protractor pterygoideus et quadrati* originate from the same muscle group (*m. constrictor internus dorsalis*), the former has not been considered in the analysis since it is mainly related to isolating the eye from jaw muscle movements (Holliday, 2009).

### 2.2 | Network modeling

Anatomical network analysis is the application of the tools and conceptualizations of network theory to the topological organization of anatomical systems made by multiple parts, for example, the musculoskeletal organization of the CMC. Letting aside information about size and shape, the primary information about the anatomical system that the method captures is the connection between their constitutive parts, formalized as a network, which is a graph whose vertices (or nodes, as they are commonly termed in Network Science; Barabási, 2016) are the physical parts of the system (muscles and bones), and whose edges (or links) are the connection between these parts. Following musculoskeletal network modeling made by previous authors (Diogo et al., 2015, 2019; Esteve-Altava et al., 2015, 2018), a musculoskeletal anatomical

**TABLE 1** Source of taxa analyzed in the present study.

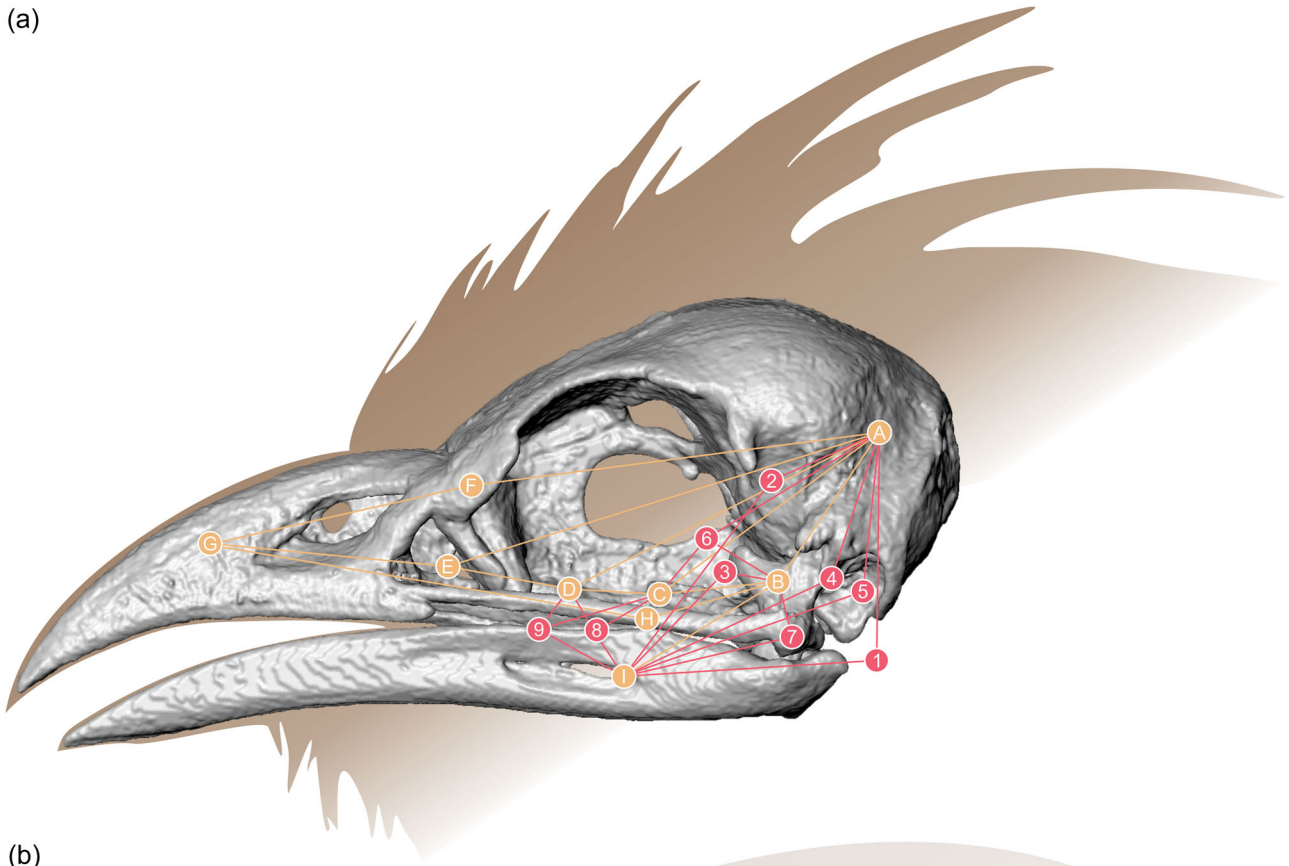
Family	Species analyzed in the original source	Source
Accipitridae	<i>Buteo buteo</i>	Lautenschlager et al. (2014); Jollie (1976), (1977a, b, c)
Alcedinidae	<i>Dacelo novaeguineae</i>	Quayle et al. (2014)
Alcidae	<i>Cephus grylle</i> , <i>Uria lomvia</i> , <i>Uria aalge</i>	Badikoba et al. (2015)
Apodidae	<i>Aerodramus vanikorensis</i> , <i>Apus pacificus</i> , <i>Hirundapus caudacutus</i>	Morioka (1974)
Columbidae	<i>Columba livia</i> , <i>Ducula aenea</i> , <i>D. badia</i> , <i>Streptopelia chinensis</i> , <i>S. decaocto</i> , <i>Treron phoenicopterus</i>	Bhattacharyya (1994); Korzun et al. (2008); Jones et al. (2019)
Cuculidae	<i>Centropus superciliosus</i> , <i>Crotophaga ani</i> , <i>Cuculus canorus</i> , <i>C. clamosus</i> , <i>Geococcyx californianus</i> , <i>Guira guira</i> , <i>Phaenicopterus tristis</i> , <i>Piaya cayana</i>	Korzun et al. (2003); Pestoni et al. (2018)
Diomedeidae	<i>Phoebastria immutabilis</i>	Holliday and Witmer (2007)
Galbulidae	<i>Brachygalba lugubris</i> , <i>Galbula albirostris</i> , <i>G. ruficauda</i> , <i>G. galbula</i> , <i>G. cyanicollis</i> , <i>Jacamerops aureus</i>	Donatelli (1992)
Gruidae	<i>Grus americana</i>	Fisher and Goodman (1955)
Momotidae	<i>Momotus momota</i>	Pascotto and Donatelli (2003); Korzun et al. (2004)
Picidae	<i>Blythipicus rubiginosus</i> , <i>Chrysophlegma mentale</i> , <i>C. minaceum</i> , <i>Dinopium javanense</i> , <i>Dinopium rafflesii</i> , <i>Picus puniceus</i> , <i>Reinwardtipicus validus</i>	Donatelli (2012)
Podicipedidae	<i>Podilymbus podiceps</i>	Zusi and Storer (1969)
Pteroclididae	<i>Pterocles alchata</i> , <i>P. orientalis</i> , <i>Syrhaptes paradoxus</i>	Korzun et al. (2008)
Spheniscidae	<i>Aptenodytes forsteri</i> , <i>A. patagonicus</i> , <i>Eudyptes chrysolophus</i> , <i>E. crestatus</i> , <i>Pygoscelis adeliae</i> , <i>P. antarctica</i> , <i>P. papua</i> , <i>Spheniscus magellanicus</i>	Zusi (1975)
Caprimulgidae	<i>Systellura longirostris</i>	Demmel Ferreira et al. (2019)
Thinocoridae	<i>Attagis gayi</i> , <i>Thinocorus orbignyianus</i> , <i>T. rumicivorus</i>	Korzun et al. (2009)
Tinamidae	<i>Crypturellus soui</i> , <i>C. transfasciatus</i> , <i>C. erythropus</i> , <i>C. cinnamomeus</i> , <i>C. parvirostris</i> , <i>C. tataupa</i> , <i>Eudromia elegans</i> , <i>E. formosa</i> , <i>Nothoprocta ornata</i> , <i>N. perdicaria</i> , <i>N. cinerascens</i> , <i>N. pentlandii</i> , <i>Nothura maculosa</i> , <i>N. darwinii</i> , <i>Rhynchotus rufescens</i> , <i>Tinamotis pentlandii</i> , <i>Tinamus major</i>	Elzanowski (1987)
Trochilidae	<i>Calliphlox evelynae</i> , <i>Eulampis jugularis</i> , <i>Glaucis hirsutus</i> , <i>Heliodoxa xanthogonyx</i> , <i>Metallura tyrianthina</i> , <i>Patagona gigas</i> , <i>Thalurania furcata</i>	Zusi and Bentz (1984)

network model was made for the CMC of *Systellura* and all the species in our data set considering each mobile part of the skull and each independent muscle as nodes. Bone–bone, bone–muscle, and muscle–muscle contacts were represented as the unweighted and undirected links between pairs of nodes. In the case of the muscles, these contacts represent their origins and insertions (Figure 1). The resulting musculoskeletal network models were stored as edge lists (Munagala & Ranade, 1999), which are matrices that save all the connections only as of the edges of the graph, with every line having a starting node and a destiny node (although, as the links are undirected, is the same, which is the starting and which is the destiny node). Following the same guidelines, we analyze the matrices excluding the muscles to evaluate the congruence between both analyses. All the edge lists are presented in Supporting Information: Table S1. A brief introduction to anatomical network analysis can be found in Diogo et al. (2019).

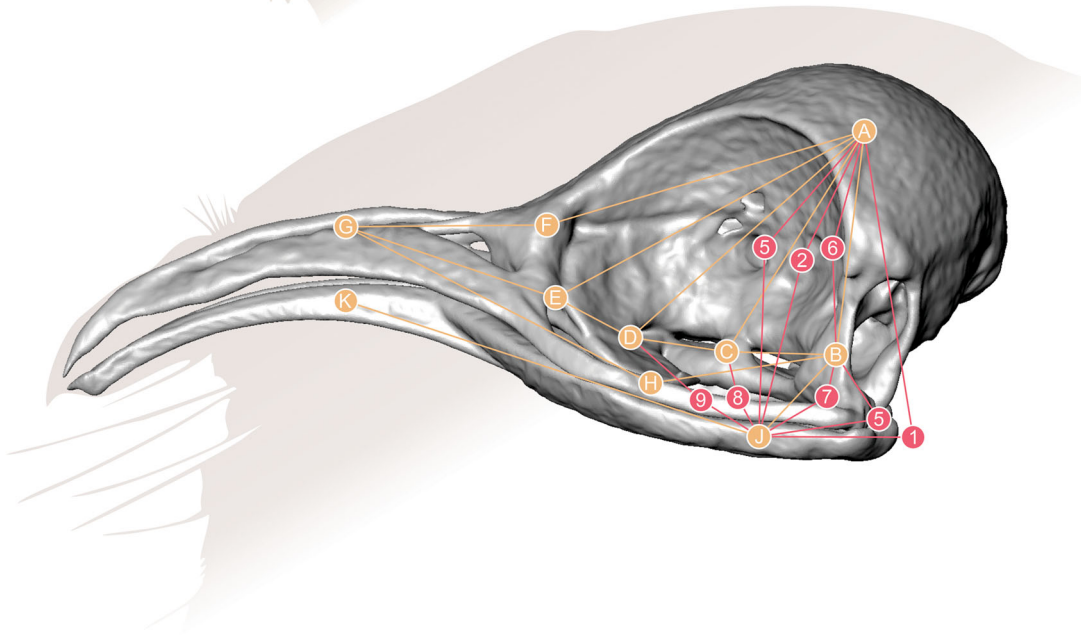
### 2.3 | Network analysis

Following Esteve-Altava et al. (2019) and Fernández et al. (2020), different parameters from each network were obtained using the R package Igraph (Csardi & Nepusz, 2006): (1) number of nodes (*N*); (2) number of links (*L*); (3) density (*D*), which is a measure of how close is the network to be a complete graph, and is obtained by dividing the number of links by the number of maximum possible links in the network; (4) average cluster coefficient (ACC), which is the average of the local cluster coefficient, a measure of each node related to the connectivity of the adjacent nodes; (5) average shortest path length (APL), which is the average length of all shortest or geodesic paths (i.e., the minimal number of links connecting every two nodes) in a network; (6) heterogeneity (*H*), which is a measure of how even are the nodes according to their number of connections; (7) average degree (AD), which is the average number of links of each node; (8) network diameter (ND), which is the length of the longest

(a)



(b)



**FIGURE 1** Connectivity patterns differences in the skull of Neoaves. (a) *Guira guira*; (b) *Systellura longirostris*. Schematic representation of the anatomical elements involved in the analysis. Bones and links between bones are indicated in light orange and muscles and links through muscles are indicated in pink. A, neurocranium; B, os quadratum; C, os pterygoideum; D, os palatinum; E, vomer; F, os lacrimale; G, upper beak; H, arcus jugalis; I, mandible; J, pars caudalis and caudal portion of the pars intermedia; K, pars cranialis and cranial portion of the pars intermedia; 1, m. depressor mandibulae; 2, m. pseudotemporalis superficialis; 3, m. pseudotemporalis profundus; 4, m. adductor mandibulae externus superficialis; 5, m. adductor mandibulae externus profundus; 6, m. protractor pterygoidei et quadrati; 7, m. adductor mandibulae posterior; 8, m. pterygoideus ventralis; 9, m. pterygoideus dorsalis.

geodesic path; and (9) modularity (Q). Modularity was calculated by dividing all the networks in different communities using the algorithm clustering walktrap, which detects communities by short random walks, as random walks in a graph tend to be trapped into densely connected subgraphs (Pons & Latapy, 2005); then the resulting membership structure was used to calculate Q (Newman & Girvan, 2004). Although heuristic, the modularity algorithm gives consistent results in different runs, allowing repeatability, and has been successfully used in previous works to compare many anatomical networks as a part of a large evolutionary study (e.g., Esteve-Altava, 2020; Plateau & Foth, 2020). Additionally, we compared every network according to the relative centrality of the different nodes, measured by (10) the connectivity degree ( $k_i$ ), which is the sum of connections that a specific node has to other nodes in the network; (11) the betweenness centrality ( $b$ ), which is the frequency of occurrence of a node in shortest paths between any pair of nodes in the whole network; and (12) the local clustering coefficient or transitivity, explained above. All these node-level data were also obtained with the R package Igraph. Network visualizations were made with the software Gephi (Amat, 2014; Bastian et al., 2009). The morphological interpretation of each variable has been discussed by Esteve-Altava et al. (2019), Bruner et al. (2019), Fernández et al. (2020), and Lee et al. (2020). In short terms, most node level measures are related to the importance of that node in the system and how much the node is related to subsystems; while all the network level measures are indicators of modularity and complexity, the later taken as how much interconnected the network is.

## 2.4 | Statistical analysis

All statistical analysis and visualizations were performed in R 4.1.1 (R Core Team, 2021). A principal component analysis was made using the nine connectivity variables of the entire network for the musculoskeletal system and for the skeletal system alone, both using the function `prcomp` of the base package of R. The phylomorphospace was generated with the `phylomorphospace` function of the package `phytools` (Revell, 2020) using the phylogenetic proposal of Prum et al. (2015). Also, based on this phylogenetic proposal, the amount of phylogenetic signal was assessed for the connectivity parameters. For this, the kappa statistic ( $\kappa$ ) (Blomberg et al., 2003) was calculated, under a Brownian motion model of evolution. The test was performed using the `phylosig` function of the `geiger` package (Harmon et al., 2007).

## 3 | RESULTS

Regarding node parameters, the neurocranium (n) and mandible (m) are the nodes with the highest connectivity degree ( $k_i$ ) for all species, except for *Systellura* whose mandible is split into four independent nodes (Supporting Information: Table S2).

Regarding network parameters, the number of nodes (N) ranged from 12 to 17 when skull bones are considered alone, to 30–34 when the whole CMC (bones and muscles) is considered. Particularly, *Systellura* has the highest number of nodes ( $N = 17$ ) within its skull

**TABLE 2** Network parameters for the skull of the analyzed taxa.

	N	L	D	ACC	APL	H	AD	ND	Q
Alcidae	14	23	0.252747	0.234014	1.978022	0.498361	3.285714	3	0.338049
Accipitridae	16	27	0.225	0.210714	2.191667	0.528649	3.375	4	0.354022
Momotidae	12	17	0.257576	0.102778	2.015152	0.471923	2.833333	4	0.339339
Picidae	14	24	0.263736	0.291497	1.945055	0.533093	3.428571	3	0.327026
Pteroclididae	14	22	0.241758	0.159184	2.021978	0.512402	3.142857	4	0.333448
Columbidae	14	26	0.285714	0.419218	1.901099	0.542881	3.714286	3	0.32926
Halcyonidae	14	25	0.274725	0.291497	1.901099	0.487632	3.571429	3	0.339218
Gruidae	14	24	0.263736	0.291497	1.945055	0.533093	3.428571	3	0.327026
Cuculidae	14	24	0.263736	0.291497	1.945055	0.533093	3.428571	3	0.344467
Diomedeidae	14	27	0.296703	0.296599	1.879121	0.391963	3.857143	3	0.339814
Podicipedidae	14	24	0.263736	0.291497	1.945055	0.533093	3.428571	3	0.3258
Spheniscidae	14	25	0.274725	0.240816	1.956044	0.406713	3.571429	3	0.365894
Caprimulgidae	17	27	0.198529	0.240056	2.389706	0.547942	3.176471	5	0.368575
Tinamidae	14	26	0.285714	0.301361	1.923077	0.453329	3.714286	3	0.356191
Thinocoridae	14	22	0.241758	0.159184	2.021978	0.512402	3.142857	4	0.354126
Trochilidae	12	15	0.227273	0	2.5	0.31909	2.5	5	0.34843

Abbreviations: ACC, average cluster coefficient; AD, average degree; APL, average path length; D, density; H, heterogeneity; L, links; N, nodes; ND, network diameter; Q, modularity.



network, but a similar number of nodes to the rest of the species within its CMC network. *Systellura* also has a high number of links ( $L$ ), the lowest density ( $D$ ), and high APL and heterogeneity ( $H$ ) within its skull network; and it has a low number of links ( $L$ ), low density ( $D$ ), the lowest ACC, heterogeneity ( $H$ ) and AD, and the highest average path length (APL). All the network parameters for each analyzed species are summarized in Tables 2 and 3 and those of the CMC is also in a two-dimensional heat map for better visualization (Figure 2).

Of the nine parameters analyzed, for both skull only and whole CMC analyses, most of the parameters showed a low phylogenetic signal (Table 4), with only the ACC and heterogeneity having a slightly higher value than one for both. This indicates that most variables carry less phylogenetic signal than expected under Brownian motion.

In the phylomorphospace based on the skull data only (Figure 3a), the sum of the first three components explains 91.11% of the variance (PC1 = 50.8%, PC2 = 30.08%, PC3 = 10.23%). For PC1, the higher values are mainly related to APL and ND, while the lower values are mainly related to  $H$ ,  $L$ , ACC, and AD. For PC2, the higher values are mainly related to  $N$  and  $Q$ , while the lower values are mainly related to  $D$ . The analyzed Strisores (i.e., Trochilidae, Apodidae, and *Systellura*) are located on the right quadrant (i.e., positive values of PC1), far from "model" birds, such as Cuculidae and Columbidae. Notably, *Systellura* has the highest values of the PC2, indicating that *Systellura* possesses a large number of nodes, but a less dense network than other Strisores.

When analyzing the whole CMC (Figure 3b), the sum of the first three components explains less variance: 84.30% (PC1 = 50.86%, PC2 = 21.58%, PC3 = 11.86%). For PC1, the higher values are mainly related to APL and ND, while the lower values are mainly related to  $L$ , ACC, and AD. For PC2, the higher values are mainly related to  $H$  and  $N$ , while the lower values are mainly related to  $D$ . All Strisores are located on the right lower quadrant (and less dispersed when compared to the skull only phylomorphospace), with *Systellura* and Trochilidae having the highest values of PC1.

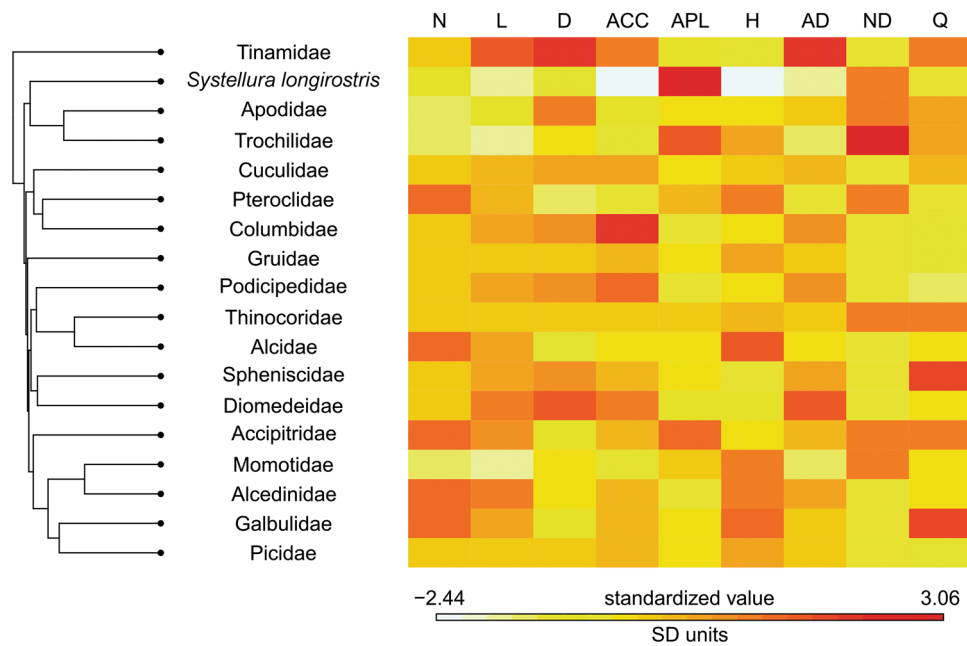
## 4 | DISCUSSION

Based on the structural organization of parts, a complex system is defined basically by four anatomical network parameters: APL, ACC, density ( $D$ ), and heterogeneity ( $H$ ) (Esteve-Altava et al., 2013; Lee et al., 2020; Rasskin-Gutman & Esteve-Altava, 2014). The lower the value of APL and the higher the values of ACC,  $D$ , and  $H$ , the greater the morphological complexity of the entire system. In other words, complex systems will have a smaller number of edges between two nodes, higher interdependence of neighboring nodes that connect to each other, higher connectivity of nodes, and higher overall disparity in individual node connectivity numbers than simpler systems. APL is the average of the smallest number of links between two nodes in the

**TABLE 3** Network parameters for the craniomandibular complex of the analyzed taxa.

	$N$	$L$	$D$	ACC	APL	$H$	AD	$D$	$Q$
Alcidae	34	67	0.11943	0.293265	2.149733	1.056259	3.941176	3	0.338049
Accipitridae	34	69	0.122995	0.324961	2.272727	0.911708	4.058824	4	0.354022
Momotidae	30	55	0.126437	0.250224	2.172414	1.006108	3.666667	4	0.339339
Picidae	32	64	0.129032	0.329054	2.147177	0.96093	4	3	0.327026
Pteroclididae	34	66	0.117647	0.274367	2.188948	1.014106	3.882353	4	0.333448
Columbidae	32	68	0.137097	0.461307	2.114919	0.906378	4.25	3	0.32926
Halcyonidae	34	71	0.12656	0.32497	2.11943	1.002884	4.176471	3	0.339218
Gruidae	32	64	0.129032	0.329054	2.147177	0.96093	4	3	0.327026
Cuculidae	32	66	0.133065	0.35197	2.139113	0.927222	4.125	3	0.344467
Diomedeidae	32	71	0.143145	0.392037	2.102823	0.858473	4.4375	3	0.339814
Podicipedidae	32	68	0.137097	0.396054	2.127016	0.906378	4.25	3	0.3258
Sphenicidae	32	67	0.135081	0.337871	2.141129	0.89443	4.1875	3	0.365894
Caprimulgidae	31	55	0.11828	0.182878	2.412903	0.752121	3.548387	4	0.335868
Tinamidae	32	74	0.149194	0.380764	2.090726	0.83965	4.625	3	0.356191
Thinocoridae	32	64	0.129032	0.318823	2.16129	0.943996	4	4	0.354126
Trochilidae	30	55	0.126437	0.247758	2.289655	0.967114	3.666667	5	0.34843
Apodidae	30	60	0.137931	0.269858	2.142529	0.907346	4	4	0.349861
Galbulidae	34	68	0.121212	0.336594	2.151515	1.040833	4	3	0.365052

Abbreviations: ACC, average cluster coefficient; AD, average degree; APL, average path length;  $D$ , density;  $H$ , heterogeneity;  $L$ , links;  $N$ , nodes; ND, network diameter;  $Q$ , modularity.



**FIGURE 2** Heatmap of the different AnNA parameters was obtained for the whole craniomandibular complex of *Systellura* and the compared birds. Parameters are standardized (SD) to have comparable variance. ACC, average cluster coefficient; AD, average degree; AnNA, anatomical network analysis; APL, average path length; *D*, density; *H*, heterogeneity; *L*, links; *N*, nodes; ND, network diameter; *Q*, modularity.

**TABLE 4** Phylogenetic signal (*K*) of each character using the phylogenetic proposal of Prum et al. (2015), calculated for the skull elements only, and the whole craniomandibular complex.

	<i>N</i>	<i>L</i>	<i>D</i>	ACC	APL	<i>H</i>	AD	ND	<i>Q</i>
Skull	0.9952	0.9859	0.9599	1.0423	0.9885	1.1493	0.9729	0.9966	0.8886
CMC	0.8747	0.9206	1.0479	1.0085	0.9981	1.1134	1.009	0.9663	0.9045

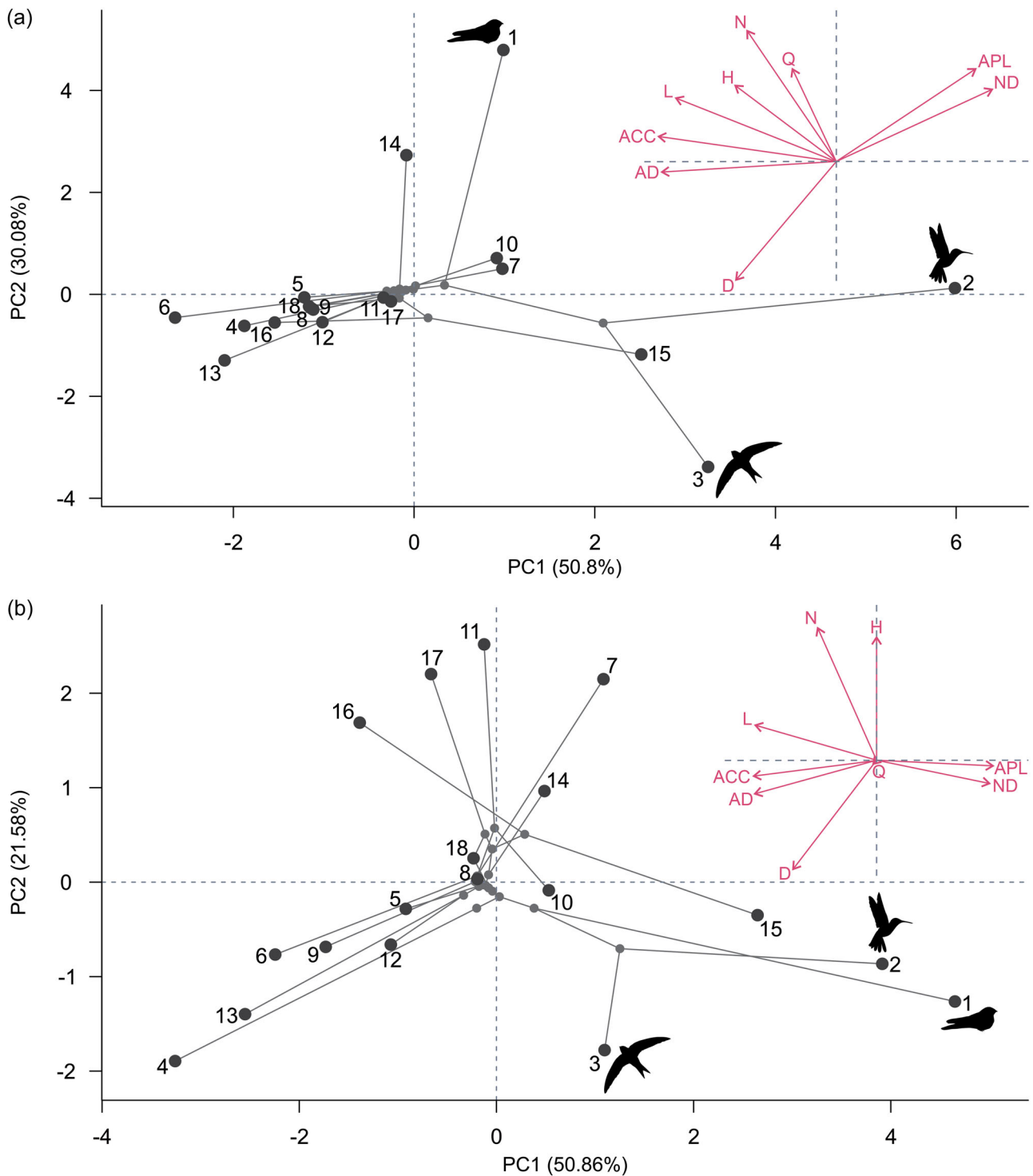
Abbreviations: ACC, average cluster coefficient; AD, average degree; APL, average path length; CMC, craniomandibular complex; *D*, density; *H*, heterogeneity; *L*, links; *N*, nodes; ND, network diameter; *Q*, modularity.

network. It is expected that a more complex network will be more interconnected (Rasskin-Gutman & Esteve-Altava, 2014), at least when the number of nodes is similar. Similarly, a high ACC means that there is a high correspondence of an anatomical part with its neighbors, so it also represents the degree of interconnection of the network (Rasskin-Gutman & Esteve-Altava, 2014). *D*, which is the relative number of connections in an entire anatomical system, also expresses the extent of the interconnection of the network and therefore is a proxy measure for complexity (Lee et al., 2020). It could be presumed that the loss of some elements could lead to an increase in the number of connections (e.g., so that all the bony parts can be activated). Finally, the *H* measures how irregular is the distribution of the connections in the whole system (Esteve-Altava et al., 2013).

One of our goals was to test if the simplification of the CMC of *S. longirostris* is also reflected in its anatomical network. As mentioned, its CMC has been characterized as “simple” when compared with model birds mainly due to the absence of two of the usual seven jaw muscles and the reduction of other muscles lacking certain origins and insertions in the skull (Demmel Ferreira et al., 2019). The CMC network of *Systellura* has the highest APL (2.41, the other taxa range from 2.09 to

2.28), the lowest ACC (0.18, the other taxa range from 0.25 to 0.46), a low *D* value (0.11 from a range of 0.11 to 0.15), and the lowest *H* (0.75, while the other taxa range from 0.83 to 1.05). Considering these complexity parameters, the CMC network of *Systellura* can be considered as simple, although some values are similar to those of other taxa. For example, *Buteo* or Trochilidae have similar APL values to *Systellura* (removing these two, the range of APL is from 2.09 to 2.18), although the other measures related to complexity in *Buteo* and Trochilidae do not reflect simplicity (Table 3). In addition, Alcidae and Pteroclididae have similar values of *D* to *Systellura*, while also not having values related to simplicity in the other parameters of morphological complexity (Table 3). Moreover, the range of *D* shows more of a gradient than the other parameters. Notably, both species considered here as having the more basic morphological model of the CMC model (Columbidae and Cuculidae) have similar complexity parameter values and both depart from the values of *Systellura*.

Our second goal was to test if the distribution of the CMC networks in a phylomorphospace is conditioned by their evolutionary history or by convergence. Five of the nine parameters analyzed (*N*, *L*, APL, ND, and *Q*) for the whole CMC showed a low phylogenetic



**FIGURE 3** Phylomorphospace of PCA values on 18 species from the time-calibrated phylogeny of Prum et al. (2015). Contribution to each component is indicated in pink in the right upper corner. (a) Skull only; (b) whole craniomandibular complex. ACC, average cluster coefficient; AD, average degree; APL, average path length; D, density; H, heterogeneity; L, links; N, nodes; ND, network diameter; PCA, principal component analysis; Q, modularity; 1, *Systellura*; 2, Trochilidae; 3, Apodidae; 4, Tinamidae; 5, Cuculidae; 6, Columbidae; 7, Pteroclididae; 8, Gruidae; 9, Podicipedidae; 10, Thinocoridae; 11, Alcidae; 12, Spheniscidae; 13, Diomedidae; 14, Accipitridae; 15, Momotidae; 16, Alcedinidae; 17, Galbulidae; 18, Picidae. Bird silhouettes correspond to the Strisores analyzed and were taken from PhyloPic (PhyloPic—Free Silhouette Images of Life Forms).



signal (i.e., lower than 1), while *D*, ACC, *H*, and AD showed a slightly higher than 1 phylogenetic signal under Brownian motion (the highest is that for *H* being 1.11). This means that phylogenetic history did not play an important role in shaping the connectivity patterns of the CMC of the birds analyzed, and other variables such as function, ecomorphology, and behavior should be considered. Avian CMC shows a high disparity related to many functions, including feeding ecology (Felice et al., 2019; Zusi, 1993; Zweers et al., 1994), nonfeeding behaviors (e.g., defense, vocalization, preen, nests building, sexual display; see Greenberg & Olsen, 2010), and physiology (e.g., thermoregulation; see Tattersall et al., 2017). Beak shape has been found in raptors to be tightly integrated with the morphology of the braincase, being highly controlled by nondietary factors like allometry (Bright et al., 2016). All these variables may explain the occupation in the phylomorphospace of the analyzed taxa.

The resulting phylomorphospace of the CMC networks shows a greater dispersion than those of skull-only networks, showing greater diversity in their connectivity patterns. Nevertheless, *Systemellura* and other Strisores are clustered together with Momotidae (Figure 3b), while in the phylomorphospace of the skull it is separated from the rest of the species analyzed (Figure 3a). This difference could be due to the singular anatomy of the mandible of *Systemellura* where there is not a single mandible node but four. Similar is the case of *Buteo* (Accipitridae), which is placed near *Systemellura* in the phylomorphospace of the skull only, but this is caused by the presence of extra superciliary bones (causing that the number of nodes is higher than the rest of the species). It is noteworthy that motmots (Momotidae) are placed close to Strisores in both phylomorphospaces (especially in the CMC phylomorphospace), having similar values of network parameters in both cases. Motmots are predators of large insects and occasionally of small vertebrates (Winkler et al., 2020). Like *Systemellura*, motmots can open their mouths widely, and the jaw is caudally broad (Pascotto & Donatelli, 2003), although it is a single bone piece. The large opening is measured based on the distance between the vertical posterior end of the upper jaw and the anterior edge of the interorbital wall (Korzun et al., 2004). As previously mentioned, the mandible is divided into several articulated parts in *Systemellura*. This reduces the role of the different jaw muscles in the whole system. For example, in most birds, the m. pseudotemporalis profundus and the m. adductor mandibulae posterior are connected to fully integrate musculoskeletal subsystems. In the same way as *Systemellura*, hummingbirds have two points of mobility along the mandible (Smith et al., 2011), although both zones are not individualized anatomically. This highlights something that is already known: the anatomical networks do not reflect anatomical particularities that are evident from anatomical descriptions. The interpretation of network and connectivity parameters in different biological systems will be surely a topic that will be more explored and discussed while the usage of AnNA expands to other biological systems (e.g., soft tissues) and other taxa.

The mandible and the neurocranium are the nodes with the highest connectivity degree in all birds (the highest number of edges). Previous authors (Carril et al., 2020; Rasskin-Gutman &

Esteve-Altava, 2018) suggested that highly connected nodes will have deeper interdependence on each other and therefore greater phylogenetic constrain, that is, they will have a higher Burden rank. Rasskin-Gutman and Esteve-Altava (2018, p. 39) stated that "Burden's main tenet is that as a morphological character evolves, it develops more relationships with other characters, becoming more and more interconnected. Through this process, the morphological character acquires more biological 'responsibilities' within the organism." Contrary to the other studied birds, *Systemellura* has four well-defined parts (nodes) in their jaw. Its mandible has syndesmotomic (fibrous) joints connecting both mandibular rami anteriorly and connecting the anterior and posterior portions of each mandibular ramus. These joints seem to be an evolutionary novelty of Caprimulgidae and may be the result of heterochronies (e.g., deceleration and/or postdisplacement processes) acting during skeletogenesis and leading to pedomorphic traits. Histological and developmental studies of the species will be necessary to test properly this hypothesis.

## 5 | CONCLUSIONS

A network-based comparison of the CMC shows that *S. longirostris* together with other Strisores and momotids segregate from the other birds analyzed including model ones. This segregation seems to be the result of convergence rather than conditioned by their phylogenetic history.

*Systemellura* has a CMC consisting of fewer muscles connecting more bones than the model species. The mandible is divided into several articulated parts in this species, for which the number of bony nodes is considerably higher than in the other compared birds. Thus, if we consider the number of integrative parts, it could be said that the skull of *Systemellura* is, actually, more complex than other birds, while its CMC is simpler. Although complexity is a topic explored in anatomical network analysis (Esteve-Altava et al., 2013; Lee et al., 2020; Rasskin-Gutman & Esteve-Altava, 2014) further work with more varied taxa and anatomical parts is needed to truly quantify musculoskeletal simplicity in the context of anatomical network analysis, and thus understand its evolutionary and biomechanical consequences. Therefore, the answer to our initial question about the consequences of the loss of elements in the system remains elusive.

## AUTHOR CONTRIBUTIONS

**Ricardo De Mendoza:** Conceptualization (lead); formal analysis (equal); investigation (equal); methodology (equal); writing—original draft (equal).

**Julieta Carril:** Conceptualization (equal); funding acquisition (equal); investigation (equal); writing—original draft (equal).

**Federico J. Degrange:** Data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); visualization (equal); writing—original draft (equal).

**María M. Demmel Ferreira:** Data curation (equal); investigation (equal); writing—original draft (equal).

**Mauro N. Nieto:** Data curation (equal); investigation (equal); writing—review & editing (equal).

**Claudia P. Tambussi:** Conceptualization (equal);

funding acquisition (lead); investigation (equal); project administration (lead); writing—original draft (equal).

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## DATA AVAILABILITY STATEMENT

Data for this study are available in Supporting Information.

## ORCID

Ricardo S. De Mendoza  <http://orcid.org/0000-0002-9642-1736>

Julieta Carril  <http://orcid.org/0000-0001-8491-1677>

Federico J. Degrange  <http://orcid.org/0000-0002-9463-4893>

María M. Demmel Ferreira  <http://orcid.org/0000-0001-9902-6021>

Mauro N. Nieto  <http://orcid.org/0000-0003-4245-4425>

Claudia P. Tambussi  <http://orcid.org/0000-0002-8711-0549>

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