



# Skull morphology and ontogenetic variation of the Southern Giant Petrel *Macronectes giganteus* (Aves: Procellariiformes)

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## Abstract

The Southern Giant Petrel *Macronectes giganteus* is the largest Procellariidae around the world. Beyond the most striking features on the skull, the strong hooked bill with tubular, dorsally-placed, external nostrils, these petrels have been the focus of diverse studies, except osteological ones. Even less is known about the osteology in juveniles and chicks. A comparative description of the skull anatomy of the Southern Giant Petrel *M. giganteus*, highlighting the differences along each postnatal ontogenetic stage, is given here. As a result, we found that the shape of the skull does not vary among the compared stages and that there is a progression in the fusion of the elements of the skull and mandible. Besides, less obvious results show a little intraspecific variation among specimens of the same ontogenetic stage, involving osteological features such as the quantity and shape of foramina within pneumatic bone surfaces, and the fact that general size is not associated with sexual dimorphism. The beak acquires its characteristic development and sturdiness from early stages. Conversely, the *fossae glandulae nasalis* is only developed in juveniles and adults, being absent in earlier stages.

**Keywords** Osteology · Anatomy · Cranium · Mandible · Procellariidae

## Introduction

Petrels are marine and pelagic birds included in the Procellariidae (Procellariiformes). These medium to large-sized seabirds are characterized by a compact and heavy body, long and slender wings, and the presence of a “tubenose”. This last feature, a pair of tubular external nostrils attached to the long and hooked bill, distinguishes Procellariiformes from any other group of birds, and seems to be related to a strong development of the sense of smell, used for the location of prey (Carboneras 1992).

The Southern Giant Petrel *Macronectes giganteus*, together with the other species of the genus, *M. halli*, is considered among the principal scavengers of the Southern Ocean, although they are also significant terrestrial predators

in some localities (Hunter 1985, 1987, 1991; Hunter and Brooke 1992; Emslie et al. 1995). For that reason, although it is not globally threatened (Carboneras 1992), *Macronectes* populations depend on seal and penguin colonies as important food resources (Conroy 1972; Hunter 1984, 1985, 1991). They not only feed on carcasses of seals, penguins, petrels and small albatrosses but also catch cephalopods, krill, and sea-surface fish discarded by ships (Johnstone 1977; Carboneras 1992).

The Southern Giant Petrel *M. giganteus* ranges from Antarctica to the subtropics, breeding on numerous islands throughout southern oceans (Carboneras 1992). Its size is variable and depends on the latitude; members of southern populations are larger in average than the northern ones (Carlos and Voisin 2008). Several reports point that Southern Giant Petrel reaches 5.60 kg in weight, and around 2.00 m in wingspan; males are always larger than females. Measurements like bill length, bill depth and weight are useful to discriminate between sexes (Conroy 1972).

Another morphological peculiarity is that, unlike most petrels, which are clumsy on land, giant petrels are the only Procellariidae that can stand and walk on land effectively (Maynard 2003). *Macronectes* species have been largely studied in connection with reproductive biology (Warham

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1962; Conroy 1972), hybridization (Voisin and Bester 1979; Hunter 1987), parasitism (Palma and Pilgrim 1987), conservation (Chupin 1997; Patterson et al. 2008; Lynch et al. 2008), physiology (Johansen and Millard 1973, 1974) and distribution (Conroy 1972; Lynch et al. 2008; Patterson et al. 2008). However, only a few of these studies have dealt with morphological aspects (Conroy 1972; Copello et al. 2006; Bugoni and Furness 2009), but in none of these cases has the osteological anatomy been studied in detail.

The main goal of the present contribution is the comparative osteology of the cranium and mandible of *M. giganteus* along postnatal ontogeny. Detailed descriptions, complemented with measurements made in each of the materials, are given below.

## Materials and methods

The skulls described here are housed in the Ornithology section (MLP-O) and in the osteological collection of the Vertebrate Paleontology Division (MLP) of the Museo de La Plata, and the Ornithology section of the Museo Argentino de Ciencias Naturales (MACN-OR). Twenty-one specimens of different ages were allocated to three ontogenetic categories following classical criteria, considering that chicks are still in the nest under parental care, juveniles are the post-fledged birds, and adults are the sexually mature individuals (e.g. Warham 1962; Trivelpiece and Trivelpiece 1998), in order to compare the development of each structure along the ontogenetic stages: chicks: MLP-O-14590, MACN-OR-68977; juveniles: MLP-O-14510, MLP-O-14691, MLP-O-14692, MLP-O-14898, MLP-O-14898, MLP-O-14898, MLP-O-14898, MLP-O-14898, MLP-O-14898, MLP-O-14898, MLP-O-14898, MLP-O-15066, MLP-O-14510, MLP-O-14590, MLP-O-14691, MLP-O-14692, MLP-O-15066, MACN-OR-68832; and adults: MLP-O-14500, MLP-O-14509, MLP-O-14869, MLP-O-14920, MLP-O-14987, MLP-O-15049, MLP-O-15050, MLP-O-15067, MLP-O-14500, MLP-O-14509, MLP-O-14869, MLP-O-14898, MLP-O-14920, MLP-O-14987, MLP-O-15049, MLP-O-15050, MLP-O-15067, MLP-812, MLP-949, MACN-OR-18251, MACN-OR-26859a, MACN-OR-26859b, MACN-OR-68029. Skull descriptions were organized by regions, comparing the features in adults, juveniles and chicks, and highlighting the differences in the development. In order to speed up the descriptions, we arranged the different regions of the skull as: braincase (i.e. neurocranium and dermatocranium), splanchnocranium, and mandible.

Terminology follows Baumel et al. (1993), supplemented by Livezey and Zusi (2006), and Dénes and Silveira (2007); new terms are indicated in the descriptions. Measurements (Fig. 1) were taken using a Vernier caliper with 0.01 mm

increments and are listed in Table 1. Photos were taken with a Sony DSC-HX200V and a Panasonic DMC-LZ40 cameras.

## Comparative description of the braincase

### Neurocranium

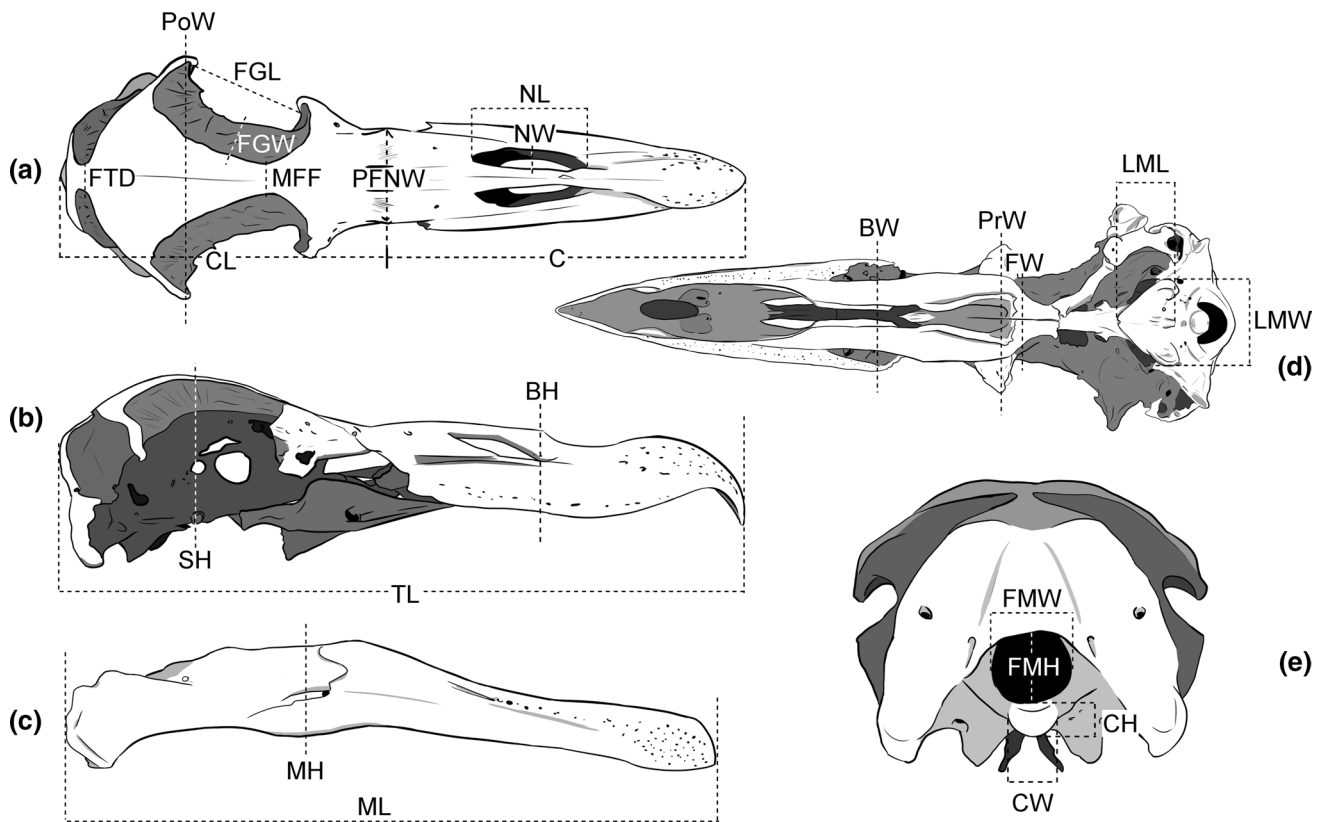
The occipital region has a quadrangular shape (in occipital view) in adults, while in juveniles it is more triangular, and is even more pronounced in chicks (Fig. 2). In this region, all the bones are fused in adults and juveniles, whereas in the chicks, the *Os supraoccipitale* can be distinguished from the dorsal *Os epioticum*. Also, in the chicks, the *Ossa exoccipitales* are not fused and contribute laterally with the formation of the *condylus occipitalis*, with the ventral *Os basioccipitale* (Fig. 3c). This last bone extends ventrally as a part of the *lamina parasphenoidalis*. In chicks, the *condylus occipitalis* is cranially displaced, leaving the *Os supraoccipitale* and the *Ossa epioticum* ventrally more exposed. This condition is not observed in juveniles and adults (Fig. 3).

Near the occiput, the *Os supraoccipitale* has a very developed and rounded *prominentia cerebellaris*, which extends caudally further the *foramen magnum* and *condylus occipitalis* level (Fig. 2). The caudal convexity of the *prominentia cerebellaris* is less pronounced in adults than in juveniles (Fig. 4). It remains cartilaginous and undefined in the chicks.

In lateral view, the *foramen magnum* forms an angle of approximately 45° with respect to the *lamina parasphenoidalis* in the *basis cranii*. The *condylus occipitalis* (Fig. 2) has a smaller diameter than the *foramen magnum* in all the ontogenetic stages. The *foramen magnum* is higher than wider in the three stages, but the aspect ratio (i.e. height/width) is different in each stage, indicating a higher foramen in juveniles than in adults (Table 1). In adults and juveniles, the dorsal region of the foramen is narrower than its ventral part, whereas an opposite condition is observed in the chicks. The *condylus occipitalis* is ventrally convex and dorsally almost flat, without an *incisura mediana condyli* in any of the compared stages.

The *crista nuchalis transversa* is similar in juveniles and adults, while in the chicks it is barely marked upon the suture between the *Os supraoccipital* and the *Os parietalis*. The *crista nuchalis temporalis* is oblique in adults and juveniles. In adults, it is disposed in the same horizontal plane, around 45° regarding the sagittal plane, whereas in juveniles it is still sigmoid, with the ends ventrally displaced in respect to the dorsal plane (Fig. 4).

In chicks, the *Ossa exoccipitales* are independent and located at both sides of the *condylus occipitalis*, while in adults and juveniles they constitute the *processi paroccipitales* (Figs. 2, 3). These processes are not completely ossified in chicks, but in adults and juveniles are well developed, and



**Fig. 1** Schematic drawings of the skull of *Macroneustes giganteus*, the measurements taken are indicated by dotted lines: **(a)** cranium in dorsal view, **(b)** cranium in lateral view, **(c)** mandible in lateral view, **(d)** cranium in palatal view, **(e)** cranium in occipital view. *BH* bill height taken at the level of the *pila supranasalis*; *BW* maximum width of the bill at the caudal end of the *rostrum maxillare*; *C* culmen length taken from the tip of the beak to the level of the suture between the *Os lacrimale* and the *processus frontalis nasalis*; *CW* width of *condylus occipitalis*; *CH* height of *condylus occipitalis*; *CL* cranium length is the total length less the culmen; *FGL* length of the *fossa glandulae nasalis* distance measured from the *Os lacrimale* to the *processus postorbitalis*; *FGW* maximum width of the *fossa glandula nasale*; *FMW* width of *foramen magnum*; *FMH* height of *foramen magnum*; *FW* minimum width between the *Ossa frontalis* taken at

the level of the contact with the *Os lacrimale*; *FTD* distance between *fossae temporalium*; *LML* length of *lamina parasphenoidalis*; *LMW* width of *lamina parasphenoidalis*; *MFF* minimum width between the *fossae glandulae nasalis*; *MH* height of the *ramus mandibulae* taken caudally to the *fenestra cranialis mandibulae*; *ML* length of the *ramus mandibulae*; *NL* *apertura nasi ossea* length; *NW* *apertura nasi ossea* width; *PFNW* width at the level of the *processus frontalis nasalis*; *PoW* width taken at the level of the *processus postorbitalis*; *PrW* preorbital width at the level of the *processus supraorbitalis* of the *Os lacrimale*; *SH* height of the cranium taken dorsally in the point of maximum height and ventrally at the level of the *processus basipterygoideum*; *TL* total length taken from the *prominentia cerebellaris* to the tip of the beak. Not to scale

extended in the same direction that the *processi lateralis parasphenoidalis*. Each *processus paroccipitalis* is ventrally projected, with its distal end medially inclined, and a latero-medial crest delimitates a shallow fossae.

In adults and juveniles, the *fossa parabasalis* is very shallow and presents four openings in caudal view surrounding the *condylus occipitalis*, (three sub-equally dimensioned and a smaller one) (Fig. 5a, b): the dorsalmost is the *foramen nervi vagi*; the medially located, closer to the *condylus occipitalis*, is the *foramen nervi hypoglossus*; the lateral and smallest is the *foramen nervi glossopharyngealis*; and the ventral most is the *ostium canalis carotici*. In addition, the *ostium canalis ophthalmici externi* opens on the edge of the *processus paroccipitalis*, and the *foramen veni occipitalis*

*externae*, latero-dorsal to the foramen magnum, are present in adults and juveniles, but are not well distinguished in chicks, although might be located in the suture between the *Os supraoccipital* and *Os epioticum* in a further stage.

The opening of the *foramen rami occipitalis arteriae ophthalmicae externae* (froaoe) is located near the lateral border of the *crista nuchalis transversa* in juveniles and in adults. Two additional small foramina, not previously described, open laterally: one of them is located laterally to the froaoe, and the other, which is the smaller one, is on the cranial side of the *crista nuchalis transversa*.

The *Ossa otica* (Fig. 5c, d) presents a complex structure in adults and juveniles, analyzed in a ventro-lateral perspective. The spatial relationship of the main elements

**Table 1** Measurements (in mm) taken on the crania and mandibles of *Macroneustes giganteus*

M	Chicks				Juveniles										
	MLP-O-14590	MACN-OR-68977	CM	MLP-O-14898	MLP-O-14691	MLP-O-15066	MLP-O-14692	MLP-O-14510	MACN-OR-68832	JM	MLP	MLP	MLP	MLP	MLP
PoW	26.26		26.26	49.50	48.52	52.66	48.62								
PrW				29.22	32.48						30.85				
FTD	9.62		9.62	8.80	9.42	5.04					7.75				
PFNW	11.00		11.00	20.00	20.00	21.96	20.36				20.58				
FMH	6.08		6.08	13.14	11.20	12.56	12.30	12.82			12.40				
FMW	6.40		6.40	9.70	10.10	9.54	9.60	10.48			9.88				
NW	3.34		3.34	6.48	6.18	7.26	6.28				6.55				
NL	15.50		15.50	24.42	25.20	29.02	25.00				25.91				
FW	10.40		10.40	20.00	19.30	21.76					20.35				
BW	13.62		13.62	22.60	23.58	25.10					23.76				
BH	8.68		8.71	15.70	16.78	19.14		10.28			15.47				
CW	5.70		5.70	5.60	5.26	6.32	6.00	6.48			5.93				
CH	2.98		2.98	3.74	4.22	4.56	3.92	4.36			4.16				
SH	20.00		20.00	34.72	35.20	36.64					35.52				
FGL	13.94		13.94	30.00	28.60	33.90					30.64		ca 30.08		
MFF	4.12		4.12	8.64	8.00	7.58					8.07				
TL	79.50		79.50	148.84	151.88	182.52					161.08				
C	41.40		41.40	83.54	88.92	104.24					92.23				
FGW	4.64		4.64	9.52	9.42						9.47				
CL	38.10		38.10	65.30	62.96	78.28					68.85				
LML	3.74		3.74	12.00	11.20	12.32	11.80				11.83				
LMW	6.98		6.98	17.90	18.30	21.38	17.86				18.86				
MH	9.06		9.05	15.70							14.44		ca 11.18		
ML	63.94		63.94	123.00							123.00				
AR	0.95		0.95	1.35	1.10	1.31	1.28	1.22			1.25				
Adults															
PoW	56.30		50.82	57.70	57.70	56.88	52.26	54.94	59.86	54.62					
PrW	37.76		33.16	36.26	36.26	39.94	32.30	36.10	40.20	34.00					
FTD	5.56		7.66	8.48	8.48	9.00	3.84	6.80	8.04	8.66					
PFNW	22.40		19.32	22.84	22.84	24.58	20.58		25.60	21.70					
FMH	11.38		11.16	11.28	11.28	12.20	11.68	11.18	12.00	11.58					
FMW	10.50		10.18	10.26	10.26	10.30	10.04	11.08	10.70	10.20					

**Table 1** (continued)

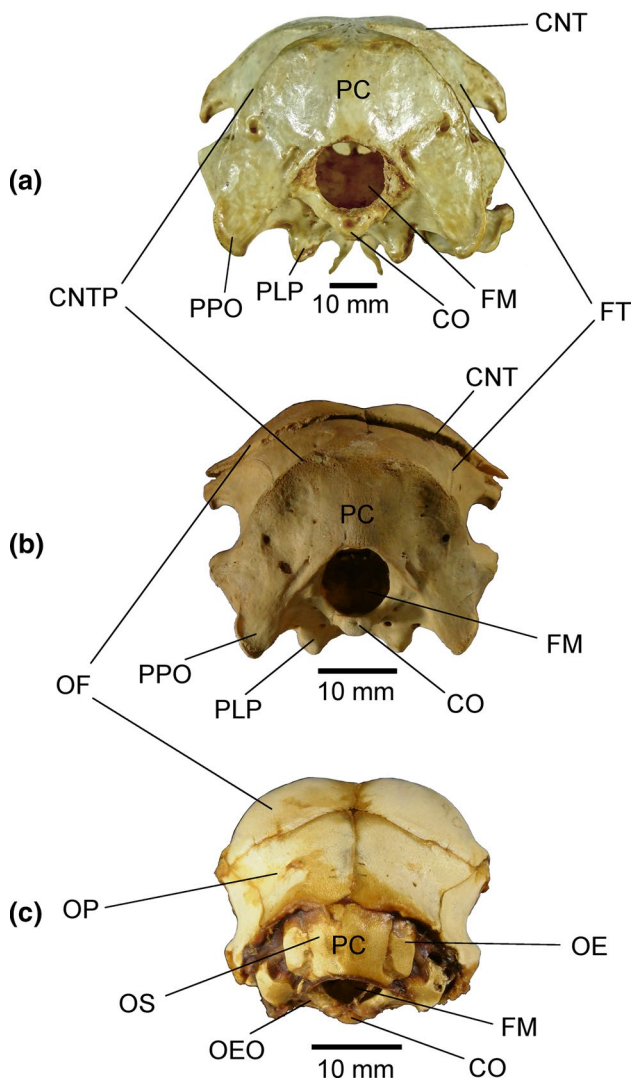
Adults										
	MLP-O-14500	MLP-O-15049	MLP-O-15067	MLP-O-15050	MLP-O-14869	MLP-O-14509	MLP-O-14987	MLP 949	MLP 812	
NW	7.26	6.38	6.54	6.34	6.88	5.96			6.62	
NL	26.60	20.58	28.96	28.14	27.76	20.40			27.68	
FW	23.14	19.12	20.42	22.10	23.24	19.42	20.24	22.68	20.80	
BW	28.00	25.60		28.52	31.98	24.78		28.74	27.72	
BH	20.58	15.70	17.46	19.32	20.60	17.56			18.74	
CW	6.28	6.50	6.42	6.30	5.70	5.06	5.18	6.28	6.62	
CH	4.32	4.18	3.78	4.30	4.62	4.04	3.94	4.58	4.32	
SH	37.00	34.38	35.90	38.24	38.58	35.08		38.36	36.28	
FGL	31.38	27.46	32.16	32.06	32.40	29.50	30.8	33.24	31.12	
MFF	7.38	7.66		7.60	23.30	6.48	8.34	6.80	9.76	
TL	171.08	141.4		171.58	178.4	148.74		180.66	164.34	
C	98.78	80.70		100.98	105.26	86.16		107.76	96.20	
FGW	10.94	8.50	9.16	11.08	11.82	10.58	8.96	11.88	10.70	
CL	72.30	60.70								
LML	13.80	10.80		12.98	13.00	12.94		14.20	13.20	
LMW	20.48	17.38		20.58	20.96	16.16		22.24	19.00	
MH	17.66	15.58		18.82	19.28	16.38		19.50	17.56	
ML	140.50	118.74		142.38	150.54	119.28		147.8	138.26	
AR	1.08	1.09	1.14	1.09	1.18	1.16	1.01	1.12	1.13	
Adults										
MACN-OR-18251										
PoW	52.76		57.44		56.70		MACN-OR-68029		55.68	
PrW	34.51		39.32		39.08				36.35	
FTD	7.30		5.80		8.24				7.38	
PFNW	22.50		22.10		22.66		MACN-OR-26856b		22.55	
FMH			10.40		11.54				11.33	
FMW	10.06		11.00		10.70				10.43	
NW			6.68		6.02				6.42	
NL			27.10		25.00				25.85	
FW	19.40		22.00		21.98				21.21	
BW	26.68		ca 28.18		ca 33.48				28.71	
BH			20.70		ca 22.90				19.69	
CW	4.82		6.64		6.30				5.89	
MACN-OR-26856a										
PoW							MACN-OR-68029			
PrW										
FTD										
PFNW										
FMH										
FMW										
NW										
NL										
FW										
BW										
BH										
CW										

Table 1 (continued)

	Adults				
	MACN-OR-18251	MACN-OR-26856a	MACN-OR-26856b	MACN-OR-68029	AM
CH	3.98	4.50	4.62	4.20	4.26
SH	31.62	41.72	39.10	35.70	37.04
FGI	29.22	30.58	32.68	29.12	31.15
MFF	8.00	6.58	8.48	10.42	9.54
TL	ca 147.70	ca 179.26	ca 172.54	ca 158.84	166.70
C	ca 89.20	ca 106.90	ca 105.10	ca 93.94	98.89
FGW	9.72	12.48	11.00	9.80	10.64
CL		72.36	67.44	64.90	68.06
LML	ca 11.40	14.86	13.04	10.70	12.91
LMW	17.00	21.58	18.90	17.80	19.35
MH	15.00	18.44	175.24	12.08	34.37
ML	120.10	147.50	145.76	127.76	137.56
AR		0.94	1.08	0.94	1.08

Only complete specimens were measured

AM adults media, AR aspect ratio of the Foramen Magnum = height/width, BH bill height taken at the level of the *pila supranasalis*, BW maximum width of the bill at the caudal end of the *rostrum maxillare*, C culmen length taken from the tip of the beak to the level of the suture between the *Os lacrimale* and the *processus frontalis nasalis*, CW width of *condylus occipitalis*, CH height of *condylus occipitalis*, CL cranium length is the total length less the culmen, CM Chicks media, FGL length of the *fossa glandulae nasalis*, distance measured from the *Os lacrimale* to the *processus postorbitalis*, FGW maximum width of the *fossa glandula nasale*, FMW width of *foramen magnum*, FMH height of *foramen magnum*, FW minimum width between the *Ossa frontali* taken at the level of the contact with the *Os lacrimale*, FTD distance between *fossae temporarium*, JM juvenile media, LML length of *lamina parasphenoidalis*, LMW width of *lamina parasphenoidalis*, M measurements, MFF minimum width between the *fossae glandulae nasalis*, MH height of the *ramus mandibulae* taken caudally to the *fenestra cranialis mandibulae*, ML length of the *ramus mandibulae*, NL *apertura nasi ossea* length, NW *apertura nasi ossea* width, PFW width at the level of the *processus frontalis nasalis*, PoW width taken at the level of the *processus postorbitalis*, PPW preorbital width at the level of the *processus supraorbitalis* of the *Os lacrimale*, SH height of the cranium taken dorsally in the point of maximum height and ventrally at the level of the *processus basipterygoideum*, TL total length taken from the *prominentia cerebellaris* to the tip of the beak



**Fig. 2** Cranium of *Macronectes giganteus* in occipital view: **(a)** adult, **(b)** juvenile, **(c)** chick. CNT *crista nuchalis transversa*; CO *condylus occipitalis*; CNTP *crista nuchalis temporalis*; FM *foramen magnum*; FT *fossa temporalis*; OE *Os epitoticum*; OEO *Os exoccipitale*; OF *Os frontale*; OP *Os parietale*; PC *prominentia cerebellaris*; PLP *processus lateralis parashenoidalis*; PPO *processus paroccipitalis*

is as follows: the *fenestra cochleae* is ventral, the *fenestra vestibuli* is dorsal, and the *foramen pneumaticum caudale* is caudal. The *pila otica* constitutes a dorsal wall, caudally wider, and separated from the *cotyla quadratica otici* that exhibits the pedicellate condition, according to Livezey and Zusi (2006). The *recessus tympanicus dorsalis* is located ventral to the *squamosum* and occupies an area that is larger than the set constituted by the *fenestra cochleae*, *fenestra vestibuli*, and *foramen pneumaticum caudale*. Cranially, in the fronto-orbital region, the opening of the *foramen nervi maxillomandibularis* is prominent and “L”-shaped. Ventrally, there is a wall distinguished from the rest of the elements, subparallel to the cranio-caudal axis, and a ventral

*canalis orbitalis*, which presents numerous foramina and recessus. This canal, present in all the stages, conducts the *ramus carotis* and *arteria sphenoida*.

The fronto-orbital region presents the circular *fonticulus interorbitalis* (Figs. 4, 5c, d) which is the greatest foramina in this region, also the most ventral and cranial one. Dorsally, the *fonticulus orbitocraneal* which is variable outlined in the different specimens, is mostly elongated (e.g. MLP-O-14500). Its width is equal to that one of the *fonticulus orbitocranialis*, and presents a ventral crest as a constriction. MLP-O-14869 presents two foramina in this position. Caudally to the *fonticulus interorbitalis* is the *foramen nervi optici*, which constitutes a single foramen (MLP-O-14500), or many foramina (MLP-O-14869) in the different specimens. *Foramen nervi ophthalmici* is in between three tiny foramina and the *foramen nervi maxillomandibularis* in adults. The *foramen nervi olfactorii* is very small, is caudal to the *foramen orbitonasal* and only present in adults.

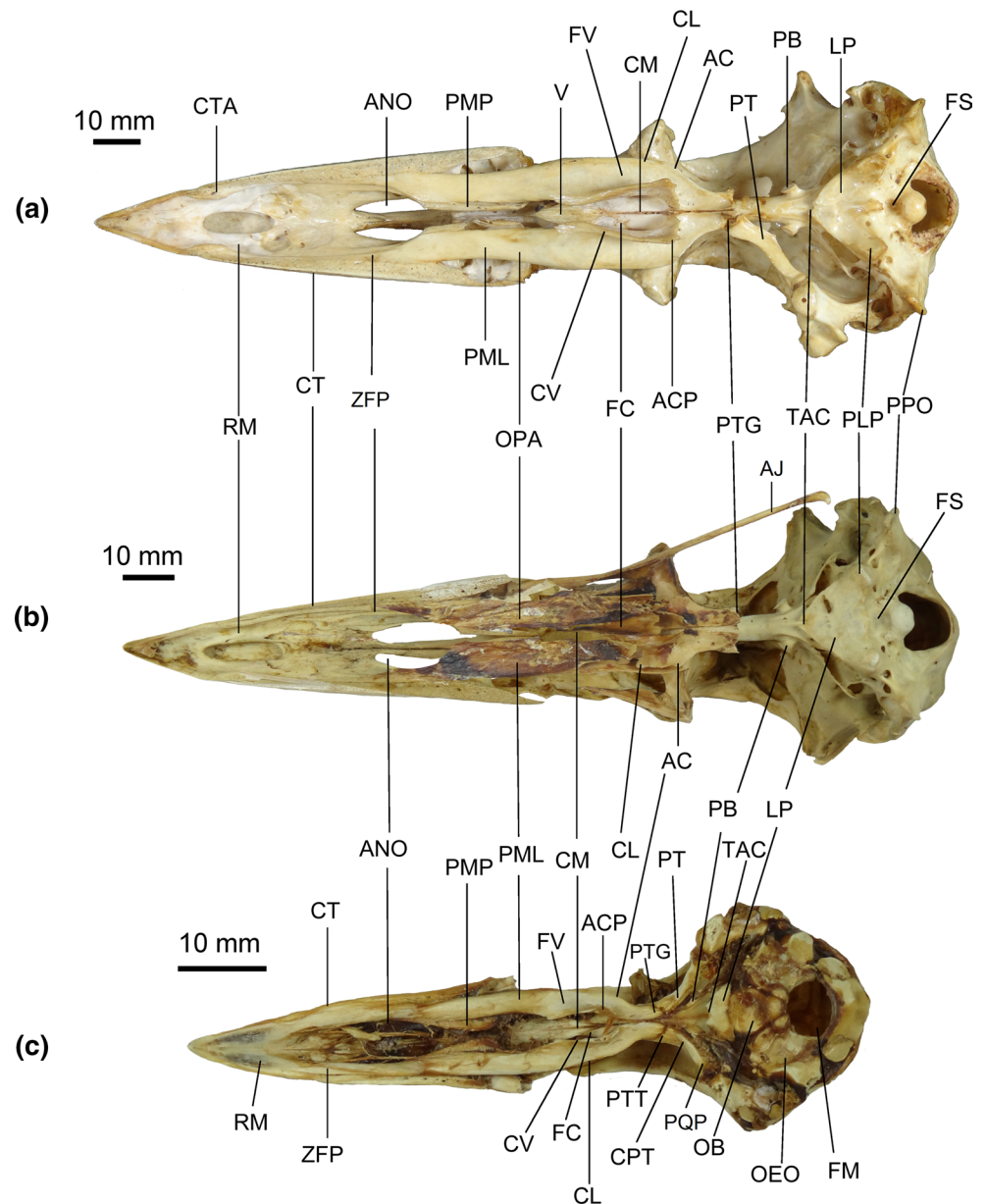
Cranio-dorsally, the *foramen orbitonasal* opens through a single foramen (MLP-O-14500) or it can be subdivided (MLP-O-14869). This foramen cannot be identified as a *foramen orbitonasal lateral* and a *foramen orbitonasal medial*, since this species present a dorso–ventral division, at least in adults. In juveniles, the *fonticulus interorbitalis* is even larger than that in adults, including the *fonticulus orbitocranialis*, the *foramen nervi optici* and the *foramen orbitonasal*. Otherwise, in juveniles, the wall of the *Os mesethmoidale* that goes from these foramina to the dorsal and caudal zone is not ossified as in adults, leaving only the *septum interorbitale*.

The orbital region (*Os mesethmoidale*) is completely ossified as a wall in adults and juveniles. Nonetheless, in chicks, it remains cartilaginous, except at the level of the *lamina dorsalis*, which is a part of the *Os mesethmoidale*. The *lamina dorsalis* is ventrally and perpendicular located respect to the *septum interorbitale* (Fig. 5e). A suture between the *Os parietales* and the ventral *Os laterosphenoidale* also appears in the chick.

The *septum nasale osseum* (Fig. 5e) is not very extended and presents an asynostotic condition with the *palatus maxillaris*. This septum is present in the adults but absent in the chicks and in the juveniles. The *sulcus nervi olfactorii* is absent, its condition probably related to the wide and extended opening of the *foramen orbitonasale* (Fig. 4).

In adults in palatal view, the *basis cranii externa* presents a triangular *lamina parasphenoidalis* with *processi lateralis parasphenoidalis* caudally directed, and laterally delimited by a crest (Fig. 3). In juveniles, these *processi* are more rounded and ventrally extended. In chicks, the *lamina parasphenoidalis* is cranially displaced and butterfly-shaped, because of the poor development of the *processi lateralis parasphenoidalis* and two other cranial smaller alae (Fig. 3c), in whose cranial ends opens the *tuba auditiva*

**Fig. 3** Cranium of *Macronectes giganteus* in palatal view: (a) adult, (b) juvenile, (c) chick. AC *angulus caudolateralis*; ACP *angulus caudomedialis palatini*; AJ *arcus jugalis*; ANO *apertura nasi osea*; FC *fossa choanalis*; FV *fossa ventralis*; CL *crista lateralis*; CM *crista medialis*; CPT *corpus pterygoidei*; CT *crista tomialis*; CTA *crista tomialis accessoria*; CV *crista ventralis*; FC *fossa choanalis*; FM *foramen magnum*; FS *fossa subcondylaris*; LP *lamina parasphenoidalis*; OB *Os basioccipitale*; OEO *Os exoccipitale*; OPA *Os palatinum*; PB *processus basiptyergoideus*; PNP *processus maxillopalatinus*; PB *processus basiptyergoideus*; PLP *procesuss lateralis parasphenoidalis*; PML *procesus maxillaris*; PMP *processus maxillaris premaxillaris*; PPO *processus paroccipitalis*; PQP *processus quadraticus pterygoidei*; PT *Os pterygoideum*; PTG *processus pterygoideus*; PTT *pes pterygoidei*; RM *rostrum maxillare*; TAC *tuba auditiva communis*; V *vomer*; ZFP *zona flexoria palatini*



*communis*. In adults and juveniles these alae are sharper and proportionally smaller, and the *lamina parasphenoidalis* has a conspicuous crest, which is absent in chicks. This crest starts at the caudal half and is caudally directed becoming more pronounced until it exceeds the *lamina parasphenoidalis* with an expansion half-moon shaped in lateral view.

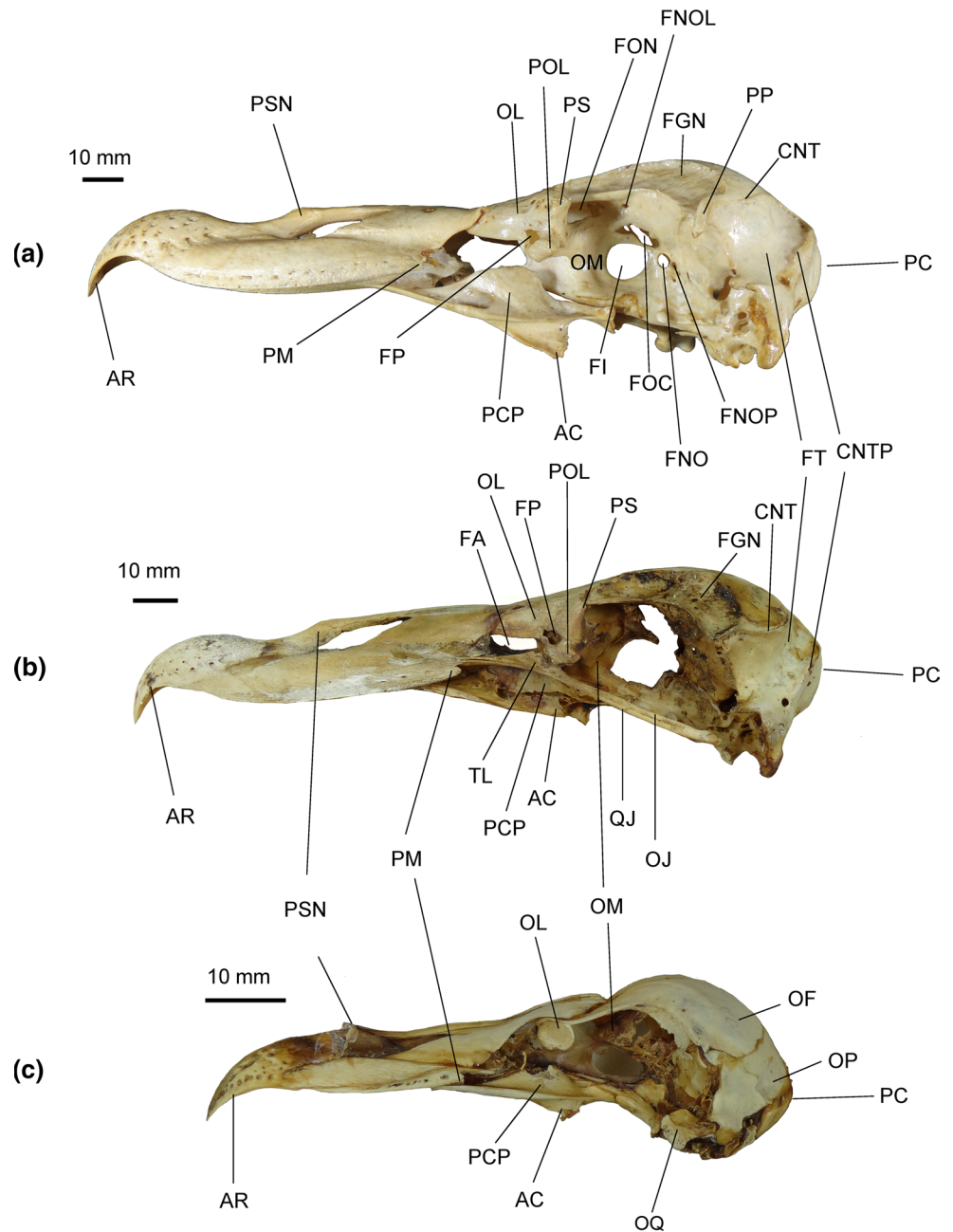
In adults, the *fossa subcondylaris* (Fig. 3), between the *lamina parasphenoidalis* and the *condylus occipitalis*, has the same width of that of the *condylus occipitalis*. In chicks, however, it is shallower and narrower. Oppositely, the *rostrum parasphenoidale* in its caudal most region is more robust in chicks than in juveniles and adults, but cranially, the rostrum is not ossified, remaining cartilaginous as in the rest of the *Os mesethmoidale* (Fig. 4c).

### Dermatocranium

Each *Os parietales* (Figs. 2, 6a–c) is separated from the rest of the bones in the chicks. In juveniles, the parietals are fused to the occipital region, and in adults they are also fused to the *Ossa frontali*. A shallow hollow appears on the chick's parietals, which develops into the *fossa temporalis*, and is deeper in juveniles than in adults. Bony texture of its surface varies among specimens. Right and left fossae dorsally extend without reaching the sagittal plane (Fig. 6a–c), remaining separated from each other by the interorbital region, which is wider in juveniles than in adults (Table 1). The boundaries of this fossa are the cranial *crista nuchalis transversa*, and the caudal *crista nuchalis temporalis*,



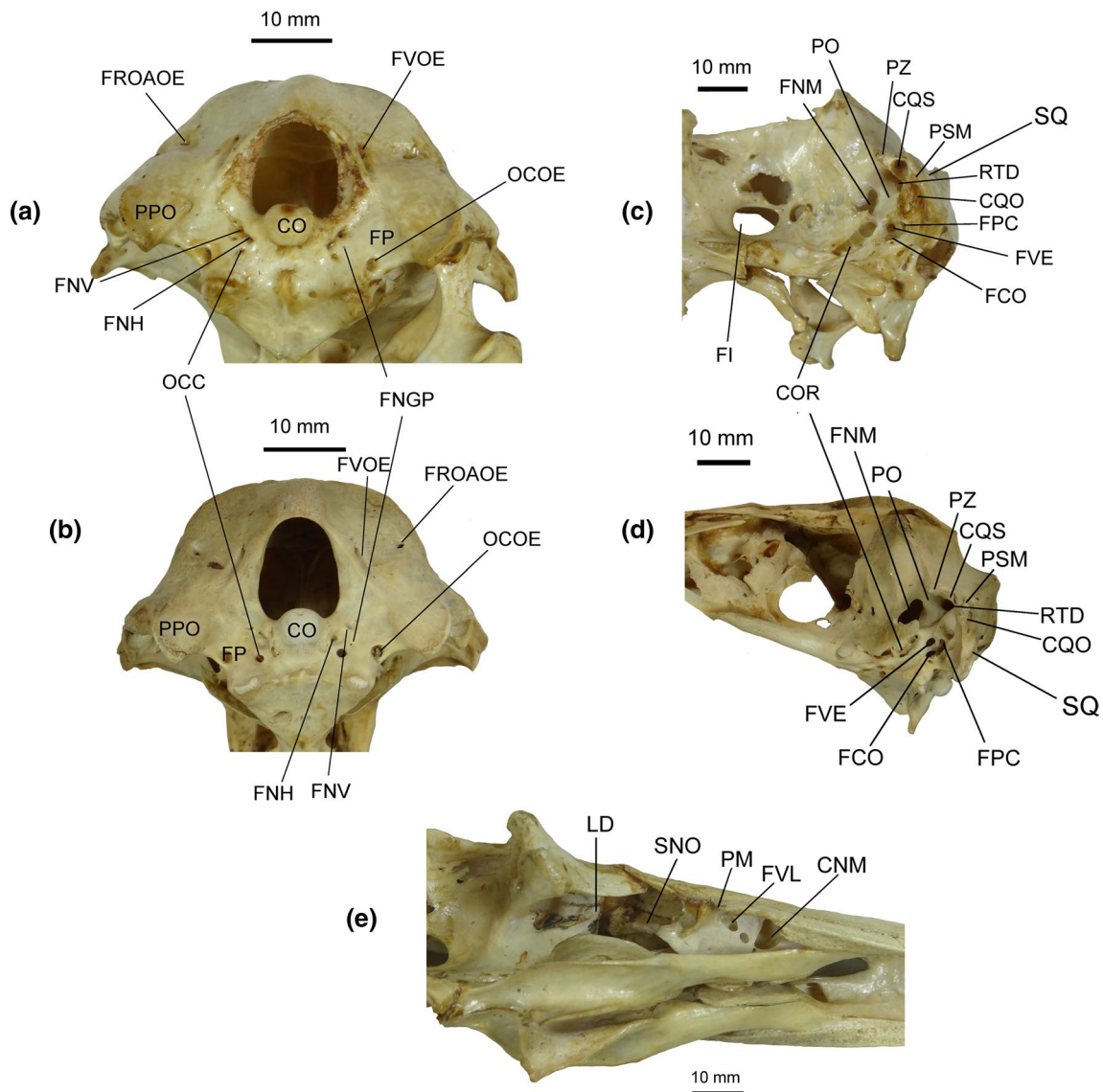
**Fig. 4** Cranium of *Macronectes giganteus* in lateral view: (a) adult, (b) juvenile, (c) chick. AC *angulus caudolateralis*; AR *apex rostri*; CNT *crista nuchalis transversa*; CNTP *crista nuchalis temporalis*; FA *fenestra antorbitalis*; FGN *fossa glandularis nasalis*; FI *fonticulum interorbitalis*; FNO *foramen nervi optici*; FNOL *foramen nervi olfactori*; FNOP *foramen nervi ophthalmici*; FOC *fonticulum orbitocraneal*; FON *foramen orbitonasal*; FP *foramen pneumaticum*; FT *fossa temporalis*; OF *Os frontale*; OJ *Os jugale*; OL *Os lacrimale*; OM *Os mesethmoidale*; OP *Os parietale*; OQ *Os quadratum*; PC *prominentia cerebellaris*; PCP *pars choanalis palatini*; PM *pons maxillarojugalis*; POL *processus orbitalis* of the *Os lacrimale*; PP *processus postorbitalis*; PS *processus supraorbitalis*; PSN *pila supranasalis*; QJ *Os quadratojugale*; TL *tuberculum lacrimale*



both of them being well developed in adults and juveniles. Although the *fossa temporalis* is shallow and poorly marked in chicks, the *crista nuchalis temporalis*, between the *Os supraoccipitale* and *Os parietalis*, is not well developed.

In chicks, the *Ossa frontali* cover an area of the cranial roof that is proportionally wider than in other stages. These bones do not have the typical triangular shape of the juveniles and adults. The suture between both *Ossa frontali* of the chicks is not longer visible in juveniles, in which it is replaced by the *depressio frontalis* and is better developed in adults. This depression, located where the *fossae glandulae nasalis* are closer to each other, is narrow and deep.

The *fossae glandulae nasalis* are deep and well delimited in juveniles and adults, their cranial ends being deeper and further away from the middle line. In chicks, this zone is only distinguished by a barely marked line. The surface of these fossae are rough, with thin caudal lines (e.g. MLP-O-14500) radiating toward the orbital zone. These lines, weaker in other specimens (MLP-O-14869, MLP-O-15050), are always present. The *margo supraorbitalis*, with a variable texture (Fig. 6a–c), is well developed in adults and juveniles. The adults MLP-O-14500, MLP-O-14897, MLP-O-15067, MLP-O-14509, and MLP-O-15049 and the juveniles MLP-O-1469, and MLP-O-14898 present a variety



**Fig. 5** Neurocranium of *Macronectes giganteus* in ventro-occipital view: (a) adult, (b) juvenile; in ventro-lateral view: (c) adult, (d) juvenile; close-up of the middle portion of the cranium in ventro-lateral view (e) adult. CNM opening of the *canalis neurovascularis maxillae*; CO *condylus occipitalis*; COR *canalis orbitalis*; CQO *cotyla quadratica otici*; CQS *cotyla quadratica squamosi*; FCO *fenestra cochleae*; FI *fonticulus interorbitalis*; FNGP *foramen nervi glossopharyngealis*; FNH *foramen nervi hypoglossus*; FNM *foramen nervi maxillomandibularis*; FNV *foramen nervi vagi*; FP *fossa para-*

*basalis*; FPC *foramen pneumaticum caudale*; FROAOE *foramen rami occipitalis arteriae ophthalmicae externae*; FVE *fenestra vestibuli*; FVL *fenestra ventrolateralis*; FVOE *foramen veni occipitalis externae*; LD *lamina dorsalis*; OCC *ostium canalis carotici*; OCOE *ostium canalis ophthalmici externi*; PM *pons maxillarojugalis*; PO *pila otica*; PPO *processus paroccipitalis*; PSM *processus suprameaticus*; PZ *processus zygomaticus*; RTD *recessus tympanicus dorsalis*; SNO *septum nasale osseum*; SQ *Os squamosum*

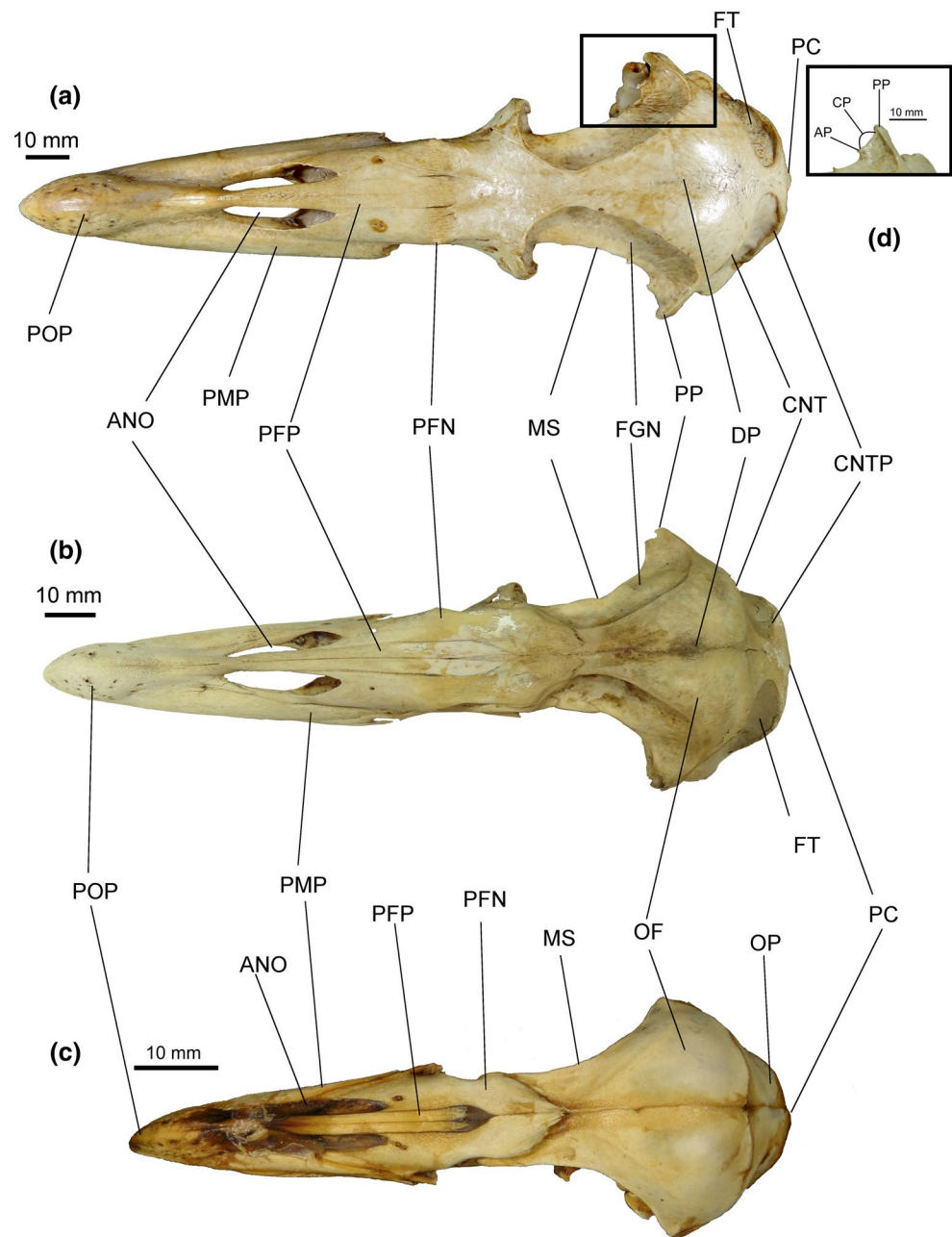
of levels of undulation. In contrast, the chicks have a *margo supraorbitalis* with a smooth surface.

Little hamuli project from the *margo supraorbitalis* in adults (e.g. MLP-O-14509 and MLP-O-14897) and juveniles (MLP-O-14691) (Fig. 6b, d). These structures are not constant, and their appearance and development vary between specimens. Immediately cranial to the *processus postorbitalis* is the *angulus postocularis* (sensu Livezey and Zusi 2006), a hamuli developed in the adults MLP-O-14500

and MLP-O-14987 that extends cranio-medially and slightly dorsal. The *angulus postocularis*, together with the *processus postorbitalis*, limits the *crista postocularis* (see Livezey and Zusi 2006), located almost perpendicular to the sagittal line. A second hamuli may appear more cranially in adults and juveniles.

The *processus postorbitalis* (Fig. 4) extends cranio-ventrally in adults, whereas it is not yet developed in the chicks. An intermediate condition is observed in juveniles, where

**Fig. 6** Cranium of *Macronectes giganteus* in dorsal view: (a) adult, (b) juvenile, (c) chick, (d) close-up of the *processus postorbitalis* area indicated with a square in (a). ANO *apertura nassi ossea*; AP *angulus postocularis*; CNT *crista nuchalis transversa*; CNTP *crista nuchalis temporalis*; CP *crista postocularis*; DP *depressio frontalis*; FGN *fossa glandularis nasalis*; FT *fossa temporalis*; MS *margo supraorbitalis*; OF *Os frontale*; OP *Os parietale*; PC *prominentia cerebellaris*; PFN *processus frontalis nasalis*; PFP *processus frontalis premaxillaris*; PMP *processus maxillopalatini*; POP *corpus ossis premaxillaris*; PP *processus postorbitalis*



there is still a suture between the *Ossa frontali* and *Ossa parietale*.

The *Os lacrimale* (Fig. 4a) is cranio-caudally elongated and fused with the *Ossa frontali* in adults; it remains separated in juveniles (Fig. 4b), and not completely ossified in the chicks (Fig. 4c). The *Os lacrimale* is also fused to the mesethmoides in its medium-caudal portion, and to the ectethmoides in its caudal portion. Otherwise, the *processus orbitalis* of the lacrimale does not contact to the ectethmoides, projecting caudally and laterally. There is a crest in its caudal region, while the cranial end is highly pneumatized, with a cranial *foramen pneumaticum*. The

*processus orbitalis*, less developed in juveniles than in adults, has a triangular shape and a slight constriction.

In adults, the *processus supraorbitalis* of the *lacrimale* is well developed, triangular, and more robust than the *processus orbitalis*. It is caudally extended, carrying a crest in caudal view. This structure is similar in juveniles, although less developed. Two small foramina (in some specimens fused in a single foramen), open cranially, communicating internally with the *foramen orbitonasale*. In all the adults and juveniles here examined, the *foramina orbitonasale medialellaterale* are fused in a single aperture, and is a non-ossified area in the chicks. A “U”-shaped notch separated

the *processus supraorbitalis* and the *processus orbitalis* in adults and juveniles.

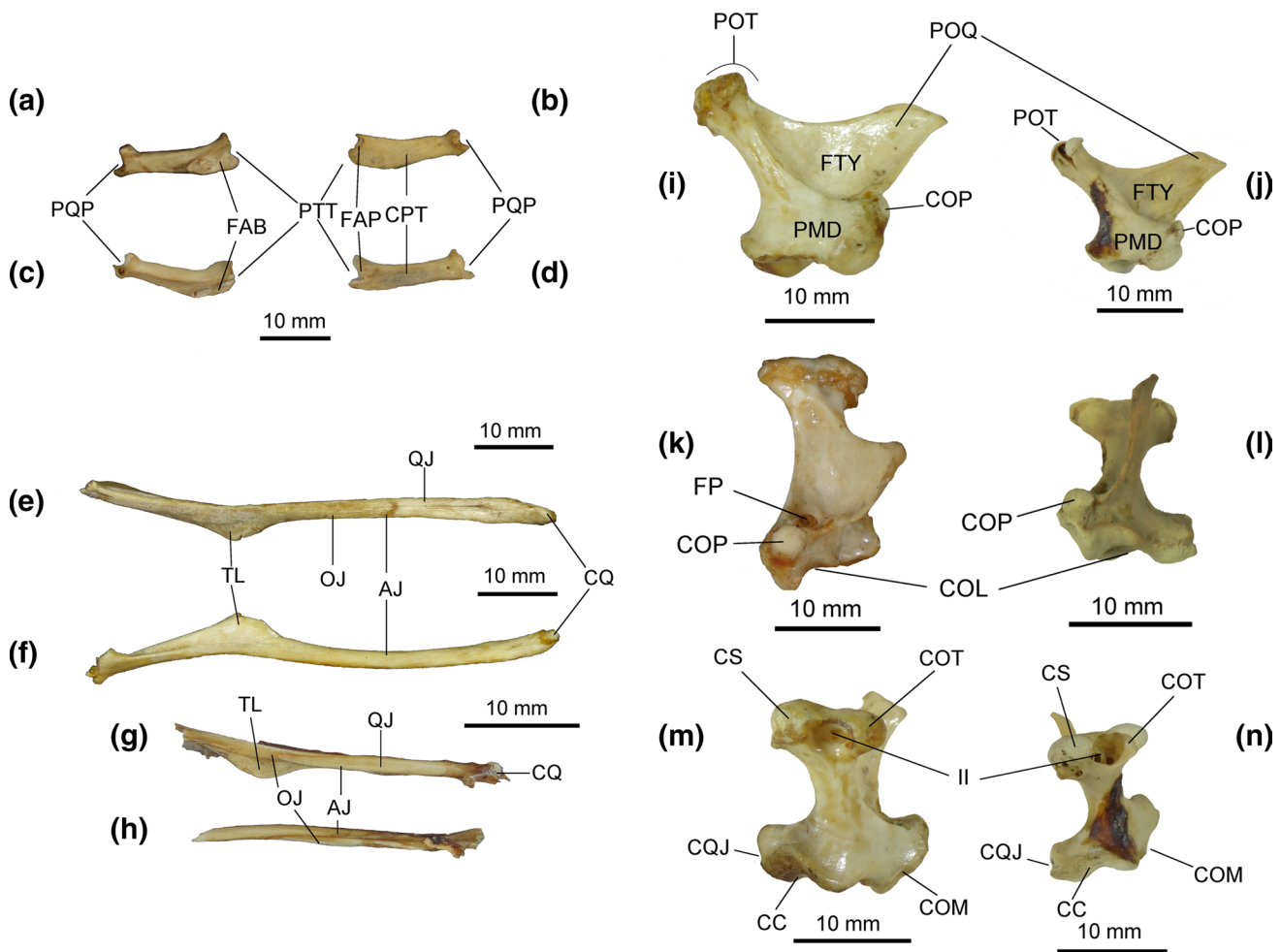
In all the specimens examined here, the *palatum* (Fig. 3) acquires a tetradiate shape constituted by the *Os pterygoideum* and *Os palatinum*. The cup-shaped *processi basiptyergoidei* are well developed, and cranio-laterally projected in juveniles and adults. In chicks, these processes are less projected, almost contacting with the *Os pterygoideum*, which is positioned further away in adults and juveniles.

The *Os pterygoideum* (Figs. 3, 7a–d) has a complex structure (see Genbrugge et al. 2011) and can be divided into three parts: *pes pterygoidei*, *corpus pterygoidei*, and *processus quadraticus pterygoidei*. A dorsal crest, probably homologous to the *processus dorsalis* described for other

birds (e.g. Baumel et al. 1993; Livezey and Zusi 2006; Genbrugge et al. 2011), is cranially bifurcated, and runs parallel to a narrow sulcus in the caudal portion (Fig. 7a–c). These same structures are developed in the three stages.

The *facies articularis basiptyergoidea* (Fig. 7a–c) (defined as the surface for the articulation with the *processus basiptyergoideum*), does not contact with these *processi* in adults (e.g. MLP-O-14500), whereas it does in juveniles (e.g. MLP-O-16066) and chicks (MLP-O-14590). However, the contact between both structures is not complete, since the *processus basiptyergoideum* is wider than the *facies articularis basiptyergoidea*.

The *facies articularis quadratica*, on the *processus quadraticus pterygoidei*, has two small condyles for the



**Fig. 7** Pterygoideum of *Macroneustes giganteus*: (a) adult in medial view, (b) adult in lateral view, (c) juvenile in dorso-medial view, (d) juvenile in lateral view; arcus jugalis of (e) adult in medial view, (f) adult in lateral view, (g) chick in medial view, (h) chick in lateral view; *Os quadratum* in medial view: (i) adult, (j) juvenile, in cranial view: (k) adult, (l) juvenile, in caudal view: (m) adult, (n) juvenile. AJ arcus jugalis; CC condylus caudalis; COL condylus lateralis; COM condylus medialis; COP condylus pterygoideus; COT capitu-

lum oticum; CPT corpus pterygoidei; CQ condylus quadraticus; CQJ cotyla quadratojugalis; CS capitulum squamosum; FAB facies articularis basiptyergoidea; FAP facies articularis palatina; FP foramen pneumaticum; FTY facies tympanica; II incisura intercapitularis; OJ *Os jugale*; PMD processus mandibularis; POQ processus orbitalis of the quadratum; PQP processus quadraticus pterygoidei; POT processus oticus; PTT pes pterygoidei; QJ *Os quadratojugale*; TL tuberculum lacrimale

articulation of the *Os quadratum* (Fig. 7c). There is a foramen in this facies, on the dorsal condyle, which is larger and sometimes subdivided in juveniles (MLP-O-14898) (Fig. 7c). Adults and juveniles present a small lateral foramen and in some adults (MLP-O-14500) (Fig. 7b–d); a larger medial one appears close to the end of this processus in adults (Fig. 7a).

In all the ontogenetic stages, the *pes pterygoidei* is very flattened and carries the *facies articularis palatina* (Fig. 7b, d), that in lateral view presents a dorso-cranial splint, the *pars palatina*, for the articulation with the *Os palatinum*, and a small *facies articularis parasphenoidalis* (Fig. 7b, d). In juveniles and chicks, the *Os palatinum* (Fig. 3), in its most caudal portion, presents a triangular form, with a narrow *processus pterygoideus* caudo-ventrally projected, along the *facies articularis palatina*. In chicks (Fig. 3c), it is more flattened and only partially ossified, consequently all the elements remain separated.

The *Os palatinum* (Figs. 3, 4) is cranially wider at the level of the *angulus caudolateralis*, from which the *crista ventralis* is cranially projected. The *crista lateralis* is pronounced in chicks (Fig. 3c) but it is barely marked in adults. The *fossa ventralis*, medial to this crest, is deeper and bounded by walls with numerous recesses and foramina in adults. At both sides of this fossa, the *lamellea ventrales, pars choanalis palatini*, is well developed and ventrally projected, constituting a triangle in lateral view. The *angulus caudomedialis palatini*, the ventral most vertex, is ventrolaterally extended, and develops some small crests in its caudal portion. The *fossa choanalis*, between both *lamellea ventrales*, has a weak mid *crista medialis*.

In juveniles and adults, the *vomer*, which is cranially located, has an oval projection with both caudal and cranial sharp ends. The cranial end comprises a thin wall, which is absent in the chicks. In lateral view (Fig. 4), the *lamella dorsalis, pars choanalis palatini*, is well developed and acquires a rounded form. In juveniles and adults, the ossification degree of this structure and the development of fossae on its surface varies among individuals and even between the left and right sides of the same specimen. For instance, in the right side of the adult MLP-O-14500, there are two fossae (cranial and caudal ones), whereas in the left side only the cranial fossa is present. Indeed, in most of the adults and juveniles, the caudal fossa is absent.

The *vomer* is cranially fused with elements of the external arch of the palatoquadrate and with the *Os Nasale* (Fig. 3). The *processi maxillarium* of the *Os nasale*, are cranially extended like two parallel bars to the sagittal plane until the *zona flexoria palatini*.

The *processi maxillopalatini* of the *Os maxillare* are medial and parallel to each other, as paired thin structures caudally separated for the *processi maxillarium*. In the adults, the *Os palatinum* is fused with the *processi*

*maxillopalatini*, the *vomer* and the *rostrum maxillare*. In juveniles and chicks, they are all separated with the exception of the *rostrum maxillare* joined to the *processi maxillopalatini* (Fig. 3b). Also, in chicks (Fig. 3c), the *processi maxillopalatini* are more laterally extended, and consequently the *processi maxillarium* are even more separated each other. In ventral view, the palatal portion of the *processus frontalis nasalis* is surrounded at both sides by the *apertura nasi ossea* (Fig. 3), which in adults presents its cranial end with a projection that corresponds to the *septum nasi osseum* (Fig. 5e), and is very reduced in this species. It is asynostotically connected with the *processus palatus maxillaris*.

In adults and juveniles, the *rostrum maxillare* (an ankylosis of the *Ossa premaxillarium*), comprises a single element, but in the juveniles and in the chicks the suture between both *Ossa premaxillarium* is still present in its caudal most region. Cranially, the *rostrum maxillare* of the *Os premaxillare* presents a large and oval fossa and caudally, and at both sides, two more fossae are connected or subdivided, with a variable number of foramina. In the chicks, there is only one shallower fossa and a single foramen on each side. The juveniles are similar to the adults, although the fossae are less subdivided.

In the most cranial region of the beak, in the place where the tip of the hook begins, a *crista tomialis accesoria* (new term), appears only in the adults. It is short and sub-parallel, joining caudally with the *crista tomialis*. Between both cristae, the *crista tomialis* and the *crista tomialis accesoria*, there is a sulcus (Fig. 3) that supports the *latericorn plate* of the rhamphotheca. The *latericorn plate* ends cranially in the place where the beak becomes more convexly expanded. In this zone is located the *premaxillary nail* of the rhamphotheca. Dorsally to the latericorn plate, and caudally to the premaxillary nail, it is disposed as a single tube; a characteristic of this group of tubenoses (Hieronymus and Witmer 2010) that extends until the *processus frontalis nasalis*. This tube opens at the level of the *pila nasalis* (this processus and pila are described below).

In medioventral view (Fig. 5e), dorsal to the *processus maxillaris*, the *fenestra ventrolateralis* opens in a dorso-caudal position in adults. Cranio-ventrally, in adults and juveniles, there is another smaller fenestra, and cranially, there is the opening of the *canalis neurovascularis maxillae*; in the chicks, all these regions remains cartilaginous. In a more caudal position, the *pons maxillarojugalis* keeps its contact through visible sutures in all the ontogenetic stages (Fig. 4).

In dorsal view (Fig. 6a–c), the *processus frontalis nasalis* forms an acute prominence on each side of the beak, at the *Os lacrimale* level. These two prominences frame a cranio-caudal elongate fossa at the caudal end of the *processus frontalis nasalis*. These prominences are located at the caudal most end of the exposed culmen (and also the culmen, due to

the tubes extend caudally to this point), and are not present either in juveniles or in the chicks. The juveniles present a suture and a small separation between the *Os lacrimale* and the *Os nasale*. However, the *Os lacrimale* in the juveniles remain weakly attached to the *Os mesethmoidale*. In the chicks, the *Ossa nasali* are separated and dorsal to the *Ossa frontali*, whereas in juveniles and adults, the opposite condition is observed; the *Ossa nasali* are ventral to the *Ossa frontali*.

In all the ontogenetic stages, the cranial end of the *processus frontalis nasalis* has one or two foramina each side, near the *apertura nasi ossea* (Fig. 6a–c). The suture that separates this process from the *processus frontalis premaxillaris* is still visible in the adults, as well as the suture between both *processi frontali premaxillarium*. In the chicks, the suture is visible throughout all the process, and its caudal part remains cartilaginous. The juveniles present an intermediate condition, with this suture stronger than that of the adults. This process is cranially projected on the dorsal surface of the *pila supranasalis* (Fig. 4), in all ontogenetic stages.

The *pila supranasalis* has an acute cranial prominence with a cranial concavity, followed by a convex protuberance in the region of the *corpus ossis premaxillaris*; the whole structure is “S”-shaped. The *corpus ossis premaxillaris* is robust, and ends in a hooked *apex rostri*, laterally covered by the *foramina neurovascularia*. Laterally, in its more ventral border, appears the *processus maxillaris premaxillaris*, which is only distinguished from the most ventral *processus maxillaris nasalis* in the chicks. Nevertheless, in juveniles and adults, the division between both processes (*processus maxillaris premaxillaris* and *processus maxillaris nasalis*) is given by the *sulcus nasi* (a synapomorphy of Procellariidae in Mayr 2004). This sulcus runs along the margin of the *apertura nasalis ossea*, extending further at both ends. In adults and juveniles, the *processi maxillarium premaxillarium* are covered by the *foramina neurovascularia* in all its ventral extension, whereas in the chicks the foramina are more caudally concentrated. Furthermore, the chicks and the juveniles have a sulcus ventral to this foramina and parallel to the *crista tomialis*. The *aperturæ nasi ossea* are oval and open horizontally, in the chicks are proportionally larger than in adults (Table 1).

The *arcus jugalis* of adults (Fig. 7e, f), juveniles (Figs. 3, 4b), and the chicks (Fig. 7g, h) is a bar constituted by three ankylosed elements: the *processus jugalis maxillare*, the *Os jugale* and the *Os quadratojugale*. The caudal end of this arch is more flattened in juveniles and the chicks. The suture between the ventral and caudal *Os quadratojugale* and the dorsal *Os jugale* is visible (Figs. 4b, 7e, g, h), extending more cranially in juveniles and the chicks. The *condylus quadraticus* is very small and hook-shaped.

The *arcus suborbitalis* is absent. The *tuberculum lacrimale* extends toward the *Os lacrimale* and forms the *fenestra*

*antorbitalis* in the adults and juveniles (Figs. 4b, 7f). The *tuberculum lacrimale* is triangular and dorso-medially projected in juveniles and adults, whereas in chicks this expansion is more dorsal and convex.

The *Os Squamosum* (Fig. 5c, d), separated from the *Os parietalis* by a suture only visible in the chicks, is “C”-shaped (with its opened side being cranial). In all the ontogenetic stages, the *processus zygomaticus* is cranially projected, and presents a dorsal notch. This process is larger than the *processus suprameaticus*, which is proportionally smaller in juveniles. The *cotyla quadratica squamosi* is between the *processus zygomaticus* and the *processus suprameaticus*, and contacts caudo-ventrally with the *cotyla quadratica otici*. The septum between them has a notch separating both cotylæ. The *fossa subtemporalis* is not developed since the external border of the *Os squamosum* is convex.

## Comparative description of the splanchnocranium

### Quadrate

In juveniles and adults, the *Os quadratum* is similar and its maximum height is barely longer than its length. In medial view (Fig. 7i, j), the *processus orbitalis* is cranio-dorsally projected with respect to the *processus mandibularis*. In the chicks, this *processus orbitalis* is not ossified, which gives the *Os quadratum* a different shape (Fig. 4c). Both processes are separated by the *crista tympanica*. The medial side (Fig. 7i, j) of the *processus orbitalis* presents a deep fossa, and the *facies tympanica*—the bone in this region—is narrower. Cranially to the *crista tympanica* opens the *foramen pneumaticum* (Fig. 7k, l), which is wider in adults than in juveniles. In both ontogenetic stages, the *processus orbitalis* (Fig. 7i, j) is dorso-cranially extended, with a slight medial inclination. It presents a quadrangular end, with its ventral tip more extended. The *processus mandibularis* is complex and compound by several structures disposed in a triangle; in medial view, only the *condylus pterygoideus* (Fig. 7i–l) can be seen, which articulates with the *Os pterygoideum*. It presents a rounded and convex articular surface, as usual in most of birds (Baumel et al. 1993). In cranial view (Fig. 7k, l), the *condylus lateralis* of the quadratum is laterally projected. It articulates with the *cotyla lateralis* of the mandible and the quadratojugale. The third process that can be seen in the medial view (Fig. 7i, j) is the *processus oticus*, which articulates with the elements of the prootic/opisthotic and squamosal. In caudal view (Fig. 7m, n), the *processus oticus* comprehends two capitula: the *capitulum oticum*, and the larger *capitulum squamosum*. The former is medially projected and is less rounded than the latter. The *incisura*

*intercapitularis* separates both capitula that develops a very pronounced and circular foramen, and in juveniles it presents recessus and foramina inside of it. In juveniles and adults, the *capitulum squamosum* is rounded and more prominent than the *capitulum oticum*, and articulates more laterally with the *Os squamosum*.

The *cotyla quadratojugalis* (Fig. 7m, n) is prominent and laterally expanded in juveniles and adults, whereas the *cotyla cranialis* is absent. The *condylus medialis* (Fig. 7m, n) articulates with the mandible and presents a shallow surface; in a caudo-ventral position (Fig. 7m, n), the *condylus caudalis* develops a small crest and gives support to the *processus postmandibularis* of the mandible.

## Comparative description of mandible

In all the ontogenetic stages, the *pars symphysialis* (Fig. 8a–c) of the *Ossa mandibula* is dorsally rounded, and the symphysis acquires a spoon shape (Fig. 8d, f, g) with a ventral sulcus (Fig. 8h–j). In the laterals of the *pars symphysialis* (Fig. 8a–c), there is a dense *foramina neurovascularia* which corresponds to the *foveae corpusculorum nervosum* for the passage of rhamphothecal keratin (see Warham 1996), which is more dense in the chicks than in juveniles and adults.

The *pars intermedia* of the *ramus mandibulae* presents lateral foramina longitudinally aligned. These foramina form a *canaliculi neurovasculares* in the most caudal part of the *pars intermedia* of the adults (Fig. 8a), whereas in the chicks, they are fused, constituting a sulcus. An intermediate condition with a partial fusion of the foramina appears in juveniles.

There is a subtle difference in the spatial location of the *crista tomialis* in the different ontogenetic stages (Fig. 8d, e, j). In adults, this crista is exactly dorsal to the ventral margin of the mandible, at least in the *pars intermedia* and the *pars symphysialis*; whereas in juveniles and the chicks (Fig. 8j), it is laterally displaced considering the ventral margin of the mandible. The opposite condition appears in the *pars caudalis* of all the ontogenetic stages, where the *crista tomialis* is medially located with respect to the ventral margin of the mandible.

In the *crista tomialis* of the mandible, a weak dorsal suture separates the *Os dentale* from the *Os spleniale*, even in the adults. The *Os prearticulare* is separated from both of them, and remains completely free in juveniles (Fig. 8e, k, l).

The *pars intermedia* extends caudally until the *zona flexoria intramandibularis caudalis*, which is indicated by the *fenestra cranialis mandibulae*, where the *pars caudalis* starts (Fig. 8a–c). The *fenestra caudalis mandibulae* is obliterated in all the ontogenetic stages. In all the adults, with the single exception of MLP-O-14500, the *fenestra*

*cranialis mandibulae* is partially obliterated which means there is a foramen but it does not get through the bone; in the juveniles, the fenestra is completely open, and in the chicks, this area remains cartilaginous. The *angulus mandibulae* is obvious and curved in all the stages. The *ramus mandibulae* (Fig. 8d, e, j) is straight in the chicks, while in adults there is a point of inflection in the most caudal part of the *pars intermedia*, which corresponds to the *angulus mandibulae*. Caudally to this point, the *partes caudalium* become subparallel to each other. Juveniles present an intermediate condition, closer to the chick morphology. At the *pars caudalis* level, the *crista tomialis* is more medially disposed than the ventral border of the mandible.

The suture between the *Os prearticulare* with the *Os dentale* and the *Os spleniale* is extended from the dorsal margin, reaching cranially to the ventral border of the *fenestra cranialis mandibulae*, and ventral to a deep *fossa aditus canalis neurovascularis* (Fig. 8e, k, l).

The *processus coronoideus* (Fig. 8a–c) is small and curved in adults and juveniles, but it is not yet developed in the chicks. In addition, in adults and juveniles, there is another caudal unnamed small process.

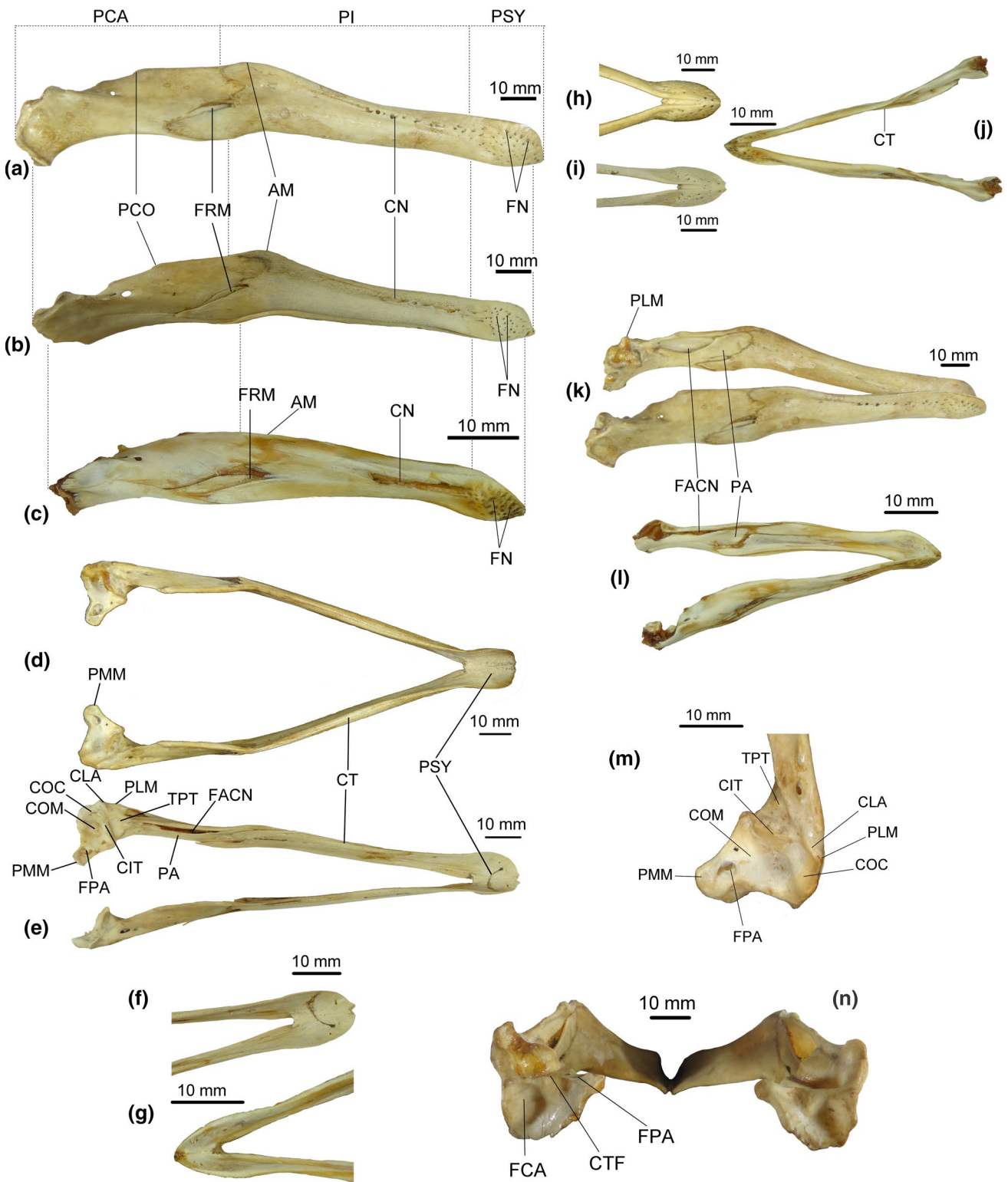
In juveniles and adults, the *processus lateralis mandibulae* (Fig. 8e, k, l) extends medially from the mandible border, through a triangular process. It develops cranio-caudally a crest, followed caudally by a notch, and another process. These areas remain cartilaginous in the chicks.

Cranially to the *processus lateralis mandibulae*, there are two different sized foramina, in all ontogenetic stages (Fig. 8a–c, e, k, l). The *processus retroarticularis* is absent. In dorsal view, the *processus medialis mandibulae* is more prominent than the lateralis (Fig. 8d, e, m), its tip is rounded, and points medially in adults, medio-dorsally in juveniles and dorsally in the chicks. In juveniles and adults, there is a dorsal and large *foramen pneumaticum articulare*, accompanied by a set of recesses and foramina within. A similar structure appears laterally in the chicks.

The *cotylae fossae articulares*, the facets of articulation with the condyli of the *Os quadratum*, are composed by the *cotyla medialis*, *cotyla lateralis*, and *cotyla caudalis*, only ossified in juveniles and adults, in which they present similar structures (Fig. 8e, m).

The *cotyla medialis* is larger and occupy most of the articular area and becomes deeper caudally. It remains separated from the others by the *crista intercotylaris* and a cranial *sulcus intercotylaris*. This crista is strong and well developed, acquiring a triangular shape, with its main axis almost perpendicular to the *ramus mandibulae*. The caudal boundary of this crest is rounded, whereas the cranial end forms a sharp ridge.

The *cotyla lateralis* and the *cotyla caudalis* are merged in a single articular facet, cranio-caudally extended and more dorsally located respect to the *cotyla medialis*.



The *tuberculum pseudotemporale* is strong (Fig. 8e, m), as in others birds with heavy beaks (see Baumel et al. 1993). It is cranial and medially projected in adults and juveniles. Caudally, there is a small foramen in adults.

In juveniles and adults, the *fossa caudalis* is very prominent in caudal view (Fig. 8n), and a dorsal crest divides a small medial fossa from a larger lateral one. The *fossa caudalis* is ventro-laterally directed. Only in juveniles and adults, where the ossification is complete, the *crista*



**Fig. 8** *Ramus mandibulae* of *Macronectes giganteus* in lateral view: (a) adult, (b) juvenile, (c) chick; in dorsal view: (d) adult, (e) juvenile (material was slightly deformed during preparation); *pars symphysialis* in dorsal view: (f) juvenile, (g) chick, in ventral view: (h) adult, (i) juvenile, (j) complete mandible of chick; mandibles in latero-dorsal view: (k) adult, (l) chick; close-up of the articular region of the mandible of an adult: (m) in dorsal view, (n) in caudal view. AM *angulus mandibulae*; CIT *crista intercotylaris*; CLA *cotyla lateralis*; CN *canaliculi neurovasculares*; COC *cotyla caudalis*; COM *cotyla medialis*; CT *crista tomialis*; FACN *fossa aditus canalis neurovascularis*; FN *foramina neurovascularia*; FRM *fenestra cranialis mandibulae*; PCA *pars caudalis*; PCO *processus coronoideus*; PCY *pars symphysialis*; PI *pars intermedia*; CIT *crista intercotylaris*; CLA *cotyla lateralis*; COC *cotyla caudalis*; COM *cotyla medialis*; CT *crista tomialis*; CTF *crista transversa fossae*; FACN *fossa aditus canalis neurovascularis*; FCA *fossa caudalis*; FPA *foramen pneumaticum articulare*; PA *Os prearticulare*; PLM *processus lateralis mandibulae*; PMM *processus medialis mandibulae*; PSY *pars symphysialis*; TPT *tuberculum pseudotemporale*

*transversa fossae* presents a medial notch, lateral to the *foramen pneumaticum articulare*.

## Discussion and conclusions

As expected, there is a progression in the ossification degree and fusion of the skull elements. Only adults present a fusion of all the elements of the braincase with the upper jaw, without visible sutures. In addition, some bones derived from the palatoquadrati and the external arc, like premaxillare and maxillare, are fused to the neurocranium. In contrast, elements of the internal arc (palatinum and pterygoideum) are separated from the neurocranium; the cranial end of the palatinum are fused.

Juveniles, on the other hand, have the elements of the occipital region fused with the *Ossa parietales*, but the *Ossa parietales* and the *Ossa frontali* remain in contact through slightly opened sutures. As seen in adults, juveniles also present a fusion of the elements of *Ossa frontali* with the rest of the cranial elements of the braincase. This cartilaginous zone is reduced in juveniles to the caudal margin of the *Ossa frontali* and the cranial margin of the *Os parietales*. Nevertheless, one of the main differences with adults is that the *Os lacrimale* remains independent from the rest of the bones in juveniles.

Chicks can be characterized by the lack of ossification in many regions of the skull. They preserve the sutures inbetween the elements, and several bones remain as separated pieces of the skull, e.g. the cartilaginous area between the *Ossa parietales* and *Ossa frontali* are widely expanded.

Skull shape, during ontogeny, remains unaltered in general terms. As an exception, the value of the aspect ratio of the foramen magnum (height/width) in adults is always near to 1.00. This indicates a circular section, whereas this value is near to 1.30 in juveniles and denotes a foramen

higher than wider. In addition, a little intra-specific variation involving osteological features was observed, such as the quantity and shape of foramina opening on pneumatic bone surfaces, and the ossification degree of several structures (see descriptions above for details). Variation in size and proportions (Table 1), not attributed to sexual dimorphism, was also detected. For instance, smaller adults (e.g. MLP-O-15049) are even smaller than juveniles (e.g. MLP-O-14898).

The shape of the occipital region changes from triangular in chicks to quadrangular in later ontogeny stages, and the *condylus occipitalis* is cranially displaced in the chicks and later becomes caudal. The *prominentia cerebellaris* remains cartilaginous in the chicks, ossified as a very pronounced structure in juveniles, and decreases in size in adults. The *crista temporalis* becomes straighter in adults.

The *Ossa frontali*, in the cranial roof, decreases in size during ontogeny and becomes triangular. Among *Ossa frontali*, there is a suture in the chicks, which is replaced in juveniles by the *depressio frontalis*. The *Os lacrimale* appears in juveniles, and it fuses with the *Ossa frontali* in adults. In the chicks, the *Ossa nasali* are separated and dorsally located to the *Ossa frontali*, whereas in juveniles and adults the opposite condition is observed, the *Ossa nasali* are ventral to the *Ossa frontali*.

The *fossae glandulae nasalis* is only developed in juveniles and adults, being absent in previous stages. The absence of this structure, that houses the salt gland, would explain why parents select low salt content items for feeding their chicks (Warham 1996). The main proportion of krill in the chicks diet would reduce the costs of osmoregulation, and improve their individual fitness (see Sievert et al. 1990; Warham 1996).

The *fonticulus interorbitalis* is larger in juveniles than in adults, constituted by the fusion of several foramina (i.e. *fonticulus orbitocranialis*, *foramen nervi optici*, and the *foramen orbitonasal*). In juveniles, the wall of *Os mesethmoidale* increases its ossification from juveniles to adults. The *septum nasale osseum* is only present in adults.

The *processi lateralis parasphenoidalis*, poorly developed in the chick, are ventrally extended in the juveniles, and caudally directed in adults. The *lamina parasphenoidalis* is cranially displaced and becomes caudal in juveniles and adults.

In adults and juveniles, the *processi maxillarium premaxillarium* are covered by the *foramina neurovascularia* in all its ventral extension, whereas in the chick the foramina are more caudally concentrated. Furthermore, the chick and the juveniles have a sulcus ventral to these foramina and parallel to the *crista tomialis*. The *aperturae nasi ossea* are oval and open horizontally while in the chicks are proportionally larger than in adults.

As we mentioned, the skull and the mandible present the characteristic grooves of the tubenoses, giving support to the

different plates of the rhamphotheca. The beak and narines acquire their characteristic development and sturdiness from early stages. The *crista tomialis* of the *pars intermedia* and the *pars symphysialis* is exactly dorsal to the ventral margin in adults, while in the juveniles and the chicks it is laterally displaced. The *crista tomialis accesoria* only appears in the adults.

The *ramus mandibulae* is straight in the chick, while in adults there is an inflex point in the most caudal part of the *pars intermedia*. Juveniles present an intermediate condition, closer to the chick morphology. The tip of the *processus medialis mandibulae* points medially in adults, medio-dorsally in juveniles and dorsally in the chick. In most of the adults, the *fenestra cranialis mandibulae* is partially obliterated, whereas in the juveniles is completely open, and in the chick this area remains cartilaginous.

As we indicated above, the acquisition of the adult skull configuration is a gradual process that does not equally affect all the regions at the same time. Ossification and fusion of elements are the general trend along the ontogeny, although a significant variation is observed within each stage.

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## Compliance with ethical standards

**Conflicts of interest** Authors declare no conflicts of interest.

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