

## ORIGINAL ARTICLE

# Comparative morphology and soft tissue histology of the remote-touch bill-tip organ in three ibis species of differing foraging ecology

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**Abstract**

Ibises (order: Pelecaniformes, family: Threskiornithidae) are probe-foraging birds that use 'remote-touch' to locate prey items hidden in opaque substrates. This sensory capability allows them to locate their prey using high-frequency vibrations in the substrate in the absence of other sensory cues. Remote-touch is facilitated by a specialised bill-tip organ, comprising high densities of mechanoreceptors (Herbst corpuscles) embedded in numerous foramina in the beak bones. Each foramen and its associated Herbst corpuscles make up a sensory unit, called a 'sensory pit'. These sensory pits are densely clustered in the distal portion of the beak. Previous research has indicated that interspecific differences in the extent of sensory pitting in the beak bones correlate with aquatic habitat use of ibises, and have been suggested to reflect different levels of remote-touch sensitivity. Our study investigates the interspecific differences in the bone and soft tissue histology of the bill-tip organs of three species of southern African ibises from different habitats (mainly terrestrial to mainly aquatic). We analysed the external pitting pattern on the bones, as well as internal structure of the beak using micro-CT scans and soft tissue histological sections of each species' bill-tip organs. The beaks of all three species contain remote-touch bill-tip organs and are described here in detail. Clear interspecific differences are evident between the species' bill-tip organs, both in terms of bone morphology and soft tissue histology. Glossy Ibises, which forage exclusively in wetter substrates, have a greater extent of pitting but lower numbers of Herbst corpuscles in each pit, while species foraging in drier substrates (Hadedda and Sacred Ibises) have more robust beaks, fewer pits and higher densities of Herbst corpuscles. Our data, together with previously published histological descriptions of the bill-tip organs of other remote-touch foraging bird species, indicate that species foraging in drier habitats have more sensitive bill-tip organs (based on their anatomy). The vibrations produced by prey (e.g., burrowing invertebrates) travel poorly in dry substrates compared with wetter ones (i.e., dry soil vs. mud or water), and thus we hypothesise that a more sensitive bill-tip organ may be required to successfully locate prey in dry substrates. Furthermore, our results indicate that the differences in bill-tip organ anatomy between the species

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reflect complex trade-offs between morphological constraints of beak shape and remote-touch sensitivity requirements, both of which are likely related to each species' foraging behaviour and substrate usage. Our study suggests that structures in the bone of the bill-tip organ could provide valuable osteological correlates for the associated soft tissues, and consequently may provide information on the sensory ecology and habitat usage of the birds in the absence of soft tissues.

#### KEYWORDS

bill-tip organ, ecomorphology, Herbst corpuscles, links between soft tissue and bone morphology, remote-touch, sensory ecology, tactile foraging, Threskiornithidae

## 1 | INTRODUCTION

Probe-foraging birds feed on prey that are either submerged in water or buried in mud/soil, and thus often face the challenge of detecting 'invisible' prey concealed within opaque substrates. Some species (such as oystercatchers, stilts, rails, and ibisbills) use a method of probing reliant on direct tactile contact with prey, usually combined with other sensory cues (visual, auditory, chemical and/or olfactory) to locate prey (Cullen, 1994; Franklin et al., 1979; Hamilton, 1975; Hulscher, 1982; Pierce, 1986; Zembal & Fancher, 1988). Such direct-contact probing requires prey density to be relatively high to be energetically cost effective (Hulscher, 1982). Other species possess a specialised sensory modality known as 'remote-touch'. Remote-touch entails the detection of buried prey at a distance from the beak through perception of high-frequency acceleration components of mechanical vibrations in the substrate (Gottschaldt, 1985). These stimuli result from either the movement of the prey within the substrate, or from changes in pressure gradients in wet granular substrate caused by the birds' repeated probing action around hard-shelled prey items (Gerritsen & Meiboom, 1985; Gottschaldt, 1985; Piersma et al., 1998). Birds that use remote-touch to locate submerged prey often do so in combination with their other senses (Cunningham et al., 2009; Gerritsen & Meiboom, 1985; Van Heezik et al., 1983).

Remote-touch probing appears to have evolved independently in three families of modern birds: ibises (Threskiornithidae), shorebirds (Scolopacidae), and kiwi (Apterygidae) (Cunningham et al., 2007; Cunningham, Castro, et al., 2010b; du Toit et al., 2020; Gerritsen & Meiboom, 1985; Nebel et al., 2005; Piersma et al., 1998). The ability to use remote-touch as a tactile sensibility for foraging in these families has been confirmed in various behavioural assays: *Calidris alba* (Sanderlings, Family: Scolopacidae) were shown to be able to detect prey using the vibrations in the substrate caused by their prey's movement (Gerritsen & Meiboom, 1985). Piersma et al. (1998) showed that *C. canutus* (Red knots) detect stationary hard-bodied prey using changes in pressure gradients in the substrate. The ability to successfully locate moving prey in the absence of all other sensory cues has been shown in Madagascar Crested Ibises (*Lophotibis cristata*) (Cunningham, Castro, et al., 2010b) and in kiwi (Cunningham et al., 2007).

Anatomical studies of the sensory regions of the brains of birds that use remote-touch provide further evidence to support its

importance. Both scolopacid shorebirds and kiwi species possess hypertrophy in the brain regions responsible for the processing of tactile information from the beak (predominantly the principal sensory trigeminal nucleus) compared with other bird species which do not use remote-touch (Cunningham et al., 2013). The same is true for other taxa of birds which use their beaks for different types of specialised tactile foraging or food manipulation, including waterfowl (ducks, geese and allies) and parrots (Cunningham et al., 2013; Martin & Martin, 2021).

Remote-touch is facilitated by a specialised tactile bill-tip organ. This comprises groups of mechanoreceptors (Herbst corpuscles) embedded within densely clustered foramina in the distal regions of both the premaxilla and mandible (Bolze, 1968; Cunningham et al., 2013; Cunningham, Alley, et al., 2010a; du Toit et al., 2020; Gottschaldt, 1985; Nebel et al., 2005). Herbst corpuscles are avian mechanoreceptors which detect changes in acceleration components of mechanical vibrations and detect vibrations that originate from sources that are not in direct contact with the structure they are part of (Gottschaldt, 1985). The clusters of Herbst corpuscles are centred around nerve fibres that run through the foramina into the neurovascular canals of the beak bones, forming branches of the trigeminal nerve (responsible for relaying sensory information from the beak, Barnikol, 1954; Dubbeldam & Karten, 1978). The foramina in the bone and the soft tissues within them are together referred to as 'sensory pits', as the external openings of the foramina on the surface of the beak bones resemble small pits/holes. The bill-tip organ refers to the entire structure of the multiple sensory pits and associated neurovascular tissues in the distal portion of the beak. In the absence of soft tissues, the presence of a tactile bill-tip organ can be inferred from the number and proximity of the sensory pits on the external surfaces of the beak bones, and when combined with the shape of the beak, the function of the organ can also be determined (du Toit et al., 2020).

A potential link between habitat type and interspecific differences in bill-tip organ morphology was proposed by Cunningham, Alley, et al. (2010a), based on differences in the number of pits in the beak bones and the extent (percentage of beak length) of pitting between species of ibises. These differences in bill-tip organ morphology correlate with the birds' habitat usage: birds living in more aquatic habitats have larger bill-tip organs (relative to beak size) and higher numbers of sensory pits on their beak bones. This pattern holds when including

data from kiwi species, which live in drier habitats and have fewer pits in their bill-tip organs compared with ibises. Cunningham (2010) proposed that these differences in the bill-tip organ morphology may be linked to different sensitivities required to detect the vibrations in substrates with different water contents.

If more extensive pitting does correlate with higher sensitivity, the more extensively pitted bill-tip organs of aquatic-foraging species are at odds with the fact that substrates with higher water content transmit vibrations more easily than drier substrates (Biot, 1956, 1962). Cunningham (2010) attempted to address this potential conundrum by hypothesising that there will be more 'noise' in wetter substrates from other sources that needs to be filtered out to detect useful signals coming from prey. However, there is as yet no behavioural evidence that higher extent of pitting correlates with higher sensitivity of the bill-tip organ to vibratory stimuli, and a better anatomical measure of sensitivity would be a comparison of the mechanoreceptor arrangements between species of ibises (Zweers & Gerritsen, 1997).

Ibises and spoonbills form the family Threskiornithidae, which falls within the Pelecaniformes order (Jarvis et al., 2014; Prum et al., 2015). Ibises have long, thin, downcurved bills, which they probe into water, mud and/or soil to extract buried prey items. Ibises occupy various foraging habitats (Ali & Ripley, 1983; Cramp et al., 1983; Hockey et al., 2005; Matheu & del Hoyo, 1992), though most ibis species do tend to forage in wetlands (Ali & Ripley, 1983; Cramp et al., 1983; Hockey et al., 2005; Kushlan, 1977, 1978; Matheu & del Hoyo, 1992). Remote-touch has been experimentally confirmed in ibises (Cunningham, Castro, et al., 2010b; du Toit, 2022), and all studies of ibis beak morphology indicate the presence of remote-touch capable bill-tip organs (Cunningham, Alley, et al., 2010a; du Toit et al., 2020; Swennen & Yu, 2004).

In this study, we investigate whether ibis species foraging in wetter habitats have more sensitive bill-tip organs than those adapted for terrestrial habitats, by assessing whether there is a positive correlation between sensory pitting extent and density of Herbst corpuscles. We compare the soft tissue histology and bone morphology of the bill-tip organs of three southern African ibis species from different habitats: Hadedea Ibis (*Bostrychia hagedash*), African Sacred Ibis (*Threskiornis aethiopicus*) and Glossy Ibis (*Plegadis falcinellus*). We describe the interspecific differences in soft tissue histology of the bill-tip organs with specific reference to the Herbst corpuscle arrangement, as the receptors themselves (not just the foramina in the bones) are likely to be driving the sensitivity of the bill-tip organs (Zweers & Gerritsen, 1997). We discuss the implications of these findings for understanding the foraging ecology of ibises and other remote-touch capable birds.

## 2 | MATERIALS AND METHODS

### 2.1 | Ecology of study species

All three species of ibises (Hadedea, Sacred and Glossy Ibises) use probe-foraging as their primary foraging technique, but differ in their foraging habitats. Hadedea Ibises are mostly terrestrial, though they will also use

wetlands on occasion (Hockey et al., 2005; Skead, 1951). In the past century they have experienced a range expansion in South Africa, now using urban gardens and agricultural land alongside their historical forested habitats (Macdonald et al., 1986), apparently facilitated by artificial irrigation and growing of lawns and pastures (Duckworth et al., 2010). Glossy Ibises forage almost exclusively in or around bodies of fresh water (Frederick & Bildstein, 1992; Hockey et al., 2005; Matheu & del Hoyo, 1992; Taylor & Taylor, 2015). Sacred Ibises are generalist in both their foraging habitat and behaviour: they forage in terrestrial and aquatic habitats (Clergeau & Yésou, 2006; Hockey et al., 2005; Yésou et al., 2017), sometimes foregoing probing to capture large vertebrate prey (e.g., eggs and chicks of other birds Williams & Ward, 2006), and will also feed on carrion (Chane & Balakrishnan, 2016). In recent years, Sacred Ibises have become urban exploiters, feeding on human refuse (Calle & Gawlik, 2011; Clark, 1979; Clergeau & Yésou, 2006; Yésou et al., 2017).

### 2.2 | Specimens used

Skeletal samples of all three species were sourced from natural history museums around the world (museum accession number abbreviations in brackets): Iziko South African Museum, Cape Town (SAM); Smithsonian National Museum of Natural History, Washington, DC (USNM); Natural History Museum at Tring, UK (NHM); University of Cambridge Zoology Museum, UK (UCZM); and Muséum National d'Histoire Naturelle, Paris (MNHN).

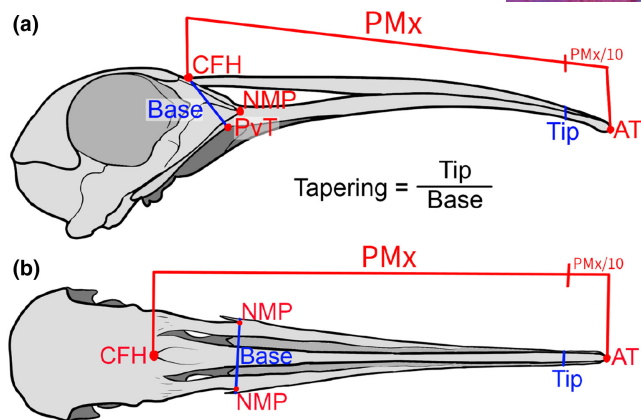
All the samples used for histological sectioning were sourced from recently deceased birds from the Western Cape Province of South Africa. These birds all died for reasons unrelated to this study (either as casualties of vehicle impacts or attacked by domestic animals) and were donated to the project by various wildlife organisations and members of the public.

We sampled six skeletal specimens per species of Glossy and Sacred Ibises, and four Hadedea Ibises (for a list of skeletal specimens used, see Supporting Information, Table S1). For the histological analyses, we sectioned two specimens per species of Glossy and Sacred Ibises, and three specimens of Hadedea Ibises (for a list of specimens sectioned for histology, see Supporting Information, Table S2). Similar numbers per species have been used in various other studies of bird beaks (Crole & Soley, 2014; Cunningham et al., 2007, 2013; Demery et al., 2011; Gottschaldt & Lausmann, 1974; Piersma et al., 1998).

### 2.3 | Measures of pitting pattern from photographs

Each skeletal specimen (using specimens which had the rhamphotheca removed) was photographed using a digital camera (*Canon PowerShot SX620 HS*) and light table. Six images per specimen were analysed: lateral, ventral and dorsal views of both the mandible and maxilla.

Measurements extracted for each specimen were: total number of pits; distance of each pit from the tip of the bill; and bill-tip organ length (measured as the average maximum distance of pits from the distal tip of the bill; used to calculate extent of pitting and density



**FIGURE 1** Drawing of a Hadeda Ibis skull, showing where measurements were taken to calculate the tapering of the beak shape. Tapering was measured as the ratio between the tip depth/width to the base depth/width (depth/width depending on lateral or dorsal view respectively). 'Tip' depth/width measured at a distance (PMx/10) of 1/10th of the total premaxilla length (PMx) from the distal-most tip of the premaxilla (AT). (a) Lateral view showing depth measurements; 'Base' depth measured as lateral distance from the craniofacial hinge (CFH) to the posteroventral tip of the premaxilla (PvT). (b) Dorsal view showing width measurements; 'Base' width measured across left and right symphyses of the nasal bone and maxillary processes [NMP— anatomical position indicated more clearly from lateral view in (a)].

of pits). The premaxilla length was measured from the distal tip to the craniofacial hinge and was used as a standard measure of beak length (see 'PMx' on Figure 1a).

To compare the 'tapering' in beak shape (the change in size between the base and the tip of the beak), we calculated the ratio of tip width to base width and tip depth to base depth of the premaxilla (see Figure 1 for points of measurement; 'width' from dorsal view and 'depth' from lateral view). The two ratios of tapering were calculated separately (i.e., one ratio for width and one for depth) by dividing the tip by the base measurements.

The numbers and distances from the tip of the beak of sensory pits in the bone were measured from the photographs using the software *ImageJ2* (Rueden et al., 2017), following the workflow described by du Toit et al. (2020).

## 2.4 | Three-dimensional imaging of beak bones

We used X-ray micro computed-tomography ( $\mu$ -CT) to image the internal bone structure of the specimens at very high resolutions, following similar methods to Cunningham et al. (2013). Scans were done by the Central Analytical Facilities Lab at Stellenbosch University (Stellenbosch, South Africa) using the *General Electric VTomex L240* (*General Electric Sensing and Inspection Technologies/Phoenix X-ray*, Germany) scanner (du Plessis et al., 2016). Specimens were mounted vertically in the scanning chamber, and the entire beak was scanned, as well as additional scans for the distal most ~5 cm portions of the bill at the higher resolutions. All scans were

taken at resolutions between 7 and 20  $\mu$ m to visualise the pits in the bones at sufficient detail.

The programme *VG Studio* (© 1997-2021 *Volume Graphics*, Germany) was used to compile the voxel data from the CT scans into three dimensional models for analysis. We performed all image capture and analyses with the open-source software *MyVGL* (© 1997-2021 *Volume Graphics*, Germany).

## 2.5 | Histological sectioning, staining, and analyses

Histological sectioning and staining of specimens followed the procedure refined by du Toit et al. (2020): Samples of the distal most ~1 cm of the beaks were fixed in 10% neutral buffered formalin for storage. In order to soften the keratin of the rhamphotheca, commercially available hair removal cream (Van Hemert et al., 2012; *Veet® In shower Hair Removal Cream*) was applied to the surface of the rhamphotheca for 1–3 days (reapplied every ~6 h). The beak samples (mandible and maxilla treated separately) were split sagittally and fixed for a minimum further 48 h in 10% neutral buffered formalin. Samples were then embedded in paraffin blocks using a benchtop tissue processor (*Leica TP1020*, Germany). Kristenson's fluid (18% formic acid buffered with formate, Wallington, 1972) was used to decalcify the bone. To avoid damage to the soft tissues, Kristenson's fluid was only applied to the exposed surface of the sample about to be sectioned, for a maximum of 15 min at a time. Sagittal sections (5–10  $\mu$ m) were made using a rotary microtome (*Leica TP1020*, Germany) (see Figure S1 in the Supporting Information for a diagram showing beaks sectioned). The sections were mounted on charged glass slides, dewaxed in xylene and rehydrated using standard procedures, before being stained using a Masson's trichrome staining kit (*Sigma-Aldrich*). Finally, the stained sections were dehydrated and cleared with xylene, before being mounted in DPX Mountant (*Sigma-Aldrich*) and coverslipped.

The sections were photographed using a compound microscope (*Nikon Eclipse E200*) and attached digital camera (*Canon PowerShot D10*), and the images were captured using *NIS Elements* (*Nikon*). All measurements were taken from the images of the sections using *ImageJ2* (Rueden et al., 2017).

The arrangement and orientation of the Herbst corpuscles in the pits in the bone were described, as well as overall descriptions of the soft tissue structure of the bill-tip organs. Quantitative measurements and counts were taken of the Herbst corpuscles in each specimen, including average width and length of the corpuscles (measured from longitudinal sections of corpuscles where the central nerve axon could be clearly seen), and the number of Herbst corpuscles per sensory pit (counted for all pits visible in the section, then averaged per specimen).

It is quite challenging to successfully section and stain Herbst corpuscles in the sensory pits of the beak. This is due to the delicate nature of the Herbst corpuscles (thin outer membrane enclosing fluid filled sac), the difficulties faced in sectioning beak tissues (due mostly to the differences in density of the tissues

– very thin calcified bone tissue making up the foramina, firm keratinised rhamphotheca, soft dermal layers and delicate receptors and blood vessels); and the harsh chemicals used to soften the bone and stain the tissues. These damaged/lost corpuscles could not be measured, but the deflated corpuscles and characteristic holes left behind in the sections of the sensory pits still allowed us to count where they would have been.

## 2.6 | Statistical analyses and generation of figures

The raw data measurements were compiled in *Microsoft Excel* (2013). All statistical analyses and plotting of data were done using *RStudio* (RStudio Team, 2016). All figures showing photographs of skulls, histological sections and images generated from the  $\mu$ -CT scans were compiled in *Adobe Photoshop* (2004).

All plots were generated using the *R* (R Core Team, 2018) package *ggplot2* (Wickham, 2011). Due to the small sample sizes, we used non-parametric Kruskal–Wallis *H*-tests to assess the statistical significance of differences in pitting numbers and densities on the beak bones between the three species of ibis. Post hoc Wilcoxon signed-rank tests were applied when statistical significance ( $p < 0.05$ ) was found in the Kruskal–Wallis *H*-tests. To plot the *P*-values and significance codes on the figures, we used the *R* packages *ggsignif* (Ahlmann-Eltze, 2019) and *ggpubr* (Kassambara, 2018).

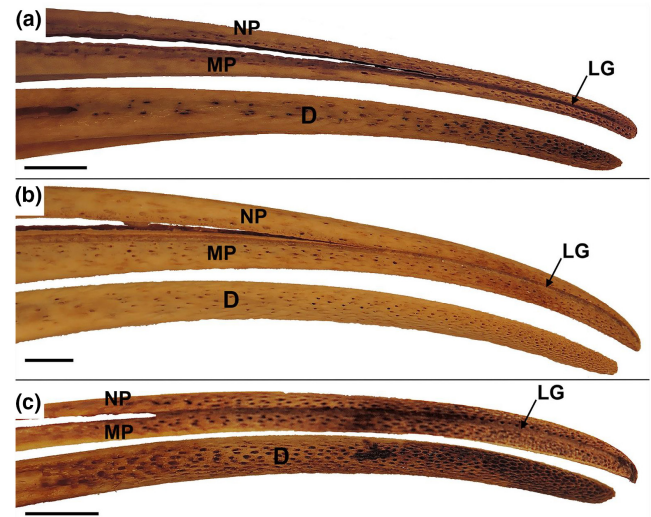
No statistical tests were performed on the data from the CT scans or histological sections, as these all had small sample sizes ( $n = 2/3$  for each ibis species). Such small sample sizes per species are however the norm for these types of morphological descriptions (Avilova et al., 2018; Cunningham et al., 2007, 2013; Cunningham, Alley, et al., 2010a; Gottschaldt & Lausmann, 1974), and were sufficient for the purposes of this study. The 95% confidence intervals shown for the number of Herbst corpuscles per pit for each species were generated from the counts of Herbst corpuscles in each pit.

## 3 | RESULTS

### 3.1 | Beak bone morphology

All three ibis species have similar external (Figure 2) and internal (Figure 3) beak bone structures. The premaxilla is made up of three distinct processes (Figure 2): the nasal process is positioned dorsally along the median of the lower two maxillary processes. The nasolabial grooves along either side of the premaxilla (between the nasal and maxillary processes) create a clear distinction between them (see Figure 2). The distal portion of the mandible is separated into two dentary bones, which are fused in the very distal region of the beak by a thin strip of bone (two dentaries' fused into a synostosis, forming the mandibular symphysis; see the coronal sections in Figure 3a), and then split apart proximally into two rami.

Two large neurovascular canals run alongside each other in the distal portion of the premaxilla, which are fused proximally. This can

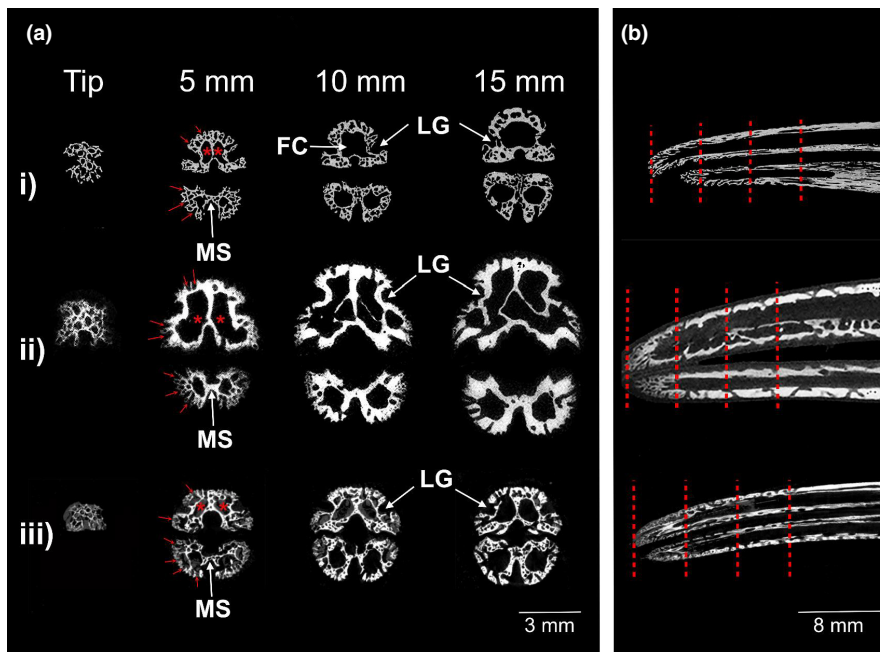


**FIGURE 2** External features on the distal portions of the beak bones of the three species of ibis, showing the external openings of the sensory foramina. (a) Hadedda Ibis (*Bostrychia hagedash*, SAM.ZO 58022); (b) Sacred Ibis (*Threskiornis aethiopicus*, SAM.ZO 57162); (c) Glossy Ibis (*Plegadis falcinellus*, SAM.ZO 58483). Note the distinction between the nasal (NP) and maxillary (MP) processes on the premaxillary bone of all three species. These form distinct units separated by the nasolabial groove (LG) in the bone. (D) dentary bone of the mandible. Scale bars: 5 mm.

be seen in the coronal sections of the beak bones (Figure 3a) and is most clear in the Hadedda Ibises (Figure 3a(i)): at 5 mm from the tip of the beak, the two canals are separate, but are fused by 10 mm [this fusion takes place more proximally in Sacred and Glossy Ibis premaxillae, between 20 and 25 mm from the tip]. The canals are predominantly filled by branches of the trigeminal nerve (the *ramus medialis* in the premaxilla, Crole & Soley, 2016), along with blood vessels supplying the length of the beak. The neurovascular canals in the distal portions of the mandible (containing branches of the *nervus intramandibularis*) remain separate in the two dentary bones.

The sensory foramina of the bill-tip organ open to the external surfaces of the beak bones (forming the 'pit' structures on the surface of the bones—see Figure 2b) and extend through the bone to connect to the central neurovascular canals of the beak (see Figure 3). None of the foramina cross into other processes of the beak from that in which they originate.

The foramina become more densely packed towards the tip of the beak (see Figure 2b). The longest foramina (foramen length measured from the opening on the external surface of the bone to the joining with the central neurovascular canal in the beak bone) are found on the distal surfaces of both the premaxilla and mandible (see first 5 mm of the bones in Figure 3b). The shallowest foramina (and the lowest density of foramina) are found on the inner surfaces of the beak bones (the inside of the birds' beaks; dorsal surface of mandible and ventral surface of premaxilla). Glossy Ibises have the shallowest foramina on average ( $230 \pm 30 \mu\text{m}$ ), followed by Sacred Ibises ( $400 \pm 50 \mu\text{m}$ ), with Hadedda Ibises having the deepest foramina on average ( $580 \pm 110 \mu\text{m}$ ).



**FIGURE 3** Micro-CT sections through bill-tip bones of three ibis species: (i) Hadeda Ibis (*Bostrychia hagedash*); (ii) Sacred Ibis (*Threskiornis aethiopicus*); (iii) Glossy Ibis (*Plegadis falcinellus*). (a) Consecutive coronal sections starting from the tip of the premaxilla, with slices 5 mm apart. Red arrows showing examples of foramina (which form the 'sensory pits'). Red asterisks indicate two branches of the neurovascular canal in distal portions of the premaxilla; these are fused into a single canal in the proximal regions, which can be seen in the Hadeda Ibis ('FC') at 10 mm (fusion occurs more proximally in Sacred and Glossy Ibises). (b) Sagittal sections of the same specimens. Vertical red dashed lines indicate the position of the coronal slices shown in (a). LG: nasolabial grooves; MS: mandibular symphysis.

### 3.2 | Relative beak shape

Whether viewed laterally or dorsally, the beaks of all three species are widest at their bases and taper distally. From a dorsal view, they all have a thin distal beak tip (see Figure 1 for definitions and places of measurement), ranging from 3.7 to 5.9 mm on average for each species (see Table 1). The degree of tapering (the difference in size between the base and tip of the beak) is unequal between the three species: Hadeda Ibises have the greatest degree of tapering in beak depth (from a lateral view), with the base of their beaks measuring almost seven times thicker than the distal tip (Figure 4a). Glossy Ibises have the least amount of lateral tapering, with their premaxilla bases being less than three times thicker than their tips, meaning that their beaks stay relatively thin across their entire length (Figure 4a). The same pattern emerges when measuring the tapering in beak width for all three species (from dorsal view, see Figure S2 in the Supporting Information). Furthermore, Glossy Ibises have the thinnest beak bases from both views (average depth of 9.5 mm, compared with 17.2 mm and 20.0 mm for Sacred and Hadeda Ibises respectively—see Table 1 for more details).

### 3.3 | Soft tissue histology

All three species have sensory pits extending outwards in all directions from the central neurovascular canals of their beaks, all of which contain multiple Herbst corpuscles (Figure 5). All the foramina

sectioned in the distal-most ~1 cm of the beak comprise sensory pits (identifiable by the central nerve fibre surrounded by Herbst corpuscles – further details below). Most of the sensory pits appear to be longitudinally sectioned in the sagittal sections of the bill-tips (see Figures S3–S5 in the Supporting Information for large sections of each species), though some lateral cross sections can be observed (see examples of lateral cross-sectioned pits in Figure 6G).

In the large sections of the ibises' premaxillae (Figures S3 and S5), the different processes of the beak bones (nasal and maxillary processes; see Figure 2b) are associated with distinct units in the soft tissues as well: the premaxilla is bisected by infolding of the rhamphotheca into the nasolabial grooves, with no nerves or blood vessels found in these grooves (see Figure S5). This arrangement of bone and rhamphotheca creates separate partitioning in the beak, confining the sensory pits to certain areas as they do not extend through the infoldings of the rhamphotheca or into other processes of the bone—see Figure 6I for an enlarged view of this region.

Each sensory pit has a nerve fibre running through it, which connects to the central nerve branches in the neurovascular canals of the beak bones (see multiple examples in Figure 6). This nerve fibre is surrounded by numerous Herbst corpuscles. Some adjacent sensory pits merge before joining the central neurovascular canal (see Figure 6D), though the majority remain separate across their entire length. Sensory pits (or occasional pairs of pits) are separated from each other by thin walls of bone, keeping each pit a distinct unit.

The Herbst corpuscles appear to be arranged to maximise their number in each sensory pit, depending on the amount of space.

**TABLE 1** Summary of various beak measurements for three species of ibis. Values are quoted as means. All width and depth measurements were taken from the premaxillary bone. 'Width' measured from dorsal view, 'Depth' from lateral view (see Figure 1). Species labels: 'Hadeda' = *Bostrychia hagedash*; 'Sacred' = *Threskiornis aethiopicus*; 'Glossy' = *Plegadis falcinellus*.  $n$  = number of specimens (could not count sensory pits on all due to preservation condition of some specimens)

Species	$n$ (total)	$n$ (used to count pits)	Bill length (mm)	Bill-tip width (mm) <sup>a</sup>	Base width (mm)	Tip/base width ratio	Bill-tip depth (mm) <sup>a</sup>	Base depth (mm)	Tip/base depth ratio	Total number of pits	Bill-tip organ length (mm) <sup>b</sup>	Percent bill length pitted	Pit density (pits/mm)
Hadeda	4	4	141.5	3.7	21.5	0.17	3.0	20.0	0.15	2206	33.6	23.61	68.3
Sacred	6	5	157.6	5.9	20.6	0.29	4.9	17.2	0.29	3155	63.5	40.54	49.4
Glossy	6	4	121.7	4.6	14.1	0.33	3.3	9.5	0.35	4354	63.3	52.43	68.3

<sup>a</sup>Measured at distance 1/10th of the total premaxilla length from the distal tip of the beak (see Figure 1).

<sup>b</sup>The maximum distance of sensory pits from the distal tip of the bill (average for all surfaces of premaxilla and mandible).

Thus, the highest numbers of Herbst corpuscles are found in the longest/largest sensory pits (predominantly those on the distal surfaces of the beak—see Figure 6A–C). The lowest numbers of Herbst corpuscles per pit are found on the interior surfaces of the beaks, as these are the shallowest pits (see Figure 6E,F).

Each Herbst corpuscle is made up of a central nerve axon (see Figure 7), which is surrounded by specialised Schwann cells (arranged along either side of the nerve axon, together making up the 'inner core' of the corpuscle). The nerve axon of each corpuscle connects to the central nerve fibre of the sensory pit, while the terminal end of the axon forms a round protrusion. The inner core is enclosed by an outer capsule, and between them lies an interconnected matrix of lamellae.

The orientation of the Herbst corpuscles is not consistent across the entire beak, but they are usually oriented in the same direction within each sensory pit (see Figure 6C,E,H). Where Herbst corpuscles in the same pit appear in different orientations, it is often because some of the foramina do not follow a straight line, but bend/curve to reach the external beak surfaces (for examples, see Figure 6A,B,D), though this is not always the case (Figure 6G).

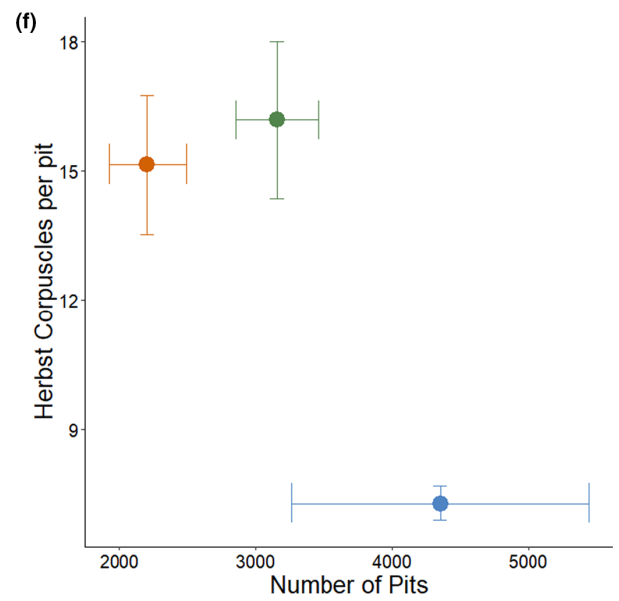
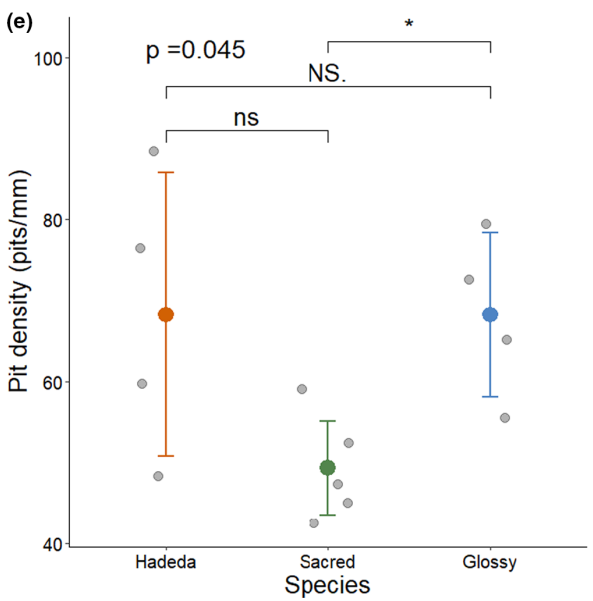
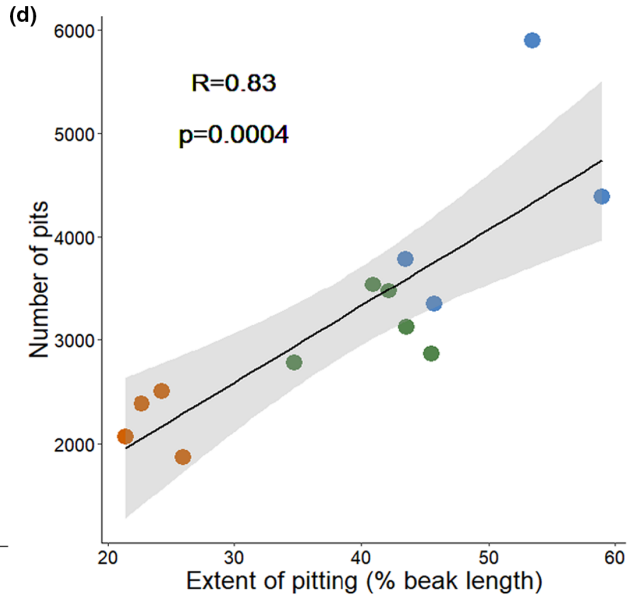
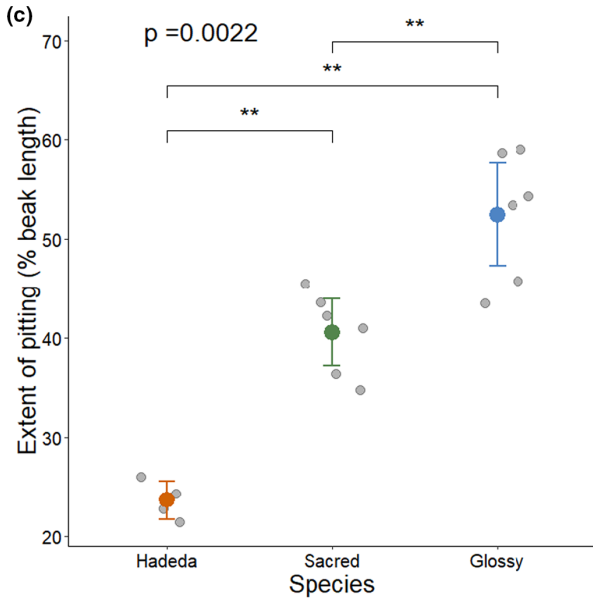
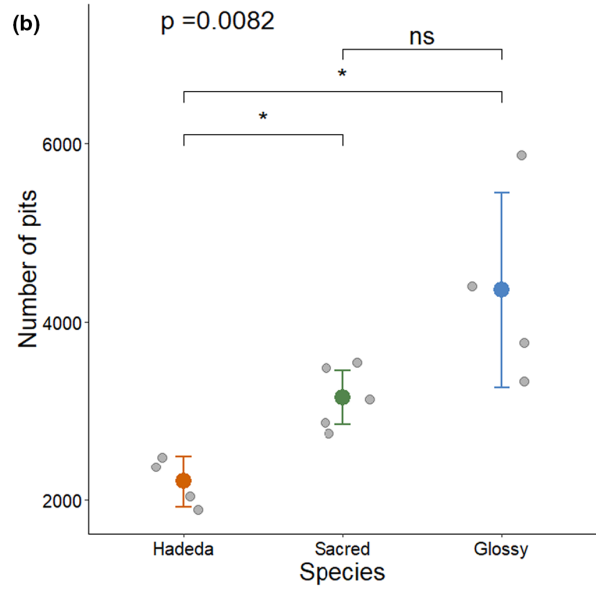
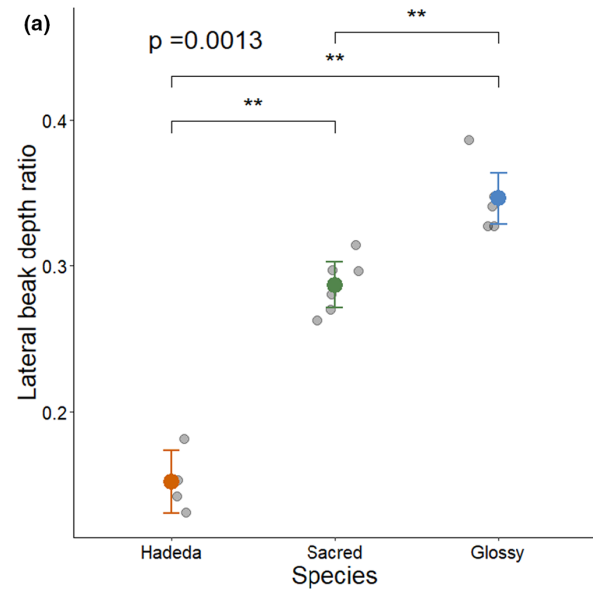
The size of the Herbst corpuscles do not differ greatly between the three species (see Table 2); however, Hadeda Ibises have slightly smaller Herbst corpuscles than Sacred Ibises (in both length and width, see Table 2).

### 3.4 | Distribution of sensory pits and Herbst corpuscles

All three species of ibis have a mean of >2000 sensory pits in their bill-tip organs (see Table 1). Hadeda Ibises have significantly lower numbers of pits ( $2206 \pm 285$  pits) than the other two species (Figure 4b). There was no significant difference in the total number of pits between Sacred and Glossy Ibises ( $3155 \pm 302$  pits &  $4354 \pm 1092$  pits respectively; see Table 1 and Figure 4b). There are statistically significant differences between all three species when looking at the percentage of the beak length pitted (Figure 4c): Hadeda Ibises have the smallest percentage of beak length pitted ( $23.61 \pm 1.95\%$ ), Sacred Ibises have an intermediate extent of pitting ( $40.54 \pm 3.37\%$ ), and Glossy Ibises have the highest pitting extent ( $52.43 \pm 5.19\%$ ). There is a strong significant positive correlation between the extent of pitting and the total number of pits across all three species ( $R = 0.83$ ; Figure 4d).

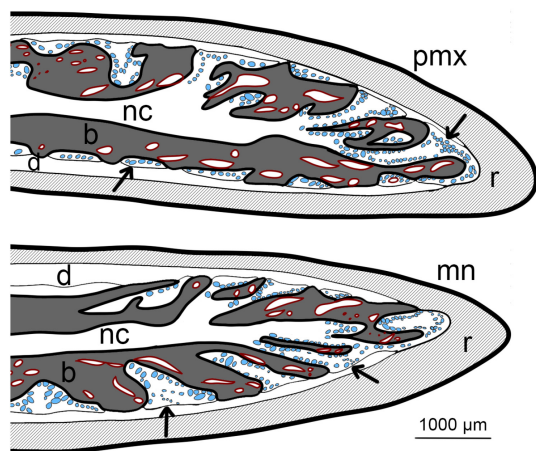
Sacred Ibises have significantly lower pitting densities ( $49.4 \pm 5.8$  pits/mm, measured by the total number of pits divided by the bill-tip organ length) than Glossy Ibises ( $68.3 \pm 10.1$  pits/mm)—see Figure 4e. Hadeda Ibises have pitting densities that are not significantly different from the other two species ( $68.3 \pm 17.4$  pits/mm).

Each species of ibis represents a different morphospace in terms of the relationship between average numbers of sensory pits and the average number of Herbst corpuscles per pit (see Table 2 and Figure 4f). Sacred Ibises have high numbers of both pits and Herbst corpuscles (HC) per pit ( $16.2 \pm 1.8$  HC/pit); Hadeda Ibises have low numbers of pits but high numbers of Herbst corpuscles per pit ( $15.1 \pm 1.6$  HC/pit);





**FIGURE 4** Interspecific differences in beak bone and bill-tip organ morphology between three species of ibises. (a) Ratio of premaxillary bone tip-to-base depth, showing relative amount of distal tapering in beak depth. See [Figure 1](#) for the location of measurements, and [Figure S2](#) (Supporting Information) for dorsal (width) tapering (same pattern as for lateral depth). (b) Total number of sensory pits on the surfaces of the beak bones. (c) Extent of the bill-tip organ as a percentage of beak length. (d) Correlation between the extent of pitting and the total number of sensory pits on the beak bones. (e) Density of sensory pits in the bill-tip organ (total number of pits divided by bill-tip organ length). (f) Morphospace of the remote-touch bill-tip organs of each species represented by the total number of pits on the beak bones vs average number of Herbst corpuscles within each pit (based on counts from histological sections). (a–c, e, f): Small grey circles represent individual specimens. Large coloured circles show mean value for species, coloured brackets showing 95% confidence intervals. In (d), coloured circles represent data from individual specimens, black line showing regression and grey shaded region the 95% confidence interval. Correlation coefficient and significance in (d) calculated using Pearson method. Quoted *p*-values (a–c, e) from non-parametric Kruskal–Wallis tests; significance codes between species from post hoc paired Wilcoxon tests: \* =  $p < 0.05$ ; \*\* =  $p < 0.01$ ; ns =  $p > 0.05$  (no significant difference). ALL: Species labels & colour key: 'Hadededa' = *Bostrychia hagedash* (orange); 'Sacred' = *Threskiornis aethiopicus* (green); 'Glossy' = *Plegadis falcinellus* (blue). See [Tables 1](#) and [2](#) for details.



**FIGURE 5** Sketch of mid-sagittal section of the distal tip of the beak of an ibis showing the gross internal anatomy of the bill-tip organ and location of Herbst corpuscles [based on histological sections of Sacred Ibises, *Threskiornis aethiopicus* (see Supporting Information, [Figure S4](#) for the actual plates, as well as [Figures S3](#) and [S5](#) for sections of the other two ibis species)]. Blue circles represent Herbst corpuscles, located within sensory pits (several examples of individual sensory pits are indicated by arrows on the sketch) in the bones (b) of the beak. The neurovascular canals (nc) within the beak bones contain large branches of the trigeminal nerve [*ramus medialis* in the premaxilla (pmx) and *nervus intramandibularis* in the mandible (mn)]. Blood vessels are shown in red outlines. d, dermis; r, rhamphotheca.

Glossy Ibises have high numbers of pits but low numbers of Herbst corpuscles per pit ( $7.3 \pm 0.4$  HC/pit). As the same region of the beak is compared for all three species, these numbers can be used to compare the species, but do not represent the actual values of each species as it was not possible to count the Herbst corpuscles in 3D space.

## 4 | DISCUSSION

### 4.1 | Remote-touch bill-tip organs

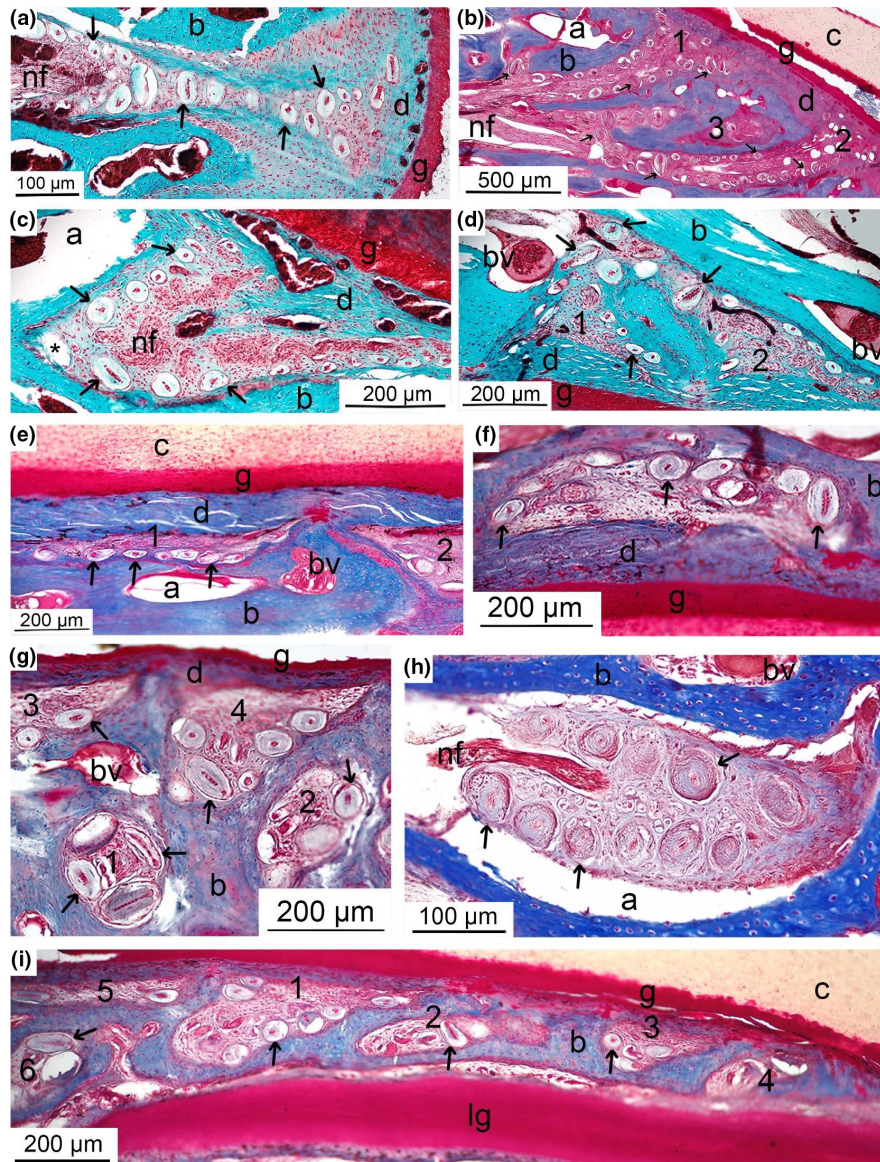
All three ibis species show similar beak bone structure and soft tissue arrangement to other ibises and remote-touch probe-foraging birds (Bolze, 1968; Cunningham et al., 2013; Cunningham, Alley,

et al., 2010a; Gottschaldt, 1985; Nebel et al., 2005). The beaks of all three species have high numbers of foramina densely packed together in the distal regions of their beak bones, typical of the remote-touch bill-tip organ (du Toit et al., 2020). These foramina contain clusters of Herbst corpuscles, which as a unit (the foramen, nerves and mechanoreceptors) form the characteristic remote-touch 'sensory pit'. The structure of the Herbst corpuscles is consistent with those found in the bill-tip organs of other species of ibises and scolopacid shorebirds (Bolze, 1968; Cunningham, Alley, et al., 2010a; Gottschaldt, 1985; Nebel et al., 2005). It is therefore highly likely that all three species use remote-touch to locate prey while probe-foraging (confirmed experimentally for Hadededa Ibises, du Toit, 2022).

### 4.2 | Interspecific differences in pitting on the beak bones and their relation to the arrangement of Herbst corpuscles, remote-touch sensitivity and foraging habitat

Consistent with the patterns found by Cunningham, Alley, et al. (2010a) in their study of eleven ibis species, the pattern of increased numbers of foramina and a greater extent of the beak length pitted in more aquatic-dwelling ibis species is reflected in the species sampled in our study: Hadededa Ibises, which use the most terrestrial habitats, have the lowest numbers and extent of pitting on their beak bones of the three species; Glossy Ibises, which use mainly aquatic habitats, have the highest numbers and extent of pitting; and Sacred Ibises, which are generalists in their habitat usage, show intermediate numbers and extent of pitting (habitat usage data from Clergeau & Yésou, 2006; du Toit, 2022; Frederick & Bildstein, 1992; Hockey et al., 2005; Matheu & del Hoyo, 1992; Shead, 1951; Taylor & Taylor, 2015; Yésou et al., 2017). Cunningham, Alley, et al. (2010a) sampled the beaks of two additional specimens of Glossy Ibises, and their results are consistent with those of our study (when accounting for discrepancies in total pit counts, likely due to advances in digital photograph resolution in the 10 years between the studies).

Cunningham, Alley, et al. (2010a) also found a positive correlation between sensory pit density and use of more aquatic habitats in ibises, but in our study pitting density (pits/mm beak

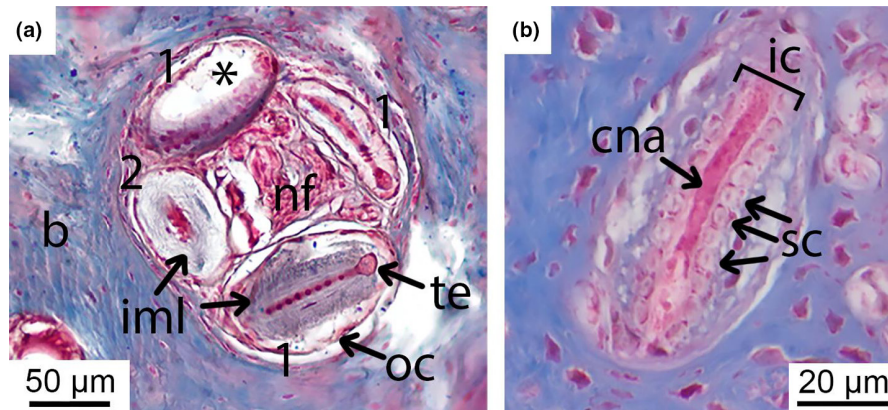


**FIGURE 6** Cross sections of various sensory pits from the bill-tip organs of three species of ibises showing the arrangement, orientation and number of Herbst corpuscles (we have not indicated all that are visible to avoid cluttering the figure, but several examples of Herbst corpuscles are indicated in each plate by small arrows) and other soft tissues within the pits. Where more than one sensory pit is shown in a plate, each pit has been numbered. Pits on the external surfaces of the beak (A–C) are longer and contain higher numbers of Herbst corpuscles than pits found on the internal surfaces of the beak (E, F) on average. The longest pits are found on the distal-most surfaces of the beak (A, B). D: two adjacent pits on the internal surface of the beak: note the fusion of the two pits before they connect to the central neurovascular canal. G: a section of the external portion of the premaxilla, showing multiple adjacent pits in various different orientations (i.e., pits 1 and 2 have been cross sectioned, while 3 and 4 have been longitudinally sectioned. Pit 1 can be seen at a higher magnification in [Figure 7a](#)). H: proximal (in relation to the central neurovascular canal of the mandible) portion of a sensory pit in the mandible, showing how some foramina curve along their length. I: pits in the section of the premaxilla bisected by the nasolabial groove (lg) of the rhamphotheca [which is made up of cornified (c) and germinative (g) layers]. a: sectioning artefact; b: bone; bv: blood vessel; d: dermis; nf: nerve fibre within sensory pits. Asterisk (C) indicates a hole left behind where a section of a Herbst corpuscle fell out during staining. Masson's trichrome stains used. A,C,D,H: Hadeda ibis (*Bostrychia hagedash*). B,E: Sacred ibis (*Threskiornis aethiopicus*). F,G,I: Glossy ibis (*Plegadis falcinellus*). For exact positioning of the pits on the beaks refer to Figures S3–S5 in the Supporting Information.

length) did not correlate with the number of pits or aquatic habitat usage in the three species sampled. Therefore, the extent of pitting and number of pits in the bill-tip organ are probably better osteological correlates than pitting density for estimating

aquatic habitat usage in ibises, as the former trends were supported in both studies.

Remote-touch sensitivity may be affected by interspecific differences in bill-tip organ morphology, as hypothesised by



**FIGURE 7** Sections of Herbst corpuscles within sensory pits of the bill-tip organs of ibises showing the structural organisation of the mechanoreceptors (all from sagittal sections of the distal portions of the bill-tip organ; see Figure 6 for lower magnifications). (A) cross section of a sensory pit in the bone (b) of the beak from a Glossy ibis (*Plegadis falcinellus*), containing four Herbst corpuscles, which have different orientations within the pit (1 = sectioned longitudinally; 2 = cross sectioned). (B) a single Herbst corpuscle (longitudinal section) from the beak of a Hadeda ibis (*Bostrychia hagedash*). The Herbst corpuscles are made up of a central nerve axon (cna), which connects to the nerve fibre (nf) of the sensory pit, and the terminal end (te) of the axon forms a round/bulbous head. The central nerve axons are enclosed by a sheath of specialised Schwann cells (sc), making up the inner core (ic) of the corpuscle. The central nerve axons can be seen as dark purple spots alongside the axon in A. The inner core is surrounded by and connected to an interconnected matrix of lamellae (iml), and the entire corpuscle is surrounded by an outer capsule (oc). The asterisk in A indicates a Herbst corpuscle which has 'ruptured' (iml separated from the oc) as an artefact of the sectioning and staining procedures. Masson's trichrome stains used.

**TABLE 2** Dimensions and counts of the Herbst corpuscles and sensory foramina for the distal portions of the bill-tip organs in three ibis species. Values are quoted as mean  $\pm$  standard error. Species labels: 'Hadeda' = *Bostrychia hagedash*; 'Sacred' = *Threskiornis aethiopicus*; 'Glossy' = *Plegadis falcinellus*

Species	Foramina length <sup>a</sup>	n (number of foramina measured)	Number of Herbst corpuscles per pit <sup>b</sup>	n (number of pits counted)	Herbst corpuscle <sup>b</sup>		n (number of corpuscles measured)
					Length	Width	
Hadeda	580 $\pm$ 110 $\mu$ m	50	15.1 $\pm$ 1.6	42	79.0 $\pm$ 8.6 $\mu$ m	48.2 $\pm$ 4.0 $\mu$ m	13
Sacred	400 $\pm$ 50 $\mu$ m	90	16.2 $\pm$ 1.8	52	111.5 $\pm$ 7.7 $\mu$ m	62.6 $\pm$ 4.9 $\mu$ m	25
Glossy	230 $\pm$ 30 $\mu$ m	53	7.3 $\pm$ 0.4	98	94.1 $\pm$ 8.6 $\mu$ m	46.8 $\pm$ 6.2 $\mu$ m	8

<sup>a</sup>Measured as the distance from the opening on the surface of the bone to the opening into the central neurovascular canal (measured from micro-CT scans of the distal most ~5 cm of beak).

<sup>b</sup>Counted/measured from the sagittal histological sections of the distal most ~10mm of the beak.

Cunningham (2010). Zweers and Gerritsen (1997) determined that the only way remote-touch probing species can increase their sensitivity to vibratory cues is to increase the numbers of Herbst corpuscles within each sensory pit. If so, our results suggest that Hadeda and Sacred Ibises have more sensitive bill-tip organs than Glossy Ibises, consistent with the poorer transmission of mechanical vibrations in the drier substrates in which Hadeda and Sacred ibises forage (Biot, 1956, 1962). Another anatomical feature of the bill-tip organ that could affect remote-touch sensitivity is the actual sensitivity thresholds of individual Herbst corpuscles to different intensities of stimuli (Zweers & Gerritsen, 1997), which are specific to each corpuscle (Gottschaldt, 1985). However, there is as yet no way of determining this without isolating whole corpuscles and testing their response thresholds to stimuli. There may also be other anatomical factors which increase the sensitivity of bill-tip organs as a whole, but these have not been described or studied yet.

### 4.3 | Tradeoffs and constraints on bill-tip organ morphology

Overall beak shape may constrain the maximum number of Herbst corpuscles per sensory pit in our three study species. All probe-foraging birds have long, thin beaks to minimise resistance while probing (Zweers & Gerritsen, 1997). This beak shape restricts the bill-tip organ's total surface area: the beak tip of a probe-foraging bird cannot expand into a wide disk shape (as seen in spoonbills), as this would prevent birds from probing their beaks into anything except water. Thus, remote-touch probing birds face a trade-off between maximising the surface area for the bill-tip organ while maintaining the narrow bill profile to reduce the energetic cost of probing (Zweers & Gerritsen, 1997). Furthermore, the size and shape of the foramina in the bone are confined by overall beak shape—i.e., species with wider beaks and thicker beak bones (e.g., Sacred and Hadeda Ibises) can and do have longer

foramina (which span the width of the bone from the external surface to the central neurovascular canal). The length of the foramina in turn appears to limit the maximum numbers of Herbst corpuscles per sensory pit: the species with the shallowest foramina (e.g., Glossy Ibises) have the lowest average numbers of Herbst corpuscles per pit.

By comparing the three species, we hypothesise that each has faced unique trade-offs in environmental constraints that may have shaped their bill-tip organ structure. Glossy Ibises do not forage in dry soils (du Toit, 2022; Taylor & Taylor, 2015). This is likely due in part to their very narrow beak shape, which would be prone to damage when probing in compacted substrates (Westergaard, 2013). However, their narrow beak profiles are ideal for reducing the energetic cost of probing (Zweers & Gerritsen, 1997). Furthermore, as soft, wet substrates generally allow birds to probe deeply (Cunningham et al., 2007; du Toit, 2022; Kelsey & Hassall, 1989), aquatic foraging ibises like Glossy Ibises may benefit from a high extent of pitting, as this would increase the surface area of their bill-tip organ in contact with the substrate when probing deeply (Zweers & Gerritsen, 1997). The narrow beak shape of Glossy Ibises also means that the foramina in the beak bones are constrained to be shallow, and therefore have space to include relatively low numbers of Herbst corpuscles. These low numbers of Herbst corpuscles per sensory pit in Glossy Ibis beaks may mean that they do not possess the required sensitivity to detect vibrations in drier substrates. Thus, Glossy Ibises appear to have faced an evolutionary tradeoff between bill-tip organ sensitivity and a more streamlined beak shape. They may be able to 'afford' this, as high remote-touch sensitivity may not be required in very wet substrates, due to the improved transmission of vibratory signals (Biot, 1956, 1962).

Conversely, species such as Hadedda Ibises that probe in relatively dry, hard substrates (Hockey et al., 2005) face different constraints: The need for a sturdy proximal region of the beak when probing in such substrates has been described and documented in various studies (Barbosa & Moreno, 1999; Bock, 1966; Zweers et al., 1994; Zweers & Berge, 1996; Zweers & Gerritsen, 1997). The greatest strain from probing in harder substrates is conferred to the proximal regions of the beak, resulting in selective pressure for this region to be wider and have denser bone (Bock, 1966; Zweers & Gerritsen, 1997), the latter of which would be compromised by a high degree of pitting on the proximal regions of their beaks. Consequently, species such as Hadedda Ibises might be constrained to have bill-tip organs limited to the tip of the beak bones only. This could place them at an overall disadvantage when foraging in wetter substrates, as their extent of bill-tip organ pitting is relatively low—i.e., even when they are able to probe their beak more deeply (in more penetrable substrates) they would not increase the contact between the substrate and the sensitive areas of their beaks, as the latter is restricted to the most distal region. Hadedda Ibises appear to have evolved a sturdy beak and potentially more sensitive (as evidenced by their high densities of Herbst corpuscles), though smaller, bill-tip organ.

Sacred Ibises (and potentially other generalist species) seem to have forgone specialising their beaks for a particular substrate type,

in keeping with their generalist foraging habits (Hockey et al., 2005; Yésou et al., 2017): they have high densities of Herbst corpuscles (likely advantageous for foraging in drier substrates), as well as a large extent of pitting (likely useful when probing in softer, wetter substrates). Sacred ibises' beak shape is intermediate between the other two studied species, lacking either the 'sturdy' base required for probing in the hardest of substrates (apparent in Hadedda Ibises) or the narrow 'energy-efficient' profile seen in Glossy Ibises (which would restrict Sacred Ibises' Herbst corpuscle densities, and likely in turn their ability to detect prey in drier substrates).

Determining whether these patterns apply across probe-foraging species with remote touch bill-tip organs would require study of the histology of the bill-tip organs of a larger sample of species. However, the three ibis species studied here represent a spectrum of foraging habitat usage, making them a good pilot group. Our results provide evidence that studying the internal sensory anatomy of the beaks in comparison with their gross morphology may yield important information on the evolution of different foraging strategies and habitat usage in ibises and other remote-touch probe-foraging birds.

#### 4.4 | Morphological patterns in comparison with other remote-touch probing birds

Several of the trends described in our sample group are consistent with patterns in the morphology and histology of other species with remote-touch sensitive bill-tip organs.

For example, spoonbills (members of the Threskiornithidae family and nested within the Old World ibises, Chesser et al., 2010) forage almost exclusively in water and, like other ibises, have a bill-tip organ (Swennen & Yu, 2004). As they do not probe-forage, they are not constrained to a narrow beak shape as the other ibises are, and instead have a characteristic disc-shaped expansion of their beak tip. This significantly increases the surface area of their bill-tip organs (Swennen & Yu, 2004). Like Glossy Ibises, they have high numbers of foramina which are densely packed together (see du Toit et al., 2020), further indicating that this arrangement is best suited for foraging in saturated substrates. Based on the trends in ibises, we would expect spoonbills have relatively low numbers of Herbst corpuscles per sensory pit (similar to Glossy Ibises). They appear to have a highly modified bill-tip organ (du Toit et al., 2020; Swennen & Yu, 2004), potentially representing a further specialisation within the groups of remote-touch capable birds. Histological examination of their bill-tip organs and behavioural experiments assessing their tactile sensory capability are thus warranted.

Kiwi follow the trend shown in ibises in terms of the relationship between their bill-tip organ bone morphology and habitat usage (Cunningham, Alley, et al., 2010a). With reference to our study sample, kiwi have relatively high numbers of Herbst corpuscles per pit, and similar foramen size and pitting extent to Hadedda Ibises (Cunningham et al., 2007, 2013; du Toit et al., 2020). This further reinforces that this type of bill-tip organ morphology is suitable for remote-touch foraging in drier substrates, and that this has evolved

convergently between ibises and kiwi. Furthermore, kiwi possess a 'sensory pad'—a bulged protuberance at the tip of the premaxilla—which Cunningham et al. (2007) hypothesised the birds use to provide general assessment of prey availability and for locomotive guidance (Cunningham & Castro, 2011). None of the ibises sampled possess this sensory pad on their premaxilla, though Hadede Ibises did show slight overlapping of the premaxilla over the tip of the mandible (best seen in the CT scans), which could suggest that this overlap or bulge of the premaxilla may assist birds (such as Hadede Ibises and kiwi) which probe in drier substrates.

The shorebirds (family: Scolopacidae) show a lot of interspecific variation in their bill-tip organ morphology. They tend to have lower numbers of sensory pits compared with the ibises (Cunningham, 2010; du Toit et al., 2020). However, they have mixed extents and densities of pitting and numbers of Herbst corpuscles per pit (Bolze, 1968; du Toit et al., 2020). Of the three families of extant birds which make use of remote-touch, they are the most diverse (91 species of scolopacids, compared with 35 species of ibises and five species of kiwi; Clements et al., 2019). Most scolopacid species forage close to bodies of water, though the types of substrates they utilise are varied (Gerritsen & Van Heezik, 1984). Some species also make use of novel foraging techniques, such as surface tension feeding on biofilms (Elnor et al., 2005; Pohle et al., 2007), which may also affect their use of remote-touch. To determine whether scolopacid shorebirds follow similar ecomorphological trends as those described in ibises and kiwi, future research would need to look at detailed interspecific differences in substrate usage of shorebirds in relation to their bill-tip organ morphology.

## 5 | CONCLUSIONS

All three species of ibises sampled possess the beak morphology indicative of remote-touch bill-tip organs. In combination with data from the literature on their foraging behaviour (Clergeau & Yésou, 2006; du Toit, 2022; Frederick & Bildstein, 1992; Hockey et al., 2005; Matheu & del Hoyo, 1992; Skead, 1951; Taylor & Taylor, 2015; Yésou et al., 2017), we conclude that all three species are able to use remote-touch. By comparing the number of Herbst corpuscles per sensory pit in the ibises' bill-tip organs, our preliminary findings suggest that species of ibises foraging in more terrestrial habitats may have more sensitive bill-tip organs than those foraging predominantly in wetter environments. The main anatomical factor that seems to be limiting the number of Herbst corpuscles per pit is the length of the sensory pits themselves, which in turn is limited by the overall shape of the beak. Thus, the interspecific differences in the morphology of the bill-tip organ in our three species appears to have been driven by trade-offs between sensitivity and durability, both of which can be linked to the type of substrates and habitats in which the species predominantly forage. This is supported through comparison with previously published studies on other taxa of remote-touch

foraging birds. Our data reaffirm the positive correlation between the number of pits and extent of pitting in the bone and the use of more aquatic habitats for foraging in ibises. Thus, we support the previous suggestion (Cunningham, Alley, et al., 2010a) that these measures are suitable proxies for studying the foraging habitat of various extinct and extant species of remote-touch probing birds. Furthermore, our results suggest that the length of the neurovascular foramina in the bone are a good osteological correlate for the density of Herbst corpuscles in the remote-touch bill-tip organ, and consequently could also serve as a correlate for bill-tip organ sensitivity in the absence of soft tissues. Further studies of this correlation in more species and how it affects remote-touch sensitivity are thus greatly warranted.

## AUTHOR CONTRIBUTIONS

C.J.d.T. took the photographs of the specimens; collected the data on bone morphology; prepared and analysed the soft tissue histology sections; analysed the CT scan data; performed all statistical analyses; designed the figures and wrote the manuscript draft. C.J.d.T. and S.J.C. developed the methodology for measuring the structures on the external surfaces of the beak bones. S.J.C. and A.C. provided supervision and advice in the data collection and analyses. All authors were involved in the editing of the manuscript.

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## CONFLICT OF INTEREST

The authors declare that they have no conflict of interests.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on the University of Cape Town's open access digital repository, ZivaHub (powered by Figshare): <https://doi.org/10.25375/uct.20411640>.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

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