BILL MORPHOLOGY OF IBISES SUGGESTS A REMOTE-TACTILE SENSORY SYSTEM FOR PREY DETECTION

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Abstract.—Birds that forage by probing must often use senses other than vision to find their prey. Remote touch is a sense based on the interception of vibrations produced by moving prey in the substrate or on the evaluation of pressure patterns produced by hard-shelled sessile prey. In probing birds, this system is mediated by an organ made up of clusters of mechanoreceptors housed within pits in the bone of the bill-tips. This bill-tip organ was first described in probing shorebirds (Scolopacidae), and more recently in kiwi (Apterygidae). Here, we describe this bill-tip organ in a third family of probing birds, the ibises (Threskiornithidae). We examined the bill morphology of 11 species of ibis from 8 genera. We found bill-tip organs in species in a wide range of habitat types, from predominantly terrestrial to predominantly aquatic, which suggests that ibises may use remote touch when foraging both in water and in granular substrates. Our data imply a link between bill-tip morphology and habitat use—a pattern that we believe warrants further investigation. *Received 10 March 2009, accepted 17 September 2009.*

Key words: Apterygidae, habitat use, Herbst corpuscles, remote touch, Scolopacidae, sensory pits, Threskiornithidae.

La Morfología del Pico de los Ibises Sugiere un Sistema Sensorial Táctil Remoto para la Detección de las Presas

Resumen.—Las aves que forrajean por sondeo deben usualmente usar otros sentidos fuera de la visión para encontrar sus presas. El tacto remoto es un sentido basado en la intercepción de vibraciones producidas mediante el movimiento de las presas en el sustrato o en la evaluación de patrones de presión producidos por presas sésiles de concha dura. En las aves que sondean sus presas, este sistema está mediado por un órgano formado por conjuntos de mecano-receptores albergados en el interior de huecos en el hueso de la punta del pico. Este órgano en la punta del pico fue descripto por primera vez en las aves playeras que sondean sus presas (Scolopacidae), y más recientemente en el kiwi (Apterygidae). Aquí, describimos este órgano de la punta del pico en una tercera familia de aves sondeadoras, los ibises (Threskiornithidae). Examinamos la morfología del pico de 11 especies de ibis correspondientes a 8 géneros. Encontramos los órganos de la punta del pico en especies de un amplio rango de tipos de hábitat, desde predominantemente terrestres a predominantemente acuáticas, lo que sugiere que los ibises pueden usar el tacto remoto cuando forrajean en el agua y en sustratos granulosos. Nuestros datos insinúan un vínculo entre la morfología de la punta del pico y el uso de hábitat—un patrón que creemos que amerita investigaciones adicionales.

Birds that forage by probing exist in many habitats and in a diversity of families (e.g., Scolopacidae, Threskiornithidae, and Apterygidae). Most possess long, sometimes down-curved bills that facilitate probe-foraging. Although tracks, burrows, and substrate disturbance may visually indicate the location of some prey items, probing birds must often rely on nonvisual sensory systems to locate their food.

Sandpipers in the genus *Calidris* (Charadriiformes: Scolopacidae) locate their prey by using chemosensory systems such as taste and perhaps olfaction (Gerritsen et al. 1983, Van Heezik et al. 1983), through chance location (directly touching prey), and by using a specialized sensory system called "remote touch" (Gerritsen and Meiboom 1986, Piersma et al. 1998). Remote touch is mediated by an organ composed of numerous pits in the bone of the bill-tips that are packed with two types of mechanoreceptors, Herbst corpuscles and terminal cell receptors (Bolze 1968, Zweers and Gerritsen 1997, Piersma et al. 1998, Nebel et al. 2005). The physical properties of Herbst corpuscles make them the more likely of the

two to be involved in remote touch (Zweers and Gerritsen 1997). Herbst corpuscles detect seismic signals from invertebrates burrowing through the substrate and pressure disturbances caused by sessile prey at some distance from the bill-tip (Gerritsen and Meiboom 1986, Piersma et al. 1998) and thus allow a probing shorebird to locate prey more efficiently than by direct touch. In some cases, remote touch may allow the bird to quickly assess prey density in an area and, thus, the profitability of foraging there (Gerritsen and Meiboom 1986). A shorebird-like bill-tip organ has recently been described in kiwi (Apterygiformes: Apterygidae), a family of nocturnal probing birds from forest habitats in New Zealand (Cunningham et al. 2007), which suggests that the faculty of remote touch may be shared by other groups of probing birds.

Ibises (Ciconiiformes: Threskiornithidae, subfamily Threskiornithinae) are a cosmopolitan family of probing birds. Ibis species use many habitats, ranging from lakes and wetlands through bogs, fens, and marshes to forests, dry shrub, and grasslands (Matheu and del Hoyo 1992). Their long down-curved bill enables them to forage for invertebrates and small vertebrates by probing and sweeping in lagoons and estuarine mud, in grasslands, in leaf litter and soil, and in cracks in dry ground (e.g., Skead 1951, Keith et al. 1974, Kushlan 1978, Dzerzhinsky 1998). Ibises are usually described as "tactile" hunters (e.g., Kushlan 1978). Therefore, some foraging studies have assumed that ibises detect prey only by direct contact with the bill-tips and that the time involved in chasing prey once it has been discovered is therefore negligible (e.g., Kushlan 1979).

Spoonbills (Ciconiiformes: Threskiornithidae, subfamily Plataleanae), the closest relatives of the ibis group, are distinguished by their dorso-ventrally flattened, spatulate bill. They are exclusively aquatic feeders that forage by sweeping their bill from side to side in shallow water (Matheu and del Hoyo 1992). The bill of the Black-faced Spoonbill (*Platalea minor*) was studied in detail by Swennen and Yu (2004), who discovered that both the upper and the lower jaws were densely covered with pits similar to, though arranged differently from, those found in the bills of Scolopacidae. Although histological evidence is lacking, they suggested that the pits would likely house Herbst corpuscles, as found in shorebird bills (Swennen and Yu 2004). Swennen and Yu (2005) observed that the Black-faced Spoonbill kept its bill spoon in the water during pursuit of prey and that sudden pecks were sometimes made at prey beyond the bill-tip. These observations suggest that the bill-tip organ of the Black-faced Spoonbill is functional for remote touch (Swennen and Yu 2005). Dzerzhinksy (1998) mentioned the presence of sensory pits in the bill of the White Ibis but presented no histological examination of the bill for mechanoreceptors.

We examined the bill-tip morphology of ibises in eight genera for bony pits that might indicate the presence of a bill-tip organ similar to that found in shorebirds (see Table 1 for scientific names of species examined). The bill-tip of the Australian White Ibis was examined histologically to verify whether the pits contained mechanoreceptors and to confirm that ibis species possess such a bill-tip organ. We investigated species with habitat types ranging from predominantly terrestrial to mainly aquatic. For exploratory purposes, we examined the data on ibis bill morphology in relation to habitat use and included data from four species of kiwi, a terrestrial probing bird, for comparison. We discuss the implications of a remote touch sense in the Threskiornithidae and

hypothesize that there may be links between habitat use and bill morphology in this group.

Methods

Morphology.—We examined 28 ibis skeletal specimens representing 11 species in 8 genera (*Threskiornis*, *Geronticus*, *Plegadis*, *Lophotibis*, *Eudocimus*, *Phimosus*, *Theristicus*, and *Bostrychia*) at Te Papa Tongarewa–Museum of New Zealand, Auckland War Memorial Museum, San Diego Natural History Museum, and the American Museum of Natural History. We noted the presence of sensory pits in the bill and, using Kincrome Vernier calipers, measured bill length (upper bill, measured from the naso-frontal hinge), skull length (measured from the bill-tip to the back of the skull), the dorsal and lateral extent of pitting in the upper bill, and the lateral and ventral extent of pitting in the lower bill of each specimen. We photographed the upper and lower bills of each specimen from the dorsal, ventral, lateral left, and lateral right views, taking care to include the entire area of sensory pitting in each photograph. For practical reasons, where photograph and specimen quality allowed, the number of sensory pits in the bill-tip was estimated by counting those visible in the photographs. Femur length (maximum) and tarsometatarsus width (minimum) were also measured as a gauge of the size of each individual.

Bill-tip organ measurements.—We measured four aspects of the bill-tip organ: (1) the absolute length of the bill-tip organ (mm), calculated by averaging the extent of pitting on the dorsal, ventral, and lateral sides of the bill (measured from the bill-tip to the most caudal sensory pit on each side); (2) the percentage of bill length occupied by the bill-tip organ (calculated by dividing bill-tip organ length, as measured above, by the total length of the bill $\times$ 100); (3) the total number of sensory pits present on all surfaces (dorsal, lateral, and ventral) of both the upper and lower bills and the number of sensory pits on the outside surfaces of the bill only (dorsal and lateral surface of the upper bill, ventral and lateral surfaces of the lower bill); and (4) the average density of pits per millimeter of bill-tip organ length, calculated by dividing the number of sensory pits on the outside surfaces of the bill by the absolute length of the bill-tip organ.

Histology.—Fresh tissues were obtained from a single juvenile Australian White Ibis (permit WT2008-2289, Australian Government Department of the Environment, Water, Heritage and the Arts) that was euthanized for reasons unrelated to this project. The head and bill were fixed immediately after death in 10% buffered formalin. The bill-tip was then trimmed into six pieces: the first 14 mm of both the upper and lower bill-tips were split medially for sectioning on the saggital plane, and a 2-mm-thick trimming was made from the cut ends of both the upper and lower bill for sectioning coronally. The keratin rhamphotheca was softened following Luna's (1968) method, and trimmed sections were decalcified using neutral EDTA (Bancroft and Stevens 1982), routinely processed, embedded in paraffin, sectioned at 3 μm, and stained with haematoxylin and eosin (Luna 1968). A single 5-μm section from the saggital plane and another from the coronal plane were stained with a silver stain (Sevier and Munger 1965) to target nervous tissue.

We measured width, depth, and angle with respect to the bill-tip, and number of sensory pits, width, length, area, and numbers of Herbst corpuscles from digital photomicrographs of silver-stained sections. All measurements were made using the

TABLE 1. Summary of ibis species sampled, including sample sizes, habitat index, average bill and leg measurements, and sensory-pit counts. Figures presented are averages where n > 1.

Species	n (total)	n (used to count sensory pits)	Habitat index	Bill length (mm)	Bill-tip width (mm)	Bill-tip depth (mm)	Femur length (mm)	Upper jaw			Lower jaw			Percent bill length pitted	Pit density (pits mm^{-1})	Total number of pits
								Number of pits on outer surface	Number of pits on inner surface	Total	Number of pits on outer surface	Number of pits on inner surface	Total			
Wattled Ibis (*Bostrychia carunculata*)	3	2	1.33	130.91	2.76	3.09	71.35	134.0	72.0	206.0	222.5	41.0	263.5	9.84	27.7	469.5
White Ibis (*Eudocimus albus*)	4	2	3.80	141.61	4.60	4.75	61.98	774.0	46.5	820.5	658.5	74.0	732.5	34.11	29.7	1,553.0
Scarlet Ibis (*E. ruber*)	6	2	3.80	146.72	4.74	4.51	58.53	635.0	17.5	652.5	639.5	25.5	665.0	28.84	30.1	1,317.5
Northern Bald Ibis (*Geronticus eremita*)	2	0	1.00	131.15	2.80	3.68	62.60	Rhamphotheca present						—	—	—
Madagascar Crested Ibis (*Lophotibis cristata*)	1	1	1.63	128.88	3.07	3.25	71.52	398.0	31.0	429.0	270.0	34.0	304.0	19.56	26.5	733.0
Bare-faced Ibis (*Phimosus infuscatus*)	1	0	3.5	109.96	2.36	2.28	50.34	—	—	—	—	—	—	12.64	—	—
White-faced Ibis (*Plegadis chihi*)	4	3	3.5	114.21	4.49	4.44	57.99	1,157.0	161.3	1,318.3	916.3	167.7	1,084.0	36.04	50.4	2,402.3
Glossy Ibis (*P. falcinellus*)	2	2	4.33	116.80	4.41	4.61	57.83	1,026.5	167.0	1,193.5	928.5	176.5	1,105.0	37.19	45.0	2,298.5
Buff-necked Ibis (*Theristicus caudatus*)	3	3	1.75	147.71	3.10	3.43	67.35	161.7	77.7	239.3	122.3	32.5	154.8	8.39	22.9	394.2
Black-faced Ibis (*T. melanopis*)	1	1	1.00	153.63	2.55	2.11	71.71	129.0	81.0	210.0	Lower jaw missing			9.50	8.8	—
Australian White Ibis (*Threskiornis molucca*)	1	1	2.60	151.82	4.10	3.60	73.62	528.0	80.0	608.0	286.0	115.0	401.0	22.85	23.5	1,009.0
Average/total *n*	28	17	2.57	133.94	3.54	3.61	64.07	549.2	81.6	630.8	505.5	83.3	588.7	21.90	29.4	1,272.1

IMAGEJ (National Institutes of Health 2008) digital image analysis system and are given as means ± SD below.

Habitat data.—BirdLife International Data Zone online species data sheets (BirdLife International 2008) summarize information on the types and relative importance of habitats used by avian species. We used this information to create an index of habitat use for each of our 11 ibis species, to facilitate exploratory comparisons between habitat use and bill morphology. The index was calculated by combining information on habitat type (*H*) and the relative importance of each habitat (*U*) for all species. Habitat types were ranked from "wettest" to "driest" and then assigned a score from 1 to 5 according to their rank (higher scores indicated more "aquatic" habitats). Habitat rankings were decided on the basis of subjective assumptions about the presence of surface water and the relative dampness of the ground in different habitat types (e.g., lagoons were ranked as "wetter" habitats than pasture). Where it was not obvious that one habitat should be ranked as more or less aquatic than another (e.g., grasslands and pasture), habitats were assigned identical scores. The scale is a rough estimate for purposes of data exploration rather than an exact measurement of water saturation across habitats. Habitats are categorized in the BirdLife International Data Zone data sheets as being of critical, major, minor, insignificant, or unknown importance to each species. We assigned a weighting value to each category, from 4 for critical habitats to 1 for insignificant and unknown habitats. A weighting value of 1 was also assigned where the importance of a habitat was not stated ("unset"), to ensure that the habitat was represented within the species' final score while being conservative about its importance. Data on habitat types used by each species, weighted by their importance, were converted to a habitat use index (HI) using the formula HI = $\Sigma(HU) / \Sigma(U)$, where increasing values of HI are equivalent to increasingly aquatic habitat use.

Data on percent of bill pitted and number of pits in the bill-tip organs of four kiwi species—North Island Brown Kiwi (*Apteryx mantelli*), Tokoeka (*A. australis*), Great Spotted Kiwi (*A. haasti*), and Little Spotted Kiwi (*A. owenii*)—were obtained from a paper on kiwi bill morphology (Cunningham et al. 2007). The HI was calculated for these species using the method described above. These data were added to the ibis data to provide a comparison with unrelated terrestrial probe-foraging species.

Morphological variables for ibises and kiwi were plotted against the HI to explore the possibility of differences in morphology related to habitat use. The strength of potential relationships between HI and bill morphology for ibises alone and together with kiwi was investigated using Spearman's rank correlations (r_s).

RESULTS

Bill morphology.—Sensory pits were found in the bill-tips of all ibis species investigated, except for Northern Bald Ibis. We were unable to examine the bills of the two specimens of the latter species because the keratin rhamphotheca was still present. The oval-to-polygonal sensory pits were found on all bill surfaces, including the inside of the tips. Pits on the outer bill surfaces were concentrated toward the tips, forming a "honeycomb" of closely packed pits similar to that seen in the Apterygidae and in many species of Scolopacidae. There were two distinct types of sensory-pit distribution on the inner surfaces of the bill. In the majority of species, pits were found around the outside edges of both jaws, separated from a deep central groove by an area of transverse ribbing of the bone. In the genera *Theristicus* and *Bostrychia*, pits were more evenly distributed at the inner tip of the upper jaw and were not separated by a central groove until several millimeters caudal to the tips (Fig. 1). We counted sensory pits in 17 of 28 individuals
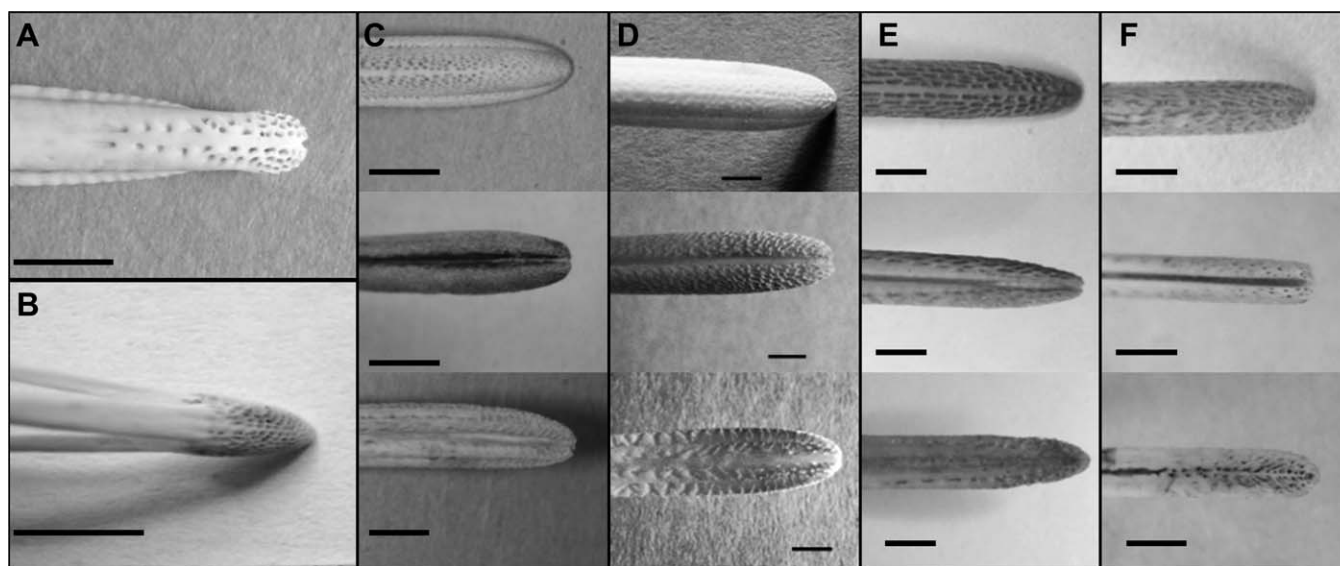

FIG. 1. (C–F) Sensory pits in the bills of four ibis species (top to bottom: dorsal tip of premaxilla, ventral tip of mandible, ventral tip of premaxilla), with dorsal views of (A) North Island Brown Kiwi and (B) Sanderling (*Calidris alba*) bills for comparison. (C) White-faced Ibis, (D) Australian White Ibis, (E) Madagascar Crested Ibis, and (F) Buff-necked Ibis. Scale bars = ~5 mm. (Photographs by S. Cunningham and T. Jensen; © (A) and (D) Te Papa Tongarewa—Museum of New Zealand).

(9 of 11 species). In all 9 species, the highest numbers of sensory pits were on the outer surfaces of the bill (Table 1). In most species, the ventral surface of the lower jaw was divided longitudinally by a deep groove (Fig. 1, central row of pictures), whereas the upper jaw carried a longitudinal, lateral groove on either side.

Histology: Australian White Ibis.—Coronal and saggital sections of both upper and lower bill tips of the Australian White Ibis showed sensory pits packed with Herbst corpuscles. Corpuscles were sectioned on various angles and varied in size from 44×33 µm to 312×134 µm (average: $118 \pm 43 \times 78 \pm 29$ µm; $n = 417$ corpuscles). Silver stains confirmed the presence of nerve axons within the centers of each Herbst corpuscle, nerve bundles within the centers of the sensory pits, and thick nerve branches running the length of both upper and lower bills.

Coronal section, upper bill.—The upper bill measured 4.04 mm deep $\times$ 6.76 mm wide at 14 mm caudal from the bill-tip. It carried deep 1.31 mm medial lateral grooves on each side. Two large nerve bundles, presumably branches of the trigeminal nerve, were encased within the bone of the premaxilla, adjacent to the groove on either side. Nerve bundles measured approximately 914×393 µm in diameter on the left side and 824×399 µm on the right side. Several sensory pits were visible on the dorsal and lateral sides of the bill in cross section. The ventral surface of the upper bill was corrugated with ridges and grooves. A single sensory pit was visible in the ventral surface of the premaxillary bone on either side. The sensory pits measured, on average, 376 ± 212 µm deep and 335 ± 56 µm wide. Between 1 and 15 Herbst corpuscles were visible within each pit in cross section (average: 3.6 ± 3.6, $n = 14$ pits; Fig. 2A).

Coronal section, lower bill.—The lower bill measured 3.44 mm deep $\times$ 5.83 mm wide at 14 mm caudal from the bill-tip. It carried a deep 1.67 mm medial longitudinal groove in the lower surface. Two large nerve bundles, presumably parts of the mandibular branch of the trigeminal nerve, were encased within the center of the bone on each side of this groove and flanked by large blood vessels. Nerve bundles measured approximately 674×620 µm in cross section on the left side and 779×709 µm on the right side at 14 mm caudal from the bill-tip. Several sensory pits were visible on the ventral and lateral sides of the bill. A single sensory pit was visible at the extreme outer edge of the dorsal surface of the mandible on each side, beneath a deep groove in the keratin layer. Pits measured, on average, 481 ± 181 µm deep from the surface of the bone to the base of the pit and 280 ± 61 µm wide at the bone surface ($n = 11$ pits). Between 1 and 12 Herbst corpuscles were visible within each pit in cross section (average: 5.3 ± 4.0, $n = 11$ pits; Fig. 2B).

Saggital section, lower bill.—Numerous sensory pits were visible in a medial saggital section of the first 14 mm of the lower bill-tip. Nine pits opened to the ventral surface of the mandibular bone, and partial sections of three more were visible beneath these. Sensory pits were angled toward the tip of the bill at an average of $130.8 \pm 26.1°$ in relation to the outer ventral surface of the beak. Pits were widest at the bone surface, narrowing with depth. Some appeared to open into horizontal chambers beneath the bone surface (e.g., Fig. 3A). Pit depth increased with proximity to the bill-tip ($r_s = 0.62$, $P = 0.033$, $n = 12$), and the number of Herbst corpuscles visible per pit increased with pit depth ($r_s = 0.74$, $P = 0.006$, $n = 12$), resulting in an increasing number of Herbst
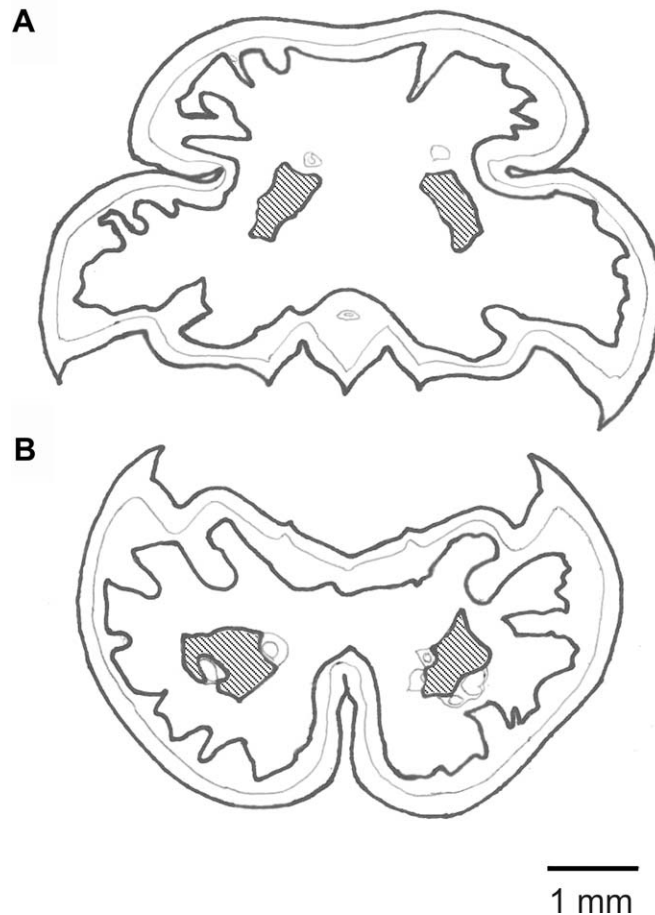

FIG. 2. Diagram of coronal sections through (A) the upper and (B) the lower jaws of the Australian White Ibis, ~14 mm from the bill-tip. Bold lines indicate the outer surface of the keratin layer and the outlines of the premaxillary and mandibular bones (which appear ragged because of the presence of numerous sensory pits). Fine lines indicate the junction between the dermal and keratin layers and the outlines of larger blood vessels. Hatched areas represent cross sections through the major nerves, which are present in both upper and lower bills.

corpuscles per pit toward the tip of the bill (average sensory pit width at bone surface: $1,074 \pm 340$ µm, depth: $1,152 \pm 946$ µm; average number of Herbst corpuscles visible per pit: 18 ± 12).

The majority of Herbst corpuscles in the lower jaw were embedded within sensory pits, though a few small corpuscles were visible in the dermal layer between the bone and keratin of the bill, and a row of Herbst corpuscles was visibly associated with the ventral side of the large nerve dorsal to the main body of the mandible bone. A large, distinct cluster of 14 Herbst corpuscles was also present in the dermis at the extreme tip of the bill, not associated with any sensory pits (Fig. 3B). Herbst corpuscles within the sensory pits measured, on average, 121 ± 43 µm long $\times 81 \pm 26$ µm wide (area: $8,500 \pm 5,478$ µm²), whereas those along the dorsal nerve measured 114 ± 25 µm $\times 62 \pm 8$ µm (area: $5,259 \pm 1,586$ µm²) and those in the bill-tip cluster measured 77 ± 17 µm $\times 41 \pm 6$ µm (area: $2,589 \pm 795$ µm²).
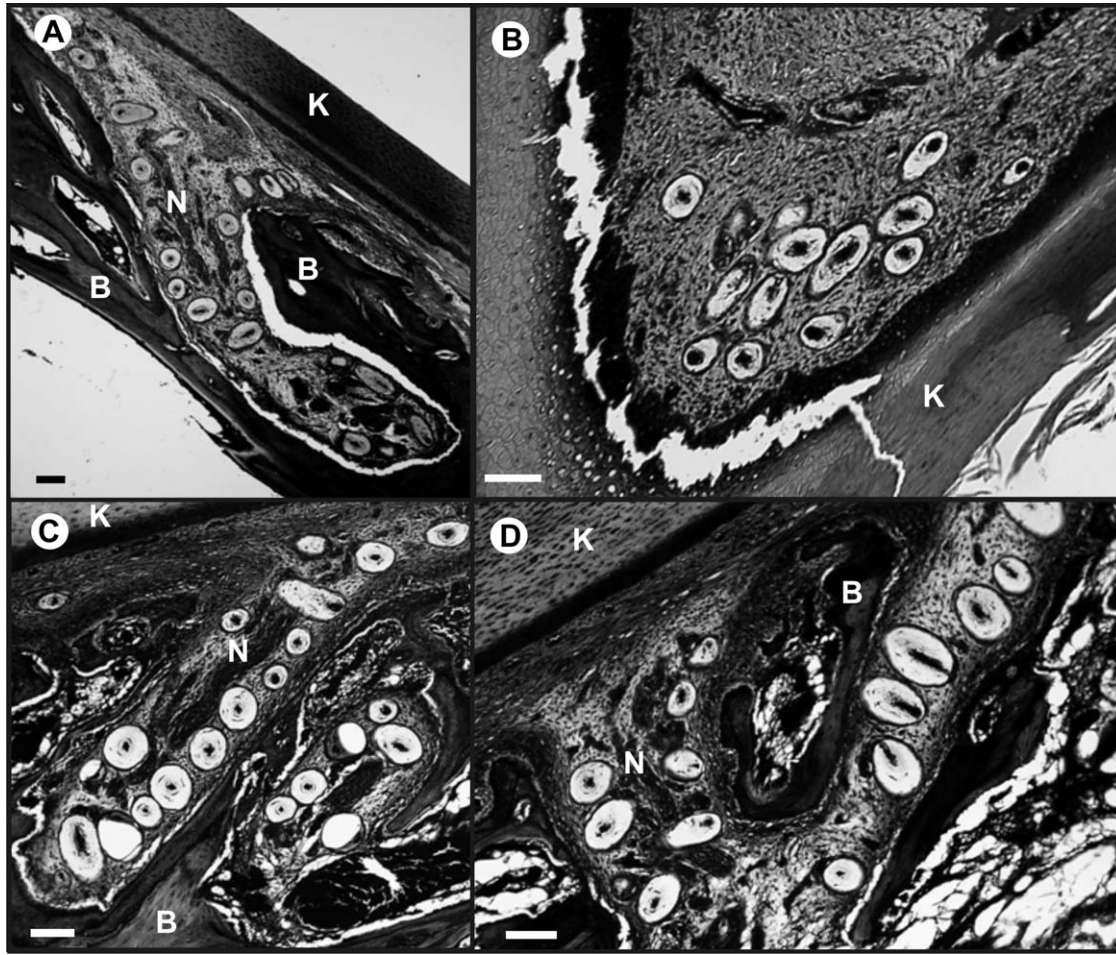
FIG. 3. Location of Herbst corpuscles and types of sensory pits within the Australian White Ibis bill. (A) A sloping sensory pit in the mandible, containing numerous pale, ovoid Herbst corpuscles of varying sizes with agyrrophilic central axons, opens to a horizontal chamber under the bone surface. (B) A cluster of irregularly shaped Herbst corpuscles within the dermis at the very tip of the mandible, not associated with a sensory pit. (C) Two adjacent sensory pits in the premaxilla, showing numerous Herbst corpuscles along the sides of the pits and strands of nervous tissue in the center. (D) Two adjacent sensory pits in the premaxilla joined at the base to form a "double" pit. Large, pale ovoid Herbst corpuscles are obvious within both pits. Slides are silver-stained. K = outer keratin layer, B = bone, N = nervous tissue. Scale bars = ~100 µm.

Saggital section, upper bill.—Ten sensory pits were visible along the dorsal side of the premaxillary bone, in a medial saggital section of the first 14 mm of the upper jaw. Two of these pits branched near the base, forming a "double" pit (Fig. 3C, D). These sensory pits, like those in the lower jaw, were angled forward toward the bill-tip at an average of $138 \pm 7°$ in relation to the outer dorsal surface of the beak. Two narrow and deep ($1,666 \pm 39$ µm deep $\times 836 \pm 54$ µm wide) sensory pits were visible at the apex of the bill-tip, and a partial section of a third apical sensory pit was present proximal to these. Five sensory pits were present in the ventral surface of the premaxillary bone, also opening forward toward the bill-tip with an average angle of $129 \pm 24°$. As in the lower jaw, sensory pits were widest at the opening and narrowed toward the base, but no increase in depth of sensory pits toward the tip of the upper bill was observed, apart from the very deep pits in the tip of the beak ($r_s = -0.09$, $P = 0.803$, $n = 10$). Sensory pits on the dorsal side of the bill were generally deeper and narrower than those on the ventral side (dorsal pits: $1,015 \pm 406$ µm deep $\times 946 \pm 256$ µm wide; ventral pits: 859 ± 733 µm deep $\times 1,297 \pm 788$ µm wide).

The majority of Herbst corpuscles in the upper jaw were embedded within sensory pits, though a few corpuscles were visible in the dermal layer between the bone and keratin of the bill on the dorsal side. No cluster of small Herbst corpuscles was present at the bill-tip. Herbst corpuscles in the upper jaw measured, on average, 118 ± 44 µm $\times 79 \pm 31$ µm (area = $8,181 \pm 6,765$ µm^2), and the average number visible per pit was 11 ± 8.

Morphology and habitat use.—All measures of the bill-tip organ in ibises increased significantly with increasingly aquatic habitat use (increasing values of HI; Table 2). This trend was supported by the addition of data on the percent of bill length pitted and total number of sensory pits for terrestrial foraging kiwi (Table 2 and Fig. 4). There was no trend in ibis bill length with habitat use, but both tarsus width and femur length declined with increasing HI values (Table 2).

Table 2. Spearman rank-order correlations between morphological measurements and habitat index (HI). Significant results are presented in bold.

Morphological measurement		n (species)	r_s	P
Ibises only:				
Bill	Length (mm)	10	0.42	0.233
Bill-tip organ	Absolute length (mm)	10	0.76	**0.010**
	Extent as percent of bill length	10	0.81	**0.004**
	Number of sensory pits (outer surfaces of bill)	9	0.85	**0.004**
	Number of sensory pits (total)	8	0.78	**0.023**
	Density of sensory pits (pits mm^{-1})	9	0.75	**0.021**
Leg	Femur length (mm)	11	−0.67	**0.023**
	Tarsus width (mm)	11	−0.73	**0.011**
Ibises and kiwi:				
Bill-tip organ	Extent as percent of bill length	14	0.73	**0.003**
	Number of sensory pits (total)	12	0.73	**0.007**

Discussion

Our morphological and histological results from the Australian White Ibis and morphological data from nine other ibis species provide the first detailed evidence that many ibis species across a number of genera possess a bill-tip organ similar in structure to that found in the families Scolopacidae and Apterygidae. The ibis bill-tip organ is present in species that use habitats ranging from terrestrial grassland and forest (e.g., *Theristicus*, *Bostrychia*,

and *Lophotibis*) to the open water of lakes and lagoons (e.g., *Plegadis* and *Eudocimus*). More aquatic ibises appear to have more extensive and densely pitted bill-tip organs than terrestrial ibises. These birds may therefore be able to locate prey hidden both underground and within the water column, using a remote-touch sensory mechanism like that used by shorebirds (Gerritsen and Meiboom 1986, Piersma et al. 1998) and kiwi (Cunningham et al. 2009).

Implications of remote touch in ibises.—Finding a shorebird-like bill-tip organ in ibises increases the number of families with this sensory organ to three: Apterygidae, Scolopacidae, and Threskiornithidae. Each family occurs within a different order of birds, and, while ibises and shorebirds belong to the superorder Neognathae, kiwi are paleognathous. Therefore, remote touch sensory systems may have evolved multiple times within these groups of long-billed probing birds. Common phylogenetic inheritance of a bill-tip organ capable of remote touch cannot be ruled out between ibises and shorebirds, given the controversy about the relationship of the Ciconiiformes to the Charadriiformes (reviewed by Parkes 1978). However, these groups are clearly separated in the recent phylogeny published by Hackett et al. (2008). The occurrence of a bill-tip organ in the bills of probing birds in a variety of families suggests that the development of this organ is favored by a probe-foraging lifestyle and that we might expect to find it in other groups of probing birds. The presence of sensory pits has been reported in the bill of an extinct long-billed rail from New Zealand (*Capellirallus karamu*; Olson 1975), although inspection of museum specimens shows that these pits are not as dense in *Capellirallus* as in the Scolopacidae, Apterygidae, and Threskiornithidae and that they are generally not present in other rail species (S. J. Cunningham unpubl. data).

In the past, it has been assumed that probe-foraging ibises detect prey only when it touches the bill-tips (e.g., Kushlan 1979), that pursuit time between the detection and capture of prey is therefore almost nonexistent, and that the birds can assess prey characteristics only after capture (Kushlan 1979). If ibises instead
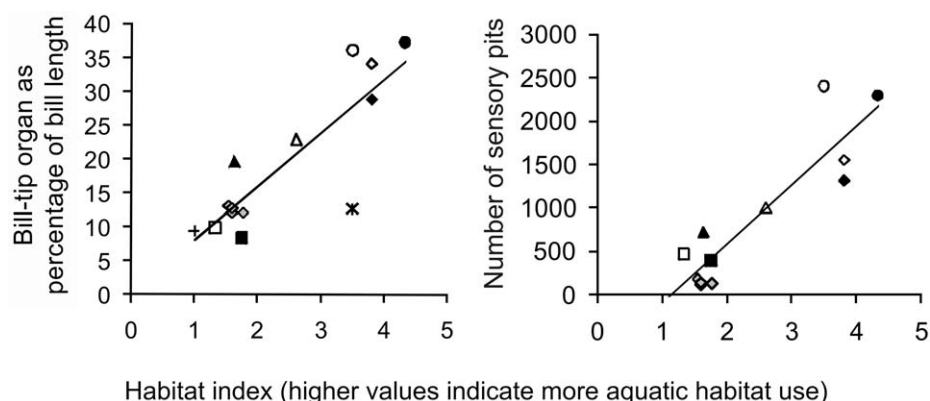

Fig. 4. Extent of the bill-tip organ as a percentage of total bill length and number of sensory pits in the bill-tip organ, in relation to habitat index. Ibises: open circles = White-faced Ibis, closed circles = Glossy Ibis, open diamonds = White Ibis, closed diamonds = Scarlet Ibis, open triangles = Australian White Ibis, closed triangles = Madagascar Crested Ibis, open squares = Wattled Ibis, closed squares = Buff-necked Ibis, plus symbol = Black-faced Ibis, and asterisk = Bare-faced Ibis. North Island Brown Kiwi, Tokoeka, Great Spotted Kiwi, and Little Spotted Kiwi are added for comparison (shaded diamonds).

use remote touch, prey items can be sensed before they come in contact with the bill, and a "pursuit" phase between detection of prey and its capture (or miss) follows. The bill-tip organ is sensitive to pressure waves produced by prey in the substrate, which may allow ibises to collect some information about prey characteristics (e.g., size) and, thus, select which prey to pursue. These possibilities should be taken into account in future studies of ibis foraging.

Morphological trends and habitat use.—The habitat index that we calculated to rank ibises in terms of habitat use is supported by published field observations of several of the species that we included in our analysis. Ogden and Thomas (1985) and Frederick and Bildstein (1992) assessed the foraging habitats used by several of the species that we examined, together with Green Ibis (*Mesembrinibus cayennensis*) and Sharp-tailed Ibis (*Cercibis oxycerca*), for which we had no specimens. The two studies ranked these species from least to most aquatic as follows: Buff-necked Ibis (dry-land forager); Green Ibis, Sharp-tailed Ibis, and Bare-faced Ibis (forage in moist soil, at water's edge, and occasionally in standing water); and White Ibis, Scarlet Ibis, and Glossy Ibis (forage almost exclusively in standing water). This rank ordering of species exactly matches the order in our habitat classification, although Bare-faced Ibis appears to be a more terrestrial forager than our index suggests, given that Frederick and Bildstein (1992) rarely found them foraging in water. Shifting the Bare-faced Ibis toward a lower HI value would improve the trend in Figure 4, so this discrepancy between our HI and field observations supports our hypothesis that ibis bill morphology is linked to habitat use. On the basis of our data and these published accounts, we predict that Green Ibis and Sharp-tailed Ibis will possess bill-tip organs similar in morphology to that of the Bare-faced Ibis.

The correlations that we found between habitat use and bill-tip morphology in ibises must be interpreted cautiously. We were able to sample only a small number of individuals per species, which potentially introduced bias. The tendency for more aquatic ibises to have more extensive bill-tip organs may also be attributable to underlying phylogenetic relatedness between ibis genera that use aquatic or terrestrial habitats. The internal phylogeny of the Threskiornithidae is not well resolved (Matheu and del Hoyo 1992); therefore, a role for phylogeny in causing this pattern can be neither confirmed nor ruled out.

However, the evidence suggests that the positive association between number of sensory pits and aquatic habitat use extends beyond the ibises, which increases the likelihood that a relationship between habitat use and bill-tip organ morphology may be selectively advantageous. For example, kiwi (terrestrial foragers) exhibit relatively low numbers of pits in the bill-tip organ (~300), with pitting extending to ~12.5% of the bill length (Cunningham et al. 2007), whereas in spoonbills (exclusively aquatic foragers), pitting extends to >50% of the bill length (Swennen and Yu 2004). Adding data for kiwi species from Cunningham et al. (2007) to the scatterplots that relate ibis bill-tip morphology to habitat use supports the observed trend, and correlations between ibis morphological variables and HI remain strong and highly significant. We therefore believe that the trend warrants further investigation, particularly given that this may lead to a greater understanding of the function of bill-tip organs in birds in different substrate types.

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