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Distribution of cephalic electroreceptor organs in weakly electric South American knifefishes (Teleostei: Ostariophysi: Gymnotiformes)

David E. Saenz*, Kevin. W. Conway* & Kirk O. Winemiller*

Sensory organs are generally fine-tuned to an organism's environment and ecological niche. Many examples of this environmentally influenced fine-tuning exist for sensory modalities, such as vision and audition, but this link is poorly understood for electroreception. This study investigates the distribution of electroreceptor pores on the heads of select members of the Gymnotiformes, Neotropical weakly electric knifefishes that use electric signals for orientation, communication, and prey localization. We evaluated the distribution and density of electroreceptors among select gymnotiform genera and discuss whether apparent differences could be consistent with ecological factors, such as habitat type and feeding behavior. Evidence for such patterns has been found in elasmobranchs; however, differences in the functional roles of the electrosensory system in gymnotiforms (e.g. electrocommunication) may alter these patterns within this diverse clade of freshwater fishes. Scanning electron microscopy was used to image the heads of specimens collected from diverse habitats. Pores associated with ampullary and tuberos electroreceptor organs were enumerated using digital image processing software and mean pore counts were compared across six different regions of the head. Previously unknown pore types and distribution patterns are described. Additionally, unique electroreceptor distributions were found in some species with specialized feeding modes. This study provides the first quantitative comparative analysis of electroreceptor distributions across multiple gymnotiform families and genera, providing an important step toward understanding the factors that have shaped the evolution of electroreception in this diverse group of Neotropical fishes.

Introduction

Sensory systems undergo strong selection to optimize how organisms obtain information about their environments. Organisms rely on sensory systems for orientation, detecting food, finding shelter, communicating with potential mates and rivals, and avoiding danger. Therefore, sensory organs are often specifically adapted to the aspects of an organism environment and ecological niche.

For example, studies manipulating the light environment have demonstrated how critical aspects of vision, such as lens properties (Kröger et al., 2001), opsin expression (Fuller et al., 2005), and the relative abundance of photoreceptor cells (Shand et al., 2008) and their neural connectivity (Wagner & Kröger, 2005), can vary. Whereas sensory modalities such as vision have been studied extensively, the influence of environmental variation on electroreception is not well understood.

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Electroreception is an ancient sensory modality that has been lost and re-evolved in multiple vertebrate lineages. One class of electroreceptors, known as ampullary receptors, are highly sensitive to DC and low-frequency AC electric fields (Boord & Campbell, 1977). They can be found in elasmobranchs, lungfishes, and coelacanths as well as some non-teleost actinopterygians, teleosts, amphibians, monotremes, and potentially also a freshwater cetacean (Bullock et al., 2006; Czech-Damal et al., 2012). Comparative studies of marine elasmobranchs have shown that variation in the distribution of electroreceptors on the body is associated with habitat differences. In a survey of 40 different species of skates, Raschi (1986) found that differences in the number of electrosensory pores and their distribution were significantly associated with habitat types. Species found at greater depths had fewer electrosensory pores and a greater proportion of pores were distributed along the dorsal surface. Furthermore, sharks occupying different habitats (e.g. pelagic, coastal, reef) show patterns in brain morphology and electrosensory pore count/distribution that coincide with their respective habitats (Kajiura et al., 2010; Kempster et al., 2012; Lisney et al., 2008). Kajiura et al. (2010) proposed that these patterns reflect specializations in foraging strategy and diet for each habitat type. Elasmobranchs only exhibit ampullary receptors, which provide passive electroreception, and although these can have other roles (e.g. orientating to Earth's magnetic field, predator avoidance), their primary function is to locate prey (Kempster et al., 2012).

Weakly electric teleosts of the orders Gymnotiformes and Osteoglossiformes (superfamily Mormyroidea) possess tuberous receptors, as well as ampullary receptors, and electric organs that generate an electric field around the body. Tuberous receptors are specialized electroreceptors tuned to the frequency of the fish's own electric organ discharge (EOD) and are used for active electrolocation and electrocommunication (Stoddard, 2002). Beyond gymnotiform and mormyroid fishes, tuberous receptors have also been documented in a single species of cetopsid catfish (*Pseudocetopsis* sp.; Andres et al., 1988), which are not known to self-generate an electric field. The weakly electric teleost fishes that possess tuberous receptors (gymnotiforms and mormyroids) are predominantly nocturnal and are known to rely heavily on their electric sense for orientation,

foraging, and communication (Kramer, 1990). Although the organization of electroreceptors largely influences the spatial resolution of the electric image (Carr et al., 1982; Kempster et al., 2012), it is unknown whether their spatial distributions exhibit patterns associated with specific habitat types or diets. With the possible exception of the weakly electric skates (Sisneros et al., 1998; Morson & Morrissey, 2007) and some stingrays (Tricas et al., 1995), elasmobranchs primarily use their electrosensory system for prey detection. However, in gymnotiforms and mormyroids electrocommunication has played a critical role in the evolution of the electrosensory system and species diversification (Hopkins, 1981; Albert & Crampton, 2005; Arnegard et al., 2010; Carlson et al., 2011; Crampton et al., 2013; Nagel et al., 2017), and therefore may influence the spatial distribution of electroreceptors (Xu-Friedman & Hopkins, 1999; Carlson et al., 2011). Most studies of electrocommunication have focused on variation in EOD frequencies and waveforms, but few studies have explored interspecific variation in the electroreceptors in gymnotiforms, and to our knowledge none have considered this variation in the context of habitat.

Due to the functional differences in the electric sense, it is unclear whether habitat associations found in the pore distributions of elasmobranchs should necessarily occur in weakly electric teleosts. Furthermore, conditions of marine habitats impose different physical constraints than those encountered in freshwater. For example, compared to freshwater teleosts, both marine elasmobranchs and siluriforms (catfishes) show similar differences in the spatial organization of ampullary receptors relative to the skin surface, presumably to account for the conductance of saltwater and relative skin resistances (Bodznick & Montgomery, 2005). Here, we provide a first look at the quantity, distribution, and density of both electroreceptor types (ampullary and tuberous) on the heads of gymnotiforms, representing multiple genera and families, collected from two broad habitat categories (river channels and floodplain lakes). We describe previously unknown patterns of electroreceptor pore distributions, explore whether these patterns mirror patterns of phylogenetic relatedness, and discuss relevant literature to speculate whether differences could be consistent with ecological factors, such as habitat type or trophic ecology.

Among the gymnotiforms, species from the same family frequently occupy similar habitats and have similar trophic niches, potentially as a consequence of traits related to the electrosensory system (Stoddard, 2002; Crampton, 2011). Given this potential conservatism, we prioritized describing electroreceptor distribution in a small number of distantly related species, placed in different genera and even different families. Our analysis focused on the head, because electrosensory capability in this region is most likely to influence food detection and feeding success. Also, the few studies that have described electroreceptor distribution in gymnotiforms report a general trend of decreasing density in the rostral-caudal direction, and the rostral region has been referred to as an electroreceptive fovea (Castelló et al., 2000); therefore, any observed differences in this region may have functional relevance.

Material and methods

Formalin-fixed, ethanol-preserved specimens were obtained from the Academy of Natural Sciences (ANSP) of Drexel University, Pennsylvania; the Biodiversity Research and Teaching Collections (TCWC) at Texas A&M University, College Station; and the Biodiversity Center (TNHC) at the University of Texas, Austin. Specimens were first inspected under a light microscope, and those that were relatively undamaged were selected for analysis. Body dimensions were measured on each specimen using calipers, with resolution to the nearest 0.1 mm. Straight-line measurements were total length (TL), from tip of snout to posterior tip of body; length from snout to posterior end of anal-fin base (LEA); and head length (HL), from tip of snout to posterior edge of opercular membrane (Mago-Leccia et al., 1985).

The electroreceptors of gymnotiform fishes lie in the corium beneath a layer of epidermis that can be further divided into four sublayers (Szabo, 1974). Ampullary receptors are found at the base of a jelly-filled canal with a pore that opens to the surface of the epidermis. Tuberous receptors are found encapsulated at the base of a canal. The canal is filled with a plug formed by elongated epithelial cells, and therefore tuberous receptors are not in contact with the surface. The naming convention used here follows Zakon (1987) and Wachtel & Szamier (1966), where the group of

encapsulated sensory receptor cells within a single canal/pore opening are collectively referred to as a receptor organ (though some receptor organs may share a pore opening, likely, during receptor organ division; Zakon, 1987). In general, each receptor organ is innervated by a single axon (but see section on *Hypopomus* sp. in Zakon, 1987 and Vischer, 1995). Receptor organs may divide over the life of a fish but are innervated by the same neuron. Collectively these are referred to as a receptor unit. For this study, we did not examine receptor innervation patterns and only quantified receptor pores (i. e. organs, not units).

Previous studies that have examined lateral-line canal and electroreceptor pore distributions in gymnotiforms have estimated receptor types by characterizing the pore overlying the receptor organ (Wachtel & Szamier, 1966; Bennett, 1967; Szamier & Wachtel, 1969; Carr et al., 1982). Ampullary organs generally have the smallest canal openings (25 μm) and occur in recognizable clusters called “rosettes” (Wachtel & Szamier, 1966; Albert & Crampton, 2005). Here we use the term cluster over rosette because, although rosettes were observed, many distinct groupings of pores were not found in this pattern. Tuberous organs reportedly have intermediate sized pores (50 μm) and may or may not cluster (Wachtel & Szamier, 1966). Clusters are formed by tuberous organs innervated by a single nerve fiber, forming *receptor units* (Zakon, 1984). Both ampullary and tuberous electroreceptor organ pores can be differentiated from the pores of the lateral-line canals in gymnotiforms based on their smaller size (25–50 μm vs. ~100 μm) (Bennett, 1967; Carr et al., 1982).

We used scanning electron microscopy (SEM) to investigate ampullary and tuberous receptors on the surface of the head. The thin layer of mucus and epidermis was first removed using fine forceps under a light microscope (Zeiss Stemi 2000). Next, the head was dissected from the body using a razor blade (slicing along the vertical line passing through the proximal margin of the pectoral fins), placed in 90% ethanol for 12 hours, and then chemically dried using a protocol based on Jusman et al. (2014) and Pinion et al. (2021). After drying, each specimen was mounted on a custom-made aluminum stub using Ted Pella colloidal silver paint, coated with gold using a Cressington 108 sputter coater, and imaged using a TESCAN Vega 3 SEM at the Texas A&M Microscopy & Imaging Center.

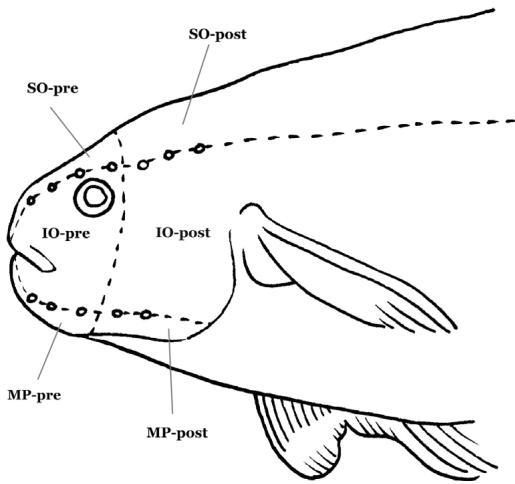


Fig. 1. Illustration of *Adontosternarchus* with dotted lines demarcating zones used for electroreceptor organ pore density comparisons on the head in this study. Circles represent schematized pores associated with the supraorbital, otic (above) and preoperculo-mandibular (below) cephalic lateral-line canals that were used as landmarks to delineate zones across species. The dorsal and ventral lines separate the supraorbital (SO) zone and the preoperculo- mandibular (MP) zone from the infraorbital zone (IO). These were further divided into -pre and -post orbital zones by eye position (pores of the infraorbital lateral-line canal are not shown to avoid confusion with zone delineation).

An average of 20 images were taken per specimen on the dorsal, ventral and lateral surfaces of one side (typically the left) of each specimen. Efforts were made to maintain the same working distance and magnification for each image. For a few cases, a change in working distance was necessary due to the rotating mechanism of the Vega 3, and appropriate adjustments were made later to scale image areas by the magnification used. FIJI was used to process the images and count the pores using a cell counter plug-in (Schindelin, 2012). In some regions of the head, not all pores could be counted either because they were covered by remnants of epidermis or the dermis was slightly damaged. In these cases, a grid (mesh size: 0.1 mm²) was superimposed on the image, and the average pore density of the immediately surrounding squares was used to estimate pore density in the missing area. FIJI also was used to measure the surface area in image sections where pores were counted.

Image distortion associated with variance in the z-plane may have yielded a small degree of error in image area and count estimates, an unavoidable consequence of measuring distances in 2-dimensional images of a 3-dimensional object. At the magnification used for counting, some images differed in the z-plane more than others; and error due to cursor placement and/or pore orientation was comparable to the few microns in actual pore size differences. Consequently, the precise distribution of different size classes could not be represented here; however, size differences between pore classes were confirmed in images taken at higher magnification with no effect of the z-plane.

The arrangement of cephalic lateral-line canals in gymnotiforms match those found in most teleost fishes (Coombs et al., 1988; Webb, 1989a–b). Lateral-line canal pores were used by Carr et al. (1982) as landmarks to compare receptor distribution in specimens of *Apteronotus albifrons* of varying sizes and by Vischer (1989) to investigate lateral-line canal development in *Eigenmannia*. Therefore, in addition to the eye, lateral-line canal pores were used to delineate six zones on the head of each fish, including three pre-orbital and three post-orbital areas (Fig. 1). The six zones were designated as follows. The region dorsal to the supraorbital (SO) lateral-line canal, with electroreceptor organ pores along the canal inclusive, was divided into two zones: (1) SO-pre = anterior to and including the eye; (2) SO-post = posterior to the eye. The region ventral to the preoperculo-mandibular (MP) lateral-line canal, with electroreceptor organ pores along the canal inclusive, was divided into two zones: (3) MP-pre = anterior to and including the eye; (4) MP-post = posterior to the eye. Lastly, the regions in between the SO and MP canals were designated as the infraorbital (IO) zone, divided into the following two zones: (5) IO-pre = anterior to and including the eye; (6) IO-post = posterior to the eye.

Electroreceptor organ pores (henceforth simply as pores) were counted for each zone and divided by the surface area to determine zone pore density. We evaluated a total of 8 species from 4 different gymnotiform families. Due to the labor-intensive nature of the methodology and to limit destructive sampling of museum specimens, only one adult specimen was evaluated per species. While this prevents us from making any assumptions about intraspecific differences of pore distributions, it should be sufficient for

revealing interspecific differences. Furthermore, other studies that have quantified electroreceptor pores report consistent densities within a single

species (Carr et al, 1982; Castelló et al., 2000). Pore densities and distributions across zones and species were compared graphically using the package

Table 1. Summary of tuberous and ampullary organ pore densities and total counts across six zones (see text for explanation of zones). Abbreviations: IO, infraorbital; MP, preoperculo-mandibular; SO, supraorbital; Tube, tuberous organ pores; Amp, ampullary organ pores.

Species	Zone	Tube density	Amp density	Tube total	Amp total
<i>Adontosternarchus clarkae</i>	IO post	24.3	0.6	155	8
	IO pre	34.3	0.6	91	3
	MP post	17.8	6.7	116	49
	MP pre	397.3	57.8	663	141
	SO post	54.0	35.1	187	94
<i>Brachyhyopomus diazi</i>	SO pre	71.6	26.8	101	38
	IO post	85.3	29.2	621	205
	IO pre	102.5	79.4	382	316
	MP post	44.6	18.5	204	84
	MP pre	74.2	60.7	333	283
<i>Eigenmannia muirapinima</i>	SO post	81.4	16.7	435	93
	SO pre	204.7	101.0	440	244
	IO post	67.7	5.4	567	38
	IO pre	128.5	3.3	1311	34
	MP post	42.1	6.2	223	33
<i>Porotergus gimbeli</i>	MP pre	356.1	2.6	1077	9
	SO post	71.9	7.1	414	60
	SO pre	170.0	17.9	886	25
	IO post	47.8	10.8	467	119
	IO pre	47.5	18.3	290	116
<i>Parapteronotus hasemani</i>	MP post	23.4	10.7	148	78
	MP pre	169.7	70.6	604	371
	SO post	26.9	1.3	167	15
	SO pre	44.2	8.1	193	79
	IO post	64.2	9.3	684	33
<i>Rhabdolichops eastwardi</i>	IO pre	402.6	85.6	1362	54
	MP post	58.1	11.0	393	21
	MP pre	221.7	40.8	170	13
	SO post	92.6	8.9	411	4
	SO pre	267.4	71.1	423	9
<i>Rhamphichthys pantherinus</i>	IO post	100.1	60.8	807	414
	IO pre	226.4	195.2	637	305
	MP post	121.2	56.2	295	130
	MP pre	167.1	71.2	767	306
	SO post	286.7	226.2	716	634
<i>Steatogenys elegans</i>	SO pre	367.5	283.2	273	364
	IO post	70.0	6.2	402	49
	IO pre	313.4	89.4	1225	325
	MP post	20.6	4.1	79	18
	MP pre	282.9	47.6	365	59
<i>Steatogenys elegans</i>	SO post	76.7	7.2	362	32
	SO pre	473.6	117.0	389	70
	IO post	40.3	3.7	337	33
	IO pre	78.9	9.7	790	99
	MP post	82.2	3.9	346	22
<i>Steatogenys elegans</i>	MP pre	165.7	4.9	877	24
	SO post	22.5	1.6	151	8
	SO pre	15.3	3.5	61	14

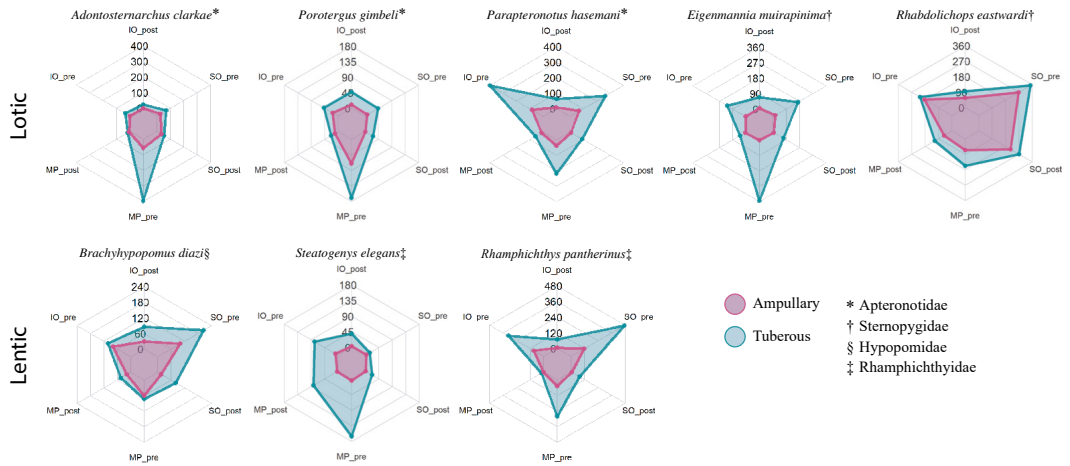


Fig. 2. Radar plots showing the relative distribution of electroreceptor organ pore densities across the six designated zones. Note that the scale is different for each species. Species collected from lotic habitats are shown on the top row and those collected from lentic habitats are on the bottom row. The zones starting from the top and proceeding clockwise are IO-post, SO-pre, SO-post, MP-pre, MP-post, IO-pre (see text for explanation). Abbreviations: IO, infraorbital; MP, preoperculo-mandibular; SO, supraorbital.

‘fmsb’ in the open-source software R (Nakazawa & Nakazawa, 2019). Raw SEM images are available upon reasonable request to the first author.

Material examined. APTERONTIDAE: *Adontosternarchus clarkae*, ANSP 197666, 2, 108.8–122.1 mm TL, 81.2–87.0 mm LEA; *Parapteronotus hasemani*, TCWC 16723.1, 107.9 mm TL, 100.7 mm LEA; *Porotergus gimbeli*, ANSP 197665, 158.4 mm TL, 138.2 mm LEA. HYPOPOMIDAE: *Brachyhypopomus diazi*, TNHC 12608, 83 mm TL, 70.0 mm LEA. RHAMPHICHTHYIDAE: *Rhamphichthys pantherinus*, TNHC 13097, 137.1 mm TL, 102.8 mm LEA; *Steatogenys elegans*, TCWC 16766.02, 158.6 mm TL, 103.2 mm LEA. STERNOPYGIDAE: *Eigenmannia muirapinima*, TCWC 16615.04, 88.5 mm TL, 63.9 mm LEA; *Rhabdolichops eastwardi*, ANSP 196613, 154.9 mm TL, 95.0 mm LEA.

Results

All species exhibited a general decline in pore density in the rostral to caudal direction on the head. Densities among the six zones of the head varied considerably across species, with most exhibiting either a dorsal or ventral skew in pore distribution (Fig. 2). Total pore counts were not a linear function of species total length or head length (p -values = 0.69 and 0.97, R^2 = 0.03 and 0.0002, respectively). Similarly, no pattern was observed when pore density was evaluated in relation to total length or head length (p -values = 0.91 and

0.34, R^2 = 0.002 and 0.15, respectively). Overall, *Rhabdolichops eastwardi* (Sternopygidae) had the highest total pore density (tuberosus + ampullary) and the highest pore counts (Table 1). *Steatogenys elegans* (Rhamphichthyidae) had the lowest total pore density, and *Adontosternarchus clarkae* (Apterontidae) had the lowest total number of pores. In general, the center of the operculum had the lowest density of pores, with *R. eastwardi* and *Brachyhypopomus diazi* (Hypopomidae) having the highest densities in IO-post (Table 1). Nearly all species exhibited tuberosus and ampullary pores with dimensions that did not match previously published descriptions. In some species, tuberosus organs appeared to have pores with a large range of sizes. In *Steatogenys elegans* (Rhamphichthyidae) some, but not all pores labeled as ampullary pores (ca. 16–25 μ m) displayed the classic rosette pattern (Fig. 3) described in *Apteronotus albifrons* (Apterontidae) (Carr et al., 1982). The pores of tuberosus organs appeared to have two size classes. Smaller pores (ca. 30–40 μ m) were mostly found in the preorbital zones, especially in MP-pre. Mean pore size increased in the rostral to caudal direction, and larger pores (ca. 55–63 μ m) were predominantly found in the postorbital zones. Interestingly, pores associated with the cephalic lateral-line canal system were similar in size to these larger tuberosus pores and were sometimes difficult to differentiate. Highest pore densities

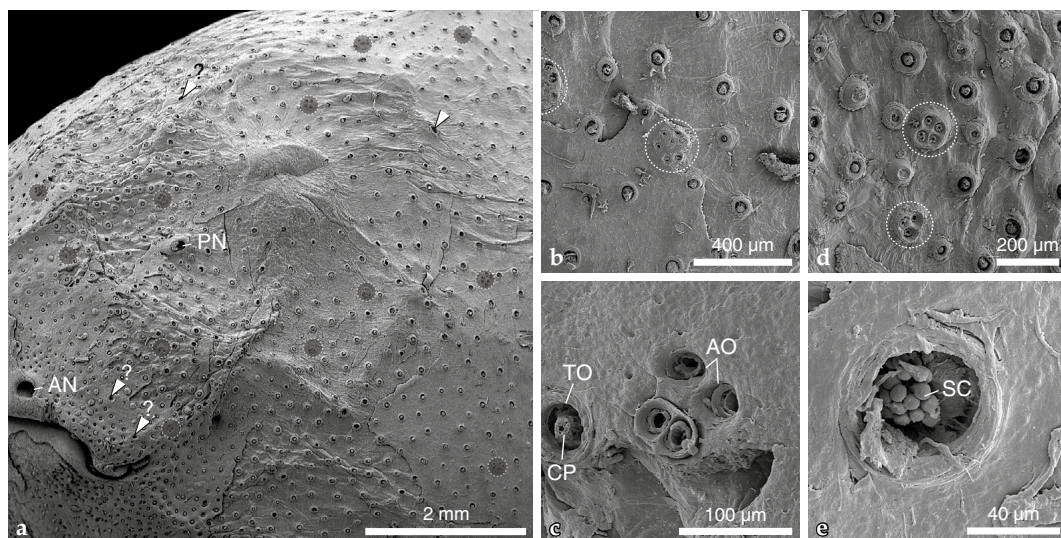


Fig. 3. Scanning electron micrographs of *Steatogenys elegans*, TCWC 16766.02, 158.6 mm TL, 103.2 mm LEA. **a**, Low magnification image of center of head, left side in lateral view; **b**, Intermediate magnification image of pore cluster associated with ampullary organs in the classic rosette pattern; **c**, Intermediate magnification image of pores also labeled, according to pore diameter, as ampullary organ pores. It is unclear whether the separating tissue indicates the organs were in the process of dividing; **d**, Higher magnification image of pores associated with a tuberosus organ on the left and ampullary organs on the right; **e**, Higher magnification close up of a single tuberosus receptor with canal plug removed and sensory cells visible. White arrow heads in **a** point to pores of cephalic lateral-line canals; white arrow heads associated with question mark symbols (?) indicate uncertainty regarding identification of opening as cephalic lateral-line canal pore. Grey circles with white dashed outline highlight clusters of ampullary organs in **a-c**. Circles with white dashed outline highlight clusters of ampullary organs in **b-c**. Abbreviations: AO, ampullary organ; AN, anterior nostril; CP, canal plug; PN, posterior nostril; SC, sensory cell; TO, tuberosus organ.

were observed in ventral zones, with the highest counts in MP-pre and the second highest in MP-post. Interestingly, the eye is densely surrounded by pores, and it appears that only the skin covering the lens is devoid of electroreceptor pores (Fig. 3).

Rhamphichthys pantherinus (Rhamphichthyidae) was unique in that none of the pore types were organized into obvious clusters (Fig. 4). There was large and fairly continuous variation in pore size. Similar to *S. elegans*, pore diameter tended to increase in the rostral to caudal direction. The smallest pores (ca. 15–20 µm, labeled as ampullary) and an intermediate class (ca. 25–33 µm, labeled as tuberosus) were predominant on the snout. Larger pores (ca. 40–50 µm, also labeled as tuberosus) were most common in the caudal zones. In a 33 mm² sample from the snout, the ratio between the large, intermediate, and smallest size classes was approximately 9:4.5:1. The highest pore density was found on SO-pre, and this was the highest pore density recorded

for a single zone among all species. Nevertheless, all three pre-orbital zones had high densities. Ampullary pores showed a similar distribution pattern to tuberosus pores.

Porotergus gimbeli (Apteronotidae) revealed strong clustering of ampullary receptors (Fig. 5). Tuberosus receptors appeared to have two different size classes, ca. 40–50 µm and ca. 70–90 µm. The highest density was found in MP-pre, just posterior to the lower lip, a region hereafter referred to as the “chin” for brevity. Both pore types were found on the snout, but the larger pores were predominantly found in the caudal zones (although at lower density) with a relatively uniform distribution. Similar to *S. elegans*, pores associated with the cephalic lateral-line canal system were nearly indistinguishable in size from tuberosus organ pores (Fig. 5).

Adontosternarchus clarkae (Apteronotidae) (not figured) was similar to *Porotergus gimbeli* in that the highest pore density was found at MP-pre,

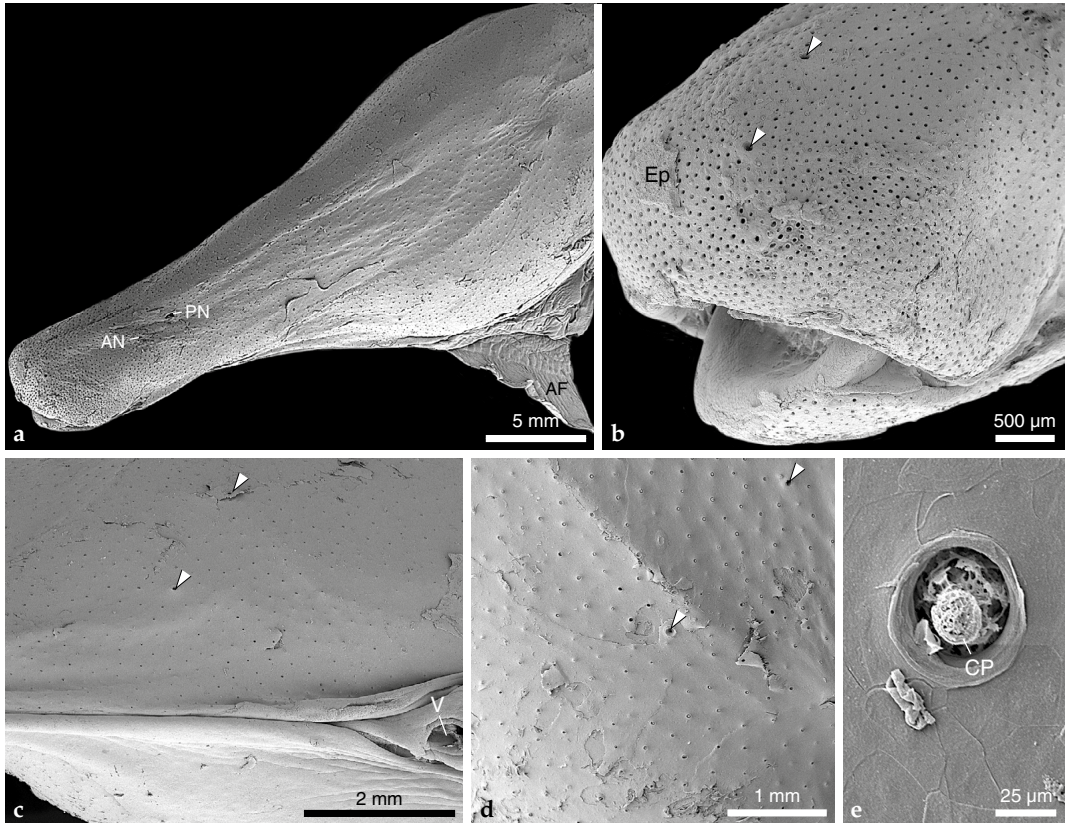


Fig. 4. Scanning electron micrographs of *Rhamphichthys pantherinus*, TNHC 13097, 137.1 mm TL, 102.8 mm LEA. **a**, low magnification overview of head, left side in lateral view; **b**, Intermediate magnification image showing anterodorsal tip of tubed snout; **c**, Intermediate magnification image showing ventral surface of head at area of isthmus and vent; **d**, Higher magnification image showing skin on ventrolateral surface of tubed snout; **e**, Higher magnification close up of single tuberous organ, canal plug visible. White arrow heads in **b–d** point to pores of cephalic lateral-line canals. Abbreviations: AN, anterior nostril; AF, anal fin; CP, canal plug; Ep, epidermis; PN, posterior nostril; V, vent.

although the density of this zone was two times greater in *A. clarkae*. In *A. clarkae*, pore density was much greater in MP-pre compared to the other zones (10:1). This ratio of pore density in MP-pre compared to the average from other zones is much higher than those for other species examined here (e.g. *P. gimbeli* had the second highest ratio of 4.5:1). Ampullary pores (ca. 15–20 μm) also occurred in clusters. Tuberous pores were generally large and uniform in size (ca. 50–60 μm); however, the chin region had pores of varying sizes (ca. 27–35 μm and ca. 50–60 μm).

Parapteronotus hasemani (Apteronotidae) (not figured) was the only species examined in which the highest density of tuberous pores occurred on a lateral zone, specifically IO-pre. Overall,

tuberous pores were more evenly distributed in the pre-orbital zones, similar to the finding for *R. pantherinus*, and the distribution of ampullary pores followed this same pattern. Three main size classes of pores were identified. Larger pores (ca. 60–68 μm, labeled as tuberous) were primarily found in caudal regions. Intermediate pores varied much more in size (ca. 31–50 μm), though most measured ca. 38–44 μm. The smallest size class (ca. 24–30 μm) mostly, but not always, exhibited clustering patterns and were interpreted as ampullary pores.

In *Eigenmannia muirapinima* (Sternopygidae) both ampullary and tuberous pores occurred in clusters (Fig. 6). Tuberous pores that clustered were generally smaller (ca. 30 μm) in diameter

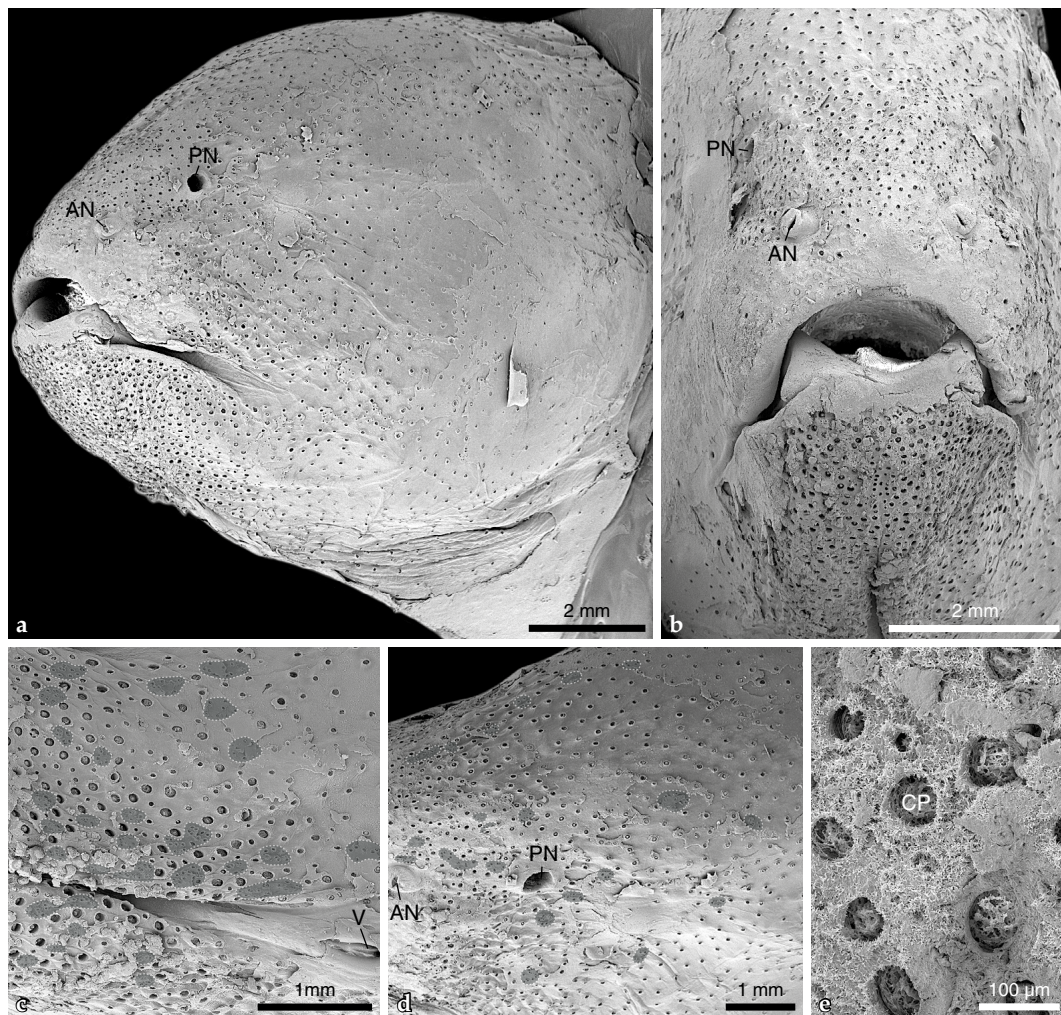


Fig. 5. Scanning electron micrographs of *Porotergus gimbeli*, ANSP 197665, 158.4 mm TL, 138.2 mm LEA. **a**, Low magnification overview of head, left side in lateral view; **b**, Low magnification overview of head and snout, anterior view; **c**, Intermediate magnification image showing ventral surface of head at area of isthmus and vent; **d**, Intermediate magnification image showing dorsolateral surface of snout and head above eye, oblique dorsolateral view; **e**, Higher magnification image of field of tuberosous organs, with canal plug removed. Grey shapes with white dashed outline highlight clusters of ampullary organs in **c-d**. Abbreviations: AN, anterior nostril; CP, canal plug; PN, posterior nostril; V, vent.

than non-clustering pores (ca. 39–43 μm) and primarily found in preorbital zones. The entire snout is well covered, with IO-pre and SO-pre having relatively high densities, although the highest concentration was observed in MP-pre (Fig. 2). Few ampullary pores (ca. 15–25 μm) were identified in *E. muirapinima*, and those that were identified tended to be relatively uniform in distribution, a pattern similar to that observed

in *S. elegans*. Pores associated with the cephalic lateral-line canal system were notably larger (140 μm) than other pores (Fig. 6).

The highest total pore count and the highest overall pore density among all the species examined was found in *Rhabdolichops eastwardi* (Sternopygidae) (Fig. 7). This species also appears to have the broadest distribution of pores (Fig. 2). The entire dorsal region (both SO-pre

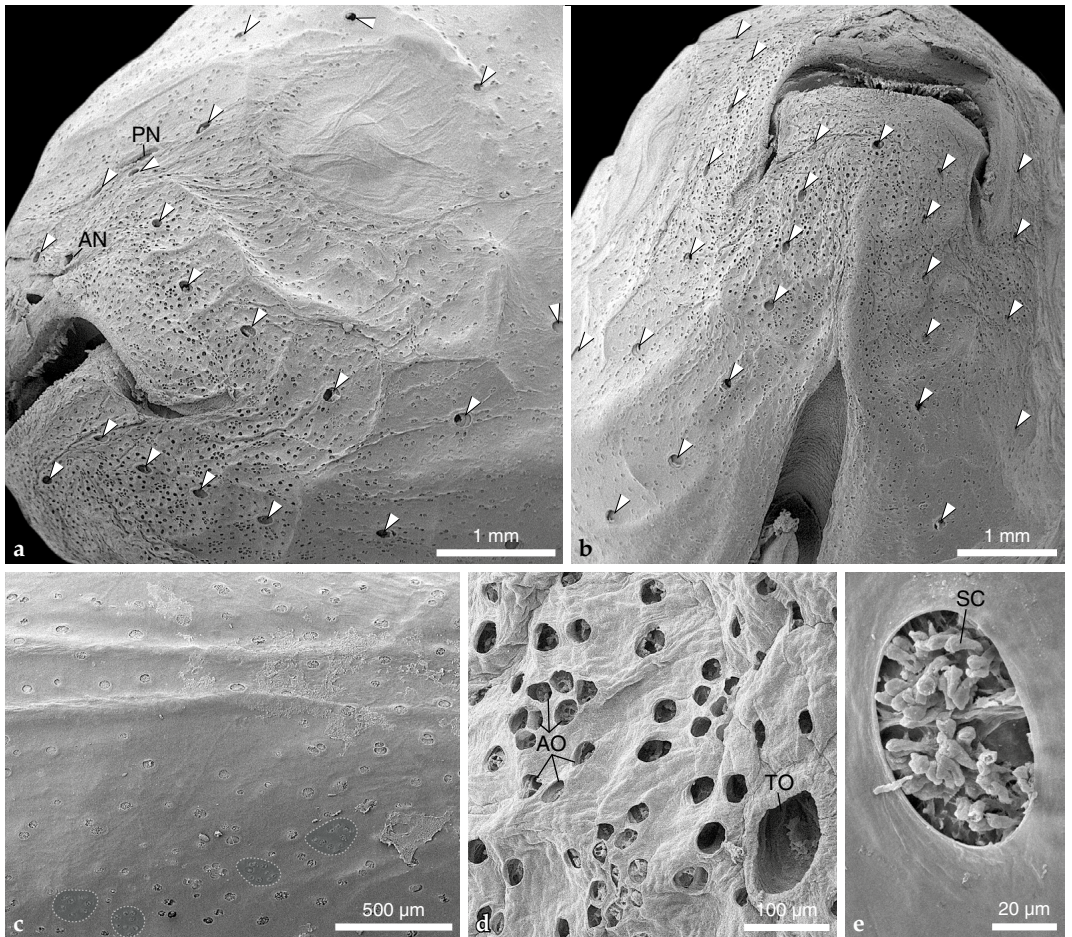


Fig. 6. Scanning electron micrographs of *Eigenmannia muirapinima*, TCWC 16615.04, 88.5 mm TL, 63.9 mm LEA. **a**, Low magnification overview of head, left side in oblique ventrolateral view; **b**, Low magnification overview of lower jaw and ventral surface of head, anteroventral view; **c**, Intermediate magnification of dorsolateral surface of head posterior to orbit, left side in oblique dorsolateral view; **d**, Higher magnification image showing clusters of ampullary organs and a single tuberosus organ with canal plugs removed; **e**, Higher magnification image of single tuberosus organ with canal plug removed. White arrow heads in **a–b** point to pores of cephalic lateral-line canals. Grey shapes with white dashed outline highlight clusters of ampullary organs in **c**. Abbreviations: AO, ampullary organ; AN, anterior nostril; PN, posterior nostril; SC, sensory cell; TO, tuberosus organ.

and SO-post) had high pore densities, with the highest density in SO-pre. Along with *S. elegans*, *R. eastwardi* was the only other species for which at least one post-orbital zone had a higher density than the pre-orbital zones, although IO-pre and MP-pre nonetheless had high pore densities.

Rhabdolichops eastwardi had a range of pore sizes that did not easily separate into discrete size categories (Fig. 7), even for the larger tuberosus pores (ca. 40–68 µm). Pores were often observed in clusters, but within clusters, pores were not

always uniform in size (Fig. 7). Instead, we often observed a range of sizes, with both small (ca. 12–16 µm) and intermediate pores (ca. 20–36 µm) clustering together. In combination with potential bias associated with the image z-plane, high pore density made it difficult to consistently differentiate between size classes in lower magnification images while counting (pore sizes were measured in higher magnification images), and there likely is overlap between pores classified as ampullary and tuberosus. This may account for the large

density of pores classified as ampullary organs in this species. Another pattern observed only in *R. eastwardi* was the ring-like clustering of smaller pores around a single large tuberous pore (Fig. 7).

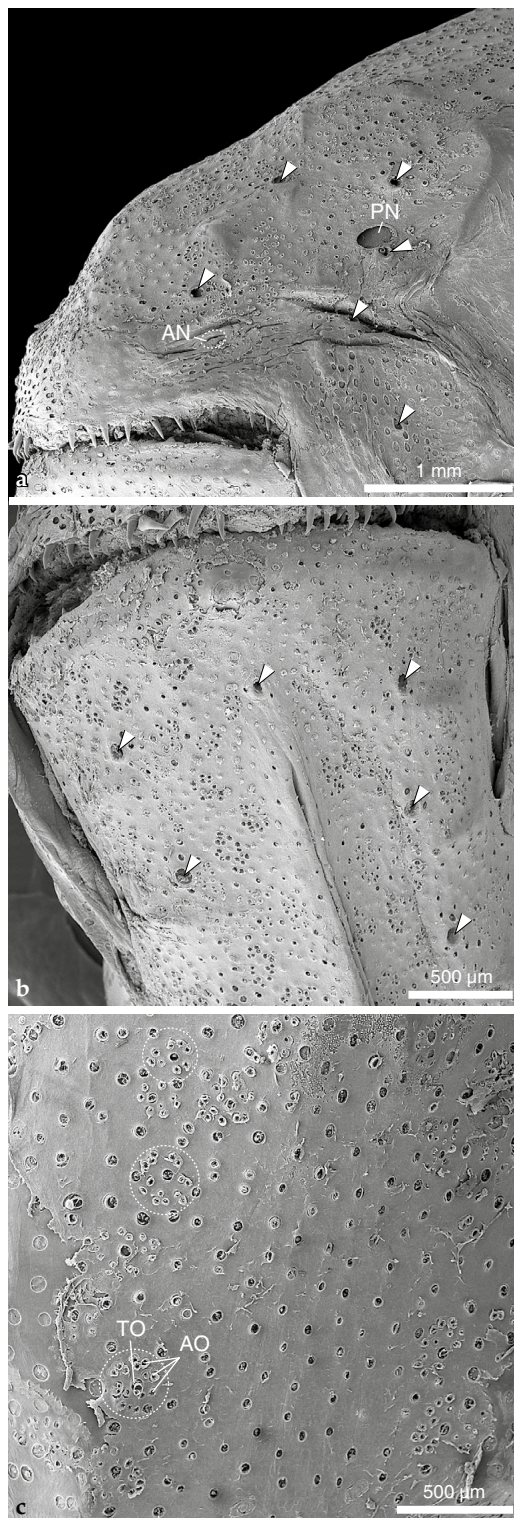
In *Brachyhypopomus diazi* (Hypopomidae) (not figured), small pores (ca. 15 μm) occasionally occurred in clusters and were labeled as ampullary pores. Two intermediate size classes (ca. 20–30 μm and ca. 45–55 μm), and one large class (ca. 70–76 μm) of pores were counted as tuberous organs. The preorbital dorsal zone SO-pre had the highest pore density. Other zones had similar pore densities, with the exception of MP-post with the lowest pore density.

Discussion

The distribution of electroreceptor pores on the heads of gymnotiforms varies widely among species. As shown in previous studies, most of the species studied here exhibited a general decline in pore density in the rostral to caudal direction; however, these densities vary greatly on a dorso-ventral axis, leading to some exceptions in this trend. To our knowledge, this study is the first to contrast electroreceptor pore densities in gymnotiforms at this scale, and therefore represents an important step toward understanding ecological and phylogenetic factors associated with the distribution of these sensory organs.

Physiologically, there are two general types of tuberous receptors in gymnotiforms, those that code EOD amplitude information and those that code EOD timing or phase information (Bullock et al., 2006). A few studies have reported patterns in the spatial distribution of morphologically and physiologically distinct receptor subtypes (Szabo, 1965, 1974; Bastian, 1977; Yager & Hopkins, 1993).

Fig. 7. Scanning electron micrographs of *Rhabdolichops eastwardi*, ANSP 196613, 154.9 mm TL, 95.0 mm LEA. **a**, Low magnification overview of snout, left side in oblique ventrolateral view; **b**, Low magnification overview of lower jaw and ventral surface of head, antero-ventral view; **c**, Intermediate magnification showing a section of the dorsal posterior region, dorsal view, anterior to top. White arrow heads in **a** and **b** point to pores of cephalic lateral-line canals. The white dotted circles in **c** outline a unique ring pattern in which pores labeled as ampullary organ pores surround an intermediate sized tuberous organ pore. Abbreviations: AN, anterior nostril; AO, ampullary organ; PN, posterior nostril; TO, tuberous organ.



Therefore, it is tempting to suggest that variation in pore sizes and distribution observed here could be related to these receptor subtypes. However, receptor subtypes have not been studied for more than a few species, nor at the spatial scale examined here, and histological and physiological studies of electroreceptors in these species are needed to confirm this. Variation in pore size also may be associated with age. Some receptor organs grow by adding more receptor cells and eventually divide, increasing the number of organs per receptor unit (Zakon, 1984, 1987). Indeed, we occasionally observed pores that appeared to be splitting (e.g. see Fig. 3d).

Within species, the density of receptor organs (and therefore pores) appears to remain the same in fish of different lengths (Carr et al., 1982; Zakon, 1987; Castelló et al., 2000), likely maintaining the resolution of the electric sense relative to the size of the individual. During the development of *Eigenmannia* sp., electroreceptor organs (ampullary and tuberous) in the trunk show a clear spatial gradient of development, with new organs developing caudal and dorsal to older ones, away from the lateral-line. However, the opposite is observed on the head where electroreceptors begin to develop randomly without any particular spatial gradient on the head, suggesting receptor distribution in the head may be more plastic than along the trunk (Vischer, 1989).

Ecological and phylogenetic perspectives on electroreceptor distributions. An additional intention of this study was to provide a first step toward exploring whether receptor pore distributions may exhibit associations with habitat or feeding behavior and whether pore distributions are associated with phylogenetic relatedness. Fish in lotic habitats often face directly into the flow of water and thereby may encounter drifting particles (e.g. food, debris); in contrast, fish in lentic habitats are unconstrained by water current. Therefore, it is possible that fish from lotic habitats may have proportionally higher pore densities in rostral regions, and species from lentic environments might have comparatively more uniform electroreceptor distributions.

The data presented here are insufficient to ascertain whether broad lentic and lotic habitat categories or phylogenetic relationship are good predictors of electroreceptor pore distributions. However, in combination with information obtained from the literature (discussed below)

and the observed interspecific differences, it is tempting to suggest that phylogenetic relatedness, head morphology, and feeding behavior are associated with and may play a role in determining electroreceptor pore distribution. We discuss a few instances where these associations seem most likely and may benefit from additional research.

Apterontidae. Most apteronotids inhabit rivers (Crampton, 1998; Albert & Crampton, 2005), some may seasonally occupy habitats in floodplains or small streams (Winemiller, 1989), and a few can be found in lentic habitats year-round (Carol Arantes, West Virginia University, unpublished data from the lower Amazon River). Based on recently available phylogenetic hypotheses (e.g. Tagliacollo et al., 2016; Alda et al., 2019; Peixoto et al., 2019, 2022), the three genera of apteronotids examined herein (*Adontosternarchus*, *Parapteronotus* and *Porotergus*) do not form a monophyletic group and are distributed across the apteronotid clade. General similarities in electroreceptor pore distributions between two of the three aforementioned genera (*Porotergus* and *Adontosternarchus*) may represent a convergent condition, or alternatively a retention of the ancestral (plesiomorphic) condition.

Species of the genus *Adontosternarchus* possess a unique V-shaped mouth as well as an accessory electric organ derived from the fibers of electrosensory nerves in the chin (Bennett, 1970). This chin organ discharges independently from the main electric organ and likely only activates receptors in the head/chin region (Bennett, 1971).

Adontosternarchus species are captured almost exclusively using bottom trawl nets, and gut contents analyses have revealed benthic invertebrates, such as cladocerans, nematodes, and rotifers (Mago-Leccia et al., 1985; Lundberg et al., 1987; Lundberg & Cox Fernandes, 2007). This information suggests that the impressive density of electroreceptors in the chin region may facilitate a benthic feeding strategy. *Porotergus gimbeli* is also known to consume benthic invertebrates (de Santana & Crampton, 2010), which also may contribute to a relatively high pore density in the MP-pre zone. Interestingly, this species exhibits polymorphic swelling of the chin region (Santana & Crampton, 2010), but the specimen examined here (ANSP 197665) lacked this feature.

Parapteronotus hasemani exhibited a different pore distribution (Fig. 2) that was more similar to that of the tube snouted *Rhamphichthys pantherinus*

(Rhamphichthyidae), but with the highest density on the side of the snout (IO-pre) rather than the dorsal surface. Interestingly, *P. hasemani* exhibits sexually dimorphic jaw morphology, with males showing large variation in jaw morphology, including individuals with greatly elongated snouts (Cox Fernandes et al., 2002). The specimen examined here (TCWC 16723.1) did not have an elongated snout, but it would be interesting to test whether similar distribution patterns of electroreceptor pores are observed in both sexes and males with elongated snouts. Further study in species that have sexually dimorphic head morphologies, such as *Compsaraia samueli* and *Apteronotus rostratus* (Albert & Crampton, 2009; Evans et al., 2018), might reveal an influence of head morphology and development on electroreceptor distribution. The males in these species independently evolved elongated snouts that are hypothesized to play a role during contests for dominance (Evans et al., 2018).

Sternopygidae. Similar to the apteronotids *Pottergus gimbeli* and *Adontosternarchus clarkae*, the sternopygid *Eigenmannia muiirapinima* had high total pore densities in MP-pre, but also had relatively high densities in other preorbital zones. Findings from a diet study on *E. trilineata* indicate consumption of prey found throughout the water column with a preference for benthic invertebrates (Giora et al., 2005), suggesting the electroreceptor distribution seen in *Eigenmannia* could reflect feeding behavior.

Rhabdolichops eastwardi was found to have the highest density of receptor pores among all species examined. Aspects of the ecology of this species may provide clues as to why. *Rhabdolichops* is found in great abundance in flowing, deep river channels (though it may occasionally be found in adjacent floodplain channels near the outflow from tributaries) (Correa et al., 2006; Lundberg et al., 1987; Lundberg & Mago-Leccia, 1986). Most members of the genus possess numerous, long gill rakers that are associated with a zooplanktivorous feeding strategy, and *R. eastwardi* is hypothesized to specialize on planktonic copepods (Lundberg & Mago-Leccia, 1986). This evidence induces speculation that a high density of electroreceptors, especially on the dorsal (SO-pre and SO-post) and lateral (IO-pre) zones, is important for locating and capturing prey from deep within the water column of turbid rivers (Lundberg et al., 1987). The enlargement of certain cephalic lateral-line ca-

nals in *Rhabdolichops* and other sternopygids (Lundberg & Mago-Leccia, 1986; Correa et al., 2006; Peixoto et al., 2020; Dutra et al. 2021) may also represent a specialization for locating prey from a certain area of the water column. The unique method of locomotion found in all gymnotiforms may be especially useful for *Rhabdolichops* to move forward and backward to capture prey drifting overhead in flowing water. *Rhabdolichops* also possess long pectoral fins useful for generating upward thrust in a manner observed during prey capture by piscivorous *Rhaphiodon vulpinus* and *Hydrolycus* spp. (Cynodontidae, Characiformes) (K. Winemiller, personal observation).

Rhamphichthyidae. Rhamphichthyids are most often found in streams and floodplain habitats (Crampton, 1998; Albert & Crampton, 2005). Although the two species studied here were captured in a small stream and a floodplain channel, they sometimes are collected from deep river channels (Albert & Crampton, 2005; Carvalho & Albert, 2015). The two rhamphichthyid species examined here had different electroreceptor pore distributions, which is perhaps not unexpected considering their differences in head morphology and feeding behavior. *Rhamphichthys* species possess long tube-like snouts used to probe for aquatic invertebrates in holes and crevices in root wads, leaf packs and other benthic substrates (Marrero, 1987; Marrero et al., 1987; Marrero & Winemiller, 1993). Once located, the prey item is ingested via suction through the tube-like snout. Unsurprisingly, the snout of *R. pantherinus* is densely covered in electroreceptor pores relative to the post-orbital zones, with an especially high density on the dorsal surface of the snout (SO-pre).

In contrast to *Rhamphichthys pantherinus*, the short-snouted *Steatogenys elegans* is an ecological generalist. The species occurs in diverse habitats throughout lowlands of the Amazon and Orinoco basins and the Guianas, ranging from shallow to deep (up to 50 m) and nutrient rich to nutrient poor water (Crampton et al., 2004). Interestingly, all rhamphichthyids possess accessory electric organs (Giora & Carvalho, 2018). *Steatogenys elegans* and *R. pantherinus* both have a submental accessory organ that runs along the ventral region of the jaw and is thought to be non-homologous in these species. Additionally, *R. pantherinus* has a subpectoral accessory organ, and *S. elegans* has a humeral accessory organ. Unlike the observed pore densities associated with the chin organ in

A. clarkae, no obvious clustering of electroreceptor pores was identified in association with these organs on the head.

Hypopomidae. Hypopomids generally occur in lentic habitats, such as channel backwaters, floodplain lakes and sluggish streams (Albert & Crampton, 2005; Crampton et al., 2016a). *Brachyhypopomus diazi*, which is commonly found in floating aquatic macrophytes or dense stands of submerged vegetation, exhibited a relatively even distribution of electroreceptor pores (Fig. 2), but with highest density on the dorsal surface. Species of *Brachyhypopomus* have been reported to feed on aquatic insect larvae, microcrustacean, and other small aquatic invertebrates (Winemiller & Adite, 1997; Giora et al., 2014; Crampton et al., 2016b).

Electrocommunication. Habitat use and feeding behavior are not the only factors that could influence the evolution of electroreceptor patterns in gymnotiform fishes. Electrocommunication also could select for different patterns of pore distribution. The sensory drive hypothesis (Endler, 1992) posits that environmental aspects influence the evolutionary trajectory of communication signals and their corresponding sensory systems. In gymnotiforms, a general relationship between EOD discharge rate and habitat type is well-known. Wave-type species (Apteronotidae, Sternopygidae) with continuous EODs are typically found in lotic habitats; whereas pulse type species (Gymnotidae, Hypopomidae, Rhamphichthyidae) with intermittent EODs more often occur in lentic habitats (Crampton, 1998; Albert & Crampton, 2005). However, we are unaware of any evidence indicating that a particular EOD discharge frequency or waveform is more effective for communication within a given habitat type. Additionally, differences in the physical properties of electric signals relative to acoustic or visual signals suggest that signal refraction or reflection by the animal's environment have little effect on the electric sense (Brenowitz, 1986; Hopkins, 1999a–b; Crampton et al., 2013). Therefore, it is unclear how communication may “override” environmental influences on the evolution of electroreceptor distribution for electrolocation or electrocommunication.

Mormyrids, on the other hand, have specialized electroreceptors termed “Knollenorgans” (Franz, 1921). These receptors and their associated central processing pathways are exclusively

responsible for mediating electrocommunication (Bullock et al., 2006). Equivalent receptors are not found in gymnotiforms. There is evidence that the spatial arrangement of Knollenorgans is important for determining the directionality of conspecific signals (Xu-Friedman & Hopkins, 1999; Carlson et al., 2011). A recent study suggests that mormyrid species that rely on the electric sense with little reliance on visual sense differ from species that use both senses with regard to the spatial distribution of Knollenorgans as well as habitat use (Vélez et al., 2018). The tuberous receptors responsible for orientation and electrolocation in mormyrids are termed mormyromasts, but to our knowledge, their distributions have not been well studied. One recent study demonstrated that morphological differences in the tube-snouts of species in the mormyrid genus *Campylomormyrus* are associated with preferences for feeding on different substrates (Amen et al., 2020). It would be interesting to examine whether mormyromast distribution patterns in these species are associated with feeding in various microhabitats.

Conclusions. In the present study, distinct differences were observed in electroreceptor pore distributions, pore-type sizes, and pore clustering in a small, but diverse, sample of gymnotiform fishes. This evidence together with ecological information from the literature suggests that phylogenetic relatedness as well as some trait combinations involving habitat use and feeding behavior may play a role in the evolution of electroreceptor spatial distribution in gymnotiforms. More comparative research involving more species from more habitat types and trophic niches is needed to explore these potential relationships. Also meriting further study is the relationship of electroreceptor distribution with species-specific EOD waveforms. Bastian (1977) showed that the frequency response of electroreceptors varies with their position on the body of the fish. Castelló et al. (2000) provided evidence of how properties of the fish's body (e.g. body geometry and tissue organization) can funnel electric currents toward the head. It is well known that electric field potentials vary spatiotemporally along a fish's body as a function of the EOD waveform (Caputi, 1999).

Some studies (Aguilera et al., 2001; Crampton et al., 2013) have supported the idea that the specific phases of the EOD waveform can be decomposed into two functional components, one for electrolocation and one electrocommunication – a

concept originally proposed by Trujillo-Cenóz et al. (1984). If true, it is possible that electroreceptor distributions could reflect feeding strategies on the head and communication specialization on the trunk. However, there is compelling evidence that different EOD phases do not have compartmentalized functions (Schuster & Otto, 2002). It would be interesting to expand the interspecific comparison of electroreceptor distribution on the head to the rest of the body and with additional species that use specific microhabitats. In addition to more detailed ecological information (e.g. habitat conditions, diet), comparisons of electroreceptor tuning properties and pore distributions for additional species (Castello et al., 2000) would further elucidate the drivers of electroreceptor evolution. Beyond furthering the theoretical understanding of the evolution of sensory organs, these studies can generate practical information. For example, they provide valuable data for studies developing aquatic robots that use electric sensors for navigation, which often use bio-inspired estimates of electroreceptor densities for developing models of electrosensory space (Snyder et al., 2007; Neveln et al., 2013).

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Cover photograph

Gobiobotia bouommatos (Photograph by Man Wang)

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