Ichthyol. Explor. Freshwaters, Vol. 31, No. 4 pp. 367–384, 7 figs., 1 tab., June 2024

LSID: http://zoobank.org/urn:lsid:zoobank.org:pub:E6F85B45-3B77-4CBF-95A1-7360E3C184E8
DOI: http://doi.org/10.23788/IEF-1199 Published 29 May 2024

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 tuberous 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.

* Department of Ecology and Conservation Biology, Texas A&M University, College Station, TX, 77843, USA. Emails: d.erniesb@gmail.com (DES), kevin.conway@tamu.edu (KWC, corresponding author), k-winemiller@tamu.edu (KOW)

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).

Acknowledgements

For technical assistance we thank Thomas Stephens, Amanda Pinion, and Kole Kubicek. We also thank Harold Zakon for helpful discussions. Mark Sabaj, Mariangeles A Hernandez (ANSP), Adam Cohen (TNHC), and Heather Prestridge (TCWC) provided access to museum specimens or provided curatorial assistance. We also thank the staff of the Texas A&M University Microscopy and Imaging Center Core Facility (RRID:SCR_022128) for their help and for granting access to equipment and Guilherme Dutra and Luiz Peixoto for providing critical review of the manuscript. DES acknowledges funding from the Tom Slick and Aviles-Johnson fellowships, Texas A&M University. KWC acknowledges financial support from Texas A&M AgriLife Research (TEX09452). KOW acknowledges funding from the Estate of Carolyn Weirichs Kelso and George Kelso. This study represents publication number 1689 of TAMU Biodiversity Research and Teaching Collections and publication number 14 of the TAMU Aquarium Research Laboratory.

Literature cited

Aguilera, P. A., M. E. Castello & A. A. Caputi. 2001. Electroreception in *Gymnotus carapo*: differences between self-generated and conspecific-generated signal carriers. Journal of Experimental Biology, 204: 185–198.

Albert, J. S. & W. G. R. Crampton. 2003. Seven new species of the Neotropical electric fish *Gymnotus* (Teleostei, Gymnotiformes) with a redescription of *G. carapo* (Linnaeus). Zootaxa, 287: 1–54.

Albert, J. S. & W. G. R. Crampton. 2005a. Electroreception and electrogenesis. Pp. 431–472 in: D. Evans (ed.), The physiology of fishes (3rd ed.). C.R.C. Press, New York.

Albert, J. S. & W. G. R. Crampton. 2005b. Diversity and phylogeny of neotropical electric fishes (Gymnotiformes). Pp. 360–409 in: T. H. Bullock, C. D. Hopkins, A. N. Popper & R. R. Fay (eds.), Electroreception. Springer Handbook of Auditory Research. Springer, New York.

Albert, J. S. & W. G. R. Crampton. 2009. A new species of electric knifefish, genus *Compsaraia* (Gymnotiformes: Apteronotidae) from the Amazon River, with extreme sexual dimorphism in snout and jaw length. Systematics and Biodiversity, 7: 81–92.

Alda, F., V. A. Tagliacollo, M. J. Bernt, B. T. Waltz, W. B. Ludt, B. C. Faircloth, M. E. Alfaro, J. S. Albert & P. Chakrabarty. 2019. resolving deep nodes in an ancient radiation of Neotropical fishes in the presence of conflicting signals from incomplete lineage sorting. Systematic Biology, 68: 573–593.

Amen, R., R. Nagel, M. Hedt, F. Kirschbaum & R. Tiedemann. 2020. Morphological differentiation in African weakly electric fish (genus *Campylomormyrus*) relates to substrate preferences. Evolutionary Ecology, 34: 427–437.

Andres, K.H., M. von Düring & E. Petrasch. 1988. The fine structure of ampullary and tuberous electroreceptors in the South American blind catfish *Pseudocetopsis* spec. Anatomy and Embryology, 177: 523–535.

Arnegard, M. E., P. B. McIntyre, L. J. Harmon, M. L. Zelditch, W. G. R. Crampton, J. K. Davis, J. P. Sullivan, S. Lavoué & C. D. Hopkins. 2010. Sexual signal evolution outpaces ecological divergence during electric fish species radiation. The American Naturalist, 176: 335–356.

Bastian, J. 1977. Variations in the frequency response of electroreceptors dependent on receptor location in weakly electric fish (Gymnotoidei) with a pulse discharge. Journal of Comparative Physiology, 121: 53–64.

Bennett, M. V. L. 1967. Mechanisms of electroreception. Pp. 313–393 in: P. H. Cahn (ed.), Lateral line detectors. Indiana University Press, Bloomington.

Bennett, M. V. L. 1970. Comparative physiology: electric organs. Annual Reviews in Physiology, 32: 471–528.

Bennett, M. V. L. 1971. Electric organs. Pp. 347–491 in: W. S. Hoar & D. J. Randall (eds.), Fish Physiology. Volume 5. Academic Press, New York and London.

Bodznick, D. & J. C. Montgomery. 2005. The physiology of low-frequency electrosensory systems. Pp. 132–153 in: T. H. Bullock, C. D. Hopkins, A. N. Popper & R. R. Fay (eds.), Electroreception. Springer Handbook of Auditory Research. Springer, New York.

Boord, R. L. & C. B. G. Campbell. 1977. Structural and functional organization of the lateral line system of sharks. American Zoologist, 17: 431–441.

Brenowitz, E. A. 1986. Environmental influences on acoustic and electric animal communication. Brain, Behavior and Evolution, 28: 32–42.

Bullock, T. H., C. D. Hopkins, A. N. Popper & R. R. Fay. 2006. Electroreception. Springer, New York.

Caputi, A. A. 1999. The electric organ discharge of pulse gymnotiforms: the transformation of a simple impulse into a complex spatio-temporal electromotor pattern. Journal of Experimental Biology, 202: 1229–1241.

Carlson, B. A., S. M. Hasan, M. Hollmann, D. B. Miller, L. J. Harmon & M. E. Arnegard. 2011. Brain evolution triggers increased diversification of electric fishes. Science, 332: 583–586.

Carr, C. E., L. Maler & E. Sas. 1982. Peripheral organization and central projections of the electrosensory nerves in gymnotiform fish. Journal of Comparative Neurology, 211: 139–153.

Carvalho, T. P. & J. S. Albert. 2015. A new species of *Rhamphichthys* (Gymnotiformes: Rhamphichthyidae) from the Amazon basin. Copeia, 103: 34–41.

Castelló, M. E., P. A. Aguilera, O. Trujillo-Cenóz & A. Caputi. 2000. Electroreception in *Gymnotus carapo*: pre-receptor processing and the distribution of electroreceptor types. Journal of Experimental Biology, 203: 3279–3287.

Coombs, S., J. Janssen & J. F. Webb. 1988. Diversity of lateral line systems: evolutionary and functional considerations. Pp. 553–593 in: J. Atema, R. R. Fay, A. N. Popper, W. N. Tavolga (eds.), Sensory biology of aquatic animals. Springer, New York.

Correa, S. B., W. G. R. Crampton & J. S. Albert. 2006. Three new species of the Neotropical electric fish *Rhabdolichops* (Gymnotiformes: Sternopygidae) from the Central Amazon, with a new diagnosis of the genus. Copeia, 2006: 27–42.

Cox Fernandes, C., J. G. Lundberg & C. Riginos. 2002. Largest of all electric-fish snouts: hypermorphic facial growth in male *Apteronotus hasemani* and the identity of *Apteronotus anas* (Gymnotiformes: Apteronotidae). Copeia, 2002: 52–61.

Crampton, W. G. R. 1998. Electric signal design and habitat preferences in a species rich assemblage of gymnotiform fishes from the upper Amazon basin. Anais da Academia Brasileira de Ciências, 70: 805–848.

Crampton, W. G. R. 2011. An ecological perspective on diversity and distributions. Pp. 165–189 in: J. S. Albert & R. Reis (eds.), Historical biogeography of Neotropical freshwater fishes. University of California Press, Berkeley.

Crampton, W. G. R., D. H. Thorsen & J. S. Albert. 2004. *Steatogenys ocellatus*: a new species of Neotropical electric fish (Gymnotiformes: Hypopomidae) from the lowland Amazon Basin. Copeia, 2004: 78–91.

Crampton, W. G. R., D. H. Thorsen & J. S. Albert. 2005. Three new species from a diverse, sympatric assemblage of the electric fish *Gymnotus* (Gymnotiformes: Gymnotidae) in the lowland Amazon Basin, with notes on ecology. Copeia, 2005: 82–99.

Crampton, W. G. R., A. Rodriguez-Cattaneo, N. R. Lovejoy & A. A. Caputi. 2013. Proximate and ultimate causes of signal diversity in the electric fish *Gymnotus*. Journal of Experimental Biology, 216: 2523–2541.

Crampton, W. G. R., C. D. de Santana, J. C. Waddell & N. R. Lovejoy. 2016a. Phylogenetic systematics, biogeography, and ecology of the electric fish genus *Brachyhypopomus* (Ostariophysi: Gymnotiformes). PloS One, 11: e0161680.

Crampton, W. G. R., C. D. de Santana, J. C. Waddell & N. R. Lovejoy. 2016b. A taxonomic revision of the Neotropical electric fish genus *Brachyhypopomus* (Ostariophysi: Gymnotiformes: Hypopomidae), with descriptions of 15 new species. Neotropical Ichthyology, 14: e150146.

Czech-Damal, N. U., A. Liebschner, L. Miersch, G. Klauer, F. D. Hanke, C. Marshall, G. Dehnhardt & W. Hanke. 2012. Electroreception in the Guiana dolphin (*Sotalia guianensis*). Proceedings of the Royal Society B, 279: 663–668.

de Santana, C. D. & W. G. R. Crampton. 2010. A review of the South American electric fish genus *Porotergus* (Gymnotiformes: Apteronotidae) with the description of a new species. Copeia, 2010: 165–175.

Dutra, G. M., L. A. W. Peixoto, V. P. Abrahão, W. B. Wosiacki, N. A. Menezes & C. D. de Santana. 2021. Morphology-based phylogeny of Eigenmanniinae Mago-Leccia, 1978 (Teleostei: Gymnotiformes: Sternopygidae), with a new classification. Journal of Zoological Systematics and Evolutionary Research, 59: 2010–2059.

Endler, J. A. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist, 139: 125–153.

Evans, K. M., M. J. Bernt, M. A. Kolmann, K. L. Ford & J. S. Albert. 2018. Why the long face? Static allometry in the sexually dimorphic phenotypes of Neotropical electric fishes. Zoological Journal of the Linnean Society, 186: 633–649.

Franz, V. 1921. Zur mikroskopischen Anatomie der Mormyriden. Zoologische Jahrbücher: Abteilung für Anatomie und Ontogenie der Tiere, 1: 119–129.

Fuller, R. C., K. L. Carleton, J. M. Fadool, T. C. Spady & J. Travis. 2005. Genetic and environmental variation in the visual properties of bluefin killifish, *Lucania goodei*: evolvable sensory systems. Journal of Evolutionary Biology, 18: 516–523.

Giora, J., C. B. Fialho & A. P. S. Dufech. 2005. Feeding habit of *Eigenmannia trilineata* Lopez & Castello, 1966 (Teleostei: Sternopygidae) of Parque Estadual de Itapuã, RS, Brazil. Neotropical Ichthyology, 3: 291–298.

Giora, J., H. M. Tarasconi & C. B. Fialho. 2014. Reproduction and feeding of the electric fish *Brachyhypopomus gauderio* (Gymnotiformes: Hypopomidae) and the discussion of a life history pattern for gymnotiforms from high latitudes. PloS One, 9 e106515.

Hopkins, C. D. 1981. On the diversity of electric signals in a community of mormyrid electric fish in West Africa. American Zoologist, 21: 211–222.

Hopkins, C. D. 1999a. Design features for electric communication. Journal of Experimental Biology, 202: 1217–1228.

Hopkins, C. D. 1999b. Signal evolution in electric communication. Pp. 461–491 in: M. D. Hauser & M. Konishi (eds.), The design of animal communication. MIT Press, Cambridge.

Jusman, Y., S. C. Ng & N. A. Abu Osman. 2014. Investigation of CPD and HMDS sample preparation techniques for cervical cells in developing computer-aided screening system based on FE-SEM/EDX. The Scientific World Journal, 2014: 289817.

Kajiura, S., A. Cornett & K. Yopak. 2010. Sensory adaptations to the environment electroreceptors as a case study. Pp. 393–433 in: J. C. Carrier, J. A. Musick & M. R. Heithaus (eds.), Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. Marine Biology. CRC Press.

Kempster, R. M., I. D. McCarthy & S. P. Collin. 2012. Phylogenetic and ecological factors influencing the number and distribution of electroreceptors in elasmobranchs. Journal of Fish Biology, 80: 2055–2088.

Kramer, B. 1990. Electrocommunication in teleost fishes: behavior and experiments. Springer, Berlin, xii + 240 pp.

Kröger, R. H. H., M. C. W. Campbell & R. D. Fernald. 2001. The development of the crystalline lens is sensitive to visual input in the African cichlid fish, *Haplochromis burtoni*. Vision Research, 41: 549–559.

Lisney, T. J., K. E. Yopak, J. C. Montgomery & S. P. Collin. 2008. Variation in brain organization and cerebellar foliation in chondrichthyans: batoids. Brain Behavior and Evolution, 72: 262–282.

Lundberg, J. G. & C. Cox Fernandes. 2007. A new species of South American ghost knifefish (Apteronotidae: *Adontosternarchus*) from the Amazon Basin. Proceedings of the Academy of Natural Sciences of Philadelphia, 156: 27–37.

Lundberg, J. G., W. M. Lewis, J. F. Saunders & F. Mago-Leccia. 1987. A major food web component in the Orinoco River channel: Evidence from planktivorous electric fishes. Science 237: 81–83.

Lundberg, J. G. & F. Mago-Leccia. 1986. A review of *Rhabdolichops* (Gymnotiformes, Sternopygidae), a genus of South American freshwater fishes, with descriptions of four new species. Proceedings of the Academy of Natural Sciences of Philadelphia, 138: 53–85.

Mago-Leccia, F., J. G. Lundberg & J. N. Baskin. 1985. Systematics of the South American freshwater fish genus *Adontosternarchus* (Gymnotiformes, Apteronotidae). Contributions in Science (Los Angeles), 358: 1–19.

Marrero, C. 1987. Notas preliminares acerca de la historia natural de los peces del Bajo Llano: 1: comparación de los habitos alimentarios de tres especies gymnotiformes, en el Río Apure (Edo Apure, Venezuela). Revue D'Hydrobiologie Tropicale, 20: 57–63.

Marrero, C., O. Castillo & A. Machado-Allison. 1987. Primera cita del genero *Traverella* Edmunds 1948 (Insecta, Ephemeroptera, Leptophlebidae), para Venezuela y comentarios preliminares acerca de la importancia del bentos en la dieta de los peces Gymnotiformes del Río Apure. Biollania, 5: 123–128.

Marrero, C. & K. O. Winemiller. 1993. Tube-snouted gymnotiform and mormyriform fishes: convergence of a specialized foraging mode in teleosts. Environmental Biology of Fishes, 38: 299–309.

Morson, J. M. & J. F. Morrissey. 2007. Morphological variation in the electric organ of the little skate (*Leucoraja erinacea*) and its possible role in communication during courtship. Pp. 161–169 in: D. A. Ebert & J. A. Sulikowski (eds.), Biology of skates. Springer.

Nagel, R., F. Kirschbaum & R. Tiedemann. 2017. Electric organ discharge diversification in mormyrid weakly electric fish is associated with differential expression of voltage-gated ion channel genes. Journal of Comparative Physiology A, 203: 183–195.

Neveln, I. D., Y. Bai, J. B. Snyder, J. R. Solberg, O. M. Curet, K. M. Lynch & M. A. MacIver. 2013. Biomimetic and bio-inspired robotics in electric fish research. Journal of Experimental Biology, 216: 2501–2514.

Nakazawa, M. & M. M. Nakazawa. 2019. Package 'fmsb'. Available from https://cran.r-project.org/web/packages/fmsb/fmsb.pdf.

Peixoto, L. A. W., G. M. Dutra & W. B. Wosiacki. 2015. The electric glass knifefishes of the *Eigenmannia trilineata* species-group (Gymnotiformes: Sternopygidae): monophyly and description of seven new species. Zoological Journal of the Linnean Society, 175: 384–414.

Peixoto, L. A. W., A. Datovo, R. R. Campos-da-Paz, C. D. de Santana & N. A. Menezes. 2019. Anatomical, taxonomic, and phylogenetic reappraisal of a poorly known ghost knifefish, *Tembeassu marauna* (Ostariophysi: Gymnotiformes), using X-ray microcomputed tomography. PLoS ONE 14: e0225342.

Peixoto, L. A., M. N. Pastana & G. A. Ballen. 2021. New species of glass knifefish genus *Eigenmannia* (Gymnotiformes: Sternopygidae) with comments on the morphology and function of the enlarged cephalic lateral-line canals of Sternopygidae. Journal of Fish Biology, 98: 142–153.

Peixoto, L. A. W., R. Campos-da-Paz, N. A. Menezes, C. D. de Santana, M. Triques & A. Datovo, A. 2022. Systematics of Neotropical electric knifefish *Tembeassu* (Gymnotiformes, Apteronotidae). Systematics and Biodiversity, 20: 1–19.

Pinion, A. K., D. Siegel, R. Britz, R. Martínez-García, C. A. Álvarez-González & K. W. Conway. 2021. The larval attachment organ of the Tropical Gar *Atractosteus tropicus* Gill, 1863 (Lepisosteiformes: Lepisosteidae). Journal of Fish Biology, 99: 418–424

Raschi, W. 1986. A morphological analysis of the ampullae of Lorenzini in selected skates (Pisces, Rajoidei). Journal of Morphology, 189: 225–247.

Sazima, I., L. N. Carvalho, F. P. Mendonça & J. Zuanon. 2006. Fallen leaves on the water-bed: diurnal camouflage of three night active fish species in an Amazonian streamlet. Neotropical Ichthyology, 4: 119–122.

Schindelin, J., I. Arganda-Carreras, E. Frise, V. Kaynig, M. Longair, T. Pietzsch, S. Preibisch, C. Rueden, S. Saalfeld, B. Schmid & J. Y. Tinevez. 2012. Fiji: an open-source platform for biological-image analysis. Nature Methods, 9: 676–682.

Schuster, S. & N. Otto. 2002. Sensitivity to novel feedback at different phases of a gymnotid electric organ discharge. Journal of Experimental Biology, 205: 3307–3320.

Sisneros, J.A., T. C. Tricas & C. A. Luer. 1998. Response properties and biological function of the skate electrosensory system during ontogeny. Journal of Comparative Physiology, A, 183: 87–99.

Shand, J., W. L. Davies, N. Thomas, L. Balmer, J. A. Cowing, M. Pointer, L. S. Carvalho, A. E. O. Trezise, S. P. Collin, L. D. Beazley & D. M. Hunt. 2008. The influence of ontogeny and light environment on the expression of visual pigment opsins in the retina of the black bream, *Acanthopagrus butcheri*. Journal of Experimental Biology, 211: 1495–1503.

Snyder, J. B., M. E. Nelson, J. W. Burdick & M. A. MacIver. 2007. Omnidirectional sensory and motor volumes in electric fish. PLoS Biology, 5: e301.

Stoddard, P. K. 2002. Electric signals: predation, sex, and environmental constraints. Advances in the Study of Behavior, 31: 201–242.

Szabo, T. 1974. Anatomy of the specialized lateral line organs of electroreception. Pp. 13–58 in: A. Fessard (ed.), Electroreceptors and other specialized receptors in lower vertebrates. Springer, Berlin.

Szabo, T. 1965. Sense organs of the lateral line system in some electric fish of the Gymnotidae, Mormyridae and Gymnarchidae. Journal of Morphology, 117: 229–249.

Szamier, R. B. & A. W. Wachtel. 1969. Special cutaneous receptor organs of fish III: the ampullary organs of *Eigenmannia*. Journal of Morphology, 128: 261–289.

Tagliacollo, V. A., M. J. Bernt, J. M. Craig, C. Oliveira & J. S. Albert. 2016. Model-based total evidence phylogeny of Neotropical electric knifefishes (Teleostei, Gymnotiformes). Molecular Phylogenetics and Evolution, 95: 20–33.

Tricas, T. C., S. W. Michael & J. A. Sisneros. 1995. Electrosensory optimization to conspecific phasic signals for mating. Neuroscience Letters, 202: 129–32.

Trujillo-Cenóz, O., J. A. Echagüe & O. Macadar. 1984. Innervation pattern and electric organ discharge waveform in *Gymnotus carapo* (Teleostei; Gymnotiformes). Journal of Neurobiology, 15: 273–281.

Vélez, A. & B. A. Carlson. 2018. Sensory specializations of mormyrid fish are associated with species differences in electric signal localization behavior. Brain, Behavior and Evolution, 92: 125–141.

Vischer, H. A. 1995. Electroreceptor development in the electric fish *Eigenmannia*: a histological and ultrastructural study. Journal of Comparative Neurology, 360: 81–100.

Vischer, H. A. 1989. The development of lateral-line receptors in *Eigenmannia* (Teleostei, Gymnotiformes). I. The mechanoreceptive lateral-line system. Brain, Behavior and Evolution, 33: 205–222.

Wachtel, A.W. & B. Szamier. 1966. Special cutaneous receptor organs of fish: The tuberous organs of *Eigenmannia*. Journal of Morphology, 119: 51–80.

Wagner, H.-J. & R. H. H. Kröger. 2005. Adaptive plasticity during the development of colour vision. Progress in Retinal and Eye Research, 24: 521–536.

Webb, J. F. 1989a. Developmental constraints and evolution of the lateral line system in teleost fishes. Pp. 79–97 in: S. Coombs, P. Görner & H. Münz (eds.), The mechanosensory lateral line. Springer, New York.

Webb, J. F. 1989b. Gross morphology and evolution of the mechanosensory lateral line system in teleost fishes. Brain, Behavior and Evolution, 33: 34–53.

Winemiller, K. O. 1989. Patterns of variation in life history among South American fishes in seasonal environments. Oecologia, 81: 225–241.

Winemiller, K. O. & A. Adite. 1997. Convergent evolution of weakly-electric fishes from floodplain habitats in Africa and South America. Environmental Biology of Fishes, 49: 175–186.

Xu-Friedman, M. A. & C. D. Hopkins. 1999. Central mechanisms of temporal analysis in the knollenorgan pathway of mormyrid electric fish. Journal of Experimental Biology, 202: 1311–1318.

Yager, D. D. & C. D. Hopkins. 1993. Directional characteristics of tuberous electroreceptors in the weakly electric fish, *Hypopomus* (Gymnotiformes). Journal of Comparative Physiology A, 173: 401–414.

Zakon, H. H. 1984. Postembryonic changes in the peripheral electrosensory system of a weakly electric fish: addition of receptor organs with age. Journal of Comparative Neurology, 228: 557–570.

Zakon, H. H. 1987. Variation in the mode of receptor cell addition in the electrosensory system of gymnotiform fish. Journal of Comparative Neurology, 262: 195–214.

Received 2 February 2024
Revised 13 March 2024
Accepted 3 May 2024

The whole contribution can be purchased as PDF file.

Availability

Generally all our publications are available as PDF files; full publications as a general rule after the printed version is out of print. If you have questions concerning particular contributions please contact us by e-mail:
pdf@pfeil-verlag.de.

The PDF files are protected by copyright.

The PDF file may be printed for personal use.
The reproduction and dissemination of the content or part of it is permitted.
It is not allowed to transfer the digital personal certificate or the password to other persons.

Prices

Books: Prices are to be found in the catalog.

Articles in journals and single contributions or chapters in books:

10 EURO basic price per order (including the first 10 pages),
and
0.50 EURO per page, beginning with the 11th page.

Page numbers are found in the contents of the publications.

Orders

Use our order form for PDF files or send your order informal per e-mail (pdf@pfeil-verlag.de). The only accepted payment is by credit card. While using the order form for PDF files, your data will be transmitted by secure link (ssl). You also may send the informations informally by e-mail, fax, phone or mail.

Handling

As soon as possible, depending on our business hours and your order, you will receive your PDF file together with the certificate and password by e-mail.
Larger PDF files can be downloaded from our webspace, if necessary.
Your invoice will be sent out by e-mail after we charged your credit card.

To open the encrypted PDF files you have to install your personal certificate after your first order. All PDF files with the same certificate can be opened from that time on.

Dieser Beitrag kann als PDF-Datei erworben werden.

Verfügbarkeit von PDF-Dateien
Prinzipiell sind von allen unseren Publikationen PDF-Dateien erhältlich. Komplette Publikationen in der Regel erst nachdem die gedruckte Version vergriffen ist. Anfragen bezüglich bestimmter Beiträge richten Sie bitte per E-Mail an pdf@pfeil-verlag.de.

Die PDF-Dateien sind urheberrechtlich geschützt.
Ein Ausdruck der PDF-Dateien ist nur für den persönlichen Gebrauch erlaubt.
Die Vervielfältigung von Ausdrucken, erneutes Digitalisieren sowie die Weitergabe von Texten und Abbildungen sind nicht gestattet.
Das persönliche Zertifikat und das Passwort dürfen nicht an Dritte weitergegeben werden.

Preise
Bücher: Die Preise sind dem Katalog zu entnehmen.
Zeitschriftenbeiträge und einzelne Kapitel aus Sammelbänden bzw. Büchern:
10 EURO Grundbetrag pro Bestellung (einschließlich der ersten 10 Seiten),
und
0,50 EURO pro Seite ab der 11. Seite.
Den Umfang der Beiträge entnehmen Sie bitte den Inhaltsverzeichnissen.

Bestellungen
Bestellungen sind mit dem PDF-Bestellformular oder formlos per E-Mail (pdf@pfeil-verlag.de) an uns zu richten. Die Bezahlung ist ausschließlich per Kreditkarte möglich. Bei Verwendung unseres Bestellformulars werden die Kreditkartendaten über eine gesicherte Verbindung (ssl) übermittelt. Sie können die Daten aber auch formlos per E-Mail, Fax, Post oder telefonisch übermitteln.

Abwicklung
So bald wie möglich, aber abhängig von unseren Bürozeiten und der gewünschten Bestellung, schicken wir Ihnen die PDF-Datei(en) zusammen mit Ihrem persönlichen Zertifikat und dem zugehörigem Passwort per E-Mail. Größere Dateien bieten wir Ihnen gegebenenfalls zum Herunterladen an.
Der fällige Betrag wird von Ihrer Kreditkarte abgebucht und Sie erhalten die Rechnung ebenfalls per E-Mail.
Um die verschlüsselten PDF-Dateien öffnen zu können, muss bei der ersten Bestellung das passwortgeschützte persönliches Zertifikat installiert werden, welches anschließend auf dem Rechner verbleibt. Alle mit diesem Zertifikat verschlüsselten Dateien können anschließend auf diesem Rechner geöffnet werden.