

Behavioral evidence of chemical communication by male caudal fin organs of a glandulocaudine fish (Teleostei: Characidae)

Clayton Kunio Fukakusa*

All fishes in the tribe Glandulocaudini have hypertrophied tissue with club cells in the caudal fin (the caudal organ). Because this structure is present only in adult males, it is hypothesized that these cells secrete a reproduction-related pheromone. The hypothesis that the caudal organ releases chemicals that attract females is tested in *Mimagoniates inaequalis*. In a Y-maze and an aquarium, females were attracted to a caudal organ extract and to water that was conditioned with caudal organ-bearing males, respectively, but not to caudal-fin lobe extract or water conditioned with males from which the caudal organs were removed (control stimuli). In tests with male-female pairs, there were no differences in the responses to caudal organ extract and male caudal organ-conditioned water, but the responses to both stimuli differed in relation to the controls. Male-female pairs engaged in fewer courtship events and more agonistic interactions than they did without chemical stimuli and with control stimuli. These results provide evidence for a possible pheromonal system in *M. inaequalis*. The caudal organ is a specialized secretory structure that produces a chemical signal that attracts females and increases the aggressiveness of males.

Introduction

The ability of animals to obtain information about their physical and social environment is essential for their survival and reproductive success (Ward et al., 2007). In the last case, intersexual communication to attract, locate or assess the quality of potential reproductive partners may involve visual, tactile, auditory, and chemical signals (Gaskell, 2007).

Fishes of the teleost cohort Otomorpha (Betancur-R et al., 2017), that comprise seven order, are mostly oviparous and externally fertilizing strategists. However, in some species of Characi-

formes (Kutaygil, 1959; Nelson, 1964a; Burns et al., 1995, 1997, 2000; Malabarba, 1998; Weitzman & Menezes, 1998; Castro et al., 2003; Weitzman et al., 2005; Javonillo et al., 2009; Quagio-Grassiotti et al., 2012) and Siluriformes (von Ihering, 1937; Loir et al., 1989; Burns et al., 2000; Meisner et al., 2000; Spadella et al., 2008, 2012; Javonillo et al., 2009) sperm has been reported in the ovaries, along with unfertilized eggs, and therefore the term insemination has been used to characterize the strategy adopted by these fishes (Burns et al., 1995, 1997; Azevedo et al., 2000; Burns & Weitzman, 2005; Javonillo et al., 2009).

* Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, 91501-970 Porto Alegre, RS, Brazil.
E-mail: claytonfukakusa@gmail.com

Literature cited

- Arbuckle, W. J., A. J. Bélanger, L. D. Corkum, B. S. Zielinski, W. Li, S.-S. Yun, S. Bachynski & A. P. Scott. 2005. In vitro biosynthesis of novel 5 β -reduced steroids by the testis of the round goby, *Neogobius melanostomus*. General and Comparative Endocrinology, 140: 1-13.
- Atkins, D. L. & W. L. Fink. 1979. Morphology and histochemistry of the caudal gland of *Corynopoma riisei* Gill. Journal of Fish Biology, 14: 465-469.
- Azevedo, M. A., C. B. Fialho & L. R. Malabarba. 2016. Reproductive strategies in two inseminating species of Glandulocaudini, *Mimagoniates microlepis* and *Mimagoniates rheocharis* (Characiformes: Characidae: Stevardiinae). Journal of Fish Biology, 89: 431-444.
- Azevedo, M. A., L. R. Malabarba & C. B. Fialho. 2000. Reproductive biology of the inseminating glandulocaudine *Diapoma speculiferum* Cope (Teleostei: Characidae). Copeia, 2000: 983-989.
- Azevedo, M. A., L. R. Malabarba & J. R. Burns. 2010. Reproductive biology and development of gill glands in the inseminating characid, *Macropsobrycon uruguayanae* Eigenmann, 1915 (Cheirodontinae: Compsoptini). Neotropical Ichthyology, 8: 87-96.
- Barata, E. N., R. M. Serrano, A. Miranda, R. Nogueira, P. C. Hubbard & A. V. M. Canário. 2008. Putative pheromones from the anal glands of male blennies attract females and enhance male reproductive success. Animal Behaviour, 75: 379-389.
- Bélanger, A. J., W. J. Arbuckle, L. D. Corkum, D. B. Gammon, W. Li, A. P. Scott & B. S. Zielinski. 2004. Behavioural and electrophysiological responses by reproductive female *Neogobius melanostomus* to odours released by conspecific males. Journal of Fish Biology, 65: 933-946.
- Betancur-R, R., E. O. Wiley, G. Arratia, A. Acero, N. Bailly, M. Miya, G. Lecointre & G. Ortí. 2017. Phylogenetic classification of bony fishes. BMC Evolutionary Biology, 17: 1-140.
- Burns, J. R. & S. H. Weitzman. 1996. Novel gill-derived gland in the male swordtail characin, *Corynopoma riisei* (Teleostei: Characidae: Glandulocaudinae). Copeia, 1996: 627-633.
- Burns, J. R. & S. H. Weitzman. 2005. Insemination in ostariophysan fishes. Pp. 107-134 in: H. J. Grier & M. C. Uribe (eds.), Viviparous Fishes. Volume 11. New Life, Homestead.
- Burns, J. R., S. H. Weitzman, H. J. Grier & N. A. Menezes. 1995. Internal fertilization, testis and sperm morphology in Glandulocaudine fishes (Teleostei, Characidae, Glandulocaudinae). Journal of Morphology, 224: 131-145.
- Burns, J. R., S. H. Weitzman & L. R. Malabarba. 1997. Insemination in eight species of cheirodentine fishes (Teleostei: Characidae: Cheirodentinae). Copeia, 1997: 433-438.
- Burns, J. R., S. H. Weitzman, L. R. Malabarba & A. Downing-Meisner. 2000. Sperm modifications in inseminating Ostariophysan fishes, with new documentation of inseminating species. P. 255 in: B. Norberg et al. (eds.), Proceedings of the 6th International Symposium on the Reproductive Physiology of Fish. Institute of Marine Research and University of Bergen, Bergen.
- Bushmann, P. J., J. R. Burns & S. H. Weitzman. 2002. Gill-derived glands in glandulocaudine fishes (Teleostei: Characidae: Glandulocaudinae). Journal of Morphology, 253: 187-195.
- Castro, R. M. C., A. C. Ribeiro, R. C. Benine & A. L. A. Melo. 2003. *Lophiobrycon weitzmani*, a new genus and species of glandulocaudine fish (Characiformes: Characidae) from the rio Grande drainage, upper rio Paraná system, southeastern Brazil. Neotropical Ichthyology, 1: 11-19.
- Colombo, L., A. Marconato, P. C. Belvedere & C. Friso. 1980. Endocrinology of teleost reproduction: a testicular steroid pheromone in the black goby, *Gobius joso* L. Bollettino di Zoologia, 47: 355-364.
- Crow, R. T. & N. R. Liley. 1979. A sexual pheromone in the guppy, *Poecilia reticulata* (Peters). Canadian Journal of Zoology, 57: 184-188.
- Ferreira, K. M., N. A. Menezes & I. Quagio-Grassiotti. 2011. A new genus and two new species of Stevardiinae (Characiformes: Characidae) with a hypothesis on their relationships based on morphological and histological data. Neotropical Ichthyology, 9: 281-298.
- Gammon, D. B., W. Li, A. P. Scott, B. S. Zielinski & L. D. Corkum. 2005. Behavioural responses of female *Neogobius melanostomus* to odours of conspecifics. Journal of Fish Biology, 67: 615-626.
- Garber, J. C., R. W. Barbee, J. T. Bielitzki, L. Clayton, J. Donovan, C. Hendriksen, D. Kohn, N. Lipman, P. Locke & J. Melcher. 2011. Guide for the care and use of laboratory animals. National Academies, Washington D.C.
- Gaskett, A. C. 2007. Spider sex pheromones: emission, reception, structures, and functions. Biological Reviews, 82: 27-48.
- Géry, J. 1977. Characoids of the world. T.F.H., Neptune City, 672 pp.
- Gonçalves T. K., M. A. Azevedo, L. R. Malabarba & C. B. Fialho. 2005. Reproductive biology and development of sexually dimorphic structures in *Aphyocharax anisitsi* (Ostariophysi: Characidae). Neotropical Ichthyology, 3: 433-438.
- Javonillo, R., J. R. Burns & S. H. Weitzman. 2009. Sperm modifications related to insemination, with examples from the Ostariophysi. Pp. 723-763 in: A. B. G. M. Jamieson (ed.), Reproductive biology and phylogeny of fishes. Volume 8. Science, Enfield.
- Javonillo, R., L. R. Malabarba, S. H. Weitzman & J. R. Burns. 2010. Relationships among major lineages of characid fishes (Teleostei: Ostariophysi: Characiformes), based on molecular sequence data. Molecular Phylogenetics and Evolution, 54: 498-511.

- Kutaygil, D. L. 1959. Insemination, sexual differentiation and secondary sex characters in *Stewardia albipinnis* Gill. Hydrobiologia University Istanbul Fen Fakültesi Mecmuası, 24: 93–128.
- Lambert, J. G. D. & J. W. Resink. 1991. Steroid glucuronides as male pheromones in the reproduction of the African catfish *Clarias gariepinus* – a brief review. The Journal of Steroid Biochemistry and Molecular Biology, 40: 549–556.
- Li, W., A. P. Scott, M. J. Siefkes, H. Yan, Q. Liu, S.-S. Yun & D. A. Gage. 2002. Bile acid secreted by male sea lamprey that acts as a sex pheromone. Science, 296: 138–141.
- Locatello, L., C. Mazzoldi & M. B. Rasotto. 2002. Ejaculate of sneaker males is pheromonally inconspicuous in the black goby, *Gobius niger* (Teleostei, Gobiidae). Journal of Experimental Zoology, 293: 601–605.
- Loir, M., C. Cauty, P. Planquette & P.-Y. Le Bail. 1989. Comparative study of the male reproductive tract in seven families of South-American catfishes. Aquatic Living Resour, 2: 45–56.
- Malabarba, L. R. 1998. Monophyly of the Cheirodoninae, characters and major clades (Ostariophysi: Characidae). Pp. 193–233 in: L. R. Malabarba et al. (eds.), Phylogeny and classification of Neotropical fishes. Edipucrs, Porto Alegre.
- Meisner, A. D., J. R. Burns, S. H. Weitzman & L. R. Malabarba. 2000. Morphology and histology of the male reproductive system in two species of internally inseminating South American catfishes, *Trachelyopterus lucenai* and *T. galeatus* (Teleostei: Auchenipteridae). Journal of Morphology, 246: 131–141.
- Menezes, N. A. & S. H. Weitzman. 1990. Two new species of *Mimagoniates* (Teleostei: Characidae: Glandulocaudinae), their phylogeny and biogeography and a key to the glandulocaudin fishes of Brazil and Paraguay. Proceedings of the Biological Society of Washington, 103: 380–426.
- Menezes, N. A. & S. H. Weitzman. 2009. Systematics of the Neotropical fish subfamily Glandulocaudinae (Teleostei: Characiformes: Characidae). Neotropical Ichthyology, 7: 295–370.
- Meyer, J. H. & N. R. Liley. 1982. The control of production of a sexual pheromone in the female guppy, *Poecilia reticulata*. Canadian Journal of Zoology, 60: 1505–1510.
- Mirande, J. M. 2018. Morphology, molecules and the phylogeny of Characidae (Teleostei, Characiformes). Cladistics, 35: 282–300.
- Nelson, K. 1964a. Behavior and morphology in the Glandulocaudine fishes (Ostariophysi, Characidae). University of California Publications in Zoology, 75: 59–152.
- Nelson, K. 1964b. The evolution of a pattern of sound production associated with courtship in the characid fish, *Glandulocauda inequalis*. Evolution, 18: 526–540.
- Nelson, K. 1964c. The temporal patterning of courtship behaviour in the Glandulocaudine fishes (Ostariophysi, Characidae). Behaviour, 24: 90–145.
- Oliveira, C., G. S. Avelino, K. T. Abe, T. C. Mariguela, R. C. Benine, G. Ortí, R. P. Vari & R. M. C. Castro. 2011. Phylogenetic relationships within the speciose family Characidae (Teleostei: Ostariophysi: Characiformes) based on multilocus analysis and extensive ingroup sampling. BMC Evolutionary Biology, 11: 1–25.
- Oliveira, C., L. C., L. R. Malabarba & J. R. Burns. 2012. Comparative morphology of gill glands in externally fertilizing and inseminating species of cheirodontine fishes, with implications on the phylogeny of the family Characidae (Actinopterygii: Characiformes). Neotropical Ichthyology, 10: 349–360.
- Pfeiffer, W. 1963. Alarm substances. Experientia, 19: 113–123.
- Pfeiffer, W. 1967. Schreckreaktion und Schreckstoffzellen bei Kneriidae und Phractolaemidae (Isospondyli, Pisces). Naturwissenschaften, 54: 177.
- Pfeiffer, W. 1977. The distribution of fright reaction and alarm substance cells in fishes. Copeia, 1977: 653–665.
- Quagio-Grassiotti, I., L. R. Malabarba, M. A. Azevedo, J. R. Burns, C. M. Baicere-Silva & R. Quevedo. 2012. Unique derived features in spermiogenesis and sperm morphology supporting a close relationship between the species of *Hollandichthys* and *Rachoviscus* (Characiformes: Characidae). Copeia, 2012: 609–625.
- Resink, J. W., R. van den Hurk, R. F. O. Groeninx van Zoelen & E. A. Huisman. 1987. The seminal vesicle as source of sex attracting substances in the African catfish, *Clarias gariepinus*. Aquaculture, 63: 115–127.
- Resink, J. W., P. K. Voorthuis, R. van den Hurk, R. C. Peters & P. G. W. J. van Oordt. 1989. Steroid glucuronides of the seminal vesicle as olfactory stimuli in African catfish, *Clarias gariepinus*. Aquaculture, 83: 153–166.
- Serrano, R. M., E. N. Barata, M. A. Birkett, P. C. Hubbard, P. S. Guerreiro & A. V. M. Canário. 2008a. Behavioral and olfactory responses of female *Salarias pavo* (Pisces: Blenniidae) to a putative multi-component male pheromone. Journal of Chemical Ecology, 34: 647–658.
- Serrano, R. M., O. Lopes, P. C. Hubbard, J. Araújo, A. V. M. Canário & E. N. Barata. 2008b. Seasonal cell differentiation and olfactory potency of secretions by the anal glands of male peacock blenny *Salarias pavo*. Journal of Fish Biology, 73: 1790–1798.
- Shrestha, B., R. Javonillo, J. R. Burns, Z. Pirger & A. Vertes. 2013. Comparative local analysis of metabolites, lipids and proteins in intact fish tissues by LAESI mass spectrometry. Analyst, 138: 3444–3449.
- Siefkes, M. J., A. P. Scott, B. Zielinski, S.-S. Yun & W. Li. 2003. Male sea lampreys, *Petromyzon marinus* L., excrete a sex pheromone from gill epithelia. Biology of Reproduction, 69: 125–132.
- Sorensen, P. W. & N. E. Stacey. 2004. Brief review of fish pheromones and discussion of their possible uses in the control of non-indigenous teleost fishes.

- New Zealand Journal of Marine and Freshwater Research, 38: 399–417.
- Spadella, M. A., C. Oliveira, H. Ortega, I. Quagio-Grassiotto & J. R. Burns. 2012. Male and female reproductive morphology in the inseminating genus *Astroblepus* (Ostariophysi: Siluriformes: Astroblepidae). *Zoologischer Anzeiger*, 251: 38–48.
- Spadella, M. A., C. Oliveira & I. Quagio-Grassiotto. 2008. Morphology and histology of male and female reproductive systems in the inseminating species *Scolopax distolothrix* (Ostariophysi: Siluriformes: Scolopacidae). *Journal of Morphology*, 269: 1114–1121.
- Stacey, N. 2003. Hormones, pheromones and reproductive behavior. *Fish Physiology and Biochemistry*, 28: 229–235.
- Stacey, N. & P. Sorensen. 2006. Reproductive pheromones. Pp. 359–412 in: K. A. Sloman et al. (eds.), *Behaviour and physiology of fish*. Volume 24. Elsevier Academic, Amsterdam.
- Thomaz, A. T., D. Arcila, G. Ortí & L. R. Malabarba. 2015. Molecular phylogeny of the subfamily Stevardiinae Gill, 1858 (Characiformes: Characidae): classification and the evolution of reproductive traits. *BMC Evolutionary Biology*, 15: 146–171.
- van den Hurk, R. V. D. & J. G. D. Lambert. 1983. Ovarian steroid glucuronides function as sex pheromones for male zebrafish, *Brachydanio rerio*. *Canadian Journal of Zoology*, 61: 2381–2387.
- von Ihering, R. 1937. Oviductal fertilization in the South American catfish, *Trachycorytes*. *Copeia*, 1937: 201–205.
- Ward, A. J. W., M. M. Webster & P. J. B. Hart. 2007. Social recognition in wild fish populations. *Proceedings of the Royal Society B*, 274: 1071–1077.
- Weitzman, S. H. & S. V. Fink. 1985. Xenobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae). *Smithsonian Contributions to Zoology*, 421: 1–121.
- Weitzman, S. H. & N. A. Menezes. 1998. Relationships of the tribes and genera of the Glandulocaudinae (Ostariophysi: Characiformes: Characidae) with a description of a new genus, *Chrysobrycon*. Pp. 171–192 in: L. R. Malabarba et al. (eds.), *Phylogeny and classification of Neotropical fishes*. Edipucrs, Porto Alegre.
- Weitzman, S. H., N. A. Menezes, H.-G. Evers & J. R. Burns. 2005. Putative relationships among inseminating and externally fertilizing characids, with a description of a new genus and species of Brazilian inseminating fish bearing an anal-fin gland in males (Characiformes: Characidae). *Neotropical Ichthyology*, 3: 329–360.

Received 8 October 2019

Revised 30 December 2019

Accepted 17 July 2020

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.