

- 15 Kramer, B., Electric and motor responses of the weakly electric fish, *Gnathonemus petersii* (Mormyridae) to play-back of social signals. *Behav. Ecol. Sociobiol.* 6 (1979) 67–79.
- 16 Kramer, B., and Westby, G. W. M., No sex difference in the waveform of the pulse type electric fish, *Gnathonemus petersii* (Mormyridae). *Experientia* 41 (1985) 1530–1531.
- 17 Landsman, R. E., and Moller, P., Testosterone changes the electric organ discharge and external morphology of the mormyrid fish, *Gnathonemus petersii* (Mormyridae). *Experientia* 44 (1988) 900–903.
- 18 Landsman, R. E., Jou, S. H., and Moller, P., Stress obscures signalling of sexual identity in *Gnathonemus petersii* (Mormyridae), in: *Reproductive Physiology of Fish 1987*, p. 307. Eds D. R. Idler et al. Proc. 3rd Int. Symp. Reprod. Physiol. Fish, St. John's, Newfoundland 1987.
- 19 Leopold, A. S., The nature of heritable wildness in turkeys. *Condor* 46 (1944) 133–197.
- 20 Lückner, H., and Kramer, B., Development of a sex difference in the preferred latency response in the weakly electric fish, *Pollimyrus isidori* (Cuvier et Valenciennes) (Mormyridae, Teleostei). *Behav. Ecol. Sociobiol.* 9 (1981) 103–109.
- 21 Mazeaud, M. M., and Mazeaud, F., Adrenergic responses to stress in fish, in: *Stress and Fish*, pp. 49–75. Ed. A. D. Pickering. Academic Press, New York 1981.
- 22 Moller, P., Electroprecognition. *Oceanus* 23 (1980) 44–54.
- 23 Moller, P., Electroprecognition and the behaviour of mormyrid fish. *Trends Neurosci.* 3 (1980) 105–109.
- 24 Moller, P., Serrier, J., and Bowling, D., Electric organ discharge displays during social encounter in the weakly electric fish *Brienomyrus niger* L. (Mormyridae). *Ethology* 82 (1989) 177–191.
- 25 Moore, F. L., and Miller, L. J., Stress-induced inhibition of sexual behavior: corticosterone inhibits courtship behaviors of a male amphibian (*Taricha granulosa*). *Horm. Behav.* 18 (1984) 400–410.
- 26 Moore, F. L., and Zoeller, R. T., Stress-induced inhibition of reproduction: evidence of suppressed secretion of LH-RH in an amphibian. *Gen. comp. Endocr.* 60 (1985) 252–258.
- 27 Moore, F. L., and Deviche, P., Neuroendocrine processing of environmental information in amphibians, in: *Processing of Environmental Information in Vertebrates*, pp. 19–45. Ed. M. H. Stetson. Springer-Verlag, New York 1988.
- 28 Ozon, R., Androgens in fishes, amphibians, reptiles, and birds, in: *Steroids in Nonmammalian Vertebrates*, pp. 328–389. Ed. D. R. Idler. Academic Press, New York 1972.
- 29 Richter, C. P., The effects of domestication and selection on the behavior of the Norway rat. *J. natl. Cancer Inst.* 15 (1954) 727–738.
- 30 Rivier, C., Rivier, J., and Vale, W., Stress-induced inhibition of reproductive functions: role of endogenous corticotropin-releasing factor. *Science* 231 (1986) 607–609.
- 31 Safford, S., and Thomas, P., Effects of capture and handling on circulating levels of gonadal steroids and cortisol in the spotted seatrout, *Cynoscion nebulosus*, in: *Reproductive Physiology of Fish 1987*, p. 312. Eds D. R. Idler et al. Proc. 3rd Int. Symp. Reprod. Physiol. Fish, St. John's, Newfoundland 1987.
- 32 Sapolsky, R. M., The endocrine stress-response and social status in the wild baboon. *Horm. Behav.* 16 (1982) 279–292.
- 33 Singh, H., Griffith, R. W., Takahashi, A., Kawachi, H., Thomas, P., and Stegeman, J. J., Regulation of gonadal steroidogenesis in *Fundulus heteroclitus* by recombinant salmon growth hormone and purified salmon prolactin. *Gen. comp. Endocr.* 72 (1988) 144–153.
- 34 Sumpter, J. P., Carragher, J., Pottinger, T. G., and Pickering, A. D., The interaction of stress and reproduction in trout, in: *Reproductive Physiology of Fish 1987*, pp. 299–302. Eds D. R. Idler et al. Proc. 3rd Int. Symp. Reprod. Physiol. Fish, St. John's, Newfoundland 1987.
- 35 Westby, G. W. M., and Kirschbaum, F., Emergence and development of the electric organ discharge in *Pollimyrus isidori*. I. The larval discharge. *J. comp. Physiol.* 122 (1977) 251–271.
- 36 Westby, G. W. M., and Kirschbaum, F., Sex differences in the electric organ discharge of *Eigenmannia virescens* and the effect of gonadal maturation, in: *Sensory Physiology of Aquatic Lower Vertebrates*, Adv. Physiol. Sci., vol. 31, pp. 179–194. Eds T. Szabo and G. Czeh. Pergamon Press, Budapest 1981.
- 37 Westby, G. W. M., and Kirschbaum, F., Sex differences in the waveform of the pulse-type electric fish, *Pollimyrus isidori* (Mormyridae). *J. comp. Physiol.* 145 (1982) 399–403.
- 38 Wingfield, J. C., Changes in reproductive function of free-living birds in direct response to environmental perturbations, in: *Processing of Environmental Information in Vertebrates*, pp. 121–148. Ed. M. H. Stetson. Springer-Verlag, New York 1988.

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## Research Articles

### Multiple prismatic calcium phosphate layers in the jaws of present-day sharks (Chondrichthyes; Selachii)

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**Summary.** Jaws of large individuals, over 2 m in total length, of the shark species *Carcharodon carcharias* (great white shark) and *Isurus oxyrinchus* (mako shark) of the family Lamnidae, and *Galeocerdo cuvieri* (tiger shark) and *Carcharhinus leucas* (bull shark) of the family Carcharhinidae were found to have multiple, up to five, layers of prismatic calcium phosphate surrounding the cartilages. Smaller individuals of these species and other known species of living chondrichthyans have only one layer of prismatic calcium phosphate surrounding the cartilages, as also do most species of fossil chondrichthyans. Two exceptions are the fossil shark genera *Xenacanthus* and *Tamiobatis*. Where it is found in living forms, this multiple layered calcification does not appear to be phylogenetic, as it appears to be lacking in other lamnid and carcharhinid genera and species. Rather it appears to be functional, only appearing in larger individuals and species of these two groups, and hence may be necessary to strengthen the jaw cartilages of such individuals for biting.

**Key words.** Chondrichthyes; sharks; jaws; prismatic calcium phosphate.

Chondrichthyan fishes are characterized by having skeletons composed of cartilage and lacking bone<sup>1</sup>. However, most species have some of their cartilages surrounded by calcium phosphate prisms to strengthen various skeletal elements<sup>2</sup>. The extent and degree of this calcification appears to be functional, as it is heaviest in the cartilages of the jaws, vertebral column, cranium, etc.<sup>3</sup>. Schaeffer<sup>4</sup> stated that living chondrichthyans and at least the fossil shark genus *Hybodus* possess only a single layer of prismatic calcium phosphate surrounding their cartilage structures, whereas at least two fossil shark genera, *Xenacanthus* and *Tamiodontis*, have numerous layers of prismatic calcium phosphate surrounding the cartilages, and this seems to be of phylogenetic importance. While examining Recent shark jaws for tooth morphology, we discovered four Recent species in the families Lamnidae and Carcharhinidae which possess multiple layers of prismatic calcium phosphate surrounding the cartilages in large individuals.

Cross-sections of jaws and other cartilages were examined on dried chondrichthyan specimens in the Muséum National d'Histoire Naturelle, Paris (MNHN), and in the British Museum (of Natural History), London (BMNH). Ground, thin sections of some species were made for light microscopical observations, and preparations for scanning electron microscopy were made using a modification of the method described by Dingerkus and Koestler<sup>5</sup> for some species. When the total length of the animal was not recorded, estimations of the total length for *Carcharodon carcharias* (great white shark) were made from the tooth length – total length curve of Randall<sup>6</sup>, and total length estimations for *Isurus oxyrinchus* (mako shark) and *Galeocerdo cuvieri* (tiger shark) were made by plotting tooth length – total length curves from measurements of whole animals<sup>7</sup>.

In all the aforementioned species, it was found that above a total length of about 2 m, the animals had additional layers of prismatic calcium phosphate around the jaw cartilages. In longer individuals, more layers of prismatic calcium phosphate were added, up to a maximum number of five in *Carcharodon carcharias* with a total length of over 5 m (figs 1 and 2). These added layers do not correlate exactly with total length, as there is considerable overlap between total length and the number of layers of prismatic calcium phosphate (fig. 1). In the two jaws of *Carcharhinus leucas* (bull shark) observed, a small one from an individual of probably about 1.5 m total length had only one layer of prismatic calcium phosphate, whereas another much larger jaw from an individual longer than 2 m clearly had two layers of prismatic calcium phosphate.

Large adult specimens were examined from over 50 other species in the families Chlamydoselachidae, Hexanchidae, Heterodontidae, Rhincodontidae, Scyliorhinidae, Triakidae, Odontaspidae, Alopiidae, Squalidae, and Squatinidae, as well as other species from the families Lamnidae (including *Cetorhinus*) and Carcharhinidae,

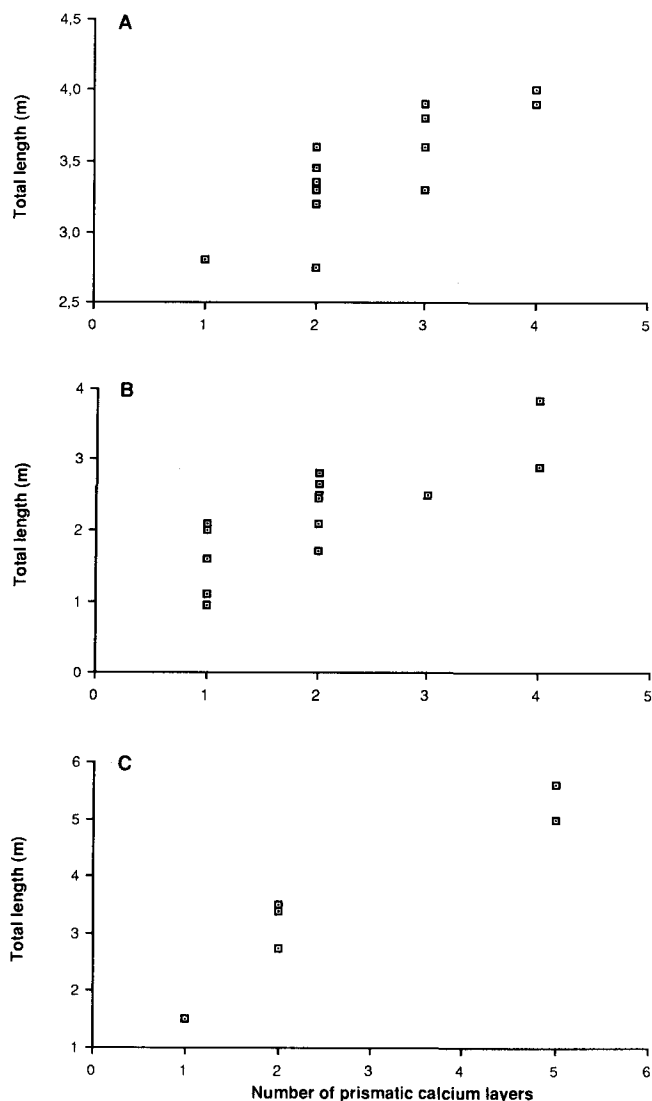


Figure 1. Graphs of total length versus the number of prismatic calcium phosphate layers in: A) *Galeocerdo cuvieri*; B) *Isurus oxyrinchus*; C) *Carcharodon carcharias*.

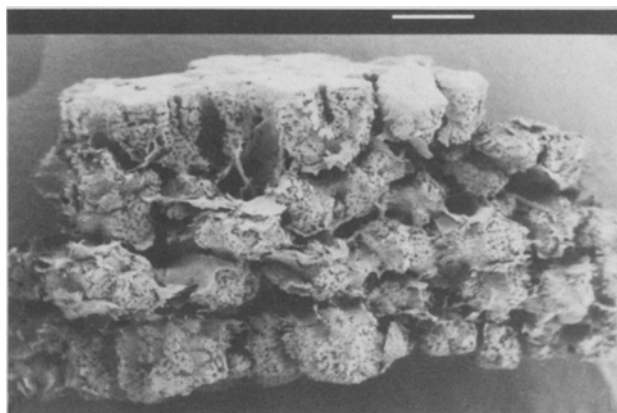


Figure 2. Scanning electron micrograph of a section of the prismatic calcium phosphate layers surrounding the jaw cartilage of *Carcharodon carcharias*, specimen No MNHN AB. 25. Scale bar equals 1 mm, exterior is at the top.

but all were found to have only a single layer of prismatic calcium phosphate. The same was also true of other groups of chondrichthyans examined, namely chimaeroids and batiforms. Also, only the jaw cartilages were found to have these additional layers of prismatic calcium phosphate; all other skeletal cartilages only had a single layer of prismatic calcium phosphate surrounding them.

The fact that these multiple prismatic calcium phosphate layers are found in only some species of the families Lamnidae and Carcharhinidae leads us to the conclusion that they are not of phylogenetic importance in living chondrichthyans. Rather, because the layers are only found in the largest species of these two families, it would appear that they are a functional attribute. Perhaps, as these large carnivorous fishes grow to such a large size, the strength of their bite becomes so strong that without these additional prismatic calcium phosphate layers sur-

rounding their jaw cartilages to strengthen them, their jaws would not be able to sustain the pressures exerted by the jaw muscles when biting.

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- 1 Romer, A. S., *The Vertebrate Body*. W. B. Saunders Co., Philadelphia & London 1950.
- 2 Roth, W., *Morph. Jahrb.* 42 (1911) 485.
- 3 Daniel, J. F., *The Elasmobranch Fishes*, 3rd edn. University of California Press, Berkeley, California 1934.
- 4 Schaeffer, B., *Bull. Am. Mus. nat. Hist.* 169 (1981) 1.
- 5 Dingerkus, G., and Koestler, R. J., *Scan. Electron Microsc.* 1986, 513.
- 6 Randall, J. E., *Science* 181 (1973) 169.
- 7 Unpublished data of the authors.

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## Evidence for spontaneous neuro-melanophore activity in *Pseudopleuronectes americanus* (Teleostei; Pleuronectiformes) during total darkness

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**Summary.** In total darkness, melanophores of much of the integumentary pattern of *Pseudopleuronectes americanus* display intermediate melanosome distribution, whilst the  $\alpha$ -adrenoceptor antagonist phentolamine evokes their complete dispersion. The intermediate condition is not attained in total darkness in locally decentralized melanophores. It is proposed that, in the absence of photic stimulation, spontaneous neural activity sustains a partial melanosome aggregation in this species.

**Key words.** Melanophores; integumentary nerve plexus; phentolamine; spontaneous neural activity.

It is well established that albedo has aggregating and dispersing effects on melanosomes when teleosts are subjected to contrasting illuminated backgrounds, resulting in changes in integumentary hue. Such responses involve varying relative degrees of neural and hormonal regulation in different species<sup>1,2</sup>, being predominantly neural in the pleuronectid flatfish *Pseudopleuronectes americanus*<sup>3</sup>. The neural control of teleost melanosome aggregation is sympathetic<sup>4,5</sup>, with noradrenalin the neurotransmitter<sup>6-8</sup>. In total darkness it has been demonstrated<sup>1,9,10-14</sup> that several teleost species, including winter flounder<sup>12</sup>, develop various intermediate hues. The purpose of the present work was to determine whether the intracellular distribution of flounder melanosomes in total darkness involves neural mediation, or whether it constitutes a more passive intrinsic condition of the melanophores.

## Methods

Locally collected *Pseudopleuronectes americanus* (300–400 g), were initially laboratory acclimated in stock tanks. Melanophore activity in the mid region of the integumentary pattern, i.e. in the extensive general background component<sup>3,12</sup> was investigated. This component displays no chromatic sexual dimorphism (Burton, unpublished observations) and unsexed, postspawned and mature flounders were background adapted in individual black (B) or white (W) plexiglas aquaria (400 × 225 × 203 mm) supplied with running seawater (6.5–7.0 °C). The aquarium system was surrounded by a frame covered with a double screen of heavy duty black polyethylene arranged to eliminate extraneous illumination, whilst permitting access of personnel. Flounders were maintained under a diurnal photocycle regime (dark 9.5 h, light 14.5 h; 60 W 1 m above the fish) with