

Fig. 4. Immature stages of *N. pinetum* in opened cocoons. Two female pupae are above and below; the pronymph on the right has developed characteristic body shape and a dark pupal eye, visible through the larval skin. The eonymph on the left is in diapause

that was needed to break the diapause of eonymphs (Fig 3b). The combination of a short critical photoperiod with a less intense diapause betrays the species' adaptation to a more southern latitude, probably during glaciation. This mechanism became a relict when the species acquired more appropriately longer critical photoperiods and an intense diapause on its postglacial northward migration.

Diapause adaptations do not purely reflect local climatic conditions. The *N. abietis* complex on balsam fir probably provides the best example where an early hatching larva and a late hatching larva can feed on the same trees with hardly any overlap. Similarly, *N. hettricki* larvae make their appearance two weeks later than the sympatric *N. pratti* on loblolly pine in eastern Virginia.

Changes in diapause patterns, accompanied by a novel preadaptation to a new host are the main forces that can reduce competition and promote speciation. Hybridization experiments with Florida and Ontario populations of *N. lecontei* have shown that the northern characters of intense diapause and long critical photoperiods are recessive traits controlled by only a few alleles. Slight genetic alterations can therefore precipitate large changes in the life history of mutant populations. This sequence of events must have occurred in the *N. abietis* complex, when populations first became established on the moderately protected spruce before jumping at least twice to the well protected balsam fir. One invasion coincided with the loss of the aestival diapause in the "early strain", thus ensur-

ing a complete allochronic isolation from the "late strain", a more recent colonizer. Application of this concept on a larger scale could explain the evolution of four closely related *Neodiprion* species in eastern North America. Members of the complex are unique by their oviposition pattern of inserting a single egg just above the needle sheath [4]. Speciation probably involved changes in the overwintering stage and the colonization of new pine hosts during the northward migrations at interglacial periods. Ancestors of the multivoltine and polyphagous *N. excitans* of Florida and the Carolinas could have given rise to an egg-diapausing population on loblolly pine at its northern lim-

it (*N. hettricki* in Virginia). Further advances hinged on a switch to a new host, pitch pine, while retaining the egg diapause (*N. pinirigidae* in New Jersey). The final jump occurred unto the northernmost host, jack pine, accompanied by a change to larval diapause (*N. swaini* in Ontario and Quebec).

Received December 15, 1982

1. Tauber, M.J., Tauber, C.A.: Ann. Rev. Ent. 21, 81 (1976)
2. Knerer, G., Atwood, C.E.: Science 179, 1090 (1973)
3. Wilkinson, R.C.: Fla. Entomol. 61, 26 (1978)
4. Ghent, A.W., Wallace, D.R.: For. Sci. 4, 264 (1958)

Myogenic Electric Organ Precedes the Neurogenic Organ in Apterodontid Fish

F. Kirschbaum

Zoologisches Institut der Universität,
Lehrstuhl für Experimentelle Morphologie, D-5000 Köln

Electric organs derive phylogenetically from muscle tissue [1, 6]. Up to now it has generally been assumed that the apteronotid family (South American knife-fishes; gymnotiformes) is the only exception: the electric organs of the adult apteronotid fish are modified axons of spinal neurons [2].

In this paper results are presented which hint that in early development of *Apterodontus leptorhynchus* there exists a functional myogenic organ which precedes the neurogenic one of the adult fish and favour the aspect that the neurogenic organ appeared later in phylogeny. These results reveal

that electric organs in fish originate without exception from muscle tissue. Gymnotiform [3] and mormyrid fish [4] can be bred by variation of environmental factors. The same technique proved to be successful in *A. leptorhynchus* raising.

Mature *A. leptorhynchus* spawn with regular intervals (fractional spawners, 6-14 days interval) rather big eggs (3 mm in diameter on average). The larvae hatch after 3 days and begin to discharge on day 9 (27 °C). The first discharges are discontinuous as has been reported for *Eigenmannia* [5]. Once the discharge has become contin-

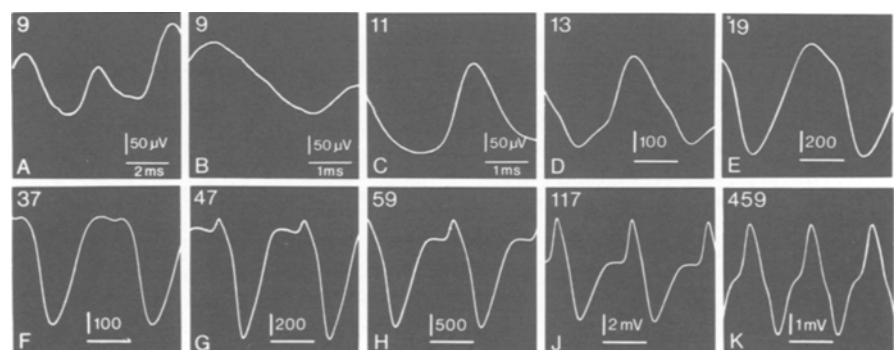


Fig. 1. Various stages in the development of the discharge from 9-day-old larva (onset of discharge) up to the characteristic adult discharge (K) of larva Nr. 4 (♀). The corresponding age is indicated. Time base scale (1 ms) applies to B-K. Head positivity up

uous and increased in amplitude the discharge of the larva is quite different from the adult fish. The waveform shapes continuously during ontogeny till it acquires its final character in the 8–10 cm fish (about 1 year old; at this age the fish can reach maturity for the first time). Some typical stages in discharge development are pictured in Fig. 1.

The larvae begin to discharge at about 300 Hz. The frequency typical of the adult fish (about 800 Hz for the males and 700 for the females) is reached after a year, approximately.

Curare experiments (Fig. 2) revealed that there exist two functionally different organs: in 11-day-old fish (Fig. 2A) injection of curare abolishes the discharge completely. The recovering discharge (Figs. 2B–D) each time resembles the original waveform (Fig. 2A). As a conclusion we may say that in 11-day-old fish only the myogenic organ (MO) seems to be functional. In 20-day-old fish after the injection of curare the discharge is kept (Fig. 2F) showing a lower amplitude and a quite

different waveform than before injection (Fig. 2E). This waveform is the result of the electric activity of the neurogenic organ (NO). With the diminishing influence of the curare (Figs. 2G, H) the waveform tends to become identical to the original one (Fig. 2E). In 31-day-old fish the remaining waveform – after curare injection – is very similar to that of the 20-day-old larva, its amplitude reaches 4/5 of the original one (Figs. 2K vs. N). Comparing the electric discharges K, L, M (Fig. 2) of the 31-day-old fish during curare application with that it shows 4, 7, and 12 days after curare injection it becomes obvious that the discharges are identical (Figs. 2M/Q; L/P; K/O). The amplitude of the NO (Fig. 2O) of the larva (43 days old at this stage) apparently has considerably increased (compared to the 20-day-old fish) the discharge of this larva is only produced by the NO – curare injection in a 44-day-old larva no longer changed the waveform – and the amplitude of the MO is negligible.

The early ontogenetic change in the waveform up to the 43-day-old larva can thus be explained by an age-dependent continuous change in the relative discharge amplitudes produced by the NO and MO. The later ontogenetic change in waveform (observed in

43-day-old larva up to adult fish) points to structural and/or physiological changes of the axons of the spinal neurons.

First evidences for the existence of two electric organs were brought about by histological examinations. Fig. 3 shows the extension of the NO and the MO of a 22-day-old larva (both organs are active). Fig. 3B reveals that both organs can be found in the ventral part of the hypaxial muscles.

The NO grows considerably during ontogeny. As histological research indicates (Fig. 3C) the NO is nonfunctional in 9-day-old larvae. In contrast to this a larva, 22 days old, shows a well developed NO (Fig. 3D), twice as big as the 9-day-old one. The 40- (Fig. 3E) and the 64-day-old larvae (Fig. 3F) show larger NOs.

In Figs. 3G–K the development of the MO in the same 4 larvae is shown. The main features are the constant size of the electrocytes and their early degeneration during ontogeny. First degeneration can be traced in the 40-day-old larva, and in the 64-day-old fish (4 cm long) only rudiments of the MO (Fig. 3K) can be identified.

To sum it up, four aspects, the curare experiments, as well as the occurrence of the electrocytes of the MO in between muscle fibres, their morphology

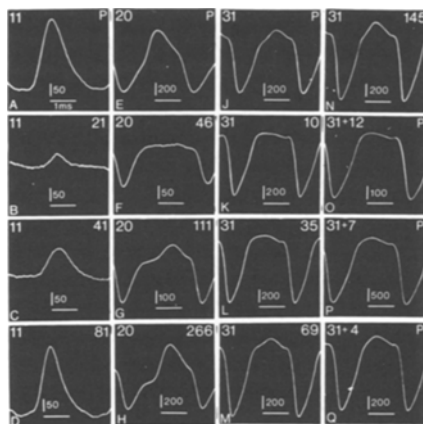


Fig. 2. Curare experiments conducted at various stages (larvae 11, 20 and 31 days old) revealing the two components of the discharge: the discharge of the myogenic organ (A) and that of the neurogenic one (F, K, O), both occurring with different relative amplitudes according to the developmental stage. Some intermediate stages during recovery from the curare injection are also found to appear during normal development (L vs. P, M vs. Q) in the 31-day-old fish. The amount of curare injected was about 1 mg curarin-asta/kg fish. Time base scale (1 ms) applies to all figures. μ V values and min after curare injection (p = pre-injection) are indicated. Head positivity up

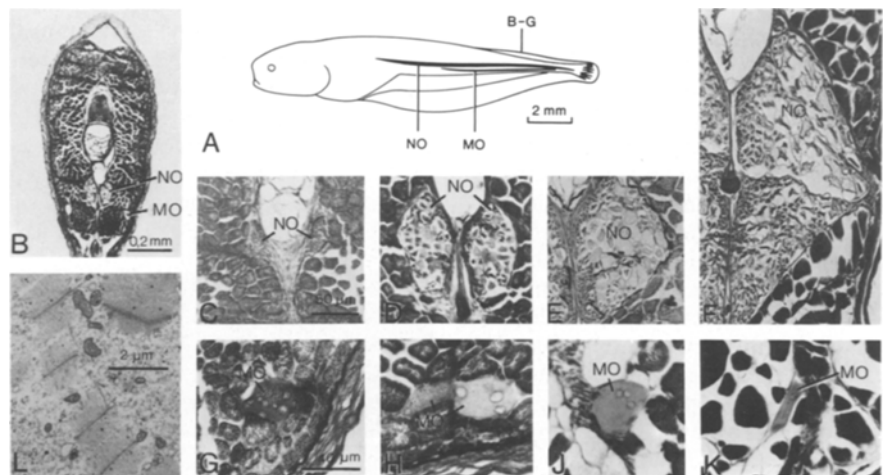


Fig. 3. (A) Schematic drawing of a 22-day-old larva, 16 mm long. The extension of the 2 electric organs, the myogenic organ (MO) and the neurogenic organ (NO), are indicated, both being functional at this stage (see Fig. 2). The level of the cross sections of Figs. (B–G) is indicated. (B–K) Light micrographs of various stages (9-day-old larva C, G; 22-day-old larva, B, D, H; 40-day-old larva, E, J; and 64-day-old larva, F, K) showing the differentiation of the NO (C–F) and the ontogeny of the MO (G–K). (L) Electron micrograph with myofilaments in the electrocytes of the MO supporting the idea that this organ derives from muscle tissue. Scale for Figs. C–F and G–K identical each time

– which is rather similar to muscle fibres – and the occurrence of myofibrils in the electrocytes of the MO (Fig. 3L) justify the conclusion that the MO has evolved from muscle tissue. As the ontogenetic sequence – the MO preceding the NO – indicates it must be taken into consideration that the NO represents an evolutionary progress based on the pre-existence of phylogenetically older MO. So even in apteronotid fish the NO of the adult species possesses an active MO-predecessor. This conclusion is supported by the fact that the MO of *A. leptorhynchus* is very similar to the primitiv

larval myogenic organ found in *Eigenmannia* during early ontogeny [6].

I would like to thank E. Wolff for technical assistance, C. Leyhausen for critical reading of the manuscript and correcting the English. This work was supported by a grant from the Deutsche Forschungsgemeinschaft (Ki 189/5, 189/6-2).

Received December 3, 1982

1. Ogneff, J.: Arch. Anat. Physiol., Physiol. Abt. 270 (1897); Ewart, J.C.: Phil. Trans. Roy. Soc. London 183, 389 (1892);

White, E.C.: Pap. Dept. Mar. Biol. 12 (252), 139 (1918); Dahlgren, U.: Pap. Tortugas Lab. 6 (183), 161 (1914); Johnels, A.G.: Quart. J. Micr. Sci. 97, 455 (1956)

2. de Oliveira Castro, G.: Anais Acad. Brasil. Cien. 27, 557 (1955); Bennett, M.V.L.: Ann. Rev. Physiol. 32, 471 (1970)
3. Kirschbaum, F.: Behav. Ecol. Sociobiol. 4, 331 (1979)
4. Kirschbaum, F.: 4th Congr. Eur. Ichthyol. Abstr. 149 (1982)
5. Kirschbaum, F., Westby, G.W.M.: Experientia 31, 1290 (1975)
6. Kirschbaum, F.: Naturwissenschaften 64, 387 (1977)

Buchbesprechungen

The Identification of Slags from Archaeological Sites. By H.-G. Bachmann. London: Institute of Archaeology 1982. 70 pp., £ 8. –.

Das vorliegende Heft von 37 Textseiten mit 37 Tafeln, Referaten und Analysentabellen beschäftigt sich mit einem Material, das bisher – unverdienterweise – die Rolle eines Stiefkindes in der Archäologie gespielt hat: den Schlacken, also den Resten vor- und frühgeschichtlicher Verfahrenstechnik. Es gibt eine kurzgefaßte, aber prägnante Übersicht über die Gesichtspunkte, die bei der Feldarbeit des Archäologen zu beachten sind, eine allerdings sehr kurze Aufstellung der Untersuchungsmethoden im Laboratorium und eine sehr nützliche Darstellung der verschiedenen Phasen, die in den kompliziert zusammengesetzten Schlacken zu beobachten sind. Die Darstellung wird erläutert durch eine Sammlung sehr guter und in dieser Form einmaliger Schliffbilder von archäologisch relevanten Schlacken. Insgesamt eine wirklich wertvolle Arbeit auf diesem wenig bekannten Gebiet. H. Moesta (Saarbrücken)

Entstehung und molekulare Evolution des Lebens. Von H. Reinbothe und G.-J. Krauß. Jena: Fischer 1982. 306 S., 65 Abb., 21 Tab., 24,00 M.

Die Autoren unternehmen einen Versuch, auf dem knappen Raum, der durch den Umfang eines Taschenbuchs vorweggenommen ist, einen Überblick über den gegenwärtigen Stand des Wis-

sens vom Ursprung des Lebens zu geben. Das Buch ist gut gegliedert und, was bei der Fülle des zur Verfügung stehenden Materials nicht immer leicht ist, auch sehr übersichtlich aufgebaut. Selbstorganisation der Materie ist der rote Faden, der durch das Büchlein leitet, von der Entstehung der Erde bis zu den höheren Organismen, den Eukaryoten. Ohne Zweifel mußten die Autoren, um ein einigermaßen klares Bild zu geben, vieles an widersprüchlichen Fakten, und derer gibt es genug, weglassen. Trotzdem ist dem Büchlein auch unschwer zu entnehmen, wo die wissenschaftlichen „weißen Flecken“ zu diesem unerhört vielschichtigen Wissensgebiet liegen. Wenn auch für nahezu alle Teilgebiete, in die die Autoren eindringen, zur Zeit ausgezeichnete, aber umfangreichere Übersichten vorliegen, so ist das Buch infolge seiner Zusammenschau eine Bereicherung der Literatur. Es wird jedem empfohlen, der sich rasch über die verschiedenen Ansätze zu einer Analyse der Vorgänge um die Entstehung des Lebens orientieren will. P. Schuster (Wien)

Geologie der Schweiz. Von T.P. Labhart. Bern-Stuttgart: Hallwag 1982. 164 S., 84 Abb., DM 19,80.

Das in seiner Ausstattung sehr ansprechende Taschenbuch wendet sich an den Naturfreund, der sich für Mineralien, Gesteine sowie für die Landschaften der Schweiz interessiert und mehr über ihre Entstehung wissen möchte. Der Rahmen ist weit gespannt: vom

geologischen Gesamtbild Europas zum Bau von Alpen, Mittelland und Juragebirge, mit Beiträgen zur alpinen Metamorphose und Zerrklüftmineralien – und von der voralpinen Geschichte seit dem Kambrium, vor 570 Millionen Jahren, bis zur jüngsten Entstehung des heutigen Alpenreliefs. Kapitel über geologische Forschung, Rohstoffe, Erdbeben, Meteoritenfälle und Gesteins- und Mineraliensammlungen sowie Angaben über Literatur und geologische Karten bringen vielfältige Information. Die klare und übersichtliche Darstellung entspricht dem neuesten Stand der Forschung; viele originelle Beiträge können selbst dem Spezialisten Neues bieten. Eindrückliche Landschaftsaufnahmen und gut gelungene Farbphotos von Gesteinen sowie zahlreiche Karten und Profile sprechen den Leser direkt an. Das in jeder Beziehung gut gelungene Buch zeugt von Begeisterung für die Geologie; es sollte einen weiten Leserkreis finden.

E. Jäger (Meikirch)

Wilhelm Ostwald. Von J.-P. Domschke und P. Lewandrowski. Leipzig-Jena-Berlin: Urania 1982. 112 S., M 14,80.

Wenn ein Forscher – und Gelehrter – so vielseitig und immens schriftstellerisch tätig gewesen ist wie Wilhelm Ostwald, ist es verlockend, von Zeit zu Zeit und unter dem jeweiligen Zeitaspekt sein Lebenswerk darzustellen. Das, was jeweils zeitgemäß ist, macht sich gut, und das, was nicht paßt, macht die Lektüre attraktiv. Da Wil-