

Table 1. Copulatory response of some lepidopterous insects to various models

Models	<i>P. operculella</i> (Gelechiidae)	<i>B. mori</i> (Bombycidae)	<i>P. interpunctella</i>	<i>C. cautella</i> (Phycitidae)	<i>A. kuehniella</i>
A. Of the same species					
dried ♂	++ <sup>a</sup>	++	++	++	—+
♂ wing <sup>b</sup>	++	++	++	++	+±
(♂) scale	++	+	++ <sup>c</sup>	++	—± <sup>c</sup>
♂ scaleless wing <sup>b</sup>	+	—	+	+	±
B. Filter paper	—	—	—	—	—
C. Of the other species <sup>d</sup>	++	++	++	++	++
	Cc (scale)	Ac (body)	Po, Cc (wing)	Po, Pi (wing)	Po, Cc (wing)
D. Flat model of the same species	++ (scale)	++ (wing)	— (wing)	— (wing)	± (wing)

<sup>a</sup> ++: responded very actively; +: responded; ±: responded seldom; —: did not respond

<sup>b</sup> Only fore wings were used as models except for *B. mori*

<sup>c</sup> Scales of both female and male wings were used in the tests of *P. interpunctella* and *A. kuehniella*

<sup>d</sup> Cc: *Cadra cautella*, Ac: *Arcte coerulea*, Po: *Phthorimaea operculella*, Pi: *Plodia interpunctella*

moth, *Bombyx mori*, the Indian meal moth, *Plodia interpunctella*, the almond moth, *Cadra cautella*, and the Mediterranean flour moth, *Anagasta kuehniella*.

For each species, the response of the male to different models under the presence of sex pheromone was observed in the laboratory. Dried specimens and several types of filter-paper models, different in size and posture for each species, respectively, were used as objects in all cases. In addition, paper models covered with the wing or the scales as described previously [4] were also examined. The results including the data for *P. operculella* are summarized in Table 1.

Male moths of all the species actively attempted copulation with the wing model as well as with the dried male specimens of their own species and with the scale model to some extent. However, they showed little

or no response to the scaleless wing model. The models made from other species also released very active responses in the male moths of all species tested, indicating that they could not discriminate the scales of their own species from those of other species. However, the flattened models in which the wings or the scales were stuck flat on the base sheet released responses only in *P. operculella* and *B. mori* males.

Thus, the scales undoubtedly play an important role in the induction of the copulation attempt in these lepidopterous insects, and the stimulus concerned seems to be tactile in every species. There were, however, subtle differences in the role of the scales among species. In *B. mori*, for example, the stimulus provided by the scales may be particularly effective for the maintenance of the copulation attempt or the evocation of searching for copulation site

by the abdominal tip, because the copulation attempt per se is also released by the sex pheromone to a certain extent. Also, in phycitid moths, the important factors for the evocation of the copulation attempt are not only the presence of the scales but also the posture of the object covered by the scales, since the males show a more restricted response to the flattened model.

The role of the scales in mating behavior of Lepidoptera has hitherto been emphasized by many workers only as a media for visual [2, 5] or olfactory [1, 3, 6, 7] stimuli. The observations reported here revealed, however, that the scales act as an important tactile stimulus for evoking copulation attempt by male moths among species belonging to three different families, indicating that the phenomenon may be fairly widespread in Lepidoptera.

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## Electric-Organ Ontogeny: Distinct Larval Organ Precedes the Adult Organ in Weakly Electric Fish

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Electric organs in electric fish originate from muscle tissue [1–5]. In *Electrophorus* [4], *Malapterurus* [3], and mormyrids [5] the results are only preliminary because of the poor availability of their larvae. In weakly electric gymnotids no ontogenetic information concerning the origin of electric organs is available.

A detailed study of the ontogeny of electric

organs in *Pollimyrus isidori* (Mormyridae) and *Eigenmannia virescens* (Gymnotoidei) was undertaken, as it has recently become possible to breed these species in the laboratory [6]. In both species distinct larval electric organs were found, thereby giving new insight into the evolution of electric organs.

*Eigenmannia*: In 7.8 mm long fish (7 days

old) electrocytes can be found for the first time in the hypaxial muscle. These cells, which originate metamERICALLY near the myosepts, extend caudally from the level of the anus over  $\frac{1}{3}$  of the total length of the fish. New cells differentiate caudally as the fish gets older and in 13.5-mm fish the newly formed electrocytes have reached the tip of the tail. Then additional cells differentiate—first caudally and then rostrally—between the pinnalis analis externalis muscles. When these cells have reached their most rostral point the cells in the hypaxial muscle (Fig. 1a) are gradually reduced and in 55.5-mm long fish the electric organ, typical of an adult fish, has

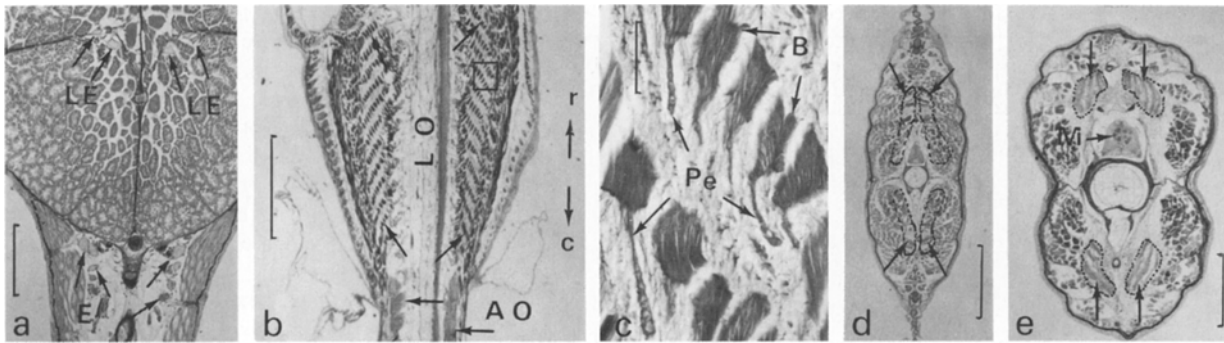


Fig. 1. (a) *Eigenmannia*, 19 mm, 41 days, transverse section. Note the electrocytes (*LE*) of the larval electric organ and those (*E*) between the pinnalis analis externalis muscles. Bar=80  $\mu$ m. (b-e) *Pollimyrus* (*P*). (b, c) *P*, 14 mm, 48 days. Sagittal section showing larval electric (*LO*)—rostral and caudal limits indicated by arrows—and adult organ (*AO*), not functional at this stage. Bar=1 mm, *r* rostral, *c* caudal. (c) Detail of (b) (see rectangle). Cell bodies (*B*) of larval electrocytes with irregularly arranged myofibrils and long pedicles (*Pe*). Bar=50  $\mu$ m. (d, e) *P*, 14.5 mm, 48 days. (d) Transverse section (TS) at midpoint of dorsal fin. Position of electrocytes of the *LO* indicated by arrows. Bar=500  $\mu$ m. (e) TS at the rostral limit of the caudal peduncle. Position of the developing, still nonfunctional, electrocytes of the *AO* indicated by arrows. Note the electromotor neurons (*M*) in the spinal cord. Bar=200  $\mu$ m. (a, d, e): dorsal up, ventral down.

developed. The electrocytes in the hypaxial muscle that appear first, are subsequently reduced, and found only in larvae will be called the larval electric organ. The electrocytes of the larval organ are apparently the most primitive ones compared with the cells in the caudal and rostral parts of the adult electric organ.

*Pollimyrus*: In this species first a larval and then a quite different adult discharge appears [7]. Curare experiments [8] proved that the 2 discharges were of different topographic origins and that a larval electric organ, producing the larval discharge, was located somewhere in the deep lateral muscle. In larvae, 14 mm long, 48 days old, this organ could be identified in the medial part of the deep lateral muscle (Fig. 1 b, d). The larval electrocytes contain a lot of disorganized myofibrils and possess long pedicles (Fig. 1 c), which receive the innervation [9]. These cells originate from the medial part of the deep lateral muscle as apparently well-organized muscle fibres and develop only gradually into these specialized cells. The sum of these cells will be called the larval electric organ. This or-

gan disappears later after the differentiation of the typical mormyrid electric organ (=adult organ). The electrocytes of the adult organ originate caudally in the medial part of the deep lateral muscle (Fig. 1 e).

If we accept the convincing argument that strongly electric fish have evolved from weakly electric fish [10] then *Eigenmannia* offers an explanation for the evolution of *Electrophorus*. The larval electric organ of *Eigenmannia* would then correspond to the main organ of *Electrophorus*, the Sachs' organ would be the homologue of the caudal part of the adult electric organ of *Eigenmannia* and the organs between the pinnalis analis externalis muscles (Hunters' organ in *Electrophorus* and the rostral part of the adult organ in *Eigenmannia*) would also be homologous structures.

In *Pollimyrus* the electrocytes of both the larval and adult organs originate in the deep lateral muscle (Fig. 1 d, e) and can thus be called homologous structures. The adult organ is the more specialized structure, which has obviously appeared later in evolution in the caudal part of the fish. In *Gymnarchus*, a Mormyridae closely related to the Mormyridae, the electrocytes originate in the medial part of the deep lateral muscle [2]. Developing electrocytes closely resemble the differentiated electrocytes of the larval organ of *Pollimyrus*, and the form and duration of the discharge of *Gymnarchus* [9] and of the larval discharge of *Pollimyrus* [7] are very similar. From these results the following conclusions can be made: The larval and adult electric organs of *Pollimyrus* and the electric organ of *Gymnarchus* are homologous structures of which the larval organ of the mormyrid is the most primitive one. The electric organ of *Gymnarchus* is the modified larval mormyrid organ. The adult organ of mormyrids is a further specialization of the caudal part of the larval organ. As soon as the adult organ is differentiated

and functional it replaces the larval organ, which then disappears. The larval discharge in mormyrids might function as a larval signal. The male of *Pollimyrus* guards the fry for several weeks near the nest and shows aggression toward the young fish after the appearance of the adult discharge.

In the mormyrid *Stomatorhinus corneti* the discharge of the larva is different from that of the adult fish [11]. The interpretation given is that this is due to the incomplete differentiation of the adult organ. This is apparently incorrect. In fact, the adult organ is only functional when it is fully developed [8].

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