THE JOURNAL OF COMPARATIVE NEUROLOGY 244:313-330 (1986)

Species Differences in Electric Organs of Mormyrids: Substrates for Species-Typical Electric Organ Discharge Waveforms

ANDREW H. BASS
Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853;
Laboratoire de Physiologie Nerveuse, Centre National de la Recherche Scientifique, Gif sur Yvette, France 91190

ABSTRACT
The organization of electric organs is described for the mormyrid fishes from Africa. The electric organ's spike-generating cells or electrocytes are wafer-shaped cells with a special geometry that relates to the number of phases and polarity of their pulsatile electric organ discharge (EOD) waveform. Six "families" of electrocytes are recognized on the basis of cell geometry. Each family includes species with EODs of similar polarity and phase number. Despite such similarities, there are still dramatic species differences in EOD waveforms for a given family that may further depend on specialized features of the electrocyte's excitable membranes. It is each species' particular electrocyte "profile" that must underlie the development of species-specific and hormone-dependent sex differences in the EOD waveforms.

Key words: electric fish, electrocyte, EOD, spike-generating

Several groups of fishes have evolved specialized neuroeffector pathways for the production of electric organ discharges or EODs (Fig. 1; reviews: Bennett, '71; Bass, in press (a)). Some species, such as the electric ray (*Torpedo*), electric catfish (*Malapterurus*), and electric eel (*Electrophorus*), produce electric pulses on the order of 60 to several hundred volts. These so-called strongly electric fish utilize their EOD for prey capture and defensive maneuvers. However, many electric fish, namely mormyriforms and gymnotiforms, produce weak electric discharges on the order of hundreds of millivolts or several volts that are important in both communication (electrocommunication) and guidance (electrolocation) systems (reviews: Heiligenberg, '77; Hopkins, '83). The African mormyriforms can be divided into two families (after Taverne, '72)—the monotypic Gymnarchidae and the Mormyridae—which include nearly 200 species. This report concerns the mormyrids of the Ivindo River district of Gabon, West Africa, where Hopkins ('80) identified nearly 20 different species with mostly distinctive EODs.

We are interested in the anatomical and physiological bases for the production of EODs. The EOD has two elements, the *EOD waveform* and the *EOD rhythm* (or SPI, sequence of pulse intervals; Hopkins and Bass, '81), each subserved by distinct peripheral and central neuroanatomical substrates. The EOD waveform describes a single cycle of the electric pulse produced by the electric organ itself. The individual cells or electrocytes of the electric organ are often spike-generating, as in mormyrids, and the properties of their action potentials can determine the appearance of the EOD waveform (Bennett and Grundfest, '61; also see Bennett, '71). The EOD rhythm, which is controlled by a central motor pathway that innervates the electric organ, describes the rate or frequency at which the electric pulse is generated (review: Bennett, '71). Electric fish are often classified as pulse or wave species, depending on the appearance of the EOD rhythm (Fig. 2). Pulse fish, like mormyrids, produce brief-duration discharges that are separated by long intervals. Among wave fish, like gymnarchids, the interval between pulses is short compared to the

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Accepted October 18, 1985.

Address reprint requests to Andrew H. Bass, Section of Neurobiology and Behavior, W227 Seeley G. Mudd Hall, Cornell University, Ithaca NY 14853.

Abbreviations

a	anterior
af	anterior face
br	branches of stalk after penetrating through electrocyte body
cbl	cerebellum
ct	connective tissue
dl	first penetration site of double-penetrating stalk
d2	second penetration site of double-penetrating stalk
d,dp	double-penetrating stalk
E	electrocyte body
el	electrocyte
elll	electroreceptive lateral line lobe
emn	electromotor nucleus
eo	electric organ
hy	hypothalamus
m	midline
me	medial nucleus
mn	medullary command and relay nucleus (see Bell et al., '83)
my	myofilaments
n	electromotor nerve
np	nonpenetrating stalk element (*Stomatorhinus*)
nu	nucleus of electrocyte
p	posterior
pe	stalk penetration site
pf	posterior face
sc	spinal cord
se	connective tissue septa
S,ST, st	stalk
tel	telencephalon

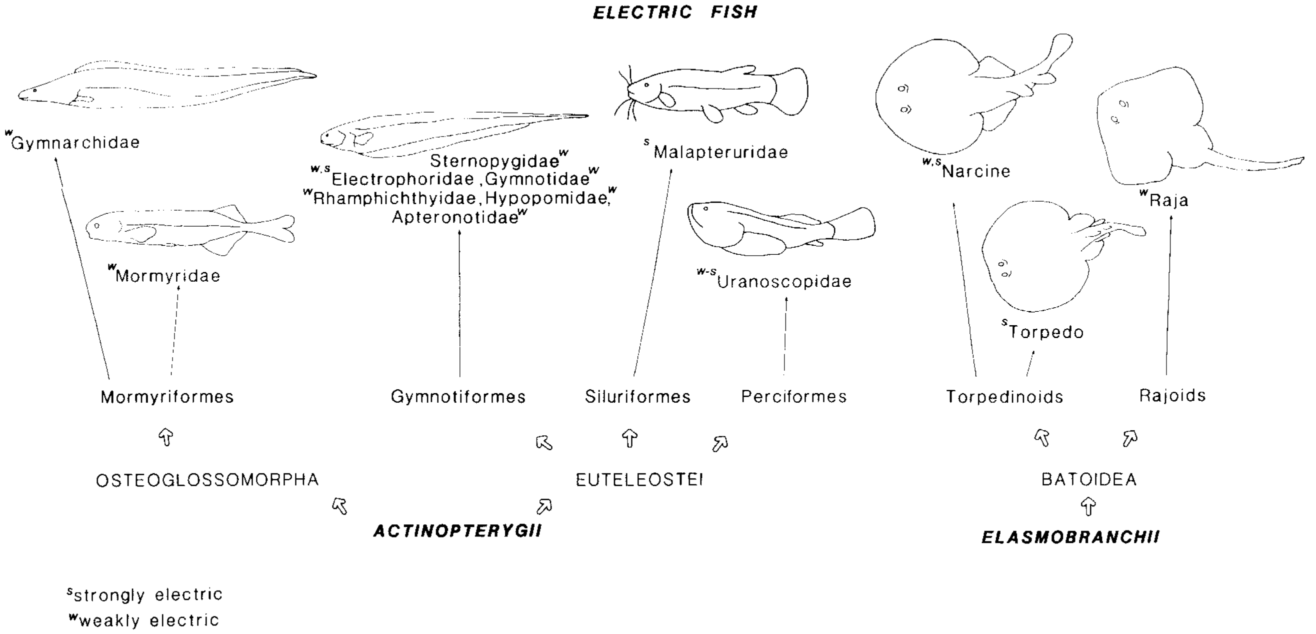

Fig. 1. Electric fish phylogeny. Shown are representative line drawings of members of the two groups of fishes, the actinopterygians and elasmobranchs, that include species with electric organs. Among actinopterygians, two major groups, the osteoglossomorphs and euteleosts (after Greenwood et al., '66; Greenwood, '73), include electric fish. The order Mormyriformes has two families, the Mormyridae and the monotypic Gymnarchidae (also Taverne, '72). Three orders of euteleosts have electric species: The Gymnotiformes are the largest order with six families (after Mago-Leccia '76), while the Siluriformes include only the electric catfishes (Malapteruridae). Only some members of the family Uranoscopidae (the stargazers) have electric organs. Among elasmobranchs, two orders of batoids—the torpedinoids and rajoids—have electric organs (Compagno, '77). The majority of species produce weak (w) electric discharges on the order of millivolts or several volts. The electric eels (Electrophoridae) and one torpedinoid, *Narcine*, produce both weak and strong (s) electric discharges, the latter on the order of several hundred volts. The electric catfishes and *Torpedo* have only a strong discharge, while the stargazer produces a signal somewhat intermediate in strength between a weakly and strongly (w-s) electric fish.

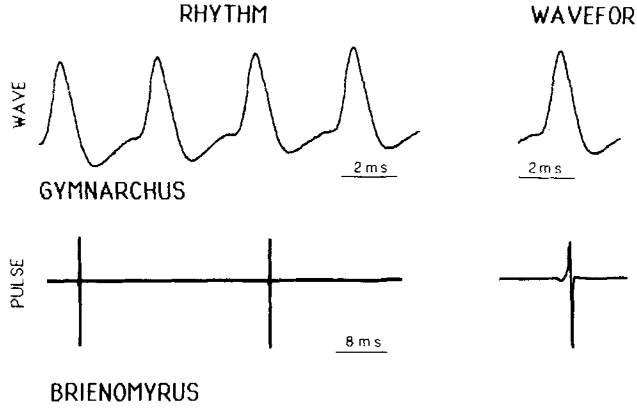

Fig. 2. The electric organ discharge (EOD) of "wave" and "pulse" fish. Shown here is a representative EOD from the two families of electric osteoglossomorphs—the wave Gymnarchidae (*Gymnarchus*) and the pulse Mormyridae (*Brienomyrus*). Among *wave* species, the interpulse interval is similar to or less than the pulse duration so that the rhythm has a quasi-sinusoidal wavelike appearance. For *pulse* species, the interval between successive pulses is long compared to the duration of the pulse waveform itself.

pulse itself so that the EOD rhythm has the appearance of a quasi-sinusoidal "wavelike" discharge.

This report is a light microscopic study that describes the organizational features underlying species differences in the anatomy of mormyrid electric organs; a second (Bass et al., submitted) concerns the ultrastructural features of, and hormone-dependent sex differences in, electrocytes. Both studies were prompted, in part, by the discovery that gonadal steroid hormones can induce among juveniles and females the EOD waveform typical of mature males of species with a sex difference in the EOD waveform (Bass and Hopkins, '83–'85; Bass, '86). Steroid-induced changes in EOD waveforms are associated with dramatic changes in electrocyte morphology (Bass et al., '84) and the duration of electrocyte action potentials (Bass and Volman, '85). Eventually, we want to understand the effects of steroid hormones on the relationship between the anatomical and physiological features of electrocytes. But a proper analysis of the development and evolution of hormone-dependent sexual dimorphisms in electrocytes requires a study of their interspecific variation, which is the focus here.

MATERIALS AND METHODS

The electric organs of 19 species of mormyrids were collected during the periods of October–December, 1979 and 1981, in Gabon, West Africa. All tissue samples were obtained from specimens that were given an overdose of MS222 (tricaine methanesulfonate) and then perfused transcardially with either (1) 0.7% saline followed by AFA (90 cc of 80% ethanol, 5 cc formalin, 5 cc glacial acetic acid) or (2) 0.1 M phosphate buffer (pH 7.2) followed by 2% gluteraldehyde in phosphate buffer (pH 7.2). The tail was removed near the caudal margin of the ventral fin (see Fig. 3) and stored in fixative (AFA) or 0.1 M phosphate buffer (pH 7.2) (glutaraldehyde-fixed tissue) prior to embedding. The brain was saved for other analyses (see Bass et al., '82). AFA-fixed material was first decalcified and dehydrated, and then embedded in paraffin, while glutaraldehyde-fixed material was postfixed in osmium tetroxide and then embedded in plastic (Araldite or Polybed 812). The paraffin-embedded tissue was serially sectioned at 15 μm in either the sagittal or the transverse plane. Plastic-embedded tissue was sectioned in the transverse, sagittal, and horizontal planes at 1 μm and stained with toluidine blue, or thin-sectioned and prepared for electron microscopy (see Bass et al., submitted, for details).

For some species, single electrocytes were dissected free from AFA-fixed material and then stained as a whole mount with methylene blue to reveal the electrocyte's stalk pattern (adapted from Bennett and Grundfest, '61). Outlines of stalk patterns were then made by using a drawing tube attachment on a Leitz Ortholux microscope.

The following species are included in this analysis: *Isichthys henryi*, *Stomatorhinus corneti*, *Pollimyrus kingsleyae*, *Petrocephalus* sp., *Ivindomyrus opdenboschi*, *Mormyrops zanclirostris*, *Hippopotamyrus batesii* (reversed polarity), *H. batesii* (triphasic), *H. castor* (biphasic), *H. castor* (monophasic), *Boulengeromyrus knoepffleri*, *Brienomyrus brachyistius* (biphasic), *B. brachyistius* (triphasic), *B. brachyistius* (long biphasic), *B. brachyistius* (monophasic), *B. curvifrons*, *Marcusenius paucisquamatus*, *Marcusenius conicephalus* and *Paramormyrops gabonensis*. Each of the latter species has nearly distinctive EODs as discovered by C.D. Hopkins ('80), who first identified these specimens for A.H. Bass. Electric organs of *Brienomyrus niger*, *Gnathonemus petersii*, *G. tamandua*, and *Pollimyrus isidori* were also available for analysis.

RESULTS

General overview

Weakly electric mormyrids (and gymnotiforms) have separate larval and adult electric organs (Kirschbaum, '77, '79, '83; Kirschbaum and Westby, '75; Westby and Kirschbaum, '77, '78; Denizot et al., '78, '82). Only adult electric organs are discussed here.

The general organization of the electromotor system of mormyrids is reviewed in Figure 3. The outputs of electric organs arise in part from the synchronous activity of many electrocytes arranged in series and parallel (see Bennett, '71). The electric organ of mormyrids is derived from seven to ten myotomes (Szabo, '60; Denizot et al., '82) and is located in the tail (Fig. 3a). It consists of two columns of serially stacked, disk-shaped cells (electrocytes) (Fig. 3c,f) located on either side of the midline (Fig. 3b,e). Each column is enclosed within a connective tissue tube (see Fig. 6). Both Marcusen (1864) and Lissmann ('58) also note the presence of the so-called "Gemminger's bones" (not shown in Fig. 3) along the dorsal and ventral borders of the organ, which probably help maintain its rigidity and the integrity of a uniform electric field.

The electric organ is innervated by a special set of motoneurons, known as electromotoneurons, which are excited by a descending signal from a "relay" nucleus in the medulla oblongata (Bennett et al., '67). The electromotor nucleus lies in the spinal cord at the level of the electric organ itself (Fig. 3b,d,g). Recently, the relay nucleus has been divided into a dorsal group of large cells (relay nucleus proper) that directly innervate the electromotoneurons, and a ventral group of smaller cells ("command" nucleus) that excite the relay cells (Bell et al., '83). The command nucleus alone is considered to make final "decisions" as to the EOD firing frequency, i.e., the EOD rhythm.

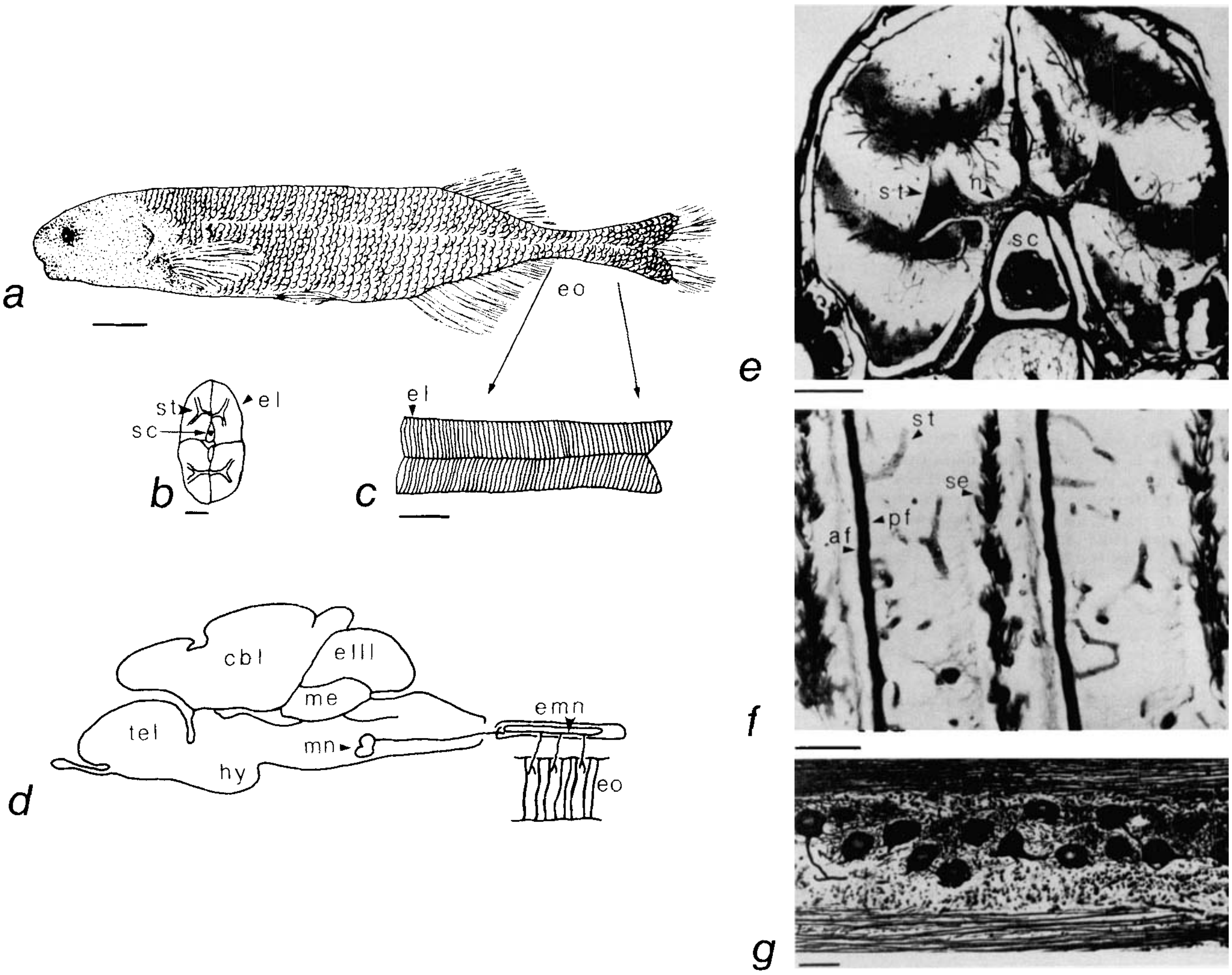

Fig. 3. The electromotor system of mormyrids. The electromotor system has two major elements–the peripheral electric organ and a central electromotor pathway. a. The electric organ (eo) is located in the tail. b. The organ consists of four columns of electrocytes (el), two on either side of the midline (transverse view). c. Electrocytes are serially stacked within each column (sagittal view). d. Electrocytes are innervated by a spinal electromotor nucleus (emn) that is at the same level as the electric organ; the emn is excited by a relay nucleus in the medulla (mn). Bar scale is 10 mm for a, 80 μm for b, and 1 mm for c. e–g. Photomicrographs of electrocytes and electromotoneurons. e. Transverse section from *Stomatorhinus corneti* of two electrocytes from the dorsal columns that are innervated at their stalk (st) by spinal nerves (n) that originate from electromotoneurons in the spinal cord (sc). Refer to Figure 3b. Bar scale is 0.2 mm. f. Sagittal view through one column of electrocytes from *Pollimyrus kingsleyae*. Each electrocyte has well-defined anterior (af) and posterior faces (pf); the stalk arises from the posterior face. Neighboring cells are separated by connective tissue septa (se) into compartments that are filled with a gelatinous mucopolysaccharide. Bar scale is 0.05 mm. g. Sagittal view of the electromotoneurons of *Brienomyrus brachyistius* (long biphasic); Bodian-stained section. Bar scale is 0.05 mm. Additional abbreviations: tel, telencephalon; cbl, cerebellum; hy, hypothalamus; elll, electroreceptive lateral line lobe; me, medial nucleus.

Mormyrid electrocytes

Electrocytes of most fishes are essentially modifications of a cylindrical form that often have definable anterior and posterior faces because of their orientation within the transverse body plane. One face may have an evagination known as a stalk where electromotoneurons terminate.

Figure 4 presents an overview of the anatomy of electrocytes from mormyrids. The electrocytes are wafer-shaped, multinucleated cells whose diameter (2–3 mm) is much greater than their thickness (10–40 μm). Each cell has anterior and posterior faces with a stalklike structure that is an evagination of one face (usually the posterior). The stalk and its major branches are best visualized in methylene-blue-stained, whole electrocytes (Fig. 4a–d). The stalk almost appears in bas-relief from the electrocyte's face (Fig. 4a,b); the many nuclei composing each cell can also be seen (Fig. 4c,d). A particularly dark-staining area near the base of the stalk demarcates the site where the axons of spinal electromotoneurons terminate (Fig. 4a–d). Nearly the entire stalk can be seen in transverse sections (Fig. 4e,f), highlighting the distinct nature of the stalk, as well as its discrete zone of electromotor nerve input. The end branches of the stalk are continuous as fingerlike projections of the posterior face (see Figs. 3f, 5–7).

Mormyrid electrocytes have two *primary* patterns of or-

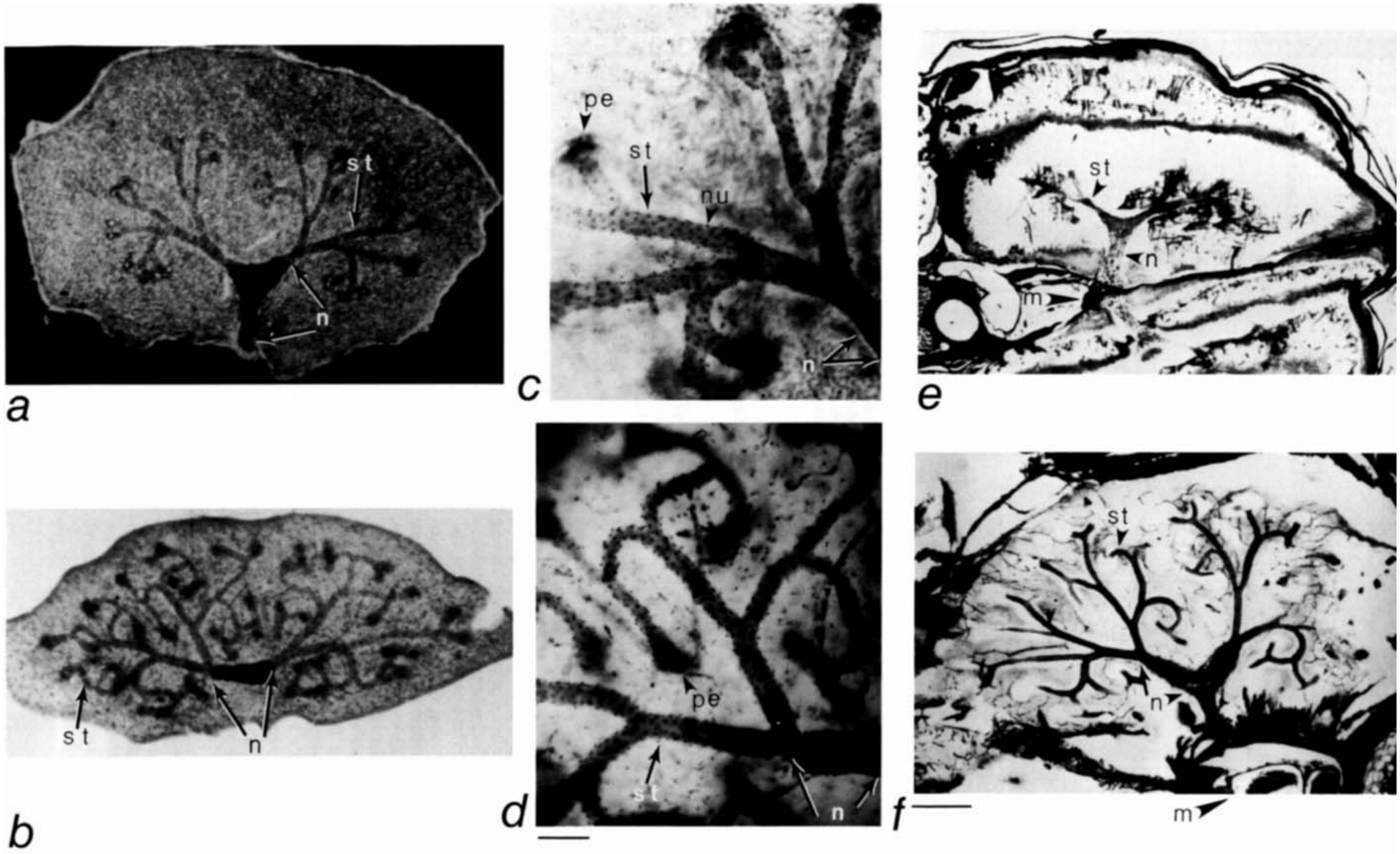

Fig. 4. a–d. Anterior face views of whole electrocytes stained with methylene blue. a. Darkfield photomicrograph of *Brienomyrus brachyistius* (long biphasic) electrocyte showing stalk (st) and electromotor nerve (n) that terminates around base of stalk. b. Electrocyte of *B. brachyistius* (biphasic) has a stalk with more branches extending to cell's periphery. c,d. Higher magnification of stalk in, respectively, a and b. Electrocytes are multinucleated; individual nuclei (nu) are seen. Regions of dense staining are penetration sites (pe) where the stalk actually pierces the electrocyte body proper (see Fig. 5). Bar scale is 0.1 mm for c and d. e,f. Photomicrographs of transverse sections of Mallory-stained electrocytes of *B. brachyistius* (long biphasic) (e) and *B. brachyistius* (biphasic) (f). Midline (m) is indicated. Dorsal is to the right in e and to the left in f. Bar scale is 0.2 mm for e and f, and 0.3 mm for a and b.

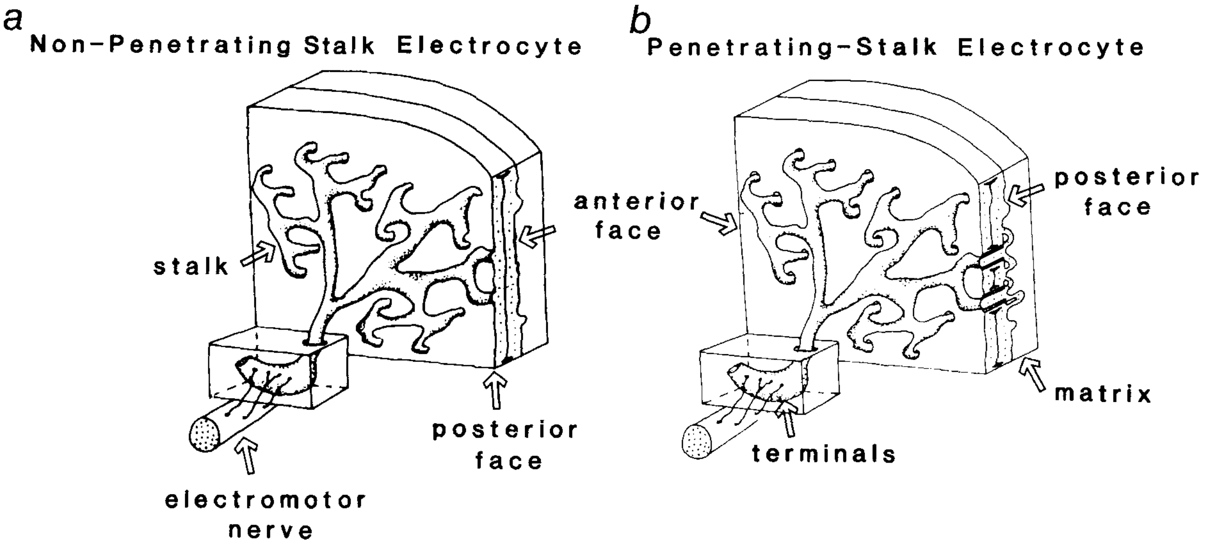

Fig. 5. Schematic representation of a cutaway view of mormyrid electrocytes, showing the two primary geometrical patterns: nonpenetrating and penetrating stalk electrocytes. In the nonpenetrating cell (a), the stalk emerges from the posterior face and then fuses to form a main trunk where electromotor axons terminate. In the penetrating case (b), the stalk emerges from the posterior side as several branchlets that fuse and then penetrate the main body of the cell to emerge on the anterior side where the stalk is innervated (Design after Szabo, '58).

ganization that I refer to as *nonpenetrating* and *penetrating* (after Bennett and Grundfest, '61) *stalk electrocytes* (Fig. 5). In nonpenetrating stalk electrocytes (Fig. 5a), the stalk "tree" emerges directly from the posterior face and is innervated by electromotor axons on that side of the cell. However, in some species (such as those depicted in Fig. 4), the stalk actually penetrates through the electrocyte body to emerge opposite its face of origin and then fuses into a major trunk that is also innervated in a restricted zone (Fig. 5b; also see Fig. 4a–d). In most cases, the stalk arises from the posterior side and penetrates to the anterior side where it is innervated (Fig. 5b). Both the size of the stalk and the number of penetration sites can vary widely among different species (Fig. 6). An understanding of electrocyte geometry (used here in a restricted sense to describe the presence or absence of a penetrating stalk) is of importance to the modelling of directional current flow along the organ and the formation of the pulselike EOD waveforms that characterize mormyrids (see Discussion).

Aside from the stalk, there are species differences in the gross morphology of the anterior face (Fig. 7). In particular, the anterior face may have foldings or papillae (after Schwartz et al., '75) that greatly increase its surface area. The size of the folds may even vary within a single electric organ, as for *Isichthys henryi* (Fig. 7b,d).

The entire electrocyte is separated from its neighbor by connective tissue septa (Figs. 3f, 6, 7) that enclose the cell in a gelatinous matrix. The lateral margins of the electrocytes appear swollen, increasing surface contact with the connective tissue tube (see Fig. 7c), which presumably decreases possible current leakage around each cell (see Bell et al., '76). A central zone of myofilaments denotes the electrocyte's origin from muscle (Fig. 7b–d; also see Bass et al., submitted).

Species differences in electrocyte geometry: Families of electrocytes

Mormyrid EODs are characterized by their number of phases, the polarity of each phase, the presence of inflection points or bumps in each phase, and total EOD duration (Hopkins, '80). EOD duration is one of the more dramatic variables, ranging from 250 μsec to over 8 msec (Figs. 8, 9). Some species have a sex difference in their EOD pulse, where the EOD of males may be twice the duration of that of females and juveniles (Fig. 9). Among the Gabon mormyrids, there are six patterns of electrocyte organization as summarized in Figures 8 and 9. The anatomical results highlight an association between electrocyte geometry and the polarity and number of phases of the EOD waveform.

Most species have a nonpenetrating stalk electrocyte (as schematized in Fig. 5a) where a single stalk system arises directly from the posterior face. All species with this pattern (Fig. 8) have a biphasic EOD waveform characterized by an initial head-positive phase followed by a negative phase. Figure 8 (as in Fig. 9) emphasizes that while species may "share" the same electrocyte geometry and EOD polarity and phase number, there is still variation in the actual appearance of each EOD phase and total EOD duration. For example, compare the EOD of *Marcusenius paucisquamatus*, which has two symmetrical phases, to the nearly monophasic EOD of *Brienomyrus brachyistius* (monophasic, MP).

A second electrocyte pattern is found for *Isichthys henryi* and *Paramormyrops gabonensis*, which have more than one nonpenetrating stalk system that arise from the posterior face, each with its own site of innervation (Fig. 8; see also Szabo, '58; Bennett and Grundfest, '61). Both species also have a biphasic EOD waveform, although their EODs are

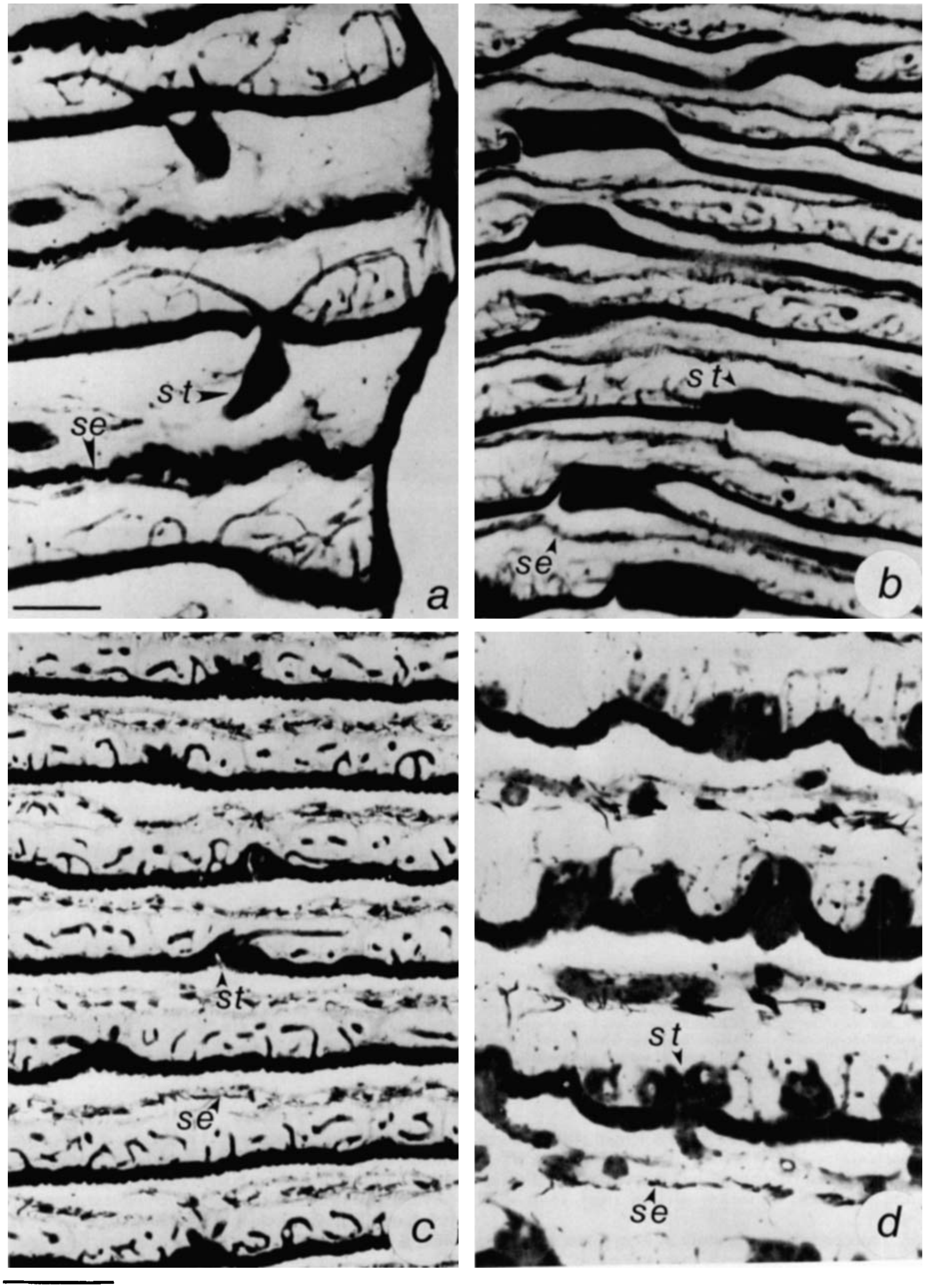

Fig. 6. Photomicrographs of sagittal sections of Mallory-stained electrocytes with penetrating stalks. a. *Brienomyrus brachyistius* (biphasic). b. *B. brachyistius* (triphasic). c. *B. brachyistius* (long biphasic). d. *Hippopotamyrus batesii* (triphasic). In all cases, posterior is up, anterior is down. Bar scales are 0.05 mm for a, d, and 0.1 mm for b, c. Abbreviations: st, stalk; se, connective tissue septa.

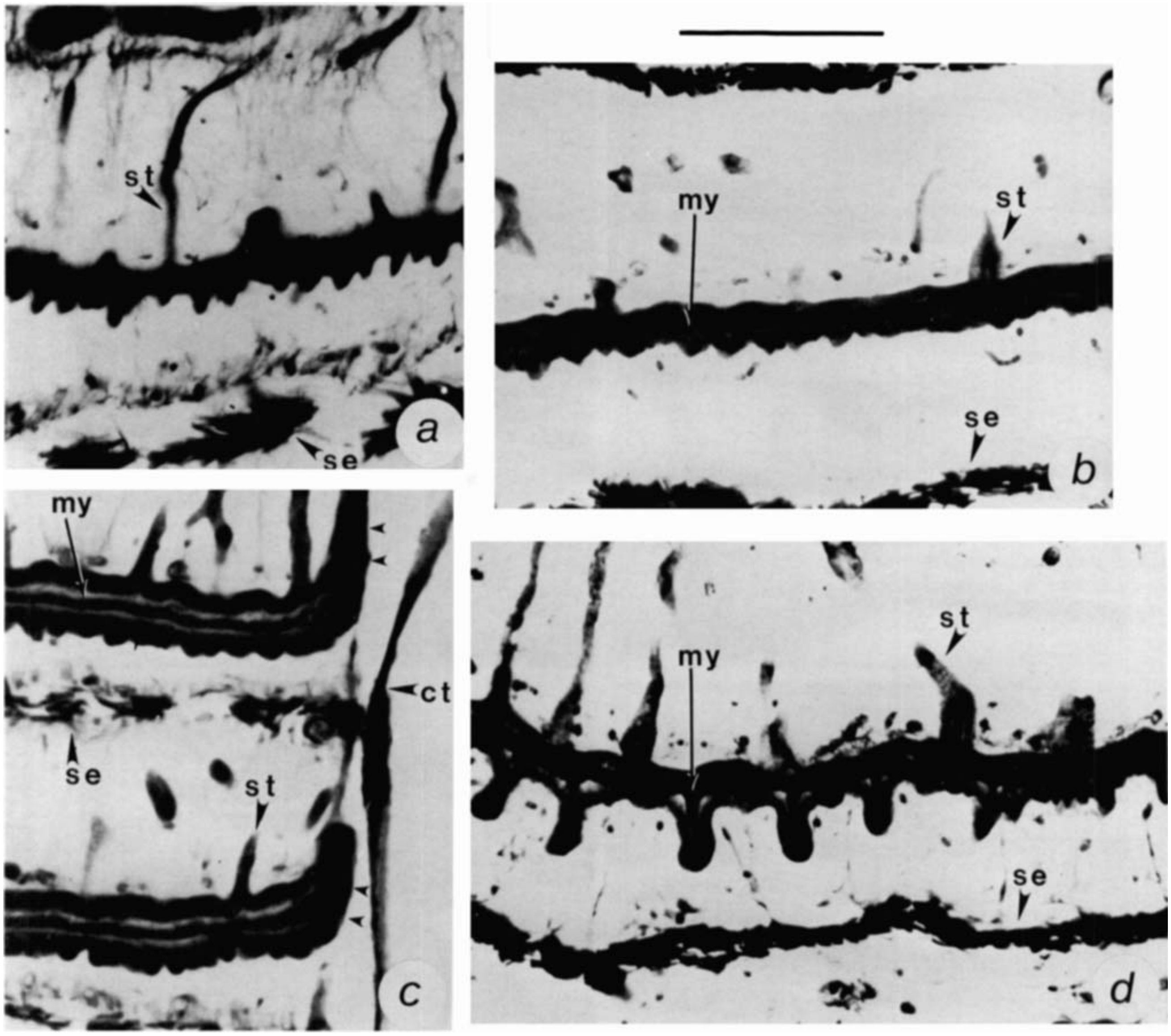

Fig. 7. Photomicrographs of sagittal views of Mallory-stained electrocytes. Anterior is down, posterior is up. a. *Brienomyrus curvifrons*. b. *Isichthys henryi*. c. *Brienomyrus brachyistius* (long biphasic). d. *Isichthys henryi*. In *I. henryi*, the size of the surface foldings varies within a single column of electrocytes, the most posterior cells (d) having larger foldings than anterior ones (b). The deeply staining central zones of several electrocytes (b–d) denote the presence of myofilaments (my). Also shown in c are the connective tissue "tube" (ct) that normally encloses (peeled away) a column of electrocytes, and the swelled margins (double arrows) of the electrocytes. Bar scale at top right is 0.1 mm for a–d. Abbreviations: st, stalk; se, connective tissue septa.

of longer duration than those with a single stalk system. Again, each species' EOD is distinct, as in *I. henryi*, where the initial head-positive phase has a prominent inflection point and the EOD duration is less than that of *P. gabonensis*.

A third pattern is a single stalk system (pattern A, Fig. 9) that arises from the posterior face, but secondarily penetrates the electrocyte body (as schematized in Fig. 5b). After emerging on the anterior side, the stalk's branches fuse into a single trunk that is innervated in a restricted zone. The five species with this pattern have a triphasic EOD waveform with an initial head negative phase. But, as with other patterns, there are still dramatic species differences in the appearnce of the EOD waveform. Compare the size of the initial negative phase in *Hippopotamyrus batesii* (reversed polarity, RP) to that of *Brienomyrus brachyistius* (triphasic, TP). Some members of this electrocyte "family" have sex differences in the EOD waveform; both sexes have the same cell geometry.

Mormyrops zanclirostris has a penetrating-stalk electrocyte (Fig. 9, pattern B) with an inverted polarity of innervation because the stalk arises from the anterior face and then penetrates the electrocyte body to arise on the cell's posterior side (also see Grosse and Szabo, '60; Bennett and

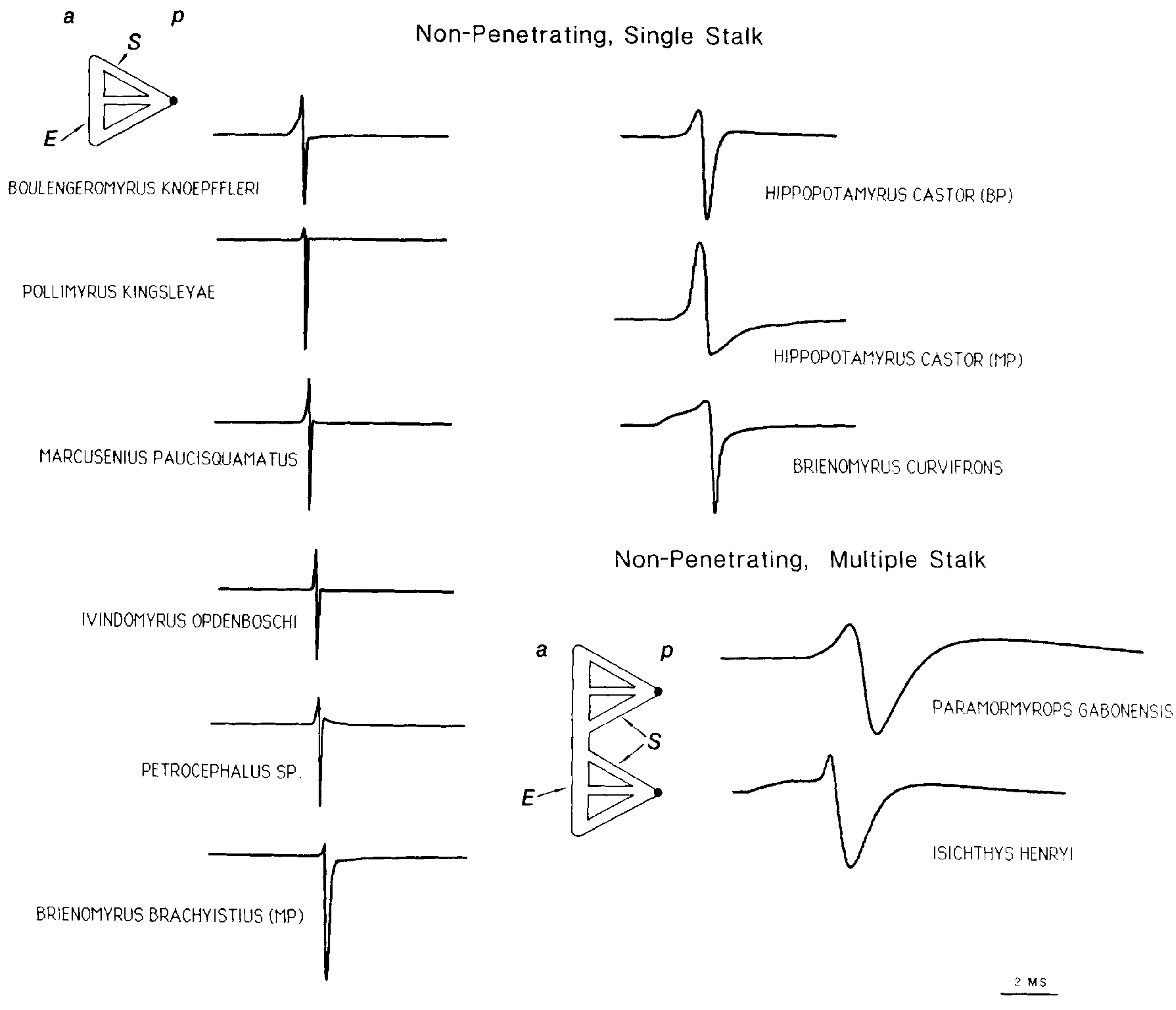

Fig. 8. Schematic representation of the geometrical patterns for mormyrid fishes from Gabon, West Africa. Each electrocyte pattern is associated with a "family" of EOD waveforms. Shown here are species with nonpenetrating stalks. Some species have a single stalk arising from the posterior face, while others have more than one stalk per cell and so multiple sites of innervation (dot). All species shown have a biphasic EOD waveform; those with a multiple-stalk pattern tend to have longer duration EODs. Abbreviations: a, anterior side; p, posterior side; S, stalk; E, electrocyte body. Bar scale is 2 msec.

Grundfest, '61). The EOD waveform is essentially biphasic (head negative, then positive), although Bennett ('71) reports a small initial head-positive phase with high amplification. We do not see the initial head positivity, but differences in water conditions could account for the presence or absence of this small initial phase (see Bell et al., '76). So, the EOD, like the electrocyte's geometry, is essentially inverted compared to those species with a penetrating stalk arising from the posterior face.

Another variant of the penetrating stalk pattern is present in *Marcusenius conicephalus*, which has multiple stalks arising from the posterior face that penetrate the electrocyte body (Fig. 9). Each stalk is innervated by electromotor axons on the anterior side of the cell. As with the single-stalk case, this species' EOD is triphasic with an initial head negativity. The initial positive phase of this fish has a prominent inflection point. The EOD of *M. conicephalus*, like that of other species with a multiple-stalk system (Fig. 8), tends to be of longer duration than the EOD of species with a single-stalk system.

A sixth and final pattern is represented by *Stomatorhinus corneti*, which has the most complicated electrocyte geometry and EOD waveform (Figs. 9, 10). The EOD waveform of *S. corneti* has four phases, with a sex difference in the pulse. As in other species (above), male and female electrocytes have the same geometry. Among juveniles and females, the initial phase may be either head positive or head negative (see Bass and Hopkins, '85; also see Moller, '80). As portrayed in Figures 9 and 10, *S. corneti* has a single stalk with both penetrating and nonpenetrating elements. The

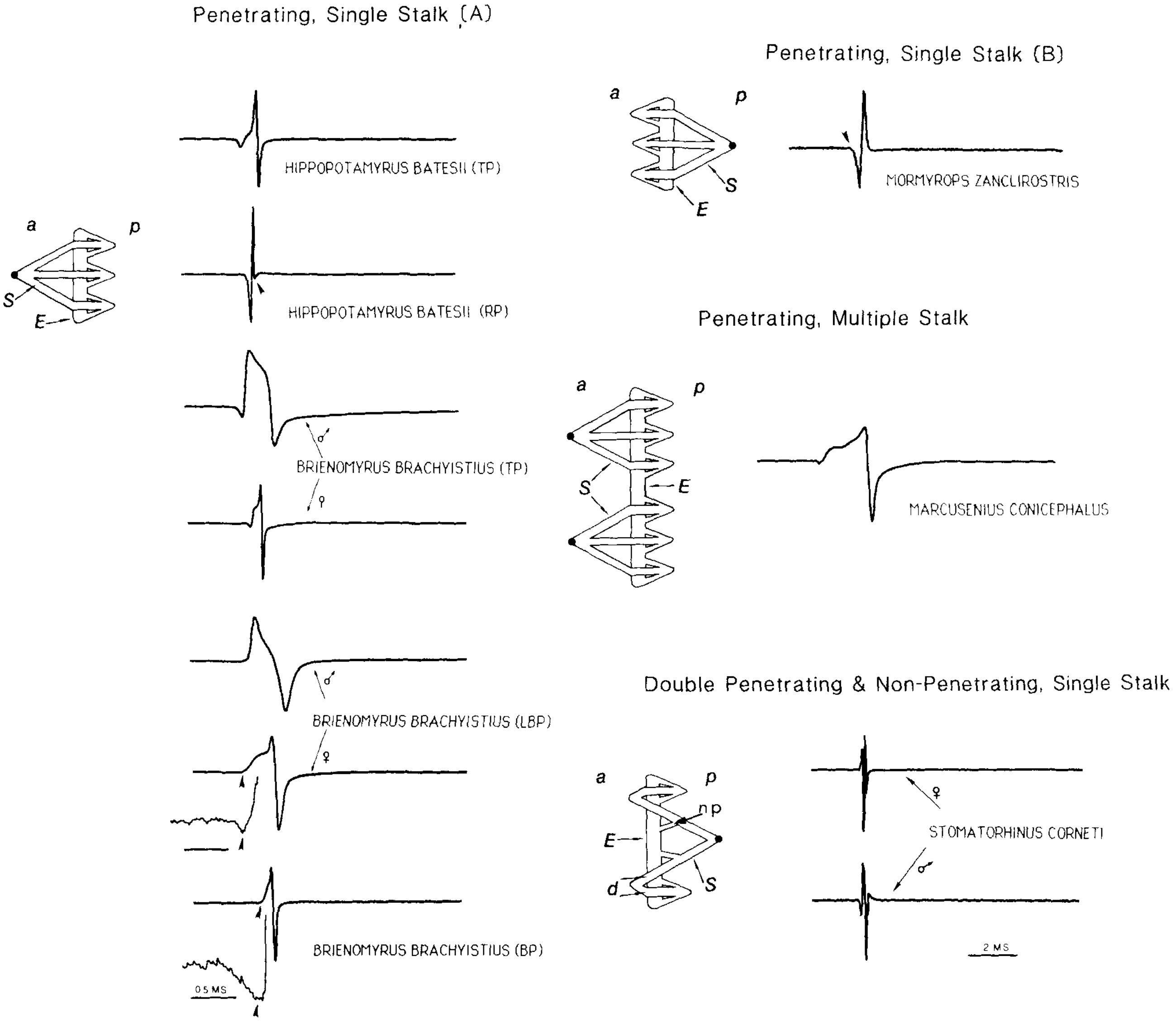

Fig. 9. Schematic representations of electrocytes with a penetrating stalk; all have EOD waveforms with three or four phases. The largest group (pattern A) includes those species with a single stalk that originates on the posterior side (p) and penetrates the cell to emerge on the anterior side (a) where it is innervated (dot). These species have triphasic EODs characterized by an initial negative phase. The size of the initial negative phase varies dramatically between species. The initial negativity for *Brienomyrus brachyistius* (long biphasic, LBP) and *B. brachyistius* (biphasic, BP) is seen only with higher amplification (insets). One species, *Marcusenius conicephalus*, has a multiple penetrating stalk system that originates on the posterior face and has a triphasic EOD waveform. *Mormyrops zanclirostris* has an inverted single stalk system (pattern B) where the stalk originates on the anterior side and then penetrates to the posterior side where it is innervated. Its EOD is essentially inverted compared to pattern A (a small initial positivity (arrow) is reported by Bennett, '71). *Stomatorhinus corneti* has the most complicated electrocyte pattern and EOD waveform. Its stalk (S) has one element that does not penetrate (np) and a second (d) that penetrates the electrocyte body (E) twice. Bar scale is 2 msec for all EODs, excepting inserts of *B. brachyistius* (0.5 msec).

stalk arises from the posterior face. One element first penetrates the electrocyte body to the anterior side and then penetrates a second time to reemerge on the posterior side where it is innervated. A second portion of the stalk consists of branches that also arise from the posterior face, but are directly continuous with the double-penetrating element.

The above findings show that although species differences in the polarity and phase number of EOD waveforms can be associated with electrocyte geometry, there is still species variability in the overall appearance of the EOD for a given geometry. This conclusion is underlined by the *Brienomyrus brachyistius* complex. Hopkins ('80) describes four groups of *B. brachyistius* that appear similar on the basis of external morphology, but differ in their EOD waveform (and so the suffixes "monophasic," "biphasic," "long biphasic," or "triphasic,"; Fig. 11). One group, *B. brachyistius* (monophasic), has a nonpenetrating, single-stalk electrocyte (as described above). The remaining three—*B. brachyistius* (biphasic), *B. brachyistius* (long biphasic), and *B.*

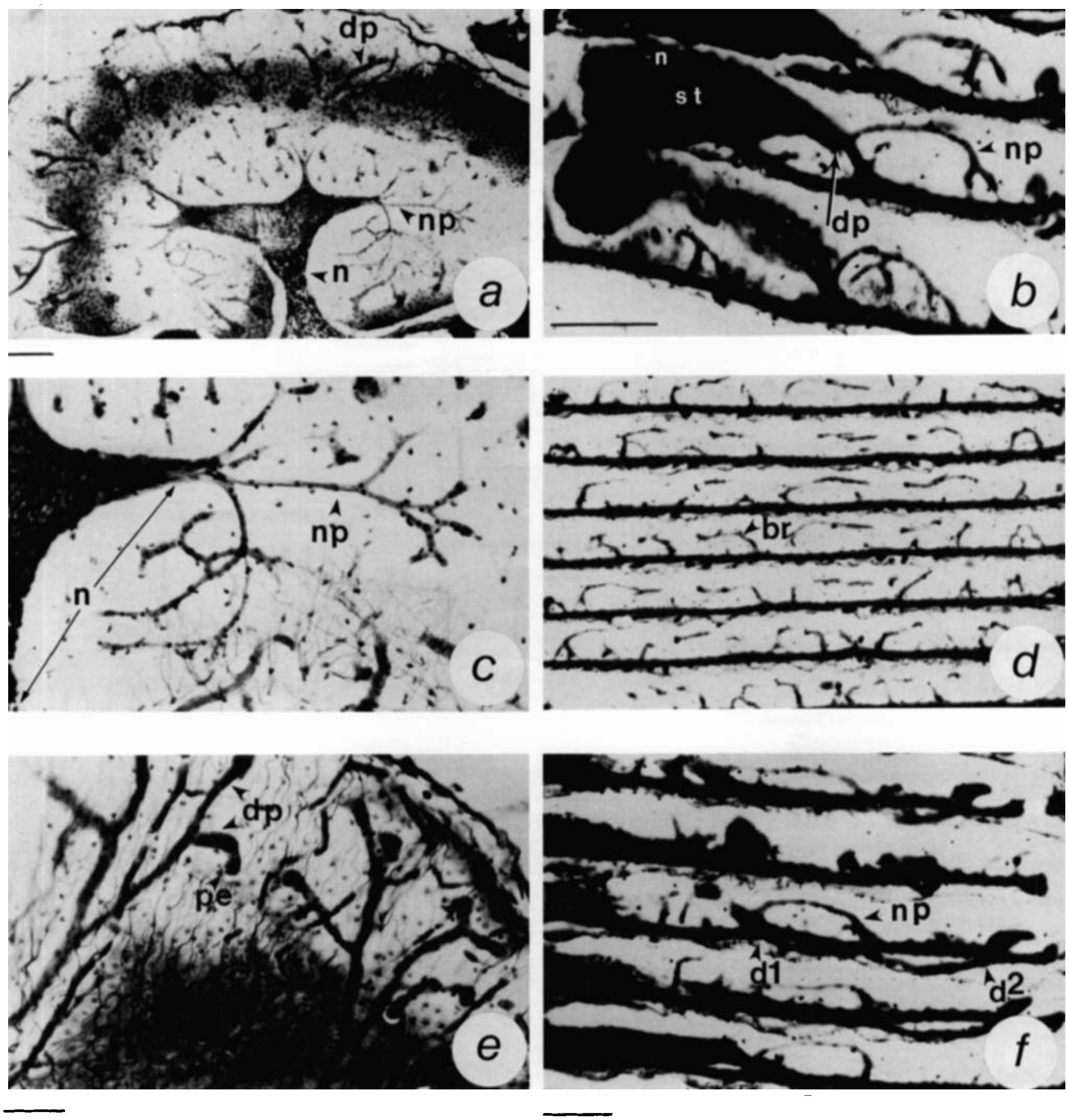

Fig. 10. The electrocyte of *Stomatorhinus corneti*. As depicted in Figure 9, the electrocyte of *S. corneti* is a single stalk system with both penetrating and nonpenetrating elements. Shown here are photomicrographs of Mallory-stained sections. a,c,e. Transverse sections. b,d,f. Sagittal sections; anterior is down. a. Face-on view showing nonpenetrating elements of the stalk (np) that are localized in the center of the cell (higher magnification in c), and double-penetrating elements of the stalk (dp) that fuse with the electrocyte's posterior face near its periphery (higher magnification in e). Electromotor nerve (n) also shown. b. The "np" branch originates from the "dp" branch near the base of the stalk (st) where the nerve (n) terminates. c. Close-up of "np" branches near base of stalk. d. The "np" branch divides into smaller branches (br) that are continuous along the posterior face. e. Close-up of "dp" elements as it extends along the anterior side of the cell before repenetrating at peripheral sites (pe) to the posterior side (see Fig. 9). f. The "dp" element penetrates first (dl) to the anterior side and secondarily (d2, which = "pe" site in 10e) back to posterior side. Bar scales are 0.1 mm for a; 0.5 mm for b,d,f; 0.025 mm for c,e.

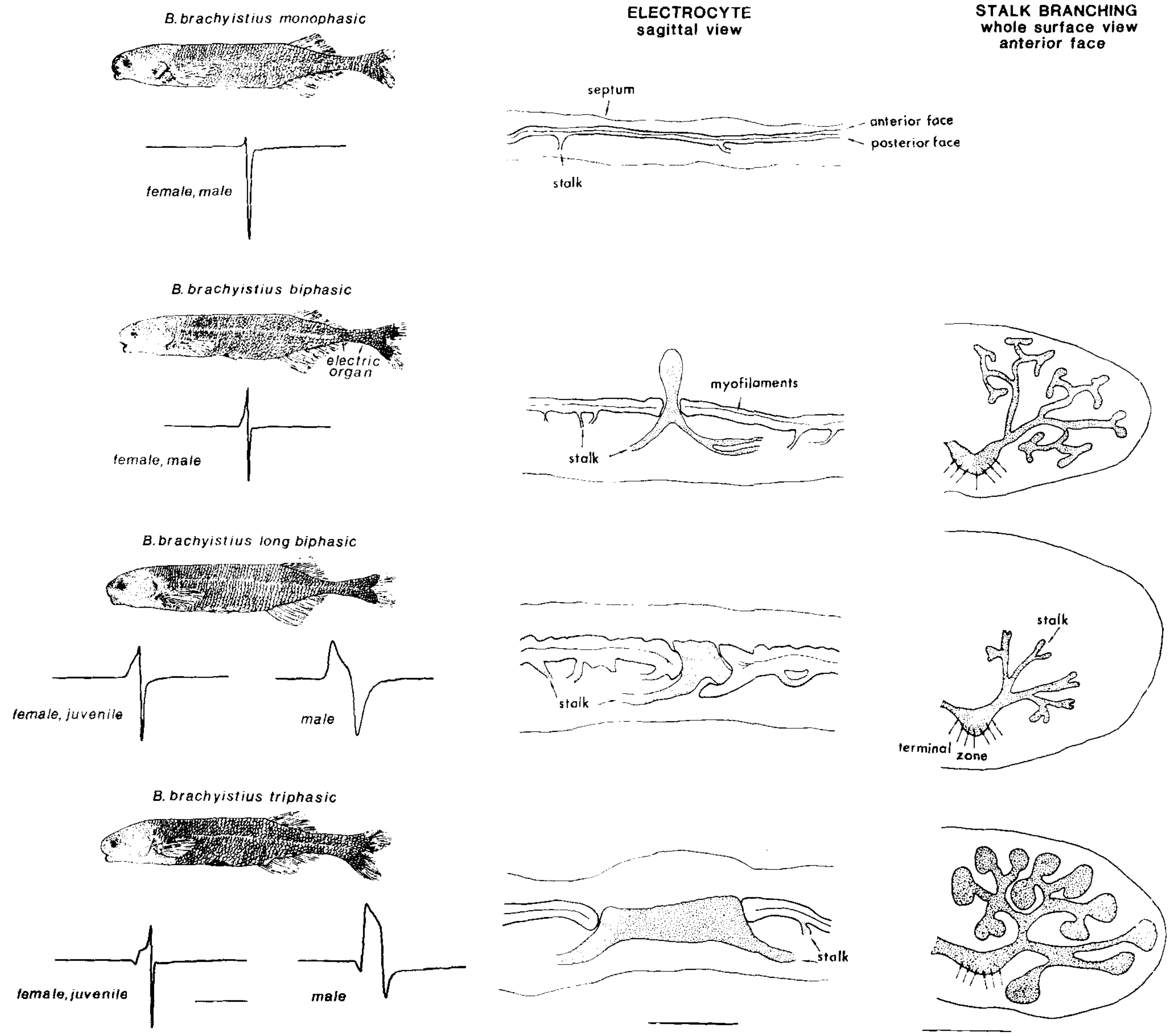

Fig. 11. Electrocytes of *Brienomyrus brachyistius* complex. Hopkins ('80) identifies four separate groups, characterized by differences in the EOD waveform as shown in the left frame. Bar scale is 2.5 msec. There are distinct anatomical differences between the electrocytes of each group (line drawings of actual Mallory-stained sagittal sections; middle frame; bar scale is 0.1 mm). The stalk's branching pattern also varies as shown to the far right for line drawings of methylene-blue-stained single electrocytes (see Fig. 4; data not available for *B. brachyistius* monophasic; bar scale is 1.0 mm).

brachyistius (triphasic)—have a penetrating single-stalk system and a triphasic EOD with an initial head negativity (also Fig. 9). Despite such similarities, there are still species and sex differences in EOD waveform appearance and electrocyte morphology. EOD duration alone ranges from 0.6 msec (*B. brachyistius* biphasic) to nearly 3.0 msec (males of *B. brachyistius* (long biphasic) and *B. brachyistius* (triphasic)). The amplitude of the initial negative phase, the duration of each phase, as well as the presence of inflection points in the major positive phase, also vary.

Bennett and Grundfest ('61) suggest that as the number of penetration sites increases for an electrocyte, so does the size of a pulse's initial negativity. The number of penetration sites for the *Brienomyrus* complex is depicted in Figure 11 for methylene-blue-stained electrocytes (see Fig. 3); it increases from ten sites in *B. brachyistius* (long biphasic) to twelve in *B. brachyistius* (triphasic) to eighteen in *B. brachyistius* (biphasic). Although the number of penetration sites may relate to the initial negative phase's amplitude, the total volume of the stalk that penetrates through an entire cell may be as significant. For example, the initial negative phase of *B. brachyistius* (triphasic) is larger in amplitude than *B. brachyistius* (biphasic), although the latter has more recognizable penetration sites. However, the size of the stalk at the penetration site (and so probably total stalk volume) is clearly much greater in *B. brachyis-*

tius (triphasic). But still, the initial negative phase and number of penetration sites of *B. brachyistius* (biphasic) is greater than that of *B. brachyistius* (long biphasic) (see higher amplifications in Fig. 9). (*Hippopotamyrus batesii* (triphasic) and *H. batesii* (reversed polarity) also have a large number of penetration sites and a large initial negative phase, Figs. 6d, 9). *B. brachyistius* (long biphasic) not only has the fewest penetration sites, but the sites do not extend to the periphery of the electrocyte. Since its posterior face has stalk branchlets along its entire surface, its stalk must have branches that extend across the posterior side of the cell to its periphery.

The stalk of *B. brachyistius* (triphasic) is quite different in size from that of any other species and deserves further comment. The penetration sites are widespread over the cell's surface (Figs. 6b, 11). Because of its large size, the stalk almost forms its own anterior and posterior faces at the penetration site (Figs. 11, 12a). In an anterior face view, the stalk forms large, mushroomlike penetrations (Figs. 11, 12b), which give off rootlike branches after emerging on the posterior side (Fig. 12a,c).

As with other mormyrids, there are also differences in the appearance of the anterior face of the electrocyte for the *Brienomyrus* complex. *B. brachyistius* (long biphasic) has surface foldings that increase its gross surface area relative to the posterior face (Fig. 7c). Similar surface folding also characterize the anterior face of *Hippopotamyrus batesii* (triphasic) (Fig. 6d), *H. batesii* (reversed polarity), *Isichthys henryi* (Fig. 7b,d), *Brienomyrus curvifrons* (Fig. 7a), *Marcusenius conicephalus*, *Paramormyrops gabonensis*, and *Mormyrops zanclirostris*. The surface area of the anterior face may be further amplified by surface invaginations, known as canaliculi or tubules, as discussed in Bass et al. (submitted).

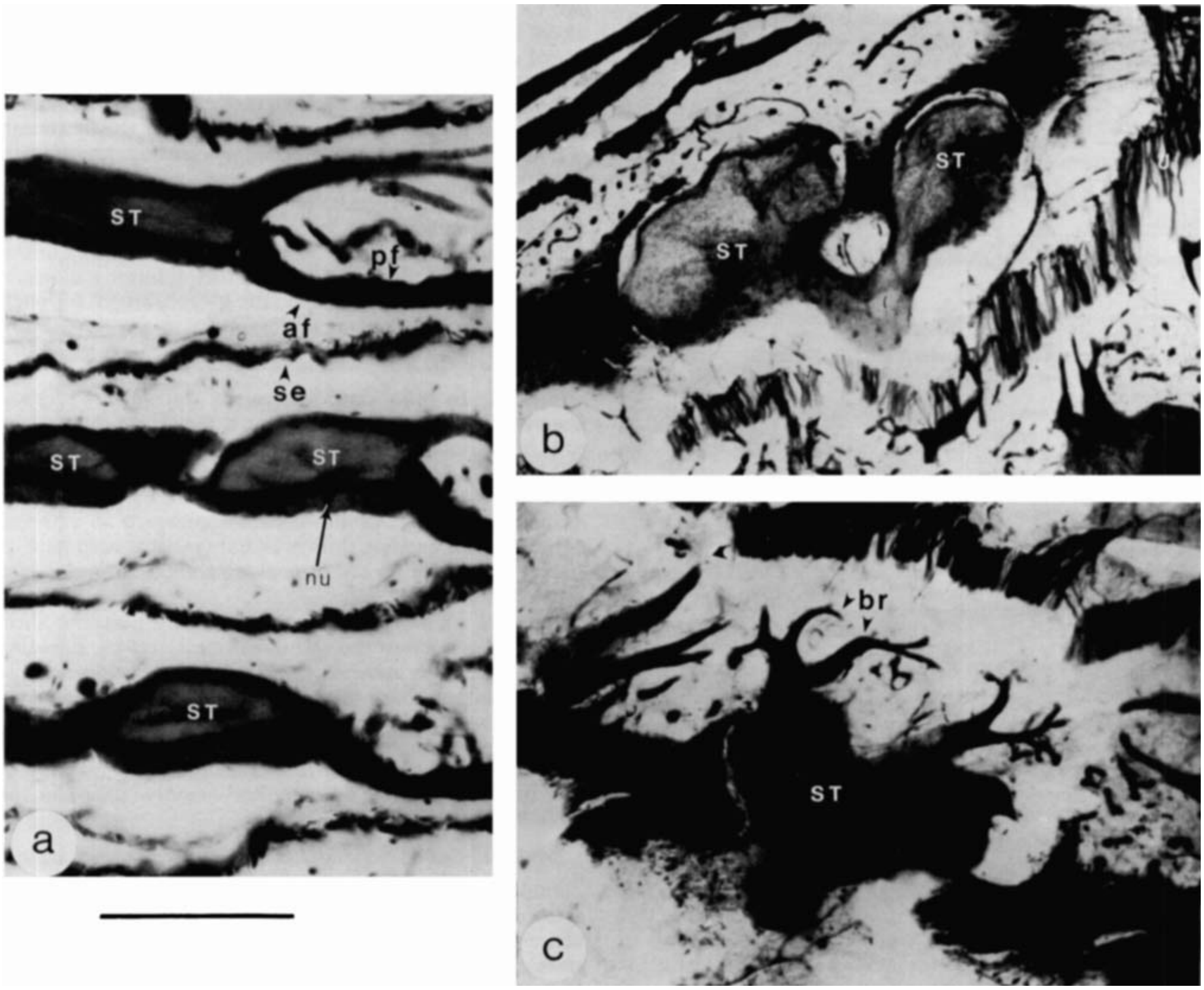

Fig. 12. The electrocyte stalk of *Brienomyrus brachyistius* (triphasic). a–c. Photomicrographs of sagittal (a) and transverse (b,c) sections of Mallory-stained electrocytes. a. The large stalk (ST) at the penetration site forms its own anterior and posterior faces, with nuclei (nu) distributed along its periphery. Connective tissue septa (se) are also seen. b. The stalk has a mushroomlike shape prior to penetration. c. The stalk has several branches (br) after penetrating to the posterior side. Bar scale is 0.1 mm for a–c.

Electrocyte number

There are species differences in the number of electrocytes per column (Table 1). Electrocyte number ranges from an average of 21 for *Paramormyrops gabonensis* to 91 for *Ivindomyrus opdenboschi* and *Hippopotamyrus batesii* (reversed polarity). While we presume that electrocyte number will affect the absolute amplitude of the EOD waveform (as in other mormyrids, Bennett and Grundfest, '61; Bell et al., '76), there is no quantitative data available for the Gabon species. For species where a sufficent sample size is available (*Stomatorhinus corneti*, *B. brachyistius* (long biphasic), *B. brachyistius* (triphasic), *H. batesii* (triphasic)), electrocyte number varies between individuals (Table 1), although there is no correlation with EOD duration, sex, or total body length. The latter suggests that mormyrids do not add on electrocytes with increasing size, i.e., age. The species with the least number of electrocytes, nearly half that of any other, are *P. gabonensis* (average of 21), *Hippopotamyrus castor* (biphasic) (24), and *H. castor* (monophasic) (29). All of the latter have nonpenetrating stalk systems. But, as with other variables, there is no strict correlation between electrocyte geometry and number; *Ivindomyrus opdenboschi* also has a nonpenetrating stalk electrocyte with 91 electrocytes per column.

TABLE 1. Electrocyte Number[1]

Species	Sex	Cells/ column	Species average of cells/ column	Size (mm)
Hippopotamyrus batesii (triphasic)	F	80, 80		76
	F	79, 81, 78, 74		90
	F	83, 83	80	90
Hippopotamyrus batesii (reversed polarity)	J	91, 91	91	80
Hippopotamyrus castor (monophasic)	M	28, 30, 28, 30	29	115
Hippopotamyrus castor (biphasic)	F	24, 23, 23, 25	24	118
Isichthys henryi	M	41, 41, 43, 48	43	210
Brienomyrus curvifrons	F	54, 50	52	105
Paramormyrops gabonensis	M	20, 21, 22, 22	21	166
Ivindomyrus opdenboschi		91, 91	91	125
Boulengeromyrus knoepffleri		>81		–
Petrocephalus sp.	M	80	80	75
Mormyrops zanclirostris		72, 74	73	160
Pollimyrus kingsleyae		>79		–
Brienomyrus brachyistius (monophasic)		82	82	–
Brienomyrus brachyistius (biphasic)	M	64, 65, 61, 61	63	97
Brienomyrus brachyistius (triphasic)	F	66, 68		50
	F	61, 65		58
	J	72		67
	M	65, 70		82
	F	66		90
	M	67		91
	F	64, 65		–
	M	68, 66	66	–
Brienomyrus brachyistius (long biphasic)	F	73, 77		68
	F	63, 63		69
	F	79, 80		85
	F	80, 79		98
	F	73, 73		102
	F	87, 83		102
	M	80, 82, 84, 80	77	115
Stomatorhinus corneti	F	67, 63		41
	F	76, 76		44
	M	65, 62, 60		47
	M	70, 68		51
	F	55, 52, 52, 51	63	55

[1] Abbreviations: F, female; M, male; J, juvenile. Size in mm is total body length. One to four columns were measured per individual, depending on available material. The average number of cells is indicated only for the species. In some cases, the entire electric organ was not sectioned, and the minimal number of cells is indicated by " > "; no average is indicated for these species.

DISCUSSION

Anatomical modelling of mormyrid EOD waveforms

This study supports a correlation between electrocyte geometry and the polarity and number of phases to the EOD waveform, as first proposed by Bennett and Grundfest ('61). Bennett and Grundfest ('61) discovered that each face and stalk of the mormyrid electrocyte generates an action potential. With electrodes placed anterior and posterior to a single cell, they recorded an electrical waveform that resembled the entire EOD waveform as recorded external to the fish with electrodes at the head and tail. While Bennett and Grundfest only studied a few species of mormyrids, their results suggested that the activity of a single electrocyte thus predicts the appearance of the EOD waveform. Based on their understanding of the electrocyte's geometry and the presence of essentially three excitable membranes, two faces and a stalk, Bennett and Grundfest proposed a model to explain the formation of an EOD waveform. Their model applies to *Gnathonemus petersii*, which has a single penetrating stalk electrocyte (as in Fig. 5b; also see Bruns, '71) and an EOD waveform with three phases. The model is redrawn in Figure 13 along with a model for the formation of a biphasic waveform from a nonpenetrating, single-stalk electrocyte.

Two points are crucial. One is that the electromotoneurons synchronously fire the electrocytes (Aljure, '64; Bennett et al., '67). Secondly, the electrocyte is oriented in the transverse body plane and has distinct anterior and posterior faces that can account for the establishment of longitudinal current flow along the organ.

Biphasic EOD waveform model (Fig. 13a-c)

Phase I. In those cases where the stalk arises directly from the posterior face and does not penetrate the electrocyte body, innervation occurs on the posterior side of the cell (see Fig. 5a). Following excitation, a spike propagates along the stalk's branchlets (active membrane indicated by dashed line in Fig. 13) but does not generate an external pulse because current flow is radial (vertical arrows, Fig. 13a) and there is no net flow along the posterior-anterior body axis.

Phase II. When the spike invades the posterior face, current flows across the cell (horizontal arrows, Fig. 13b) in a posterior to anterior direction and accounts for the initial positive phase of the head-positive biphasic waveform (as recorded with head-positive external electrode, dashed line of sine wave; Fig. 13b).

Phase III. The anterior face is excited by phase II; current flow reverses and forms a final negative phase for the biphasic pulse (Fig. 13c).

Triphasic waveform model (Fig. 13d-f)

Phase I. Electromotor axons terminate on the electrocyte's stalk on the anterior side of the electrocyte (see Fig. 5b); a spike is generated which then propagates along the stalk's membrane. As above, current enters the stalk in a radial fashion (Fig. 13d) and there is no net longitudinal current flow. But Bennett and Grundfest's model states that at the site where the stalk penetrates the electrocyte body, current is trapped by the stalk-body junction and directed from anterior to posterior (horizontal arrows, Fig.

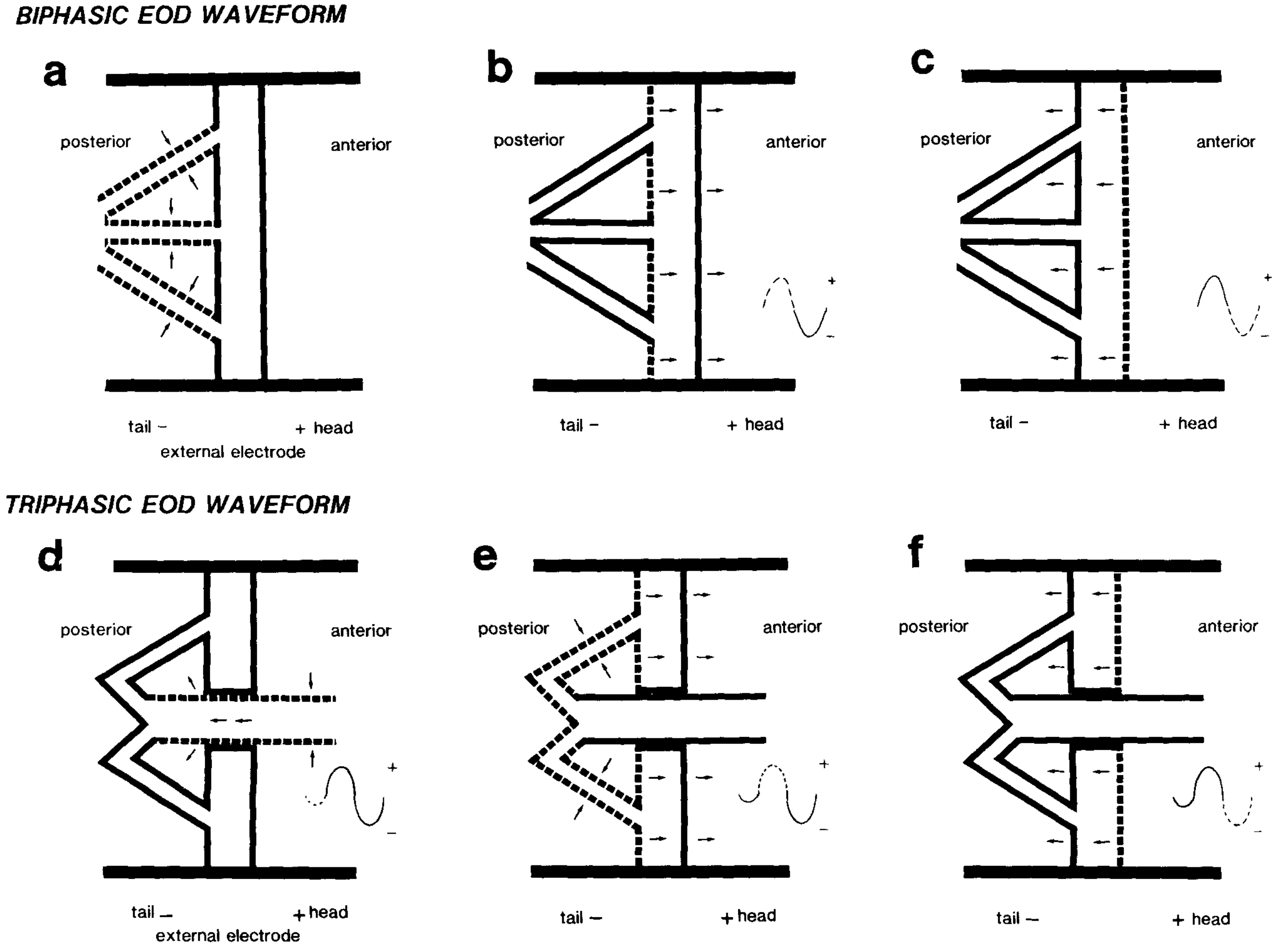

Fig. 13. Diagrammatic representation of the anatomical basis for the development of an EOD waveform based on the geometry of the cell; adapted from Bennett and Grundfest ('61). The excited membrane is shown by dashed lines. Arrows indicate the direction of current flow. An EOD waveform (schematized as a single sine wave; the active phase also indicated by a dashed line) as recorded externally with a head-positive electrode, is shown in the lower right of frames b–f. a–c. *Biphasic model*: The stalk is excited by electromotor axons and a spike propagates along the stalk (a) until it invades the posterior face of the electrocyte (b). The resultant posterior-anterior current flow (along the stalks and across the posterior face) generates a positive phase in an EOD waveform. The anterior face is subsequently depolarized, current flow reverses (c), and a final negative phase is generated for the biphasic waveform. d–f. *Triphasic model*: A spike propagates along the stalk (d) until it invades the posterior face (e). As current enters the stalk near the site of penetration, it is trapped and directed longitudinally, parallel to the anterior-posterior body axis; an external negativity is recorded (d). When the posterior face is excited (e), current flows across this face and a positive phase is recorded externally. Finally, the posterior-anterior current flow excites the anterior face, current flow is reversed (f), and a final negative phase is recorded for the triphasic waveform.

13d). Current tends not to leak around the edges of the cell because of the close opposition of the electrocyte's edges and the connective tissue tube enclosing them. Our external, head-positive electrode records an initial negative phase for the EOD waveform (Fig. 13d). Beyond the penetration site, current flow is again radial.

Phase II. The spike propagates along the stalk's branchlets until it invades the posterior face of the electrocyte where a second spike is generated (Fig. 13e). Current now flows across the cell in a posterior to anterior direction so that an external positivity is recorded, forming the second phase of the triphasic waveform.

Phase III. As current flows across the electrocyte, the anterior face will subsequently be depolarized and current flow reverses, now going from anterior to posterior as during phase I (Fig. 13f). A third, and final, negative EOD phase is recorded.

The models predict the number of phases and their polarity for EOD waveforms of the Gabon species (Figs. 8, 9). Additional correlations between electrocyte geometry and EOD waveform appearance:

(1) The longest-duration pulses are found for species with multiple stalks: *Isichthys henryi*, *Marcusenius conicephalus*, *Paramormyrops gabonensis*. Since there are multiple innervation sites, this may relate to asynchronous activation of different sites along the posterior face of the electrocyte (see Bennett and Grundfest, '61).

(2) Inflection points in the major positive phase of the

EOD are found both among species with and without a penetrating stalk system.

(3) For those species so far examined, the presence of sex differences in the EOD waveform correlates with a penetrating, single-stalked electrocyte.

Electrocyte morphology: A species-typical character

There is considerable variability in the actual appearance of the species-specific EOD waveforms for a given electrocyte geometry. What is crucial is recognizing that each species has its own "profile" of characters; i.e., no single morphological character predicts the appearance of the EOD pulse. Differences in membrane surface area—either stalk size (Fig. 6) or gross foldings of one face (Fig. 7) or degree of surface invaginations (Bass et al., submitted)—are as striking a morphological character as the presence or absence of a penetrating stalk. A discussion of the possible relationship between surface area and electrical properties is found in Bass et al. (submitted).

From a taxonomic viewpoint, electrocyte morphology may be a species-typical character used to predict the association of an EOD with a particular species. For example, Hopkins ('80) recognizes four major EOD groupings for *Brienomyrus brachyistius*. Each EOD subgroup, ("monophasic," "biphasic," "long biphasic," "triphasic") can now be associated with a distinct electrocyte morphology (Fig. 11), reinforcing a consideration of them as distinct species. Both *males* and *females* of sexually dimorphic species, as *B. brachyistius triphasic*, have very different EOD pulses, but the *same electrocyte geometry* (there is a sex difference in the size of electrocytes and membrane surface area; see Bass et al., submitted). Field studies show that steroid hormones can induce the male-typical EOD in females (Bass and Hopkins, '84, '85). So electrocyte anatomy can predict species relatedness for individuals whose EOD waveform can have more than one form, as with sex differences.

Thus, *Hippopotamyrus batesii* (triphasic) and *H. batesii* (reversed polarity) may be a single species. They have a similar electrocyte number (Table 1), and morphology characterized by frequent penetration sites (Fig. 6d). The possible significance of the "reversed polarity" form is unclear. Perhaps it is some stage of a sexually dimorphic EOD waveform. A sex difference in EOD duration is already reported for *H. batesii* (triphasic) (Bass and Hopkins, '85). While the sample size is small, the anatomy suggests these specimens are the same species. Only more detailed field studies can clarify such points.

Mormyrid central electromotor pathway and EOD waveforms

There is little data implicating an underlying role for the central electromotor pathway (Fig. 3) in determining the appearance of the EOD waveform. For mormyrids, the spinal electromotoneurons that synchronously fire the electrocytes are themselves synchronously activated by a descending signal from a medullary relay nucleus (Bennett et al., '67; see Fig. 3). The electromotoneurons generate a three-spike "command" signal in response to medullary excitation (Aljure, '64; Bennett et al., '67). The temporal properties of the command signal appear similar between species (Bennett, '71; Russell and Bell, '78; Bass and Hopkins, '83, '85), sexes, and hormone-treated and untreated individuals with normal or transformed EOD waveforms (Bass and Hopkins, '83, '85).

Phylogenetic trends among Mormyriformes

The order Mormyriformes includes two families: the mormyrids and the monotypic gymnarchids. The "wave" gymnarchids (Fig. 2) are considered the more primitive of the two groups (Taverne, '72); their electrocytes are disc-shaped as are those of the "pulse" mormyrids, but innervation occurs directly along the entire posterior face as in many gymnotiforms and marine species (Bennett, '71; Srivastara and Szabo, '72; A.H. Bass, unpublished observations). Petrocephalinae, the most primitive group of mormyrids (Taverne, '72), has a single, nonpenetrating stalk system with a restricted zone of innervation (Fig. 8). Among the other, more advanced mormyriforms (see Taverne, '72), there are a variety of penetrating and nonpenetrating stalk configurations as depicted for the mormyrids from Gabon (Figs. 8, 9). Thus, the evolution of a pulse waveform among mormyriforms is clearly associated with the development of a stalk with a restricted site of innervation.

For all mormyrids so far examined, there is nearly an equal distribution of penetrating and nonpenetrating stalk patterns (review: Bass, in press (a)). In some cases, electrocyte geometry does not even characterize genera. For example, *Marcusenius paucisquamatus* and *M. conicephalus* have, respectively, nonpenetrating and penetrating stalk systems (Figs. 8, 9). Similarly, *Brienomyrus brachyistius* (monophasic) has a nonpenetrating stalk while its close relatives have a penetrating stalk (Fig. 11). *Pollimyrus isidori* has a double-penetrating stalk (Denizot et al., '82; A.H. Bass, unpublished observations) while *Pollimyrus kingsleyae* has a nonpenetrating stalk electrocyte (Fig. 3f). Such intrageneric variation may relate to problems in classification. However, other characters such as brain size and morphology characterize the same genera (Bass et al., '82; A.H. Bass, unpublished observations). The data suggest that electrocyte morphology can vary at the species level.

Comparisons with electric organs of Gymnotiformes

Bennett ('71) and Bass (in press (a)) review the comparative neurobiology of electric organ structure and function. Intragroup variation in electrocyte morphology and EOD waveforms is most apparent among the weakly electric, freshwater fishes. Among gymnotiforms (see Fig. 1), electrocyte shape ranges from the ribbon-shaped cells of *Electrophorus* to the tubular-shaped cells of sternopygids, to the drum-shaped cells of gymnotids, hypopomids, and rhamphichthyids (Bennett, '71; Schwartz et al., '75). Both rhamphicthyids and hypopomids have a simple, conelike stalk that extends from the posterior face of the electrocyte, where innervation occurs. There are no gymnotiforms, or for that matter any other electric fish, that have electrocytes with a complicated stalk morphology comparable to mormyrids. One striking correlate of a specialized stalk system in mormyrids is the evolution of extremely brief duration EOD waveforms (e.g., 0.6 msec in *Brienomyrus brachyistius* (biphasic) and 250 μsec in *Stomatorhinus corneti*). In contrast, EOD pulse duration among gymnotiforms seems to have a lower limit of 1 msec (Hagiwara and Morita, '63; Bennett, '71; Bastian, '76; Hopkins and Heiligenberg, '78; Heiligenberg and Bastian, '80).

Unlike mormyrids, EOD diversity among gymnotiforms appears to relate more to the asynchronous firing of different subgroups of electrocytes, than to the specialization of the electrocytes themselves (review: Bass, in press (a)). What is especially striking is the presence of multiple electric organs, the best known example of which is the electric eel, *Electrophorus*, which has three—Main, Hunters', and Sachs'—organs (Keynes and Martins-Ferriera, '53).

Evolution of pulse vs. wave species

Most species of weakly electric fish have a pulse-type EOD; i.e., the interval between successive EOD waveforms is greater than the duration of the waveform itself. Two families of Gymnotiformes—the Sternopygidae and Apteronotidae—and one family of Mormyriformes—the Gymnarchidae—have a wave-type EOD (Fig. 2). The apteronotids appear to have maximized their EOD repetition rate or frequency (up to 1,700 Hz) by evolving a neurogenic electric organ derived from axons of spinal motoneurons, and thus "dispensing" with myogenic electrocytes and the chemical nerve- electrocyte (i.e., neuromuscular) synapse (see Bennett, '71).

Both sternopygids and gymnarchids have myogenic electric organs and are considered the most primitive members of their respective orders (Taverne, '72; Mago-Leccia, '76; Fink and Fink, '81). In each case, the electrocytes are the least specialized for the order. Sternopygid electrocytes have a long, tubular shape, reminiscent of the electrocytes in larval forms (Kirschbaum, '77; Denizot et al., '78). Gymnarchid electrocytes have no stalk, unlike mormyrids. One possible interpretation is that pulse species evolved from wave species and that development of a pulse-type EOD depended upon divergence in electric organ morphology. Of course, it is still possible that sternopygids and gymnarchids originated from pulse-type species, and secondarily evolved a wave-type EOD by modifying the EOD's rhythm generator in the medulla.

ACKNOWLEDGMENTS

The author is indebted to Thomas Szabo of the C.N.R.S., Gif sur Yvette, for the invitation to work in his laboratory and the generous use of his equipment; and to Denise Rouilly of the C.N.R.S. for her expert technical assistance throughout the study. Special thanks to Carl D. Hopkins for introducing me to the mormyrids of Gabon; to Margaret Marchaterre for help with the illustrations and the text; to Terri Natoli and Sally Mancil for typing the manuscript; and to anonymous reviewers for their helpful comments. This work was supported by NIH research grant RO1-NS19942-01A1 to A.H. Bass and C.N.R.S. grants to T. Szabo. Early stages of the research were also supported by NIH postdoctoral fellowship IFSN-NS06309 to A.H. Bass and NIMH research grant MH 26140 to C.D. Hopkins.

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