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Electric fishes research in the nineteenth century, following the steps of Carlo Matteucci and Giuseppe Moruzzi

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ABSTRACT

The history of the research on electric fish and animal electricity is briefly reviewed. In 1964, Giuseppe Moruzzi published an important article on Carlo Matteucci, who made fundamental contributions to these fields. Studies of electric fish played an important role in the birth of modern electrophysiology, largely through the research of Luigi Galvani. They also contributed to Alessandro Volta's invention of the electric battery. Electric fishes were widely studied by physiologists, physicists and zoologists in the nineteenth century.

Key words
Eletric fishes • Torpedo • Luigi Galvani • Alessandro Volta • History of electrophysiology

Electric fish research and two scientific revolutions in Enlightenment science

The aim of this article is to survey some historical aspects of research on the so-called electric fishes, i.e. the ubiquitous flat-shaped sea torpedoes, some elongated fish of the South-American rivers superficially resembling the eels (and therefore called "electric eels"), and a particular type of catfish of the African rivers, often referred to as Nile silurus. These singular fishes are capable of producing a strong shock which, until the eighteenth century, could not be accounted for satisfactorily within the framework of the available scientific paradigms. As we shall see, the history of electric fish research is ideally connected to the themes of a recent meeting held at Corliano, near Pisa, and dedicated to Carlo Matteucci and Giuseppe Moruzzi; both contributed to the development of electrophysiology in the last two centuries.

The research carried out on electric fishes, particularly in the eighteenth and nineteenth centuries, represents one of the main lines of scientific endeavour underlying the great development of modern electrophysiology (and more generally of neurosciences). This is mainly because of its importance in the investigation path which led to the discovery of the electric nature of nervous signal and muscle excitation. The starting point of this line of investigation is generally traced to the pioneering studies on frog preparations carried out by Luigi Galvani in Bologna. The results were published in 1791, in the last volume of the *Commentaries* of the Bologna Academy of Sciences. The connection linking Galvani to investigations of electric fishes is that his research was stimulated by the then recent studies suggesting that the shock of the singular fishes could be electrical (Piccolino and Bresadola, 2003). The crucial phases in the path leading to the electric nature of the shock from fish were associated especially with the experimental endeavours of an

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Englishman, John Walsh (1726-1795). In 1772, working at La Rochelle, on the Atlantic coast of France, Walsh showed that the shock of these fish is propagated along electric conductive materials, and interrupted by insulating bodies, exactly as happens with genuine electricity. Four years later, in London, he could produce a visible spark from another type of fish, the so called "trembling eels", imported from the Dutch Guyana. This experiment was considered as the crucial evidence necessary for establishing the electric nature of the shock. The evidence obtained in the eels was considered applicable not only to these fish, but also to torpedoes, and to catfish of the African rivers, thus contributing to the "electrification" of the all three fishes (Piccolino and Bresadola, 2002; Piccolino, 2003).

The electric hypothesis of the fish shock, supported by Walsh's experiments, supplanted the mechanical theory put forward in the previous century by the "new scientists" (*novatores*) of the Galilean revolution (and notably by Francesco Redi, Giovanni Alfonso Borelli and Stefano Lorenzini). At the beginning of the eighteenth century, the mechanical explanation had been endorsed by one of the most influent scientists of the Enlightenment, René-Antoine Ferchault de Réaumur, thus becoming the reference hypothesis for the shock from a fish until the emergency of the electric hypothesis.

The reason why Walsh's results with electric fish acted as a catalyst for Galvani's experiments on the involvement of electricity in nerve and muscle excitability relates to one of the main discussions of the eighteenth century physiology. The possibility that electricity could be the agent of the nervous conduction had indeed been suggested in the first half of the century when physical investigation showed that the "electric fluid" could propagate at distance along a conductive wire without any appreciable delay. This "neuro-electric" theory had been, however, discredited on the basis of a series of important objections pointing to the impossibility that body fluids, being electrically conductive, could maintain the electrical disequilibrium needed for the propagation of a signal from one extremity of a nerve to the other. It was argued, moreover, that, were the nervous conduction electric, nervous signals would propagate from one fibre to the adjacent ones making impossible any precise and localised movement.

By showing that electricity might have a role in fish physiology, that is in a type of animal which not only has a conductive body (like all animals), but also lives in an conductive medium, Walsh's research invalidated all these objections. It thus made realistic the possibility of electricity being involved in the physiology of less singular animals and, particularly, in the functioning of their nerves and muscles. This explains why it prompted Galvani's investigations which were started few years after the news of Walsh's research spread around Europe.

In a different – but correlated – context, electric fish research also stimulated the investigation of Alessandro Volta, leading, toward end of 1799, to the invention of the electric battery. In a letter addressed on March of the following year to the president of the Royal Society of London announcing the new invention, Volta dubbed the new instrument *organe électrique artificiel*. As he explicitly stated, this was due to the fundamental inspiration he drew from his reflections on the organ of electric fish (Piccolino, 2000a, 2003).

By prompting Galvani's research on animal electricity and Volta's invention of battery, electric fish investigation stimulated two of the most notable achievements of eighteenth century science. There had been a productive, albeit conflicting, interaction between Galvani and Volta in their investigations of the relation between physical and physiological electricity. Eventually, however, the success of Volta's battery contributed to reducing the influence of Galvani's hypothesis concerning the electric nature of nerve and muscle excitability. This was because Volta had arrived at a completely different conclusion to Galvani's on the origin of the electricity involved in his experiments on frog preparations. As a matter of fact, by repeating Galvani's experiments, Volta convinced himself that muscle contractions could be explained simply on the basis of the response to an external, purely physical, form of electricity, without assuming the existence of an intrinsic, animal form of electricity. For Volta, this external electricity was produced by the contact of the two different metals composing the arc normally used by Galvani in his experiments to connect nerve and muscle.

It was by developing this interpretation that Volta invented the battery, which, in his view, worked simply by adding up the electricity generated by the large number of bimetallic disc-couples, stacked one above the other, in an orderly fashion. On similar lines, Volta interpreted the production of electricity in the fish organs, which he considered to differ from the physical instrument only in being composed exclusively of humid discs, instead of metals. For Volta only electric fishes are endowed with a genuine form of animal electricity, i.e. one ‘essentially linked to life, which would depend on some of the functions of animal economy’. Contrary to Galvani’s assertion, Volta’s opinion was that such processes did not occur in ordinary animals (Piccolino and Bresadola, 2003).

In the first decades of the nineteenth century, Volta’s conceptions of the battery electricity as due exclusively to the contact of different metals was gradually abandoned. This was because it became clear, particularly after the experiments by Humphry Davy at the Royal Institution of London, that the functioning of the battery involves chemical reactions. These reactions take place in the liquid discs interspersed between the metallic discs (a fundamental aspect of the design of the battery). The relation between electricity and chemistry which started to be manifest in this way represented a first insight into the intimate relation between electricity and the deep constitution of inanimate matter, a basic landmark of modern physics.

As Volta’s ideas were increasingly criticized, Galvani’s hypothesis of the existence of a genuine form of electricity within the body of ordinary animals gradually re-emerged. This stimulated a new interest in electric fish, particularly because the electricity of these fishes seemed to open an important window on a possible tight association of this form of energy with the phenomena of life.

The latter idea was expressed in a clear way in a part of a treatise on electricity and magnetism published in 1836 by French physicist Antoine Caesar Becquerel. Becquerel was one of the many scientists actively engaged in electric fish studies. Together with his collaborator Gilbert Breschet, he had just made important observations on torpedoes caught near Venice in 1835. Becquerel wrote: “I have paid particular attention to everything that concerns electric fish since if some day one would happen to discover that electric fluid intervenes in the phenomena of life, this would likely be after having studied the singular property that these fishes have” (Becquerel, 1836, vol. IV, p. XIV).

Starting particularly from the 1820s the warm shores of the Mediterranean (and other southern European seas) became a kind of Holy Land or Mecca for these scientific pilgrims. In particular Italy was the preferred site for these electric fish pilgrimages (Finger and Piccolino, 2011).

Matteucci, Moruzzi and animal electricity: frog batteries, twitching legs and sparking torpedoes

A young Italian physicist, Carlo Matteucci, would eventually enter this field and play an important role, both direct and indirect, in some of the most important achievements of electric fish research of his epoch, and more generally in the investigation on animal electricity. The book in which he would publish the results of his electrophysiological studies, the *Traité des phénomènes électro-physiologiques des animaux* (Matteucci, 1844), is one of the most important works of nineteenth century electrophysiology. It provided the basis on which scientists of the calibre of Hermann Helmholtz, Emil du Bois-Reymond, Eduard Pflüger, Ludimar Hermann and Julius Bernstein would lay the ground for the great development of this science in the next century.

Matteucci is one of the two scientists to whom the Corliano meeting is dedicated. The other is Giuseppe Moruzzi, another great figure of Italian electrophysiology, whose life span is separated by about one century from that of his predecessor. Matteucci and Moruzzi are tied in many ways and particularly because, in his lifelong interest in history of science, Moruzzi dedicated a fundamental article to Matteucci’s electrophysiological work (Moruzzi, 1964, 1996).

Personally I am greatly indebted to this article. Reading Moruzzi’s text several years ago played an important role in orienting my cultural interest toward the history of science and particularly toward to the study of the historical foundations of modern electrophysiology. In his analysis of Matteucci’s scientific endeavours, Moruzzi combined his great historical sensibility with a deep knowledge of electrophysiology. He underlined the importance of Matteucci’s achievements for the subsequent development of electrophysiological thinking, and contributed to make Matteucci’s work known to the modern neuroscience community. Moruzzi's analysis of Matteucci's research is far from being purely eulogistic. Despite his admiration for his predecessor, Moruzzi did not refrain from remarking how, in some crucial moments of his experimental endeavour (as for instance in the case of the discovery of the induced-twitch), Matteucci failed to grasp the significance of his observations, thus missing the chance to foster in a more decisive way the birth of modern electrophysiology.

It is impossible to review here in detail the many important points of Moruzzi's analysis of Matteucci's electrophysiological work. It is, however, appropriate to present a few images from Matteucci's experiments which, in a highly expressive way, depict the importance of some of his achievements in the field of electrophysiology. The first image is that concerning Matteucci's experiment with the pile of frog half-thighs. This experiment allowed Matteucci to provide for the first time the unequivocal evidence of the animal origin of the electric current measured from a frog muscle.

A short comment is necessary to grasp the significance and importance of this experiment. As mentioned above, after Volta's invention of the battery, Galvani's theory of animal electricity seemed largely discredited. This is likely to be why, in the 1820s, the Italian physicist Leopoldo Nobili attributed a physical – and not a biological – origin to the electricity that he was able to record from a frog preparation by using a sensitive instrument (his "astatic" galvanometer) (Nobili, 1825, 1828). Matteucci continued Nobili's research and used his recording device. He was able to show that a current can be measured from a muscle only when one electrode is placed on an intact muscle surface while the other is on an injured region. This observation is easily understandable on the basis of the modern physiological knowledge, because the injured region provides a path of low resistance to the interior of muscle fibres.

In order to provide firm evidence that the current measured in his experiments does not simply depend on the contact between metals and animal tissues and is of genuine biological origin, Matteucci made recourse to the pile of frog half-thighs illustrated in Fig. 1. In this preparation the intact side of every individual thigh is connected to the injured side of

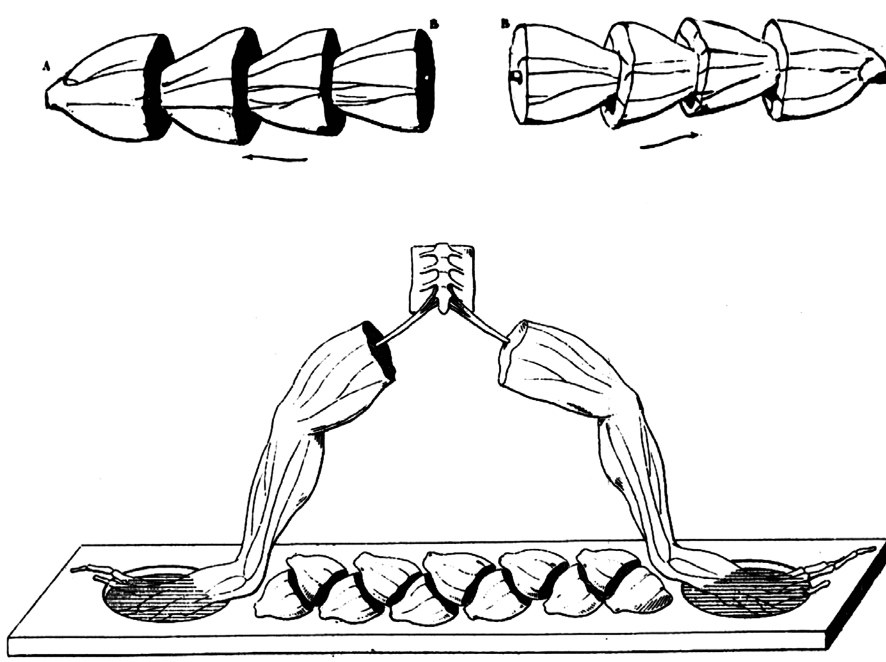

Fig. 1. - The "pile" of frog half-thighs used by Matteucci in some of his galvanometric measurements of animal electricity. In the lower part of the figure the electricity produced by the frog pile is used to stimulate a frog leg preparation.

the adjacent thigh. The deflection of the galvanometer needle was found to increase in progressive steps with every new half-thigh added to the pile, while the number and type of liquid-metal junctions remained constant. No doubt therefore that the current measured with the galvanometer originated from the frog muscle and was not simply an artefact due to the contact between the metallic electrodes and the humid animal tissues.

Another fundamental observation made by Matteucci in his investigation on animal electricity (amply discussed by Moruzzi in his historical article) is that concerning the already mentioned induced-twitch (Fig. 2). On the thigh of a typical frog preparation is laid the nerve of another preparation. When a contraction is induced in the first frog (by any kind of stimulation: electrical, chemical, mechanical), the second leg also moves. By varying the experimental conditions, Matteucci could discount the possibility that the contraction of the second frog depends on mechanical irritation of its nerves, induced by the movement of the first frog. Initially he correctly assumed that the effect was the consequence of an electric current propagated along the excited muscle (of the first preparation), which acted as a stimulant of the nerve in the second preparation.

Unfortunately, for reasons which are well discussed in Moruzzi's article, Matteucci eventually changed his views and came to the conclusion that nerve signal is not a genuine electric phenomenon. In Moruzzi's words "with the discovery of the induced twitch" Matteucci had "the keys to modern electrophysiology", but he missed making the conceptual connection. As a matter of fact, the induced-twitch experiment indicated that the propagation of the signal along nerves and muscles was due to the conduction of an electric wave capable of re-generating itself in the course of its propagation, by acting as a stimulus for the following segment of the fibre. After Matteucci, this view would emerge in a clear way, between the second half of the nineteenth and the beginning of the twentieth century. This was due particularly to the experiments of du Bois-Reymond, Hermann, and Bernstein in Germany, although the final explanation of the underlying mechanisms would be provided only in 1952 with the landmark studies of Alan Hodgkin and Andrew Huxley in Cambridge (reviewed in Hodgkin, 1964, 1992).

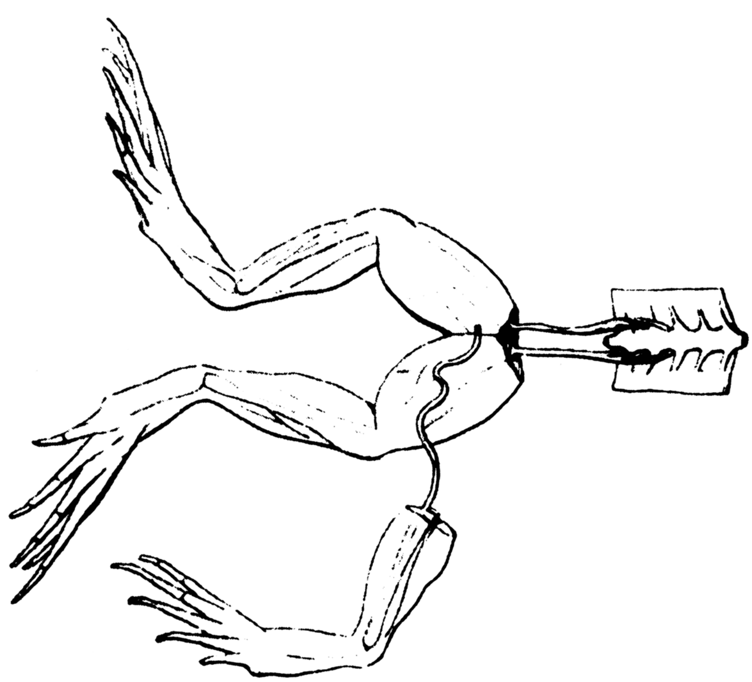

Fig. 2. - The arrangement for Matteucci's induced-twitch experiments with prepared frogs. These experiments provided the first demonstration that the electric signal propagating along nerve and muscle fibers is capable of exciting the zone ahead in the direction of the propagation.

The third aspect of Matteucci's research, worthy of allusion even in a brief survey, is that of his electric fish investigation, which was one of the main directions of his electrophysiological work and a central theme of the present article. Matteucci devoted a great number of scientific papers to the experimental study of torpedo shock, most of which were published on the *Comptes rendus* of the French *Académie* des Sciences, starting from 1836 until the last years of his life (Matteucci, 1836, 1837 and 1865; see Moruzzi, 1964, 1996).

Matteucci's first communication to the Académie concerned an experiment which had been unsuccessfully attempted several times by many scientists since the previous century. This experiment was successfully conducted by Matteucci in collaboration with Santi Linari, a colleague who was then professor at the University of Siena. As a matter of fact Linari performed the experiment a few months before Matteucci. He worked on torpedoes caught on the Tyrrhenian coast of Tuscany, while Matteucci worked on the Adriatic coast of Romagna, his native region (Linari, 1836). The experiments carried out by the two Italian physicists consisted in the production of a spark from the shock of a torpedo (Linari, 1836). The reason why many before Linari and Matteucci had failed in this experiment is because of the relatively low voltage (ca. 50 volts) of the shock of common torpedoes. Walsh, who had tried unsuccessfully with the torpedoes in La Rochelle, could only obtain a spark from the shock of electric eels in London because of the stronger electric intensity of these fish. As we know now, the voltage produced by the electric eel can be up to about 500 volts, thus being about ten times stronger than that of the torpedoes.

In their initial experiments on the torpedo, Linari and Matteucci employed a special arrangement in order to make fish electricity effective in producing the spark: the current was passed along an induction coil and the spark appeared when the discharge circuit was suddenly interrupted soon after the shock production. The spark was produced because the electric effect induced by the circuit interruption resulted in the production of a voltage much higher than that associated with the shock. The two physicists were applying to their investigation of the fish shock the advances brought about by the recent studies of Michael Faraday in the field of electromagnetic induction.

The first communication of the torpedo spark experiment was sent to the Académie by Matteucci in July 1836, also on behalf of Linari. This led to a long and harsh quarrel between the two scientists about the priority of the discovery (Matteucci, 1837; Linari, 1838), which is discussed by Moruzzi in his article.

The other important aspect of Matteucci's research on the torpedo concerns the experiments in which he provided definite evidence of the control exerted by the central nervous system on the shock production. In the previous century, first Lazzaro Spallanzani and later Galvani had shown that the fish could not produce the shock if the central nervous system had been destroyed (Piccolino, 2000b; Piccolino and Bresadola, 2003). Matteucci confirmed and extended these observations and, importantly, showed that the control centre of the torpedo shock is localised in a precise encephalic region, the "fourth lobe" (i.e. in the medulla). As Moruzzi points out, with this experiment Matteucci earned the esteem of several important European scientists, and notably Alexander von Humboldt, the German scholar who had a deep interest in electric fish research.

Humboldt, who had unsuccessfully tried to join Napoleon's expedition to Egypt in order to study the Nile silurus, had eventually succeeded in investigating electric eels in 1800 at Calabozo in Venezuela. This occurred during a famous five-year journey to the "equinoctial regions of the world" made together with French botanist Aimé Bonpland. In 1805, upon coming back to Europe from this journey, Humboldt made experiments on torpedoes in Naples, in collaboration with the famous French physicist and chemist Joseph Louis Gay-Lussac (Finger and Piccolino, 2011).

The two great scholars were largely unsuccessful in these experiments: they could not produce the spark from the fish shock, failed in the attempt of recording fish electricity with a physical instrument, and could not even show that the shock can be transmitted along electric conductors: they experienced the shock only by directly touching the fish body (possibly because the animals had a weak vitality). These failures may account for why, many years later, Humboldt, who still maintained a strong interest in electric fish, strongly praised Matteucci's achievements with torpedoes.

Fig. 3 combines three images concerning torpedo experiments from Matteucci's 1844 *Traité* which

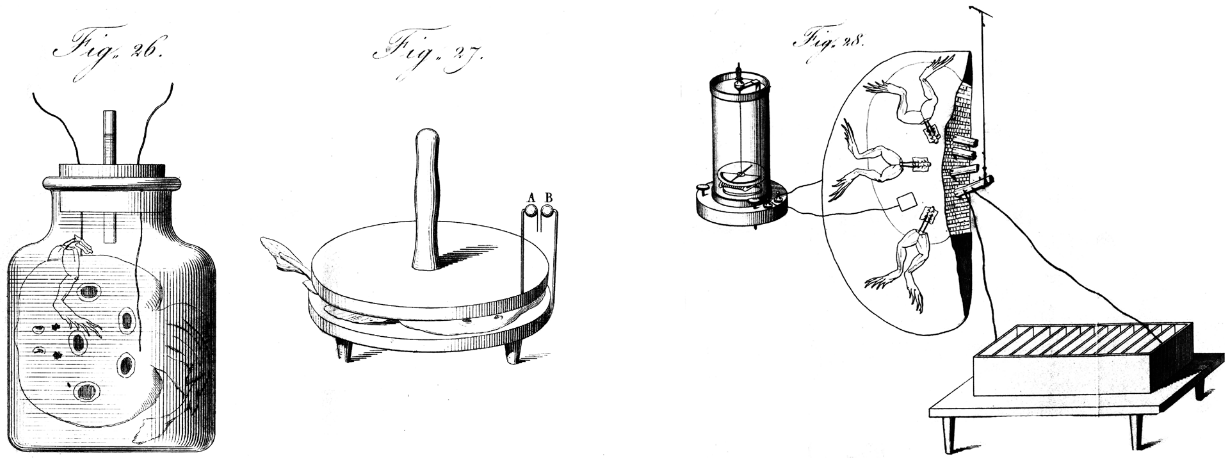

Fig. 3. - Three images of Matteucci's experiments on the torpedo from his *Traité*. Left: an experiment by which Matteucci could demonstrate that the production of the shock does not involve any reduction of the electric organs volume. The frog preparation laid down on the fish body is used to monitor the occurrence of the shock. Middle: the arrangement used to maximize the derivation of the fish current at the instant of the shock in order to produce the spark. Right: an experiment in which the current associated to the shock is recorded with the astatic galvanometer, while, at the same time it produces electrochemical effects. As in the figure at the left, also in this case frog preparations are used to monitor shock production.

illustrate both the sagacity and visual creativity of their author (see the legend for an explanation).

Matteucci made experiments only on torpedoes. He prompted, however, some of his colleagues at Pisa University to investigate other electric fishes in addition to the common torpedoes. His *Traité* contains a long appendix by the naturalist and zoologist Paolo Savi, with an accurate study of torpedo anatomy and particularly of the innervation of the electric organs. As we learn from Moruzzi's article, in 1850, while Matteucci was living in the Villa di Corliano (the location in which our meeting was held in 2010), he wrote some letters to Cesare Studiati, a young scientist living a short distance away, in Molina di Quosa. He asked Studiati, who was then lecturer in physiology, to investigate the structure of the electric organs of African catfish and of South America electric eels and to compare them with that of torpedoes. Matteucci was then planning a second edition of his *Traité*, which, however, would never be published.

Few years later, in 1855, Matteucci asked the professor of surgery, Andrea Ranzi, to make experiments on the African catfish in order to ascertain the polarity of the shock (Matteucci and Ranzi, 1855). Ranzi was then in Cairo where he served as physician to Viceroy Abbas I. Following the directions received from Matteucci, he could demonstrate that the catfish's tail becomes positive with respect to the head region during a shock (this was just the opposite of what happens with electric eels). Matteucci would publish the important result obtained by Ranzi as a short note on a new journal, *Il Nuovo Cimento*, that he had recently founded in collaboration with Raffaele Piria, professor of chemistry in Pisa. Also in this case Matteucci preceded du Bois-Reymond who obtained the same results in 1858 working on some electric fishes arrived to Berlin from Africa (du Bois-Reymond, 1858).

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