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Description of a new Central African earthworm, *Petroscolex centenarius* gen. et sp. nov. (Crassiclitellata, Eudrilidae), celebrating the 100th birthday of Pietro Omodeo

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Abstract

Prof. Pietro Omodeo (University of Siena, Italy), the world-renowned earthworm taxonomist and evolutionary biologist, was born in Cefalù, Sicily, Italy on the 27th September, 1919. He celebrates his 100th birthday in 2019 and members of the international community of earthworm taxonomists salute him with *Petroscolex centenarius* **gen. et sp. nov.**, a new megadrile taxon discovered in 1991 by him but which has not been formally described until now. The many important contributions of Omodeo to oligochaetological research are briefly mentioned.

Riassunto

Pietro Omodeo (Università di Siena, Italia), oligochetologo e biologo evoluzionista di fama mondiale, è nato a Cefalù, in Sicilia, Italia, il 27 settembre 1919. Celebra il suo centesimo compleanno nel 2019 e la comunità internazionale di tassonomia dei lombrichi lo saluta con *Petroscolex centenarius* gen. et sp. nov., un nuovo taxon di megadrili da lui scoperto nel 1991, fino ad oggi non formalmente descritto. I molteplici importanti contributi di Omodeo alla ricerca oligochetologica sono brevemente ricordati.

Key words: Centenarium, Oligochaeta, taxonomy, new genus, Central-Africa

Introduction

Pietro Omodeo (born in Cefalù, Palermo, Italy, 27 September 1919) has worked on oligochaetes since the age of 20, when he wrote his master's thesis (University of Pisa; supervisor: Giuseppe Colosi) on the blood circulation of

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Octodrilus complanatus. Returning from nearly 7 years of war and captivity in North Africa, he became the assistant of Umberto Pierantoni in Naples, and worked on his doctoral thesis (Scuola Normale Superiore, Pisa, 1947) focused on the embryological oddities of *Aporrectodea trapezoides*. The cocoons of this species almost always hatched as two monozygotic twins, with a high frequency of double or triple monsters (Omodeo 1948). This study had precedents in research conducted during the 1800s (Dugès 1828, Kleinenberg 1878) but Omodeo's evidence was much richer and his account more detailed. Having studied cytogenetics under Alberto Chiarugi, Omodeo felt ready to approach this new field of research in earthworms by exploring the chromosome sets and problems associated with polyploidy. At the same time, the teaching of Colosi and Pierantoni had instilled in him an evolutionary view along with mature taxonomic judgment which showed through even in his early notes on Italian earthworms. This granted him an excellent reputation, particularly abroad: Curt Kosswig, a German zoologist in Istanbul, entrusted him with material from Turkey, the Swedish spelaeologist Knut Lindberg sent him cave samples from Afghanistan, and Giorgio Marcuzzi entrusted him with collections from Venezuela and the Dolomites. Other scientists sent material to him from the Ivory Coast and Angola. The most fabulous collection, however, was sent by Maxime Lamotte: it originated from the Nimba mountain, a nature reserve situated at the cross point of Guinea, the Ivory Coast and Liberia, and contained dozens of new species belonging to eight oligochaete families, particularly Acanthodrilidae (Omodeo 1958). One third of the latter belonged to genera represented also in South America, like *Neogaster* and *Wegeneriella*: such a high amphi-Atlantic proportion was more than was expected and stimulated Omodeo's interest in biogeography (Omodeo 1963). In Europe he found, in particular, the family Hormogastridae—endemic to the western Mediterranean lands—lent themselves to biogeographical considerations, due to their endogeic habits, physiological adaptation to prolonged periods of drought, and low vagility. At mid 1950s, Omodeo was invited to study the collections of Arctic earthworms at the natural history museum of Copenhagen, a survey with biogeographic, ecological and cytogenetic implications (Omodeo 1957). The Greenland and Icelandic populations turned out to be very different from the conspecific ones from England and the Alps, which made transportation by man an unlikely explanation of their origin, and the survival in loco in ice-free nunataks the most probable explanation. During a 1962 symposium on the history of North Atlantic biota in Reykjavik, Iceland, organized by Askell Löve (an Icelandic botanist based in Canada), Omodeo revived the theory of Wegener, then in great disrepute although the geologists had begun to reconfirm it. He also denied that all European species of earthworms in North America were introduced by European settlers during the last few centuries and suggested the existence of a pre-Quaternary Holarctic earthworm fauna. In 1950, Omodeo was warmly welcomed as a new assistant at the Biology Institute of Siena by the then director Emanuele Padoa, man of great culture and humanity. There he resumed studying the cytogenetics of earthworms and documented, simultaneously with Sylfest Muldal, the relevance of polyploidy and parthenogenesis in these animals (Omodeo 1952). Omodeo was the first to clearly identify the mechanism that allowed unfertilized eggs to develop (premeiotic doubling of the chromosomes), and also explained how and why the male germ cells degenerated. The English botanist Irene Manton simultaneously described and interpreted identical phenomena in ferns. Furthermore, Omodeo discovered that different polyploid strains may coexist in local populations of many lumbricid species. The work (published in *Caryologia*), although written in Italian, had great international success. It received the compliments of Cyril Dean Darlington, Michael J. D. White, Hans Bauer, and others. In 1954 Omodeo became director of the Siena Biology Institute and published a second caryological monograph (Omodeo 1955) which was equally successful. By 1956 he proposed a redefinition of the genera of Lumbricidae based on a careful evaluation of morphoanatomical characters (where possible, analysed by statistical tools), as well as of biological (diapause and secondary growth) and embryological (organogenetic gradients) features, for the purposes of a phylogenetic reconstruction of the family (Omodeo 1956). All his new subgenera, *Dendrodrilus, Octodrilus, Cernosvitovia, Microeophila* and *Eiseniona* have later been promoted to full rank. Marcel Avel, experimental biologist in Bordeaux, France, cited Omodeo's work many times in his chapter on oligochaetes in Grassé's *Traité de Zoologie* (Avel 1959), and in a letter to Omodeo he acknowledged that Omodeo had made this difficult branch of systematics alive and fascinating as the study of microevolution should be.

While a full professor in Siena, and also after moving to universities in Padua (in 1966) and Rome Tor Vergata (in 1984), Omodeo focused mostly on the fauna of the Mediterranean region, exploring Tuscany and its archipelago, Sardinia and the surrounding islands (with about ten collecting expeditions), Sicily, wide areas of the Alpine and pre-Alpine arc, the Ligurian Apennine, and some crucial regions of France and Spain (Provence, Corsica, Pyrenées, Catalonia, Balearic Islands). This work was aimed at consolidating the faunal data, compiling a national catalogue, and delimiting the areas of endemism. An updated analysis of the Hormogastridae (Cobolli Sbordoni *et al.* 1992)

used the new powerful tool of *electrophoresis* for the study of *microevolutionary* processes and recent palaeogeographic data based on plate tectonics. The current reconstruction of the phylogenetic relationships within that family has been facilitated by those results and by meticulous observations of morphological variations recorded by Omodeo. Another major research of Omodeo concerned the endemic lumbricids of Tyrrhenian districts, including the Sardo-Corsican subfamily Diporodrilinae Bouché, 1970 (an isolated taxon with some archaic traits that was probably already present when the area was still attached to Catalonia). Outside Europe, his effort was mostly focused on Turkey (extensively explored in 1987 and 1990) and the Maghreb (five collecting journeys). Among the Lumbricidae of Turkey he observed the adaptive radiation of some endemic genera in the soils of Anatolia and suggested their attribution to a subfamily Spermophorodrilinae. The overall results on earthworm diversity and land evolution in the Mediterranean area were summarized in 2008 (Omodeo & Rota 2008). In 1998 and again in 2000, Omodeo attempted a reconstruction of the origin and evolution of Clitellata based mainly on the vascular system and on the female and copulatory apparatuses; in it he hypothesized a polyphyletic origin of megadriles, i.e. the orders Megascolecina, Lumbricina and Eudrilina, from the Alluroididae (via the Ocnerodrilidae?), the Haplotaxidae (via some primitively aquatic genera), and directly from the Alluroididae, (Omodeo 1998, 2000). For a full list of publications, see Rota (2009).

FIGURE 1. Members of the international community of earthworm taxonomists, participants in the 2nd IOTM, Cluj, Romania, 2005. Persons left to right: Randall Wood, Csaba Csuzdi, Ana Moreno, Tarmo Timm, Danuta Plisko, Tomás Pavlíček, **Pietro Omodeo**, Sam James, Anna Rożen, Antonia A. Pop, Gábor Cech, Victor V. Pop (Photo: Patricia Cardet).

30 years ago, Prof. Omodeo and co-author Kanyonyo ka Kayondo wrote a paper on a small collection of Central African worms belonging to an enigmatic genus of Eudrilidae (Eudrilinae). The worms possessed unusual prostatic and spermathecal pore positions (xiii and xviii, respectively, which mean reversed positions of the genital pores) and calciferous glands in xiv instead of the usual position in xii or xiii. That manuscript was sent for review to the late András Zicsi, who discussed this strange genus with the first author (Cs.Cs.) of this present paper. In the meantime the journal ceased to exist and the new taxon ("Simsiella irangiana") remained undescribed.

During a visit to the Natural History Museum, London, U.K., in 1994, the first author of this present paper (Cs.Cs.) found several specimens fitting the above diagnosis but did not report it, waiting to see if Omodeo's paper would ever be published. Although the original submission likely has been lost forever, we now have the opportunity to celebrate Pietro Omodeo's 100th birthday, honouring him and highlighting his contributions to Oligochaetology with the description of these peculiar worms.

Material and Methods

The earthworms were collected in the Kivu Region, Democratic Republic of Congo by Gazana N'Doli in 1973. In the description of this taxon, the terminology of Sims (1971) and Csuzdi *et al.* (2015) is used. Segment positions are indicated with lower case Roman numerals ("xii, xiii"), intersegments with Arabic numerals ("12/13"). The type material is deposited in the Natural History Museum, London, U.K., (NHMUK) and in the Hungarian Natural History Museum, Budapest, Hungary, (HNHM).

Taxonomy

Family Eudrilidae Claus, 1880

Subfamily Eudrilinae Claus, 1880

Petroscolex Csuzdi, Szederjesi & Sherlock, gen. nov.

Type species. *Petroscolex centenarius* **sp. nov**.

Diagnosis. Eudrilinae with single midventral prostatic pore in xiii and single midventral spermathecal pore in xviii. Female pores paired in xiv close to 14/15 near *d*. Oesophageal gizzard in vi, intestinal gizzards absent. Dorsal blood vessel simple throughout. Paired calciferous glands in xiv and unpaired chylus-sacs in ix, x, xi. Male genital apparatus proandric with sperm reservoirs in x and vesicles in xi. Excretory system holoic, vesiculate. Ovo-spermathecal apparatus paired with a dorsal interconnecting duct. Penial setae lacking.

Etymology. The new genus is named in honour of Prof. Pietro Omodeo.

Remarks. The new genus is unique among Eudrilidae due to the forward shift of the prostatic pore and the position of calciferous glands in segment xiv.

Petroscolex centenarius Csuzdi, Szederjesi & Sherlock, sp. nov.

(Figures 2, 3)

Holotype. NHMUK 1997.1594 clitellate adult. DR Congo, Kivu, Irangi. Leg. Gazana N'Doli, 20.02.1973.

Paratypes. HNHM AF/3555 1 ex. clitellate adult, NHMUK 1997.1595 1 ex. clitellate adult broken in two pieces. Locality and date same as of the Holotype. NHMUK 1997.1548–1549 1 ex. clitellate adult, 1 ex. juvenile, HNHM AF/3539 1 ex. clitellate adult, DR Congo, Kivu, Irangi. Leg. Gazana N'Doli, 08.03.1973. NHMUK 1997.1526–1529 1 ex. clitellate adult, 1 ex. aclitellate adult, 2 ex. juvenile, NHMUK ANEA 2019.7368 1 ex. clitellate adult, HNHM AF/5754 1 ex. clitellate adult, DR Congo, Kivu, Irangi. Leg. Gazana N'Doli, 09.03.1973. NHMUK 1997.1530 1 ex. aclitellate adult, DR Congo, Kivu, Irangi. Leg. Gazana N'Doli, 07.06.1973.

Etymology. The specific epithet refers to the 100th birthday of Prof. Pietro Omodeo.

Description. *Holotype*: Preserved length 160 mm, diameter after clitellum 5 mm, segment number 196. *Paratypes*: 150–190 mm in length, 4–5 mm in diameter. Segment number 153–206, anteclitellar segments frequently multiannulate, segments ii–xi carinate. Colour preserved brownish, alive unknown. Head epilobous 1/2 open, dorsal pores lacking. Setae: *ab* distant *cd* paired, setal ratio after clitellum *aa:ab:bc:cd:dd* = 4:3:3.6:1:12. Nephridial pores begin on segment ii, aligned somewhat dorsal to setal line *c*.

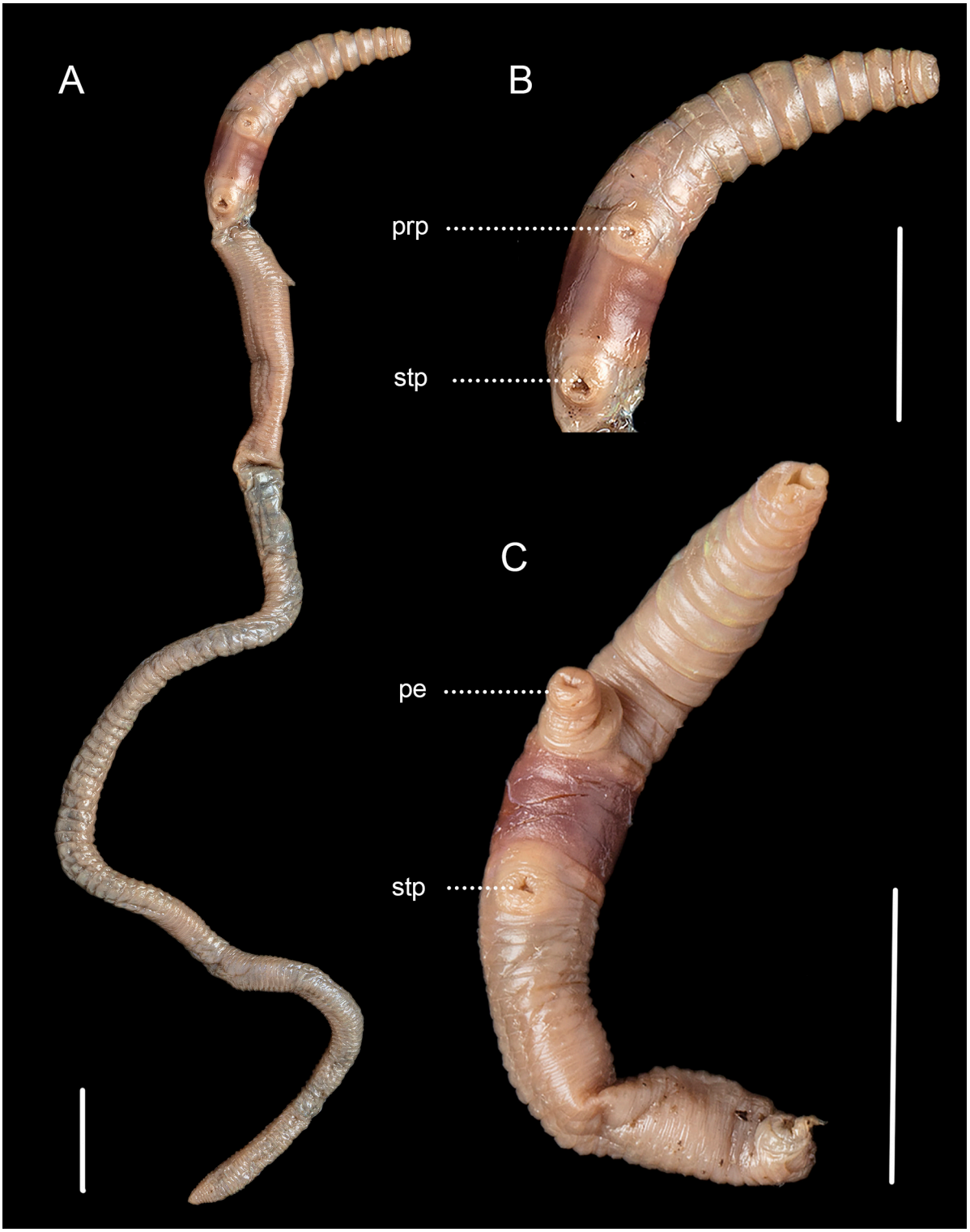

FIGURE 2. *Petroscolex centenarius* **sp. nov.**, photographs of type material. **A.** Holotype, complete worm, ventral view. **B.** Details of A, enlarged. **C.** Paratype NHMUK 1997.1595, ventral view, anterior body end. *pe* = penis (=everted bursa copulatrix); *prp* = prostatic pore; *stp* = spermathecal pore. Scale bar = 1 mm.

Clitellum annular on segments ½xiii–½xvii. Prostatic pore midventral on a spherical papilla in xiii, near to the 12/13 intersegmental furrow which sometimes emerges as a penis-like organ. Female pores small dots on xiv, close to the intersegmental furrow 14/15 just below setal line *d*. Spermathecal pore single midventral on xviii (Fig. 2A–C).

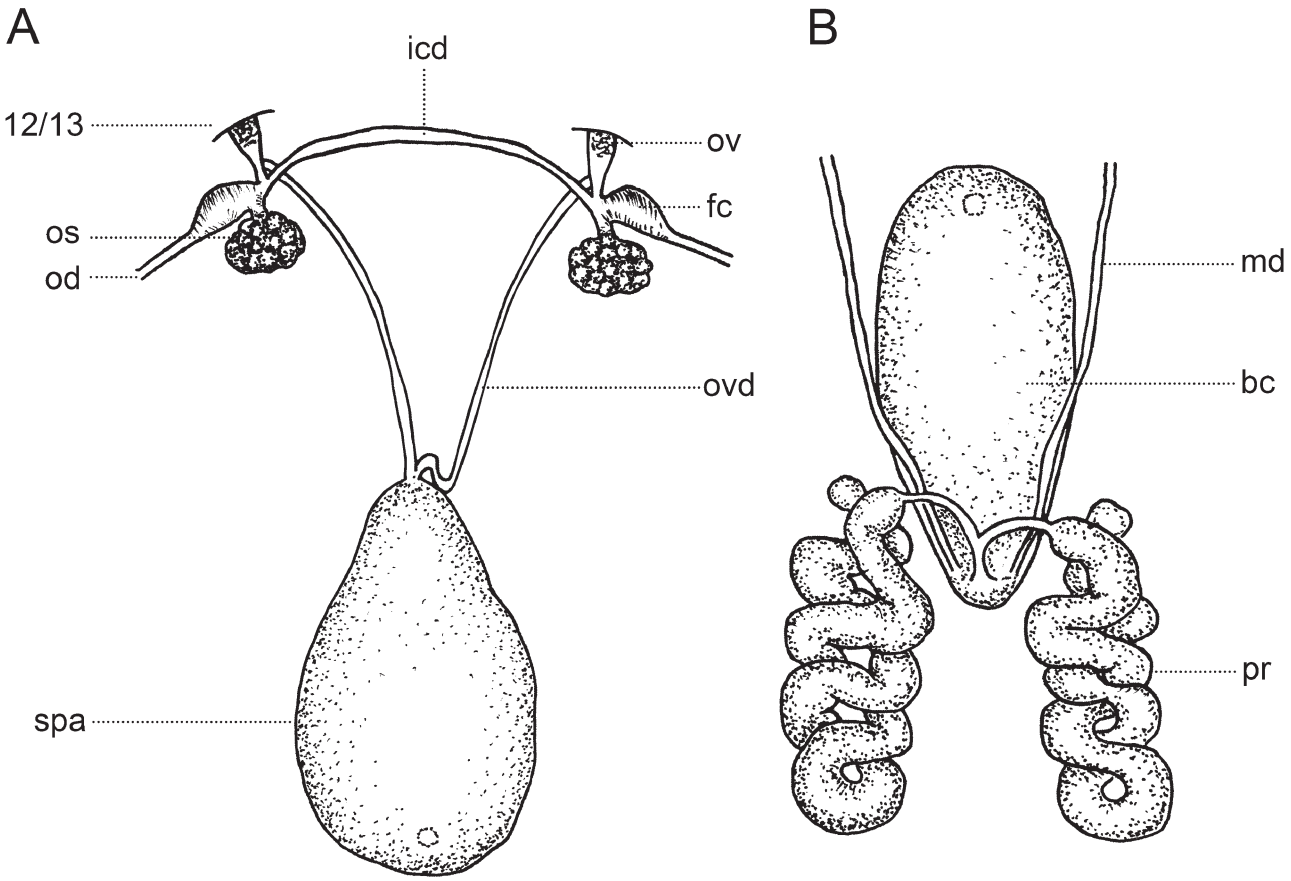

FIGURE 3. *Petroscolex centenarius* **sp. nov.**, reproductive organs. A. Ovo-spermathecal system. B. Prostates with bursa copulatrix. Note that the structure shown in B is situated dorsally of that shown in A. *bc* = bursa copulatrix; *fc* = fertilisation chamber; *icd* = intercommunicating duct; *md* = male duct; *od* = oviduct; *os* = ovisac; *ov* = ovarium; *ovd* = ovo-spermathecal duct; *pr* = prostate; *spa* = spermathecal atrium.

Internal characters: Muscular gizzard in vi, large, cylindrical. Septa 7/8–10/11 moderately, 11/12 slightly thickened. Calciferous glands paired in xiv, large mouflon-horn shaped. Small chylus-sacs in ix, x, xi. Dorsal blood vessel simple throughout. Hearts in x–xi, moniliform. Nephridial system holoic with thin biramous nephridial bladders. Typhlosole lacking.

Proandric. Testes and sperm funnels in x enclosed in a coiled sperm-reservoir. Seminal vesicles large in xi. Ovaries in xiii enclosed in an ovarian capsule pendant from septum 12/13. This ovarian capsule laterally continuing in a short, hardly recognizable ovarian duct joining the fertilisation chamber and bearing a pendant ovisac. From the fertilisation chamber a straight oviduct leads to the female pore in xiv. The ovarian capsule medially communicates on both sides with a delicate ovo-spermathecal duct running alongside the bursa copulatrix and joining apically to the pear-shaped, highly muscular spermathecal atrium (Fig. 3A). This atrium opens midventrally on segment xviii. The left and right ovarian apparatus connected by a small intercommunicating duct running above the intestine (Fig. 3A).

Prostates a pair of long spiral tubes, joining the bursa copulatrix (copulation pouch) via a common Y-shaped duct. Bursa copulatrix situated above the spermathecal atrium and completely covers it dorsally. Bursa copulatrix highly muscular, somewhat spindle-shaped, oriented headwards and opening (through the prostatic pore) on a penis-like protuberance on xiii (usually retracted). The two male ducts run backward along both sides of this copulatory pouch, and join to it subapically near each other (Fig. 3B). Penial setae lacking.

Discussion. Eudrilidae is the only earthworm family with internal fertilisation (Clausen 1965; Jamieson 1967; Sims 1969), which requires intercommunication of the ovarial and spermathecal systems resulting in a common ovo-spermathecal apparatus. This ovo-spermathecal apparatus is highly variable among different taxa both in its structure and external opening (Sims 1987).

The external opening of the spermatheca, usually located near the front of the clitellum, is frequently shifted back: for example, in *Beddardiella* Michaelsen, 1910 (spermathecal pore at 16/17), *Keffia* Clausen, 1963 (in xix), or in *Parapolytoreutus* Segun, 1980 (as far back as segment 22/23). Sometimes it shows wide variation even inside a genus: for example, in *Buettneriodrilus aequatorialis* Michaelsen, 1935 the spermathecal pore is in 12/13, while in *Buettneriodrilus armatus* (Michaelsen, 1913) it is in segment xix (Zicsi & Csuzdi 1986; Sims 1987). The position of the prostate pores is less variable; in the genera within the family described to date, it can be found in xvii, 17/18 or in xviii. *Petroscolex* **gen. nov.** is the first genus in Eudrilidae with prostatic pore in xiii, anterior to the clitellum.

The new genus is also unique in the position of calciferous glands in xiv, not xii or xiii as in other species of the subfamily. Sims (1987) distinguished two groups of genera based on this character, one group with calciferous glands in xii, distributed in West Africa, and another one with calciferous glands in xiii, distributed across tropical Africa. *Petroscolex* **gen. nov.** with its calciferous glands in segment xiv is more similar to the latter group because all the genera with backward shifted spermathecal pores possess calciferous glands in xiii. The distribution of the new genus supports this as well, the type locality Irangi, Kivu is at the eastern border of the Congo-basin.

A third peculiarity of the new species is the proandric condition of the testes. In Eudrilidae the male apparatus is mostly holandric, although a few genera show metandric reduction: *Metascolex* Michaelsen, 1903, *Polytoreutus* Michaelsen, 1890 or *Okudrilus* Csuzdi & Sherlock, 2015. *Petroscolex* **gen. nov.** is the first eudrilid genus with proandric reduction.

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