Ophiotaenia echidis n. sp. (Cestoda: Proteocephalidae) from the saw-scaled viper, Echis carinatus sochureki Stembrller (Ophidia: Viperidae), one of the world’s deadliest snakes, from the United Arab Emirates

Alain de Chambrier a, Philippe V. Alves b, Rolf K. Schuster c, Tomáš Scholz d,*

a Natural History Museum, PO Box 6434, CH-1211, Geneva 6, Switzerland
b Departamento de Parasitologia, Instituto de Ciencias Biologicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brasil
c Central Veterinary Research Laboratory, Dubai, PO Box 597, United Arab Emirates
d Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, Branisovská 31, 370 05, České Budějovice, Czech Republic

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ABSTRACT

Ophiotaenia echidis n. sp. (Cestoda: Proteocephalidae) is described from the intestine of one of the world’s deadliest snakes, the saw-scaled viper Echis carinatus sochureki Stemberller (Ophidia: Viperidae) in the United Arab Emirates. The new species differs from other species of the non-monophyletic Ophiotaenia by the position of testses in two longitudinal lines on both sides of the uterus, and by the large size of an embryophore (diameter of 44-55 μm versus less than 40 μm in other species). Phylogenetic reconstructions based on lsrDNA and concatenated lsrDNA + COI datasets place the new species among proteocephalids from unrelated zoogeographical realms but mostly infecting venomous snakes. In all analyses, O. echidis n. sp. exhibited a strongly supported sister relationship with O. lapata Rambeloson, Ranaivoson et de Chambrier, 2012, a parasite of a pseudox-yrophid snake endemic to Madagascar. Despite a shared close evolutionary history between these taxa, morphological synapomorphies remain unclear, which impedes the erection of a new genus to accommodate them. A list of the 71 tapeworms of the former, non-monophyletic subfamily Proteocephalinae, parasitising snakes and lizards, including species inquirendae, and the phylogenetically closely related Thaumasioscolex didelphidis from opossum, with selected characteristics, is also provided, together with a checklist of helmint parasites reported from E. carinatus.

1. Introduction

Ophiotaenia La Rue, 1911 is the most species-rich genus of proteocephalid cestodes (Onchoproteocephalidea), with a hundred species (88 according to de Chambrier et al., 2017 plus 12 taxa considered species inquirendae) parasitising reptiles and amphibians throughout the world (Rego, 1994; de Chambrier et al., 2017). Despite the overall morphological uniformity of most species of Ophiotaenia, the most comprehensive phylogenetic analysis (lsrDNA-based) for proteocephalids assessed by de Chambrier et al. (2015), revealed multiple colonisation events in snakes worldwide. These authors recognised three main clades containing species of Ophiotaenia. The generic name should be restricted to species of Clade O of de Chambrier et al. (2015), which includes the type species Ophiotaenia perspicua La Rue (1911) from North American colubrid snakes (La Rue, 1911, 1914), and also Ophiotaenia europaea Odening, 1963 from Palaeartic colubrids (de Chambrier et al., 2015).

Viperid snakes of the genus Echis Merrem, also known as saw-scaled vipers, are small to medium-sized animals widely distributed across xeric areas from Africa (countries north to the Equator) to India and Sri Lanka, including most regions of the Middle East (Pook et al., 2009); they exhibit a diversified diet usually corresponding to a particular species of the genus, e.g., vipers of the E. carinatus (Schneider) and E. pyramidatum (Geoffroy Saint-Hilaire) groups prey mostly upon arthropods, whereas species of the E. coloratus Günther group feed almost exclusively on vertebrates (Barlow et al., 2009).

The World Health Organization (2020) classified most species of Echis within Category 1 of risk, i.e., of the highest medical importance, which is reasonable since these vipers are presumably responsible for the greatest number of snakebite deaths per year in Africa and also being important causes of mortality and morbidity in India (see Pook et al.,...
2009 and references therein). Despite the relevance of *Echis* spp. to human health, their cestode fauna is poorly known, with just a few reports in faunistic surveys (see Sharpilo, 1976; Gibson et al., 2005). Data on helminth parasites of the saw-scaled viper are also scarce and most of them were published by Soviet authors in the 1950’s and 1960’s (see Sharpilo, 1976). Since most papers were written in Russian and are not easily accessible, a checklist of helminths parasitising *Echis carinatus* is provided to facilitate availability of information largely published in local journals and proceedings (‘sbornik’).

In the present paper, a new species of *Ophiotanenia* from the saw-scaled viper, *Echis carinatus sochureki* Stemmler, in the United Arab Emirates is described and its phylogenetic position is discussed.

2. Materials and methods

2.1. Morphological data

Tapeworms were found in the small intestine of six saw-scaled vipers, *Echis carinatus sochureki* Kemmler found in different localities of the United Arab Emirates and examined from 2003 to 2020. This subspecies occurs in northern India, Bangladesh, southern Afghanistan, Pakistan, central Iran, southern Iraq and the United Arab Emirates, with an isolated population in southeastern Arabian Peninsula (Uetz et al., 2020). The nominotypical subspecies *E. carinatus carinatus* (Schneider) is limited in its distribution to peninsular India (Uetz et al., 2020). None of 33 other snakes examined was infected, namely one *Echis omanensis* Babocsay, five *Cerastes gasperetti* Leviton et Anderson (both Viperidae), ten *Eryx jayakari* Bouleuger (Boidae), one *Malpolon moilensis* (Reuss), 13 *Paspamphob schokari* (Forská) (both Pommipodidae), and three *Platyceph rhodarachis* (Jan) (Colubridae). A total of 58 tapeworms in different states of maturity were found, but some specimens were kept in tap water until their strobila were totally relaxed. Therefore, only a few specimens collected in a fresh snake (host code No. UAE 4) fixed in 4% ethanol series, clarified by eugenol (clove oil) and mounted in Canada Balsam is permanent preparations. For histology, pieces of strobila were embedded in paraffin, transversely sectioned at 12–15 μm intervals, stained with Weigert’s haematoyxlin, and counterstained with 1% cosin B (acidified with five drops of pure acetic acid for 100 ml solution) (see de Chambrier, 2001). Eggs were studied in distilled water. For scanning electron microscopy (SEM) observations, one scolex was dehydrated through a graded ethanol series, dried in hexamethyldisilazane, coated with gold (thickness of 10–20 nm) and examined in a JEOL JSM-7401 F scanning electron microscope at the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences. All measurements in morphological description are given in micrometres unless otherwise indicated. Abbreviations used in description (usually if the number of measurements was >5) are: x = mean; n = number of measurements. Host and zoogeographical realm classifications follow Uetz et al. (2020) and Holt et al. (2013), respectively. Material studied is deposited in the Natural History Museum, Geneva, Switzerland (acronym MHNG-PLAT), and in the Helminthological Collection of the Institute of Parasitology, České Budějovice, Czech Republic (IPCAS).

A piece of another specimen (paragenophore from host UAE 03; MHNG-PLAT-120508) was used for DNA sequencing (courtesy of J. Brabec) of the large subunit nuclear ribosomal RNA (lsrDNA; D1–D3 domains) and the partial mitochondrial cytochrome c oxidase subunit I (COI) following the methodology outlined by de Chambrier et al. (2019). The sequences were assembled and inspected for errors using Geneious version R11 (Kearse et al., 2012), and submitted to GenBank (MW703700 – lsrDNA; MW703548 – COI); COI gene assembly was trimmed to the protein-coding region using the echinoderm translation code. Two alignments were created using the newly obtained sequences and selected members of the Proteocephalidae mostly corresponding to Clade K of de Chambrier et al. (2015) (these taxa were informed by a more comprehensive analysis of currently unpublished data) using default parameters of MAFFT (Katoh and Standley 2013) implemented in the Guidance2 web server (http://guidance.tau.ac.il/; Sela et al. 2015): (i) alignment including only the lsrDNA sequence data, and (ii) a concatenated alignment (lsrDNA + COI) including only those representatives with available sequences for both markers (see Table 1). Unreliable positions in the alignments were identified and removed using the Gblock web server (https://mbi.iastate.edu/gblocks/; Dereeper et al., 2008) with less stringent settings.

Phylogenetic reconstructions were performed with the maximum likelihood (ML) criterion using the evolutionary models implemented in ModelFinder (Kalyaanamoorthy et al., 2017) within IQ-TREE (Trifinopoulos et al., 2016), based on the small sample size corrected Akaike Information Criterion (AICc). The models chosen were as follows: TIM3 + F + R2 for the lsrDNA dataset alone; K3P + I for 1st codon position and GTR + F + G4 for lsrDNA, 2nd and 3rd codon positions using the concatenated dataset. The ML trees were generated via IQ-TREE and clade supports were estimated with 5000 replicates of the ultrafast bootstrap (UFBoot – Minh et al., 2013) and an SH-aLRT test with 5000 replicates (Guindon et al., 2010). To avoid overestimation of UFBoot, we used a hill-climbing nearest neighbour interchange (NNI), as recently recommended by Hoang et al. (2018). Clades with support values of both UFBoot >95 and SH-aLRT > 80 were considered strongly supported, while clades with only one of UFBoot >95 or SH-aLRT > 80 were weakly supported; nodes with both UFBoot <95 or SH-aLRT < 80 were unsupported. All the above-mentioned analyses were run on the computational resource CIPRES (Miller et al., 2010).

3. Results

3.1. *Ophiotanenia echidis* n. sp. Figs. 1–3

**Type- and only host:** *Echis carinatus sochureki* Stemmler, 1969 (Serpentes: Viperidae).

**Type-locality:** Houbara Breeding Centre (25.10418; 55.11283), Dubai, United Arab Emirates.

**Other localities:** Camelf Reroduction Centre, Dubai (25.08752; 55.38819); Dubai Safari (25.17971; 55.45056); Emirates Industry for Camel Milk Products, Dubai (25.02290; 55.41492), all in the United Arab Emirates.

**Prevalence:** Six snakes of 20 examined (i.e., 30%) in March 2007, July 2014, July and December 2017, and June 2020 were positive.

**Intensity of infection:** A total of 58 tapeworms were found in six positive hosts, i.e., mean intensity of infection was 10 tapeworms/host; minimum four tapeworms in June 2020, maximum 21 specimens in December 2017.

**Site of infection:** Small intestine.

**Distribution:** United Arab Emirates.

**Type-material:** Holotype MHNG-PLAT-0137383, 18 slides (complete whole-mounted specimen on three slides and 15 slides with serial sections) and two slides (with serial sections) IPCAS C-876/1 from host field number UAE 04, Houbara Breeding Centre, collected in July 2017; one paratype MHNG-PLAT-0137384, 21 slides (one complete whole-mounted specimen on three slides and 18 slides with serial sections), and two slides (with serial sections) IPCAS C-876/1 field number UAE 04, Houbara Breeding Centre (July 2017); two paratypes, IPCAS C-876/1 (two complete whole-mounted specimens on three and two slides, field number UAE 04-T2a-3a), Houbara Breeding Centre (July 2017), all Emirates Industry for Camel Milk Products in Dubai, examined by R. Schuster in June 2020.

**Other material:** Vouchers MHNG-PLAT-120508 (paragenophores), 14 slides (seven slides with whole-mounted specimen and seven slides serial sections from host field number UAE 03, Dubai Safari; IPCAS C-876/1 (one whole-mounted specimen); MHNG-PLAT-88912, Houbara Breeding Centre (March 2007), one specimen without scolex, 17 slides (three whole-mount and 14 serial sections), field number UAE 01;
MHNG-PLAT-120507, one specimen without scolex, 35 slides (four whole-mounts and 31 with serial sections) Houbara Breeding Centre, field number UAE 04, all from E. carinatus; see above.

Etymology: The specific name is derived from the generic name of the host.

Representative DNA sequences and phylogenetic relationships: one isolate (MHNG-PLAT-120508) yielded partial lsrDNA (MW703700; 1489 bp long) and COI (MW703548; 921 bp long) sequences. The final alignment of only lsrDNA dataset comprised 1012 positions including 124 parsimony informative sites, whereas the concatenated alignment comprised 1615 positions (1012 of lsrDNA and 603 of COI) including 250 parsimony-informative sites. The trees resulting from the ML analyses of both single and concatenated datasets showed a strongly supported sister relationship between O. echidis n. sp. and Ophiotenia lapata (Fig. 2C) in their analysis, our results show only weak support for this group (Fig. 4) that encompasses, besides snake cestodes, the only protocelphalid from a mammal, Thaumasioscolex didephidis Schlegel (Pseud oxyphriophiidae) endemic to Madagascar (Fig. 2A) (Rambeloson, Ranaivoson et de Chambrier, 2012, from Madagasgarcophis colubrinus Rambeloson, Ranaivoson et de Chambrier, 2012, from... (Fig. 2C) in their analysis, our results show only weak support for this group (Fig. 4) that encompasses, besides snake cestodes, the only protocelphalid from a mammal, Thaumasioscolex didephidis Schlegel (Pseud oxyphriophiidae) endemic to Madagascar (Fig. 2A) (Rambeloson, Ranaivoson et de Chambrier, 2012, from Madagasgarcophis colubrinus Rambeloson, Ranaivoson et de Chambrier, 2012, from...
proglottid, occupying very small area (Fig. 2C, G, 3). Cirrus-sac ovoid, thick-walled, 220–290 long, i.e. 20–34% (\(x = 24\%\), \(n = 22\)) of proglottid width, 100–140 wide (Fig. 2G). Cirrus occupies 73–80% of length of cirrus-sac (Fig. 2C). Genital atrium narrow; genital pores irregularly alternating, slightly postequatorial to equatorial, situated at 49–61% (\(x = 56\%\), \(n = 21\)) of proglottid length (Fig. 3).

Ovary small, bilobed, 370–540 wide, occupying 52–60% (\(x = 57\%\), \(n = 20\)) of proglottid width (Figs. 2B and 3); relative size of ovary, i.e., ratio of surface of ovary to surface of proglottid (see de Chambrier et al., 2012), 1.1–1.6% of proglottid size. Ovary length represents 2.5–4.2% of proglottid length. Vagina predominantly anterior (79%), rarely posterior (21%, \(n = 24\)) to cirrus-sac, lined with intensely stained cells in its terminal (distal) part and surrounded by small circular sphincter (diameter of 70–80) near genital atrium (Fig. 2C, F). Mehlis’ gland 70–100 in diameter, representing 8–13% of proglottid width.

Vitelline follicles oval, very small (30–60 long, 30–60 wide), arranged in two lateral, longitudinal columns on dorsal side of proglottid (Fig. 3), not interrupted on poral side dorsally at level of terminal genitalia (cirrus-sac and vagina – Fig. 2G). Follicles not reaching anterior margin of proglottids (Fig. 3); posteriorly, follicles may reach ovary,
Fig. 2. *Ophiotaenia echidis* n. sp. from *Echis carinatus sochureki*, United Arab Emirates. A – scolex, IPCAS C-876/1 (UAE 04). B – posterior part of proglottid, holotype, MHNG-PLAT-0137383, dorsal view. C – terminal genitalia with evaginated cirrus and vaginal sphincter, MHNG-PLAT-0137385, ventral view. D – cross section at level of anterior part of pregravid proglottid, MHNG-PLAT-0120507. E – egg with a trilayered embryophore, drawn in distilled water, MHNG-PLAT-0120507. F – cross section at level of the vagina, showing the vaginal sphincter, mature proglottid, MHNG-PLAT-0120507. G – terminal genitalia, C-876/1 (UAE 04 TS), dorsal view. H, I – eggs with a trilayered embryophore, drawn in distilled water, MHNG-PLAT-0120507. Abbreviations: ci: cirrus; cs: cirrus-sac; doc: dorsal osmoregulatory canal; ec: ejaculatory duct; em: trilayered embryophore; ilm: internal longitudinal musculature; ln: longitudinal nerve cord; loc: lateral osmoregulatory canal; Mg: Mehlis' glands; oc: secondary osmoregulatory canals; oe: outer envelope; on: oncosphere; ot: ootype; ov: ovary; sc: subtegumental cells; te: testes; tg: tegument; ud: uterine diverticula; up: uterine pore; us: uterine stem; ut: uterus; va: vas deferens; vc: vaginal canal; vd: vitelline duct; vf: vitelline follicles; voc: ventral osmoregulatory canal; vs: vaginal sphincter.
occupying porally 89–94% and aporally 88–92% of proglottid length, respectively.

Primordium of uterine stem ventral, with 47–55 (x = 50, n = 8) lateral branches (diverticula) on each side (Fig. 3B), never reaching posteriorly beyond ovarian isthmus (Fig. 2B). Formation of uterus of type 1 of de Chambrier et al. (2004) as follows: Uterine stem present as undifferentiated longitudinal median concentration of chromophilic cells in immature proglottids. In mature proglottids, uterine stem straight, occupying almost entire length of proglottids. Lumen appears in first mature proglottids. Lateral branches formed when eggs appear in uterus. Thin-walled lateral branches grow in pregravid and gravid proglottids (Fig. 3B), occupying up to 72% of proglottid width, and opening by elongate, slit-like uterine pore.

Eggs large, oval to spherical, with thin, hyaline outer envelope, up to 120 (n = 12) in diameter, somewhat collapsed in distilled water (Fig. 2E, H, I). Inner envelope consists of trilayered embryophore, with thick external layer, 44–53 in diameter, and nucleated envelope of irregular shape, 40–49 in diameter. Oncosphere surrounded by additional thick layer, 20–23 in diameter; oncospheres spherical, 11–12 in diameter, with 3 pairs of embryonic hooks 5–6 long (Fig. 2E, H, I).

Fig. 3. Ophiotaenia echidis n. sp. from Echis carinatus sochureki, United Arab Emirates. A - pregravid proglottid, holotype, MHNG-PLAT-0137383, dorsal view. B - gravid proglottid, paratype, IPCAS C-876/1, ventral view. Abbrevations: cs: cirrus-sac; eci: everted cirrus; oc: osmoregulatory canal; ov: ovary; te: testes; ut: uterus; vc: vaginal canal; vf: vitelline follicles.
3.3. Differential diagnosis

The new species is placed in *Ophiotaenia* (the former subfamily Proteocephalinae) because of the medullary position of the vitelline follicles, the unarmed scolex with uniloculate suckers and testes forming two separate fields (Rego, 1994). Based on molecular data, the new species is placed in Clade K of de Chambrier et al. (2015), which currently includes species of (non-monophyletic) *Ophiotaenia* (= *Ophiotaenia* sensu lato); *Australophiotaenia* de Chambrier, Beveridge and Scholz (2018); *Macrobothriotaenia* Freze, 1965; and *Thaumasioscolex* Caneda-Guzmán, de Chambrier et Scholz, 2001 (de Chambrier et al., 2015).

The new species differs from all species of *Ophiotaenia* (sensu lato) by the position of testes in single lines alongside the uterus, and by a large embryophore (44–53 μm versus less than 40 μm) (see Table 2).

In addition, *O. echidis* n. sp. possesses a trilayered embryophore, which is present only in a few species of *Ophiotaenia* from snakes, such as *Ophiotaenia lapata* Rambeloson, Ranaivoson et de Chambrier, 2012 from *Madagascarcacobilis communis* (Schlegel), *Ophiotaenia georgievi* de Chambrier, Ammann et Scholz, 2010 from *Leioheterodon gayoi* (Mocquard) (both host, *Pseudoxystrophophiidae*), and *O. bugarii* de Chambrier, Binh et Scholz, 2012 from *Bungarus fasciatus* (Schneider) (Elapidae) (see de Chambrier et al., 2010; 2012; Rambeloson et al., 2012).

*Ophiotaenia echidis* differs from the closely related *O. lapata* (see Fig. 4) by the absence of an apical organ and by the larger size of the scolex (400–725 μm versus 190–280 μm). The new species can be differentiated from *O. bugarii* by the position of the genital pore (at 49–61% of the proglottid length versus 29–48%) and by the smaller relative size of the ovary (1.1–1.6% versus 3.3%). *Ophiotaenia echidis* differs from *O. georgievi* by the number of uterine diverticula (47–55 versus 23–28) and smaller relative size of the ovary (1.1–1.6% versus 2.5–4.3%).

Eight species that belong to Clade Q in Fig. 4 (subclade of Clade K of de Chambrier et al., 2015) share the presence of a third embryophoric layer, in contrast to the three remaining species in the Clade K (Fig. 4), namely *O. jarara* (Fuhrmann, 1927), *O. grandis* La Rue, 1911, and *T. didelphidis*, which possess only a bilayered embryophore (Table 2). Interestingly, all but one species of Clade K listed above have an embryophore of a similar size (diameter always less than 34 μm), the only exception being the new species, *O. echidis*, with extraordinarily large embryophore (diameter 44–53 μm). The presence of a third layer in the embryophore is not common in the Proteocephalidae and has been observed only in some proteocephalids parasitising reptiles from different genera, such as *Australophiotaenia*, *Cairella* Coquille et de Chambrier, 2008, a parasite of the polychrotid lizard *Norops trachyderma* (= *Anolis trachyderma* Cope) in Ecuador (Coquille and de Chambrier, 2008; Scholz et al., 2013; de Chambrier et al., 2018, 2020). The only proteocephalid parasitising amphibians that possesses a third embryophore layer is *Ophiotaenia alessandraceae* Marsella et de Chambrier, 2008 from *Boa boans* (= *Boaana boans* (Linnaeus)) in Ecuador (Marsella and de Chambrier, 2008). This indicates that the presence of a trilayered embryophore is a homoplastic character that has evolved in several groups of proteocephalids parasitising tetrapods independently.

3.4. Checklist of helminth parasites of the saw-scaled viper, *Echis carinatus*

The present checklist is primarily based on data compiled by...
Table 2
List of tapeworms of the former, non-monophyletic subfamily Proteocephalinae, parasitising snakes and lizards, including species inquirendae, and phylogenetically closely related *Thaumasioscolex didelphidis* from opossum with selected characteristics (see de Chambrier et al., 2017).

| Species (clade/ subclade)* | Type host | Country | Total length (mm) | Width of scolex (μm) | Testis number | Relative cirrus-sac length | Genital pore position | Position of vagina | Vaginal sphincter | No. uterine diverticula | Apical organ | Ovary surface | Diameter of embryophore (no. layers) | Embryophore |
|-----------------------------|-----------|---------|-------------------|----------------------|---------------|-------------------------|----------------------|------------------|-----------------|------------------------|-------------|--------------|-------------------------------|------------|
| *Australophoebium* amphiboluri (Nybelin, 1917) | Pogona barbata | Australia | ? | absent | 127–152 | 10–14% | 62–73% | ant–post | present | 29–32 | ? | 6.7% | 30–35 | bilayered |
| *A. gallardi* (Johnston, 1911) (clade K & subclade Q) | *Pseudechis porphyriacus* | Australia | 400 | 960 | 72–80 | 25% | 50% | anterior | absent | numerous | present | 3.2% | ? | trilayered |
| *A. longmani* (Johnston, 1916) (clade K & subclade Q; not included in our analyses – no 16S rDNA data) | *Apidites ramsayi* (Lialis burtonis) | Australia | 94 | 800 | ? | 25% | 50% | anterior | present | 25–35 | absent | 2.3% | 32–36 | trilayered |
| *A. mjobergi* (Nybelin, 1917) | *Demania psammophila* | Australia | 150 | 700–850 | 200–300 | 73% | 50% | anterior | present | 30–40 | absent | 4.7% | 30–34 | trilayered |
| *A. striata* (Johnston, 1914) | *Lialis burtonis* | Australia | 33 | 330–465 | 64–83 | 13–17% | 48–51% | anterior | absent | 18–27 | absent | 1.5% | 27–30 | ? |
| *Crepidobothrium gerrardi* (clade B) | *Boa constrictor* | Brazil | 560 | 1820–2120 | 237–370 | 23–33% | 35–53% | anterior | present | 18–35 | present | ? | 17–23 | ? |
| *Macrobothriotaenia fctica* (Meggitt, 1931) (clade K & subclade Q) | *Bitis arietans* | Africa | 300–400 | 55–600 | 170–220 | 20–25% | 50% | anterior | present | 40–50 | present | 2.1% | ? | ? |
| *O. azevedoi* | *Erythrolamprus miliaris* | Brazil | 80 | 390 | 70 | 41–42% | 35–45% | anterior | ? | about 60 | absent | 5.1% | ? | ? |
| *O. atretiumi* (Devi, 1973) | *Atreium schismatum* | India | 160–190 | 210–280 | 70–95 | 17–20% | 45–59% | anterior | absent | 10–15 | present | 6.5–8.5% | 15 | ? |
| *O. avae* | *Bothrops jararaca* | Brazil | 415 | 630–735 | 88–212 | 17–26% | 40–55% | anterior | present | 45–61 | present | 1.9% | 27–31 | bilayered |
| *O. barbouri* | *Tretoarhizus variabilis* | Cuba | 16–18 | 730 | 46–58 | ? | 33% | posterior | ? | 18–22 | absent | 2.9% | 26–28 | ? |
| *O. barthi* | *Bungarus fasciatus* | Vietnam | 240 | 360–420 | 100–150 | 29–30% | 29–48% | anterior | present | 50–65 | present | 3–3.3% | 28–32 | trilayered |
| *O. calmettei* (Barrois, 1898) | *Botheocephala lanceolata* | Martinique | 270–800 | 1000–1300 | 130–160 | 17–25% | 50% | posterior | present | 24–35 | absent | 2.2% | ? | ? |
| *O. carteflisi* | *Botheocephala lanceolata* | Brazil | 124–240 | 990–1220 | 107–158 | 14–22% | 40–54% | anterior | present | numerous | present | 2.1% | 15–23 | bilayered |
| *O. chaturajii* | *Naja naja* | India | 24–26 | 300–360 | 140–160 | 18% | 45–47% | ? | ? | 10–26 | present | 2.9% | 27–30 | ? |
| *O. congolensis* (Southwell & Lake, 1939) | *Boaedon olivaceus* | Zaire | 80 | ? | 65 | 25% | 50% | anterior | ? | 15–20 | ? | 4.3% | 15 | ? |
| *O. crofti* | *Crotalus durissus* | Venezuela | 520 | absent | 308–412 | 7–12 | 41–43% | ? | present | 8–16 | ? | 2.8% | 27–30 | ? |
| *O. cupeni* | *Crotalus durissus* | Brazil | 210–260 | 94–98 | 19% | 50% | posterior | ? | 15–18 | absent | 3.8% | 26 | ? |

(continued on next page)
| Species (clade/clade K & subclade Q) | Type host | Country | Total length (mm) | Width of sclex (μm) | Testis number | Relative cirrus-sac length | Genital pore position | Position of vagina | Vaginal sphincter | No. uterine diverticula | Apical organ | Ovary surface | Diameter of embryo-phore | Embryophore (no. layers) |
|-----------------------------------|-----------|---------|------------------|-------------------|--------------|--------------------------|-------------------|-------------------|----------------|-------------------------|------------|--------------|------------------------|----------------------|
| O. croatopeltis (clade K)         | Crotaphopeltis tornieri | Lake Tanganyika | 130 | 202–283 | 87–166 | 25% | 33–(76%) | ant-post | absent | 20–26 | absent | 9.8% | ? | ? |
| O. dubini (clade K)               | Coronella australis | Ukraine | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? | ? |
| Ophiotaenia eichidis sp. (clade K) | Echis carinatus sochureki | UAE | 230–275 | 400–725 | 118–205 | 20–34% | 49–61% | ant-post | present | 47–55 | absent | 1–1.6% | 44–55 | trilayered |
| O. elapoidae (clade K)            | Elapoidoa guentherii | ‘a small snake’ | Brazil | 30–40 | ? | ? | ? | ? | ? | ? | ? | 25–42% | ant-post | present | ? | ? |
| O. europaeus Odening, 1963 (clade K) | Matrix matrix | Europe | 280–540 | 222–313 | 189–344 | 25–43% | 33–66% | posterior | absent | 28–73 | absent | 12.7% | 18–22 | ? | ? |
| O. eustri de Chambrier et Vaucher, 1992 | Bothrops jarara | Brazil | 45 | 300–310 | 116–141 | 25–34% | 24–42% | ant-post | present | ? | absent | 2.2% | ? | ? |
| O. faranciae (clade K)            | Farancia abacura | USA | >180 | 500 | 390–420 | 22% | 16–25% | posterior | ? | 30–50 | present | 2.1% | ? | ? |
| O. fins (Meggitt, 1927)            | Amphisea stolatum | India | ? | 200 | 68–89 | 25–33% | 135% | posterior | ? | 27–33 | absent | 3.4% | ? | ? |
| O. fixst (Meggitt, 1927)           | Amphisea stolatum | India | 50 | absent | 71–94 | 20% | 33–40% | ant-post | ? | 20–24 | ? | 3.8% | ? | ? |
| O. flavus Rudin, 1917              | Coluber sp. | Brazil | 50–60 | 500–600 | 45–60 | 50% | 20–40% | ant-post | absent | ? | absent | 3.6% | 28–30 | ? | ? |
| O. gabonica (Beddard, 1913)       | Bitis gabonica | Africa | 380 | 300 | 130–170 | 20% | 1–43% | posterior | present | 38–46 | absent | 2.8% | 39 | ? | ? |
| O. gorgosi de Chambrier, Ammann et Scholz, 2010 | Leioheterodon grophi | Madagascar | 57 | 225–235 | 92–140 | 19–32% | 44–56% | posterior | present | 23–28 | absent | 2.5–4.3% | 31–35 | trilayered |
| O. gilberti Ammann et de Chambrier, 2008 | Thanomodyndastes pallidus | Paraguay | 60–120 | 140–145 | 57–91 | 15–23% | 42–50% | ant-post | present | 28–41 | present | 3.7% | 27–28 | bilayered |
| O. grandis La Rue, 1911 (clade K) | Agkistrodon piscivorus | USA | 300–400 | 1000–1200 | 200–250 | 20–33% | 5% | ant-post | present | 40–60 | absent | 2.1% | 21–23 | bilayered |
| O. greeri (Bursey, Goldberg et Kraus, 2006) | Sphenomorphus aegyptius | Papua New Guinea | 7–15 | 205–410 | 29–51 | 5–17% | 38–47% | anterior | present | 14–24 | present | 6.8% | 15–18 | ? | ? |
| O. habanensis Freze et Rysavy, 1976 | Trophidia pardalis | Cuba | 57–67 | 360 | 31–51 | >50% | env.60% | ? | present | 26–32 | absent | 2.7% | 22–28 | ? | ? |
| O. hyalina Rudin, 1917             | Coluber sp. (Liophis ?) | Brazil | 120 | 680–800 | 50–55 | 50% | ?33% | ant-post | present | ? | absent | 5.5% | ? | ? |
| O. indica Johri, 1955              | Naja naja | India | 110–180 | 200–370 | 31–32 | 33% | 50% | ?anterior | ? | 15–17 | absent | 5.4% | 24–30 | ? | ? |
| O. japonensis Yamaguti, 1935        | Rhhabdophis tigrinus | Japan | 400 | 330–500 | 90–130 | 72% | 50% | ant-post | present | 20–30 | absent | 1.9% | 39 | ? | ? |
| O. jarara Fuhrmann, 1927 (clade K) | Bothrops jarara | Brazil | 140 | 1100–1200 | 150 | 27–34% | 50% | anterior | present | 27–32 | ? | 2.4% | 23 | bilayered |
| O. jarase de Chambrier et Paulino, 1997 | Xenodon naswiedii | Brazil | 140–250 | 480–790 | 147–210 | 14–25% | 28–56% | ant-post | present | 26–49 | absent | 3.1% | 26–30 | bilayered |
| O. kuantamesius Yeh, 1956           | Ophiophagus hannah | Malaysia | 100 | 2400 | 250–350 | 20% | <50% | ant-post | ? | 35–40 | absent | 5.1% | 33 | ? | ? |
| O. lapata Rambelson, 1985           | Madagascarpis colubrinus | Madagascar | 295 | 190–280 | 89–170 | 19–25% | 43–53 | ant-post | present | 41–68 | present | 2.1–2.9% | 34–39 | trilayered |
| O. lacne (Leidy, 1855)             | Nerodia sipedon | USA | ? | ? | ? | ? | ? | ? | ? | absen | ? | ? | ? | ? |

(continued on next page)
Table 2 (continued)

| Species (clade/subclade)* | Type host | Country | Total length (mm) | Width of scolex (μm) | Testis number | Relative cirrhus-sac length† | Genital pore position* | Position of vagina | Vaginal sphincter | No. uterine diverticula | Apical organ | Ovary surface | Diameter of embryo- phore | Embryophore (no. layers) |
|---------------------------|-----------|---------|------------------|---------------------|---------------|-----------------------------|----------------------|-------------------|-----------------|-------------------------|-------------|--------------|--------------------------|------------------------|
| O. macrobothria Rudin, 1917 | Micrurus corallinus | Brazil | 50 | 400-500 | 50-60 | >50% | 20-33% | ant-post | absent | ? | 4.4% | ? | ? |
| O. marmorata (Barrois, 1899)* | Aphiastes plicatus | USA | 400 | 1200-2000 | 150-240 | 25-33% | 50% | anterior | ? | 20-30 | absent | 2.6% | 20 | ? |
| O. megatti Hilmy, 1936* | Atheris chloris | Liberia | 68 | absent | 86-104 | 33% | >50% | ant-post | 35.00 | ? | 2.3% | ? | ? |
| O. microspilota (Shoop et Cokum, 1982) | Micrurus diastema | Mexico | 259-290 | 720-760 | 121-169 | 14-20% | 48-56% | posterior | absent | 35-53 | 3.2% | 20-23 | ? | ? |
| O. monigi Fuhrmann, 1924 | Crotaphophis hattomboeia | Africa | 50 | ? | 80 | 10% | 50% | anterior | present | 50-57 | ? | 3.1% | 25 | bilayered |
| O. najae (Beddard, 1913) | Naja tripudians | India | 180 | 248-300 | 120-165 (165) | 25-33% | 50% | anterior | absent | 14-25 | 3.5% | 25 | ? | ? |
| O. nankangensis (Ji, 1935) | Pysa dhamnades | China | 105-124 | 320 | 147-166 | 17% | <50% | ant-post | present | 36-40 | 3.0% | ? | ? | ? |
| O. nattereri (Parona, 1901) | Coluber sp. | Brazil | 75-250 | 250 | 80-100 | 28-33% | <50% | ant-post | present | 15-30 | absent | ? | 22-26 | ? |
| O. nicolicci Mettrick, 1963 | Thecadactylus rapicauda | Ecuador | 230-351 | 325-340 | 142-204 | 21-33% | 34-53% | ant-post | present | 13-27 | present | 4.9% | 32-36 | bilayered |
| O. nigricollis Mettrick, 1963 | Naja nigricollis | Zimbabwe | 170 | 300-310 | 176-210 | ~25% | ~35% | ant-post | ? | 16-20 | ? | 6.3% | 26-33 | ? |
| O. nybelini Hilmy, 1936 | Metadosoma coronatus | Africa | 52 | 105 | 67-90 | 16-20% | ?50% | ant-post | ? | 25-40 | 3.6% | 25 | ? | ? |
| O. ophidoc Mettrick, 1960* (clade K & subclade Q) | Casua rhombeatus | Zimbabwe | 210-270 | 790-1140 | 110-120 | 25% | 45-54% | ant-post | present | 30-42 | absent | ? | 27-36 | ? |
| O. paraguanensis Rudin, 1917 (clade N) | Hydrodynastes gigas | Paraguay | 550-600 | 240 | 238-344 | 12-19% | 27-39% | ant-post | present | 20-36 | absent | 3.3% | 21-24 | ? |
| O. perspicus La Rue, 1911 (clade O; type species) | Nerodia rhomberi | USA | 360 | 255-410 | 150-215 | 25-33% | 33-50% | anterior | present | 20-30 | present | 2.3% | ? | ? |
| O. phillipus (Burt, 1937) | Trimeresurus tritonoccephalus | Sri Lanka | 400-920 | 670-1400 | 170-230 | ~50% | ~50% | posterior | present | 60-80 | absent | 2.1% | 24-30 | ? |
| O. racemosus (Rudolphi, 1819) | Coluber sp. | Brazil | 160 | 540-650 | 80-120 | ~33% | ~33% | ant-post | present | 40-50 | ? | 4.3% | 24 | ? |
| O. rabdophidus (Burt, 1937) | Anfibema striatum | Sri Lanka | 250 | 130-187 | 110-140 | 20-25% | 33-50% | ant-post | ? | 30-45 | present | 3.1% | 22-27 | ? |
| O. sanbernardinosis Rudin, 1917 (clade N) | Helicops leopardsinus | Paraguay | 100-120 | 230-250 | 70-102 | ? | 20-40% | ant-post | present | 27-33 | absent | 5.0% | 22-23 | ? |
| O. sinensis Cheng et Lin, 2002 | Rhadophis tigrinus | China | 460-694 | 247-325 | 256-320 | ~25% | ~45% | ? | ? | ? | 2.5% | ? | ? | ? |
| O. southwi Freze, 1965* | Casua rhombeatus | Africa | 90 | 1500 | 170-230 | ? | ~50% | ant-post | ? | 8-12 | ? | 3.4% | 30 | bilayered |
| O. spazky Freze and Sharpio, 1967* | Vipera berus | Russia | 70-90 | 295-355 | 179-271 | 20-25% | ~30% | ant-post | present | 19-31 | ? | 9.1% | ? | ? |
| O. theileri Rudin, 1917 | Naja haje | Africa | 300 | 400 | 160-310 | 20-25% | ~50% | ant-post | absent | 35-40 | 4.5% | ? | 36% | ? | ? |
| O. trimersoni (Parona, 1898)* | Trimeresurus formosus (= T. sumatratus) | Mentawai Islands | 105 | 750 | 100-108 | 20-30% | ~50% | ant-post | present | 20-30 | absent | 3.6% | ? | ? |
| O. variabilis Brooks, 1978 | Nerodia cyclopor | North America | 300 | 170-200 | 77-253 | 22-33% | 15-30% | ant-post | absent | 25-45 | 2.8% | ? | ? | ? |
| O. wygierski Cheng, Yuyuang et Zao He, 2007 | Trimeresurus gramineus | China | 460-700 | 245-325 | 256-320 | 23% | ~45% | ? | ? | ? | 2.8% | ? | ? | ? |
| O. xochakki Rudin, 1917 | Naja haje | South Africa | 550-600 | 400 | 160-200 | 20-25% | ~50% | ant-post | ? | ? | absent | 6.4% | ? | ? |

(continued on next page)
Sharpilo (1976) and Gibson et al. (2005), with a subsequent search of primary, especially literature written in Russian.

Cestoda – tapeworms

Cyclophyllidea: Anoplocephalidae Cholodkovsky, 1902

1. *Oochoristica fedtschenkoi* Bogdanov et Markov, 1955
   This species was described from several species of viperid snakes, including *E. carinatus*, from Turkmenistan and Uzbekistan. The highest infection rate was reported for the saw-scaled viper (prevalence of 4.2%, mean intensity of infection 26, range 1–50 worms) (Bogdanov and Markov, 1955; Markov et al., 1970; Sharpilo, 1976).

2. *Oochoristica sindensis* Farooq, Khanum et Ansar, 1983
   This cestode was described from the saw-scaled viper in Pakistan by Farooq et al. (1983).

Cyclophyllidea: Dipylidiidae Stiles, 1896

3. *Diplopylidium acanthotetra* (Parona, 1898)– larvae
   Metacestodes of this tapeworm were found in the body cavity of *E. carinatus* in Turkmenistan (Markov et al., 1970). The most common intermediate host of *D. acanthotetra* is the Caspian bent-toed gecko, *Tenuidactylus caspius* (Eichmann), and its metacestodes were found in Algeria, Egypt, Israel, Iraq and Italy (Sharpilo, 1976).

4. *Diplopylidium noelleri* (Skrjabin, 1924)– larvae
   Larvae of this cestode occur in the liver, intestinal wall and body cavity of reptiles of distantly related groups, such as geckoes, lacertids, agamas and colubrid snakes (Sharpilo, 1976). They were also found in *E. carinatus* from Turkmenistan (Markov et al., 1970).

5. *Joyeuxiella echinorhynchoides* (Sonsino, 1889)– larvae
   Metacestodes are frequently found in the liver, intestinal wall and body cavity of a wide spectrum of reptiles, including viperid snakes (Sharpilo, 1976). Markov et al. (1970) found *J. echinorhynchoides* in *E. carinatus* from Turkmenistan.

Onchoproteocephalidea: Proteocephalidae La Rue, 1911

6. *Ophiotaenia* sp.
   Markov et al. (1970) reported unidentified species of *Ophiotaenia* from *E. carinatus* in Turkmenistan. However, the authors did not provide morphological characterisation and illustrations, and no voucher specimens have been deposited. Therefore, it is impossible to compare tapeworms found in Middle Asia with those found in the United Arab Emirates by the present authors.

Acanthocephala – spiny-headed worms

Archiacanthocephala: Gigantorhynchidae Hamann, 1892

7. *Centrorhynchus aluconis* (Müller, 1780)– larvae
   Cystacanths of this very common parasite of owls have also been found in *E. carinatus* from Turkmenistan (Markov et al., 1970). Markov et al. (1970) found *J. echinorhynchoides* in *E. carinatus* from Turkmenistan.

Archiacanthocephala: Oligacanthorhynchidae Southwell et Macfie, 1924

8. *Centrorhynchus globocaudatus* (Zeder, 1800)– larvae
   Markov et al. (1970) reported cystacanths of this parasite of owl and raptors from *E. carinatus* in Turkmenistan, but Sharpilo (1976) did not list this species in his survey of helminth parasites of reptiles in the former USSR.
9. Centrorhynchus sp. – larvae

Unidentified larvae (cystacanths) of another species of Centrorhynchus Lühe, 1911 were found in E. carinatus from Turkmenistan by Markov et al. (1970). Their identification is not possible because the authors did not provide any morphological data and illustrations.

10. Oligacanthorhynchus sp. – larvae

Cystacanths of unidentified species of Oligacanthorhynchus Travassos, 1915 were found in the body cavity and liver of various reptiles, including E. carinatus from Turkmenistan (Markov et al., 1970).

Nematoda – nematodes (roundworms)

Rhabditida: Ascarididae Blanchard, 1849

11. Hexametro skrabini Markov et Bogdanov, 1960

This nematode was described from the small intestine and stomach of the spotted desert racer, Coluber karelini Brandt (= Platyceps karelini) (Colubridae), dwarf sand boa, Eryx millaris (Pallas) (Boidae), and E. carinatus from Dagestan (Russia) and Turkmenistan (Markov and Bogdanov, 1960; Markov et al., 1970).

Rhabditida: Habronematidae Chitwood et Wehr, 1932

12. Agamosphirura sp. – larvae

Markov et al. (1970) reported larvae of unidentified species of Agamosphirura Henry et Sisoff, 1913 from E. carinatus in Turkmenistan.

Rhabditida: Pharyngodonidae Travassos, 1919

13. Spauldingon australiensis (Seurat, 1917)

Only immature worms were found in E. carinatus from Turkmenistan by Bogdanov and Markov (1955, 1960), and Markov and Bogdanov (1956). This record of the nematode that occurs in Algeria, Egypt and France needs verification (Sharpilo, 1976).

Rhabditida: Physalopteridae Railliet, 1893

14. Abbreviata uzbekistana Bogdanov and Markov (1955)

This parasite of the stomach, rarely of the oesophagus and intestine, was described by Bogdanov and Markov (1955). It has been found in several distantly related reptiles, such as agamas, geckoes and the saw-scaled viper from Dagestan (Russia), Turkmenistan and Uzbekistan (Sharpilo, 1976). Echis carinatus is probably postcylic, not definitive host of this spirurine nematode.

In addition, larvae of the following nematodes unidentified to the genus or even family level were reported from E. carinatus: Acuaroidea gen. sp. in Turkmenistan (Velikanov, 1984); Omeinidae gen. sp. (Quimperiidae) in Turkmenistan (Markov et al., 1970). One of the present authors (R.K.S.) found the following helminths in the saw-scaled viper from the United Arab Emirates, but these records were presented only at an international conference (Schuster and Sivakumar, 2013); cestodes Joyeuxiella sp., most probably J. pasquaeti (Diamare, 1893), and Diplopyleidium noelleri (Cestoda); acanthocephalan larvae Centrorhynchus alcuonis and Macroncanchorhynchus catulinus Kostylev, 1927; and larvae of spirurine nematodes, most probably Physcephalus dromedari Muschkambarova, 1967.

4. Discussion

Ophiotaenia is a composite genus pending taxonomic revision. Validity of its species should be re-assessed and poorly characterised taxa redescribed. However, this task is difficult because of the large number of species (88 according to de Chambrier et al., 2017 plus 12 species inquirendae) and difficulties in obtaining new, properly fixed material suitable for molecular studies. The generic name Ophiotaenia should be retained only for taxa of Clade O of de Chambrier et al. (2015), because it includes the type species O. perspicua from colubrid snakes in North America. Interestingly, species of this clade have proportionally larger ovaries than those in the other species of Ophiotaenia (Clades K and N of de Chambrier et al., 2015). Species in individual clades also differ in uterine development: Type 1 according to de Chambrier et al. (2004) is present in species of Clade K, whereas a Type 2 uterus occurs in species of Clades N and O (de Chambrier et al., 2015). It is clear that species of Clades K and N need to be allocated to other (new) genera, which also affects the new species described in the present paper.

However, there are two principal obfuscates in erecting a new genus for the new species and the closely related O. lapata: (i) molecular data are available for a limited number of species of Ophiotaenia only; and (ii) the absence of obvious morphological synapomorphies of the new species and O. lapata, which would unequivocally differentiate them from the other taxa of Clade K. For example, the scolecites of most species of all but two genera are rather uniform; only species of monotypic Macrobothriotaenia and Thaumasioscolex have distinct scolecites (Cañeda-Guzmán et al., 2001; Scholz et al., 2013). In addition, some species of Australophiotenia and M. ficta (Meggitt, 1931) have a trilayered embryophore, similar to O. echidis n. sp. (see de Chambrier et al., 2018). Therefore, the new species is provisionally placed in Ophiotaenia, even though this genus is not monophyletic (de Chambrier et al., 2015).

Clade K (updated in this study in Fig. 4) is composed almost exclusively of parasites of snakes, namely Boidae, Elapidae, Pseudoxyrhophiidae, Pythonidae, Viperidae (three of the 18 species of Ophiotaenia from vipers sequenced), and Xenopeltidae, throughout the world and the only proteocephalid parasitising a mammal, the common opossum (D. marsupialis), in Neotropical Mexico in the case of T. didelphidis. According to de Chambrier et al. (2015), species of Clade K may represent a relatively recent colonisation of unrelated groups of snakes in most continents or a trace of a very ancient colonisation of these snake hosts. Based on the most informative tree presented here (using only the 16S rDNA dataset), the early colonisation of Clade K representatives in vertebrates (snakes and the common opossum) currently distributed across the Americas is hypothesised, followed by colonisation of snakes in the Afrotropical, Australian, Madagascar, Oriental, and Saharo-Arabian zoogeographical realms (see Fig. 4). Nevertheless, for proposing a more precise scenario of the evolution of this clade of Ophiotaenia, a broader spectrum of related taxa should be analysed, including diverse proteocephalids in Australian reptiles (de Chambrier et al., 2018), which might provide stronger statistical support for internal nodes.

Recently, de Chambrier et al. (2018) erected a new genus, Australophiootaenia, to accommodate species of Ophiotaenia from snakes in the Australian region, including A. gallardi (Johnston, 1911) from Clade K of de Chambrier et al. (2015). In the present analyses, two species of this genus, A. gallardi and Australophiootaenia sp. 1, grouped together (Fig. 4). Australophiootaenia is characterised by the following characteristics: a tubular, thin-walled embryophore, a scolex only large, anteriorly directed suckers, an exclusively dorsal and paramuscular position of vitelline follicles (i.e., follicles may penetrate into the medulla between fibres of the inner longitudinal musculature), and a postequatorial to equatorial genital pore in most species (de Chambrier et al., 2018).

The present study supports the assumption about strict (oioxenous) host specificity of species of Ophiotaenia from reptilian hosts (see de Chambrier et al., 2010, 2017, 2020) because the new species was found only in E. carinatus sochukeri, but not in any of 33 other snakes of six
planktonic copepods (first intermediate host), fish or amphibian tadpoles (second intermediate host) and reptiles (definitive host), and to consider the similar diet of vipers of the E. carinatus and E. pyrrohidium groups (Barlow et al., 2009), new studies should focus on these potential hosts.

The taxonomic history of Echis has been convoluted, which has direct implications for human health, given that venom composition is highly variable among species resulting in several cases of a lack of antivenom cross-neutralisation (Pook et al., 2009). That having been said and considering the assumption of ooxenous host specificity, the fauna of proteocephalids of these venomous snakes may help to inform us about distinct evolutionary lineages of their hosts, which ultimately may be used to guide searches for specific antivenoms. In the present study, we examined five specimens of Cerastes gasperettii but none was infected. The common European adder, Vipera berus (Linnaeus), which is the definitive host of Ophiotaenia spasskyi Freeze et Sharpilo, 1967 in Europe, clustered with species of Echis in a weakly supported clade (Alencar et al., 2016). Therefore such comparison is not informative enough.

Literary search for data on the helminth parasites of the saw-scaled viper has revealed that most information was accumulated by Soviet researchers, especially G.S. Markov and O.P. Bogdanov, from Turkmenistan in the 1950’s and 1960’s. More recent data are scarce and include just a few reports (Farooq et al., 1983; Nama, 1984; Velikanov, 1984). The helminth fauna of E. carinatus includes 14 species and another two larvae of nematodes unidentified to the genus level. This fauna is composed of adult cestodes (3 spp.), their larvae (3 spp.), larval acanthocephalans (4 spp.), adult nematodes (3 spp.) and their larvae (3 spp.). Noteworthy is the complete absence of any trematode ( Digenea), with no involvement of intermediate or paratenic vertebrate host (Biserov and Kostadinova, 1997). It remains unclear how O. echidus n. sp. is transmitted to its definitive host, but considering the similar diet of vipers of the E. carinatus and E. pyrrohidium groups (Barlow et al., 2009), new studies should focus on these potential hosts.

Declarations of competing interest

There is no conflict of interest.

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DECLARATION OF COMPETING INTEREST

There is no conflict of interest.
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