

# New data on the morphology of *Comephoronema oschmarini* (Nematoda, Cystidicolidae), a little-known gastrointestinal parasite of *Lota lota* (Teleostei) in Palaeartic Eurasia

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## Abstract

The nematode *Comephoronema oschmarini* Trofimenko, 1974 (Cystidicolidae) was found in the stomach of the burbot *Lota lota* (Linnaeus) of Lake Geneva, Savoy, France, collected on 23 March 2000 [prevalence 60% (3/5); intensity of infection 2–66 (mean 35)]. This material made it possible to study in detail the morphology of this so far little-known parasite, using both light and scanning electron microscopy (the latter not previously used for this species). The SEM examination showed taxonomically important morphological features, not previously reported, including the presence of distinct terminal pseudolabial projections (protuberances), four submedian labia, four bilobed submedian sublabia, and only four cephalic papillae. Deirids were found to be bifurcated. A description of the true arrangement of the two last pairs of minute caudal papillae and phasmids in the male is given. Species of *Comephoronema* Layman, 1933 are considered to be closely related to those of *Ascarophis* van Beneden, 1871. A key to valid species of *Comephoronema* is provided.

## Key words

Parasitic nematode, *Comephoronema*, morphology, fish, *Lota lota*, Lake Geneva, France

## Introduction

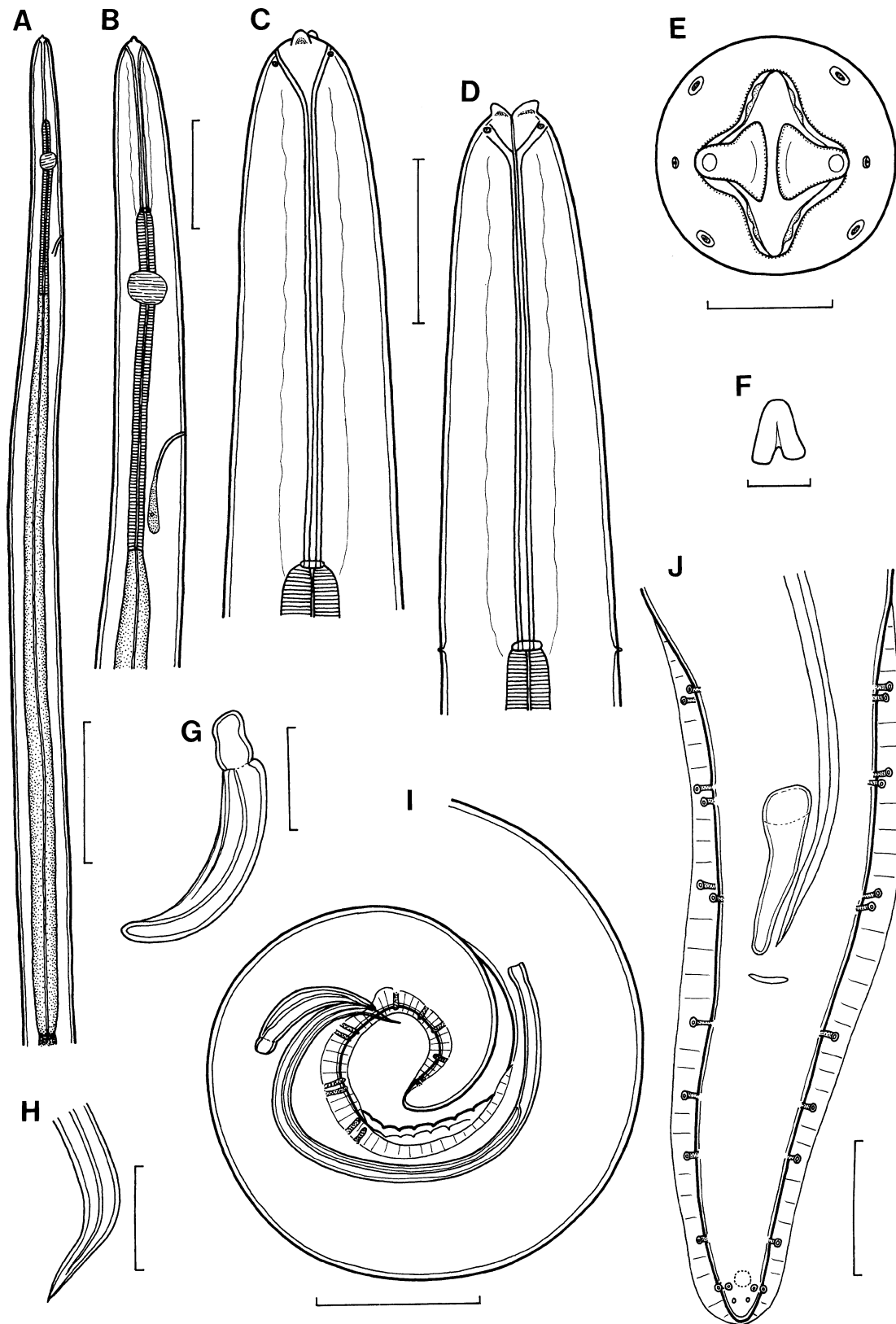
The present taxonomy of nematodes of the family Cystidicolidae Skryabin, 1946 is unsatisfactory, because several genera have been based on details in the cephalic structures visible only with the aid of scanning electron microscopy (SEM), although this method has not yet been used for the majority of species and for representatives of some genera. As stated by Ferrer *et al.* (2005), Moravec *et al.* (2006) and Moravec and González-Solís (2007), it will be evident whether or not these tiny features are of generic importance only after more cystidicolids are described or redescribed using SEM and comparative molecular data is available. At present, a total of 19 cystidicolid genera are usually considered valid (see Moravec and Klimpel 2007).

Until recently, one of the cystidicolid genera the members of which were not studied by SEM was *Comephoronema* Layman, 1933. It contained only two species, *C. werestschagini* Layman, 1933 (type species), a parasite of the digestive tract of the endemic scorpaeniform fishes in the Lake Baikal

basin (Siberia, Russia), and *C. oschmarini* Trofimenko, 1974, a stomach parasite of burbot, *Lota lota* (L.), in Palaeartic Eurasia (Trofimenko 1974, Vismanis *et al.* 1987, Moravec *et al.* 1999). Only Moravec and Klimpel (2007) described an additional species, *C. macrochiri* Moravec et Klimpel, 2007, a stomach parasite of the marine notacanthiform fish *Halo-sauropsis macrochir* (Günther) in the Atlantic Ocean, and transferred to this genus another species, *C. beatriceinsleyae* (Holloway et Klewer, 1969), a gastrointestinal parasite of the zoarcid *Lycodichthys dearborni* (DeWitt) from Antarctica, which was originally assigned to *Rhabdochona* Railliet et Henry, 1916 (see Holloway and Klewer 1969). Additional two species, *Comephoronema johnsoni* Arya, 1978 and *C. mac-kiewiczzi* Malhotra et Rautela, 1984, poorly described from fishes in India (Arya 1979, Malhotra and Rautela 1984), are considered *species inquirendae* probably belonging to other genera (Moravec and Klimpel 2007).

Moravec *et al.* (1999) recorded *C. oschmarini* in *Lota lota* from Lake Annecy, France, but only one male of this species was found. Later, many specimens of *C. oschmarini*, includ-

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**Fig. 1.** *Comephoronema oschmarini* Trofimenko, 1974: **A** – anterior part of body, lateral view; **B** – anterior end, lateral view; **C** and **D** – cephalic end, lateral and dorsoventral views; **E** – cephalic end, apical view; **F** – deirid, lateral view; **G** – small (right) spicule; **H** – distal end of large (left) spicule; **I** and **J** – caudal end of male, lateral and ventral views. Scale bars = 200  $\mu$ m (**A**), 100  $\mu$ m (**B-D**, **I**), 50  $\mu$ m (**J**), 30  $\mu$ m (**G**, **H**), 10  $\mu$ m (**E**), 2  $\mu$ m (**F**)

ing both males and gravid females, were collected by V. Hanzelová from *L. lota* from the nearby Evian, Lake Geneva, France, in March 2000. This made it possible to study the morphology of this nematode in detail, using both light and scanning electron microscopy. The results obtained are presented herein.

## Materials and methods

Burbot ( $n = 5$ ; total body length 245–290 mm) were sampled in Lake Geneva near Evian on 23 March 2000. These were immediately examined for the presence of helminth parasites in the laboratories of Station d'Hydrobiologie Lacustre in Thonon, France. For morphological studies, the live nematodes recovered from the fish stomachs were fixed in hot 4% formaldehyde solution. For light microscopical examination, nematodes were cleared with glycerol. Drawings were made with the aid of a Zeiss microscope drawing attachment. Specimens used for scanning electron microscopy (SEM) were postfixed in 1% osmium tetroxide, dehydrated through a graded ethanol series, critical point dried and sputter-coated with gold; they were examined using a JEOL JSM-6300 scanning electron microscope at an accelerating voltage of 15 kV. All measurements are in micrometres unless otherwise stated. Fish names follow FishBase (Froese and Pauly 2007).

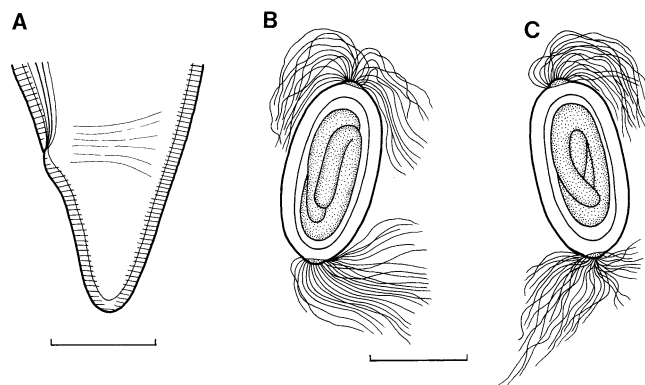
## Results

### *Comephoronema oschmarini* Trofimenko, 1974 (Figs 1–4)

General: Medium-sized, whitish nematodes. Cuticle with fine transverse striations. Cephalic end rounded, with two conspicuous pseudolabial terminal protrusions with rounded tips (Figs 1C, D and 3A, C). Oral aperture oval, with lateral extensions. Lateral pseudolabia rather large, each provided with conspicuous terminal protrusion; in apical view, flat inner parts of pseudolabia partly cover mouth and are distinctly dorsoventrally expanded, forming two (1 dorsolateral and 1 ventrolateral) extensions on each; inner margins of both pseudolabia dorsoventrally straight, parallel to each other (Figs 1E and 3B). Four submedian labia and four bilobed submedian sublabia well developed (Figs 1E and 3A–C). Four submedian cephalic papillae and pair of lateral amphids present (Figs 1E and 3B). Vestibule (stoma) long, with funnel-shaped anterior prostom. Glandular oesophagus 4–5 times longer than muscular. Nerve ring encircles muscular oesophagus approximately at border of its first and second fourths; excretory pore between nerve ring and anterior end of glandular oesophagus; deirids small, with distal end laterally expanded and bifurcated (Figs 1F and 3D), situated at level or somewhat posterior to end of vestibule (Fig. 1D).

Male (5 specimens; measurements of additional 2 juvenile specimens in parentheses): Length of body 9.40–10.01 (6.12–6.53) mm, maximum width 87–109 (68). Height of cephalic

protrusions 3–4 (3). Vestibule including prostom 150–177 (153–159) long; prostom 15–18 long and 15–18 wide (prostom of juvenile males indistinct). Length of muscular oesophagus 330–384 (300), maximum width 15–18 (12); length of glandular oesophagus 1.62–1.70 (0.90–0.94) mm, maximum width 36–48 (30–33); length ratio of muscular and glandular parts of oesophagus 1:4.2–5.1 (1:3.0–3.1). Length of entire oesophagus and vestibule represents 20–24 (21–23)% of total body length. Nerve ring, excretory pore and deirids 233–264 (219–233), 381–408 (351–366) and 159–195 (156–180), respectively, from anterior extremity. Posterior end of body spirally coiled, provided with wide caudal alae. Preanal papillae: 6 pairs forming on either side three groups, each consisting of two papillae situated close together. Postanal papillae: 6 pairs present, including 5 pairs of pedunculate subventral papillae and 1 pair of minute ventral sessile papillae located approximately at level of last pair of subventrals (Figs 1J and 3F, G). In addition, a pair of small ventral papilla-like phasmids present posterior to ventral papillae (Fig. 3G). Small median ventral caudal protuberance present between both ventral papillae (Fig. 3G). Ventral cuticular ridges (area rugosa) anterior to cloaca well developed, consisting of longitudinal rows of tessellated ornamentations (Fig. 3E). Large (left) spicule 348–405 (198–225) long, with pointed distal tip (Fig. 1H); its shaft 90–105 (78) long, forming 23–26 (39)% of overall length of spicule. Small (right) spicule broad, 87–90 (78) long, with rounded distal end (Fig. 1G). Length ratio of spicules 1:3.9–4.5 (1:2.5–3.4). Tail conical, 132–168 (81–90) long, with rounded tip.

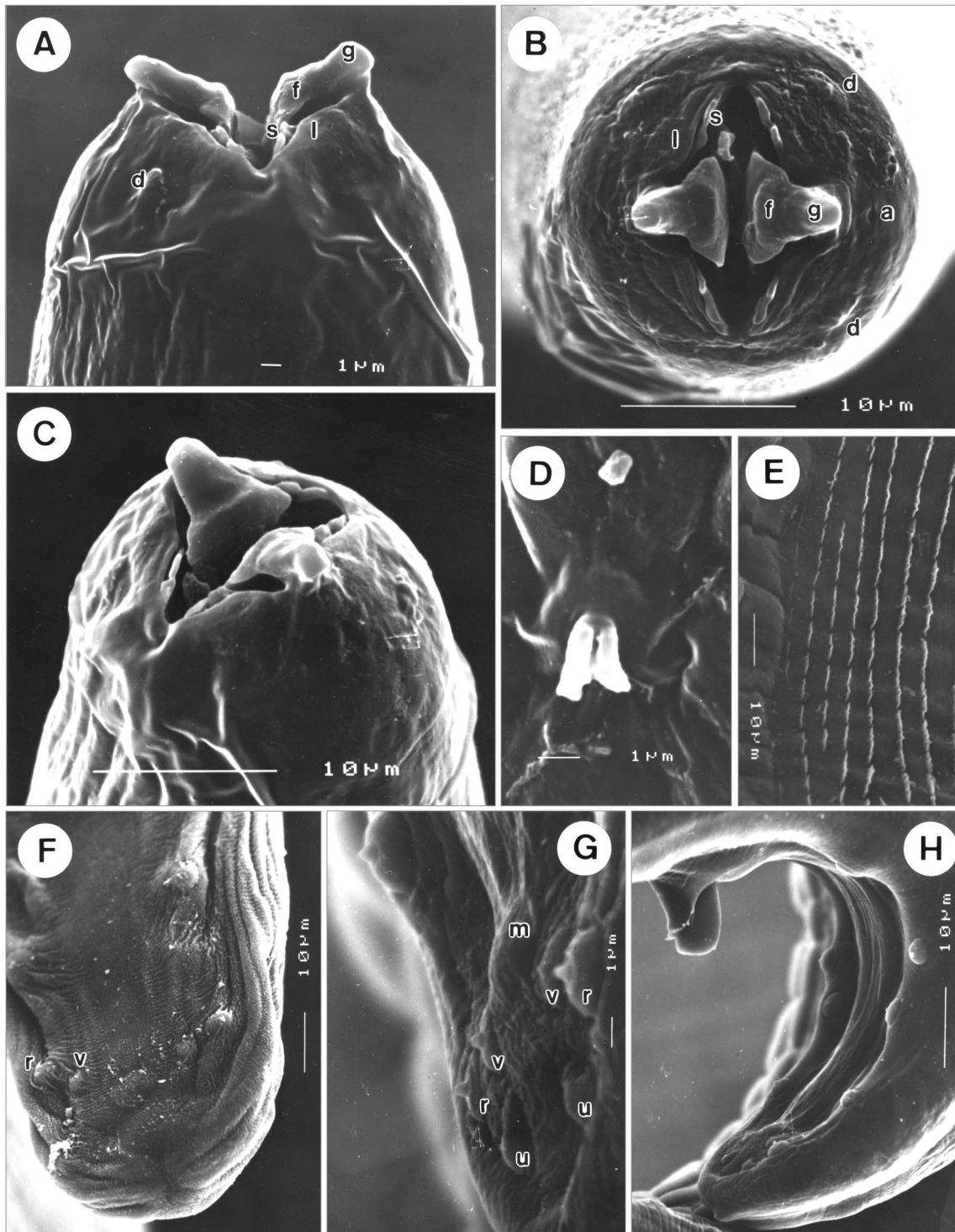


**Fig. 2.** *Comephoronema oschmarini* Trofimenko, 1974: **A** – tail of gravid female, lateral view; **B** and **C** – fully developed eggs. Scale bars = 50  $\mu$ m (A), 30  $\mu$ m (B, C)

Female (5 gravid specimens with fully developed eggs): Length of body 16.13–18.54 mm, maximum width 133–136. Height of cephalic protrusions 3–4. Vestibule including prostom 150–168 long; prostom 15–18 long and 15–18 wide. Length of muscular oesophagus 381–394, maximum width 15–18; length of glandular oesophagus 1.74–1.96, maximum width 45; length ratio of muscular and glandular parts of oe-

sophagus 1:4.5–5.1. Length of entire oesophagus and vestibule represents 14% of total body length. Nerve ring, excretory pore and deirids 240–264, 381–394 and 168–213, respectively,

from anterior extremity. Tail conical, 69–75 long, with a small, low terminal knob in smaller specimens. Vulva slightly postequatorial, situated 10.95–12.24 mm from anterior end



**Fig. 3.** *Comephoronema oschmarini* Trofimenko, 1974, SEM micrographs: **A–C** – cephalic end, dorsoventral, apical and ventrolateral views, respectively; **D** – deirid; **E** – ventral precloacal ridges (area rugosa); **F** and **G** – caudal end of male, ventral and sublateral views; **H** – tail of male, lateral view. **Abbreviations:** a – amphid, d – cephalic papilla, f – pseudolabium, g – pseudolabial protrusion (protuberance), l – submedian labium, m – median caudal ventral elevated area (protuberance), r – postanal papilla of last subventral pair, s – bilobed sublábium, u – phasmid, v – ventral postanal papilla

of body, at 66–69% of body length; vulval lips not elevated. Amphidelphic. Uterus filled with numerous eggs, occupies major part of body. Fully developed eggs (containing larvae) elongate oval, thick-walled, size 57–63 × 27–30; thickness of egg wall 6. Each pole of egg provided with distinct protuberance bearing tuft of very numerous fine filaments up to 45–66 µm long (Fig. 2B, C).

Host: Burbot, *Lota lota* (Lotidae, Gadiformes).

Site of infection: Stomach.

Locality: Lake Geneva, Evian, Savoy, France (collected 23 March 2000).

Prevalence and intensity: 60% (3/5); 2–66 (mean 35) nematodes per fish.

Number of specimens studied: 61 (21 males, 40 females).

Deposition of voucher specimens: Helminthological Collection of the Institute of Parasitology, Biology Centre of the ASCR, České Budějovice (Cat. No. N-721).

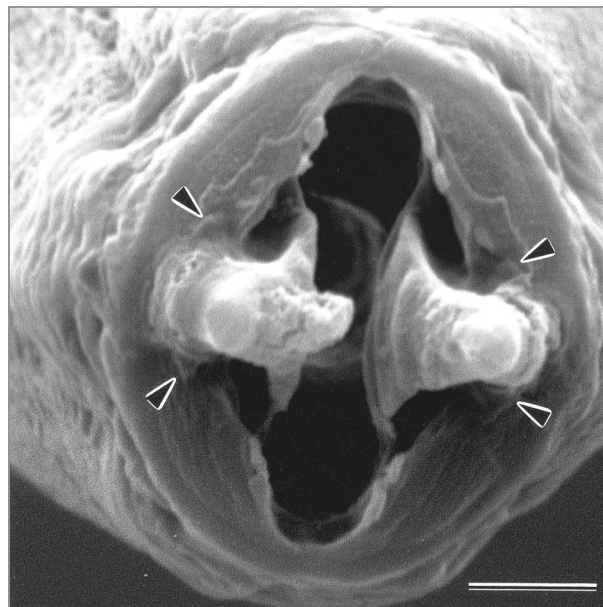
## Discussion

The general morphology of nematodes of the present material corresponds to *Comephoronema oschmarini*, as it has been described in the papers by Trofimenko (1974) and Moravec *et al.* (1999), differing only in some morphological details, and there is no doubt that they belong to this species. However, the SEM examination, used for the first time for this species, revealed some additional morphological features, which could not be previously studied by LM. This concerns mainly the structure of the cephalic end, which was examined (by LM) in an apical view by Trofimenko (1974).

In contrast to data by Trofimenko (1974), the present study shows a somewhat different shape and structure of pseudolabia: In an apical view, their flat inner parts covering partly the mouth are markedly dorsoventrally expanded, forming two distinct (one dorsolateral and one ventrolateral) extensions on each (Figs 1E and 3B). In a dorsoventral view, each pseudolabium bears a large rounded, anteriorly directed protuberance near the edge of the oral aperture, from which its upper part is gradually depressed towards the inner, low pseudolabial ridge extending dorsoventrally (Figs 1D and 3A, C); in this position, the shape of pseudolabia of *C. oschmarini* somewhat resembles that of *Cystidicola farionis* Fischer, 1798 (see fig. 1B of Moravec and Rokicki 2002), a swimbladder parasites of salmonids, but the outer large pseudolabial protuberance is conical and the inner pseudolabial ridge is reduced to a small protuberance in *C. farionis*.

Trofimenko (1974) reported eight cephalic papillae arranged in two circles in *C. oschmarini*, but the SEM examination did not confirm the presence of the four small papillae of the internal circle (Fig. 3A–C); only four cephalic papillae as in *C. oschmarini* are also reported for other cystidicolid species studied by SEM (e.g., Moravec and Nagasawa 1999, Frantová and Moravec 2003, Ferrer *et al.* 2005, Moravec and Justine 2007, Moravec and Klimpel 2007). In the SEM micrograph of *C. oschmarini* from Russia recently sent to the senior

author (F.M.) by S.G. Sokolov, two minute protuberances situated on sides of the basal part of each pseudolabium are visible in an apical view (Fig. 4), which might have been mistaken for inner cephalic papillae by Trofimenko (1974); in fact, these seem to be just cuticular elevations associated with bases of pseudolabia, not visible in all specimens.



**Fig. 4.** *Comephoronema oschmarini* Trofimenko, 1974: SEM micrograph of cephalic end of specimen from Russia with four minute cuticular elevations (see arrowheads) associated with bases of pseudolabia. Scale bar = 5 µm. Courtesy S.G. Sokolov

The presence of four submedian labia and four submedian bilobed sublabia (Fig. 3A–C) in *C. oschmarini* is described in this paper for the first time. The SEM examination of this species also revealed that the deirids of this species are bifurcated (Fig. 3D); the shape of deirids has recently been found to be an important taxonomic feature in cystidicolids (e.g., Muñoz *et al.* 2004, Ferrer *et al.* 2005, Moravec *et al.* 2006, Moravec and Justine 2007, Moravec and Klimpel 2007).

Both Trofimenko (1974) and Moravec *et al.* (1999) reported six pairs of postanal papillae in *C. oschmarini* males, of which papillae of the two last pairs are very small and close to each other; the authors could study the male caudal ends only in a lateral view, but these posteriormost minute papillae are poorly visible in this position under the LM. The SEM micrographs show (Fig. 3F–H) that five pairs of postanal papillae are pedunculate, subventral and that there is another pair of minute sessile papillae situated ventrally at the level or slightly posterior to the last pair of subventrals (Fig. 3F, G); the ventral papillae are followed by a pair of minute papilla-like phasmids (Fig. 3G). This number and arrangement of postanal papillae is typical of most other cystidicolids of different genera. Figure 3G shows the presence of a median elevated area (protuberance) situated somewhat anterior to the level of ventral postanal papillae, not previously reported for

*C. oschmarini*; a similar formation located between the last two pairs of postanal papillae has been observed in *Cystidicola farionis* (see Fagerholm 1982, Moravec and Rokicki 2002) and *Spinitectus petrowi* Belous, 1965 (see Moravec *et al.* 2004). Ventral precloacal ridges (area rugosa) (Fig. 3E) have already been reported for *C. oschmarini* by Trofimenko (1974) and Moravec *et al.* (1999); they occur in the majority of cystidicolids.

According to Trofimenko (1974), the fully developed eggs of *C. oschmarini* are provided with numerous thin filaments present not only on the egg poles but over the entire surface of the egg. However, this was not observed in the present material, where the eggs had only polar filaments, as is found in other cystidicolids. Lateral filaments, in addition to a tuft of filaments at each egg pole, were also reported by Berghe (1935) in *Cystidicola farionis*, but their presence was not confirmed by Moravec and Ergens (1970) in *C. farionis* from former Czechoslovakia (Slovakia) and Mongolia. In contrast to other species of *Comephoronema* from marine fishes and the majority of cystidicolids, the egg filaments of *C. oschmarini* are very numerous and fine, resembling those of *C. werestschagini* (see Layman 1933).

The only other species of *Comephoronema* studied by SEM is *C. macrochiri* (see Moravec and Klimpel 2007). It distinctly differs from *C. oschmarini* in a different shape of deirids (distal end of deirids considerably distended, but not bifurcated) and a somewhat different shape of pseudolabia, in addition to some other features visible by LM, such as the presence of filaments only on one egg pole or smaller eggs ( $48\text{--}51 \times 21\text{--}24 \mu\text{m}$ ).

*Comephoronema* was considered by Chabaud (1975) to be a junior synonym of *Cystidicola* Fischer, 1798, but Moravec and Nagasawa (1999) revalidated this genus on the basis of Trofimenko's (1974) data on the cephalic structure of *C. oschmarini*, pointing out that it shows affinities more to *Salvelinema* Trofimenko, 1962 than to *Cystidicola*. However, the present SEM study of the cephalic structure of *C. oschmarini*, as well as those of *Comephoronema macrochiri* and *Cystidicola farionis* (see Moravec and Rokicki 2002, Moravec and Klimpel 2007), show that *Comephoronema* is in fact closest to *Ascarophis* van Beneden, 1871 (see Ko 1986), differing from it only in the more numerous pairs of preanal papillae in the male (Moravec and Klimpel 2007).

*Comephoronema oschmarini* is a Palaearctic species parasitizing *Lota lota* in Europe and Asia. It has so far been recorded from Russia (Onega Lake and lakes in Karelia, lower reaches of the Yenisey River, lakes of eastern Siberia – Lake Baikal, Lake Keta) and France (Lakes Annecy and Geneva in Savoy) (Trofimenko 1974, Vismanis *et al.* 1987, Moravec 1994, Moravec *et al.* 1999, present data). The intermediate hosts of *C. oschmarini* are the gammarids *Palassea quadrispinosa* Sars and *Echinogammarus baicalensis* Messjatzeff (see Vismanis *et al.* 1987).

It has been mentioned above that, to date, four valid species can be assigned to *Comephoronema*. Differences among them can be seen from the following key.

### Key to species of *Comephoronema*

- 1 Parasites of freshwater fishes. Mature eggs with a tuft of very numerous fine filaments on either pole ..... 2
  - Parasites of marine fishes. Mature eggs at most with 4 thread-like filaments on one or on both poles ..... 3
- 2 Preanal papillae 8–10 pairs or 8 and 11 in number. Body length of male and female 3.9–6.1 mm and 6.8–7.4 mm, respectively. Parasitic in scorpaeniform fishes (Abyssocottidae, Comephoridae, Cottocomephoridae) endemic in Lake Baikal (Siberia, Russia) ..... *C. werestschagini*
  - Preanal papillae 6 pairs. Body length of male and female 9.7–10.5 mm and 15.1–18.5 mm, respectively. Parasitic in *Lota lota* (Lotidae, Gadiformes) in Palaearctic Eurasia (Europe, Siberia) ..... *C. oschmarini*
- 3 Only one egg pole with filaments (2). Left spicule 297–375  $\mu\text{m}$  long. Length ratio of spicules 1:3.3–3.7. Body length of male and female 4.5–7.4 mm and 11.2–14.2 mm, respectively. Parasitic in deep-sea fish *Halosauropsis macrochiri* (Halosauridae, Notacanthiformes) in Mid-Atlantic Ridge ..... *C. macrochiri*
  - Both egg poles with filaments (2–4 on each pole). Left spicule 485–571  $\mu\text{m}$  long. Length ratio of spicules 1:4.0–5.4. Body length of male and female 7.9–15.2 mm and 15.8–32.2 mm, respectively. Parasitic in *Lycodichthys* spp. (Zoarcidae, Perciformes) in Antarctica ..... *C. beatriceinsleyae*

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