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**An emendation of the generic diagnosis of the monotypic *Glanitaenia*
(Cestoda: Proteocephalidae), with notes on the geographical distribution of *G. osculata*,
a parasite of invasive wels catfish**

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Abstract: The generic diagnosis of the monotypic *Glanitaenia* is amended based on a detailed morphological examination of newly collected specimens of *G. osculata* (Goeze, 1782) (syn. *Proteocephalus osculatus*) found in wels catfish, *Silurus glanis* Linnaeus, 1758, from Neuchâtel, Switzerland. Several morphological characteristics of *G. osculata* are described for the first time or better specified, such as uterine development (type 2 according to the classification by de Chambrier *et al.*, 2004, 2015), the presence and peculiar position of a vaginal sphincter (previously not reported), its egg morphology, description of scolex microtriches and a dense network of osmoregulatory canals in the posterior part of the scolex and the anterior region of the neck (proliferative zone). The anterior position of the vagina, which opens anterior to the cirrus-sac, not ventral as typical for most of the closely related species of the *Proteocephalus* aggregate, may represent apomorphy of this taxon. *Glanitaenia osculata* is reported from Italy (River Po basin), Romania (River Danube delta) and Switzerland (Aare/Rhine River basin) for the first time. This expansion of the parasite distribution area may be related to a recent introduction of wels catfish to West Europe.

Keywords: Cestoda, *Glanitaenia osculata*, morphology, redescription, freshwater fish, geographical distribution, Europe.

INTRODUCTION

The cestode genus *Glanitaenia* de Chambrier, Zehnder, Vaucher & Mariaux, 2004 (Proteocephalidea: Proteocephalidae) was erected by de Chambrier *et al.* (2004) based on the phylogenetic position of its type and only species, *G. osculata* (Goeze, 1782) [syn. *Taenia osculata* Goeze, 1782; *Proteocephalus osculatus* (Goeze, 1782) La Rue, 1911; *Gangesia osculata* (Goeze, 1782) Reichenbach-Klinke, 1962] from wels catfish, *Silurus glanis* Linnaeus, 1758, among Palaearctic proteocephalideans. It grouped with morphologically distinct *Paraproteocephalus parasiluri* (Yamaguti, 1934), another parasite of silurid catfishes, thus making the genus *Proteocephalus* sensu stricto (called *Proteocephalus*-aggregate by de Chambrier *et al.*, 2004) paraphyletic. The erection of *Glanitaenia* as a separate genus was supported by phylogenetic analyses based on 5.8S + ITS2, V4 region of the 18S rRNA and 28S rRNA gene sequences (Hypša *et al.*, 2005; Scholz *et al.*, 2007; de Chambrier *et al.*, 2015).

Glanitaenia was differentiated from the other genera of the subfamily Proteocephalinae by the possession of a well-developed, functional apical sucker with a deep cavity (the apical sucker in other species of the *Proteocephalus*-aggregate is vestigial, without any cavity, or completely absent – see Scholz *et al.*, 1998). In the diagnosis of *Glanitaenia*, de Chambrier *et al.* (2004) relied mainly on the morphological features of *G. osculata* described by previous authors, especially Nybelin (1942), Freze (1965), Scholz & Hanzelová (1998), and Scholz *et al.* (1998). However, some morphological details, including characteristics that are recently considered to be of potential taxonomic and phylogenetic importance, such as the development of the uterus, relative size of the ovary, morphology of the eggs and terminal genitalia (the distal part of the vaginal canal), and the course of osmoregulatory canals (see de Chambrier *et al.*, 2012, 2015), were not provided.

Therefore, the generic diagnosis of *Glanitaenia* is amended in the present paper and the current distribution of *G. osculata* is reviewed based on new geographical

records from Europe and in relation to the current expansion of its fish host, wels catfish, which is classified as an invasive species (Copp *et al.*, 2009).

MATERIAL AND METHODS

The present study is mainly based on morphological evaluation of 25 tapeworms found in a single wels catfish, *Silurus glanis* Linnaeus, 1758 (total length of 211 cm, weight of 68 kg) from Neuchâtel, Switzerland (River Aare basin) examined on 25 March 2010 by the senior author (A. de C.). Specimens for morphological study were fixed immediately after dissection of the host with hot 4% neutral formaldehyde solution and then stored in 75% ethanol. They were stained with Mayer's hydrochloric carmine solution, dehydrated in a graded ethanol series, cleared with eugenol (clove oil) and mounted in Canada balsam. Pieces of strobila were embedded in paraffin wax, transversely sectioned at 12–15 μm , stained with Weigert's haematoxylin and counterstained with 1% eosin B (acidified with five drops of pure acetic acid for 100 ml solution) (de Chambrier, 2001; Oros *et al.*, 2010). Voucher specimens have been deposited in the collection of the Natural History Museum in Geneva (acronym MHNG-PLAT; Collection numbers 68395–68397, 68699, 68700, 68709, 84707–84712, 91260) and in the helminthological collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences in České Budějovice (acronym IPCAS; Collection number C-49/1).

Scolexes of two specimens were prepared for scanning electron microscopy (SEM) as follows: specimens were dehydrated in a graded ethanol series, then transferred to a graded amylacetate series, critical point-dried in CO_2 , sputter-coated with gold and examined in a Zeiss DSM 940A electron microscope at the Natural History Museum, Geneva. Microthrix terminology follows that of Chervy (2009).

Eggs were studied in the water after their spontaneous release from gravid tapeworms found in *S. glanis* from the River Vltava at the Orlik water reservoir near Štědrónín, Czech Republic, examined by T. S. on 13 October 1997 (host field nos. 2244 & 2245 – see below) and used for experimental infection of copepods (see Scholz, 1999). Measurements of egg envelopes, oncosphere and embryonic hooks are expressed in micrometres (μm) as range with the mean \pm standard deviation and number of measurements in parentheses.

In addition, the following comparative material of *G. osculata* from *S. glanis* deposited in IPCAS was studied:

(i) 5 specimens from the Rivers Latorica in Slovakia and Tisa near Szolnok and Kőtelek (Hungary) (see Scholz, 1989);

(ii) tapeworms from the Orlik water reservoir on the River Vltava at Štědrónín, South Bohemia, Czech Republic, collected on 12 May 1996 (8 specimens; host field No. FM5504), 18 September 1996 (1 spec.), 22 May 1997 (6 spec.; Nos. 2146 & 2147), 4 June 1997 (34 spec.; No. 2186), 11 June 1997 (2 spec.; Nos. 2241–2243) and 13 October 1997 (8 spec.; Nos. 2244 & 2245) (see Scholz *et al.*, 1998; Scholz & Hanzelová, 1998);

(iii) 1 specimen from Horusický fishpond, South Bohemia, Czech Republic (Moldau/Elbe River basin) collected on 19 October 2009;

(iv) 4 specimens from Bodensee, Germany, collected in 1999 by Alexander Brinker;

(v) 1 specimen from River Po in Ferrara, Italy, collected in July 2009 by Bahram S. Dezfuli;

(vi) 1 specimen from Chilia Branch of the Danube River, Romania, collected in July 2013 by Petr Horák (all specimens listed above – IPCAS C-49/1).

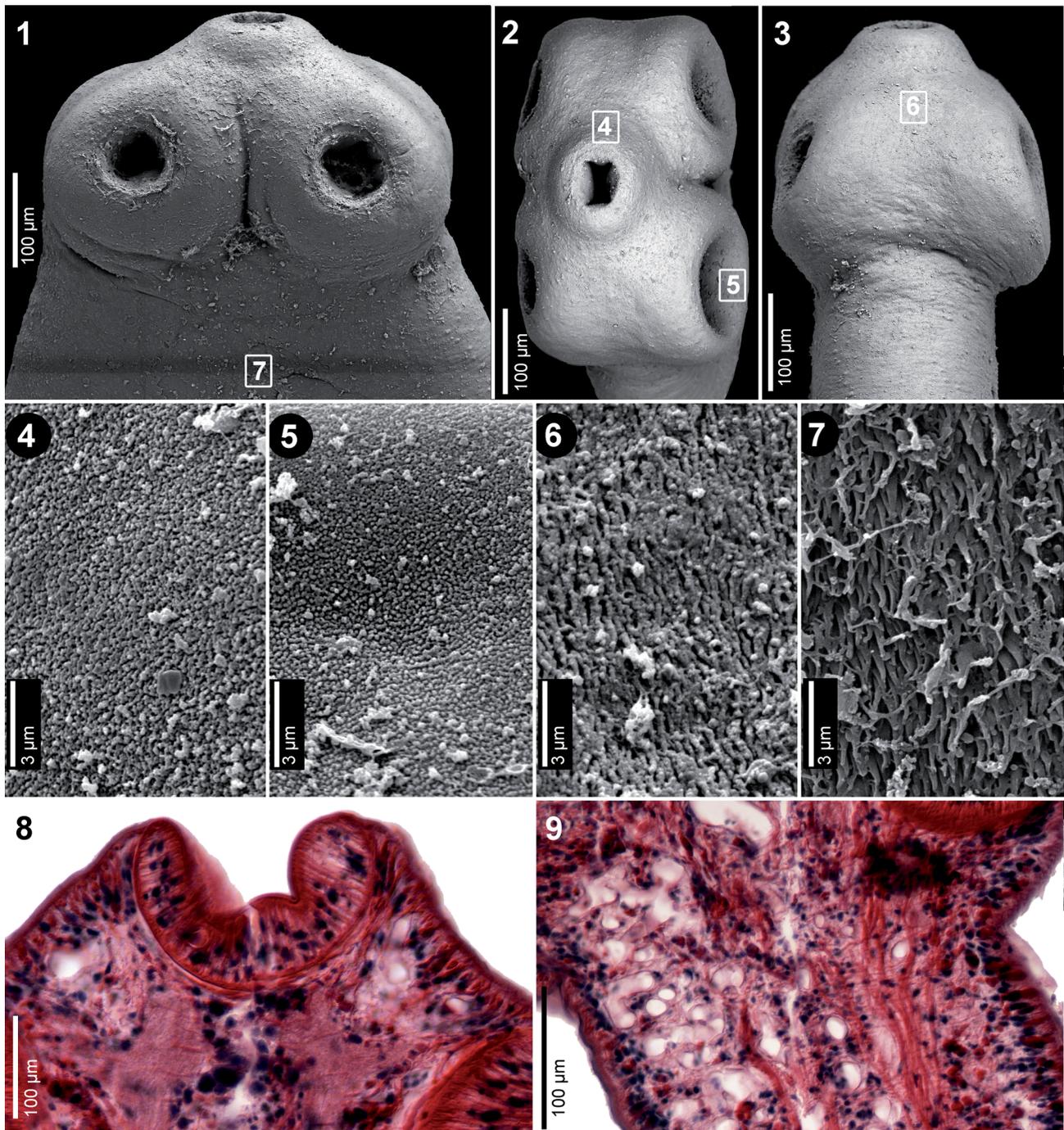
Relative size of the ovary, i.e. the proportion of its size in relation to the size of the proglottid, was calculated as outlined by de Chambrier *et al.* (2012). A copy of the illustration of the proglottid was cut out and weighed using a high precision balance (Mettler AE 163). Then a copy of the ovary itself was cut out and weighed, and the proportion of its weight to that of the entire proglottis was calculated (in %).

RESULTS

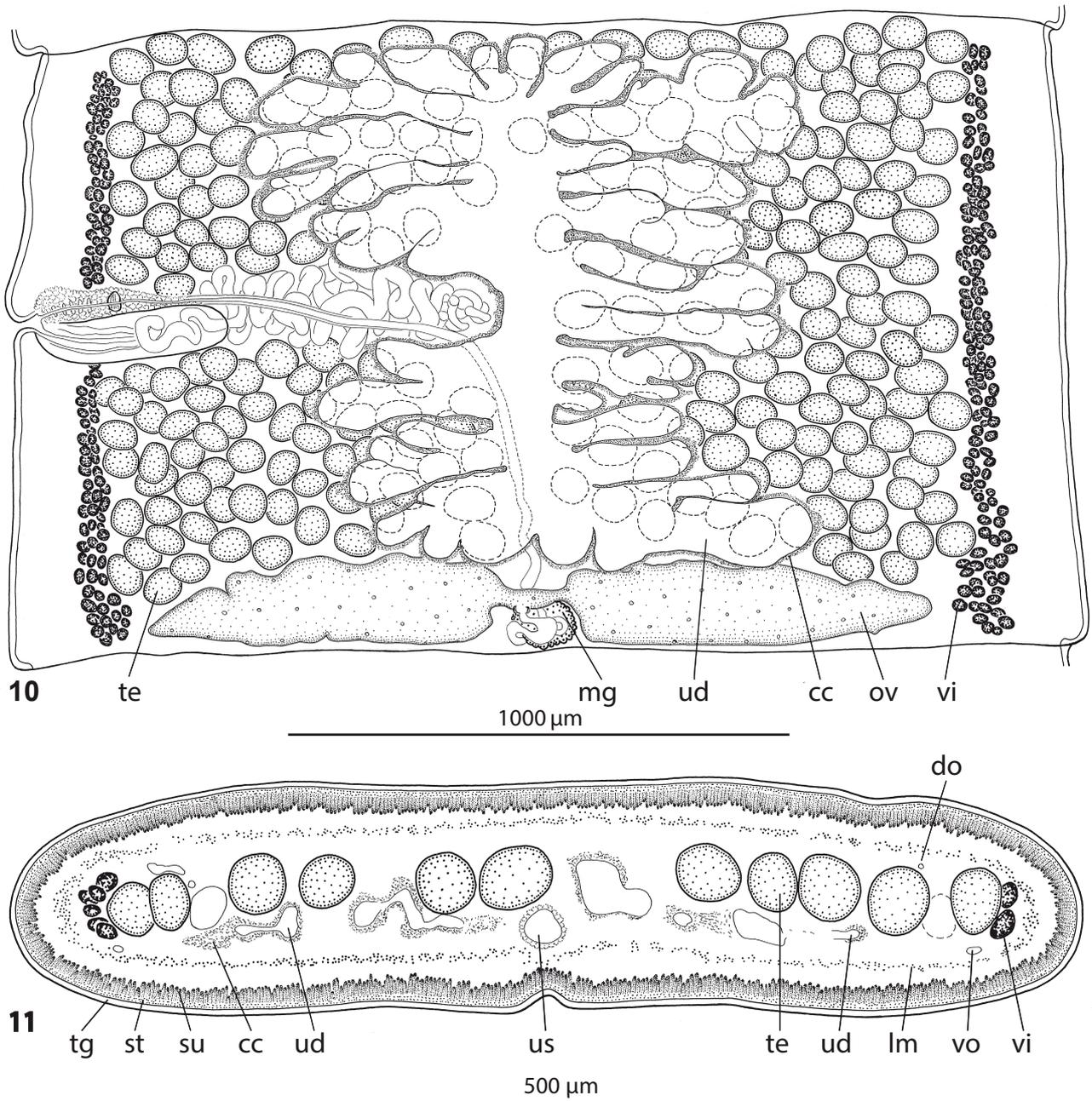
Examination of newly collected cestodes from Switzerland as well as voucher specimens from the Czech Republic, Germany, Hungary, Italy, Romania and Slovakia made it possible to supplement the morphological description of *Glanitaenia osculata*, with morphological data, which were previously not reported or not described sufficiently (Figs 1–15).

1. Development of the uterus

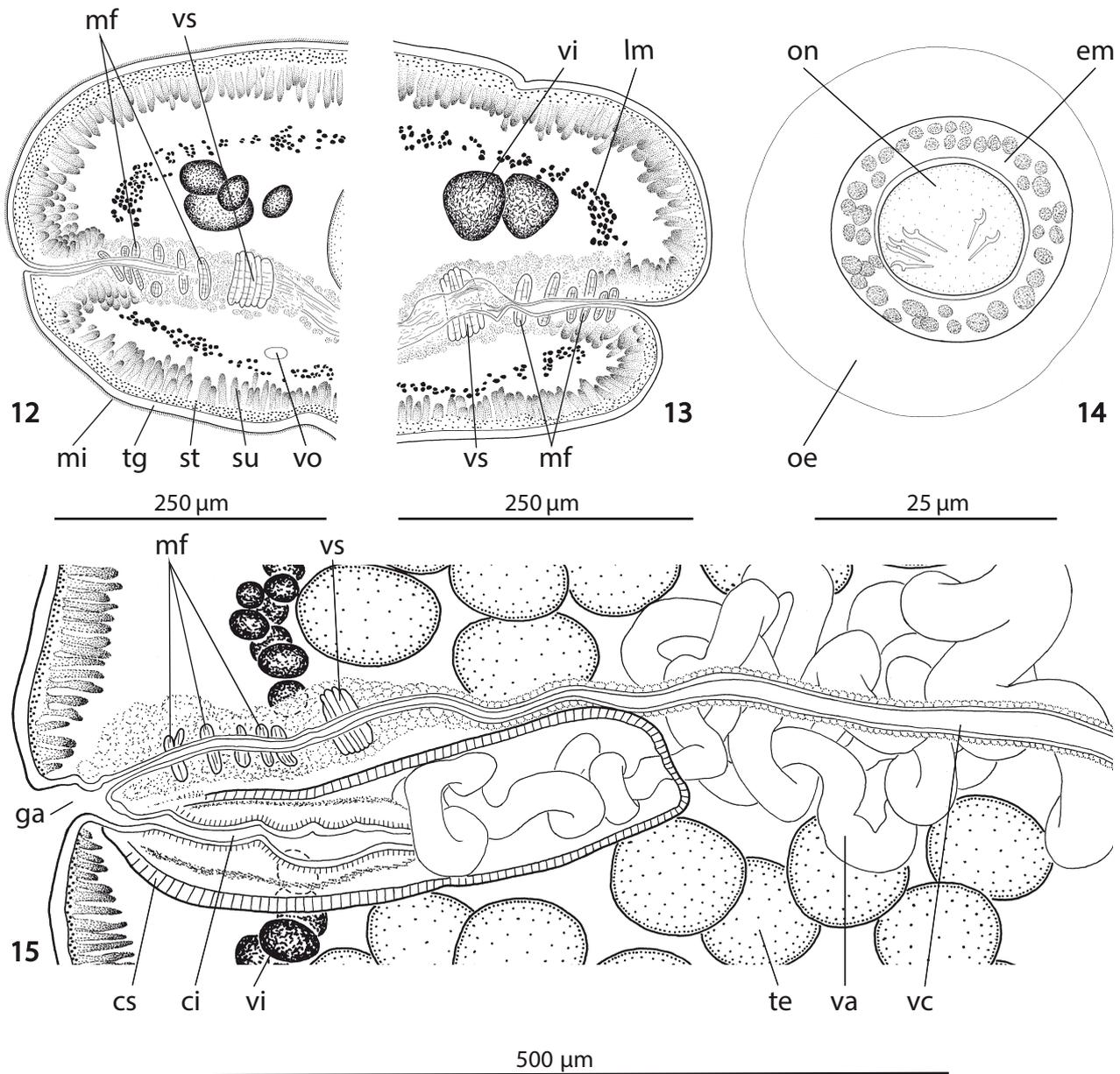
The uterine development of *G. osculata* is of type 2 according to the classification of de Chambrier *et al.* (2004, 2015). In immature proglottids, the uterine stem is lined by numerous weakly-staining cells, sometimes difficult to observe, on both sides. Thereafter, elongated ramified digitations appear lateral to the stem; their apical part contains undifferentiated chromophilic cells. In the last immature proglottids, the lumen of the uterine stem occupies up to 34% of the proglottid width. In mature proglottids, the lumen gradually extends from its base to the apex of each digitate diverticulum and occupies up to 44% of the proglottid width; the apex is lined with numerous chromophilic cells. Lateral ramified diverticula enlarge in gravid proglottids, occupying up to 59% of the proglottid width (Figs 10, 11).



Figs 1-9. *Glanitaenia osculata* from *Silurus glanis*, Switzerland. 1-7. Scanning electron micrographs (INVE-PLAT-91260). (1) Scolex, dorsoventral view. (2) Scolex, apical view. (3) Scolex, lateral view. (4) Acicular filitriches on the apex of the scolex. (5) Papilliform filitriches on the internal surface of suckers. (6) Capilliform filitriches between the suckers. (7) Gladiate spinitriches on the external surface of the proliferation zone (neck). (8, 9.) Photomicrographs of longitudinal sections of the scolex (INVE-PLAT-91260). (8) Detail of the apical part of the scolex showing an apical sucker. (9) Detail of the dense network of osmoregulatory canals in the posterior part of the scolex and the anterior part of the neck (proliferation zone).



Figs 10, 11. *Glanitaenia osculata* from *Silurus glanis*, Switzerland. (10) Pregravid proglottid, ventral view (MHNG-PLAT-84710). Note the shape of the ramified lateral diverticula of the uterus. (11) Cross section of a pregravid proglottid at the level of the preperal region. Abbreviations: cc: chromophilic cells; do: dorsal osmoregulatory canal; lm: internal longitudinal musculature; mg: Mehlis' glands; ov: ovary; st: subtegumental muscle fibres; su: subtegumental cells; te: testes; tg: tegument; ud: uterine diverticula; us: uterine stem; vi: vitelline follicles; vo: ventral osmoregulatory canal.



Figs 12-15. *Glanitaenia osculata* from *Silurus glanis*, (12, 13) Cross sections of the poral part of a pregravid proglottid at the level of the vagina (MHNG-PLAT-68397). Note the presence of a proximally situated vaginal sphincter and more distally situated muscles surrounding the vaginal canal. (14) Egg spontaneously released from a gravid tapeworm collected in the Czech Republic. (15) Detail of the cirrus-sac and the distal (terminal) part of the vaginal canal (MHNG-PLAT-84710). Abbreviations: ci: cirrus; cs: cirrus-sac; em: bi-layered embryophore; ga: genital atrium; lm: internal longitudinal musculature; mf: muscle fibres; mi: microtriches; oe: outer envelope; on: oncosphere; st: subtegumental muscle fibres; su: subtegumental cells; te: testes; tg: tegument; va: vas deferens; vc: vaginal canal; vi: vitelline follicles; vo: ventral osmoregulatory canal; vs: vaginal sphincter.

2. Relative size of the ovary

The surface of the ovary of *G. osculata* represents 7.5-8.7% of the total surface of the proglottids in the newly collected material, and 10.6-10.7% in proglottids illustrated by Scholz & Hanzelová (1998) (calculated from fig. 17A, C in that paper).

3. Vaginal sphincter

The distal part of the vaginal canal of *G. osculata* is surrounded by a small circular sphincter. Unlike most other proteocephaline cestodes, it is situated more medially, ventral or medioventral to vitelline follicles (Figs 12, 13, 15), not close to the genital atrium as in other taxa. In addition to this circular sphincter of a typical appearance (ring-like, circular sphincter), the distal (terminal) part of the vaginal canal is surrounded by a few separated bundles of muscle fibres (Figs 12, 13, 15).

4. Position of the vaginal canal

The vaginal canal is almost always anterior to the cirrus-sac (in 163 of 166, i.e. 98.1%, of observed proglottids; Fig. 15), thus not overlapping it on its ventral side. In most species of the *Proteocephalus* aggregate, the vaginal canal opens at the same level as the cirrus pore, thus the distal part of the vaginal canal overlaps the terminal part of the cirrus-sac on its ventral side (Scholz & Hanzelová, 1998).

5. Egg morphology

Eggs released spontaneously to the water are spherical, with a hyaline outer envelope, 34-43 (39.3 ± 2.3 ; $n = 27$) in diameter; diameter of granular embryophore 23-27 (25.3 ± 1.2 ; $n = 24$) (Fig. 14). Oncosphere subspherical, 15-18 (16.7 ± 0.9 ; $n = 20$) long and 14-17 (14.7 ± 0.8 ; $n = 20$) wide, with three pairs of embryonic hooks (Fig. 14); lateral hooks slightly shorter, 6.5-7.7 (7.1 ± 0.3 ; $n = 25$) long, than median hooks, 6-7.5 (6.7 ± 0.4 ; $n = 20$) long.

6. Osmoregulatory canals

In the posterior part of the scolex and the anterior part of the neck region of *G. osculata*, osmoregulatory canals are strongly convoluted and form a dense network of anastomosed canals (Fig. 9).

7. Number of testes

The number of testes in the newly collected specimens is 222-281 per proglottid ($x = 249$; $n = 10$; Fig. 10).

8. Microtriches

The apical part of the scolex is covered with acicular filitriches (Fig. 4) and the internal surface of the suckers with papilliform filitriches (Fig. 5); capilliform filitriches are present between the suckers (Fig. 6) and gladiate spinitriches on the external surface of the proliferation zone (neck) (Fig. 7).

On the basis of our new observations, we amend the diagnosis of *Glanitaenia* as follows:

Glanitaenia de Chambrier, Zehnder, Vaucher & Mariaux, 2004 – amended diagnosis

Diagnosis: Proteocephalidea, Proteocephalidae. Large tapeworms with numerous slightly craspedote proglottids, wider than long including for pregravid and gravid proglottids. Inner longitudinal musculature well developed, formed by highly anastomosed, numerous bundles of muscle fibres. Scolex unarmed, with four uniloculate suckers, with convoluted osmoregulatory canals in its posterior part. Apical sucker well developed, strongly muscular, with deep cavity; apical part lined with numerous gland cells. Neck region (proliferation zone) long, containing extensively developed, convoluted osmoregulatory canals with numerous anastomoses in its anterior part. Immature proglottids numerous, begin at considerable distance posterior to scolex. Testes numerous, medullary, in one continuous field and in one layer, exceptionally with a few testes in second incomplete layer. Ovary medullary, numerous, bilobed, relatively large in relation to surface of proglottids. Vagina opening to common genital atrium anterior to cirrus-sac; vaginal canal with circular vaginal sphincter situated ventral to ventrolateral to vitelline follicles; terminal (distal) part of vaginal canal encircled by separated bundles of muscle fibres. Genital pore slightly pre-equatorial. Vitelline follicles lateral, occupying almost entire proglottid length. Uterus medullary, ventral, with ramified lateral diverticula. Development of uterus of type 2. Parasites of siluriform fish in Palaearctic Region. Type and only species: *Glanitaenia osculata* (Goeze, 1782) de Chambrier, Zehnder, Vaucher & Mariaux, 2004 [synonyms *Taenia osculata* Goeze, 1782; *Proteocephalus osculatus* (Goeze, 1782) La Rue, 1911; *Ichthyotaenia skorikowi* von Linstow, 1904; *Proteocephalus skorikowi* (von Linstow, 1904) La Rue, 1911; *Gangesia osculata* (Goeze, 1782) Reichenbach-Klinke, 1962].

DISCUSSION

In the present study, generic diagnosis of one of the earliest diverging taxon of the subfamily Proteocephalinae (see de Chambrier *et al.*, 2015) is amended, based on the examination of newly collected and museum material of its type and only species,

Glanitaenia osculata. This species was poorly known since its description as *Taenia osculata* by Goeze (1782) and La Rue (1911, 1914) placed it (as *Proteocephalus osculatus*) among *species inquirendae*, partly because it was confused with another specific parasite of wels catfish, *Silurotaenia siluri* (Batsch, 1786) (Proteocephalidea: Gangesiinae). Nybelin (1942) was the first who confirmed the validity of *P. osculatus* and provided a most detailed description of its morphology at a given time.

Freze (1965), who studied extensive material of *P. osculatus* (= *Glanitaenia osculata*) from the former Soviet Union, stated that “Nybelin’s description of *P. osculatus* [= *G. osculata*] insufficiently reflects the boundaries of its morphological variations, although Freze’s material in general corresponds to this description and pertains to the same species.” Scholz *et al.* (1998) provided detailed data on the scolex morphology of *G. osculata* (as *P. osculatus*) including SEM micrographs, and Scholz & Hanzelová (1998) redescribed the species based on newly collected specimens from the Czech Republic.

In the present study, some morphological and biometrical data are provided for the first time, which made it possible to amend the generic diagnosis of *Glanitaenia*. de Chambrier *et al.* (2004) have demonstrated potential importance of the uterine development as one of very few morphological characteristics that may reflect the evolutionary history of the order (see also de Chambrier *et al.*, 2015). The former authors classified the development of the uterus of *G. osculata* as type 2 (see fig. 1 in de Chambrier *et al.*, 2004), but did not provide any details. Surprisingly, the shape of the developed uterus of *G. osculata* with ramified lateral diverticula is most similar to that of *Ageneiella brevifilis* de Chambrier & Vaucher, 1999, a parasite of the auchenipterid catfish *Ageneiosus inermis* (Linnaeus) in the Neotropical Region (see fig. 31 in de Chambrier & Vaucher, 1999), which belongs to a most derived clade of proteocephalidean cestodes (de Chambrier *et al.*, 2015).

The new material of *G. osculata* also enabled us to provide data on the relative size of the ovary (see de Chambrier *et al.*, 2012). The surface of the ovary of *G. osculata* represents 7.5–8.7% of the total surface of proglottids (and 10.6–10.7% in specimens illustrated by Scholz & Hanzelová, 1998), which well corresponds to the values in other species of proteocephalideans from teleost fishes and it is markedly larger than those in most species of *Ophiotaenia* La Rue, 1911 from reptiles (see table 1 in de Chambrier *et al.*, 2015).

A novelty of the present study is a detailed description of a vaginal sphincter in *G. osculata* and its peculiar position and morphology. Indeed, Nybelin (1942) also described a small vaginal sphincter and illustrated it in his fig. 3, but he did not provide any details. In contrast, Scholz & Hanzelová (1998) did not report this structure at all. They illustrated a thick layer of cells lining the terminal (distal) part of the vaginal canal in their fig. 9G (cross

section at the level of the vagina), but these cells were not interpreted as a vaginal sphincter. Similarly, no sphincter was illustrated in the terminal part of the vaginal canal (fig. 16I in that paper).

One of the reasons why Scholz & Hanzelová (1998) did not report the vaginal sphincter, which is actually present in the specimens studied by these authors, could be its unusual position. It is situated at the level of vitelline follicles, i.e. much more medially than in related taxa such as *Proteocephalus longicollis* (Zeder, 1800) and *P. percae* (Müller, 1780), in which the sphincter is close to the genital atrium (see figs 14G, 18E, F and 20 H, I in Scholz & Hanzelová, 1998).

The terminal part of the vaginal canal of *G. osculata*, which is surrounded by a medially situated circular vaginal sphincter of a typical shape (ring-like sphincter) and a few separated bundles of muscle fibres situated more distally, somewhat resembles that of phylogenetically distant species from Neotropical catfish, *Mariauxiella piscatorum* de Chambrier & Vaucher, 1999 (see fig. 87 in de Chambrier & Vaucher, 1999).

The eggs of *G. osculata* are described and illustrated for the first time in the present paper, even though Scholz (1999) studied early phases of the developmental cycle of the species. However, he provided only data on metacercodes (plerocercoids) from experimentally infected copepods 12 and 21 days post infection. In fact, the eggs of *G. osculata* resemble those typical of most species of the *Proteocephalus* aggregate (see Scholz, 1999).

The anterior part of the body of *G. osculata*, specifically the posterior part of its scolex and the anterior part of a very long proliferative zone (neck region), contains strongly convoluted osmoregulatory canals that form a dense network of anastomosed canals. Scholz *et al.* (1998) observed similar networks in the scolex of most Palaearctic species of the *Proteocephalus* aggregate, but they did not focus on the presence of these canals in the proliferative zone. In addition, the canals seem to be much more developed in *G. osculata* compared to those in species of the *Proteocephalus* aggregate (see figs 1K, 3G, I, J, 5E, Q in Scholz *et al.*, 1998). A dense network of osmoregulatory canals situated in the posterior part of the scolex and the anterior part of the neck region was also observed in phylogenetically distant *Proteocephalus regoi* de Chambrier, Scholz & Vaucher, 1996, a parasite of *Hoplias malabaricus* (Bloch) (Characiformes: Erythrinidae) in the Neotropical Region (see figs 1 and 3 in de Chambrier *et al.*, 1996), and in *Sandonella sandoni* (Lynsdale, 1960) from *Heterotis niloticus* (Cuvier) (Osteoglossiformes: Arapaimidae) in the Ethiopian Region (see fig. 2 in de Chambrier *et al.*, 2008). Function of these canals and the reason of their concentration in the scolex or in the proliferative zone are not known. Cestodes seem to be osmoconformers whose excretory system plays little or no role in osmoregulation and is largely excretory (Smyth & McManus, 1989).

Glanitaenia osculata belongs to the largest cestodes of teleost fishes, with a total length reaching up to 1 m (Lühe, 1910); the longest specimen found in the present study was 74 cm long (a tapeworm from Switzerland). The body of *G. osculata* consists of numerous, rather large proglottids that contain many testes. Even though these are mostly in a single layer, their counting is difficult due to their high number and a well-developed longitudinal musculature. Nybelin (1942) reported 276-291 testes per proglottid, Freze (1965) 180-424 testes (usually about 250), but Scholz & Hanzelová (1998) only 105-171 testes. In the present study, 222-281 testes ($x = 249$, $n = 10$) were counted based on illustrations of individual proglottids, which is the most precise method of counting the testes.

This species forms, together with *Paraproteocephalus parasiluri* (Yamaguti, 1934), type and single species of *Paraproteocephalus* Chen in Dubinina, 1962 (see de Chambrier *et al.*, 2004, 2015; Scholz *et al.*, 2007). Species of both monotypic genera differ from each other in their scolex and strobilar morphology, especially in the presence/absence of a metascolex (absent in the former species versus well-developed in *P. parasiluri*, which was even placed in the subfamily Corallobothriinae – Freze, 1965), the position of bands of vitelline follicles ('typically' vertical alongside margins of proglottids

in *G. osculata* versus L-shaped, with most follicles forming a transverse band lateral to the ovary in the latter species – see figs 6 & 7 in Shimazu, 1993), and uterine diverticula (lateral in the former species as in a majority of proteocephalideans versus forming anterior and posterior branches from the transversely situated uterine stem in *P. parasiluri* – figs 6 & 7 in Shimazu, 1993).

Glanitaenia osculata resembles species of the *Proteocephalus* aggregate in the morphology of its scolex, which is devoid of any metascolex, and shape of the strobila and its proglottids, which are only slightly wider than long. It can be distinguished from species of the *Proteocephalus* aggregate by a much more developed apical sucker (versus vestigial or absent in species of the latter group – see Scholz *et al.*, 1998) and by the anterior position of the vaginal canal in relation to the cirrus-sac (ventral to the terminal part of the sac in most species of the *Proteocephalus* aggregate). In addition, *G. osculata* is much bigger and more robust than the species of the *Proteocephalus* aggregate and its proglottids contain much more proglottids, especially immature ones, and more testes (Scholz & Hanzelová, 1998; present study).

This tapeworm has been reported from the following countries of Europe and Palaeartic Asia: Bulgaria, Czech Republic, Germany, Hungary, Latvia, Lithuania, Poland, Russia, Slovakia, Sweden, Ukraine, United Kingdom, former Yugoslavia, Azerbaidzhan, Georgia, Iraq and Turkey (Fig. 16; see also Scholz & Hanzelová, 1998 and Gibson *et al.*, 2005 [but misidentification of *Postgangesia inarmata* de Chambrier, Al-Kallak & Mariaux, 2003 and *Postgangesia hemispherous* (Rahemo & Al-Niaeemi, 2001) in Iraq cannot be excluded]).

Glanitaenia osculata is a specific parasite of wels catfish, which is currently considered to be an invasive species and has recently been introduced to the western and southwestern Europe including northern Italy, Spain, France, Germany and England (Copp *et al.*, 2009; Fig. 16). Therefore, it is possible that new geographical records from two of these countries (the River Po in Italy and the River Rhine basin in Germany – River Aare is a tributary of the Rhine joining it in Koblenz, at the Swiss-German border) are a result of this recent expansion of the wels catfish throughout Europe (Fig. 16).



Fig 16. Geographical distribution of *Glanitaenia osculata* (Goeze, 1782) in Europe. Countries with previous records indicated by triangles; new geographical records (Italy, Romania and Switzerland) highlighted by asterisk; the original distribution area of wels catfish (grey silhouette; bordered by dashed line) and newly colonized regions of Europe (white silhouette; bordered by dotted line; modified from Copp *et al.*, 2009).

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