
Archaic Tergipedidae of the Arctic and Antarctic: *Murmania antiqua* gen. et sp. nov. from the Barents Sea and a revision of the genus *Guyvalvoria* Vayssière with descriptions of two new species

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ABSTRACT. The Antarctic genus *Guyvalvoria* Vayssière, 1906 is revised. The type species of the genus, *G. francaisi* Vayssière, 1906 is redescribed based on the study of the type and new material. Two new species of the genus *Guyvalvoria*, *G. gruzovi* sp. nov. and *G. savinkini* sp. nov. are described from the Davis Sea and Subantarctic Kerguelen Island. In addition, a new genus and species, *Murmania antiqua* gen. et sp. nov. is described from off the Murman coast of the Barents Sea (depth 60-300 m). The latter taxon is characterized by a wide body, numerous branched rows of the digestive gland and moderately developed notal rim with an elevated ridge. Radular teeth of *Murmania antiqua* possess unusual clusters of lateral denticles. The Antarctic genus *Guyvalvoria* and Subarctic genus *Murmania* gen. nov. have some similarities in the external appearance, presence of numerous branches of the digestive gland and a tendency to shift of the anus caudally. Morphological peculiarities of the new taxon suggest a new interpretation of the head composition in the family Tergipedidae: the tergipedid head is formed with involving of the postoral lobes of the anterior foot, as distinct from the "typical head", characteristic of most aeolidacean nudibranchs. This conclusion is supported by a number of examples from the family Tergipedidae and other families of the aeolidaceans. Both *Murmania* gen. nov. and *Guyvalvoria* Vayssière, 1906 are considered as one of most basal within the Tergipedidae; transformations of the digestive gland within the family are discussed.

Most species of the family Tergipedidae possess a slender body with simple branches of the digestive gland tending to be reduced up to one papilla per row. Only few taxa, for instance the type species of the genus *Cuthona*, *C. nana* (Alder et Hancock, 1842) have a relatively broad body and a branched digestive gland. In addition, most Tergipedidae, with minor exceptions, always have anus in the acleiproctic position. Up to now, a notal ridge was unknown for tergipedids, while all large aeolidacean families (Flabellinidae, Facelinidae, Aeolidiidae) contain several basal genera having a wide body, numerous rows of branched digestive gland, some-

times distinct notal ridge, and pleuroproctic or cleiproctic anus. The present study reveals two tergipedid genera featuring numerous elaborated branches of the digestive gland, elevated lateral ridge, posterior anus and other unusual for the family Tergipedidae characters.

Currently, two approaches to the taxonomy of the nudibranch family Tergipedidae can be recognized. Miller [1977] for the first time critically revised the large number of accumulated at that time generic names of the Tergipedidae, synonymized *Trinchesia* and *Catriona* with *Cuthona*, but retained *Cuthonella* and some other genera on the basis of pattern of the digestive gland. Williams and Gosliner [1979] revealed the presence of a supplementary gland in the male part of reproductive system in the type species of *Cuthona* and the insertion of this gland into vas deferens in "*Cuthona*" *concinna* (Alder et Hancock, 1843). In the same year, Gosliner [1979] united most of the family diversity into one genus — *Cuthona*. Millen [1986] discovered a *Cuthonella*-like species in shallow water of the Canadian Pacific, and synonymized the genus *Cuthonella* with *Cuthona*. It should be emphasized that Northern and Arctic tergipedids with supplementary gland inserted to the vas deferens form a monophyletic group including at least six species both with numerous branches of the digestive gland (*C. abyssicola* Bergh, 1884) and with lesser number of simple branches (*C. concinna*). This group was suggested to be considered as the genus *Cuthonella* [Martynov, 1992]. Recently the genus *Trinchesia* was restored and delineated from *Cuthona* [Martynov, 2002]. Miller [2004] undertook a new review of the Tergipedidae of New Zealand and also restored the genus *Trinchesia*.

Completing the first review of Nudibranchia of the Barents and White Seas, Herzenstein [1885: 712], noted that he had «two unidentified species of *Aeolis*», one of them «...a species, found in a single specimen on the depth 160 "sagènes" [probably equal to fathoms; ca. 293 m] on muddy ground off Kildin Id.», which «...is can be hardly compared with any species known to me». The mentioned

specimen (Fig. 1 G) was collected by F.F. Yarzhin-sky in 1871 off Murman coast of the Barents Sea and preserved in the collection of the Zoological Institute, St.-Petersburg. This specimen, after 110 years of storage, is at the first glance hardly attributable to any group of the Nudibranchia Aeolidacea; rather it is similar to both families Tergipedidae and Facelinidae. In addition, eight old specimens of this taxon from the Barents Sea (depth 67-292 m, soft substrates) have been studied. This species from the Subarctic is superficially similar to the obscure Antarctic genus *Guyvalvoria*. Both taxa have anus in the posterior part of the back (actually close to the middle) but the species from the Barents Sea can be clearly distinguished by numerous elaborated, not compressed rows (up to 40) of anterior and posterior digestive gland. It is considering here as a new genus and species, *Murmania antiqua* gen. et sp. nov.

Vayssi re [1906a, 1906b, 1917] gave a detailed description of his new taxon, *Guivalvoria francaisi* with unusual set of characters, from waters of the Antarctic Peninsula. Because of the presence of uni-serial radula and supplementary (= "penial") gland it has to be admitted that this animal is related to the genus *Cuthona*. However, the position of the anal opening far behind the middle of the back is quite dissimilar to the family Tergipedidae. Yet another species with similar features, "*Cuthonella*" *paradoxa*, was described a year later by Eliot [1907] from the Ross Sea, but further has not been drawn attention. It undoubtedly also belongs to the genus *Guyvalvoria*.

About 40 years passed before Odnher [1944] noticed that characters of *Guyvalvoria* not allowed to conclude definitely on its relationship: *G. francaisi* rather belongs to the genus *Cuthona*. Recently the unusual Vayssi re's taxon was shortly listed by Cattaneo-Vietti [1991]. He did not agree with Odnher's opinion on the placement of *G. francaisi* in the genus *Cuthona* but retained it as a doubtful species. Despite the good knowledge on the Antarctic nudibranch fauna since the time of Vayssi re, there were no new records of *Guyvalvoria*.

Among numerous samples of Nudibranchia collected by E.N. Gruzov and A.M. Sheremetevsky during all-year underwater researches using SCUBA in the framework of the 16th and 17th Soviet Antarctic Expedition (early 1970s), there are several specimens of two species undoubtedly belonging to the genus *Guyvalvoria*. Most of them, collected in regions of the Amery Ice Shelf and in the Davis Sea (Haswell Is.) on 15-50 m, on rocky substrate, belong to *G. francaisi* Vayssi re, 1906; the other two specimens belong to a new species. In addition, in a single sample from stomach of fish *Nothotenia rossi* caught off Kerguelen Id. several specimens were discovered of a large tergipedid in a rather good condition. A

close examination of them has led to a conclusion that they also belong to *Guyvalvoria*.

Although externally these two genera have unique features for Tergipedidae, their internal morphology is typical for the family. Thus, it is revealed in the present study that the genus *Guyvalvoria* is actually a separate tergipedid taxon.

Abbreviations of institutions:

BMNH — The Natural History Museum, London.
MNHN — Mus um National d'Histoire Naturelle, Paris.
ZIN — Zoological Institute RAS, St. Petersburg.

Murmania Martynov, gen. nov.

Type species: *M. antiqua* Martynov, sp. nov.

Gender: feminine

Diagnosis. Head with dorsal triangular ridge-like wedging in between rhinophores. Postoral lobes fused with head and forming anterior corners of foot. Body sides high, with lateral notal ridge-like elevations. Branches of digestive gland very numerous, branched, there is no direct correspondence between branches and ceratal rows. Preanal ceratal rows more than 20, postanal rows not reduced. No visible border between anterior and posterior digestive gland. Lateral edges of back in form of elevated notal ridge. Anus cleiproctic, placed in posterior part of the back, but near to middle of body. Masticatory processes of jaws bearing several sharp denticles in a single row. Radular teeth wide, arc-shaped, with strongly protracted central cusp and lateral denticles united in several clusters. Preradular teeth absent. Male and female genital openings close to each other. Vas deferens without clear distinction between prostatic and non-prostatic parts. Supplementary gland large, elongate, inserted into base of penis and covered near penial sheath with well developed connective tissue layer. Penis large, conical and unarmed. Seminal reservoir unknown.

[**Диагноз.** На дорсальной части головы имеется треугольная складка, вклинивающаяся между ринофорами. Тело высокое, по бокам имеется закраина с закругленным краем. Ветви пищеварительной железы очень многочисленные, разветвленные, без прямого соответствия ветвей рядам папилл. Преанальных цератальных рядов более 20, постанальные не редуцированы. Нет заметной границы между передней и задней частями пищеварительной железы. Анус клейпроктный, располагается около середины спины, несколько сдвинут назад. Жевательный отросток челюстей несет один ряд приостр енных зубчиков. Зубы радулы арковидные, центральный зубец сильно выдается за латеральные зубчики, которые организованы в два нечетко выраженных кластера, где чередуются узкие и широкие зубчики. Прерадулярные зубы отсутствуют. Мужское и женские отверстия располагаются рядом. Семяпровод без выраженных различий между простатической и мускульной частями. Дополнительная железа мощная,

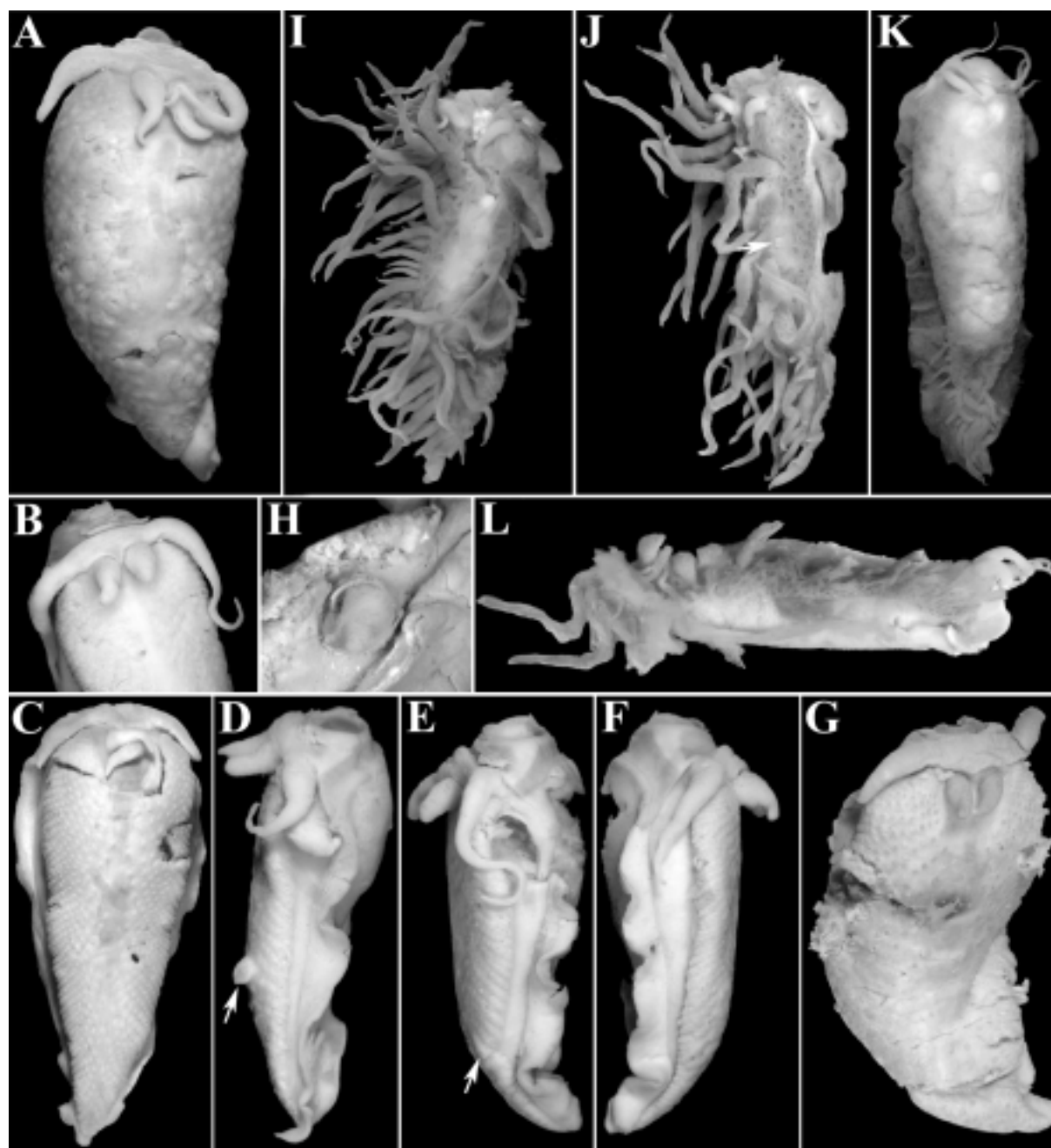


FIG. 1. A-H — *Murmania antiqua* gen. et sp. nov.: A — paratype, ZIN No. 2/24512, dorsal view, length 19 mm; B, E, F — paratype, ZIN No. 2/24512, length 19.2 mm. B — anterior dorsal view; E — right lateral view showing abnormal anus position; F — left lateral view; C — holotype (dissected), dorsal view; D — paratype, ZIN No. 2/24512, length 11 mm, right lateral view; G — historically important specimen collected by F.F. Yarzinsky in 1871, paratype, ZIN No. 3/24472, length 19 mm, dorsal view; H — genital area and penis of specimen ZIN No. 3/24472. I-L — *Guyvalvorina savinkini* sp. nov.: I — paratype, ZIN No. 2, length 32 mm, dorsal view; J — paratype, ZIN No. 2, length 32 mm, dorso-lateral view from right side; K — holotype, ZIN No. 1, length 33 mm, dorsal view; L — right lateral view of paratype, ZIN No. 3, length 42 mm (head width 10 mm). Anal opening is marked by an arrow.

РИС. 1. А-Н — *Murmania antiqua* gen. et sp. nov.: А — паратип, ЗИН № 2/24512), длина 19 мм, вид с дорсальной стороны; В, Е, F — паратип длиной 19,2 мм с аномальным положением ануса, ЗИН № 2/24512), В — вид передней части тела дорсально; Е — латеральный вид с правой стороны; F — латеральный вид с левой стороны; С — голотип (вскрытый), вид с дорсальной стороны; D — паратип, ЗИН № 2/24512), длина 11 мм, латеральный вид с правой стороны; G — исторически значимый экземпляр, собранный Ф.Ф. Яржинским в 1871 году, паратип длиной 19 мм с дорсальной стороны, ЗИН № 3/24472); H — генитальная область и penis паратипа, ЗИН № 3/24472. I-L — *Guyvalvorina savinkini* sp. nov.: I — паратип, ЗИН № 2, длина 32 мм, вид с дорсальной стороны; J — паратип, ЗИН № 2, длина 32 мм, дорсо-латеральный вид с правой стороны; K — голотип, длина 33 мм, вид с дорсальной стороны; L — паратип, ЗИН № 3, длина 42 мм (ширина головы 10 мм), латеральный вид с правой стороны. Стрелкой указан анус.

удлиненная, впадает в основание пениса. Пениальный мешок и прилегающие части дополнительной железы покрыты толстым соединительно-тканым чехлом. Пенис крупный, конический и невооруженный.]

Etymology. *Murmania* is named after Murman coast of the Barents Sea, one of the oldest regions of study of Nudibranchia in Russia. Species epithet *antiqua* (Latin), refers to the long history of discovery and description as well as to the number of archaic features in this species.

Remarks. According to morphology of the radula and the male part of reproductive system, *Murmania antiqua* gen. et sp. nov. is a member of the family Tergipedidae. The new genus differs from the genus *Cuthona* by continuous digestive gland without external distinction of anterior and posterior regions, numerous branches of the digestive gland, which do not fully correspond to ceratal rows, high body with notal ridge-like elevations along lateral sides. Radular teeth of the *Murmania antiqua* gen. et sp. nov. have an unusual feature — lateral denticles are united in several clusters. The Antarctic genus *Guyvalvoria*, which is somewhat similar to the new genus, differs from the latter in having two bands of significantly compressed branches of the digestive gland where the particular branches are hardly or not distinguishable, and ceratal rows are placed rather longitudinally than normally transversally. Anus of the all three species of the genus *Guyvalvoria* is placed on inner side of the right “band” of the digestive gland and not enclosed by the cerata, whereas in *Murmania* gen. nov. the anus is placed between branches of the digestive gland, sometimes even at the edge of the right body side. Additionally, the radular teeth of *Guyvalvoria* do not display the peculiar clusters of the lateral denticles as in *Murmania antiqua*. The alternation of thick and thin denticles is known for different tergipedids, but only few taxa, first of all the genus *Catriona* have well developed groups of such denticles.

Murmania antiqua Martynov, sp. nov.

(Figs. 1 A-H; 3 C-F; 4 G, H; 5 A; 6 G)

Precuthona peachii (sic) Roginskaya, 1971: 73, fig. XIX-5-10, non *Eolis peachi* Alder et Hancock, 1848.

Tergipedidae gen. et sp. nov.: Martynov, 1999: 15, Martynov, 2006: 65

Material. Holotype, ZIN No. 1 (in systematic catalogue). R/V “Andrei Pervozvanny”, sta. 162, job 372, March 23 (April 5), 1900, Barents Sea, 15 miles N from Svyatoi Nos Cape, 67 m, sand, collector not recorded. Paratypes, ZIN No. 2, 3 specimens. R/V “Russanov”, sta. 34, September 14, 1931, “Kara Sea, Dixon Id., intertidal”, coll. G.P. Gorbunov¹. Paratype, ZIN No. 3/24472, 1 specimen (identified by N.M. Knipovitch as *Fiona nobilis*, No. 1). 1871, Barents Sea, Kildin Id., depth 294 m, coll. F.F. Yarzhinsky. Paratype, ZIN No. 4, 1 specimen (identified by N.I. Volodchenko as *Precuthona peachi*, No.

3). R/V “Andrei Pervozvanny”, sta. 63, job 118 (119?), July 6(18), 1899, Barents Sea, 69°38.30' N, 36°45'E, depth 180-183 m, sandy mud and small stones, collector not recorded. Paratype, ZIN No. 6, 1 specimen (identified by N.I. Volodchenko as *Precuthona peachi* No. 5). R/V “Andrei Pervozvanny”, sta. 508, job 990, June 30 (July 13), 1901, Barents Sea, 75°18'N, 33°10'E, depth 247 m, shelly mud, collector not recorded. Paratype, ZIN No. 7, 1 specimen. “S-3”, sta. 12, July 13, 1948, Barents Sea, 76°40'N, 27°10'E, depth 119 m, gray mud with stones and gravel, coll. V.L. Vagin and V.M. Koltun. Paratype, ZIN No. 8, 1 specimen (identified by N.I. Volodchenko as *Coryphella salmonacea* No. 1). R/V “Andrei Pervozvanny”, sta. 65, job 130, July 07 (19), 1899, Barents Sea, 70°58'N, 37°07'E, depth 161-170 m, sand and stones, collector not recorded. ZIN No. 9/24513, 1 specimen (dried up some time ago). R/V “Andrei Pervozvanny”, sta. 292, job 684, July 6 (August 8), 1900, Barents Sea, 72°00'N, 43°10'E, depth 292 m, mud, collector not recorded.

Description. External morphology (Figs. 1 A-G). Length of 9 preserved specimens ranging from 7 to 46 mm, width ranging from 3 to 16 mm, height — from 3 to 13 mm. Average length about 20 mm. Almost all specimens were dissected by previous workers. Body elongate-triangular, very wide anteriorly and sharpened in hind part. Head about 1.5 times narrower than widest part of foot. Upper part of head thickened and by a triangular fold interposed dorsally between rhinophores. Strong conical oral tentacles placed laterally from head fold, whereas ventrally head fold covering lateral edges of anterior foot. Slightly wrinkled rhinophores thinner and about 1.5 times shorter than oral tentacles. Dorsal papillae have fallen in all specimens, except for some smallest cerata in few rows. General number of ceratal rows about 40. Ceratal rows, especially in large specimens, placed very densely, many in double and triple rows, resulting in that superficially ceratal rows looking like uniform slightly differentiated area. Ceratal rows end on not high elevations and therefore back passing to sides via roundish notal border. Ceratal formula of right side in specimen 20 mm long: 3;4;6(2,8);10;6(4,2,5);4(10,9);

¹All specimens of *Murmania antiqua* gen. et sp. nov. were found in the SE Barents Sea, on the depth no less than 67 m. The records on the labels of ZIN No. 1 and ZIN No. 2 specimens from intertidal of Dixon Id. are very doubtful. Dixon Id. is characterized by typical Arctic intertidal zone with extremely instable salinity and uncovered black stones, under which there are ephemeral populations of amphipod *Gammarus setosus* [V. Petryashev and B. Sirenko, pers. comm.]. The record in the field journal of G.P. Gorbunov for the intertidal sta. 34 of R/V “Russanov” stated “no Mollusca”. The original label for these specimens is absent. In the cruise journal of R/V “Russanov”, judged from coordinates, this locality exactly corresponded to the sta. 38, at the depth 23 m. Summing up, it is likely that the record from intertidal of Dixon Id. in the label of *M. antiqua* is a mistake. Most likely these specimens were also collected off Murman coast of the Barents Sea.

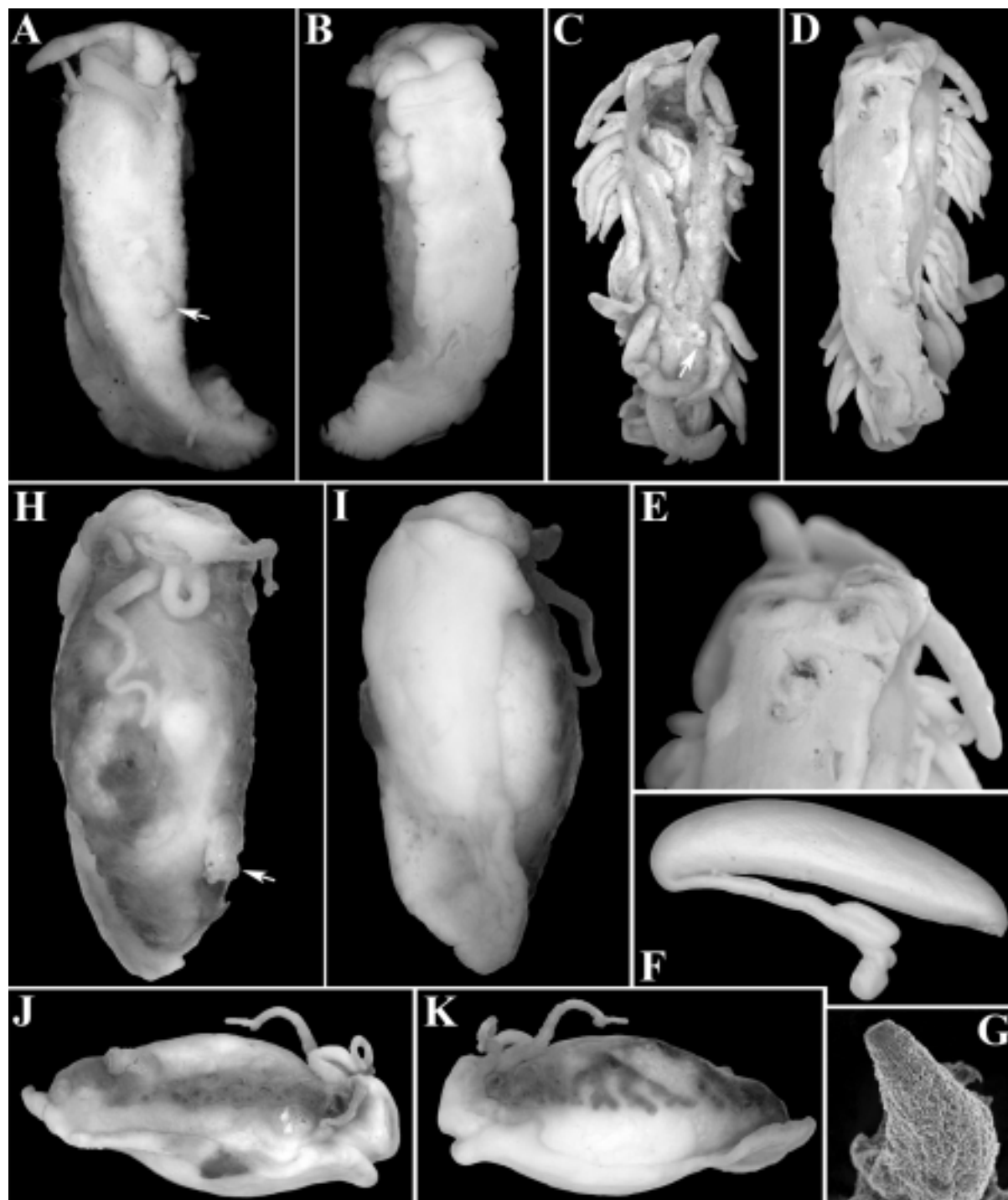


FIG. 2. A-G — *Guyvalvoria francaisi* Vayssière, 1906: A-B — ZIN No. 1, length 15 mm, A — dorsal view; B — ventral view; C-F — holotype, length 7.5 mm; C — dorsal view; D — ventral view; E — ventral view of anterior part (head width 1.5 mm); F — male supplementary gland of holotype, length 3.8 mm; G — scanning electron micrograph, ZIN No. 2. H-K — *Guyvalvoria gruzovi* sp. nov., holotype, H — dorsal view; I — ventral view; J — lateral view from the right part, normal state of digestive gland; K — lateral view from the left part, note very clear branches of digestive gland caused by swollen gonad due to fixation artifacts. Anal opening is marked by an arrow. Scale bar: G — 100 μ m.

РИС. 2. A-G — *Guyvalvoria francaisi* Vayssière, 1906: A-B — экземпляр длиной 15 мм, ЗИН № 1, А — вид с дорсальной стороны; В — вид с вентральной стороны; C-F — голотип, длина 7,5 мм; C — вид с дорсальной стороны; D — вид с вентральной стороны (ширина головы 1,5 мм); E — вид передней части тела с вентральной стороны (ширина головы 1,5 мм); F — дополнительная железа мужской части половой системы, длина 3,8 мм; G — пенис под сканирующим электронным микроскопом. H-K — *Guyvalvoria gruzovi* sp. nov., голотип: H — вид с дорсальной стороны; I — вид с вентральной стороны; J — латеральный вид с правой стороны, типичная форма пищеварительной железы; K — латеральный вид с правой стороны, раздвинутые ветви пищеварительной железы из-за вздутой при фиксации гонады. Стрелкой указан анус. Масштаб: G — 100 мкм.

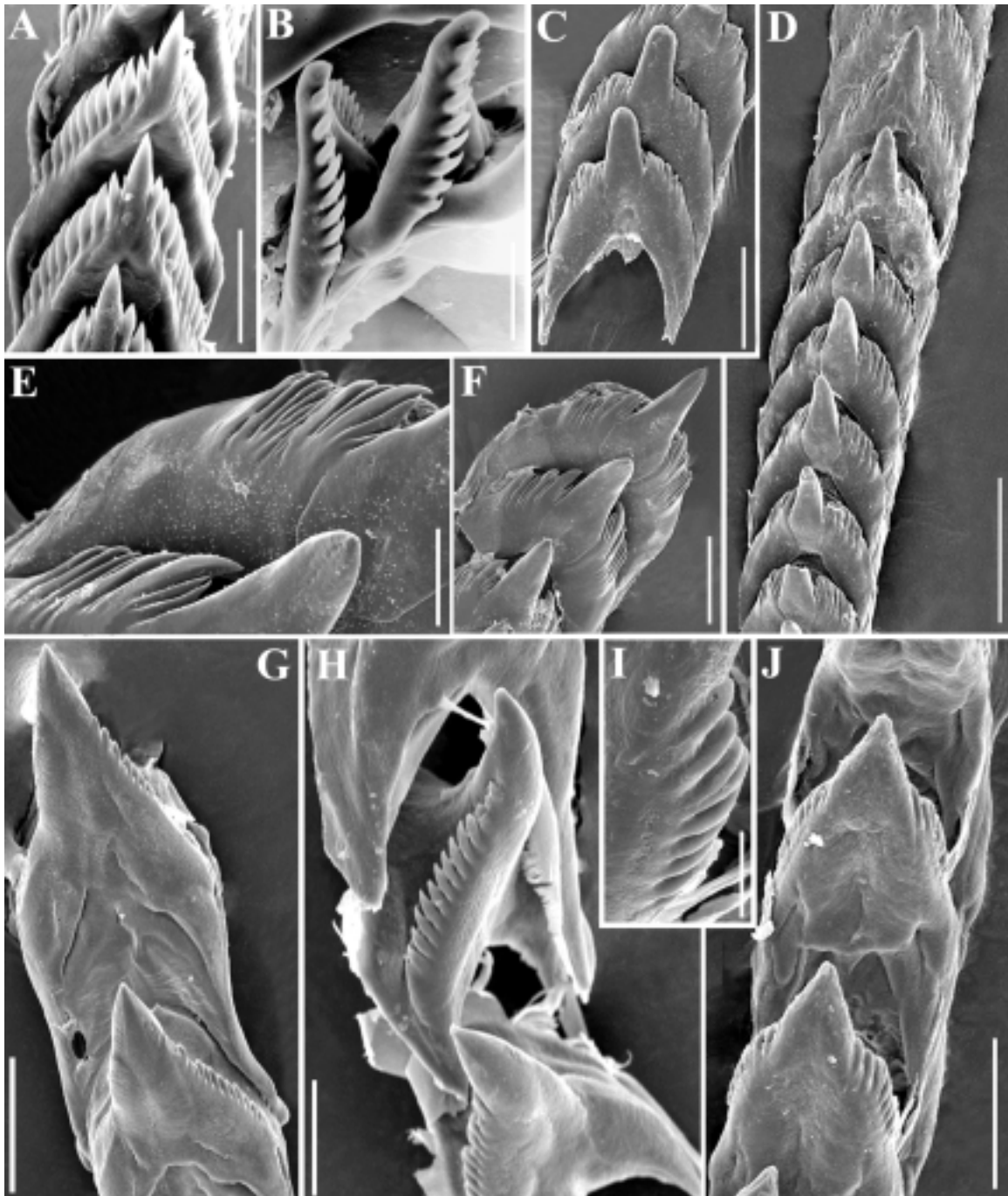


FIG. 3. Scanning electron photographs of the radula. A-B — *Guyvalvoria francaisi* Vayssière, 1906, several teeth from middle of radula. C-F — *Murmania antiqua* gen. et sp. nov., different radular teeth of paratype (ZIN No. 6), body length 46 mm; C — 15-17 teeth from anterior part of radula; D — 5-11 teeth from posterior part of radula; E — enlarged part of 1-3 teeth showing clusters of denticles; F — 1-3 teeth from posterior part of radula. G, H — *Guyvalvoria savinkini* sp. nov.: G — teeth from posterior end of radula; H — teeth from middle radula. I, J — *Guyvalvoria gruzovi* sp. nov. I — enlarged part of a tooth showing double diverged denticles; J — two teeth from middle of radula. Scale bars: A — 38 μ m, B — 38 μ m, C — 150 μ m, D — 300 μ m, E — 60 μ m, F — 150 μ m, G — 80 μ m, H — 40 μ m, I — 15 μ m, J — 60 μ m.

РИС. 3. Радулы под сканирующим электронным микроскопом. А-В — *Guyvalvoria francaisi* Vayssière, 1906, несколько зубов из середины радулы. С-Ф — *Murmania antiqua* gen. et sp. nov., зубы из различных частей радулы паратипа (ЗИН № 6) длиной 46 мм: С — 15-17 зубы из передней части радулы; D — 5-11 зубы; E — увеличенный участок 1-3 зубов из задней части радулы, демонстрирующий кластеры зубчиков; F — 1-3 зубы. G, H — *Guyvalvoria savinkini* sp. nov.: G — зубы из задней части радулы; H — несколько зубов из середины радулы. I, J — *Guyvalvoria gruzovi* sp. nov.: I — увеличенная часть зуба, демонстрирующая двойные зубчики; J — два зуба из середины радулы. Масштаб: А — 38 мкм, В — 38 мкм, С — 150 мкм, D — 300 мкм, E — 60 мкм, F — 150 мкм, G — 80 мкм, H — 40 мкм, I — 15 мкм, J — 60 мкм.

4(2(9,9),3(9,8,10));8(8,11);12(5,-7) posterior digestive gland 12;12;A;5(4,4);5(9,10);4(7,7);4(3,3);4(3,3);5;4;3;3;2. Foot wide, gradually narrowed toward tail. Anterior part of foot with slightly undulating thickened edge, anterior foot corners in form of small conical processes. Anus cleiproctic, placed in posterior part of body, near to middle of back, opened at ends of rather high papillae. Genital openings on right side of body in its first quarter.

Anatomy. Digestive system. Jaws broadly triangular. There are about 27 protruding narrow triangular denticles on masticatory edges (Figs. 4 G, H). Teeth of radula wide, arc-shaped, with strong protracted cusp (Figs. 3 C, D, F). Specimens 23 mm and 9 mm long (paratypes, ZIN No. 6 and No. 8) have 20-21 teeth. Lateral denticles in peculiar clusters, with alternating thin and thick denticles (Fig. 3 E). However, in different teeth these clusters not always clearly developed. There are about 8-14 denticles of different size in two clusters in young teeth (Fig. 3 E, F) and about 8 in old teeth (Fig. 3 C).

Reproductive system (Fig. 5A). Ampulla huge and voluminous, especially in the largest specimen (holotype), bending and slightly convoluted. Post-ampullar duct bifurcating into oviduct and a relatively short vas deferens. No clear distinction between prostatic and non-prostatic parts of vas deferens. Prostate is narrow tube, almost uniform along its length, making two irregular loops, then passed to non-prostatic part, slightly narrower and nearly straight, entering under thick connective tissue layer and at some distance inserting at top of conical penial sheath, the latter also covered by same thick layer of connective tissue, beyond walls proper. Supplementary gland very large, bending and elongate, at base united with penial sheath by thick layer of connective tissue, inserted to top of sheath together with vas deferens. Unarmed penis, a rather massive elongate cone (Fig. 1 H). Receptaculum seminis not detected due to poor condition of reproductive system.

Remarks. Volodchenko labelled this species in the Zoological Institute (St.-Petersburg) in the 1930s under three different names from two families including a new species from the genus *Precuthona*. The latter species has never been published by Volodchenko. Since she applied very different names to one species, it is completely unclear that was mentioned exactly. Roginskaya in his Ph. D. Dissertation [1971] illustrated the radula and male reproductive system of one of the present specimens of this species under the name *Precuthona peachi* Alder et Hancock, 1848 but without any explanation. *Precuthona peachi* is an undoubted synonym of *Cuthona nana* [Williams, Gosliner, 1979; Brown, 1980]. The latter taxon is very different from *Murmania antiqua* gen. et sp. nov; the distinguished characters being listed in remarks to the diagnosis of the new genus.

Guyvalvoria Vayssière, 1906

Guy-Valvoria [sic] Vayssière, 1906a: 147, 1906b: 5-6.

Type species *Guy-Valvoria francaisi* Vayssière 1906 (by original designation).

Diagnosis. Body high. Notal ridge absent. Branches of digestive gland significantly compressed in laterally and forming dorsally two continuous longitudinal narrow bands. Externally there is no distinction between anterior and posterior digestive gland. Anus cleiproctic, internal in relation to ceratal band, not surrounded by papillae. Radular teeth triangular in outline, with prominent cusp. Supplementary gland various in size, may be attached to penial sac wall. Single receptaculum seminis near beginning of vas deferens.

Remarks. According to the morphology of radula and male part of reproductive system, the genus *Guyvalvoria* undoubtedly belongs to the family Tergipedidae. There are three genera that have species with highly branched digestive gland: *Murmania* gen. nov., *Cuthonella*, and *Cuthona*. The digestive gland in *Guyvalvoria* is distinct from all these three genera and has a peculiar composition of continuous narrow laterally compressed branches. In addition, the internal, in relation to the digestive gland, position of the anus not surrounded by cerata is also a unique feature of *Guyvalvoria*. Posterior position of anus is not constant: it is near the tail in *G. gruzovi* sp. nov., more anterior in *G. francaisi* and near the middle of body in *Guyvalvoria savinkini* sp. nov.

Guyvalvoria francaisi Vayssière, 1906

(Figs. 2 A-G; 3 A, B; 4 I; 5 D)

Guy-Valvoria francaisi Vayssière, 1906a: 149; Vayssière, 1906b: 6-10, Pl. II, figs. 16-24; Vayssière, 1917: 147; Odhner, 1944: 24; Marcus, 1959: 78; *Guyvalvoria francaisi*: Powell, 1951: 167; Russell, 1971: 74; Cattaneo-Vietti, 1991: 226, 228; Valdés, Héros, 1998: 732; Martynov, 1999: 15.

Cuthonella paradoxa Eliot, 1907: 24-25, fig. 27, syn. nov.

Type material studied. Holotype, MNHN. Field label: Bc Casthage, Drague 25'', 15 Mars, 166. Other labels: *Guy-Valvoria Francaisi* A. Vayssière, No. 166 — Ile Wandel [= Renaud Id.] 15 Mars 1904. 7.5 mm long.

Material. ZIN No. 1, 2 specimens, 17 SAE, 19.02.1972, Amery Ice Shelf, sample 164, depth 35 m, rock, coll. A.M. Sheremetevsky. ZIN No. 2, 2 specimens, 17 SAE, 18.02.1972, Amery Ice Shelf, sample 161, depth 25 m, rock, small stones, coll. A.M. Sheremetevsky. ZIN No. 3, 1 specimen, 16 SAE, 24.11.1971, Davis Sea, Haswell Ids., sample 103, depth 45 m, rock, coll. E.N. Gruzov, A.M. Sheremetevsky. ZIN No. 4, 1 specimen, 16 SAE, 15.12.1971, Davis Sea, Haswell Ids., sample 114, depth 43 m, rock, coll. E.N. Gruzov, A.M. Sheremetevsky. ZIN No. 5, 1 specimen, 17 SAE, 18.02.1972, Amery Ice Shelf,

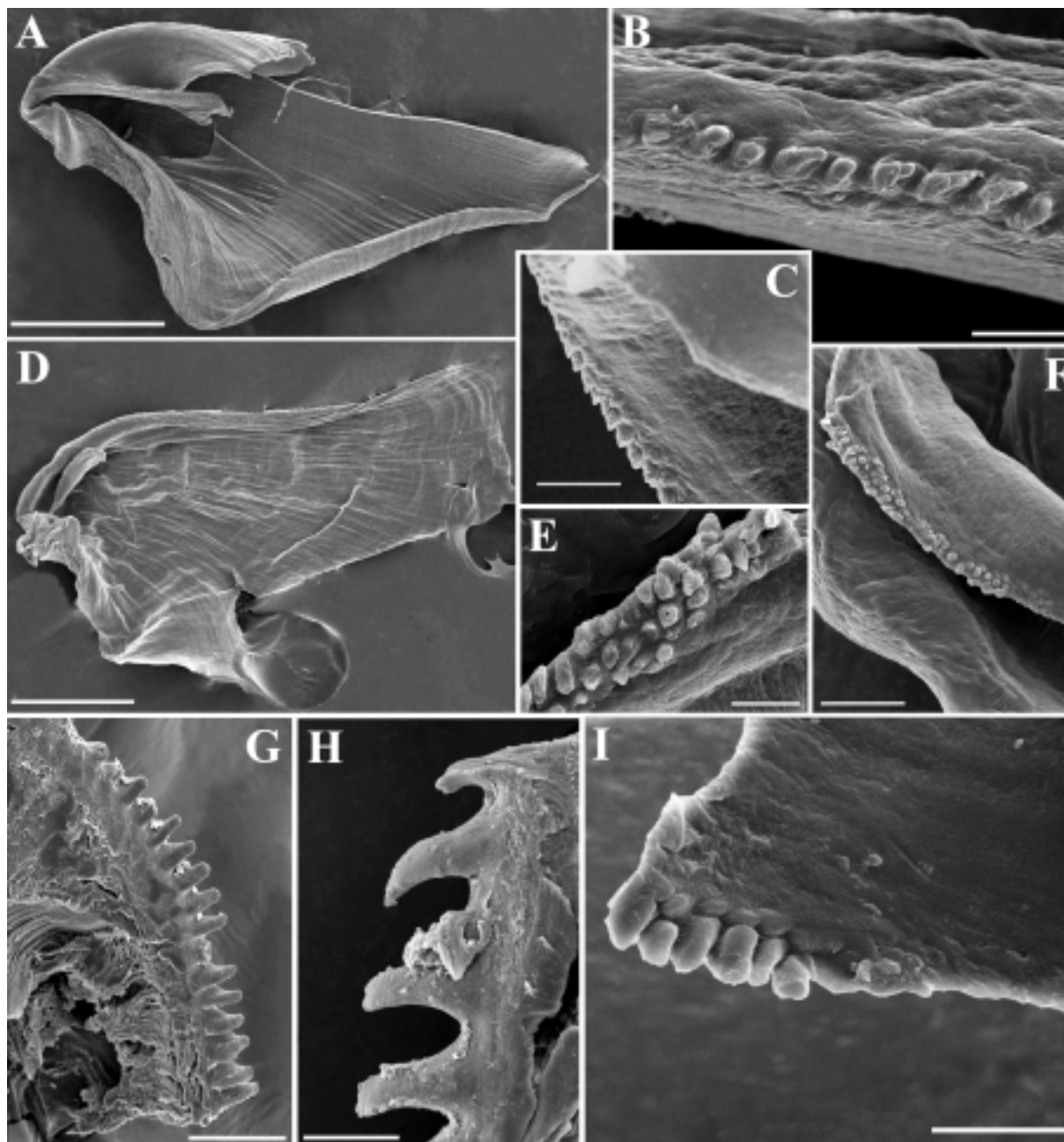


FIG. 4. Scanning electron photographs of jaws. A-C — *Guyvalvoria savinkini* sp. nov.: A — general view of left jaw from inside; B, C — details of masticatory edge. D-F — *Guyvalvoria gruzovi* sp. nov.: D — general view of left jaw from inside; E, F — details of the masticatory edge. G-H — *Murmania antiqua* gen. et sp. nov., details of masticatory edge. I — *Guyvalvoria francaisi* Vayssière, 1906, detail of masticatory edge. Scale bar: A — 800 μ m, B — 30 μ m, C — 30 μ m, D — 40 μ m, E — 12 μ m, F — 40 μ m, G — 150 μ m, H — 40 μ m, I — 20 μ m.

РИС. 4. Челюсти под сканирующим электронным микроскопом. А-С — *Guyvalvoria savinkini* sp. nov.: А — общий вид левой челюсти изнутри; В, С — детали жевательного края. D-F — *Guyvalvoria gruzovi* sp. nov.: D — общий вид левой челюсти изнутри; E, F — детали жевательного края. G-H — *Murmania antiqua* gen. et sp. nov., детали жевательного края. I — *Guyvalvoria francaisi* Vayssière, 1906, детали жевательного края. Масштаб: А — 800 мкм, В — 30 мкм, С — 30 мкм, D — 40 мкм, E — 12 мкм, F — 40 мкм, G — 150 мкм, H — 40 мкм, I — 20 мкм.

sample 162, depth 15 m, rock, coll. A.M. Sheremetevsky. ZIN No. 6, 1 specimen, 17 SAE, 18.02.1972, Amery Ice Shelf, sample not recorded, depth 45 m, rock, coll. E.N. Gruzov, A.M. Sheremetevsky (all numbers in systematic catalogue).

Description. External morphology. (Fig. 2 A, B). Length of one of the largest specimens is 14.5 mm (without enrolled tail 2 mm long), width 3.8 mm, height 4 mm. Body massive, with elongate

external appearance, only with traces of papillae attachments. Lateral sides of body high, back clear marked from sides, but without notal ridge. Head about equal to widest part of foot. Upper part of head above mouth semicircular, two conical oral tentacles inserted dorso-laterally. Posteriorly, close to foot, part of head possesses two prominent triangle elevations which pass to upper part of the head and form not deep groove. Almost smooth conical rhinophores about 2 times longer than oral tentacles. Almost all cerata fallen, excluding few small cerata at edges of back. There are about 27 fallen cerata. Papillae conical, irregularly finger-shaped. Their apex slightly lengthened and sharpened. Longest papilla 5.8 mm in length, 1.6 mm in width. Cerata round in cross-section. Traces of attachment of papillae placed along edges the back in two narrow bands, most part of back, to anus, thus being devoid of ceratal rows. Before anus there are 15-27 traces of papillae on both sides, behind anus — 9-14. Only behind anus, traces of attachment of cerata covering also middle part of back. Judging from these traces, papillae arranged in extremely short transverse rows. Each row consists of 1 to 3 papillae. Because these rows are very dense, counting exact number of rows is rather difficult. On right side to anus there are about 9 rows. Preanal digestive gland it is in oblique rows with 5-6 papillae per row; if these rows considered as significantly compressed transverse rows of “usual” tergipedids, there are 5-6 cerata behind anus on right side. “Interhepatic” space not distinct, therefore no clear demarcation between anterior and posterior digestive glands, as typical for aeolidacean nudibranchs. Anterior part of foot nearly straight, rounded at edges, without processes. Foot (including tail) is wide. Anus wide, a somewhat funnel-shape prominent tube (length 1.1 mm), placed at border between second and third parts of body, after lines of cerata right to middle of body or sometimes almost medially. Immediately before anus cerata absent, after anus there is, trace of a single papilla. Nephroproct placed before anus. Genital openings placed on right side in first third of body, caudally have weakly developed collar disappearing ventrally. Genital openings opened within massive slightly wrinkled field. Female openings slit-like.

Anatomy. Digestive system. Jaws triangularly oval, rather wide, light brown in colour. Masticatory processes with one distinct row of denticles and a single incomplete row. Denticles (24-30 in number) triangular or rounded (Fig. 4 I), sometimes bifid at top. Radula uniserial, comprised by 27-31 elongate-triangular, semitransparent yellowish teeth (Fig. 3 A, B). Central cusp rather narrow, sharpened, moderately protracted beyond 8-9 distinct lateral denticles. Before first external lateral denticles there is triangular tubercle. 9-11 teeth of radula with about 5 lateral denticles.

Reproductive system (Fig. 5 D). Gonad consisting of relatively small number of large ovotestes with separated female follicles. Ampulla rather small, irregularly kidney-shaped. Post-ampullar duct bifurcating into oviduct and a long vas deferens. Non-prostatic part of vas deferens in form of a rather long narrow tube almost uniform along entire length, initially making two irregular loops, then straightened and entering thick elongate prostate covered externally by thin layer of connective tissue. Prostate proximally directly inserted at top of rather small oval penial sheath. Supplementary gland large, completely free from walls of penial sheath, pear-shaped, with long bending narrow stalk inserted to top of sheath together with vas deferens. Penis rather massive, in form of short cone. Apically there are no any petal-shaped structures as described by Vayssi re [Vayssi re 1906b: Pl. II]. Absence of these structures was revealed by both light and scanning electron microscope studies (Fig. 2 G). Connective tissue covering vas deferens, prostate, penial sheath and supplementary gland is colourless. Receptaculum seminis not detected macroscopically in preserved material. It will be subject of further histological studies.

Remarks. The studied specimens well agree to the original description as well as to the type material of *G. francaisi* (compare Figs. 2 A, B and 2 C-E) in the general body shape and the presence of distinct thick prostate gland opened to the penial sac without muscular part of vas deferens. The prostate of the type specimen is preserved in a separate glass tube and is similar in shape to that in other material (see Fig. 2 F). In addition, the morphology of radular teeth as described in the original description corresponds well to that in studied here specimens.

In *Cuthonella paradoxa* Eliot, 1907 from the Ross Sea, according to the original description [Eliot, 1907], “The anal papilla is dorsal, set far back (7 mm from anterior end) and slightly to the median line”, which together with the pattern of ceratal arrangement described by Eliot, also suggests that this species belongs to *Guyvalvoria*. Type material of the *C. paradoxa* is not traceable [A. MacLellan (BMNH), personal communication]. Nevertheless, at least three important characters unite *C. paradoxa* with *G. francaisi*: (1) absence of anterior foot processes (Eliot specially highlighted this character: “the foot is round in front, thickened at the margin and slightly expanded, but not grooved and not produced into tentaculiform angles”); (2) a single row of denticles on masticatory processes of the jaws (instead several rows in, for instance, *G. gruzovi* sp. nov.); and (3) radular teeth with narrow cusp and distinct lateral denticles. Even if the cusp might have been figured semi-schematically, Eliot noted the distinct nature of lateral denticles. Also, the head of *G. paradoxa* has a shape of the hood and a ventral mouth same as in *G. francaisi*, whereas *G. gruzovi*

sp. nov. has distinct ventral projections and frontal mouth in both specimens studied. Thus, available from the original description characters of *G. paradoxo* suggest that it is a synonym of *G. francaisi*. Reddish brown colour of digestive gland reported for *C. paradoxa* is not known for *G. francaisi* but is characteristics for *G. gruzovi* sp. nov. Because colour in alive condition is still unknown for *G. francaisi* the above-listed morphological differences are enough for distinguishing from *G. gruzovi* sp. nov. *Guyvalvoria francaisi* is the most advanced species within the genus in the reproductive system and external features.

Guyvalvoria gruzovi sp. nov.

(Figs. 2 H-K; 3 I-J; 4 E-F; 5 C; 6 I)

Guyvalvoria paradoxa: Martynov, 1999: 15, non Eliot, 1907

Material. Holotype, ZIN No. 1 in systematic catalogue, 17 SAE, 18.02.1972, Amery Ice Shelf, sample 161, depth 25 m, rock, small stones, coll. E.N. Gruzov, A.M. Sheremetevsky. Paratype, 1 specimen, ZIN No. 2 in systematic catalogue, type locality.

Description. External morphology (Fig. 2 H-K). Length of holotype 8.2 mm, width 3.2 mm, height 3 mm. Length of single paratype 9.3 mm, width 3.5 mm, height 3 mm. Body shape similar to that of *G. francaisi* but more massive and less high, narrowed in anterior part and widened in middle part. Head slightly narrower than foot. Upper lateral part of head bearing a pair of thin oral tentacles narrowed to top. In place of transition of semicircular dorsal part of head into ventral part there are two triangular knobs, which are prolongation of a pair of thickened ridges in ventral part of head. There is a wide groove between these ridges and anterior part of foot. Rhinophores slightly wrinkled and very long, 2.5-3 times longer than oral tentacles. Rhinophores very convoluted, narrowed to their tops. Cerata of the holotype fallen almost completely, in paratype on each side saved ca.10 papillae. Cerata arranged in oblique, short, branched transverse rows with 2-3 (large and small) papillae per row. Papillae irregularly finger-shaped, sharpened at end. Longest papillae reaching 2.6 mm. Diverticulum of digestive gland in papillae occupying most part of papillae. General pattern of digestive gland similar to that of *G. francaisi*. There is a broad band on back devoid of branches of digestive gland. Through semitransparent dorsal epithelium in middle back area is seen dark stem of posterior digestive gland in form of irregular spot and dark branches under papillae. Second branch of left digestive gland best seen. It consists of short stem, dark-brown in colour, with two lateral double branches. First branch containing one simple and one double branches, second branch — only simple but longer branches, which possess

1-2 small branches without cerata. In other parts of back, digestive gland translucent as entire dark mass under traces of papillae. Along above described branches there are 2-3 papillae, and one papillae in place of branching. On right side before anus there are about 21 traces of papillae. If ceratal rows considered very oblique, then numbers of papillae per row reach 4. Behind anus from right side papillae are poorly developed — 1-2. On left side before anus there are about 24 traces of papillae in anterior digestive gland and about 9 postanal cerata. Approximate ceratal formula for the left side of body is ((1,3,3,2,3), (1,2,3,5)) A, 2,3,2,2,2). "Interhepatic" space detectable only on left side of body due to exaggeration of gonad on left side after fixation and corresponding shift of digestive gland, where border between anterior and posterior digestive gland clearly marked. Nevertheless, there is no interruption in ceratal arrangement since oblique last branch of anterior digestive gland is in close contact with posterior digestive gland. Anterior part of foot semicircular and thickened with short foot corners. Foot broad; hind part slightly produced as short flat tail. Genital opening in first third of the body. Back well delineated from sides but without notal edge. General colour of fixed specimens yellowish-pink, rhinophores, oral tentacles, lateral parts of foot, integuments around digestive gland partially pinkish. Digestive gland dark-brown.

Anatomy. Digestive gland. Jaws oval-triangular, wide, light brown, masticatory area with pinkish shadow. Masticatory processes broadly triangular, with at least two complete rows of denticles and several irregular and incomplete rows (Fig. 4 E, F). Denticles different in shape: obtuse, sharpened, almost cylindrical, or bifid. Proximally denticles decreased in size and transformed into folded tubercles. Masticatory edge has about 35 denticles. Radular teeth with wide base and strong central cusp protruded beyond small lateral denticles, conical or drop-shaped, 11-15 on each side (Fig. 3 I, J). In transition of tooth base into cusp there is a well developed triangular denticle. Radular teeth amber in colour.

Reproductive system (Fig. 5 C). Gonad consisting of relatively numerous ovotestes with not separated female follicles. Ampulla rather small, consisting of two whorls and aberrant in having scalloped appearance. Post-ampullar duct bifurcating into oviduct and a long vas deferens. There is no distinct prostate. Vas deferens in form of a narrow tube almost uniform along entire length, initially making one loop, then slightly narrowed and attached to wall of penial sheath and making 2 loops, afterward straightened and inserted at top of sheath. Supplementary gland large, attached for its half to penial sheath bent around side of penial sheath and inserted to top of sheath together with vas deferens. Proximal wider

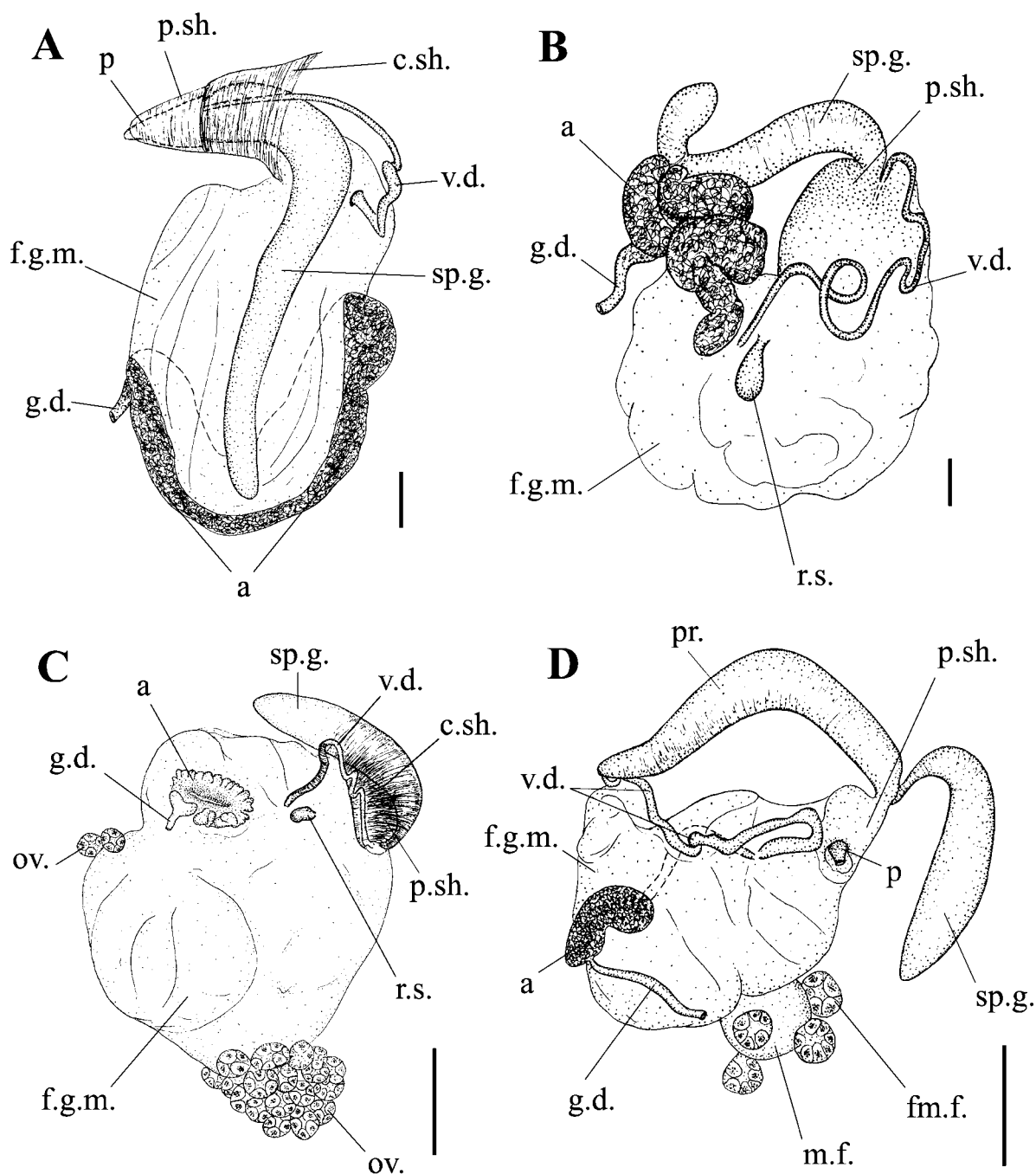


FIG. 5. Reproductive system. A — *Murmania antiqua* gen. et sp. nov. (paratype, ZIN No. 2); B — *Guyvalvoria savinkini* sp. nov. (paratype, ZIN No. 4); C — *Guyvalvoria gruzovi* sp. nov. (paratype, ZIN No. 2); D — *Guyvalvoria francaisi* Vayssièrè, 1906. Scale bars: 1mm.

Abbreviations: a — ampulla; c.sh. — connective tissue sheath; f.g.m. — female gland mass; fm.f. — female follicles; g.d. — germaphroditic duct; m.f. — male follicles; ov. — ovotestis; p — penis; pr — prostate; p.sh. — penial sheath; r.s. — receptaculum seminis; sp.g. — supplementary gland; v.d. — vas deferens.

РИС. 5. Половая система. А — *Murmania antiqua* gen. et sp. nov. (паратип, ЗИН № 2); В — *Guyvalvoria savinkini* sp. nov. (паратип, ЗИН № 4); С — *Guyvalvoria gruzovi* sp. nov. (паратип, ЗИН № 2); D — *Guyvalvoria francaisi* Vayssièrè, 1906 (особь ЗИН № 2). Масштаб: 1 мм.

half of supplementary gland is free. Female gland mass voluminous. Receptaculum seminis small, inconspicuous, oval in shape, without a stalk, entering female gland mass near beginning of vas deferens. There is reddish pigment in gonads, on vas deferens,

in connective tissue covering penial sheath, on supplementary gland.

[Диагноз. Тело массивное, умеренно высокое, закраина отсутствует. Ринофоры очень длинные, длиннее оральных щупалец в 2,5-3 раза. По обеим сторонам

вентральной части головы расположены два удлинённых треугольных выступа. На спине имеется широкая полоса, лишённая ветвей пищеварительной железы. Папиллы неправильно-пальцевидные, на конце приострённые, располагаются скошенными, сжатыми, очень короткими, поперечными рядами по 2-4 папиллы, маленькая и большая в каждом ряду. С правой стороны до ануса можно различить около 21 отверстия от папилл. После ануса, с правой стороны тела, следы от папилл очень плохо заметны — не более 1-2. Предположительная формула пищеварительной железы для левой стороны: ((1,3,3,2,3), (1,2,3,5)) A, 2,3,2,2,2). Межпеченочное пространство хорошо заметно только с левой стороны. Передняя часть ноги полукруглая, ее углы оттянуты в короткие отростки. Подошва широкая, сзади незначительно выступает в виде неширокого листовидного хвостика. Генитальное отверстие располагается в первой трети тела. Общая окраска фиксированного экземпляра желтовато-розовая, отдельные участки ринофоров, оральных щупалец, бортика ноги более розоватые, розоватый оттенок можно различить в покровах вокруг ветвей пищеварительной железы. Пищеварительная железа темно-коричневая, хорошо видна сквозь покровы. Много красноватого пигмента в комплексе женских желез и гонаде. Челюсти овально-треугольные, широкие. Жевательный отросток челюстей широко-треугольный, несёт по меньшей мере два полных ряда зубчиков и еще несколько неправильных и неполных. Всего по наружному краю около 70 зубчиков. Зубы радулы с подкововидным основанием и мощным центральным зубцом, который значительно выдается за пределы мелких латеральных зубчиков, числом 11-15 с каждой стороны. Семяпровод без четкого разделения на простатическую и мускульную части. Дополнительная железа впадает в пениальный мешок и прикреплена на две трети своей длины к его стенке посредством тонкого соединительно-тканного чехла.]

Etymology. This species is named in honour of Eugeny Gruzov (St. Petersburg) for his achievements in studying of Antarctic region.

Remarks. The pattern of digestive gland and the position of anus undoubtedly evidence belonging of this taxon to the genus *Guyvalvoria*. The new species can be distinguished from *G. francaisi* by a number of characters: a wider and more massive body, peculiarities of the digestive gland, shape of the head, presence of well developed anterior foot corners, shape of the radular teeth, and absence of the massive prostatic part in the vas deferens. *Guyvalvoria savinkini* sp. nov. clearly differs primarily by large length and pattern of the digestive gland with numerous branches and anus lie more close to the middle of the body rather than to the tail. Head of *Guyvalvoria savinkini* sp. nov. have not fully fused postoral lobes whereas *Guyvalvoria gruzovi* sp. nov. has postoral lobes completely fused with the head.

Guyvalvoria savinkini sp. nov.

(Figs. 1 I-L; 3 G, H; 4 A-C; 5 B; 6 F)

Material. Holotype, ZIN No. 1 in systematic catalogue, R/V "Scythian", 13.03.1971, sta. 1248/337, trawl 231, off

Kerguelen Id., depth 80-90 m, from the stomach of fish *Notothenia rossi* Richardson, 1844. Paratypes, ZIN Nos. 2-6 in systematic catalogue, 5 specimens, type locality.

Description. External morphology (Fig. 1 I-L). Length from 23 to 40 mm, width from 8 to 11 mm, height from 4.5 to 8 mm. Holotype 33 mm long, 6 mm wide and 5 mm high. Body large, massive, rather depressed. Lateral sides of body high, back clearly delimited from sides but notal ridge absent. Head narrower than foot. Upper part of head above mouth is semi-circular. Two long, convoluted, very thin toward to their tops, conical oral tentacles inserted dorso-laterally. At border of anterior part of foot and lower part of head, there are two prominent postoral lobes, partially fused with head. Between postoral lobes and anterior part of foot there is a deep groove. Conical convoluted rhinophores 1.5-2 times larger than oral tentacles. Cerata extremely long, irregularly conical, convoluted, decreasing in size toward body edge. Their apex is slightly attenuated and sharpened. Longest papillae about 12 mm in length. Papillae round in section. Pattern of digestive gland is two narrow bands placed closely to back edges. Most part of back devoid of ceratal rows. The pattern of ceratal rows appeared as short compressed to each other obliquely rows, which is branched terminally. However, rows sometimes are very irregular and not clear are these transverse or longitudinal rows. Largest paratype with length 42 mm has approximately 50 such ceratal "rows". Middle part of back fully devoid of papillae. Judging from traces, papillae arranged in extremely short transverse rows. Each "row" may consist of up to 6 papillae in back anterior part to 1-2 on tail. Since these rows are very dense, counting exact number of rows is impossible. On right side to anus there are about 15 rows. These rows appear as strongly compressed transverse rows of "usual" tergipedids, at least in preanal rows it is oblique rows with number papillae per row 3-6. Toward tail number of papillae per row diminishing to 1-2. Interhepatic space not distinct, therefore no clear distinction between anterior and posterior parts of digestive gland, as typical of Aeolidacea. Anterior part of foot with short corners. Foot wide, as well as tail. Anus, a rather wide tube, placed in mid-body; before and left from anus there is free space devoid of papillae, at a short distance after anus there are two papillae. Nephroproct situated before anus. Genital openings on right side in first third of body, anteriorly with a slightly developed collar.

Anatomy. Digestive gland. Jaws large, triangular, light brown (Fig. 4 A). Masticatory processes narrow, triangular, with 1-2 rows of denticles (Fig. 4 B, C). Denticles different in shape: sharpened, obtuse, and irregularly flattened. Masticatory edge with about 70 denticles. Radular teeth with wide base and a strong central cusp protracted beyond small lateral denticles, conical or drop-shaped, about

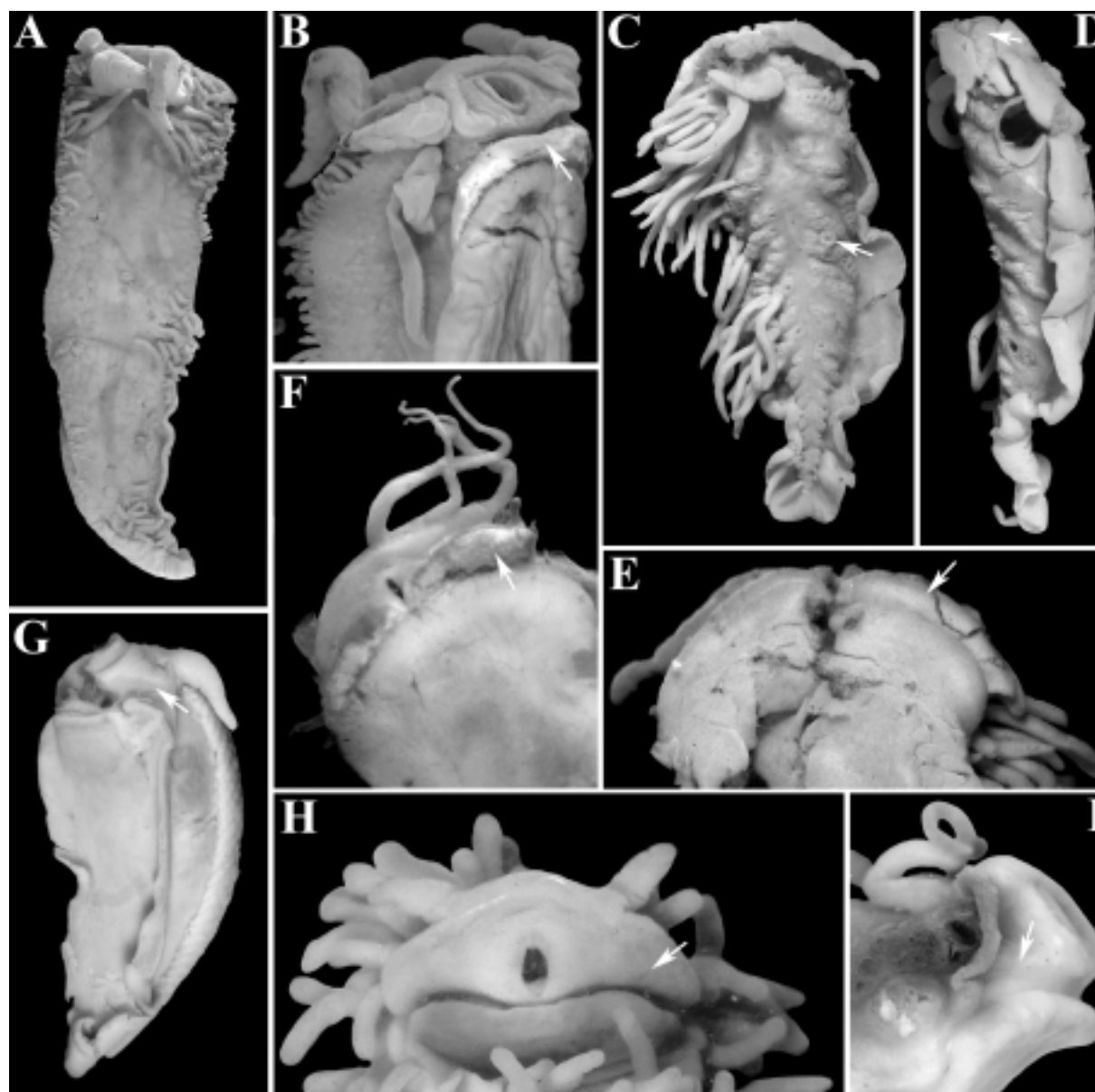


FIG. 6. A-B — *Chlamylla atypica* (Bergh, 1899), specimen ZIN No. 7 in systematic catalogue, 33 mm long, Okhotsk Sea, between Paramushir and Atlasova Id., depth 126 m. A — dorsal view, B — ventro-lateral view (from right side) of the anterior part of body (head width 5.1 mm). C-E — *Cuthona* sp. (an undescribed species), ZIN No. 1, length 19 mm (head width 6.5 mm), Laptev Sea, depth 12 m. C — dorsal view showing branching pattern of digestive gland and ceratal rows; D — lateral view from the right side; E — ventral view of the body anterior part. F — *Guyvalvorina savinkini* sp.nov., head of paratype 42 mm long (head width 10 mm). G — *Murmania antiqua* gen. et sp. nov., paratype, ZIN No. 2/24512, length 19 mm, latero-ventral view from the left side. H — head of *Cuthona* cf. *nana* (Alder et Hancock, 1842), Bering Sea, depth 150 m, mud, animal length about 9 mm, head width 4 mm. I — *Guyvalvorina gruzovi* sp. nov., holotype, right lateral view of the body anterior part. In parts B, F, G, H, I the arrows mark the postoral lobes or their derivatives. In part C the arrow indicates the anal opening.

РИС. 6. А-В — *Chlamylla atypica* (Bergh, 1899), ЗИН № 7, экземпляр длиной 33 мм, Охотское море, между о. Парамушир и о. Атласова, глубина 126 м. А — вид с дорсальной стороны; В — латеро-вентральный вид с правой стороны (ширина головы 5,1 мм). С-Е — *Cuthona* sp. (неописанный вид), ЗИН № 1, длина 19 мм (ширина головы 6,5 мм), море Лаптевых, глубина 12 м; С — вид с дорсальной стороны, демонстрирующий расположение ветвей печени и рядов папилл; D — латеральный вид с правой стороны; E — передняя часть тела с вентральной стороны. F — *Guyvalvorina savinkini* sp.nov. голова паратипа длиной 42 мм (ширина головы 10 мм); G — *Murmania antiqua* gen. et sp. nov., паратип, ЗИН № 2/24512, длина 19 мм, латеро-вентральный вид с левой стороны. H — голова *Cuthona* cf. *nana* (Alder et Hancock, 1842) с вентральной стороны, Берингово море, глубина 150 м, ил, трал Сигеби, длина особи около 9 мм, ширина головы 4 мм. I — *Guyvalvorina gruzovi* sp. nov., голотип, латеральный вид передней части тела справа. Стрелками указаны: В, F, G, H, I — посторальные лопасти или их производные, С — анус.

10-14 on each side (Fig. 3 G, H). Reproductive system (Fig. 5 B). Gonad consisting of relatively numerous ovotestes with not separated female follicles. Ampulla large, voluminous, convoluted. Post-ampullar duct bifurcating into oviduct and a long vas deferens. No distinct prostate. Vas deferens in form of a narrow tube almost uniform along entire length, making 2-3 loops, then attached to wall of penial sheath and shortly inserted at top of large wide penial sheath. Supplementary gland large, attached for its one third to penial sheath, bent around side of penial sheath and inserted to top of sheath together with vas deferens. Proximal part of supplementary gland free. Female gland mass voluminous. Receptaculum seminis not large, oval, on small stalk, entering female gland mass near beginning of vas deferens. There is reddish pigment on gonads, on vas deferens, in connective tissue covered penial sheath, and on supplementary gland.

[**Диагноз.** Тело крупное, массивное и невысокое, закраина отсутствует. Ринофоры длинные, близки по размерам оральным щупальцам. По обеим сторонам вентральной части головы две широких лопасти, объединяющих её с передней частью ноги. На спине имеется широкая полоса, лишенная ветвей пищеварительной железы. Папиллы могут достигать очень больших размеров, удлинённо-конические, располагаются скошенными, сжатыми, очень короткими, поперечными рядами по 3-6 папилл. С правой стороны до ануса можно различить около 40 отверстий от папилл. Межпеченочное пространство не выражено. Анус располагается близ середины тела. Передняя часть ноги полукруглая, ее углы оттянуты в короткие отростки. Подошва широкая, сзади выступает в виде длинного листовидного хвостика. Генитальное отверстие располагается в первой трети тела. Общая окраска фиксированного экземпляра желтовато-розовая, пищеварительная железа, включая её выросты в папиллах, с красноватым оттенком. Челюсти мощные, треугольные. Жевательный отросток челюстей узко-треугольный, несёт 1-2 полных ряда заостренных или уплощенных зубчиков. По наружному краю имеется около 70 зубчиков. Зубы радулы с подкововидным основанием и мощным центральным зубцом, который значительно выдается за пределы мелких латеральных зубчиков, в числе около 10-14 с каждой стороны. Семяпровод без четкого разделения на простатическую и мускульную части. Дополнительная железа впадает в широкий пениальный мешок и прикреплена к его стенке лишь у основания.]

Etymology. The species is named in honour of Oleg Savinkin (Moscow) for his important contribution to photographing and collecting of number of marine animals during numerous SCUBA diversings.

Remarks. This is the largest species of the genus *Guyvalvoria*. Despite that this new species is quite dissimilar to the type species of the genus, it can be assigned to *Guyvalvoria* by the following characters: the digestive gland in form of two narrow bands; middle part of the back substantially free from cerata; branches of digestive gland are strongly compressed, so transverse rows are very hard to distin-

guish; anterior and posterior parts of digestive gland pass to each other externally continuously, without distinct interhepatic space, and anus is not enclosed by papillae. Also the body is high and have traces of reduced notal ridge. From other two known species of the genus *Guyvalvoria*, *G. savinkini* sp. nov. is distinguished by large body size, numerous branches of digestive gland in more "rows", position of anus near middle of body instead the posterior part, broad buccal bulb, shape of the radula teeth, very massive supplementary gland in the male reproductive part. In the reproductive system morphology and presence of several rows of the jaws denticles the new species is most similar to *Guyvalvoria gruzovi* sp. nov. The new species is the most basal in the genus *Guyvalvoria*.

Discussion

There are two morphological peculiarities of the newly described taxa worthy to discuss in relation to other aeolidacean families. They are the pattern of digestive gland and the postoral lobes. In various opisthobranchs, the postoral lobes are a rather common structure, but they are usually defined as a transverse subdivision of propodium, and named, for instance, labium [Wägele, Willan, 2000]. However, this structure is markedly distinct from the anterior part of foot and is placed in-between of the ventral part of head and the foot (Fig. 6 B, arrow). According to its shape, the postoral lobes of Flabellinidae and Facelinidae (see an example of a flabellinid, *Chlamylla atypica* (Bergh, 1899) (Fig. 6 B) are very similar to the ventral part of head of some species of *Guyvalvoria*. The following case is of a special interest. Ventral part of the head of *Guyvalvoria savinkini* is essentially the same in shape as the postoral lobes and occupies a similar position between the anterior part of foot and the head (Fig. 6 F, compare with Fig. 6 B). Postoral lobes of *G. gruzovi* (Fig. 6 I) and *G. francaisi* (Fig. 2 B) are already completely fused with the head. There is a similar relation between *Cuthona* sp. (an undescribed species from the Laptev Sea) and *Cuthona* cf. *nana* from the Bering Sea. The former species has the lobes still connected with the anterior part of the foot (Fig. 6 D, E) whereas in the latter the lobes are completely fused with the head (Fig. 6 H). All other tergipedids never demonstrate free postoral lobes and have a wide semicircular head. These peculiarities of the new taxa allow to suggest a new interpretation of the head composition in the family Tergipedidae. Besides the typical narrow head, characteristic of most aeolidacean nudibranchs, the tergipedid head was formed by fusing ventrally of the anterior part of foot with postoral lobes. Thus, the "complex head" of Tergipedidae can be considered as a unique apomorphy for the family. Due to wide

occurrence of postoral lobes in different unrelated opisthobranchs, it is likely a plesiomorphic feature and not apomorphic as currently recognized [Wägele, Willan, 2000; Valdés, 2002]. While fusion of the postoral lobes with the head is restricted to the Tergipedidae, the reduction of the postoral lobes and further fusion with the anterior part of the foot is most common trend within different groups of nudibranchs.

For the basal Antarctic arminacean nudibranchs, a continuous, irregular and multi-branched pattern of the digestive gland is known [Wägele, 1991]. A similar pattern of the digestive gland is characteristic of the basal flabellinid genus *Chlamylla* Bergh, 1886 (Fig. 6 A). The morphology of digestive gland in *Murmania* (Fig. 1A, C) and *Guyvalvoria* (Figs. 1 J, L; 2 J) is quite similar to the above mentioned condition and dissimilar to other tergipedids (for instance the genus *Cuthona* that also has a ramified digestive gland (Fig. 6 C, D)). The digestive gland of *Guyvalvoria* is more modified than that in *Murmania*, and the digestive gland is narrowed toward body sides. It is possible to recognize two general trends of a transformation of the digestive gland within the family Tergipedidae. The first, more common, is a differentiation of the digestive gland into separate branches, exactly corresponding to the ceratal rows (Fig. 6 C, D — *Cuthona* sp.). Posterior digestive gland in this case is not reduced and anus lies relatively close to the middle of the body. It occurs in tergipedid genera *Cuthona*, *Cuthonella*, *Trinchesia* and other. The second trend in tergipedid is known exclusively for the genus *Guyvalvoria* — it is a modification of the digestive gland into two narrow bands of rather irregularly ramified comp-

ressed branches, whereas the ceratal rows do not exactly correspond to the branches of the digestive gland. The posterior digestive gland has a tendency to reduction — in two species of the genus *Guyvalvoria* the anus is correspondingly shifted to the posterior end of the body. A somewhat similar pattern is known also for arminacean genus *Janolus* [Miller, Willan, 1986]. Position of the genus *Murmania* in respect to both above described patterns of the digestive gland is rather basal. Moreover, a single specimen of the *Murmania antiqua* (ZIN No. 2) from the Kara Sea has an abnormal placement of anus within notal edge, i.e. laterally and not dorsally (Fig. 1 E). This is similar to the pleuroproctic condition, basal for all aeolidaceans.

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Архаичные Tergipedidae Арктики и Антарктики: *Murmania antiqua* gen. et sp. nov. и ревизия рода *Guyvalvoria* Vayssière с описанием двух новых видов

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РЕЗЮМЕ. Ревизован антарктический род *Guyvalvoria* Vayssière, 1906. На основе изучения новых материалов и типового экземпляра переописан типовой вид рода *Guyvalvoria francaisi* Vayssière, 1906. Кроме того, приведены описания двух новых видов рода *Guyvalvoria*, *G. gruzovi* sp. nov. и *G. savinkini* sp. nov. из моря Дейвиса и вод субантарктического острова Кергелен. Из вод Мурманского берега Баренцева моря (глубины 60-300 м) описан новый род и вид *Murmania antiqua* gen. et sp. nov. Данный таксон характеризуется широким телом, многочисленными разветвленными рядами пищеварительной железы, а также умеренно развитой закраиной с закругленным краем. Радужные зубы *Murmania antiqua* характеризуются необычной кластеризацией зубчиков. Предполагается, что *Murmania* gen. nov. является одним из наиболее архаичных таксонов семейства Tergipedidae. Антарктический род *Guyvalvoria* и субарктический род *Murmania* обнаруживают определенное сходство в габитусе, наличии многочисленных ветвей пищеварительной железы, а также в тенденции к каудальному смещению ануса. Морфологические особенности новых таксонов позволяют предложить новую трактовку состава головы в семействе Tergipedidae: помимо "обычной" головы, характерной для большинства эолидаей, в её формирования принимают участие посторальные лопасти, обычно связанные с передним краем ноги. Данное предположение иллюстрируется рядом примеров из семейства тергипедид и других семейств эолидаей. Обсуждаются трансформации пищеварительной железы в семействе тергипедид с использованием данных по вновь описанным таксонам.