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Article

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Description of the first cryptobranch onchidoridid *Onchimira cavifera* gen. et sp. nov., and of three new species of the genera *Adalaria* Bergh, 1879 and *Onchidoris* Blainville, 1816 (Nudibranchia: Onchidorididdae) from Kamchatka waters

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Abstract

The opisthobranch fauna of the SE Kamchatka peninsula (NW Pacific, Russia) has been intensively investigated for the first time resulting in 21 species found, and six new records for Kamchatka. A unique onchidoridid species with a well defined, closeable gill pocket into which gills can be fully retracted, and which does not fit with any existing genus is described as *Onchimira cavifera* **gen. et sp. nov.** in anatomical detail. *Onchimira cavifera* is remarkable in that it combines characteristic features of cryptobranch dorids with those of phanerobranch onchidoridids. Its role as a missing link and new evidence for evolutionary reduction of the gill cavity within phanerobranch dorid lineages is discussed. In addition, two new species of the genus *Adalaria*, *A. slavi* **sp. nov.** and *A. olgae* **sp. nov.**, are described based on numerous newly collected specimens showing little intraspecific variations, but clear differences to all previously described *Adalaria* species. A review of the presently known *Adalaria* species including SEM data of the radula and labial cuticle is presented in order to highlight differences among the newly discovered taxa. A new species of the nudibranch genus *Onchidoris*, *O. macropompa* **sp. nov.**, is described. A comparative table of all presently known *Onchidoris* species is presented.

Key words: Opisthobranchia, Doridacea, taxonomy, phylogeny, gill cavity (=gill pocket) evolution, North Pacific

Introduction

The North Western Pacific, including Kamchatka and Kurile Islands waters, is a vast, predominantly cold area, and one of the most biologically productive zones of the world ocean. Records of nudibranch gastropods were scarce and fragmentary. Pallas (1788) published the description of the first Russian nudibranch, *Tritonia tetraquetra* from North Kurile Ids. Further records of nudibranchs from this region can be found only in Volodchenko (1941) and in occasional collections in the framework of large-scale Soviet hydrobiological expeditions that targeted for an ecosystem study rather than taxonomical diversity. Routine opisthobranch investigations in the Russian Far-East started rather recently (e.g. Martynov 1992; 1994a, b; 1997; 1999b; Martynov & Baranets 2002; Martynov 2003; Millen & Martynov 2005; Martynov & Schrödl 2008). The first illustrated catalogue of the marine and brackish water gastropods of Russia includes a review of all Russian nudibranchs that were then known (Martynov 2006). Only ten species of Nudibranchia were recorded for Kamchatka waters. Taking into account the diverse underwater landscapes and ecosystems of that huge area this number is obviously underestimated.

In July and August of 2008 the opisthobranch fauna of the SE Kamchatka (Fig. 1) was specially investigated for the first time, from the intertidal to a depth of 26 m. Twenty one nudibranch species were discovered, including six new ones for the Kamchatka fauna: *Berthella californica* (Dall, 1900), *Acanthodoris pilosa* (Abildgaard in Müller, 1789), *Adalaria jannae* Millen, 1987, *Colga minichevi* Martynov & Baranets, 2002, *Dirona pellucida* Volodchenko, 1941 and *Cuthonella soboli* Martynov, 1992.

Besides these new records, the most important data for both nudibranch taxonomy and phylogeny were obtained at the depths 18–26 m in waters around Starichkov Island. Twenty one specimens of an unknown onchidoridid species possessing a well-defined gill pocket were discovered. Further investigation of these specimens has revealed the capability of their gill to retract completely into the gill cavity and the edges of the gill pocket can fully contract over the retracted gill, i.e. showing identical conditions as was regarded to be characteristic for cryptobranch dorids (e.g. Wägele & Willan 2000; Valdés 2002a). At the same time, the specimens show characteristic features of “phanerobranch” dorids in the family Onchidorididae, i.e. an onchidorid buccal pump and radular pattern. Previously, only one onchidoridid taxon was known to possess a gill pocket — *Calycidoris guentheri* Abraham, 1876 from Arctic seas (Abraham 1876; Roginskaya 1972). In the Pacific, the range of this species is restricted to the northern Bering Sea (Martynov 2006). The gill pocket of the genus *Calycidoris* Abraham, 1876, usually considered as a specialized feature within the family Onchidorididae, differs from true cryptobranch gill pockets due to its incapability to retract gills into the cavity and contract the edges of the pocket over the gill (Abraham 1876, 1877; Millen 1985; Fahey & Valdés

2005). The gill pocket of the newly found species is essentially similar to the true cryptobranch gill pocket, and the radula and reproductive system of the Kamchatka specimens differs considerably from the genus *Calycidoris*. Herein, external and anatomical features of onchidoridid genera are compared (Table 1), and a new genus is established to accommodate the new species.

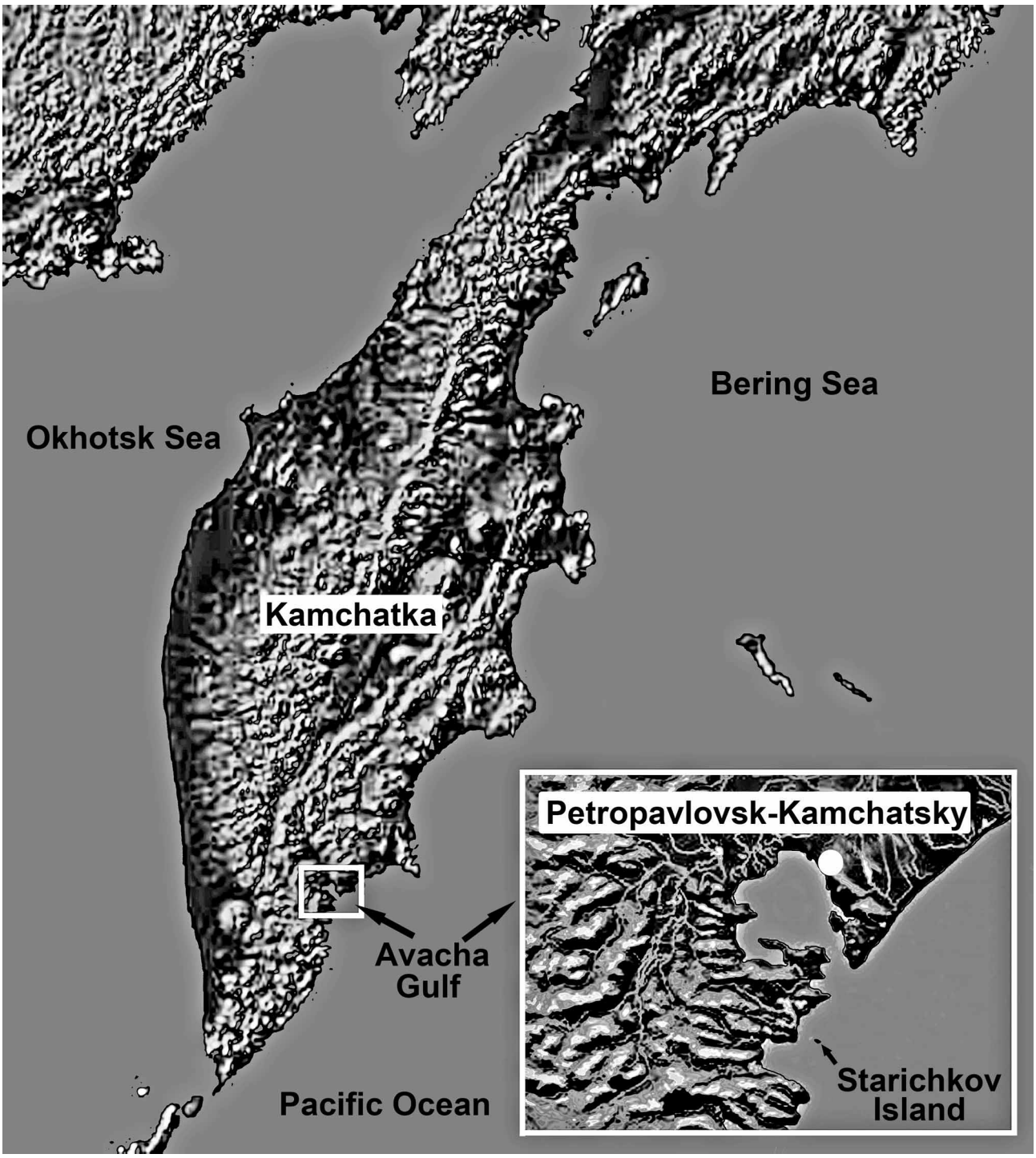

FIGURE 1. Map of the NW Pacific showing Kamchatka peninsula and collecting site.

Three further undescribed onchidoridid species were found in Kamchatka. One belongs to the genus *Onchidoris* Blainville, 1816, two others to *Adalaria* Bergh, 1879. Both genera are comprised of small phanerobranchs feeding on encrusting bryozoans. Until recently, North Pacific species of the genus *Adalaria* were considered as well known (Millen 1987; 2006), with four species recorded, including three from Russian

TABLE 1. Comparison of the genera of the family Onchidorididae possessing dorsal gills

	***Onchimira* gen.nov.**	*Calycidoris* Abraham, 1876	*Acanthodoris* Gray, 1850	*Adalaria* Bergh, 1879	*Loy* Martynov, 1994	*Onchidoris* Blainville, 1816
Notum consistency	Soft	Hard	Soft	Hard or soft	Soft	Hard or soft
Notum	Almost smooth or with low tubercles	Numerous spiniform tubercles	Numerous spiniform tubercles (smooth in a single species)	Well defined wide spiculose tubercles	Smooth	Wide spiculose tubercles in most species
Rhinophoral sheaths	Raised, smooth, even edges	No definite borders, except for several adjacent tubercles	With raised crenulated edges	No definite borders, except for several adjacent tubercles	Without definite borders and tubercles	No definite borders, except for adjacent tubercles
Oral veil shape	Subtrapezoid, wide	Two narrow elevations	Semicircular, wide, with two distinct lower lobes	Semicircular, wide, entire in most species	Two narrow separate triangular lobes	Semicircular, wide, entire
Gill shape and arrangement	Unipinnate, in complete circle	Unipinnate, in complete circle	Tripinnate, in a semi-circle	Uni- to tripinnate, semicircle or almost complete circle	Unipinnate, placed at single point	Unipinnate, in a semicircle
Gill cavity (pocket)	Present, fully contractable	Present, similar to cryptobranch type but apparently incapable of full contraction	Absent	Absent	Present, of a special type	Absent
Gill retractibility	Fully retractable	Capable of partial retraction into gill cavity	Contractile	Contractile	? Contractile	Contractile
Buccal pump	Sessile	Sessile	Sessile	Sessile or on short broad stalk	Sessile, low elevation of the anterior part of pharynx	Long stalked
Radular formula	7–9.1.1.1.9–7	3.1.0.1.3	2–7.1.0.1.7–2	3–13.1.1–0.1.13–3	7.1.1.0.1.1.7	2–0.1.0–1.1.0–2
Labial cuticle	Distinct rods	Distinct rods	Distinct short irregularly denticulated rods	Indistinct polygonal elements	Smooth	Indistinct polygonal elements
Stomach caecum	Absent	Present	Absent	Absent	Absent	Absent
Evertable part of vas deferens	Wide permanent penis with smaller inner evertable part	Long narrow, forming penis while everted	Long narrow, forming penis while everted	Long narrow, forming penis while everted	Wide short flattened permanent penis	Long narrow, forming penis while everted
Oviduct pattern	Proximal oviduct enters female gland mass	Proximal oviduct enters female gland mass	Proximal oviduct enters female gland mass	Proximal oviduct connects to allosperm receptacles or vagina	Proximal oviduct connects to allosperm receptacles	Proximal oviduct connects to allosperm receptacles or vagina
Seminal receptacle pattern	Swollen area at terminal vagina; sessile	Long stalked; vaginal arrangement	Long stalked; vaginal arrangement	Short stalk at terminal part of the vagina	Swollen part of proximal oviduct	Long duct from terminal part of the vagina
Vagina	Short	Very long	Very long	Moderately long to short	Short	Short
Source	Present study	Abraham, 1876; Roginskaya, 1972; Martynov, 2006; Present study	Alder & Hancock, 1845-1855; MacFarland, 1925, 1926; Thompson & Brown, 1984; Fahey & Valdés, 2005; Present study	Alder & Hancock, 1845-1855; Bergh, 1879, 1880; Thompson & Brown, 1984; Millen, 1987, 2006; Martynov et al., 2006; Present study	Martynov, 1994a	Alder & Hancock, 1845-1855; Schmekel & Portmann, 1982; Thompson & Brown, 1984; Millen, 1985; Martynov et al., 2006; Present study

TABLE 2. Comparison of the species of the genus *Adalaria*

	Colour	Maximum length, mm	Notal tubercles shape	Notum consistency	Rhinophore lamellae number	Gill numbers and pattern	Postbranchial gland	Oral veil shape	Labial cuticle	Buccal pump shape	Distribution	Source
A. proxima (Alder & Hancock, 1854) (=*A. pacifica* Bergh, 1880; *A. albopapillosa* Dall, 1871; *A. virescens* Bergh, 1880)	White to yellow-orange	25	Relatively wide and short spear-shaped (Atlantic form); more elongated and narrow (Pacific)	Hard	Up to 19	12, unipinnate, in a semicircle	Absent	Wide, semicircular	Indistinct irregularly polygonal elements	Medium sized, sessile	Amphiboreal species: in the North Atlantic from North Great Britain to Barents and White Seas and from Massachusetts to Greenland; in the North Pacific from Alaska to British Columbia	Alder & Hancock, 1845-1855; Bergh, 1880; Thompson & Brown, 1984; Millen, 1987; Martynov et al., 2006; Present study (Fig. 8B, C)
A. loveni (Alder & Hancock, 1862)	White, sometimes pale yellow	32	Very wide and globose, short	Soft	Up to 25	12, unipinnate, in a semicircle	Absent	Wide, semicircular	Indistinct irregularly polygonal elements	Large, sessile	Great Britain (Western Scotland) to Middle Norway	Thompson & Brown, 1984; Millen, 1987, pers. comm.
A. tschuktschica Krause, 1885 (= *A. septentrionalis* Roginskaya, 1971)	Unknown	12	Long, narrow, somewhat bent, short protruding spicules	Hard	Ca. 20	10, tri- and unipinnate incomplete circle	Absent	Wide, semicircular	Indistinct elements	Medium sized, sessile	Arctic Ocean from Laptev to Chukchi Sea and in Northern Bering Sea in NW Pacific	Krause, 1885; Roginskaya, 1971; Present study
A. jannae Millen, 1987	Translucent whitish to orange. Rhinophores and gills darker	15	Short, moderately narrow, rounded or club-shaped	Hard, spiculose	7–15	9–17, unipinnate in a semicircle	Large, prominent, globose to oval tubercle	Wide, semicircular	Distinct irregularly polygonal elements	Medium sized, on a short stalk	North Pacific from Japan Sea to SE Kamchatka and from Alaska to California	Millen, 1987; Fahey & Valdés, 2005; Martynov, 2006; Present study (Fig. 8A)

continued next page.

TABLE 2. (continued)

	Colour	Maximum length, mm	Notal tubercles shape	Notum consistency	Rhinophore lamellae number	Gill numbers and pattern	Postbranchial gland	Oral veil shape	Labial cuticle	Buccal pump shape	Distribution	Source
A. evincta Millen, 2006	White, rarely yellowish. Rhinophores and gills white or yellow	16	Globose tubercles with strongly protruding spicules on long narrow stalks	Hard, spiculose	11–17	6–13, unipinnate, incomplete circle	Small, flattened granulated area	Wide, semicircular, notched laterally	Smooth	Medium sized, on a short stalk	NE Pacific: British Columbia	Millen, 2006
***A. slavi* sp. nov.**	White with densely scattered tiny opaque white dots. Rhinophores and gills same colour	23	Globose tubercles on a short stalk, spicules not protruding	Soft, but integument contains a spicules network	11–14	6–8, bi- and tripinnate, incomplete circle	Absent	Trilobed with postero-lateral tentacles below	Indistinct irregularly polygonal elements	Medium sized, sessile	NW Pacific: SE Kamchatka, possibly all Kurile and Commander Islands	Present study
***A. olgae* sp. nov.**	Intense lemon yellow, invariable. Rhinophores similar in colour. Gills semi-transparent white	13.5	Globose or narrower on a short stalk, spicules not protruding	Soft, but integument contains a spicule network	6–9	9–12, unipinnate, incomplete circle	Absent	Semicircular appearance but two flattened lobes are well marked	Distinct irregularly polygonal elements	Medium sized, well delineated from pharynx on a short stalk	NW Pacific: SE Kamchatka, possibly all Kurile and Commander Islands	Present study

TABLE 2. (continued)

	Radula formula	First lateral teeth cusp shape	First lateral teeth denticles pattern and number	First lateral teeth basal knob and flange patterns	Outer lateral teeth shape	Prostate	Penis	Origin of combined oocyte and allosperm transporting duct ("distal oviduct")	Seminal receptacle shape and pattern	Vagina shape and length	Source
A. proxima (Alder & Hancock, 1854)	39–50 x 13–9. 1.1.1.9–13	Straight	Absent in adults and denticulate in juveniles	No knob, short projecting flange	Rectangular, several firsts outer innermost laterals with fork-shaped denticles	Long, narrow, tubular	Long, evertable, smooth ejaculatory duct without terminal processes	At vaginal duct	Relatively large, distinct from bursa, embedded into female gland mass	Almost straight, long, expanded end	Alder & Hancock, 1845-1855; Bergh, 1880; Thompson & Brown, 1984; Millen, 1987; Present study (Figs. 11G, L)
A. loveni (Alder & Hancock, 1862)	42–46 x 12–13.1.1.1.13–12	Straight	Absent	No knob, short projecting flange	Rectangular, several innermost laterals are narrow	Long, narrow, tubular	Long, evertable, smooth ejaculatory duct	At vaginal duct	Relatively large, distinct from bursa, embedded into female gland mass	Straight and very short, expanded end	Millen, 1987
A. tschuktschica Krause, 1885	30–32 x 6–8.1.1.1.8–6	Beak-shaped, curved	5–10 small denticles	No knob, indistinct flange	Elongate-oval	Long, narrow, tubular	Long, evertable (smooth?) ejaculatory duct	Unknown	Unknown	Short	Krause, 1885; Roginskaya, 1971; Present study (Figs. 11I, M)
A. jannae Millen, 1987	28–39 x 4–6.1.0.1.6–4	Beak-shaped, curved	13–21 relatively large denticles	Small knob, long narrow flange	Oval, often with fork-shaped dentilces	Short, moderately wide, tubular	Short, evertable, smooth ejaculatory duct	At vaginal duct	Relatively large, distinct from bursa, embedded into female gland mass	Bending to form a tight loop, moderate in length	Millen, 1987; Valdés & Fahey, 2005; Present study (Figs. 11J, K)

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TABLE 2. (continued)

	Radula formula	First lateral teeth cusp shape	First lateral teeth denticles pattern and number	First lateral teeth basal knob and flange patterns	Outer lateral teeth shape	Prostate	Penis	Origin of combined oocyte and allosperm transporting duct ("distal oviduct")	Seminal receptacle shape and pattern	Vagina shape and length	Source
A. evincta Millen, 2006	34–39 x 3–6.1.1.1.6–3	Beak-shaped, curved	1–12 small denticles	No knob, elongate flange	Two innermost laterals are squarish, outerones are elongate with pointed posterior end	Long, narrow, tubular	Long, evertable, smooth ejaculatory duct	At vaginal duct	Relatively large, distinct from bursa, embedded into female gland mass	Almost straight, long	Millen, 2006
***A. slavi* sp. nov.**	27–32 x 6–9.1.1.1.9–6	Beak-shaped, curved	10–15 small denticles, all similar in size	No knob, short narrow flange	Elongate with pointed posterior end	two distinct parts: long narrow, tubular and short swollen	Long, evertable, smooth ejaculatory duct	At vaginal duct	Relatively large, distinct from bursa, embedded into female gland mass	Bending to form a tight loop, long	Present study
***A. olgae* sp. nov.**	30–31 x 3–4.1.1.1.4–3	Beak-shaped, curved	4–8 denticles, first 1–3 denticles are larger than rest	Prominent basal knob, wide flange	Oval and rectangular, somewhat hook-shaped, pointed posteriorly	long, distinctly swollen	Long, evertable ejaculatory duct with two short terminal knobs	At junction of bursa base and vagina	Small knob-shaped, integrated within bursa base	Almost straight and very short	Present study

TABLE 3. Comparison of the species of the genus *Onchidoris*

	Colour	Maximum length, mm	Notal tubercles shape	Notum consistency	Rhinophore lamellae number	Rhinophoral sheaths edges	Gill numbers and pattern	Post-branchial gland	Oral veil shape	Labial cuticle	Buccal pump shape	Distribution	Source
O. bilamellata (L., 1767)	Light brown or yellowish grounds with numerous dark brown spots	40	Relatively narrow and long, with blunt tips	Soft	Up to 16	Low, indistinct, adjoin by few tubercles	Up to 29, unipinnate, in a semi-circle, posteriorly spirally coiled	Absent	Wide, semi-circular	Indistinct rod-shaped elements	Disk-shaped, laterally strongly compressed, on a long stalk	Amphiboreal species; North Atlantic from French coast to Barents and White Seas, and from New England to Greenland; North Pacific from Japan Sea to Bering Sea and from Alaska to California	Crampton, 1977; Thompson & Brown, 1984; Behrens, 1991; Fahey & Valdés, 2005; Martynov et al., 2006; Personal observations of AM & TK
O. muricata (Müller, 1776)	White to yellow	15	Wide and relatively short, mushroom-shaped; spicules slightly protruding through the top while tubercles contracted	Hard, spiculose	Up to 20	Low, indistinct, adjoin by few tubercles	Up to 18, unipinnate, in a semi-circle	Slightly distinct flattened area	Wide, semi-circular	Indistinct irregularly polygonal elements	Medium sized, sessile	Amphiboreal species; North Atlantic from French coast to Barents and White Seas, and from New Scotia to Greenland; North Pacific from Japan Sea to Bering Sea and from Alaska to California	Alder & Hancock, 1845–1855; Bergh, 1880; Thompson & Brown, 1984; Millen, 1985; Behrens, 1991; Martynov et al., 2006; Present study

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TABLE 3. (continued)

	Colour	Maximum length, mm	Notal tubercles shape	Notum consistency	Rhinophore lamellae number	Rhinophoral sheaths edges	Gill numbers and pattern	Post-branchial gland	Oral veil shape	Labial cuticle	Buccal pump shape	Distribution	Source
O. neapoliatana (Delle Chiaje, 1841)	Yellowish or pale brown notum is covered with dense and intensive reddish or purple brown; at the notal edge pigment became linear	8	Long, narrow, soft tubercles	Soft	6–8	Low, indistinct, adjoin by few tubercles	Up to 12	Absent	Wide, semi-circular	Indistinct polygonal elements	Unknown	Northern Mediterranean and Gibraltar	Schmekel & Portmann, 1982; Ortea & Ballesteros, 1982
O. depressa (Alder & Hancock, 1842)	Pale brown or whitish translucent notum with scattered orange or purple-brown speckles	9	Long, narrow, soft tubercles	Hard, spiculose	8–10	Low, indistinct, almost smooth or adjoin by a circle of tubercles	Up to 12, unipinnate, in a semi-circle	Absent	Wide, semi-circular	Indistinct polygonal elements	Unknown	Great Britain (West coast and North Sea) to Western Andalusia (Spain)	Alder & Hancock, 1845–1855; Thompson & Brown, 1984; Just & Edmunds, 1985
O. oblonga (Alder & Hancock, 1845)	Grayish or pale brown notum with scattered brown irregular spots	8	Short, rounded spiculose tubercles	Hard, spiculose	Up to 9	Low, indistinct, almost smooth	Up to 10, unipinnate, in a semi-circle	Absent	Wide, semi-circular	Indistinct polygonal elements	Unknown	Great Britain to Southern Norway	Alder & Hancock, 1845–1855; Thompson & Brown, 1984
O. pusilla (Alder & Hancock, 1845)	Notum is densely covered with small dark-brown to blackish spots	9	Tiny, hardly conspicuous rounded spiculose tubercles	Hard, spiculose	6	Low, indistinct, almost smooth	Up to 9, unipinnate, in a semi-circle	Absent	Wide, semi-circular	Unknown	Unknown	Great Britain to Southern Norway and Sweden in the North and to Gibraltar in the South	Alder & Hancock, 1845–1855; Ortea, 1979a; Thompson & Brown, 1984

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TABLE 3. (continued)

	Colour	Maxi-mum length, mm	Notal tubercles shape	Notum consis-tency	Rhino-phore lamellae number	Rhino-phoral sheaths edges	Gill numbers and pattern	Post-branchial gland	Oral veil shape	Labial cuticle	Buccal pump shape	Distribution	Source
O. sparsa (Alder & Hancock, 1846)	Pale brown notum with scattered purple-brown spots; these spots can form notum ground colour	8	Very short, rounded to conical spiculose tubercles	Hard, spiculose	9	Low, indistinct, adjoin by few tubercles	Up to 9, uni-pinnate, in a semi-circle	Absent	Wide, semi-circular	Indistinct polygonal elements	Unknown	Great Britain to Skagerrak and to Catalonia (Mediterranean)	Alder & Hancock, 1845–1855; Ortea, 1979b; Ballesteros, 1984; Thompson & Brown, 1984
O. inconspicua (Alder & Hancock, 1851)	White to pale brown (with purple tinge) notum	12	Very short, rounded or conical	? Hard, spiculose	7–8	Low, indistinct, adjoin by few tubercles	Up to 10, uni-pinnate, in a semi-circle	Absent	Wide, semi-circular	Unknown	Unknown	Great Britain (predominantly West coast) to Galicia (Spain) and Mediterranean	Alder & Hancock, 1845–1855; Ortea & Ballesteros, 1982; Thompson & Brown, 1984
O. bouvieri (Vayssière, 1919)	Light orange notum is covered with brown, reddish brown, bright orange spots, sometimes arranged in indistinct lines	9	Long pointed spiculose tubercles	Hard, spiculose	8–10	Low, indistinct, adjoin by few tubercles	Up to 10, uni-pinnate, in a semi-circle	Absent	Wide, semi-circular	"Hair-like rods"	Unknown	Northern Mediterranean	Schmekel & Portmann, 1982
O. albo-nigra (Pruvot-Fol, 1951)	White notum is covered with large violet-black spots	7	Long pointed spiculose tubercles	Soft	7–10	Low, indistinct, adjoin by few tubercles	Up to 7, in an almost closed narrow semi-circle	Absent	Wide, semi-circular	Indistinct polygonal elements	Unknown	Northern Mediterranean	Pruvot-Fol, 1951; Schmekel & Portmann, 1982; Ortea & Ballesteros, 1982

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TABLE 3. (continued)

	Colour	Maximum length, mm	Notal tubercles shape	Notum consistency	Rhinophore lamellae number	Rhinophoral sheaths edges	Gill numbers and pattern	Post-branchial gland	Oral veil shape	Labial cuticle	Buccal pump shape	Distribution	Source
O. maugeansis (Burn, 1958)	Semitransparent notum covers with orange-yellow dots	8	Long pointed apparently soft tubercles	Hard, spiculose	4	Low, indistinct, smooth	?Up to 12, uni-pinnate, in an almost closed semi-circle	Absent	Wide, semi-circular	Unknown	Unknown	Southern Australia (Torquay, Victoria)	Burn, 1958; Coleman, 2001
O. reticulata Ortea, 1979	Whitish notum is covered with numerous brownish-greenish spots in a characteristic reticulate pattern; in between of rhinophores and gills there are two broad whitish bands devoid of the pigment	9	Short, rounded to conical spiculose tubercles	Hard, spiculose	9	Low, indistinct, adjoin by few tubercles	9–10, uni-pinnate, incomplete circle	Absent	Wide, semi-circular	?Smooth	Medium sized, wide, on a short stalk	Northern Spain (Galicia)	Ortea, 1979a; Ortea et al., 1982
O. cervinoi Ortea & Urgorri, 1979	Intesively orange notum; notal edges sometimes whitish	12	Short, conical or spear-shaped tubercles	Hard, spiculose	14	Low, indistinct, adjoin by few tubercles	9–10, uni-pinnate, incomplete circle	Absent	Wide, semi-circular	? Indistinct polygonal elements	Disk-shaped, laterally strongly compressed, on a long stalk	Northern Spain (Bay of Biscay and Galicia)	Ortea & Urgorri, 1979

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TABLE 3. (continued)

	Colour	Maximum length, mm	Notal tubercles shape	Notum consistency	Rhinophore lamellae number	Rhinophoral sheaths edges	Gill numbers and pattern	Post-branchial gland	Oral veil shape	Labial cuticle	Buccal pump shape	Distribution	Source
O .tridactila Ortea & Ballesteros, 1982	Whitish notum is covered with orange or dark reddish spots; sometimes in between of the rhinophores and gills there are up to six irregular lines form by this pigment	9	Long, narrow	Hard (?), spiculose	15	High, distinct, adjoin by few tubercles	9–12, in incomplete circle, posteriorly sligthly spirally coiled	Absent	Wide, semi-circular	Unknown	Unknown	Northern Spain (Bay of Biscay)	Ortea & Ballesteros, 1982
***O. macropompa* sp. nov.**	Off-white, semitransparent notum	15	Club- or mushroom-shaped tubercles on short stalk. Larger tubercles dominate all over notum, but single irregular zigzag row of smaller tubercles appears in mid-notal line	Hard, spiculose	7–13	Low, indistinct, adjoin by few tubercles	9–10, up to 12, uni-pinnate, incomplete circle	Slightly distinct flattened area	Wide, semi-circular	Indistinct polygonal elements	Very broad, on a narrow stalk	Northern Pacific: SE Kamchatka to Commander Ids (Russia)	Present study; Martynov, 1997

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TABLE 3. (continued)

	Radula formula	First lateral teeth cusp shape	First lateral teeth base shape	First lateral teeth denticles, pattern and number	Outer lateral teeth shape	Prostate	Penis	Origin of combined oocyte and allosperm transporting duct ("distal oviduct")	Seminal receptacle shape and pattern	Vagina pattern and length	Source
O. bilamellata (L., 1767)	23–30 x 1.1.1.1.1	Beak-shaped, very long, curved	Narrow, triangular without flange fold	Absent	Rectangular with rounded edges and posterior ventral single denticle	Long, narrow, tubular	Long, evertable, smooth ejaculatory duct without terminal knobs	At vaginal duct	Relatively large, stalked, at the bursa base	Sligthly convoluted, moderately long	Thompson & Brown, 1984; Fahey & Valdés, 2005; Personal observations of AM
O. muricata (Müller, 1776)	20–36 x 1.1.1.1.1 (Thompson & Brown, 1984, have reported two outer laterals in large specimens)	Beak-shaped, short, curved	Broad and high, rectangular, without flange fold	8–18 small denticles	Rectangular with rounded edges and posterior ventral single denticle	Long, narrow, tubular	Long, evertable, smooth ejaculatory duct with one long process and two short terminal knobs	At vaginal duct	Relatively large, distinct from bursa, embedded into female gland mass	Almost straight, short, expanded end	Alder & Hancock, 1845–1855; Bergh, 1880; Thompson & Brown, 1984, Millen, 1985; Present study
O. neapoliatana (Delle Chiaje, 1841)	24 x 1.1.0.1.1	Very short, slightly raised and curved	Broad and low, rectangular strongly folded flange	4–6 distinct denticles	Rectangular with rounded edges and anteriror single denticle	Long, narrow, tubular	? Long, evertable, smooth ejaculatory duct without terminal knobs	At vaginal duct	Relatively large, distinct from bursa	Almost straight, moderately long	Schmekel & Portmann, 1982
O. depressa (Alder & Hancock, 1842)	33–34 x 1.1.0.1.1	Very short, adpressed	Broad and low, rectangular, without median fold	4–5 distinct denticles	Rectangular with rounded edges and posterior ventral single denticle	Unknown	Unknown	Unknown	Unknown	Unknown	Alder & Hancock, 1845–1855; Ortea & Ballesteros, 1982; Thompson & Brown, 1984

continued next page.

TABLE 3. (continued)

	Radula formula	First lateral teeth cusp shape	First lateral teeth base shape	First lateral teeth denticles, pattern and number	Outer lateral teeth shape	Prostate	Penis	Origin of combined oocyte and allosperm transporting duct ("distal oviduct")	Seminal receptacle shape and pattern	Vagina pattern and length	Source
O. oblonga (Alder & Hancock, 1845)	28 x 1.1.0.1.1	Beak-shaped, moderately long, slightly curved	Broad and high, triangular, without median fold	Ca. 20 small denticles	Rectangular with rounded edges and posterior ventral single denticle	Unknown	Unknown	Unknown	Unknown	Unknown	Alder & Hancock, 1845–1855; Thompson & Brown, 1984
O. pusilla (Alder & Hancock, 1845)	21–29 x 1.1.0.1.1	Beak-shaped, moderately long, considerably curved	Broad and high, triangular, without median fold	12 distinct denticles	Narrow elongate plate pointed anteriorly	Unknown	Unknown	Unknown	Unknown	Unknown	Alder & Hancock, 1845–1855; Thompson & Brown, 1984
O. sparsa (Alder & Hancock, 1846)	32–36 x 1.1.0.1.1	Very short, slightly raised, almost straight	Broad and low, rectangular, without median fold	Ca. 10 distinct denticles	Elongate rectangular plate with posterior ventral inconspicuous denticle	Unknown	Unknown	Unknown	Unknown	Unknown	Alder & Hancock, 1845-1855; Thompson & Brown, 1984
O. inconspicua (Alder & Hancock, 1851)	29 x 1.1.0.1.1	Short, raised, straight	Broad and low, rectangular, without median fold	12 small denticles	Elongate rectangular plate with posterior ventral inconspicuous denticle	Unknown	Unknown	Unknown	Unknown	Unknown	Alder & Hancock, 1845–1855; Ortea & Ballesteros, 1982; Thompson & Brown, 1984
O. bouvieri (Vayssière, 1919)	40 x 1.1.0.1.1	Moderately long, raised, narrow	? Narrow, square, with weak median fold	Ca. 6–7 small denticles	Elongate rectangular plate with anterior denticle	Unknown	Unknown	Unknown	Unknown	Unknown	Schmekel & Portmann, 1982

continued next page.

TABLE 3. (continued)

	Radula formula	First lateral teeth cusp shape	First lateral teeth base shape	First lateral teeth denticles, pattern and number	Outer lateral teeth shape	Prostate	Penis	Origin of combined oocyte and allosperm transporting duct ("distal oviduct")	Seminal receptacle shape and pattern	Vagina pattern and length	Source
O. albo-nigra (Pruvot-Fol, 1951)	30 x 1.1.0.1.1	Beak-shaped, moderately long, slightly curved	Broad and high, triangular, without median fold	Ca. 8 small denticles	Rectangular with rounded edges and anteriror single denticle	Unknown	Unknown	Unknown	Unknown	Unknown	Schmekel & Portmann, 1982
O. maugeansis (Burn, 1958)	22 rows	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Burn, 1958
O. reticulata Ortea, 1979	51–54 x 1.1.0.1.1	Short, slightly raised and curved	Broad and low, rectangular, with weak median fold	8–10 distinct denticles	Narrow elongate plate pointed anteriorly	Two short narrow tubular loops	Short, evertable ejaculatory duct	? At vaginal duct	Relatively large, elongate, free from female gland mass (?)	Long and narrow	Ortea et al., 1982
O. cervinoi Ortea & Urgorri, 1979	? x 1.0.1	Short, slightly raised and curved	Broad and low, rectangular, without median fold	Ca. 12 small denticles	Absent	Two short narrow tubular loops	Moderately long, evertable, smooth ejaculatory duct	? At vaginal duct	Relatively large, elongate, flow-through	Almost straight, moderately long and narrow	Ortea & Urgorri, 1979
O.tridactila Ortea & Ballesteros, 1982	12 x 1.1.0.1.1	Short, slightly raised and considerably curved	Broad and low, rectangular strongly folded medially	3–4 distinct denticles, all similar in size	Rectangular with rounded edges and posterior ventral single denticle	Unknown	Unknown	Unknown	Unknown	Unknown	Ortea & Ballesteros, 1982
***O. macropompa* sp. nov.**	35–38 x 1.1.1.1.1	Moderately long, raised, straight	Broad and high, rectangular, without median fold	Absent	Rectangular with rounded edges and posterior ventral single denticle	Long, narrow, tubular	Long, evertable, smooth ejaculatory duct with one very long process and two short terminal knobs	At vaginal duct	Relatively large, distinct from bursa, embedded into female gland mass	Almost straight, short, expanded end	Present study

waters (Martynov 1998; 2006). The finding of two new sympatric species is therefore remarkable. The newly discovered species are well distinguished by their external and internal characters from each other and all known *Adalaria* species (Table 2). Both new species were found in considerable numbers and show little intraspecific variation. In addition, to show the differences of the newly described *Onchidoris* species, a comparative table of all presently known species of this genus is presented (Table 3).

The new onchidoridid genus and species, two new *Adalaria* species and a new *Onchidoris* are described in the present paper.

Material and methods

The following abbreviations are used throughout the text and figures: SEM—scanning electron microscope, ZIN—Zoological Institute RAS, St. Petersburg**;** ZMMU—Zoological Museum Moscow State University; a—ampulla; an—anus; ao—external atrial opening; at—common atrium; bc—bursa copulatrix; bgl—buccal ganglia; bp—buccal pump; cgl—capsule gland; ct— central teeth; dn—reduced denticles; dov—joint distal oviduct and uterine duct; gd—genital duct; mgl—mucus gland; megl—membrane gland; ne—nephroproct; ngl—nidamental glands; oe—oesophagus; ov—oviduct; ovo—nidamental glands opening; p—penis; pm—peripheral muscle of the buccal pump; po—penial opening within common genital atrium; pov—proximal oviduct; pr—prostata; psh—penial sheath with ejaculatory duct; pv—proximal descending part of the vagina; rs—receptaculum seminis; sgl —salivary glands; tp—terminal penial processes; tv—terminal part of the vagina; ud—uterine duct; v—vagina; vb—vaginal bursa; vd—vas deferens (muscular part); vo—vaginal opening.

All specimens used in the present study have been collected by SCUBA diving. Specimens were fixed in ethanol (70–96%) or 4 % formalin. The soft part anatomy was studied under the dissecting microscope; integuments were also studied by SEM. Radulae and labial cuticles were prepared using domestic bleach, rinsed in water, dried, and studied under a CamScan SEM at the Scanning electron microscopic laboratory of the Moscow State University.

Class Gastropoda

Subclass Opisthobranchia

Order Nudibranchia

Suborder Doridacea (=Doridina, Anthobranchia)

Family Onchidorididae Gray, 1827

Onchimira gen.nov.

Type Species: *Onchimira cavifera* **gen. et sp. nov.**

Diagnosis. The notum is soft and almost smooth, relatively broad, usually covered with very short tubercles. The integument contains a sparse network of spicules. The rhinophores are lamellate. The rhinophoral pockets have well defined contractile sheaths with smooth edges. The gills are unipinnate united by a common membrane into a circle around the anus, and are retractable into a common true gill cavity. The gill cavity border is moderately raised and has a smooth edge, which is capable of closing entirely over the gills. The oral veil is well defined, trapezoid, with oblique lateral sides and a convex anterior edge. The foot is broad, not bilobed anteriorly, slightly narrowed posteriorly. The labial cuticle contains dark rods with bent tips. The

buccal pump is large, sessile, fully banded medially by a broad peripheral muscle. The salivary glands are elongate. The radula formula is 7–9.1.1.1.9–7. The central teeth are small and rectangular. The first lateral tooth is large, beak-shaped, bearing small faint denticles. Further lateral teeth are small and elongate. The stomach is relatively large, a caecum is absent. The male part of the reproductive system comprises a small single looped prostate, a moderately sized muscular vas deferens and a large, distinctly swollen penis, which contains a smaller evertable part. The penis is not armed. The ampulla bifurcates into a vas deferens, uterine duct and oviduct. The bursa copulatrix is small and rounded. The seminal receptacle does not represent a separate structure; instead it is formed by a swollen terminal part of the vagina, which is wide, massive and moderately convoluted.

Etymology. From *onchi* in referring to the family Onchidorididae and *mira* (Latin), = remarkable, extraordinary. *Onchimira* is a noun of feminine gender.

Remarks. See under species description.

***Onchimira cavifera* gen. et sp. nov.**
(Figures 2; 3A, E; 4A–C, F, J–K; 5A, B; 6A, B; 7A. Table 1)

Type material. Holotype, ZMMU Lc-37446, NW Pacific near Kamchatka peninsula, Starichkov Id., 20–26 m, large boulders, collected by T.A. Korshunova and A.V. Martynov. 14.08.2008. Paratypes, ZMMU Lc-37447, 11 specimens (three dissected), same locality and collectors as holotype, 14.08.2008. Paratypes, ZMMU Lc-37448, three specimens (one dissected), same locality and collectors as holotype, 18–24 m, 19.08.2008. Paratypes, ZMMU Lc-37449, three specimens (one dissected), same locality and collectors as holotype, 19.08.2008. Paratypes, ZMMU Lc-37450, three specimens (one dissected), same locality and collectors as holotype, 19.08.2008.

Type locality. NW Pacific, SE Kamchatka, Starichkov Id., 18–26 m depth.

Etymology. The species epithet from the Latin *cavi* (= cavity) and *fero* (= to bear) refers to the presence of a well-defined gill cavity.

Description. *External morphology.* The dimensions of the holotype are 22 mm x 12 mm (Fig. 2). The length of fifteen measured living specimens ranged from 8.5 to 25 mm, the width ranged from 4.5 to 14 mm. The consistency of the living animals is soft. The notum is rather broad, rounded in front and posteriorly. The rhinophores are long and retracted into raised sheaths with smooth, soft, sometimes slightly crenulate edges, not bearing tubercles (Fig. 2C). The rhinophoral sheath edges are capable of considerable contraction in living specimens. There are 5–9 rhinophoral lamellae. The rhinophore clavus lacks a posterior ridge. The notum is almost smooth, sparsely covered with wrinkled low elevations, sometimes raised to very low tubercles (Fig. 2A). Rays of spicules radiate from the bases of such elevations and form a sparse network in the notum (Fig. 6A), but spicules are not conspicuous externally (Fig. 2A). Each elevation contains sparsely placed spicules, which do not protrude from the tubercles. The strongly calcified spicules are of various size, most with a narrow channel inside (Fig. 6B). 10–15 (usually 12) unipinnate gills are united by a common membrane into a circle around the anus. Gills are retractable into a common true gill cavity, which is capable of closing over the gills completely (Figs. 2E–H). The border of the gill cavity is moderately raised and has a smooth edge (Figs. 2E, F). The oral veil is well defined, trapezoid, with oblique lateral sides and convex anterior edge (Fig. 2B). The foot is broad, anteriorly rounded and not thickened; posteriorly it projects slightly from the notum in crawling animals, forming a rounded tail.

Colour. The living specimens are grayish with creamy tinge (Fig. 2). The rhinophores (including lamellae) are similar to the ground colour but more intensively cream. The gills are semitransparent white, similar to the ground colour. The pinkish digestive gland is slightly visible through the notum dorsally and shines more clearly through the foot ventrally. A purple-blackish female gland mass is visible through the anterior part of the right side in some specimens.

Anatomy. *Digestive system*. The anterior part of the buccal bulb is modified into the sessile, large, buccal pump which is medially fully banded by a broad peripheral muscle (Fig. 7A). The lateral sides of the buccal pump are provided with thin muscular fibres. The rounded labial disk is covered by a brown cuticle bearing distinct, rod-shaped labial elements with bent tips (Figs. 3A, E). The radular formula in four specimens (17–23 mm length) is 25-28 x 7–9.1.1.1.9–7. The radular teeth are slightly yellowish. The central tooth is small, elongate, rectangular and folded on the lateral edges (Fig. 4A). The first lateral tooth is large and provided with a long, wide base and a strong, slightly curved beak-shaped cusp (Figs. 4A–C, F). The cusp sometimes bears small faint denticles (Fig. 4C). Outer lateral teeth are elongated small plates without cusps, all similar in size and shape (Figs. 4A, B, F). The salivary glands are relatively long and narrow (Fig. 7A). The stomach is relatively large and broad, then rapidly narrowing to the intestine. The stomach caecum is absent.

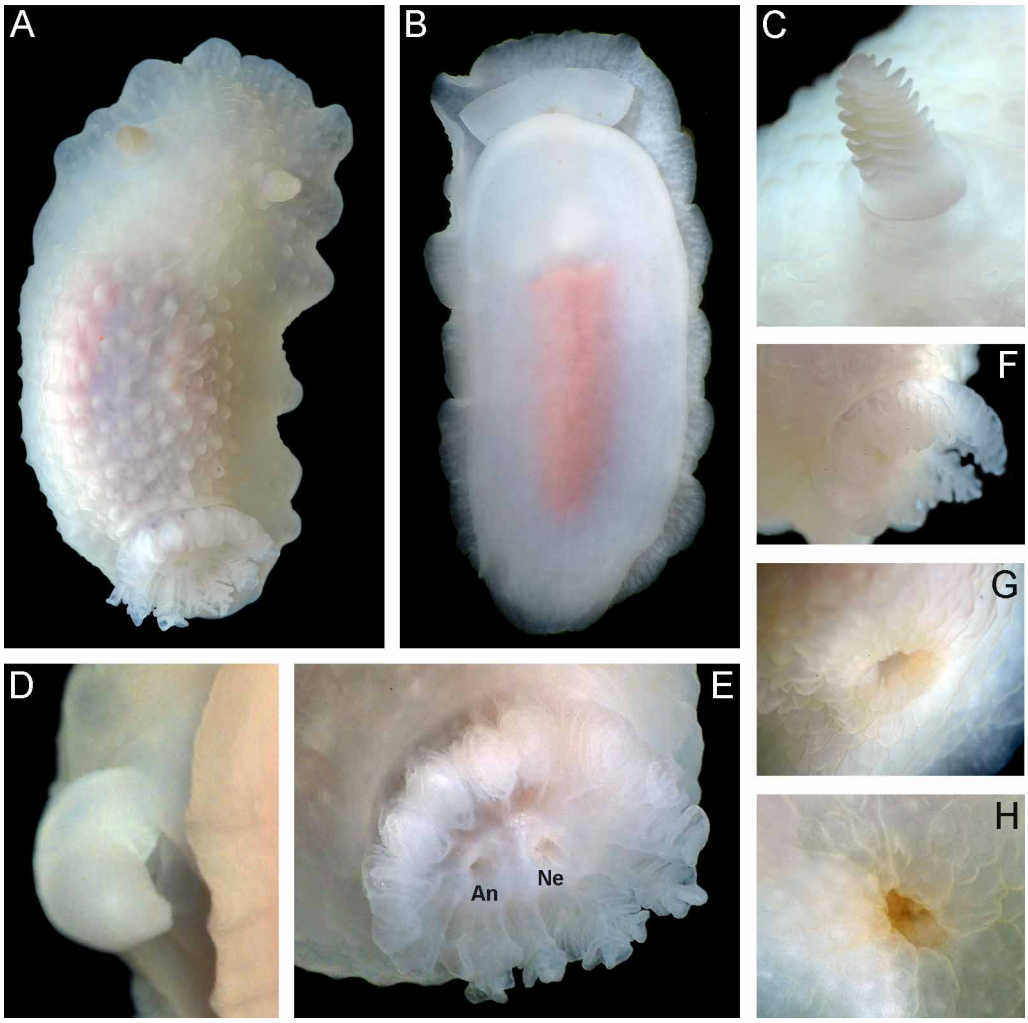

FIGURE 2. *Onchimira cavifera* **gen. et sp. nov.**, A–C, E, Holotype ZMMU Lc-37446, living animal, 22 mm length, NW Pacific, Kamchatka peninsula, Starichkov Island. A. Dorsal view; B. Ventral view; C. Rhinophore and rhinophoral pocket; D. Paratype, ZMMU Lc-37448, living animal, 17 mm length, penis everted; E. Close up of the gills and gill pocket, showing anus and nephroproct; F–H, Paratype, ZMMU Lc-37447, 18 mm length, three phases of the gill retraction: F. Extended, G. Retracted, the gill pocket edges not fully contracted; H. Retracted, the gill pocket edges fully closed over the gills. Photos: A–C Karen Sanamyan; D–H Tatiana Korshunova.

Circulatory system. In the pericardial sac the broadly triangular posterior auricle and the smaller sized oval ventricle are present. The rather massive, irregularly rectangular blood gland is located above the central nervous system.

Central nervous system. The cerebral and pleural ganglia are well separated, the latter being somewhat smaller in size. The optic nerve is very short. The eyes are relative large, with black pigment in all studied

specimens. The pedal ganglia are smaller than the cerebrals, lay below them and are connected to them by very short connectives. The rhinophoral ganglia are rather irregular, rounded or elongate. The buccal ganglia are rounded-oval (Fig. 7A). Gastro-esophageal ganglia are present. Five pairs of cerebral nerves, two pleural and three pedal ones are detected.

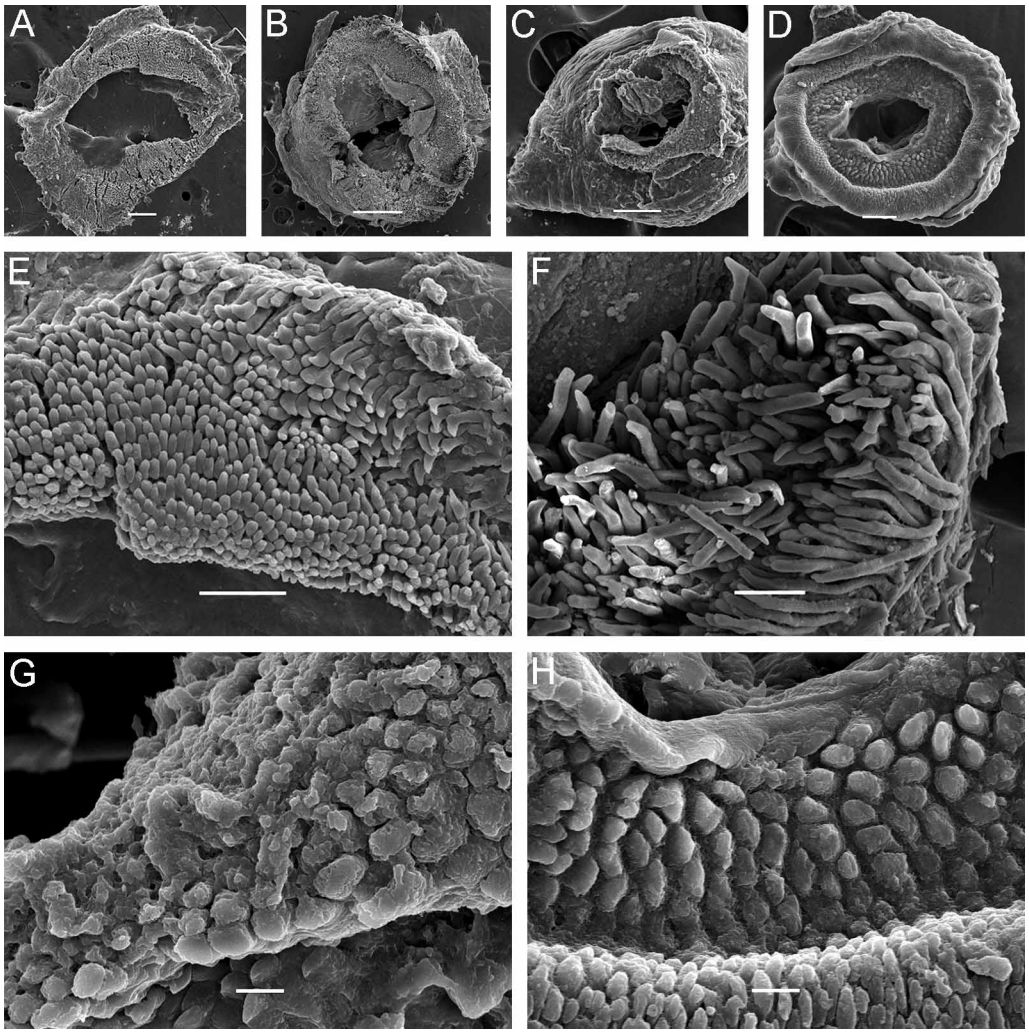

FIGURE 3. Labial cuticles, scanning electron micrographs. A–D, general views: A. *Onchimira cavifera* **gen. et sp. nov.**, paratype ZMMU Lc-37450, living specimen, 18 mm length, Starichkov Island; B. *Calycidoris guentheri* Abraham, 1876, ZIN N 40, preserved specimen, 23 mm length, Bering Sea, 66° 55,5' N 165° 55,1' W, from 22 m depth; C. *Adalaria slavi* **sp. nov.** , paratype ZMMU Lc-37457, living specimen, 18 mm length, Starichkov Island; D. *Adalaria olgae* **sp. nov.**, paratype ZMMU Lc-37455, living specimen, 9 mm length, Starichkov Id.; E–H, details: E. *Onchimira cavifera* **gen. et sp. nov.**, paratype ZMMU Lc-37450; F. *Calycidoris guentheri* Abraham, 1876, ZIN N 40; G. *Adalaria slavi* **sp. nov.**, paratype ZMMU Lc-37457; H. *Adalaria olgae* **sp. nov.**, paratype ZMMU Lc-37455. Scale bars: A—100 μm, B—500 μm, C—100 μm, D—50 μm, E—50 μm, F—50 μm, G—10 μm, H—10 μm. Photos: Alexander Martynov.

Reproductive system. (Figs. 5A, B). The ampulla is relatively short and narrow, not filled by sperm in all studied specimens (Fig. 5B, a). The ampulla trifurcates into the moderately long vas deferens, uterine duct and oviduct (Fig. 5B, pr, ud and ov). The prostatic part of the vas deferens is a very short, slightly swollen and bending duct, which does not encircle the bursa copulatrix (Figs. 5A, B, pr). The prostate transits to a moderately long and narrow single-looped vas deferens (Figs. 5A, B, vd), which rapidly widens and enters a common genital atrium (Fig. 5A, at), terminating into the large, wide, and prominent penis, which contains a smaller evertable part (Figs. 4 J, K; 5A, B, p). The vagina is relatively wide, moderately convoluted (Figs. 5A, B, v), and enters a rather small, flattened bursa copulatrix (Figs. 5A, B, bc). The uterine duct is long and narrow (Fig. 5B, ud); it begins at the ampulla bifurcation and then enters the terminal part of the vagina

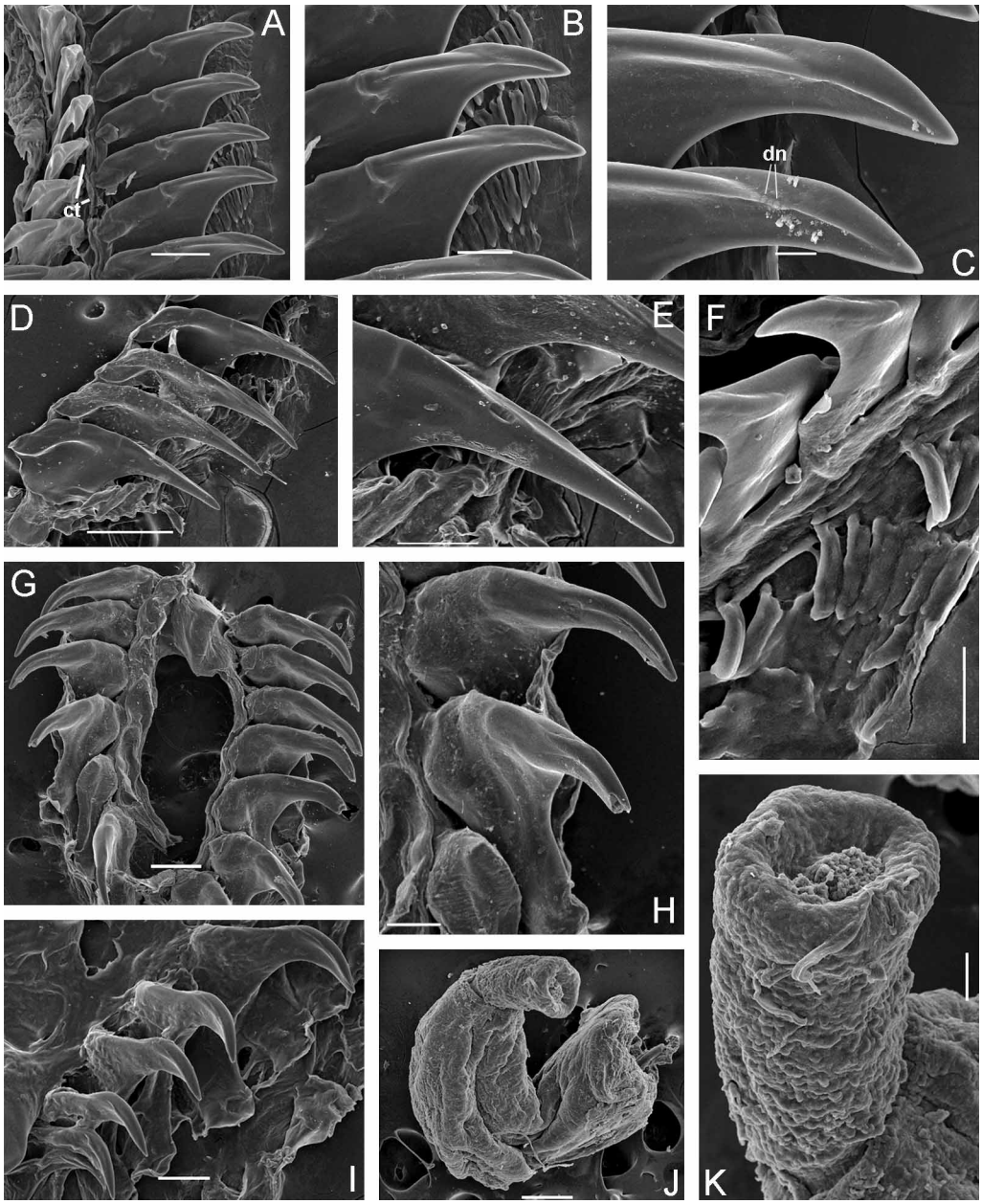

FIGURE 4. Radulae of representatives of the genera *Onchimira* **gen. nov**., *Calycidoris* Abraham, 1876, and *Acanthodoris* Gray, 1850, scanning electron micrographs. A–C, *Onchimira cavifera* **gen. et sp. nov.**, paratype ZMMU Lc-37450, living specimen, 20 mm length; A. Rows toward anterior radula end; B. Enlarged, showing distinct rows of the small outer lateral teeth; C. Enlarged cusp of two first laterals showing indistinct denticles on the lower tooth; D–E, *Acanthodoris uchidai* Baba, 1935, preserved specimen, 18 mm length, Kurile Islands, Paramushir Id., depth 20 m; D. Middle rows; E. Details of the first lateral tooth cusp and outer laterals; F. *Onchimira cavifera* **gen. et sp. nov.**, paratype ZMMU Lc-37447, living specimen, 18 mm length, three middle rows showing outer laterals; G–I, *Calycidoris guentheri* Abraham, 1876, ZIN N 40, preserved specimen, 23 mm length; G. Part of the radula; H. Enlarged two first lateral teeth from the middle rows; I. Part of the radula; J–K, *Onchimira cavifera* **gen. et sp. nov.**, paratype ZMMU Lc-37447, living specimen, 15 mm length; J. Isolated penis; K. Close up of the terminal everted part. Scale bars: A—100 μm, B—50 μm, C—20 μm, D—300 μm, E—100 μm, F—50 μm, G—200 μm, H—100 μm, I—100 μm, J—200 μm, K—50 μm. Photos: Alexander Martynov.

forming a small pointed elevation. A separate seminal receptacle is absent, but the terminal part of the vagina forms a large swollen area (Fig. 5B, tv+rs), which may serve as a receptacle. In freshly dissected living specimens, a tiny, almost inconspicuous knob-shaped structure was found on the vagina at the bursa base.

This structure possibly is a vestige of a seminal receptacle, but in the ethanol-fixed specimens it was no longer detectable. The oviduct is well defined, wide (Figs. 5A, B, ov). It starts at the ampulla, and is an irregularly convoluted duct. The capsular gland is unusually purplish-blackish in colour, having an alveolar surface (Figs. 5A, B, cgl).

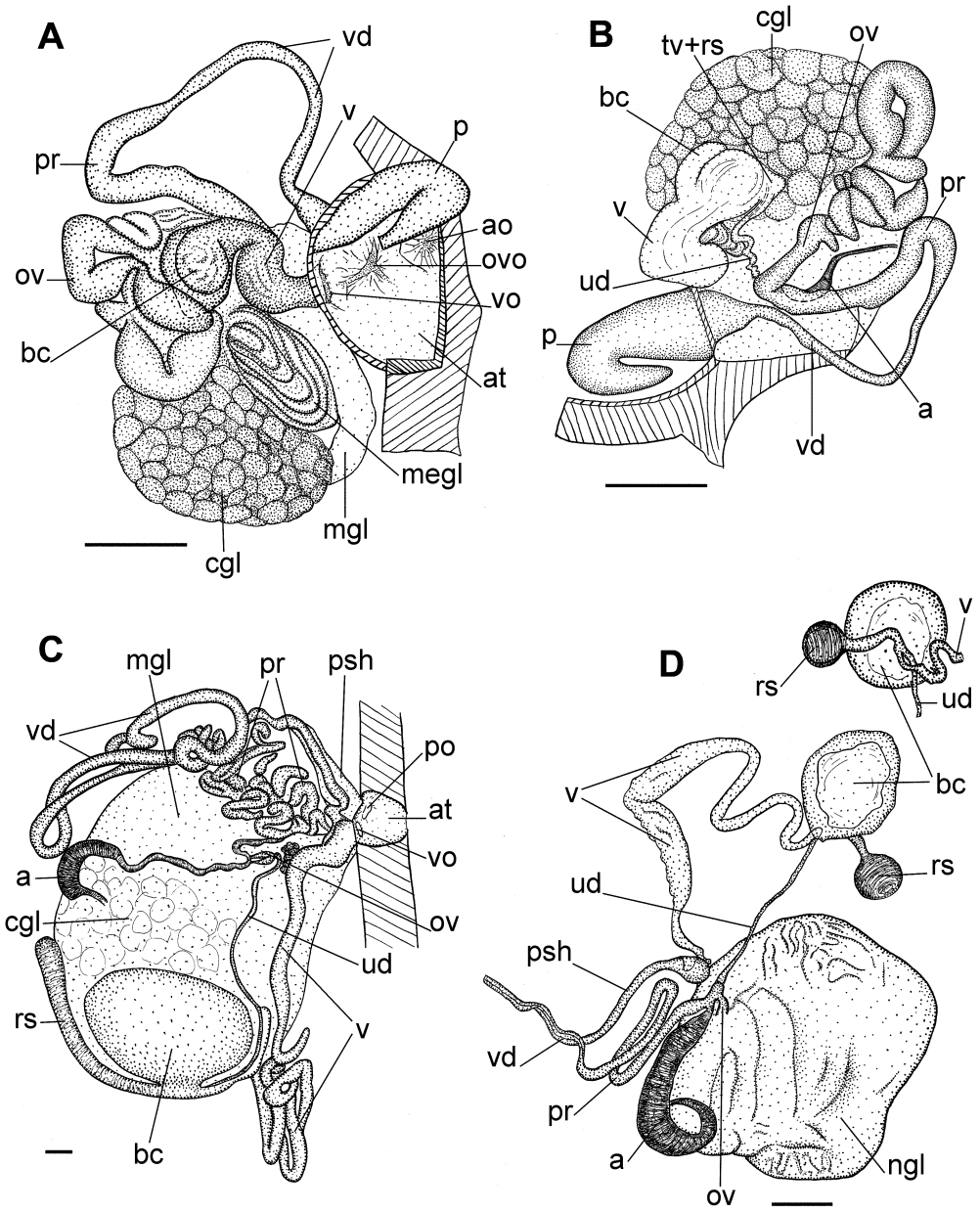

FIGURE 5. Reproductive system of members of the genera *Onchimira* **gen. nov.**, *Calycidoris* and *Acanthodoris*. A–B, *Onchimira cavifera* **gen. et sp. nov.**, based on examination of four paratypes ZMMU Lc-37447, living specimens, 17–20 mm length; A. Dorsal view, common genital atrium is dissected; B. Ventro-lateral view showing vagina and bursa connections; C. *Calycidoris guentheri* Abraham, 1876, ZIN N 40, preserved specimen, 23 mm length, dorsal view, common genital atrium is dissected; D. *Acanthodoris pilosa* (Abildgaard in Müller, 1789), preserved specimen, 15 mm length, Barents Sea, Dalne-Zelenetskaya Bay, intertidal, dorsal view. Scale bars—1 mm. Drawings by Tatiana Korshunova based on Alexander Martynov originals.

Biology. Specimens were found predominantly on large boulders covered with several species of encrusting bryozoa, at 18–26 m depth, considerably less commonly than *Adalaria slavi* **sp. nov.**

Distribution. Presently known only from the type locality.

Remarks. *Onchimira cavifera* gen. et **sp. nov.** possesses all the usual onchidoridid characters, e.g. a well-defined buccal pump which is fully banded by the peripheral muscle, a rectangular rachidian tooth (when

present), a distinct, hooked, first lateral teeth, and a number of elongate, reduced, outer laterals. The new species differs from all known onchidorids by possessing a true gill cavity of a cryptobranch dorid type. The gills are capable of complete retraction into the gill cavity, the edges of which may fully contract over the gills (Figs. 2E-H). These features clearly delineate *Onchimira* gen. nov. from other onchidoridid genera (Table 1).

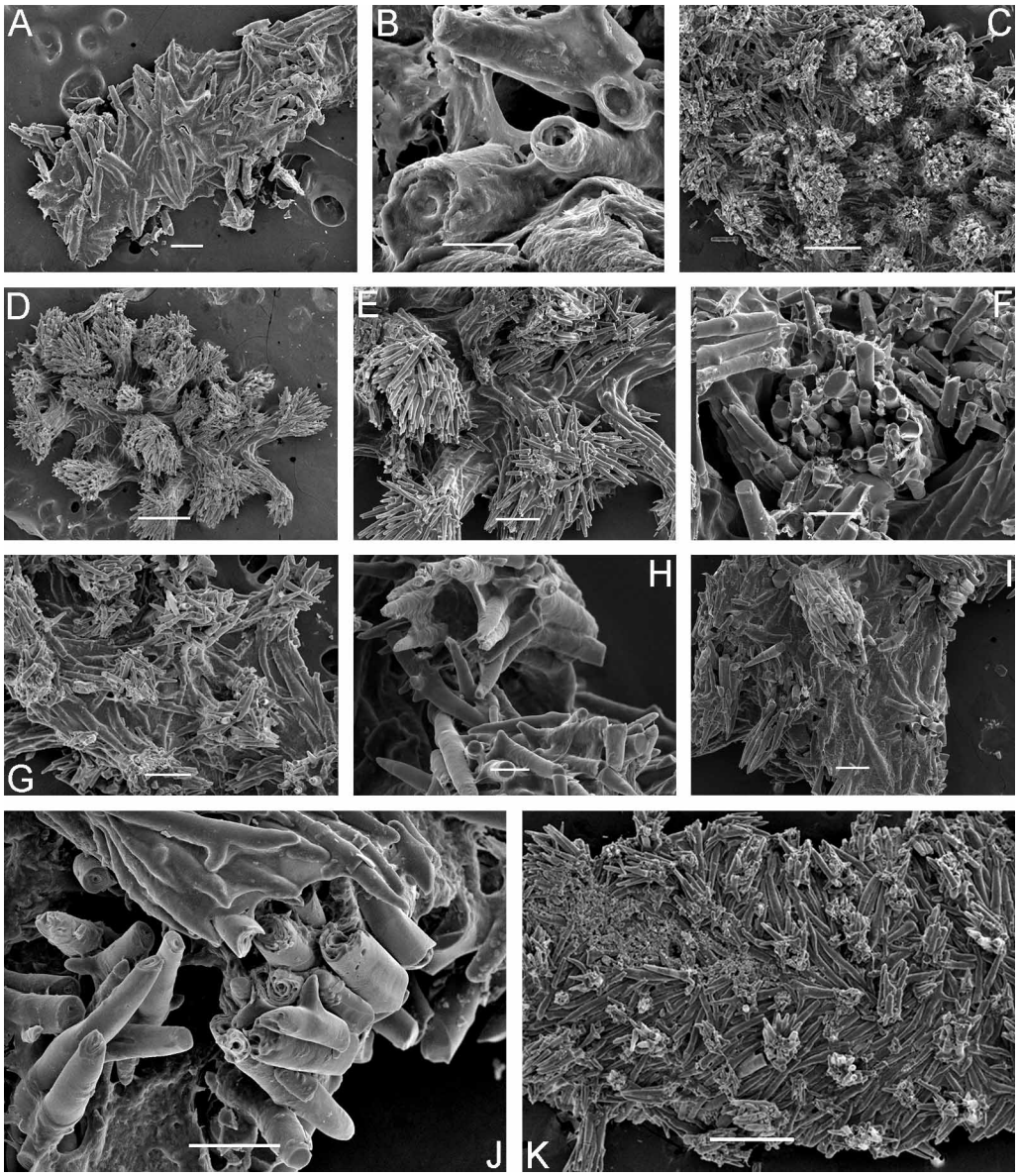

FIGURE 6. Parts of the dorsal spicule network including tubercles, scanning electron micrographs. A–B, *Onchimira cavifera* **gen. et sp. nov.**, paratype ZMMU Lc-37448; A. Living animal, 18 mm length; B. Same, details enlarged; C. *Calycidoris guentheri* Abraham, 1876, ZIN N 40, preserved specimen, 23 mm length; D–F, *Adalaria slavi* **sp. nov.**, paratype ZMMU Lc-37457; D. Living specimen, 18 mm length; E. Details of tubercles; F. Close up of the spicules; G–H, *Adalaria olgae* **sp. nov.**, paratype ZMMU Lc-37455; G. Living specimen, 9 mm length; H. Close up of the spicules; I–J, *Onchidoris macropompa* **sp. nov.**, paratype ZMMU Lc-37465; I. Living specimen, 15 mm length; J. Close up of the spicules; K. *Adalaria jannae* Millen, 1987, living animal, 8 mm length, NE Pacific, Kamchatka peninsula, Starichkov Island, from 13–15 m depth. Scale bars: A—200 μm, B—50 μm, C—500 μm, D—500 μm, E—200 μm, F—100 μm, G—200 μm, H—50 μm, I—200 μm, J—100 μm, K—500 μm. Photos: Alexander Martynov.

The only genus of the family Onchidoriddidae, which also demonstrates the presence of a well defined gill cavity, is *Calycidoris* Abraham, 1876. In the present study, numerous specimens of the single known species of this genus, *Calycidoris guentheri* Abraham, 1876, were examined for comparison (Fig. 8E). It is confirmed that *C. guentheri* possesses a well defined gill cavity, which even can contract to some degree. However, no

specimens were found with a completely closed gill pocket, i.e. with edges of the cavity fully contracted over the gills. The general external appearance of *Onchimira cavifera* is similar to that of cryptobranch dorids, e.g. *Cadlina*, in having an elevated body, and markedly differs from *Calycidoris guentheri*, which has a flattened notum (Fig. 8E). The notum spicule pattern of the genera *Onchimira* and *Calycidoris* is also different — the former has a soft notum that is sparsely filled with spicules (Figs. 2A, 6A) whereas in the latter genus the notum is hard and contains a dense spicule network (Fig. 6C).

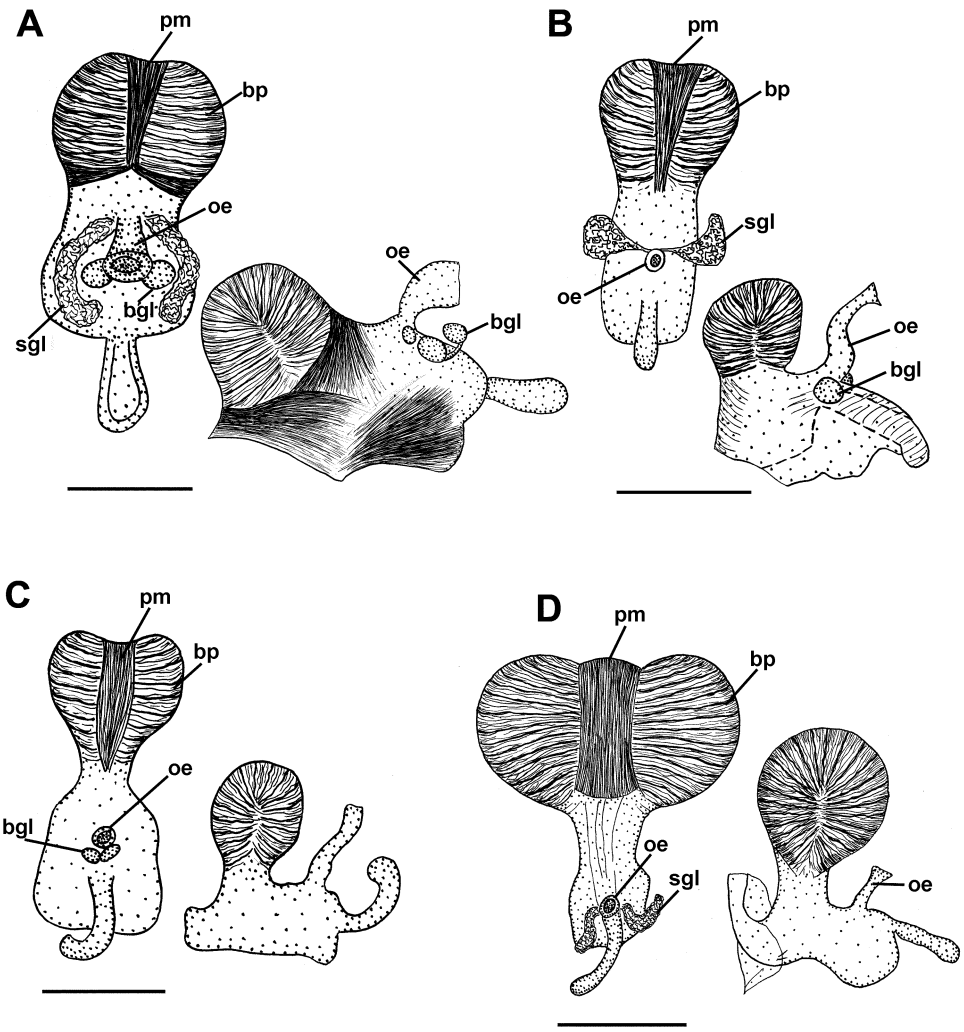

FIGURE 7. Buccal pumps, posterior and lateral views. A. *Onchimira cavifera* **gen. et sp. nov.**, paratype ZMMU Lc-37447; B. *Adalaria slavi* **sp. nov.**, paratype ZMMU Lc-37460, living specimen, 10 mm length; C. *Adalaria olgae* **sp. nov.**, paratype ZMMU Lc-37455, living specimen, 12 mm length; D. *Onchidoris macropompa* **sp. nov.**, paratype ZMMU Lc-37465, living specimen, 15 mm length. Scale bars—1 mm. Drawings by Tatiana Korshunova based on Alexander Martynov originals.

Internally, *Onchimira* gen. nov. differs from *Calycidoris* by the presence of a large distinct penis (Figs. 2D, 5A, B, p) instead of a long, narrow ejaculatory duct (Fig. 5C, psh). An especially distinctive feature is the seminal receptacle that is apparently fused with the terminal part of the vagina forming a large swollen area (Fig. 5B, tv+rs). This part of the vagina is similar to the pattern found in the genera *Adalaria* and *Onchidoris*, where possibly all known species have a wide, swollen seminal receptacle that directly transits into the vagina (e.g. Figs. 12B, rs and 15A, C, rs). In contrast, members of the genera *Calycidoris* and *Acanthodoris* possess a well-defined, long-stalked seminal receptacle (Figs. 5C, D, rs), which is distinct from the vagina, as is also found in many cryptobranch dorids. The radula of *Onchimira* gen. nov. has central teeth (Fig. 4A), while in

Calycidoris central teeth are absent (Figs. 4H, I). The lateral teeth of *Calycidoris* are very massive (Figs. 4G–I), whereas those of *Onchimira* gen. nov**.** are considerably thinner (Figs. 4A–C). The general radular appearance of *Onchimira* gen. nov. is rather similar to the genus *Acanthodoris* (Figs. 4D, E), except for the presence of the central tooth.

The poorly described *Lamellidoris beringi* Volodchenko, 1941 was indicated as having a common gill sheath (Volodchenko 1941). However, a single specimen personally identified by N.I. Volodchenko as *Onchidoris beringi* stored in the Zoological Institute, St. Petersburg, showed an external morphology that is typical for the genus *Onchidoris* (including the presence of numerous mushroom-shaped notal tubercles) and lacking a common gill sheath. Other features of *Lamellidoris beringi* indicated by Volodchenko (1941), i.e. long cylindrical notal tubercles, smooth rhinophores, narrow conical oral tentacles, short thick cusp of the first lateral tooth and 5 outer laterals, significantly differ from *Onchimira cavifera*.

Another genus traditionally placed within family Onchidorididae, *Diaphorodoris* Iredale & O'Donoghue, 1923, also possesses a small gill cavity (Millen 1985; present study), but other external and internal characters are very different from the genera *Onchimira*, *Calycidoris*, and from any other onchidoridid taxa (Table 1). Earlier it was suggested (Martynov 1999a,b) that *Diaphorodoris* is closely related to the phanerobranch family Anculidae.

Onchimira cavifera thus is a member of Onchidorididae but cannot be incorporated into any existing genus (Table 1). There are a number of important differences regarding external features as well as digestive and reproductive organ systems. Rather than widening and confusing the current generic diagnoses we establish the new genus *Onchimira*. Phylogenetic analyses including characters of the newly described taxa will support or reject this hypothesis.

Genus *Adalaria* Bergh, 1879

Adalaria: Bergh, 1879: 360

Synonyms: *Arctadalaria* Roginskaya, 1971
Type species: *Doris loveni* Alder & Hancock, 1862, by monotypy

Diagnosis. The notum is covered with well-defined spiculose tubercles of variable shape. The integument contains a dense network of spicules. The rhinophores are lamellate. The rhinophoral pockets have poorly defined, contractile smooth sheaths adjoined by several tubercles. The contractile gills are bi-tri to unipinnate, arranged separately in an almost complete circle around the anus. A common gill cavity or separated gill pits are completely absent. The oral veil is well defined, semi-circular, in one species distinctly trilobed. The foot is broad, not bilobed anteriorly, slightly narrowed posteriorly. The labial cuticle contains weakly defined polygonal elements. The buccal pump is large, prominent, sessile or on a short broad stalk, fully banded medially by a broad peripheral muscle. The salivary glands are short. The radula formula is 3–13.1.1.1.13–3. The central teeth are small and rectangular; present in most species. The first lateral tooth is large, beak-shaped, in most species bearing well defined denticles. Further lateral teeth are small elongate and characteristically excavated. The stomach is relatively small, a stomach caecum is absent. The male part of the reproductive system is comprised of a looped, moderately narrow prostate, and a long musculary sheathened ejaculatory duct. The penis is not armed. The post-ampullar gonoduct bifurcates into a vas deferens and a proximal oviduct that connects to the vagina. The combined distal oviduct / uterine duct starts separately from the vaginal duct, close to the external genital opening. The bursa copulatrix is small and rounded. The seminal receptacle is distinct but always buried within nidamental glands near bursa base. The 7 valid species (including 2 described in the present paper) are listed in Table 2. The North Pacific is the center of the genus diversity.

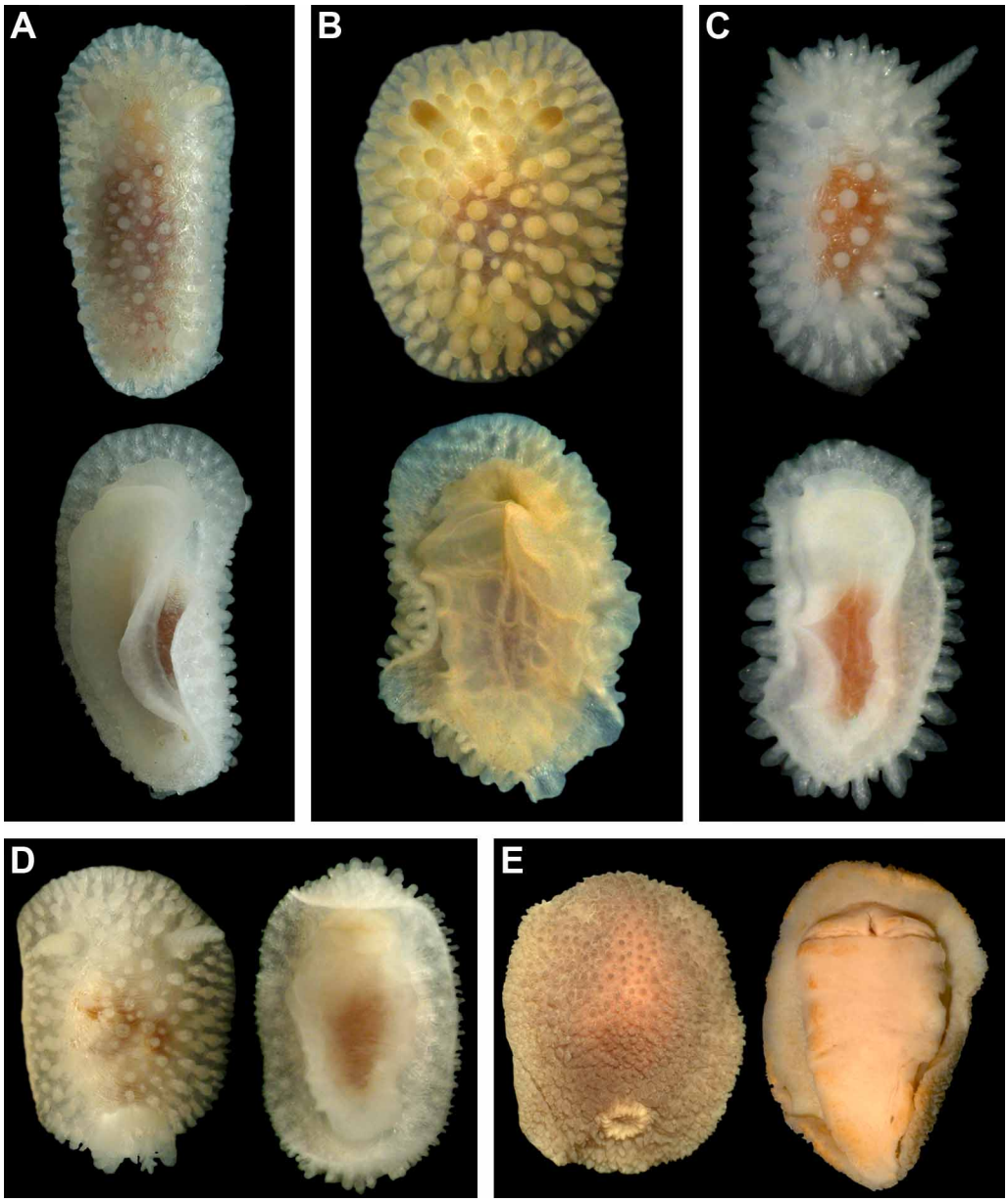

FIGURE 8. Representatives of the genera *Adalaria*, *Onchidoris* and *Calycidoris*, dorsal and ventral views. A. *Adalaria jannae* Millen, 1987, ZMMU, not registered, living animal, 8 mm length, Starichkov Island; B. *Adalaria proxima* (Alder et Hancock, 1854), ZMMU, not registered, Barents Sea, Dalne-Zelenetskaya Bay, living non-mature specimen with poorly differentiated reproductive system and smooth first lateral teeth, 13 mm length, intertidal; C. *Adalaria proxima* (Alder & Hancock, 1854), ZMMU, not registered, living juvenile, 7 mm length, White Sea, Kandalakshsky Bay, Cape Kartesh, depth 5–7 m; D. *Onchidoris muricata (*Müller, 1776), ZMMU, not registered, living animal, 7 mm length, Barents Sea, Dalne-Zelenetskaya Bay, intertidal; E. *Calycidoris guentheri* Abraham, 1876, ZIN N 40, preserved specimen, 23 mm length, Bering Sea, 66° 55,5' N 165° 55,1' W, from 22 m depth. Photos: Tatiana Korshunova.

***Adalaria slavi* sp. nov.**
(Figures 3C, G; 6D–F; 7B; 9; 11A–D; 12A, B. Table 2)

Type Material. Holotype, ZMMU Lc-37456, (23 mm length), NW Pacific near Kamchatka peninsula, Starichkov Id., 20–26 m, collected by T.A. Korshunova and A.V. Martynov, 14.08.2008. Paratypes, ZMMU Lc-37457, 28 specimens, same locality and collectors as holotype 19.08.2008. Paratypes, ZMMU Lc-37458,

seven specimens (one dissected) same locality and collectors as holotype, at 18–24 m depth, large boulders, 19.08.2008. Paratypes, ZMMU Lc-37459, five specimens (three dissected), same locality and collectors as holotype, 14.08.2008. Paratypes, ZMMU Lc-37460, 10 specimens, same locality and collectors as holotype, 19.08.2008. Paratypes, ZMMU Lc-37461, 9 specimens, same locality and collectors as holotype, 19.08.2008. Paratype, ZMMU Lc-37462, one dissected specimen, same locality and collectors as holotype, 19.08.2008.

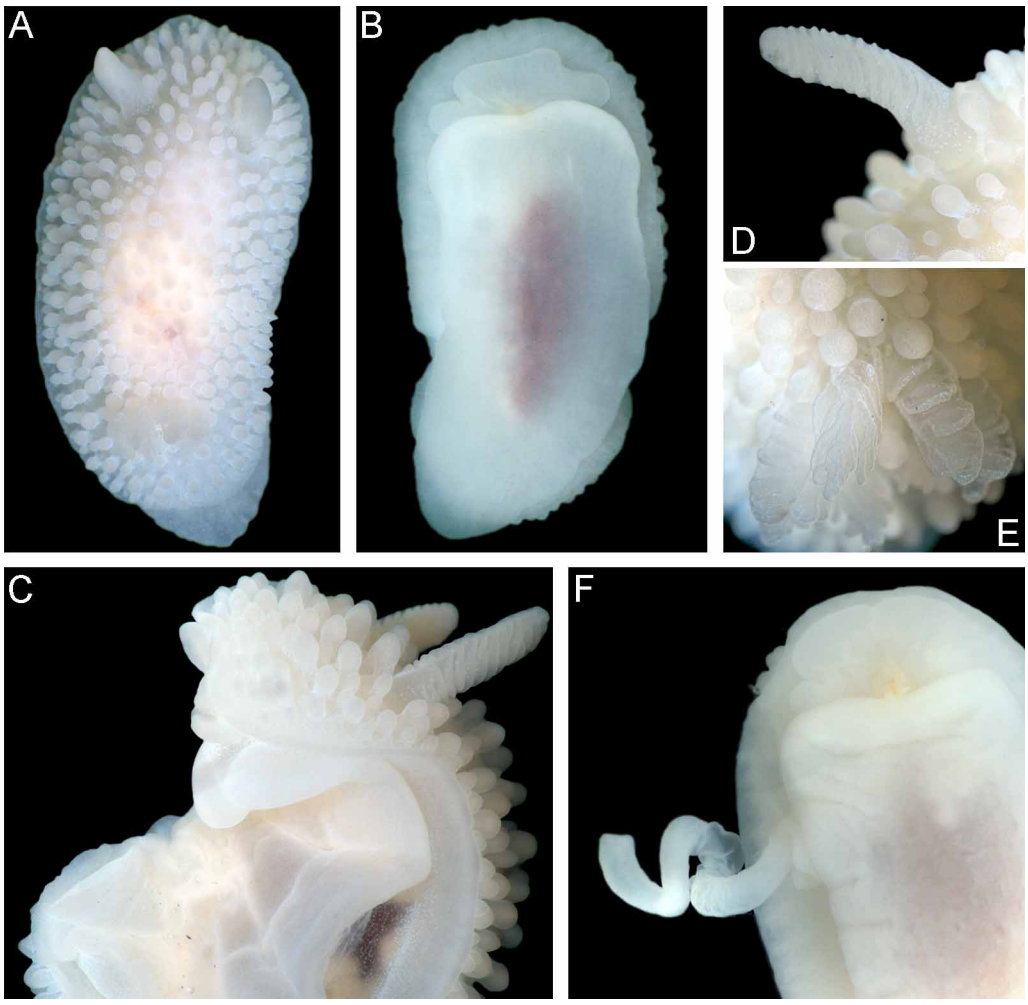

FIGURE 9. *Adalaria slavi* **sp. nov.**, living animals. A–B, Holotype, ZMMU Lc-37456, living animal, 23 mm length, NW Pacific, Kamchatka peninsula, Starichkov Island; A. Dorsal view; B. Ventral view showing a trilobed oral veil; C–F, paratype, ZMMU Lc-37457, living animal, 20 mm length; C. Left lateral view showing the distinctive pattern of numerous small white dots on the hyponotum; D. Close up of the rhinophore and rhinophoral pocket; E. Gills, enlarged; F. Ventral view showing long everted penis. Photos: A–C, F Tatiana Korshunova; D–E Karen Sanamyan.

Type locality. NW Pacific, SE Kamchatka, Starichkov Id., 18–26 m.

Etymology. This species is named in honour of Vyacheslav G. Shipilov, captain of the boat “Chaika” in recognition of his generous help in organizing scuba diving.

Description. *External morphology.* The length of the holotype is 23 mm and width 11.5 mm (Fig. 9A–B). The length of 20 living specimens ranged from 8 to 23 mm, the width ranged from 4.5 to 11.5 mm. The consistency of living animals is rather soft. The notum is moderately broad, rounded in front and posteriorly. The rhinophores are long and retracted into sheaths with smooth edges, except for 5–6 tubercles of various size that are connected with edge of each sheath (Fig. 9D). The rhinophoral sheath edges are capable of some contraction in living specimens. There are 11–14 rhinophoral lamellae. The clavus of the rhinophore has a low ridge posteriorly. The notum is densely covered with inflated cylindrical or almost globular tubercles on a short stalk. Tubercles in the central notal area are somewhat wider and more globular than those at the notal

edge. Larger tubercles are regularly intermingled with smaller ones. The rays of spicules radiating from the bases of tubercles form a sort of network under the surface of the apparently soft notum (Figs. 6D–E). The spicules are not conspicuous externally. Each tubercle contains dense bundles of spicules, not protruding through the tubercle surface. The strongly calcified spicules are of various sizes, most of them are solid (Fig. 6F). The gill cavity is absent. Six to eight bi- and tripinnate gills form an almost complete semicircle around the anus, and one tubercle may be present just behind the anus. (Fig. 9E). Three gills were detected in a juvenile of 5–6 mm length. The oral veil is large, since it consists of two pairs of processes: a single, broad trapezoid upper triangular projection that is not medially fused with the hyponotum, and two flattened lobes below (Fig. 9B). The foot is broad, anteriorly rounded, and posteriorly slightly projecting beyond the notum in crawling animals forming a rounded tail (Fig. 9A).

Colour. The living specimens are milky white, slightly transparent, with a brownish intestine scarcely visible in the middle of the notum. The integument of the notum (including hyponotum) and rhinophores are densely covered with small, faint opaque white dots (Figs. 9A, C). On the tubercle tops and rhinophoral lamellae edges the white pigment is almost entirely absent. The gill edges are covered with white dots. The white gonad shines through mature animals (including the holotype), and ventrally the reddish digestive gland can be seen.

Anatomy. *Digestive system*. The anterior part of the buccal bulb is modified into the prominent, sessile buccal pump (Fig. 7B). The buccal pump is fully banded by a relatively narrow peripheral muscle (Fig. 7B). The lateral sides of the buccal pump are provided with thin muscular fibres. The salivary glands are massive triangular lobes (Fig. 7B, left figure). The rounded labial disk is covered by yellowish cuticle bearing fine, knob-like labial elements (Figs. 3C, G). The radular formula in six studied specimens (15–21 mm length) is 27–32 x 6–9.1.1.1.9–6. Radular teeth are slightly yellowish. The central tooth is small, elongated, rectangular and folded (Figs. 11A, D). The first lateral tooth is provided with a long, wide base and a strong slightly curved beak-shaped cusp, bearing 10–15 small denticles (Fig. 11C). The outer denticles gradually reduce in size towards the internal ones. Outer lateral teeth have slightly elongated bases, with a curved, hooked cusp on its lateral corner; all are similar in size and shape (Figs. 11A, C). In smaller specimens (8–9 mm length) the denticles of the innermost lateral teeth are relatively larger and fewer (8–10) (Fig. 11D) and the cusp itself is straighter. This condition is somewhat similar to the condition in juveniles of *Adalaria proxima* (Fig. 11L) and adult specimens of *Adalaria olgae* **sp. nov.** (Figs. 11F, H). The stomach is relatively small and narrow. A stomach caecum is absent.

Circulatory system. In the pericardial sac a triangular posterior auricle and a smaller sized oval ventricle are present. The blood gland is rather large in relation to the central nervous system, lies above it and comprises from both posterior and anterior lobes.

Central nervous system. The cerebral and pleural ganglia are well separated, the latter being somewhat larger in size. The optic nerve is very short. The eyes are not large, with black pigment in all studied specimens. The pedal ganglia are similar in size to the cerebrals, lay below them and are connected to them by very short connectives. The rhinophoral ganglia are spherical. The buccal ganglia are slightly oval. Gastro-esophageal ganglia are not differentiated. Six pairs of cerebral nerves, three pleural and three pedal ones are detected.

Reproductive system. (Figs. 12A, B). The ampulla is moderately short and narrow (Figs. 12A, B, a). The post-ampullar duct bifurcates into a long vas deferens and a short proximal oviduct (Fig. 12B, pr and pov). The prostate has two distinct parts; a proximal, narrow, rather long convoluted duct partially encircles the bursa copulatrix, a distal, short but greatly swollen part is wrapped within a thin sheath and forms a few lobes (Fig. 12A, pr). The prostate transits to a long single-looped penial sheath, which contains several loops of the ejaculatory duct (Fig. 12A, psh). The inverted penial sheath and the ejaculatory duct (penis) is long and rather thick, without spines and additional terminal processes (Fig. 9F). The moderately sized, globular bursa copulatrix contains some pinkish-red substance; it enters into the vagina via a short narrow stalk (Fig. 12B, bc). The proximal oviduct (Fig. 12B, pov) is short and rather straight; it extends from near to the junction of ampulla and prostate to the vagina at the bases of the seminal receptacle and bursal stalk. The seminal

receptacle is wide, swollen, similar in diameter to the vagina and appears as its prolongation rather than as a separate structure (Fig. 12B, rs). The vagina is a long, wide and convoluted duct (Fig. 12A, v); near its opening, it has an additional pouch, the vaginal bursa (Fig. 12A, vb), and then it opens via a short distal descending part (Fig. 12A, pv) and also transits to the off-white nidamental glands by a short wide indistinct distal oviduct (Fig 12A, dov).

Biology. Specimens were found predominantly on large boulders covered with several species of encrusting bryozoa, at 18–26 m depth, where it is a very common species.

Distribution. Presently known only from the type locality.

Remarks. *Adalaria slavi* **sp. nov.** is well distinguished from other species of the genus by a number of characters. The present species is similar to *A. proxima* (Fig. 11G) and *A. loveni* in the number of outer laterals (up to 9) but markedly differs regarding the shape of the first lateral tooth (beak shaped covered with small denticles instead of smooth straight cusp), shape of the prostate comprising two parts, different shape of the notal tubercles and characteristic opaque white small dots densely scattered all over the dorsal body side. *Adalaria tschuktschica* Krause, 1885 (Figs. 11I, M) and the poorly described *Lamellidoris spiculoides* Volodchenko, 1941 were considered as nomina dubia by Martynov (2005) and Millen (2006); they differ from *Adalaria slavi* in having spiniform elongated notal tubercles, by the shape of the first lateral teeth and by a considerably fewer number of outer lateral teeth (5–6 instead of 6–9). The recently described NE Pacific *A. evincta* Millen, 2006 significantly differs from *Adalaria slavi* by the presence of globular tubercles on a very narrow stalk with protruding long spicules, by the differently shaped lateral teeth, the smaller number of outer laterals (3–6 instead of 6–9), the long, convoluted, narrow prostate, and by the colouration. Specimens of *Adalaria jannae* Millen, 1987, have been found in course of the present study from Kamchatka waters, but shallowly and never together with the new species (Fig. 8A). They are well distinguished externally from *Adalaria slavi* in having smaller and more slender notal tubercles, a very hard dorsal notum with a strong network of spicules shining through, the presence of a well defined postbranchial gland, and the semitransparent white or yellowish colour without opaque white dots. Internally *A. jannae* (Figs. 11J, K) also clearly differs from *Adalaria slavi* by its radula that is entirely devoid of central teeth, sharper denticles on the first lateral tooth cusp, fewer outer laterals (4–6 instead of 6–9), and a shorter ejaculatory duct in the reproductive system. Finally, the present species markedly differs from the sympatric *Adalaria olgae* **sp. nov.**, which inhabits the same depth, by its white colour, bi- and tripinnate gills instead of unipinnate ones, distinct tentacle lobes on the oral veil, a sessile buccal pump, the shape of the first lateral teeth, and by a larger number of outer lateral teeth which differ in their shape. *Adalaria slavi* is readily distinguished from all known *Adalaria* species by having a large trilobed oral veil with paired lower lobes and an entire upper lobe, in combination with other features such as body size, colour, and radular features that are summarized in Table 2.

The present species, like at least most other *Adalaria* and *Onchidoris* species (see Millen 1987; Schmekel & Portmann 1982; present study, Figs. 12B; 15A, C), shows an arrangement of reproductive organs that differs from usual doridoidean systems with oocytes and allosperm entering the female gland mass via separate ducts (i.e., oviduct and uterine duct): the proximal oviduct does not enter the female gland mass but connects to the vaginal system; oocytes and allosperm enter the female gland mass via a distally situated, combined duct. Contrary information on *Adalaria jannae*, *A. proxima* (Alder & Hancock, 1854), *Onchidoris bilamellata* (L., 1767) and *O. muricata* (Müller, 1776) by Fahey & Valdés (2005) likely are due to observational errors (Thompson 1966; Millen, 1987; own reexaminations of *A. jannae*, *O. bilamellata* and *O. muricata*).

***Adalaria olgae* sp. nov.**
(Figures 3D, H; 6G–H; 7C; 10; 11E, F, H; 12C–D. Table 2)

Type Material. Holotype, ZMMU Lc-37451, NW Pacific near Kamchatka peninsula, Starichkov Id., 20–26 m depth, collected by T.A. Korshunova and A.V. Martynov, 14.08.2008. Paratypes, ZMMU Lc-37452, two

dissected specimens, same locality and collectors as holotype, 20–25 m depth, 14.08.2008. Paratype, ZMMU Lc-37453, one dissected specimen, same locality and collectors as holotype, 19.08.2008. Paratypes, ZMMU Lc-37454, three specimens, same locality and collectors as holotype, 14.08.2008. Paratypes, ZMMU Lc-37455, ten specimens, same locality and collectors as holotype, 14.08.2008.

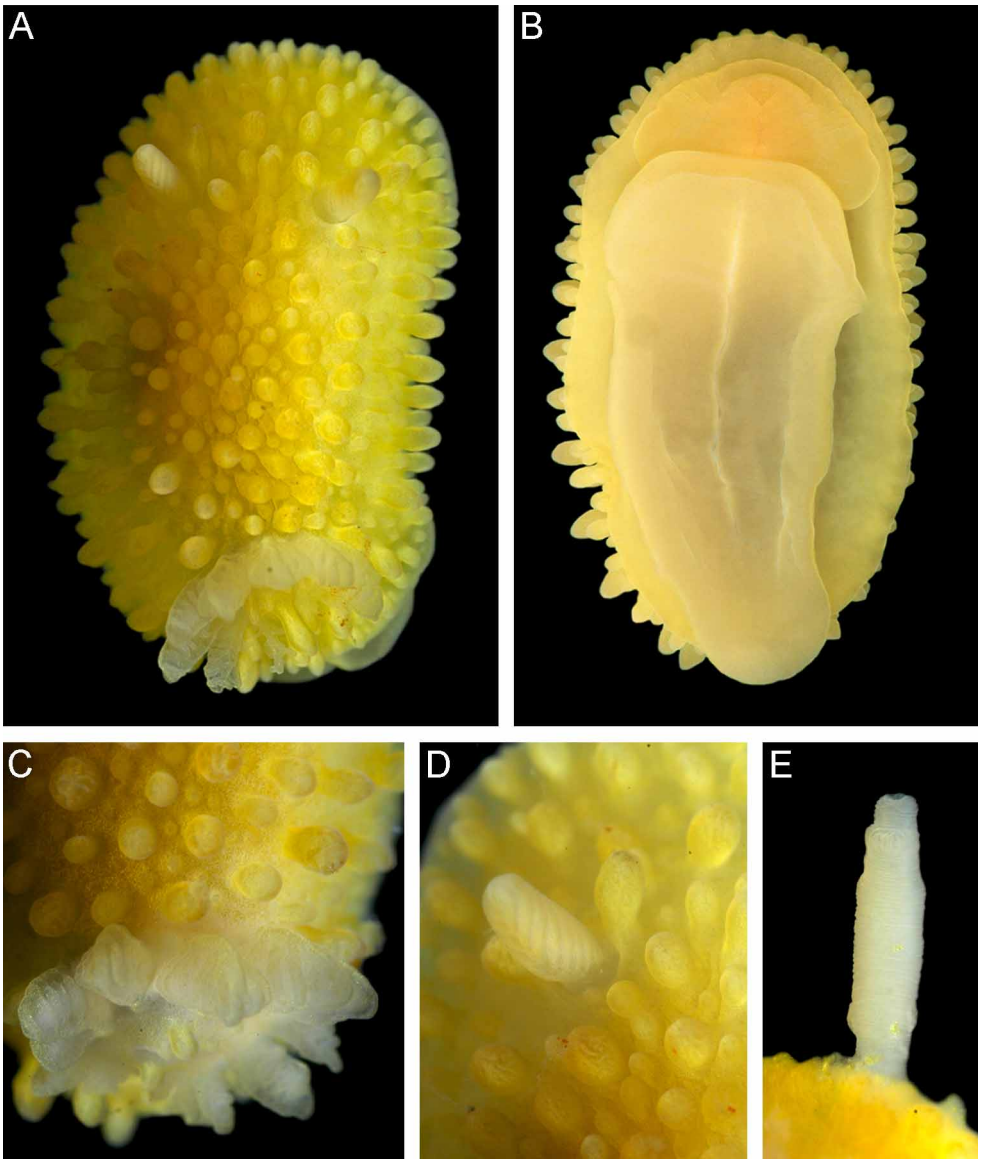

FIGURE 10. *Adalaria olgae* **sp. nov.**, living animals. A–B, Holotype, ZMMU Lc-37451, living animal, 13.5 mm length, NW Pacific, Kamchatka peninsula, Starichkov Island; A. Dorsal view; B. Ventral view; C–D, paratype, ZMMU Lc-37455, living animal 12 mm length, from the same locality as holotype; C. Close up of the gills; D. Rhinophore and rhinophoral pocket enlarged; E. Paratype, ZMMU Lc-37455, living animal, 11 mm length, from the same locality as holotype, everted penis. Photos: A–B Tatiana Korshunova; C–E Karen Sanamyan.

Type locality. NW Pacific, SE Kamchatka, Starichkov Id., 18–26 m depth.

Etymology. *Adalaria olgae* **sp. nov.** is named in honour of the daughter of two authors (AM and TK).

Description. *External morphology.* The dimensions of the holotype are 13.5 mm x 7 mm (Fig. 10). The length of 10 living specimens ranged from 5.5 to 13.5 mm, the width ranged from 3.5 to 7 mm. The consistency of the living animals is rather soft. The notum is moderately broad, rounded in front and posteriorly. The rhinophores are long and retract into sheaths with smooth edges, except for 3 tubercles of variable size at the edges of the sheaths (Fig. 10D). The rhinophoral sheath edges are capable of some contraction in living specimens. There are 6–9 rhinophoral lamellae. The clavus of each rhinophore lacks a

ridge posteriorly. The notum is densely covered with club-shaped or almost globular tubercles on a short stalk (Fig. 10A). The top of the tubercles often has a peculiar wrinkled appearance, somewhat tulip-shaped (Fig. 10C). The tubercles of the mid-notal area are somewhat wider and more globular than those at the notal edge. Larger tubercles are regularly intermingled with smaller ones. Rays of spicules radiating from the bases of tubercles form a network on the surface of the apparently soft notum (Fig. 6G). The spicules are not conspicuous externally. Each tubercle contains dense bundles of spicules, which do not protrude through the tubercle surface. The strongly calcified spicules are of various sizes, some with a narrow channel inside, some solid (Fig. 6H). A gill cavity is absent. Ten to thirteen unipinnate gills form a semicircle around the anus (Figs. 10A, C). Within the gill circlet, one long and four shorter elongate tubercles are situated just before the anus. The oral veil, as in *Adalaria slavi* **sp. nov.**, consists of a single, broad trapezoid anterior triangular projection which is medially not fused with the hyponotum, and two ventro-lateral flattened lobes (Fig. 10B). The tentacular lobes are less defined than in *Adalaria slavi*, so the general appearance of the oral veil is more similar to other *Adalaria* and *Onchidoris* species (Figs. 8A–C). The foot is broad, anteriorly rounded and thickened, and posteriorly slightly projecting beyond the notum in crawling animals forming a rounded tail (Fig. 10A).

Colour. The living specimens have a remarkable, bright lemon yellow ground colour, which is constant in all studied specimens (Fig. 10). Under magnification the yellow pigment appears as numerous small dots. The rhinophores (including lamellae) are similar in colour to the ground colour. The upper part of tubercles is lighter. The gills are semitransparent-white, without traces of the yellow pigment (Fig. 10). Bright white gill glands are in the notum at the gill bases.

Anatomy. *Digestive system.* The anterior part of the buccal bulb is modified into the prominent buccal pump having a short, broad, but conspicuous stalk (Fig. 7C). The buccal pump is fully banded by a relatively broad peripheral muscle (Fig. 7C). The lateral sides of the buccal pump have thin muscular fibres. The rounded labial disk is covered by yellowish cuticle bearing fine distinct regular polygonal elements (Figs. 3D, H). The radular formula in four specimens (11–13 mm length) is 30–31 x 3–4.1.1.1.4–3. A few anterior radular rows have only two or three outer lateral teeth, whereas most of the further radula rows possess four laterals. Radular teeth are slightly yellowish. The central tooth is small, elongated, rectangular, and folded (Figs. 11E, H). The first lateral tooth is provided with a long, wide base and a strong, slightly curved cusp. The cusp bears 4–8 denticles that are placed in a characteristic pattern. The outermost 1–3 denticles are conspicuously larger than the rest (Figs. 11F, H). There is a prominent triangular knob medial to the denticular ridge and a poorly defined medial wing. Outer lateral teeth are slightly elongated plates, with a downward directed cusp on its lower outside corner, and all are similar in size and shape (Figs. 11E–F). The stomach is relatively small and narrow. A stomach caecum is absent.

Circulatory system. In the pericardial sac the thin-walled, triangular posterior auricle and a smaller sized, oval ventricle are present. A well-defined blood gland lies above the central nervous system.

Central nervous system. The cerebral and pleural ganglia are well separated, the latter being somewhat smaller in size. The optic nerve is very short. The eyes are relatively large, with black pigment in all studied specimens. The pedal ganglia are smaller than the cerebrals, lay below them, and are connected to them by very short connectives. The rhinophoral ganglia are rather irregular, round or elongate. The buccal ganglia are roundish-oval. Gastro-esophageal ganglia are present. Five pairs of cerebral nerves, two pleural and three pedal ones are detected.

Reproductive system. (Figs. 12C, D). The ampulla is long and wide, but not filled by sperm in all studied specimens and thus generally appeared inconspicuous (Figs. 12C, D, a). The post-ampullar duct bifurcates into a thick prostatic loop and a proximal oviduct (Fig. 12D). The prostatic part of vas deferens is a relatively long thickened loop (Figs. 12C, D, pr), which does not encircle the bursa copulatrix. The prostate is wide, swollen, filled with sperm and not granulated. The prostate transitions into a long swollen single-looped penial sheath, which contains several loops of the ejaculatory part of the vas deferens (Fig. 12C, psh). The inverted penial sheath and ejaculatory duct (penis) are long and rather thick, without spines, but have two additional short terminal knobs, not united into a singular structure (Figs. 10E; 12D, p). The vagina is very

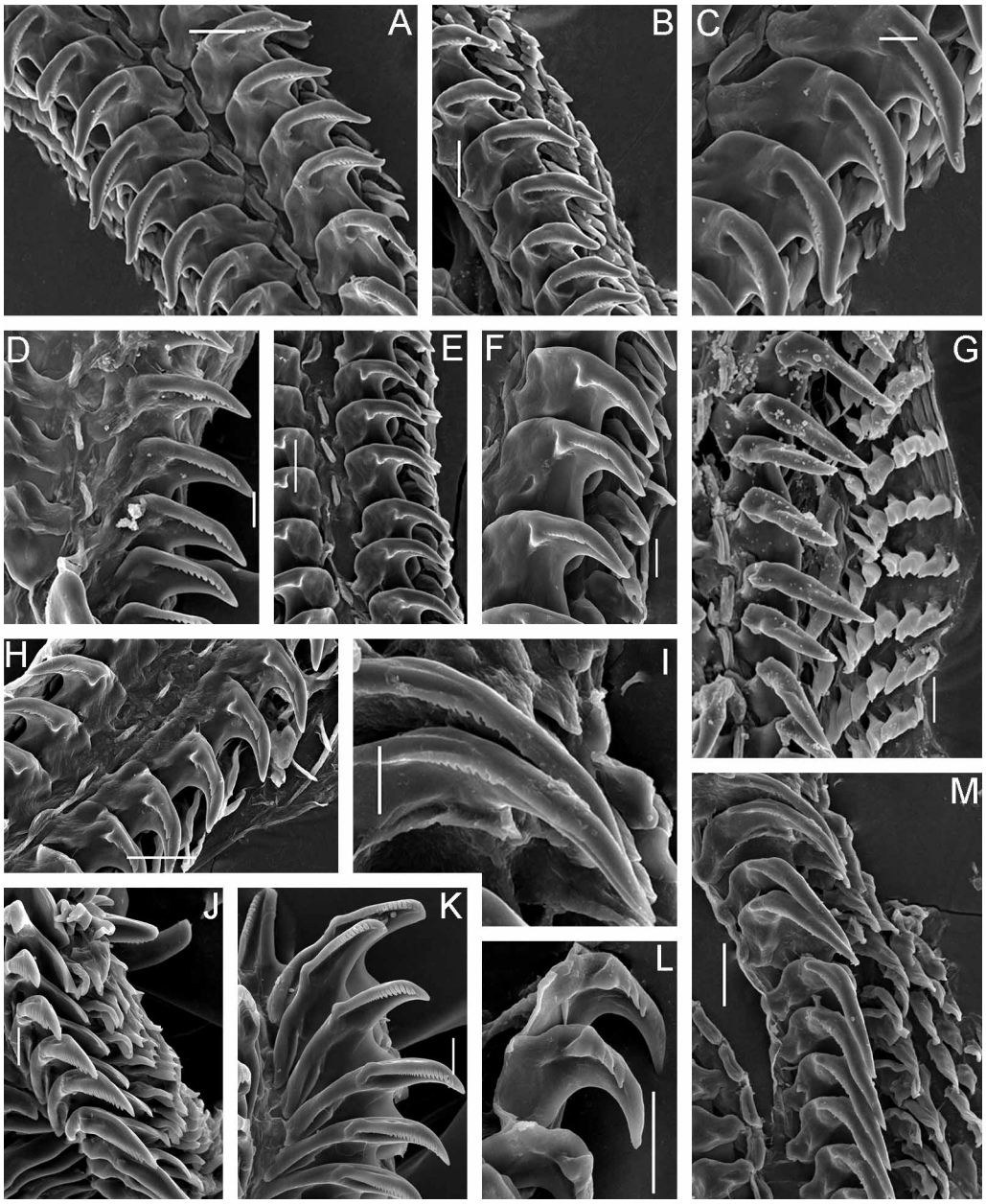

FIGURE 11. Radulae of species of the genus *Adalaria*, scanning electron micrographs. A–C, *Adalaria slavi* **sp. nov.**, paratype ZMMU Lc-37457, living specimen, 18 mm length; A. Middle part of the radula; B. Several middle rows showing outer laterals; C. Enlarged first laterals showing cusp denticle pattern; D. *Adalaria slavi* **sp. nov.**, paratype ZMMU Lc-37460, juvenile, 7 mm, middle part of the radula; E–F, *Adalaria olgae* **sp. nov.**, paratype ZMMU Lc-37454, living specimen, 9 mm length; E. Middle part of the radula; F. Few enlarged middle rows showing cusp denticles pattern of the first laterals and outer lateral teeth; G. *Adalaria proxima* (Alder & Hancock, 1854), ZMMU, not registered, Barents Sea, Dalne-Zelenetskaya Bay, living non-mature specimen with poorly differentiated reproductive system and smooth first lateral teeth, 15 mm length, intertidal, middle part of the radula; H. *Adalaria olgae* **sp. nov.**, paratype, ZMMU Lc-37455, living specimen, 10 mm length, middle part of the radula; I. *Adalaria tschuktschica* Krause, 1885, ZMMU, not registered, preserved specimen, 8 mm length, Chukchi Sea, Vrangel. Id., from 7 m depth, close up of the first laterals from the middle part of the radula showing pattern of cusp denticles; J–K, *Adalaria jannae* Millen 1987, ZMMU, not registered, living specimen, 8 mm length, Starichkov Island; J. Middle part of the radula, showing outer lateral teeth; K. Close up of the first laterals showing pattern of cusp denticles; L. *Adalaria proxima* (Alder et Hancock, 1854), ZMMU, not registered, juvenile specimen, 5 mm length, White Sea; M. *Adalaria tschuktschica*, middle part of the radula. Scale bars: A—50 μm, B—50 μm, C—20 μm, D—20 μm, E—50 μm, F—20 μm, G—30 μm, H—50 μm, I—20 μm, J—20 μm, K—20 μm, L—30 μm, M—50 μm. Photos: Alexander Martynov.

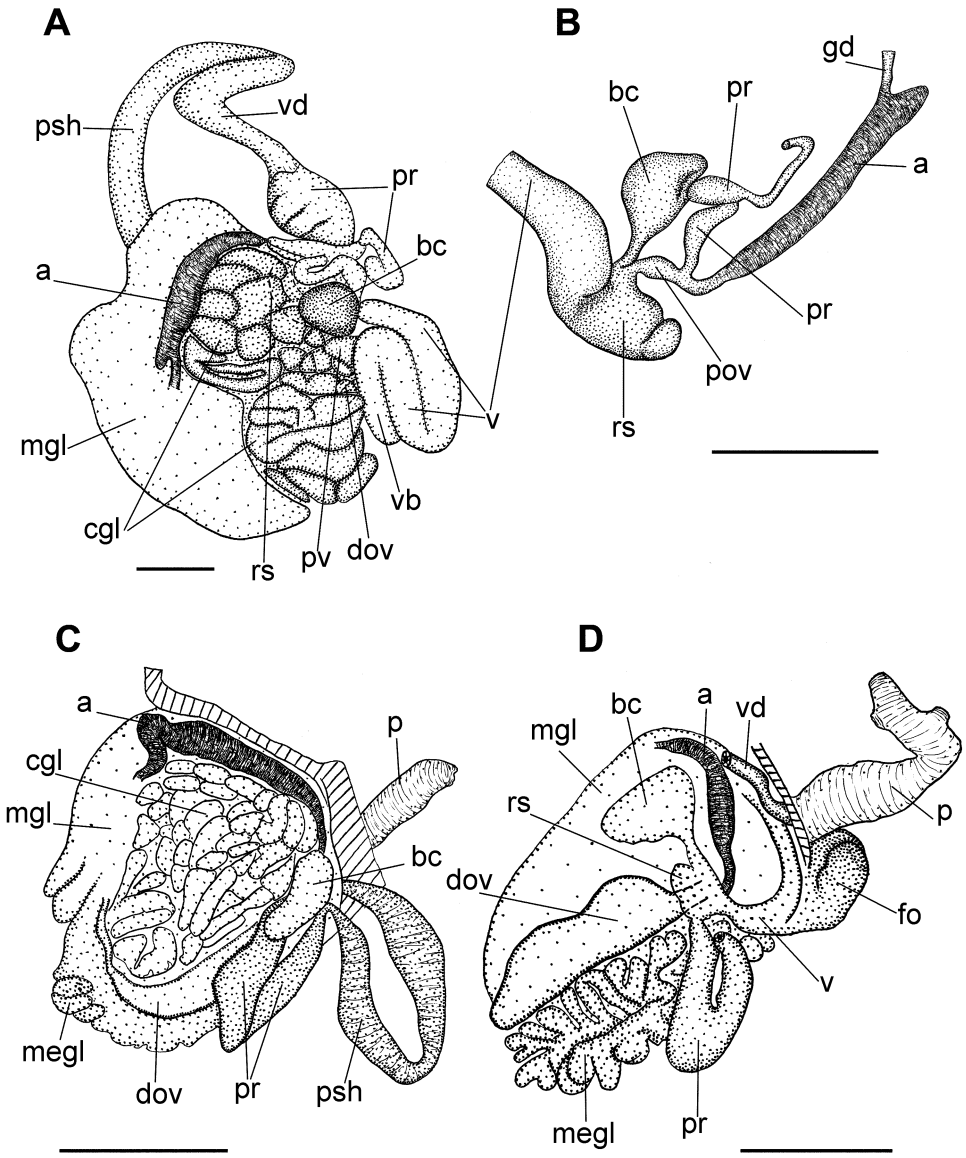

FIGURE 12. Reproductive system of members of the genus *Adalaria*. A–B, *Adalaria slavi* **sp. nov.**, based on examination of three paratypes ZMMU Lc-37447, living specimens, 18–20 mm length; A. Dorsal view; B. Details of the seminal reservoirs, vagina and connecting ducts; C–D, *Adalaria olgae* **sp. nov.**, based on examination of three paratypes, Lc-37455, living specimens, 9–12 mm length; C. Dorsal view; D. Lateral view showing oviduct, vagina and bursa connections. Scale bars—1 mm. Drawings by Tatiana Korshunova based on Alexander Martynov originals.

short and somewhat widened (Fig. 12D, v); it forms a short stalk to the relatively large globular bursa copulatrix (Fig. 12D, bc) containing a pinkish-brown substance. The proximal oviduct is very short and indistinct, entering near the base stalk of the bursa copulatrix. The seminal receptacle is hardly distinguishable and just represented by an elevation of the bursa stalk (12D, rs). The combined distal oviduct and uterine duct emerges near the junction of the ampulla and seminal receptacle. This duct is long and wide, narrowing and diminishing within the nidamental glands (Figs. 12C, D, dov).

Biology. Specimens were found predominantly on large boulders covered with several species of encrusting bryozoa, at 18–26 m depth, where the species is considerably less common than *Adalaria slavi***.**

Distribution. Presently known only from the type locality.

Remarks. *Adalaria olgae* **sp. nov.** is well distinguished from other species of the genus by a number of characters. From *A. proxima* (Figs. 8B; 11G) and *A. loveni* the present species markedly differs in having considerably fewer outer lateral teeth (3–4 instead of 9–13), by the shape of the first lateral tooth (curved beak

shaped with small denticles instead of almost straight smooth cusp) by its relatively short and markedly swollen prostate, a penis with two short terminal knobs, by the different shape of the notal tubercles, the bright yellow-lemon ground colour with off-white gills, and also by its smaller body length. *Adalaria tschuktschica* (Figs. 11 I, M) and *Lamellidoris spiculoides* differ from *Adalaria olgae* in having spiniform, elongate notal tubercles, a semicircular oral veil without evident tentacle lobes and a larger number of distinctly shaped outer lateral teeth. *Adalaria evincta* significantly differs from *Adalaria olgae* by its globular tubercles on a very narrow stalk bearing distinctly protruding long spicules, and a couple of internal features that are summarized in Table 2. *Adalaria jannae* is found in Kamchatka waters, but more shallowly and never together with the new species (Fig. 8A); it is well distinguished externally from *Adalaria olgae* in having smaller and more slender notal tubercles, a very hard notum with a translucent strong spicule network (Figs. 6K; 8A), and the presence of a well defined postbranchial gland. Internally *A. jannae* also clearly differs from *Adalaria olgae* by its radula that is entirely devoid of central teeth, among other features (Table 2). Finally, the present species differs considerably from the sympatric and syntopic *Adalaria slavi* **sp. nov.** (Figs. 9; 11A–D) regarding colour, unipinnate versus bi- and tripinnate gills, less defined tentacle lobes on the oral veil, a stalked buccal pump, fewer outer lateral teeth and their shape, a swollen prostate, and the tiny knob-shaped seminal receptaculum that is integrated at the base of the bursal duct. The coloration of *Adalaria olgae* (intense lemon yellow with semitransparent-white gills) is especially remarkable and diagnostic. Whereas for some predominantly white onchidoridid species yellowish colour variations have been reported (e.g. for *Adalaria proxima* (Fig. 8B) and *Onchidoris muricata*; Thompson & Brown 1984; Millen 1985) all collected specimens of *Adalaria olgae* showed a homogenous invariable intense lemon yellow colour, which markedly differs this new species from any yellowish onchidoridid colour varieties (including yellow and orange variants of *A. jannae* recorded from NE Pacific only). Its colour pattern also readily distinguishes *Adalaria olgae* from all other onchidoridids of similar size of the Kamchatka waters.

In the present study radulae of *Adalaria olgae* were compared with those of juvenile *Adalaria proxima* (Fig. 11 E–F and 11L respectively). *Adalaria proxima* at the length of ca. 10 mm transforms the denticulate first lateral teeth (Fig. 11L) into a smooth one (Fig. 11G) (Thompson 1958; Thompson & Brown 1984; present study). *Adalaria olgae* has denticulate first lateral teeth, and, at this size, already has a mature reproductive system. Thus, the first lateral teeth of the juvenile type persist in adult *Adalaria olgae*. Denticulation pattern, however, differs between *A. proxima* juveniles and *Adalaria olgae*: the former posess 2–3 large similar-sized denticles (Fig. 11L), whereas the new species has usually more than 5 denticles, which are differentiated into larger and smaller ones (Fig. 11F, H). All studied *A. proxima* specimens of 10–15 mm length (Barents Sea, Martynov et al. 2006) had immature, poorly developed reproductive systems but already entirely smooth first lateral teeth, whereas all investigated *Adalaria olgae* (8–13 mm) possess mature, well differentiated reproductive system and denticulated first laterals. Details of the reproductive system (for instance the very short vagina and distinct swollen prostate) and dorsal tubercles shape also significantly differ between *Adalaria olgae* and *A. proxima* (Table 2). Comparisions of the external shape of the adults and juveniles of *A. proxima* (Fig. 8B and 8C respectively) and adult specimens of *Adalaria olgae* (Fig. 10) highlight these differences. Distinguishing features of *Adalaria olgae* **sp. nov.** are summarized in Table 2.

Genus *Onchidoris* Blainville, 1816

Onchidoris: Blainville, 1816: 96

Synonyms:
Ancylodoris Dybowski, 1900
Atalodoris Iredale & O'Donoghue, 1923
Lamellidoris Alder & Hancock, 1855
Oicodespina Gistl, 1848
Onchidiorus Fèrussac, 1822

Onchidora Cuvier, 1830
Onchiodora Desmarest, 1858
Oncidoris Herrmannsen, 1847
Onchidorus Blainville, 1816
Oncidiodoris Gray, 1847
Oncodoris Agassiz 1846
Proctaporia Mörch, 1857
Villiersia Orbigny, 1837

Type species: *Onchidorus leachii* Blainville, 1816, by monotypy

Diagnosis. The notum is covered with well-defined spiculose tubercles of various shapes in most species. The integument contains a dense network of spicules. The rhinophores are lamellate. The rhinophoral pockets have poorly defined contractile smooth sheaths adjoined by several tubercles. The contractile gills are unipinnate, inserted separately in an almost complete circle around the anus. A common gill cavity or separated gill pits are completely absent. The oral veil is well defined, semi-circular. The foot is broad, not bilobed anteriorly, slightly narrowed posteriorly. The labial cuticle contains weakly defined polygonal elements. The buccal pump is large, prominent, on a narrow stalk, fully banded medially by a broad peripheral muscle. The salivary glands are short. The radula formula is 1–0.1.0–1.1.0–1 (but two outer laterals were reported from *O. muricata* by Thompson & Brown (1984)). The central teeth are small and rectangular; absent in most species. The first lateral tooth posesses a variably beak-shaped cusp, bearing small denticles in most species. The outer lateral teeth are squarish or elongate and usually posess a posterior or anterior denticle. The stomach is relatively small, a caecum is absent. The male part of the reproductive system shows a single short or looped prostate, and a long ejaculatory duct within a muscular sheath. The penis is not armed. The post-ampullar gonoduct bifurcates into a vas deferens and a proximal oviduct, which connects to the vagina. The combined distal oviduct and uterine duct starts separately from the vaginal duct, close to the external genital opening. The bursa copulatrix is small and rounded. The seminal receptacle is distinct but always buried within nidamental glands near to the base of the bursa.

The genus includes 15 valid species (one of them is described in the present paper, Table 3). The North Atlantic and the Mediterranean Sea is the center of the genus diversity. Most of the Atlantic species of the genus still are poorly known anatomically. Some species, e.g. *O. tridactila* Ortea & Ballesteros, 1982 were described only from few specimens and their deliniation from for instance *O. neapolitana* (Delle Chiaje, 1841) is not completely satisfactory; both *O. neapolitana* and *O. tridactila* share very similar first lateral teeh with a strongly folded flange.

***Onchidoris macropompa* sp. nov.**
(Figures 6I, J; 7D; 13; 14A–F; 15A, B. Table 3)

Onchidoris sp.: Martynov, 1997: 235

Material. Holotype, ZMMU Lc-37463, NW Pacific near Kamchatka peninsula, Starichkov Id., 6–7 m depth, collected by T.A. Korshunova and A.V. Martynov, 25.07.2008. Paratypes, Lc-37464, two specimens (one dissected), same locality and collectors as holotype, 25.07.2008. Paratype, ZMMU Lc-37465, one specimen (dissected), 21–26 m depth, same locality and collectors as holotype, 14.08.2008. Paratypes, ZMMU Lc-37466, two specimens (dissected), 12–15 m depth, same locality and collectors as holotype, 19.08.2008; Paratype, ZMMU Lc-37467, one specimen (dissected), Commander Ids., Medny Id., Cape Drovyanye Stolby, sample 101, 9–12 m depth, collector Oshurkov V.V., 17.07.1992. Paratype, ZMMU Lc-37468, one specimen (dissected), Commander Islands, Beringa Id., Ariy Kamen Id., sample 225, 25 m depth, rock, collector V.I. Shalukhanov, 02.08.1991. Paratypes, Lc-37469, two specimens (one dissected), Commander Islands, Mednyi Id., Kekur Korabelny Stolb Id., 18–19 m depth, rock, collector V.I. Shalukhanov, 11.07.1992.

Type locality. NW Pacific, SE Kamchatka, Starichkov Id., 6–26 m depth.

Etymology. From *macros* (Greek, = large) and *pompa* (Russian, Italian, = pump) refers to the largest relative size of the buccal pump of the present species within Onchidorididae.

Description. *External morphology.* The length of holotype is 7 mm, the width is 4 mm (Fig.13A). The length of 5 living specimens ranged from 6 to 15 mm, the width ranged from 4 to 6.5 mm. The consistency of the living animals is hard. The notum is moderately broad, rounded in front and posteriorly. The rhinophores are long and retract into sheaths with smooth edges, except for 3–4 tubercles of various sizes that are connected with the edges of the sheaths (Fig. 13F). The rhinophoral sheath edges are capable of some contraction in living specimens. There are 7–13 rhinophoral lamellae. The notum is densely covered with mushroom-shaped or club-shaped tubercles on a short stalk. The larger tubercles dominate all over the notum, but a single irregular zigzag row of smaller tubercles appears in the mid-notal line. Some smaller tubercles are also scattered around various notal areas and at the edge of the notum. The rays of the spicules that extend from the bases of tubercles form a dense network that shines through the notum surface (Figs. 6I; 13A, D). Each tubercle contains dense bundles of spicules, characteristically slightly protruding from the tubercle surface. The strongly calcified spicules are of various sizes; most have a narrow channel inside, some are solid (Fig. 6J). A gill cavity is absent. Inside the gill circlet there are several narrow tubercles of variable height. Ten to twelve unipinnate gills form a semicircle around the anus (Fig. 13D). The oral veil is semicircular (Figs. 13B, C). The foot is broad, anteriorly rounded and thickened, and posteriorly not projecting beyond the notum, forming a rounded tail (Fig. 13A).

Colour. The living specimens are off-white, semitransparent. Rhinophores (including lamellae) and gills are similar to the ground colour. Dull white gill glands are placed at the gills base. A postbranchial gland is indicated by a slightly conspicuous flattened area behind the gills.

Anatomy. Digestive system. The anterior part of the buccal bulb is modified to a prominent, large, very broad, buccal pump that sits on a short, narrow, conspicuous stalk (Fig. 7D). The buccal pump is fully banded by the broad peripheral muscle (Fig. 7D). Lateral sides of the buccal pump are provided with thin muscular fibres. The rounded labial disk is covered by colourless cuticle with indistinct labial elements. The radular formula in five specimens (8–15 mm length) is 35–38 x 1.1.1.1.1, radular teeth are almost colourless. The central tooth is distinct, relatively large, elongated, rectangular, and folded (Figs. 14A–C, E). The first lateral tooth is provided with a long, wide base and a strong, almost straight beak-shaped cusp. All teeth are entirely devoid of any denticles (Figs. 14A–F). The second lateral teeth are rectangular plates, with a downward directed cusp on its lower outside corner (Figs. 14B–C; E–F). The stomach is relatively small and narrow. The stomach caecum is absent.

Circulatory system. In the pericardial sac there is a rather wide triangular posterior auricle and a smaller sized and also triangular ventricle. The massive blood gland forms a single piece that is located above the central nervous system and projects slightly anteriorly and posteriorly.

Central nervous system. The cerebral and pleural ganglia are well separated, the latter being somewhat smaller in size. The optic nerve is very short. The eyes are relatively large, with black pigment in all studied specimens. The pedal ganglia are smaller than the cerebrals, lay below them and are connected to them by very short connectives. The rhinophoral ganglia are rather irregular, globular or elongate. The buccal ganglia are slightly oval. Gastro-esophageal ganglia are present. Five pairs of cerebral nerves, two pleural and three pedal ones are detected.

Reproductive system. (Figs. 15A, B). The ampulla is wide and swollen, somewhat kidney-shaped, and filled with sperm (Figs. 15A, a). A long post-ampullar duct is placed along a shallow groove in between the seminal receptacle and vagina and then bifurcates into a long vas deferens (Fig. 15A, pr) and the proximal oviduct (Fig. 15A, pov). The prostatic part of the vas deferens is a relatively long loop adjacent to, but not encircling the bursa copulatrix (Fig. 15A, pr). The prostate is narrow, not granulated; it narrows and then rapidly widens into a long swollen penial sheath; this forms ca. 2.5 loops, and contains several folds of the ejaculatory duct. (Fig. 15A, psh). The everted penial sheath and ejaculatory duct (penis) have two short terminal processes, and a third, very long one, that are united into a trifurcate penis (Fig. 15B, tp). The

globular bursa copulatrix (Fig. 15A, bc) contains a dark brown substance; it enters the proximal part of the vagina via a narrow, relatively long stalk. At its base, a duct, which is similar in diameter to the vagina, exits the vagina and leads to the ovoid seminal receptacle (Fig. 15A, rs). The vagina is wide and long (Fig. 15A, v). The small distal oviduct (Fig. 15A, dov) exits the vagina (Fig. 15A, v) close to the vaginal opening.

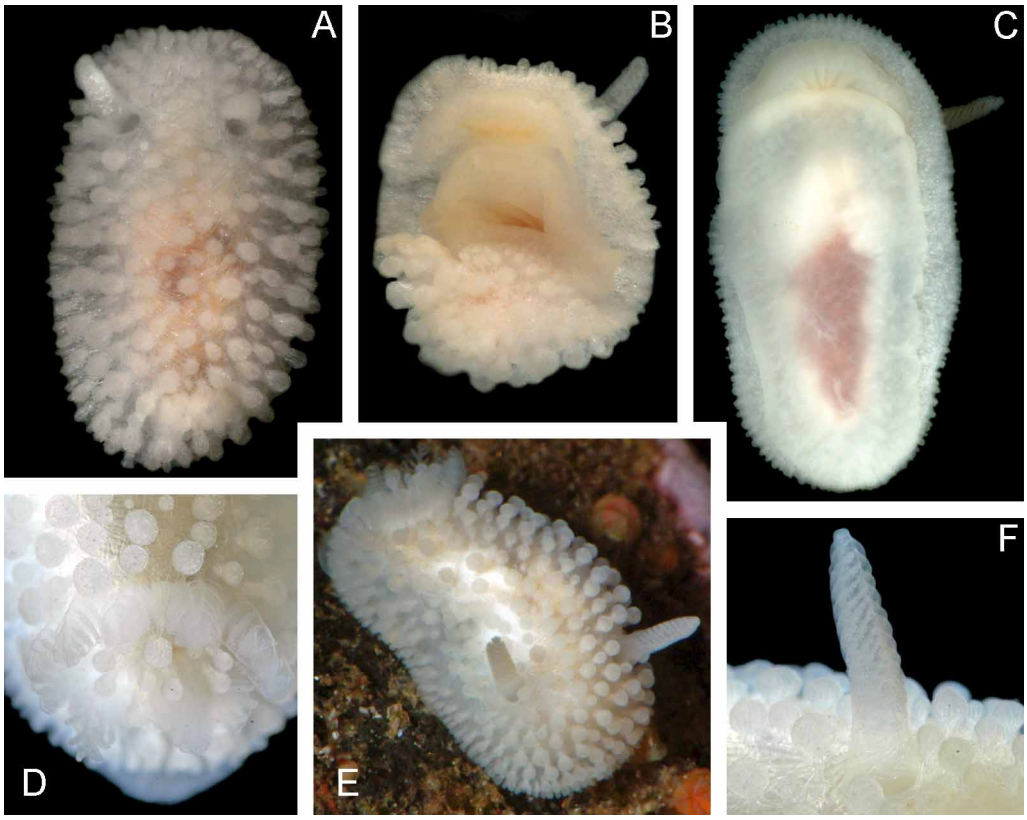

FIGURE 13. *Onchidoris macropompa* **sp. nov.**, living animals. A–B, holotype, ZMMU Lc-37463, living animal, 7 mm length, NW Pacific, Kamchatka peninsula, Starichkov Island; A. Dorsal view; B. Ventral view; C–F, paratype, Lc-37465, living animal, 15 mm length, from the same locality as holotype; C. Ventral view; D. Close up of the gills; E. Same specimen, frontal and dorsal view; F. Same specimen, close up of the rhinophore and rhinophoral pocket. Photos: A–C Tatiana Korshunova; D–F Karen Sanamyan.

Biology. Specimens were found predominantly under small stones covered with several species of encrusting bryozoa, at 6–15 m depth, rarely down to 18–25 m depth.

Distribution. Presently known only from the type locality in Kamchatka waters and from Commander Ids. (Martynov 1997, as *Onchidoris* sp.; present study).

Remarks. *Onchidoris macropompa* **sp. nov.** is externally most similar to *Onchidoris muricata* but can be readily distinguished from the latter by the smooth cusp of the first lateral teeth, completely devoid of any traces of denticles and in all studied specimens from different, distantly placed localities (i.e. from Kamchatka and from Commander Islands) (Figs. 14A–F). In contrast, numerous specimens of *Onchidoris muricata* from both North Atlantic and North Pacific waters always have revealed the presence of various numbers of cusp denticles (Thompson & Brown 1984; Millen 1985; present study, Figs. 14G–I). In addition, the cusps of the first lateral teeth of *Onchidoris macropompa* are straight (Figs. 14B–D, F), whereas in *Onchidoris muricata* it is typically distinctly curved (Figs. 14H, I). In addition, *Onchidoris macropompa* differs from most other species of the genus *Onchidoris* by presence of a central tooth in the radula (see Table 3 for comparison). The single other congener with radula formula of 1.1.1.1.1 and having smooth first lateral teeth, *O. bilamellata*, differs from *Onchidoris macropompa* by its colouration, the shape of the buccal pump, the shape of the first lateral teeth, and the pattern of the reproductive system.

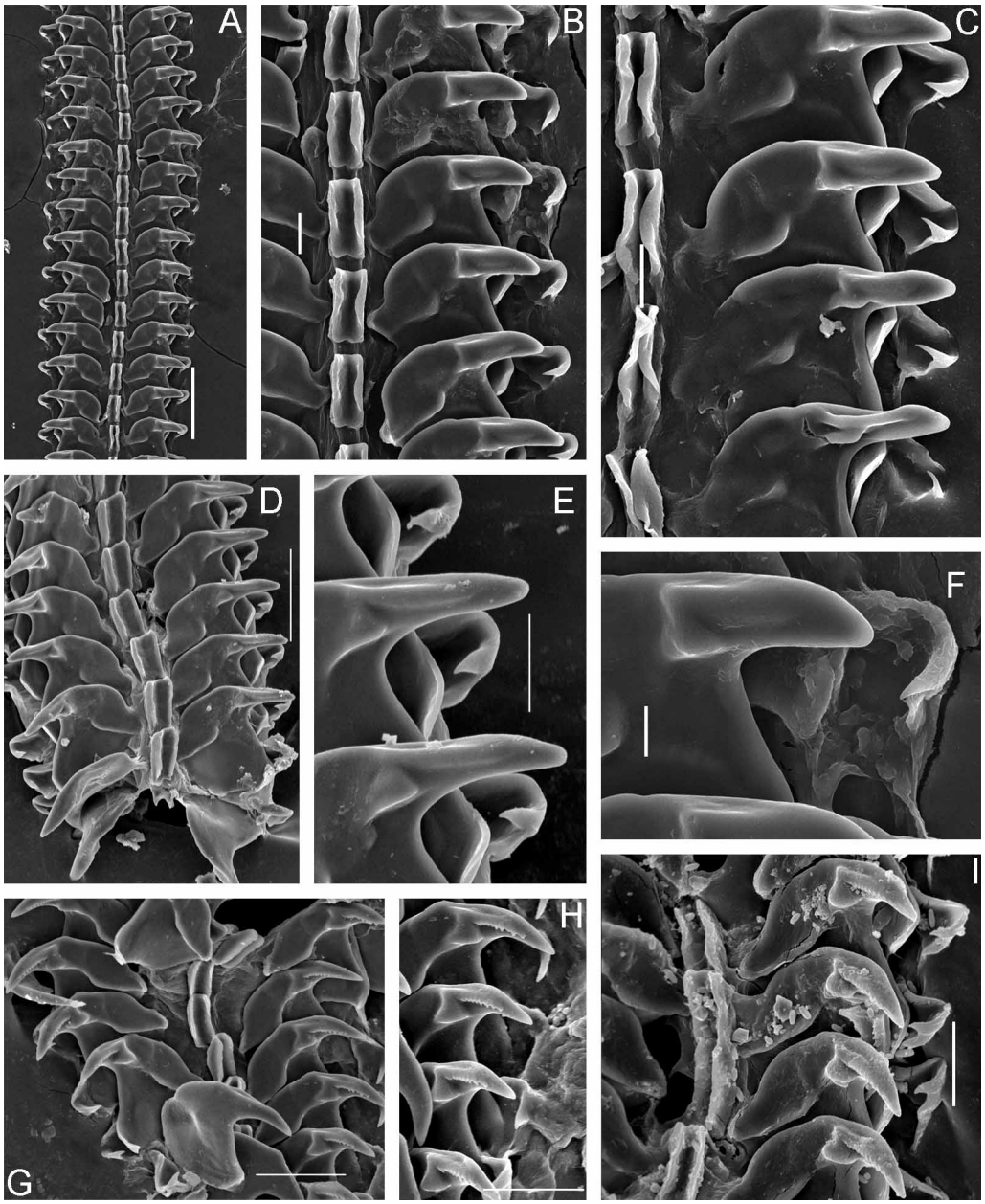

FIGURE 14. Radulae of species of the genus *Onchidoris*, scanning electron micrographs. A–C *Onchidoris macropompa* **sp. nov.**, paratype ZMMU Lc-37465, living specimen, 15 mm length, NW Pacific, Kamchatka peninsula, Starichkov Island; A. Part of the radula; B. Middle rows enlarged, showing straight smooth first lateral teeth; C. Anterior rows enlarged, showing straight smooth first lateral teeth; D. *Onchidoris macropompa* **sp. nov.**, paratype ZMMU Lc-37467, preserved specimen, 7 mm length, NW Pacific, Commander Islands, anterior part of the radula; E–F, *Onchidoris macropompa* **sp. nov.** ZMMU Lc-37465, living specimen, 15 mm length; E. Close up of cusps of first lateral teeth; F. Few rows enlarged; G–H, *Onchidoris muricata* (Müller, 1776), ZMMU, not registered, living specimen, 9 mm length, Barents Sea, Dalne-Zelenetskaya Bay, intertidal; G. Middle part of the radula; H. First lateral teeth enlarged; I. *Onchidoris muricata* (Müller, 1776), ZMMU, not registered, living specimen, 8 mm length, White Sea, Kandalakshsky Bay, Cape Kartesh, from 5–7 m depth. Scale bars: A—100 μm, B—20 μm, C—20 μm, D—60 μm, E—20 μm, F—10 μm, G—40 μm, H—50 μm, I—20 μm. Photos: Alexander Martynov.

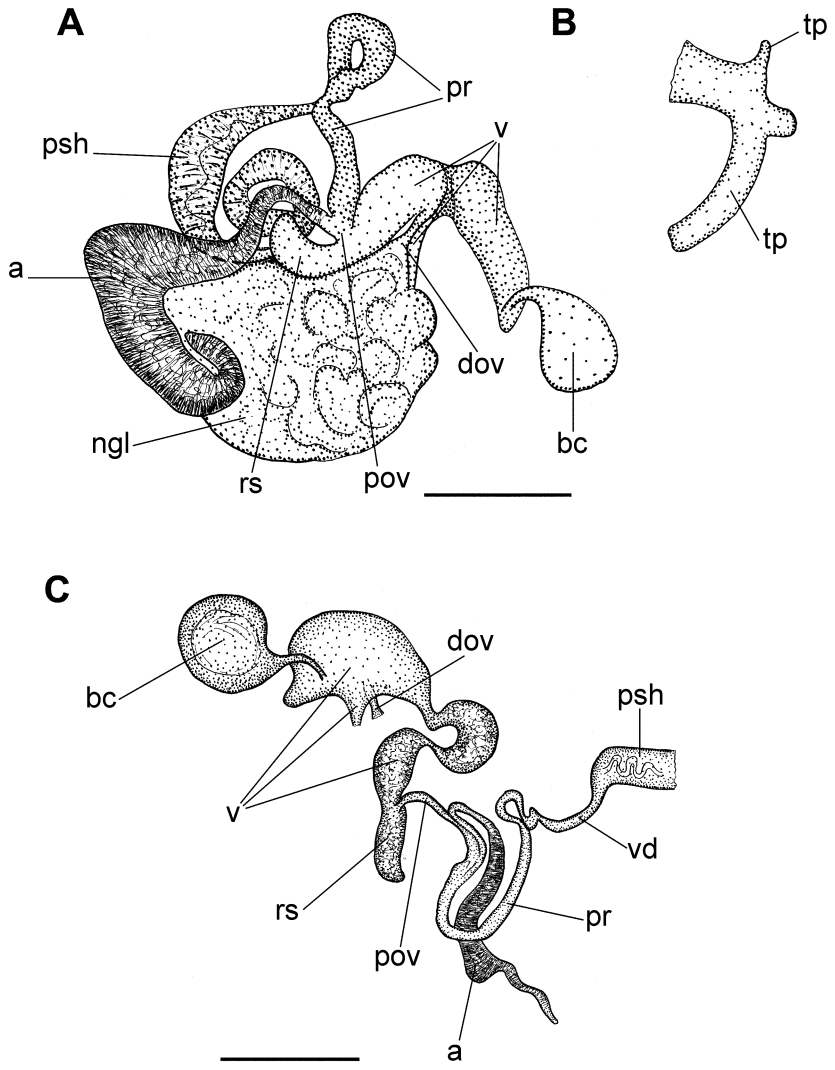

FIGURE 15. Reproductive system of members of the genus *Onchidoris*. A. *Onchidoris macropompa* **sp. nov.**, paratype ZMMU Lc-37467, dorsal view; B. *Onchidoris macropompa* **sp. nov.**, paratype ZMMU Lc-37465, terminal penial part showing the peculiar processes; C. *Onchidoris muricata* (Müller, 1776), ZMMU, not registered, living specimen, 10 mm length, Barents Sea, Dalne-Zelenetskaya Bay, dorsal view, nidamental glands and vas deferens partially omitted. Scale bars—1 mm. Drawings by Tatiana Korshunova based on Alexander Martynov originals.

Discussion

Dorid nudibranchs (Anthobranchia) comprise two major groups, the Bathydoridoidea and the Doridoidea (Wägele & Willan 2000; Schrödl et al. 2001). The Bathydoridoidea include the single family Bathydorididae that is characterized by a diaulic reproductive system (with exception of *Bathydoris spiralis* Valdés, 2002), an asymmetrical position of the anus, heart, and gills, and several other characters. The Doridoidea, in contrast, apparently all have a triaulic reproductive system (Schrödl 2000), and a symmetrical arrangement of gills forming a circle (or semicircle) around the mediodorsal anus (Wägele & Willan 2000). The latter group commonly is divided into Cryptobranchia and Phanerobranchia. Cryptobranchs were considered as a monophyletic group (Valdés 2002a), whereas several molecular and morphological studies have suggested a polyphyletic nature of Phanerobranchia (e.g. Martynov 1995; 1999a; Wollscheid & Wägele 1999; Wägele & Willan 2000; Wollscheid-Lengeling et al. 2001; Valdés 2002a; Millen & Martynov 2005). For

Bathydoridoidea a paraphyletic origin was also proposed (Valdés 2002b). Both phanerobranchs and the apparently archaic bathydoridids share the absence of the gill cavity (=gill pocket), contrary to the well-defined gill pocket in all cryptobranchs, and this was probably a reason for considering phanerobranchs as the more basal dorid groups (e.g. Valdés 2002a, b). According to the currently predominating phylogenetic hypothesis (Valdés 2002a; Fahey & Valdés 2005), the phanerobranch condition is a primary, plesiomorphic trait for dorids, whereas the possession of the gill cavity (cryptobranch condition) is regarded as an advanced feature, which was acquired once by the ancestor of cryptobranch dorids.

Despite the obvious importance of gill pockets, a special study involving a comparison of the cryptobranch and phanerobranch gills and gill cavity patterns in a broad taxonomical and phylogenetic context was never performed. Several "difficult" cases, e.g. the presence of the gill cavity in the traditional phanerobranch onchidoridid genera *Calycidoris* (Abraham 1876; Roginskaya 1972) and *Diaphorodoris* (Millen 1985) were not considered adequately. The principal difference between onchidoridid and typical cryptobranch gill cavities was claimed to be the inability in the former to contract the cavity edge over the retracted gills (Abraham 1876; Millen 1985), and the contractibility of the gills into the cavity instead of retractibility (Fahey & Valdés 2005). The gill cavity of the genera *Calycidoris* and *Diaphorodoris* was thus suggested as a special onchidoridid feature that is not homologous to the cryptobranch gill cavity (Millen 1985). However, until recently, the degree of the cavity edge contractibility in living onchidoridids was studied only in species of the genus *Diaphorodoris*, which has a weakly developed cavity (Millen 1985). *Calycidoris guentheri* instead has rather large gill cavity but it was never studied in living specimens. All approx. 150 preserved specimens of *Calycidoris guentheri* studied herein show some but never full contraction of the cavity edge over the gill (present study, Fig. 8E). The retraction of the entire gill circle into the gill pocket in cryptobranchs is caused by a strong retractor muscle (Potts 1981; Wägele & Willan 2000), which is absent in most phanerobranchs. However, *Onchidoris bilamellata*, *Calycidoris guentheri* and *Onchimira cavifera* **gen. et sp. nov.** also show a reasonably well developed retractor muscle (Potts 1981; AM unpublished data). The circulatory system, which is closely connected with the gill apparatus, also shows only minor differences between Cryptobranchia and Phanerobranchia (Potts 1981; García & García-Gomez 1990).

Even if we assume structural differences between phanerobranch and cryptobranch gill pockets, and suggest these are enough reason to conclude that the gill pocket complex is non-homologous prior to phylogenetic analysis, the recently published dorid phylogenetic analyses include considerable confusion and misunderstandings regarding gill cavities (pockets) and gill retractibility. For instance, in the data matrix provided by Fahey & Valdés (2005), the gill cavity of *Calycidoris* was coded like that of the cryptobranch *Cadlina*, i.e. as gill retractile into a true gill pocket; however, in the character list, only *Cadlina* was mentioned as having retractile gills. In contrast, Valdés (2002a) mentioned for *Calycidoris* the absence of any gill cavity. Furthermore, the small gill cavity of *Diaphorodoris* was coded as entirely absent (Valdés 2002a) or considered as "an opening" apparently not homologous to the cryptobranch cavity (Fahey & Valdés 2005).

The above mentioned contradictions may be resolved by accepting another scenario of the main events within dorid evolution as was suggested by Martynov (1994b; 1995; 1999a,b). It was proposed that the acquisition of the gill cavity is not an autapomorphy of the Cryptobranchia but an apomorphy of Doridoidea, with subsequent reduction of the cavity independently in different lineages, leading to phanerobranch dorids. This hypothesis explains the presence of a gill cavity within several genera of phanerobranch dorids, i.e. the genera *Calycidoris*, *Diaphorodoris* and *Loy*. In contrast to all previously recorded gill cavities in phanerobranchs, the herein described *Onchimira cavifera* possesses a gill cavity that is capable of full contraction over the gills (Figs. 2 F–H), which are united by a common membrane (Fig. 2E). I.e., there is not any structural difference to the "true" cryptobranch condition. *Onchimira cavifera* is thus considered here as having a gill cavity which is homologous to that of Cryptobranchia, linking between cryptobranch and fully developed or more or less reduced onchidoridid gill pockets.

An evolutionary scenario with independent acquisition of the gill cavity and of several correlated new features, like gill muscle-retractor and contractile pocket's edge, in different basal dorid lineages is hardly plausible. A reduction of such organs instead may more easily occur; various opisthobranch lines have

demonstrated repeated reduction and/or further modification of organs such as the mantle, shell, notal processes, dorsal papillae, radular rows, digestive gland etc (e.g. Schmekel 1985; Gosliner 1991; Wägele & Willan 2000). In summary, a hypothetic independent origin of the gill cavity complex in the Onchidorididae and in cryptobranch dorids is regarded as a less probable event than its repeated reduction. The major (and perhaps only) "apomorphy" of the Cryptobranchia, is thus considered to be a plesiomorphy; the basal division of Doridoidea into Phanerobranchia and Cryptobranchia is as questionable as is the current view of phanerobranchs to be the most basal dorids. Phylogenetic analyses including the newly discovered taxa and an unbiased coding of gill pocket structures are necessary to assess their homology and to reveal the evolutionary history of dorid nudibranchs.

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References

Abraham, P.S. (1876) Notes on some genera of nudibranchiate Mollusca, with notices of a new genus and some hitherto undescribed species, in the collection of the British Museum. *Annals and Magazine of Natural History*, series 4, 18, 132–146.

Abraham, P.S. (1877) Revision of the anthobranchiate nudibranchiate Mollusca, with descriptions or notices of forty-one hitherto undescribed species. *Proceedings of the Zoological Society of London*, 196–269.

Alder, J. & Hancock, A. (1842) Descriptions of several new species of nudibranchous Mollusca found on the coast of Northumberland. *Annals & Magazine of Natural History*, 9, 31–36.

Alder, J. & Hancock, A. (1845) Notice of a new genus and several new species of nudibranchiate Mollusca. *Annals & Magazine of Natural History*, 16, 311–316.

Alder, J. & Hancock, A. (1846) Notices of some new and rare British species of naked Mollusca *Annals & Magazine of Natural History*, 18, 289–294.

Alder, J. & Hancock, A. (1845-1855) *A monograph of the British nudibranchiate Mollusca: with figures of all the species*. Ray Society London, Pt. 1–7, pls. 1–48, pp. 1–54, Appendix, pp. i–xl.

Alder, J. & Hancock, A. (1862) Description of a new genus and some new species of naked Mollusca. *Annals and Magazine of Natural History*, series 3, 10, 102–105.

Ballesteros, M. (1984) *Onchidoris sparsa* (Alder y Hancock, 1846) en el Mediterráneo. *Iberus*, 4, 137–138.

Behrens, D.W. (1991) *Pacific coast nudibranchs: a guide to the opisthobranchs, Alaska to Baja California*. Second Edition. Sea Challengers, Monterey, California. 107 pp.

Bergh, R. (1879) Gattungen nordischer Doriden. *Archiv für Naturgeschichte* 45, 340–369.

Bergh, R. (1880) On the nudibranchiate gasteropod mollusca of the North Pacific Ocean, with special reference to those of Alaska, pt. 2. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 32, 40–127.

Blainville, H. (1816) Quartrième mémoire sur les mollusques, de l'ordre des cyclobranches. *Bulletin des Sciences par la Société Philomathique*, Paris 13, 93–97.

Burn, R. (1958) Further Victorian Opisthobranchia. *Journal of the Malacological Society of Australia*, 2, 20–36.

Coleman, N. (2001) *1001 Nudibranchs — Catalogue of Indo-Pacific Sea Slugs*. Neville Coleman's Underwater Geographic Pty. Ltd. Springwood, Queensland, 144 pp.

Crampton, D.M. (1977) Functional anatomy of the buccal apparatus of *Onchidoris bilamellata* (Mollusca: Opisthobranchia). *Transactions of the Zoological Society of London*, 34, 46–86.

Dall, W.H. (1871) Descriptions of sixty new forms of mollusks from the west coast of North America and the North Pacific Ocean, with notes on others already described. *American Journal of Conchology*, 7, 93–160.
Dall, W.H. (1900) A new species of *Pleurobranchus* from California. *Nautilus*, 14, 92–93.
Delle Chiaje, S. (1841) *Descrizione e notomia degli animali invertebrati della Sicilia citeriore osservati vivi negli anni 1822-1830*, Napoli, 7, plates 86–173.
Fahey, S.J. & Valdés, Á. (2005) Review of *Acanthodoris* Gray, 1850 with a phylogenetic analysis of Onchidorididae Alder and Hancock, 1845 (Mollusca, Nudibranchia). *Proceedings of the California Academy of Sciences*, Ser. *4*., 56, 213–273.
García, F.J. & García-Gomez, J.C. (1990) Anatomy of the circulatory system of the nudibranch *Platydoris argo* (Linne, 1767) with comparisons among Doridacea (Gastropoda, Opisthobranchia). *The Veliger* 33, 166–173.
Gosliner, T. M. (1991) Morphological parallelism in opisthobranch gastropods. *Malacologia* 32, 313–327.
Just, H. & Edmunds, M. (1985) North Atlantic nudibranchs (Mollusca) seen by Henning Lemche, with additional species from the Mediterranean and the north east Pacific. *Ophelia* suppl., 2, 1–170.
Krause, A. (1885) Ein Beitrag zur Kenntniss der Mollusken-Fauna des Beringsmeeres. II. Gastropoda und Pteropoda. *Archiv für Naturgeschichte* 51, 256–302.
Linnaeus, C. (1767) *Systema naturae per regna tria naturae*. Edito duodecima, reformata. Vol. 1, Regnum animale. Pt. 2. Impensis Direct. Laurentii Sakvii, Holmiae, 533-1327.
MacFarland, F.M. (1925) The Acanthodorididae of the California coast. *Nautilus*, 39, 49–65.
MacFarland, F.M. (1926) The Acanthodorididae of the California coast. *Nautilus*, 39, 94–103.
Martynov, A.V. (1992) A new species of nudibranch molluscs from the Sea of Japan with notes on the genus *Cuthonella* (Gastropoda, Opisthobranchia). *Zoologicheskiy Zhurnal*, 71, 18–24.
Martynov, A.V. (1994a) Materials for the revision of the nudibranch molluscs of the family Corambidae (Gastropoda, Opisthobranchia) Part 1. Taxonomy. *Zoologicheskiy Zhurnal*, 73, 1–15.
Martynov, A.V. (1994b) Materials for the revision of the nudibranch molluscs of the family Corambidae (Gastropoda, Opisthobranchia). Part II. The Origin. *Zoologicheskiy Zhurnal*, 73, 36–43.
Martynov, A.V. (1995) Materials for the revision of the nudibranch family Corambidae (Gastropoda, Opisthobranchia). Communication 2. Origin of the Corambidae. *Hydrobiological Journal*, 31, 59–66.
Martynov, A.V. (1997) Opistobranch gastropods at the Commander Islands with remarks on their fauna of the Russian Far Eastern Seas. In: *Benthic flora and fauna of the shelf zone of the Commander Islands*. 1997. Vladivostok, Dalnauka Press., ed. A.V. Rzhavsky, 230–241.
Martynov, A.V. (1998) Subclass Opisthobranchia. *In:* Adrianov A.V. & Kussakin O.G (Eds), *Taxanomic catalogue of biota of Peter the Great Bay*, Vladivostok, Dalnauka, pp. 204–209.
Martynov, A.V. (1999a) Buccal pumps, gills pockets and new understanding of suctorial phanerobranchial dorids. In Systematic, Phylogeny and Biology of Opisthobranch Molluscs, *(2nd International Workshop of Malacology) Menfi, Italy, June 10 – 14 1999*, 13–14.
Martynov, A.V. (1999b) *Nudibranch molluscs of North-West part of the Sea of Japan with discussion on taxonomy and phylogeny of the order Nudibranchia*. Ph. D. thesis. Zoological Institute RAS, St. Petersburg. 424 p.
Martynov, A.V. (2003) A new species of the genus *Rostanga* Bergh, 1879 (Mollusca: Opisthobranchia) from the Peter the Great Bay, the Japan Sea, with a discussion on the genus *Boreodoris* Odhner, 1939. *Ruthenica*, 13, 141–147.
Martynov, A.V. (2005) "Group" Acochlidiacea, clades Sacoglossa and Nudipleura. *In:* Yu.I. Kantor, A.V. Sysoev (Eds.), *Catalogue of Molluscs of Russia and Adjacent Countries*. Moscow: KMK Scientific Press Ltd, pp. 175–192.
Martynov, A.V. (2006) Nudipleura. *In:* Yu.I. Kantor, A.V. Sysoev (Eds.), *Marine and brackish water Gastropoda of Russia and adjacent countries: an illustrated catalogue.* Moscow: KMK Scientific Press Ltd., pp. 267–294, plates 131–138.
Martynov, A.V. & Baranets, O.N. (2002) A revision of the genus *Colga* Bergh (Opisthobranchia, Polyceridae), with description of a new species from the North Pacific. *Ruthenica*, 12, 23–43.
Martynov, A.V, Korshunova, T.A & Savinkin, O.V. (2006) Shallow-water opisthobranch molluscs of the Murman coast of the Barents Sea, with new distributional data and remarks on biology. *Ruthenica*, 16, 59–72.
Martynov, A.V. & Schrödl, M. (2008) The new Arctic side-gilled sea slug genus *Boreoberthella* (Gastropoda, Opisthobranchia): Pleurobranchoidean systematics and evolution revisited. *Polar Biology*, 32, 53–70.
Millen, S.V. (1985) The nudibranch genera *Onchidoris* and *Diaphorodoris* (Mollusca, Opisthobranchia) in the northeastern Pacific. *The Veliger* 28, 80–93.
Millen, S.V. (1987) The nudibranch genus *Adalaria*, with a description of a new species from the Northeastern Pacific. *Canadian Journal of Zoology*, 65, 2696–2702.
Millen, S.V. (2006) A new species of *Adalaria* (Nudibranchia: Onchidorididae) from the Northeastern Pacific. *Proceedings of the California Academy of Sciences*, 57, 357–364.
Millen, S.V. & Martynov, A.V. (2005) Redescriptions of the nudibranch genera *Akiodoris* Bergh, 1879 and *Armodoris* Minichev, 1972 with a new species of *Akiodoris* and a new family Akiodorididae. *Proceedings of the California Academy of Sciences*, 56, 1–22.

Müller, O.F. (1776) *Zoologiae Danicae. Prodromus seu animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium*. Heineck et Faber, Hafnia et Lipsia, 282 pp.

Müller, O.F. (1789) *Zoologica Danica sev animalium Daniae et Norvegiae rariorum ac minus notorum descriptiones et historia*, ed. 3, vol. 3, 1–71.

Ortea, J. (1979a) Dos nuevas especies ibéricas de *Onchidoris* (Mollusca Opisthobranchia, Doridacea) colectadas en Asturias. *Boletín de Ciencias de la Naturaleza* (IDEA), 24, 167–175.

Ortea, J. (1979b) *Onchidoris sparsa* (Alder and Hancock, 1846) in Asturias, Northern Spain. *The Veliger*, 22, 45–48.

Ortea, J. & Ballesteros, M. (1982) Sobre algunos *Onchidoris* Blainville, 1816 (Mollusca, Opistobranchia, Doridacea) del litoral iberico. *Investigación Pesquera* 46, 239–254.

Ortea, J., Llera, E.M & Vizcaíno, A. (1982) Segunda captura de *Onchidoris reticulata* Ortea, 1979 (Mollusca: Opisthobranchia: Doridacea). *Iberus*, 2, 85–89.

Ortea, J. & Urgorri, V. (1979) Una nueva especie de *Onchidoris* (Moluscos, Opistobranquios, Doridáceos) del Norte y Noroeste de España, *Onchidoris cerviñoi* n. sp. *Cahiers de Biologie Marine* 20, 507–513.

Pallas, P.S. (1788) Marina varia nova et rariora. *Nova Acta Academiae Scientiarum Imperialis Petropolitanae*, 2, 229–250.

Potts, G.W. (1981) The anatomy of respiratory structures in the dorid nudibranchs, *Onchidoris bilamellata* and *Archidoris pseudoargus*, with details of the epidermal glands. *Journal of the Marine Biological Association of the United Kingdom*, 61, 959–982.

Pruvot-Fol, A. (1951) Études des nudibranches de la Méditerranée (2e partie). *Archives de Zoologie Expérimentale et Générale* 88, 1–80.

Roginskaya, I.S. (1971) *Arctadalaria septemtrionalis* gen. n., sp. n. (Onchidoriddidae) a new nudibranchiate mollusc from the Laptev sea. *Zoologicheskii Zhurnal*, 50, 1154–1157.

Roginskaya, I.S. (1972) *Calycidoris guentheri* (Gastropoda, Nudibranchia). Taxonomy and distribution. *Zoologicheskii Zhurnal*, 51, 913–918.

Schmekel, L. (1985) Aspects of evolution within the opisthobranchs. *In:* Wilbur KM, ed. *The Mollusca*. London: Academic Press, pp. 221–267.

Schmekel, R.L. & Portmann A. (1982) *Opisthobranchia des Mittelmeeres, Nudibranchia und Saccoglossa*. Fauna e flora del Golfo di Napoli 40, *Monografia della Stazione Zoologica di Napoli*, pp. i–viii, 1–410, Springer-Verlag.

Schrödl, M. (2000) Revision of the nudibranch genus *Cadlina* (Gastropoda: Opisthobranchia) from the Southern Ocean. *Journal of the Marine Biological Association of the United Kingdom*, 80, 299–309.

Schrödl, M., Wägele, H., & Willan, R.C. (2001) Taxonomic redescription of the Doridoxidae Bergh, 1899 (Mollusca: Gastropoda: Opisthobranchia), an enigmatic family of deep water nudibranchs, with discussion of basal nudibranch phylogeny. *Zoologischer Anzeiger*, 240, 83–97.

Thompson, T.E. (1958) Observations on the radula of *Adalaria proxima* (A. & H.) (Gastropoda Opisthobranchia). *Proceedings of the Malacological Society of London*, 33, 49–56.

Thomspon, T.E. (1966) Studies on the reproduction of *Archidoris pseudoargus* (Rapp) (Gastropoda Opisthobranchia). *Philosophical Transactions of the Royal Society of London* (B), *Biological Sciences*, 250, 343–375.

Thompson, T.E. & Brown, G.H. (1984) *Biology of opisthobranch molluscs*, vol. 2, Ray Society, no. 156., 229 pp.

Valdés, Á. (2002a) A phylogenetic analysis and systematic revision of the cryptobranch dorids (Mollusca, Nudibranchia, Anthobranchia). *Zoological Journal of the Linnean Society*, 136, 535–636.

Valdés, Á. (2002b) Phylogenetic systematics of '*Bathydoris*' s.l. Bergh, 1884 (Mollusca, Nudibranchia), with the description of a new species from New Caledonian deep waters. *Canadian Journal of Zoology*, 80, 1084–1099.

Vayssière, A. (1919) Recherches zoologiques et anatomiques sur les Mollusques Opisthobranches du Golfe de Marseille, 2me Supplément. *Annales du Musee d'Histoire Naturelle de Marseille 17*, 53–92.

Volodchenko, N.I. (1941) New species of the nudibranchiate molluscs from the Far-Eastern seas of USSR. *Issledovaniya dalnevostochnykh morei USSR*, 1, 53–68.

Wägele, H., & Willan, R. (2000) Phylogeny of the Nudibranchia. *Zoological Journal of the Linnean Society*, 130, 83–181.

Wollscheid, E. & Wägele, H. (1999) Initial results on the molecular phylogeny of the Nudibranchia (Gastropoda, Opisthobranchia) based on 18S rDNA data. *Molecular Phylogenetics and Evolution*, 13, 215–226.

Wollscheid-Lengeling, E., Boore, J., Brown, W. & Wägele, H. (2001) The phylogeny of Nudibranchia (Opisthobranchia, Gastropoda, Mollusca) reconstructed by three molecular markers. *Organisms Diversity and Evolution*, 1, 241–256.