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The *Ophryotrocha labronica* group (Annelida: Dorvilleidae) — with the description of seven new species

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Abstract

This paper reviews the group of gonochoristic *Ophryotrocha* species, known as the "*O. labronica* group". This informal group is chararacterised by its unique maxillary P- and K-forceps and dorsomedian rosette glands. All members of the group are primarily gonochoristic and almost all have the diploid complement of chromosomes of 2n = 6. External morphological differences within the group are very slight. In males and females of all species the P-type maxillae change at maturity to the K-type with the right forceps being bifid. A jaw fossil from the Upper Cretaceous, attributable to the *O. labronica* group, attests to the long history of the group. As herein defined, the group includes: *O. labronica labronica, O. labronica pacifica, O. costlowi* **sp. nov**., *O. dimorphica, O. japonica* **sp. nov**., *O. macrovifera* **sp. nov.**, *O. notoglandulata, O. permanae* **sp. nov.**, *O. robusta* **sp. nov.**, *O. rubra* **sp. nov.**, *O. schubravyi, O. vellae* **sp. nov.**, *O. olympica*, nom. nud., *O. prolifica*, nom. nud., and *O. sativa*, nom. nud.. Seven species are formally described and diagnoses are provided for all remaining taxa in the taxonomic section. This is followed by an illustrated discussion of the morphology, reproductive traits, and relationships of the members of the informal group.

Key words: Polychaetes, taxonomy, reproduction, development, nutrient-rich waters, crossbreeding, *nomina nuda*

Introduction

Polychaetes of the genus *Ophryotrocha* Claparède & Mecznikow, 1869, found in shallow, nutrient-rich waters such as harbours, are very similar to each other in their external morphology, making species identifications on these criteria often difficult and sometimes impossible. In contrast, their reproductive patterns differ greatly, ranging from hermaphroditism to gonochorism and viviparity (Åkesson 1975). Crossing experiments of laboratory cultures led to the recognition of a number of new species. Many of these studies were published, referring to the animals by their laboratory names without formal descriptions, rendering the names as *nomina nuda*, *i.e.* names not (yet) available (Åkesson 1975, 1978; Pleijel & Eide 1996; Dahlgren *et al.* 2001; Åkesson & Paxton 2005).

We are here treating the group of gonochoristic *Ophryotrocha* sibling species which was first recognised by Åkesson (1973) for *O. labronica* La Greca & Bacci, 1962, two new species from the Mediterranean Sea and *O. notoglandulata* Pfannenstiel, 1972 from Japan. The group has been referred to as the "*O. labronica* group" and reported to include 15 species (Åkesson & Paxton 2005).

The *O. labronica* group is coherent and can be delineated from other *Ophryotrocha* species by its unique maxillary P- and K-forceps and dorsomedian rosette glands. All members of the group are primarily gonochoristic and all but two (or three) have the diploid complement of chromosomes of 2n = 6. External morphological differences within the group are very slight, in all species the P-type maxillae change at maturity to the K-type, with the right forceps being bifid. Monophyly of the *O. labronica* group was shown in an analysis employing morphological, sex strategy, and protein data by Pleijel & Eide (1996), and confirmed by the analyses of the mitochondrial genes 16S (Dahlgren *et al.* 2001), COI (Heggøy *et al.* 2007) and 16S and COI in combination with the nuclear gene H3 with bootstrap support of 100% (Wiklund *et al.* 2009).

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The fossil record of *Ophryotrocha* is scant. The oldest reported K-forceps, *O. lukowensis* Szaniawski, are from the middle Jurassic (163 Ma) and differ from the modern forms. However, K-forceps reported as *Ophryotrocha* sp. from the upper Cretaceous (85 Ma) by Eriksson & Lindström (2000) are extremely similar to those of modern *O. labronica* with respect to their general shape, right bifid forceps, and internal darker lines and pulp cavities. Its size compared to K-forceps of extant species indicates that this fossil came from a worm of similar size.

This paper will review the morphology, reproductive traits and relationships of the *O. labronica* group which includes 14 species. Only four of these species are formally described and 10 have been reported in the literature by their laboratory names or *nomina nuda*. Seven of the latter have been continuously cultured since their discovery (some as long as 40 years ago) and will be formally described below. Three species must remain as *nomina nuda*, as their cultures have not survived and they are not available as preserved specimens either.

Material and methods

Material examined. This study was largely based on the examination of live material reared in culture. The origins of the cultures are given in the individual species treatments. The cultures were handled as previously described by Åkesson (1967, 1973). The animals examined at higher magnifications were anaesthetised in 6% magnesium chloride. General drawings were prepared from specimens mounted on cavity slides, or squash preparations for jaw apparatuses. Specimens preserved for examination and/or type specimens were anaesthetised and fixed in 70% ethanol, with several later changes of alcohol. All drawings were made with the aid of a camera lucida. Photographs were taken with an Olympus SZX stereo microscope with Olympus ColorView IIFW camera (Fig. 1A–E) and an Olympus SZH stereo microscope with Sony CFW-310C colour digital camera (Fig. 1F). Scanning electron microscopy (SEM) procedures followed Rouse & Pleijel (2001). SEM preparations were fixed in 1% osmium tetroxide in seawater, critical-point dried, gold coated and examined with a JEOL JSM-6480LA. Type specimens have been deposited at the Australian Museum, Sydney (AM) and the Swedish Museum of Natural History, Stockholm (SMNH).

Presentation of Results section. Accounts of previously described species are limited to diagnoses and remarks. Because of the remarkable morphological similarity of the *O. labronica* group, the new species are described in an abbreviated form to avoid excessive repetition of similar morphology. In the "Discussion" section we discuss the morphology in detail, pointing out any observable differences between the members of the group. For completeness we also include diagnoses and remarks for the indeterminate *nomina nuda*. A comparison of size, morphology, reproduction and development of all species is given; it lists only those features that vary within the group (Table 1).

Results

Dorvilleidae Chamberlin, 1919

Ophryotrocha Claparède & Mecznikow, 1869

Type species: *Ophryotrocha puerilis* Claparède & Mecznikow, 1869 by monotypy.

Ophryotrocha labronica labronica La Greca & Bacci, 1962

Figure 2A, B, H; 4D, E; Table 1

Ophryotrocha labronica La Greca & Bacci, 1962: 15, figs 1–4, 7, 8, 11–16, 18; Pleijel & Eide 1996; Dahlgren *et al.* 2001; Simonini 2002; Åkesson & Paxton 2005; Heggøy *et al.* 2007; Simonini *et al.* 2009; Wiklund *et al.* 2009.
Ophryotrocha labronica labronica: Paxton & Åkesson 2007, figs 5–8.

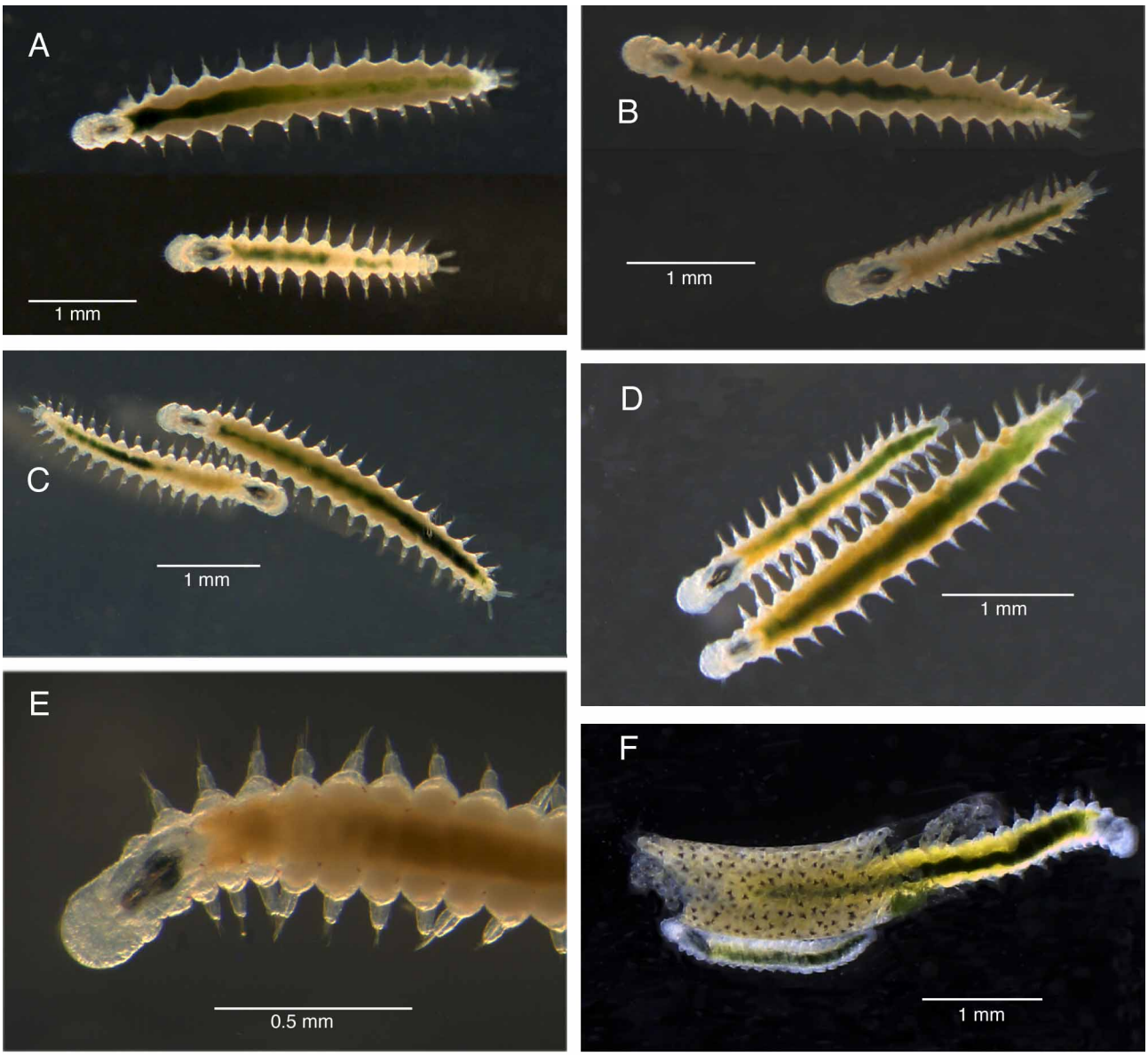

FIGURE 1. Photographs of live animals, larger animals female, smaller animals male, in dorsal view. A, *Ophryotrocha costlowi*, **sp. nov.**; B, *Ophryotrocha japonica*, **sp. nov.**; C, *Ophryotrocha macrovifera*, **sp. nov.**; D, *Ophryotrocha robusta*, **sp. nov.**; E, *Ophryotrocha rubra*, **sp. nov.**, close-up to show red spots; F, *Ophryotrocha vellae*, **sp. nov.**, egg tube with large number of larvae ready to be released, jaws of individual larvae appear as black spots, female inside tube, head towards right, male on lower surface of tube, head towards left.

Material examined. Type material: Neotype (SMNH 6422), cultured from specimens collected in the Bay of Naples (Mergellina harbour) Italy, 1965. Other material: Live cultures from same collection.

Diagnosis. Prostomium with short, ovate antennae, palps absent (Fig. 2A, B); two eyes medially connected; parapodia uniramous, lacking dorsal and ventral cirri, with dorsal protrusion; supra-acicular simple chaetae and subacicular coarsely serrated falcigers (Fig. 2H); pygidium with two cirri, pygidial median stylus absent in adults; up to five dorsal median rosette glands on posterior segments in males, up to three in females; anterior edge of mandibles with 25-28 teeth; maxillae with falcate P1-forceps, bidentate P2-forceps, K-forceps right bidentate, left falcate; gonochoristic; chromosomes 2n = 6; diameter of eggs 120–130 µm; tubular egg masses; released larvae without parapodia, with long pygidial median stylus (Figs. 4D, E).

Remarks. For a detailed description see Paxton & Åkesson (2007).

Distribution. Mediterranean and adjacent eastern North Atlantic; South Pacific: Sydney, Australia.

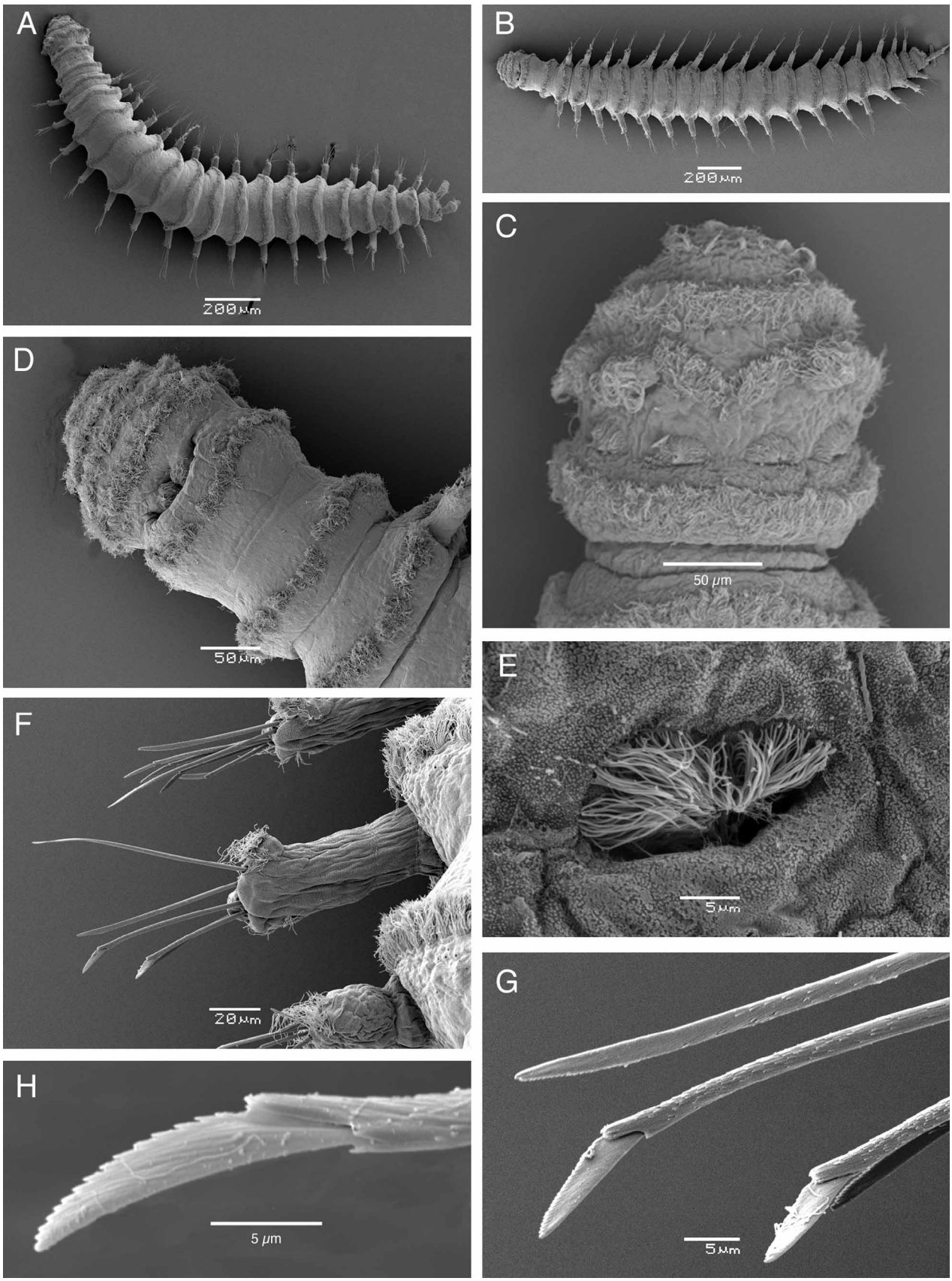

FIGURE 2. SEM images. A, Complete female *Ophryotrocha labronica labronica,* dorsal view; B, same, ventral view; C, anterior end of *Ophryotrocha vellae*, **sp. nov.**, dorsal view; D, anterior end of *Ophryotrocha macrovifera*, **sp. nov.**, ventral view; E, nuchal organ of *Ophryotrocha vellae*, **sp. nov.**; F, median parapodia of *Ophryotrocha macrovifera*, **sp. nov.**; G, chaetae of same; H, falciger of *Ophryotrocha labronica labronica.*

TABLE 1. Comparison between species of the *O. labronica* group.

Species	Maximum length mm (chaetigers)	Median connection between eyes	Serration of falcigers	Max. no. of rosette glands in males	Max. no. of rosette glands in females	No. of teeth at edge of mandible	No. of diploid chromoso-mes.	Diameter of eggs (µm)	No. of chaetigers at larval release	Length of larval pygidial stylus
O. l. labronica	4 (24)	present	coarse	5	3	25–28	6	120–130	0	long
O. l. pacifica	4 (20)	present	coarse	5	3	25–28	6	120–130	0	long
O. costlowi, sp.nov.	4 (18)	present	coarse	5	5	23–26	6	125	0	long
O. dimorphica	3 (19)	?absent	?	?present	3	17–22	?	140	0	long
O. japonica, sp.nov.	6 (28)	absent	fine	5	5	20–24	6	145–160	2–3	short
O. macrovifera, sp.nov.	5 (22)	present	fine	5	5	21–24	6	150–180	2	short
O. notoglandulata	8 (36)	present	fine	12	8	22–25	6	120–130	0	long
O. permanae, sp.nov.	4 (18)	present	coarse	5	4	24–27	6	125	0	long
O. robusta, sp.nov.	6 (22)	absent	coarse	7	7	22–25	10	120–130	0	long
O. rubra, sp.nov.	4 (20)	absent	coase	6	5	18–21	10	165–170	2	short
O. schubravyi	3 (20)	present	?	?	?	21	?8	120	0	long
O. vellae , sp.nov.	5 (20)	present	coarse	6	4	23–27	6	110	0	long
O. olympica , nom.nud.	?	absent	?	present	present	?	6	165	3	?
O. prolifica , nom.nud.	?	present	?	present	present	23–25	6	125	0	?
O. sativa , nom.nud.	?	present	?	?absent	?absent	?	6	120	0	?

***Ophryotrocha labronica pacifica* Paxton & Åkesson, 2007**
Table 1

Ophryotrocha labronica pacifica Paxton & Åkesson, 2007: 16.

Material examined. Type material: Holotype (SMNH 6423), cultured from specimens collected in Sagami Bay, Japan 1979. Other material: Live cultures from same collection.

Diagnosis. Morphology as for nominotypical subspecies; genetic distance expressed as a moderate fitness decrease in F_1 hybrids, but a severe hybrid breakdown in F_2 and lowered viability in crosses between subspecies.

Distribution. North Pacific Ocean: Sagami Bay, Japan; Hawaii; Los Angeles, California, USA.

***Ophryotrocha costlowi* sp. nov.**
Figure 1A; Table 1

Ophryotrocha costlowi nom. nud. Åkesson, 1978: 575; Pleijel & Eide 1996; Dahlgren *et al.* 2001; Åkesson & Paxton 2005; Wiklund *et al.* 2009.

Material examined. Type material: Holotype (AM W36856), complete female specimen, 2.9 mm long, 0.35 mm wide without parapodia (preserved) for 15 chaetigers; allotype (AM W36867), complete male specimen, 1.7 mm long, 0.25 mm wide without parapodia (preserved) for 12 chaetigers; 10 paratypes (AM W36868); 10 paratypes (SMNH T-8028); cultured from specimens collected at Pivers Island, near Duke University Marine Laboratory, Beaufort, North Carolina, USA, in 1974. Other material: Live cultures from same collection.

Description. Length of most live adults 2–3 mm (12–14 chaetigers), maximum length 4 mm (18 chaetigers). Live animals (Fig. 1A) translucent, preserved opaque white. Pigmentation consisting only of very small lateral red spots on some chaetigers. Prostomium anteriorly rounded, with pair of short, ovate antennae; palps absent; two eyes medially connected. Two peristomial achaetous segment-like rings.

Parapodia uniramous, lacking dorsal and ventral cirri, with dorsal protrusion, with retractile ventral lobe; 2–3 supra-acicular simple chaetae, 3–4 subacicular heterogomph falcigers and inferiormost simple chaeta; distal part of simple chaetae and blades of falcigers coarsely serrated. Pair of pygidial cirri present, pygidial median stylus absent in adults. Rosette glands, one per segment, present mid-dorsally on posteriormost segments of mature animals, up to five in males and females.

Mandibles with elongate shafts and bifid cutting plates with 23–26 tiny pointed teeth at anterior edge. Maxillary apparatus of P- and K-type in both sexes, with falcate P1-forceps, bidentate P2-forceps, K-forceps right bidentate, left falcate.

Reproduction and development. Gonochoristic; chromosomes 2n = 6; diameter of eggs 125 µm; tubular egg masses; released larvae without parapodia, with long pygidial median stylus.

Etymology. This species is named in honour of Dr. John D. Costlow Jr., former Director of Duke University Marine Laboratory, who facilitated the work of B.Å. in all possible ways during his stay at the laboratory.

Remarks. Åkesson (1978) reported the discovery of *Ophryotrocha costlowi*, **sp. nov.** from Beaufort and Morehead City, North Carolina, and the aquaria at the Bermuda Biological Station. However, the name was invalid as he did not designate type specimens, which is herewith rectified.

The new species was originally identified through crossbreeding experiments with other members of the *O. labronica* group (Åkesson 1978; Åkesson & Paxton 2005) and has been confirmed by gene sequence studies (Dahlgren *et al.*, 2001; Wiklund *et al.* 2009). According to the crossbreeding experiments it is most closely related to *O. labronica*, from which it can be distiguished only by the following small differences: rosette glands in *O. costlowi* number up to five in both sexes, while in *O. labronica* they are less numerous in females, reaching a maximum of three. The small teeth at the margin of the mandibular plate range from 23–26 in the former and 25–28 in the latter. See Table 1 for comparisons with other species.

Distribution. North Atlantic: Morehead City and Beaufort, North Carolina, USA; Bermuda.

Ophryotrocha dimorphica Zavarzina & Tzetlin, 1986
Table 1

Ophryotrocha dimorphica Zavarzina & Tzetlin, 1986: 1809, figs. 1–4; 1991, figs. 6–7.

Diagnosis. Prostomium with short, ovate antennae, palps absent; two eyes; parapodia uniramous, lacking dorsal and ventral cirri, with dorsal protrusion; supra-acicular simple chaetae and subaciular falcigers; pygidium with two cirri, pygidial median stylus absent in adults; dorsal median rosette glands on posterior segments; anterior edge of mandibles with 17-22 teeth, maxillae with falcate P1-forceps, bidentate P2-forceps, K-forceps right bidentate, left falcate; diameter of eggs 140 µm; tubular egg masses; released larvae without parapodia, with long pygidial median stylus.

Remarks. This species was described as a protandrous hermaphrodite with strongly pronounced sexual dimorphism and asexual reproduction. The authors described the males as smaller than females, but with a wider prostomium and larger K-forceps. During the sex change from male to female the K-maxillae were stated to moult once more resulting in K-maxillae with the smaller K-forceps typical of females. From our experience, *Ophryotrocha* maxillae do not moult any more once the K-type is in place.

As to the asexual reproduction, Zavarzina & Tzetlin (1986) described a restriction after chaetigers 5–7 and deterioration of the following segments resulting in fission. While the anterior part regenerated a new posterior end, the isolated posterior part remained alive for some weeks, but no regenerated heads were observed. The authors added that the frequency of fission increased with increased environmental stress. In our cultures we have recognised similar fissions in many species. It may occur if the animals are infected by intestinal or coelomic parasites or if the culture bowls are allowed to remain without adequate renewal of fresh water. The described fission is asexual, but it does not represent any reproduction as the number of individuals is the same before and after the process. On the basis of its morphology, *O. dimorphica* is a typical member of the gonochoristic *O. labronica* group. Most members of the group display some features of sexual dimorphism, especially difference in the size of the K-forceps. However, the difference in prostomial width of male and female *O. dimorphica* appears to be greater than in other species.

Distribution. Near Popov Island, Japan Sea.

Ophryotrocha japonica sp. nov.
Figure 1B; Table 1

Ophryotrocha japonica nom. nud. Pleijel & Eide, 1996; Dahlgren *et al.* 2001; Simonini 2002; Åkesson & Paxton 2005; Heggøy *et al.* 2007; Simonini *et al.* 2009; Wiklund *et al.* 2009.

Material examined. Type material: Holotype (AM W36869), complete female specimen, 2.2 mm long, 0.30 mm wide without parapodia (preserved) for 16 chaetigers; allotype (AM W36870), complete male specimen, 2.4 mm long, 0.30 mm wide without parapodia (preserved) for 16 chaetigers; 10 paratypes (AM W36871); 10 paratypes (SMNH T-8029); cultured from specimens collected in 1989 near Amakusa Marine Biological Laboratory in southern Japan. Other material: Live cultures from same collection.

Description. Length of most live adults 3–4 mm (15–18 chaetigers), maximum length 6 mm (28 chaetigers). Live animals (Fig. 1B) translucent, preserved opaque white. Pigmentation consisting only of very small lateral red spots on some chaetigers. Prostomium anteriorly rounded, with pair of short, ovate antennae; palps absent; two distinct eyes, not medially connected. Two peristomial achaetous segment-like rings.

Parapodia uniramous, lacking dorsal and ventral cirri, with dorsal protrusion; with retractile ventral lobe; 2–3 supra-acicular simple chaetae, 3–4 subacicular heterogomph falcigers and inferiormost simple chaeta; distal part of simple chaetae and blades of falcigers finely serrated. Pair of pygidial cirri present, pygidial median stylus absent in adults. Rosette glands, one per segment, present mid-dorsally on posteriormost segments of mature animals, up to five in males and females.

Mandibles with elongate shafts and bifid cutting plates with 20–24 tiny pointed teeth at anterior edge. Maxillary apparatus of P- and K-type in both sexes, with falcate P1-forceps, bidentate P2-forceps, K-forceps right bidentate, left falcate.

Reproduction and development. Gonochoristic; chromosomes 2n = 6; diameter of eggs varies from 145–160 µm in different populations, released larvae with 2–3 chaetigers, with short pygidial median stylus.

Etymology. The new species was first discovered in Japan, hence the name.

Remarks. The new species was originally identified through crossbreeding experiments in 1989 and has been confirmed by gene sequence studies (Dahlgren *et al.* 2001; Wiklund *et al.* 2009). Only four species of the *O. labronica* group have eyes not medially connected. Two of these (*O. robusta* **sp. nov.** and *O. rubra* **sp. nov.**) differ from *O. japonica* in having 10 diploid chromosomes rather than 6, in addition to different jaw and reproductive characteristics (Table 1). *Ophryotrocha olympica*, nom. nud. has the same number of chromosomes as *O. japonica*, similar egg size and the released larvae have three chaetigers, but it differs in that the eggs are white in colour rather than yellow as in *O. japonica*.

Distribution. North Pacific: Japan and Southern California, USA; Mediterranean.

***Ophryotrocha macrovifera* sp. nov.**

Figures 1C, 2D, F, G; 3C–F, H, I; 4A, B; 5A, C; Table 1

Ophryotrocha macrovifera nom. nud. Åkesson, 1975: 378; 1984; Levinton 1983; Pleijel & Eide 1996; Dahlgren *et al.* 2001; Simonini 2002; Åkesson & Paxton 2005; Simonini *et al.* 2009; W
iklund *et al.* 2009.

Material examined. Type material: Holotype (AM W36872), complete female specimen, 3.1mm long, 0.35 mm wide without parapodia (preserved) for 18 chaetigers; allotype (AM W36873), complete male specimen, 2.1 mm long, 0.25 mm wide without parapodia (preserved) for 14 chaetigers; 10 paratypes (AM W36874); 10 paratypes (SMNH T-8030); cultured from specimens collected at Kyrenia, Cyprus, 1972. Other material: Live cultures from same collection.

Description. Length of most live adults 3–4 mm (14–16 chaetigers), maximum length 5 mm (22 chaetigers). Live animals (Fig. 1C) translucent, preserved opaque white. Pigmentation consisting only of very small lateral red spots on some chaetigers. Prostomium anteriorly rounded, with pair of short, ovate antennae; palps absent (Fig. 2D); two eyes medially connected (Fig. 3C, D). Two peristomial achaetous segment-like rings.

Parapodia uniramous (Fig. 2F), lacking dorsal and ventral cirri, with dorsal protrusion, with retractile ventral lobe; 4–5 supra-acicular simple chaetae, 4–5 subacicular heterogomph falcigers and inferiormost simple chaeta; distal part of simple chaetae and blades of falcigers finely serrated (Fig. 2G). Pair of pygidial cirri present, pygidial median stylus absent in adults (Fig. 4A). Rosette glands (Fig. 4B), one per segment, present mid-dorsally on posteriormost segments of mature animals, up to five in males and females.

Mandibles with elongate shafts and bifid cutting plates with 21–24 tiny pointed teeth at anterior edge (Fig. 3E, F). Maxillary apparatus of P- and K-type in both sexes, with larval maxillae (Fig. 3H), falcate P1-forceps (Fig.3I), bidentate P2-forceps (Fig. 5A), K-forceps right bidentate, left falcate (Fig. 5C).

Reproduction and development. Gonochoristic; chromosomes 2n = 6. Diameter of eggs varies from 150–180 µm in different populations. Tubular egg masses, released larvae with two chaetigers and short pygidial median stylus.

Etymology. The name of the new species refers to its large yolky eggs.

Remarks. The new species was originally collected from Cyprus, Mediterranean Sea in 1972 and identified as a new species through crossbreeding experiments (Åkesson 1975) which have been confirmed by gene sequence studies (Dahlgren *et al.* 2001; Heggøy *et al.* 2007; Wiklund *et al.* 2009). *Ophryotrocha macrovifera* is unique among the *O. labronica* group for the following combination of characters: having medially connected eyes and larvae possessing 2–3 pairs of parapodia at hatching.

Distribution. Mediterranean: Cyprus, Genoa, Venice, Italy; Alexandria, Egypt; North Atlantic: Florida, USA, Portugal.

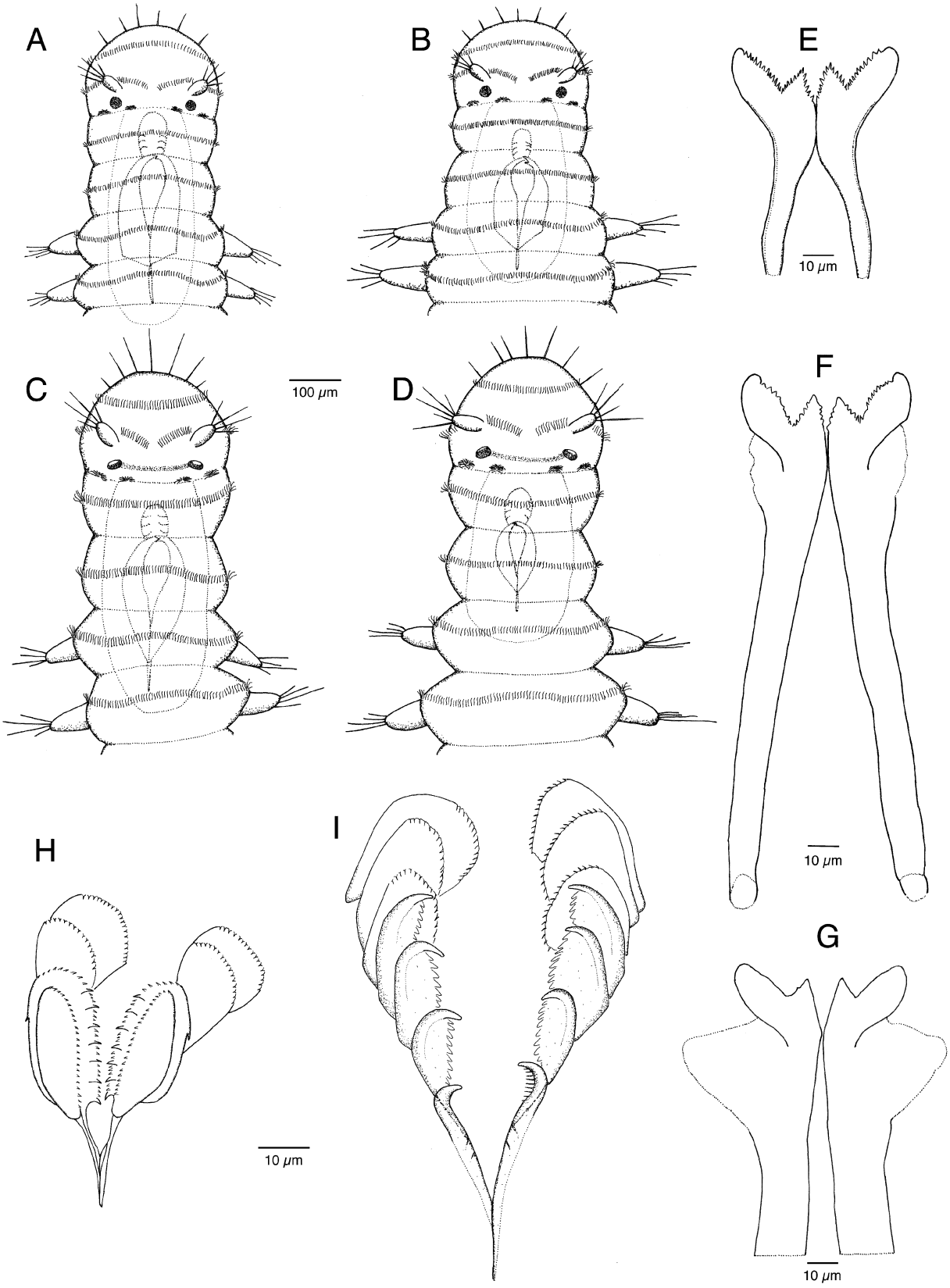

FIGURE 3. Anterior ends, dorsal view (A–D). A, Male *Ophryotrocha robusta*, **sp. nov.**; B, female of same; C, male *Ophryotrocha macrovifera*, **sp. nov.**; D, female of same. Mandibles, dorsal view (E–G). E, 8-chaetiger *Ophryotrocha macrovifera*, **sp. nov.**; F, 18-chaetiger female of same; G, 12-chaetiger *Ophryotrocha permanae*, **sp. nov.**. Maxillae, dorsal view (H, I). H, L-maxillae of 2-chaetiger larva of *Ophryotrocha macrovifera*, **sp. nov.**, I, P1-maxillae of 7-chaetiger juvenile of same.

***Ophryotrocha notoglandulata* Pfannenstiel, 1972**
Table 1

Ophryotrocha notoglandulata Pfannenstiel, 1972: 117, figs. 1-3; Pleijel & Eide 1996; Dahlgren *et al.* 2001; Heggøy *et al.* 2007; Wiklund *et al.* 2009.

Material examined. Live cultures from specimens collected at the Misaki Marine Biological Station, Sagami Bay, Japan, in 1961 by Prof. C. Hauenschild.

Diagnosis. Prostomium with short, ovate antennae, palps absent; two eyes medially connected; parapodia uniramous, lacking dorsal and ventral cirri, with dorsal protrusion; supra-acicular simple chaetae and subacicular finely serrated falcigers; pygidium with two cirri, pygidial median stylus absent in adults; up to 12 dorsal median rosette glands on posterior segments in males, eight in females; anterior edge of mandibles with 22–25 teeth, maxillae with falcate P1-forceps, bidentate P2-forceps, K-forceps right bidentate, left falcate; gonochoristic; chromosomes 2n = 6; diameter of eggs 120–130 µm; released larvae without parapodia, with long pygidial median stylus.

Remarks. *Ophryotrocha notoglandulata* can be distinguished from all other species of the *O. labronica* group by its larger maximum size and greater number of rosette glands.

Distribution. Western North Pacific: Sagami Bay, Japan.

***Ophryotrocha permanae*, sp. nov.**
Figure 3G; Table 1

Ophryotrocha permanni nom. nud. Pleijel & Eide, 1996; Dahlgren *et al.* 2001; Heggøy *et al.* 2007; Wiklund *et al.* 2009.

Material examined. Type material: Holotype (AM W36875), complete female specimen, 1.8 mm long, 0.20 mm wide without parapodia (preserved) for 15 chaetigers; allotype (AM W36876) complete male specimen, 1.6 mm long, 0.20 mm wide without parapodia (preserved) for 14 chaetigers; 9 paratypes (AM W36877); 10 paratypes (SMNH T-8031); cultured from specimens collected at Link Port, Indian River, Florida, USA, in 1994. Other material: Live cultures from same collection.

Description. Length of most live adults 2–3 mm (13–16 chaetigers), maximum length 4 mm (18 chaetigers). Live animals translucent, preserved opaque white. Pigmentation consisting only of very small lateral red spots on some chaetigers. Prostomium anteriorly rounded, with pair of short ovate antennae; palps absent; two eyes medially connected. Two peristomial achaetous segment-like rings.

Parapodia uniramous, lacking dorsal and ventral cirri, with dorsal protrusion, with retractile ventral lobe; 2–3 supra-acicular simple chaetae, 3–4 subacicular heterogomph falcigers and inferiormost simple chaeta; distal part of simple chaetae and blades of falcigers coarsely serrated. Pair of pygidial cirri present, pygidial median stylus absent in adults. Rosette glands, one per segment, present mid-dorsally on posteriormost segments of mature animals, up to five in males, four in females.

Mandibles with elongate shafts with extensive lateral sclerotisation in old animals (Fig. 3G), and bifid cutting plates with 24–27 tiny pointed teeth at anterior edge. Maxillary apparatus of P- and K-type in both sexes, with falcate P1-forceps, bidentate P2-forceps, K-forceps right bidentate, left falcate.

Reproduction and development. *Ophryotrocha permanae* is not strictly gonochoristic. Some populations are mixed, including males, gonochoristic females and thelygenic females. Chromosomes 2n = 6; diameter of eggs 125 µm; tubular egg masses; released larvae without parapodia, with long pygidial median stylus.

Etymology. This species is named in honour of Ms. Jenny Perman, who has been in charge of the extensive *Ophryotrocha* "living gene bank" cultures at our Gothenburg laboratory for many years.

Remarks. The new species was originally identified through crossbreeding experiments and has been confirmed by gene sequence studies (Dahlgren *et al.*, 2001; Heggøy *et al.* 2007; Wiklund *et al.* 2009). *Ophryotrocha permanae* is morphologically very similar to *O. labronica, O. costlowi* and *O. vellae* (Table 1).

The only difference that we could observe is that the lateral sclerotisation of mandibles in relatively large specimens of *O. permanae* can be more extensive than in any of the other species (Fig. 3G).

Distribution. North Atlantic: Florida, USA; East China Sea: Sanya and Xiamen, China; Okinawa, Japan.

***Ophryotrocha robusta* sp. nov.**
Figure 1D; 3A, B; 5B; Table 1

Ophryotrocha robusta nom. nud. Åkesson, 1975: 378; Pleijel & Eide 1996; Dahlgren *et al.* 2001; Simonini 2002; Heggøy *et al.* 2007; Simonini *et al.* 2009; Wiklund *et al.* 2009.

Material examined. Type material: Holotype (AM W36878), complete female specimen, 4.4 mm long, 0.60 mm wide without parapodia (preserved) for 22 chaetigers; allotype (AM W36879) complete male specimen, 2.3 mm long, 0.35 mm wide without parapodia (preserved) for 15 chaetigers; 10 paratypes (AM W36880); 10 paratypes (SMNH T-8032); cultured from specimens collected at Malaga, Spain in 1978. Other material: Live cultures from same collection.

Description. Length of most live adults 3–4 mm (14–16 chaetigers), maximum length 6 mm (22 chaetigers). Live animals (Fig. 1D) translucent, preserved opaque white. Pigmentation consisting only of very small lateral red spots on some chaetigers. Prostomium anteriorly rounded, with pair of short ovate antennae; palps absent; two distinct eyes, not medially connected. Two peristomial achaetous segment-like rings (Fig. 3A, B).

Parapodia uniramous, lacking dorsal and ventral cirri, with dorsal protrusion, with retractile ventral lobe; 2–3 supra-acicular simple chaetae, 2–4 subacicular heterogomph falcigers and inferiormost simple chaeta; distal part of simple chaetae and blades of falcigers coarsely serrated. Pair of pygidial cirri present, pygidial median stylus absent in adults. Rosette glands, one per segment, present mid-dorsally on posteriormost segments of mature animals, up to seven in males and females.

Mandibles with elongate shafts and bifid cutting plates with 22–25 tiny pointed teeth at anterior edge. Maxillary apparatus of P- and K-type in both sexes, with falcate P1-forceps, bidentate P2-forceps (Fig. 5B), K-forceps right bidentate, left falcate.

Reproduction and development. Gonochoristic; chromosomes 2n = 10. Diameter of eggs 120-130 µm; tubular egg masses; released larvae without parapodia, with long pygidial median stylus.

Etymology. The name of the new species is derived from the fact that sexually mature females of *O. robusta* are bigger than females of other species, e.g. *O. macrovifera*, with the same segment number.

Remarks. The new species was originally identified through crossbreeding experiments (Åkesson 1975) and has been confirmed by gene sequence studies (Dahlgren *et al.* 2007; Heggøy *et al.* 2007; Wiklund *et al.* 2009). Of the four *O. labronica* group species with separate eyes, *O. robusta* is the only one with small eggs producing larvae without parapodia when released from the egg mass. It is further characterised by having a diploid chromosome complement of 10, a characteristic it shares with only *O. rubra* in the group.

Distribution. Mediterranean and Strait of Gibraltar: Malaga, Ceuta, Tarifa, Spain; Genoa, Sicily, Italy.

***Ophryotrocha rubra* sp. nov.**
Figure 1E; Table 1

Ophryotrocha rubra nom. nud. Pleijel & Eide, 1996; Heggøy *et al.* 2007; Wiklund *et al.* 2009.

Material examined. Type material: Holotype (AM W36881), complete female specimen, 2.6 mm long, 0.40 mm wide without parapodia (preserved) for 19 chaetigers; allotype (AM W36882) complete male specimen, 1.3 mm long, 0.25 mm wide without parapodia (preserved) for 14 chaetigers; 10 paratypes (AM W36883); 10 paratypes (SMNH T-8033); cultured from specimens collected at Ceuta, Spain in 1978. Other material: Live cultures from same collection.

Description. Length of most live adults 2–3 mm (12–14 chaetigers), maximum length 4 mm (20 chaetigers). Live animals (Fig. 1E) translucent, preserved opaque white. Pigmentation consisting of very small red spots on most chaetigers, when best developed in large animals, forming rows of spots on some segments (Fig. 1E). Prostomium anteriorly rounded; with pair of short ovate antennae; palps absent; two distinct eyes, not medially connected. Two peristomial achaetous segment-like rings.

Parapodia uniramous, lacking dorsal and ventral cirri, with dorsal protrusion, with retractile ventral lobe; 2–3 supra-acicular simple chaetae, 2–4 subacicular heterogomph falcigers and inferiormost simple chaeta; distal part of simple chaetae and blades of falcigers coarsely serrated. Pair of pygidial cirri present, pygidial median stylus absent in adults. Rosette glands, one per segment, present mid-dorsally on posteriormost segments of mature animals, up to five to six in males and females.

Mandibles with elongate shafts and bifid cutting plates with 18–21 tiny pointed teeth at anterior edge. Maxillary apparatus of P- and K-type in both sexes, with falcate P1-forceps, bidentate P2-forceps, K-forceps right bidentate, left falcate.

Reproduction and development. Gonochoristic; chromosomes 2n = 10. diameter of eggs 165–170 µm; tubular egg masses; released larvae with two chaetigers, with short pygidial median stylus.

Etymology. The name of the new species refers to its numerous red spots.

Remarks. The new species was originally identified through crossbreeding experiments and has been confirmed by gene sequence studies (Heggøy *et al.* 2007; Wiklund *et al.* 2009). *Ophryotrocha rubra* is most closely related to *O. robusta*, the only other species in the *O. labronica* group with a diploid chromosome complement of 10. Both species have separate eyes but differ in their reproductive characteristics in that *O. rubra* has large eggs that develop into 2-chaetiger larvae before leaving the egg mass, while *O. robusta* has small eggs that leave as 0-chaetiger larvae.

Distribution. Mediterranean/Strait of Gibraltar: Tarifa, Ceuta, Spain.

Ophryotrocha schubravyi Tzetlin, 1980

Table 1

Ophryotrocha schubravyi Tzetlin, 1980: 666, fig. 1.

Diagnosis. Prostomium with moderately long antennae, palps absent; two eyes medially connected; parapodia uniramous, lacking dorsal and ventral cirri; with dorsal protrusion; supra-acicular simple chaetae and subacicular falcigers; pygidium with two cirri, pygidial median stylus absent in adults; anterior edge of mandibles with 21 teeth, maxillae with falcate P1-forceps, bidentate P2-forceps, K-forceps right bidentate left falcate; gonochoristic; chromosomes 2n = 8; diameter of eggs 120 µm; released larvae without parapodia, with long pygidial median stylus.

Remarks. This species, only known from its original description, appears to be a typical member of the *O. labronica* group. The antennae of *O. schubravyi* are slightly longer than in most members of the group and its only distinguishing characteristic is that its diploid number of chromosomes is reported as 8.

Distribution. *Ophryotrocha schubravyi* was discovered in a marine aquarium in Moscow and it is not known from where it was introduced.

Ophryotrocha vellae sp. nov.

Figure 1F, 2C, E, 4C, 4F; Table 1

Ophryotrocha obscura nom. nud. Pleijel & Eide, 1996: 648; Dahlgren *et al.* 2001.
Ophryotrocha Sanya sp. 2 Dahlgren *et al.*, 2001; Heggøy *et al.* 2007.

Material examined. Type material: Holotype (AM W36884), complete female specimen, 3.8 mm long, 0.40 mm wide without parapodia (preserved) for 19 chaetigers; allotype (AM W36885) complete male specimen,

1.7 mm long, 0.20 mm wide without parapodia (preserved) for 17 chaetigers; 10 paratypes (AM W36886); 10 paratypes (SMNH T-8034); cultured from specimens collected at Sanya, South Hainan, China, in 1995. Other material: Live cultures from same collection.

Description. Length of most live adults 3–4 mm (13–15 chaetigers), maximum length 5 mm (20 chaetigers). Live animals (Fig. 1F) translucent, preserved opaque white. Pigmentation consisting of very small lateral red spots on some chaetigers. Prostomium (Fig. 2C) anteriorly rounded, with pair of short ovate antennae; palps absent; two eyes medially connected; four nuchal organs (Fig. 2C, E). Two peristomial achaetous segment-like rings.

Parapodia uniramous (Fig. 2F), lacking dorsal and ventral cirri, with dorsal protrusion, with retractile ventral lobe; 2–3 supra-acicular simple chaetae, 3–4 subacicular heterogomph falcigers and inferiormost simple chaeta; distal part of simple chaetae and blades of falcigers coarsely serrated. Pair of pygidial cirri present, pygidial median stylus absent in adults. Rosette glands (Fig. 4C), one per segment, present mid-dorsally on posteriormost segments of mature animals, up to six in males four in females.

Mandibles with elongate shafts and bifid serrated cutting plates with 23–27 tiny pointed teeth at anterior edge. Maxillary apparatus of P- and K-type in both sexes, with falcate P-1-forceps, bidentate P2-forceps, K-forceps right bidentate, left falcate.

Reproduction and development. Gonochoristic; chromosomes 2n = 6; diameter of eggs 110 µm; released larvae without parapodia, with long pygidial median stylus; stylus subsequently lost (Fig. 4F).

Etymology. This species is named in honour of Ms. Nicole Vella, in gratitude for her assistance with SEM and photography.

Remarks. The type material results from a strain collected in 1995, named '*O.* Sanya sp. 2', cultured and subsequently identified as a new species through crossbreeding experiments with other members of the *O. labronica* group. At that time the culture of *O. obscura* nom. nud., discovered in 1978 in a pet store aquarium in Gothenburg, Sweden, with no indication of its origin, had already perished, preventing any crosses between these two strains. Molecular studies of the mitochondrial 16S gene demonstrated that the investigated sequence in *O. obscura* nom. nud. and *O.* Sanya sp. 2 was identical (Dahlgren *et al.* 2001). This demonstrated that the two strains are members of the same species which is here described as *O. vellae.*

Ophryotrocha vellae is closely related to *O. labronica*, *O. costlowi* and *O. permanae* and cannot be morphologically distinguished from these species. The only difference we could establish is that the diameter of *O. vellae* eggs is only 110 µm, while it is 120–130 in the other three species.

Distribution. East China Sea: Sanya, Hainan.

Ophryotrocha olympica nom. nud.

Table 1

Ophryotrocha olympica nom. nud. Pleijel & Eide, 1996: 648.

Diagnosis. Prostomium with moderately long, tapering antennae, palps absent; two distinct eyes, not medially connected; parapodia uniramous, lacking dorsal and ventral cirri; dorsal single rosette glands on posterior segments; detail of mandibles and maxillae unknown, K-forceps, right bidentate, left falcate; gonochoristic; chromosomes 2n = 6; diameter of eggs 165 µm; released larvae with 3 chaetigers.

Remarks. The specimens were collected in June 1978 in the Mukkaw Bay in the Makah Indian Reservation, about 8 km south of Cape Flattery on the Olympic Peninsula, Washington state, in gravel from a depression in the rocky shore, mid to high intertidal zone.

Crossing experiments demonstrated that this species is a typical member of the *O. labronica* group, as has been confirmed by electrophoresis (Pleijel & Eide 1996). In routine culture the adult females had 17-19 chaetigers with a maximum of 22. Males were smaller, 14-15 chaetigers and an observed maximum of 17. Adults have small, segmentally arranged brown-red pigment spots.

Since the culture no longer exists and no material was preserved, this species remains indeterminate.

Distribution. Western North Pacific: Mukkaw Bay, Olympic peninsula, Washington, USA.

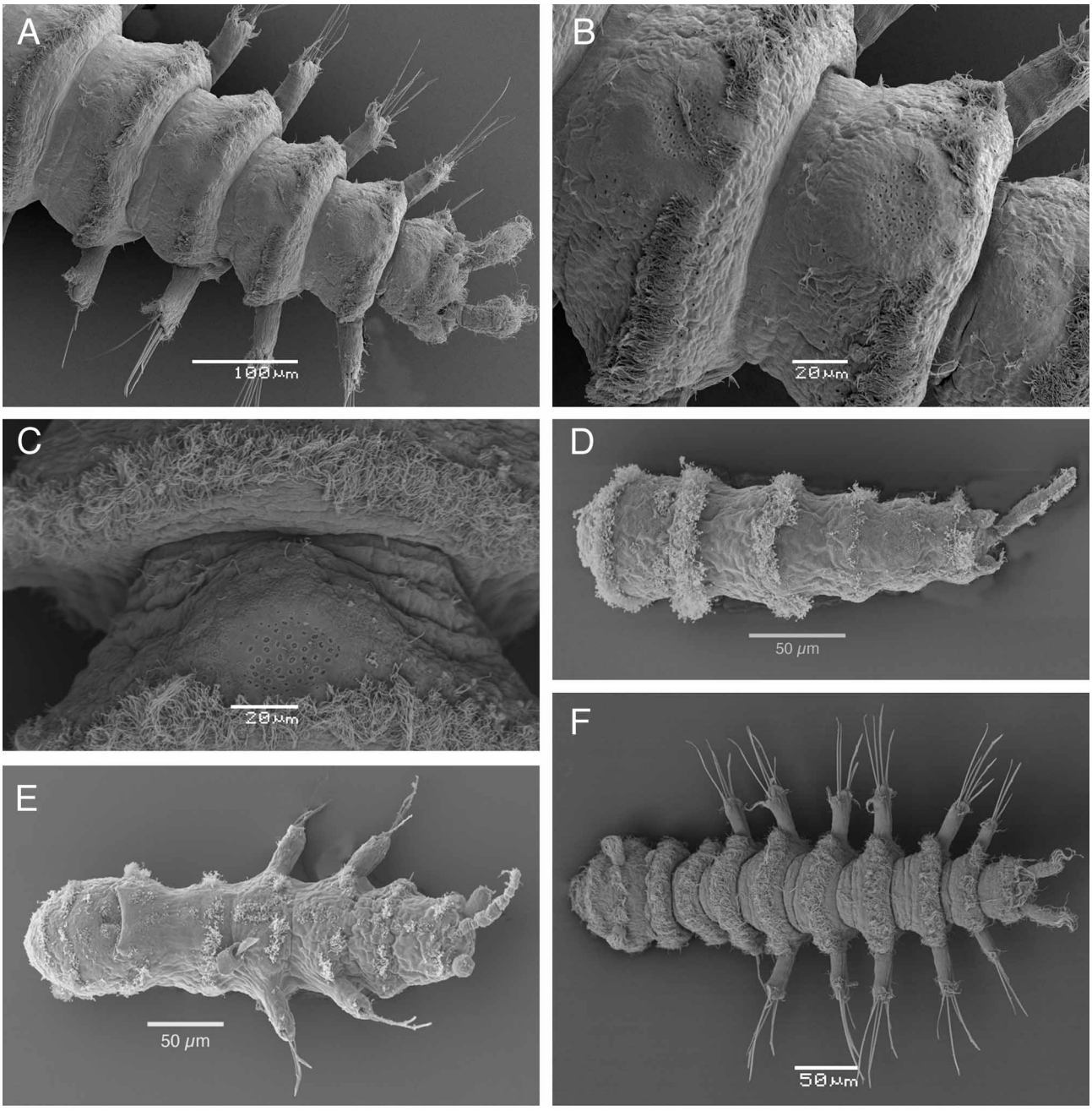

FIGURE 4. SEM images. A, Posterior end of *Ophryotrocha macrovifera*, **sp. nov.**, dorsal view; B, enlargement of same to show rosette glands; C, rosette gland of *Ophryotrocha vellae*, **sp. nov.**; D, recently released larva of *Ophryotrocha labronica labronica*, dorsal view; E, 2-chaetiger larva of same, ventral view; F, 6-chaetiger juvenile of *Ophryotrocha vellae*, **sp. nov.**, dorsal view.

Ophryotrocha prolifica **nom. nud.**

Table 1

Ophryotrocha prolifica nom. nud. Pleijel & Eide, 1996: 648.

Diagnosis. Prostomium with moderately long, tapering antennae, palps absent; two eyes medially connected; parapodia uniramous, lacking dorsal and ventral cirri; dorsal single rosette glands on posterior segments; anterior edge of mandibles with 23–25 teeth, detail of maxillae unknown, K-forceps, right bidentate, left falcate; androdioecy; chromosomes 2n = 6; diameter of eggs 125 µm; released larvae without parapodia, with pygidial median stylus.

Remarks. This species was first observed and cultured by Dr. Stanley A. Rice, University of Tampa and brought to Gothenburg in March 1979. Sex determination differs from other members of the *O. labronica* group. It is comprised of three genotypes: monogenic hermaphrodites, amphigenic hermaphrodites, and males. Sex is determined by a simple diallelic locus with a dominant allele, S, coding for hermaphroditism, and a recessive allele, s, coding for males. Monogenic hermaphrodites are SS, amphigenic hermaphrotides are Ss, and males are ss. Both outcrossing (with males) and selfing occur in the population. This rare reproductive form is known as androdioecy. It was first reported for animals by Sassaman & Weeks (1993) who described it from the conchostracan shrimp *Eulimnadia texana* (Packard). This mode of reproduction has not been reported from any other polychaete.

Based on its morphology this species is a typical member of the *O. labronica* group, as has been confirmed by electrophoresis (Pleijel & Eide 1996).

Since the culture no longer exists and no material was preserved, this species remains indeterminate.

Distribution. The specimens appeared as a contamination in an aquarium with material from Indian River on the east coast of Florida, USA.

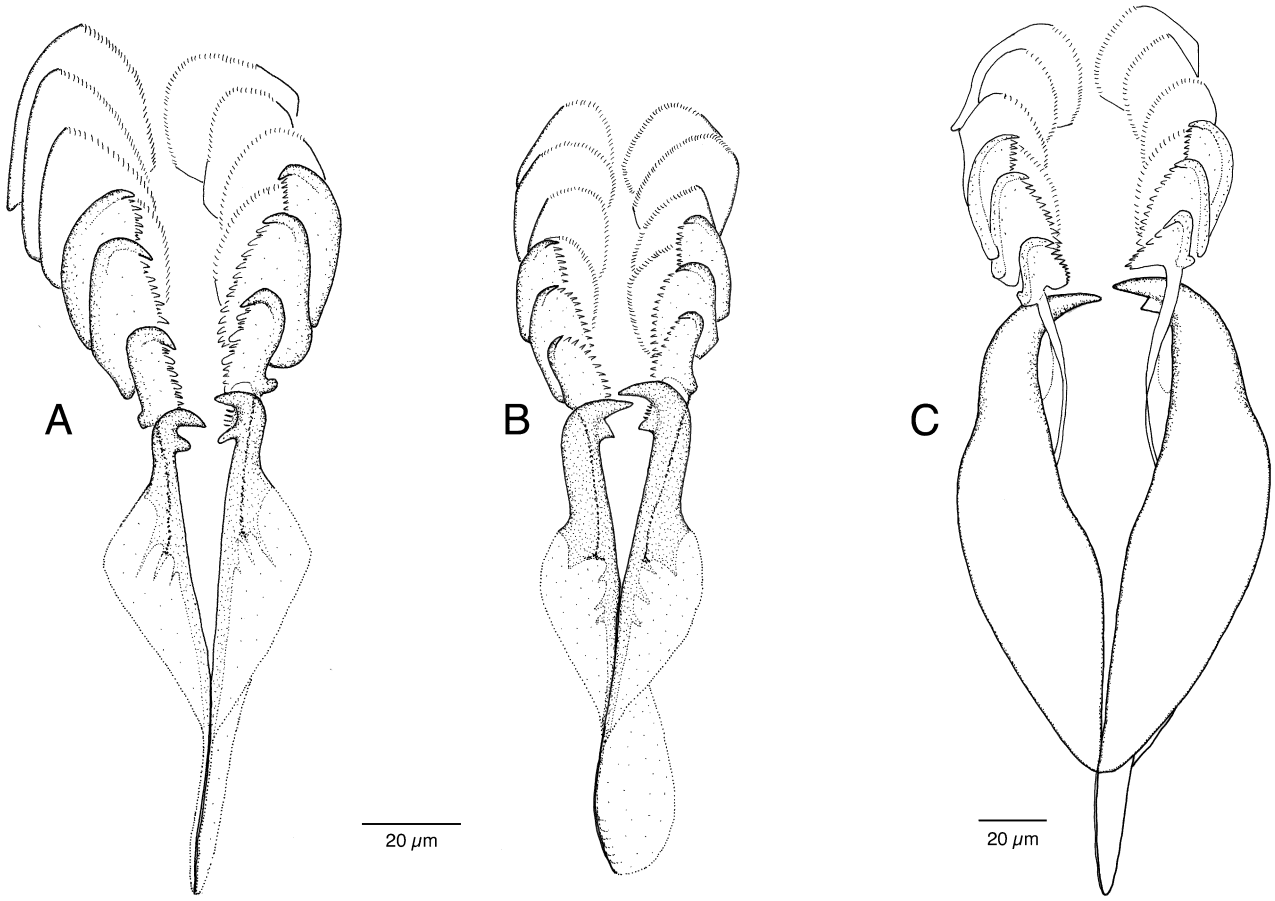

FIGURE 5. Maxillary apparatuses, dorsal view. A, P2-maxillae of 14-chaetiger *Ophryotrocha macrovifera*, **sp. nov.**; B, same of 11-chaetiger *Ophryotrocha robusta*, **sp. nov.**; C, K-maxillae of 18-chaetiger female *Ophryotrocha macrovifera*, **sp. nov.**

***Ophryotrocha sativa* nom. nud.**
Table 1

Ophryotrocha sativa nom. nud. Pleijel & Eide, 1996: 648.

Diagnosis. Prostomium with moderately long, tapering antennae, palps absent; two eyes medially connected; parapodia uniramous, lacking dorsal and ventral cirri; rosette glands reported as absent; detail of mandibles and maxillae unknown, K-forceps, right bidentate, left falcate; gonochoristic; chromosomes 2n = 6; diameter of eggs 120 µm.

Remarks. The diagnosis (except for reproductive characteristics) is based on information from Pleijel & Eide (1996). On the basis of this information and its position in the pylogenetic tree of Pleijel & Eide (1996) this species appears to be a typical member of the *O. labronica* group. However, the scored morphological characters are too general to distinguish it from the other members. Since the culture no longer exists and no animals have been preserved, this species remains indeterminate. The same species was also sampled from aquaria in four more pet stores. Data about fecundity and sex ratio were obtained from those strains.

Distribution. The distribution is unknown. The specimens were found in the aquaria of a wholesale dealer who had imported 'living stones' (pieces of coral in good condition with a variety of attached organisms) from the Philippines. They are native in a tropical environment and cannot survive at temperatures of 18ºC or lower.

Discussion

Morphology. Like most *Ophryotrocha* species, the species of the *O. labronica* group are small, with the smaller ones (e.g. *O. costlowi*) reaching 3–4 mm for 18 chaetigers and the largest (*O. notoglandulata*) having a maximum size of 8 mm for 36 chaetigers (Table 1). Males are generally smaller than females, in total length as well as numbers of chaetigers (Fig. 1). The body is cylindrical, tapering towards the posterior end (Fig. 2A, B). Live animals are translucent white, preserved ones opaque white. Pigmentation is present only as very small red spots on some or all chaetigers, best developed in *O. rubra* where they may form segmental rows of spots (Fig. 1E). The number of spots may increase with age.

The prostomium is wider than long and anteriorly rounded. In some species it appears to have an anterior peak (e.g. *O. vellae* Fig. 2C), while in others it is more rounded (e.g. *O. robusta* Fig. 3A, B). However, this is not a good taxonomic criterion as the animals can extend and withdraw the anterior tip of the prostomium. The animals have two eyes that are internal, light-reflecting structures, appearing silvery white in live animals under incident light but are invisible in preserved specimens (Fig. 2C). *Ophryotrocha* eyes are unusual rhabdomeric ocelli, almost or completely unpigmented. Their visibility in the light microscope is due to the presence of a reflector cup formed by several flat cells containing refractive crystalline platelets instead of a pigment screen (Rhode1990; Purschke 2005). Eyes of all larvae and early juveniles are separate and remain as such throughout life in some species (e.g. *O. robusta* Fig. 3A, B), while in most species of the *O. labronica* group the platelet-bearing cells spread medially to connect with the other eye when the animals consist of about five chaetigers (e.g. *O. macrovifera* Fig. 3C, D). A pair of short, ovate antennae is situated anterior to the eyes. Palps are absent, although ventrolateral bundles of cilia have been attributed to vestiges of palps by other authors.

Cilia are present as dense bands, partly to completely encircling the body, and as hair-like tactile cilia consisting of small bundles of adjoined cilia. Prostomial tactile cilia are present at the anterior margin of the prostomium and the tip of the antennae. In live animals these tactile cilia adhere to each other and appear spike-like (Fig. 3A-D), while in fixed specimens the spikes have fallen apart and the bundle is obvious (Fig. 2C). Two bands of cilia are encircling the prostomium; one complete circle, about halfway between the antennae and the tip of prostomium, and one incomplete circle at the level of the antennae. The latter circle is continuous ventrally but is dorsally interrupted. The cilia between the antennae are slanting posteriorly towards the centre. They are either continuous or more often separated by a small mid-dorsal space, forming two oblique patches of cilia appearing like eyebrows. Ventrally there is an additional semicircle of cilia posterior to the complete circles. The posterior border of the prostomium is indicated dorsally by four nuchal organs or ciliated pits (Fig. 2C, E), ventrally by the mouth (Fig. 2D). The nuchal organs are slightly behind the eyes, one pair lateral and one pair medial to the eyes. The prostomium is followed by two apodous achaetous segment-like rings representing the peristomium; both are encircled by cilia. The following chaetigers have ciliary bands that are laterally interrupted by the parapodia (Figs. 2C, D; 3A–D).

The parapodia are uniramous, lacking dorsal and ventral cirri (Fig. 2F). The distal part of the parapodium has a dorsal protrusion carrying tactile cilia, short pre- and postacicular lobes and a retractile ventral lobe, supported by a short simple chaeta. The supra-acicular fascicle has up to four simple chaetae, while the

subacicular fascicle has up to five heterogomph falcigers and the inferiormost simple chaeta. The appendages of the falcigers and the upper part of the simple chaetae are serrated and have a single distal tooth. The serrations vary from very fine (e.g. *O. macrovifera* Fig. 2G) to coarse (e.g. *O. labronica*, Fig. 2H).

The pygidium bears a dorsal anus and a pair of dorsal pygidial cirri (Fig. 4A). A ventral median pygidial stylus is present in larvae. In most species the median stylus is at least twice as long as the pygidial cirri (Fig. 4D, E), while in some species it is short, equal to or less than the cirri (Table 1). The stylus is lost when the animals consist of about five chaetigers (Fig. 4F). The pygidium is encircled by a band of cilia; tactile cilia are present at the posterior margin and at the distal tips of the cirri.

Rosette glands, large segmental epidermal glands best developed in males, were first described by Braem (1893) for *O. puerilis* and named for the circular arrangement of their oblong cells. While they are paired dorsal structures in the posterior segments of *O. puerilis*, they are single dorsal structures in the *O. labronica* group where they were first identified in *O. notoglandulata* by Pfannenstiel (1976). They are present in all species of the group in males and females and are usually more numerous in males than in females (Table 1). The lowest numbers were observed in *O. labronica* (five in males and three in females) and the highest numbers in *O. notoglandulata* (12 in males and eight in females). The surface view of a mature rosette gland as observed in SEM images shows a large raised area that is centrally closely perforated (Fig. 4A, B). The ciliary band may become interrupted as in *O. macrovifera* (Fig. 4B) or remain intact as in *O. vellae* (Fig. 4C).

The jaws consist of a pair of ventral mandibles and a dorsal maxillary apparatus. The mandibles are two elongate shafts that widen distally into bifid cutting plates with knob-like lateral projections and numerous tiny pointed teeth at the anterior edge of each plate. The structure of the cutting plates is best seen in young animals as anterior teeth are often damaged in mature specimens (Fig. 3E). The mandibles are not replaced during the lifetime of the animal. The initial parts of the mandibles to become visible in the larva are the cutting plates and sclerotisation proceeds posteriorly to form the shafts. The mandibles are very similar in the different species. The only variations are in the number of anterior teeth and in the amount of lateral sclerotisation of the shafts. The number of anterior teeth ranges from 18–21 in *O. rubra* to 25–28 in *O. labronica* and others (Table 1). Lateral sclerotisation is absent in very young specimens and accumulates with age in males and females, but is most pronounced in large males. The maximum extent in all but one species is about equal to or slightly wider than the width of the cutting plates (e.g. *O. macrovifera* (Fig. 3F), while in *O. permanae* (Fig. 3G) the lateral sclerotisation can be more than 1.5 times as wide as the cutting plates.

The maxillary apparatus goes through a series of moults from the initial larval jaws to the P1, P2, and finally the K-maxillae (Paxton 2004). Each jaw stage consists of basal plates or forceps fused with a carrier-like stucture and anterior denticles. All denticles are interconnected by thin ligaments and a more obvious ligament strut connecting the anterior denticles to the basal plates or forceps. The larval maxillae (L) (Fig. 3H) consist of two paired basal plates posteriorly fused into a carrier-like structure and two paired anterior denticles. The larger basal plate is coarsely denticulated by alternating large and small teeth, whereas the smaller plate is finely serrated, as are the anterior two rounded denticles. No variation among the different species was observed.

The moult to the P1-maxillae occurs in 5- to 7-chaetiger juveniles, resulting in forceps and six pairs of anterior denticles (D). The forceps are very slender and posteriorly fused into a carrier-like structure (Fig. 3I). The anterior tips are falcate or fang-like. The left part of the forceps has a medially smooth edge, whereas the right part is medially serrated below the fang. The anterior denticles are of the same form as those of the P2 and K-maxillae; D1-D3 have a distal fang and coarsely serrated median edge, while D4-D6 are finely serrated. The P1-stage is very brief but there is some variation in the onset of the moult to the P2-maxillae. In species with small eggs, where the larvae are released before they have developed parapodia, the moult occurs in the 7- to 9-chaetiger stage (e.g. *O. labronica*). Whereas in species where the larvae are released with 2–3 chaetigers present, the moult occurs in the 12- to 15-chaetiger stage (e.g. *O. macrovifera*).

The P2-maxillae consist of forceps and seven pairs of anterior denticles and the individual elements are larger and the forceps are bifid. The stronger sclerotised distal parts of the forceps are quite similar among the species of the *O. labronica* group in that the area between the distal fang and second tooth on the left side has a smooth edge, while the right side is serrated. However, while in most species the darker distal part is short (e.g. *O. macrovifera* Fig. 5A), it is longer in *O. robusta* (Fig. 5B) and *O. rubra*.

The moult to the K-maxillae occurs in both males and females of all species of the subgenus. However, a sexual dimorphism can be observed in that the males attain the K-type at an earlier age and their forceps are considerably larger than in females (Fig. 1A–D; 3A–D). The right distal tip of the K-forceps is bidentate while the left is falcate (Fig. 5C). The second tooth of the right side is very delicate and appears to be a sheath into which the left distal tip slides when the jaw is locked. The ligament strut connecting the seven anterior denticles to the forceps is clearly visible at this stage. Newly moulted and female K-maxillae are more lightly sclerotised, while those of males are black in colour.

Reproductive traits. The literature covering reproduction and development of the group, particularly *O. labronica*, is extensive; a general summary for that species was presented by Paxton & Åkesson (2007). Here we focus on some reproductive traits of the group. Members of the group are, with one exception, gonochoristic, and some species have a tendency towards hermaphroditism and viviparity.

Hermaphroditism. *Ophryotrocha labronica* was formally described by La Greca & Bacci (1962) from the harbour of Leghorn, Italy. They described the new species as a protandrous hermaphrodite that could self-fertilise. Their observations were confirmed by Parenti (1960) and Zunarelli (1962, 1967). The new species was described as 3 mm long with a maximum of 18–20 chaetigerous segments and with a chromosome complement of 2n = 6. Both La Greca & Bacci and Zunarelli reported the same species was also present in the Gulf of Naples, but all detailed observations were made on material from Leghorn and the conspecificity of the two populations was not tested by crosses.

Parenti (1960) reported that an intense spermatogenesis began at a size of 7–8 chaetigers and oocytes began to grow at 9–10 chaetigerous segments, while the amount of spermatozoa gradually decreased and the sex change was completed at about 13 chaetigers. Self-fertilisation could be related to a secondary spermatogenesis. The egg masses were rather small, only 40–50 eggs with a diameter of 120–130 µm.

In a sample of *O. labronica* from Genoa Sella & Zambaldi (1985a, b) identified one single self-fertilising hermaphroditic individual that could transfer its self-fertilising ability to four successive generations. In the first generation the progeny consisted of both sexes in a proportion of about 1:1, but in the following three generations thelygenic progeny were produced. Over the generations only a fraction of the hermaphrodites could self-fertilise (Sella, pers. comm.). The authors performed a control sample by crossing gonochoristic individuals from the same Genoa population. But, judging from the reports, no crosses were performed between members of the hermaphroditic strain and the gonochoristic animals. Thus, we do not know whether this exceptional hermaphrodite really was an *O. labronica* individual or if it represented a sibling species.

Another aberration was found in three *O. labronica* populations (from Faro in S. Portugal (Åkesson 1975); Malaga and Formia (unpubl.)), where a few males produced oocytes which eventually became resorbed, as has also been reported for a population from Naples by Pfannenstiel (1976). We extended our experiments further and found that the secondary females retained their male potential and could produce progeny together with normal (primary) females (Åkesson 1975). Recently we obtained secondary females in intrapopulation crosses with the PAX I strain from Sydney (Åkesson & Paxton 2005). These secondary females had already functioned as males (together with primary females) before they produced progeny together with primary males. The resulting fecundity and sex ratio were both significantly lower.

Reproduction in *Ophryotrocha prolifica*, nom. nud. is fundamentally different from all other species treated in this report, although its morphology, release of eggs when spawning, shape of egg mass, and development are all typical for the *O. labronica* group. This population contained males and two kinds of hermaphrodites, both of which could either self-fertilise or cross-fertilise. Sex determination is related to one single locus with two alleles, one dominant and one recessive. This kind of sex determination was first described by Sassaman & Weeks (1993) in the conchostracan shrimp *Eulimnadia texana* as an example of androdioecy. A detailed report of crossing experiments will be published separately.

Thelygeny. The exception to the gonochoristic pattern is *O. permanae*, which deviates from the others by having mixed populations with males, gonochoristic females and thelygenic females. The progeny of these thelygenic females is purely female. Thus, for each new generation males have to be added from a normal, gonochoristic strain. We have maintained cultures of two such thelygenic strains, one from Indian River on the east coast of Florida, USA, the other one from Xiamen, China. The Xiamen strain has been cultured

through more than 30 generations. All attempts to transfer the trait to other species or even to other populations of *O. permanae* have failed. It appears that this thelygeny is a genetic aberration.

Viviparity. A tendency towards viviparity has been observed in several *Ophryotrocha* species, three of them belonging to the *O. labronica* group: *O. labronica*, *O. notoglandulata*, and *O. macrovifera*. After the spawn has been moulded into the tubular shape and the external walls have hardened, a few 0-chaetiger larvae can occasionally be seen together with the newly laid spherical eggs. These larvae may have been trapped in the female's coelom and been fertilised by entering spermatozoa during a previous spawning. This is supported by the fact that such larvae never appear in the spawn from the female's first breeding (Åkesson 1994).

Sex ratio. *Ophryotrocha labronica* is the most widespread species within the group. Of the many strains maintained as laboratory cultures for many years, the original sex ratios (expressed as percentage of males) are unchanged. Our oldest strain, Naples I, was sampled in 1965. The sex ratio was then 31.6%. The strain was maintained at two separate laboratories from 1970 to 1984. Both strains retained the same sex ratio and behaved like one single strain when tested in crosses after this period. In other strains the male ratio is above 40%, but none has a sex ratio of 1:1. The sex ratio depends on genetic factors and the male ratio can be increased through selection (Åkesson 1972) or decreased (Sella & Zambaldi 1985a).

The male-dominated Moscow strain had a sex ratio of 65% when it was brought to our laboratory in 1986 and is still not significantly different. Whereas long term culture does not change sex ratios, a strong variation has been observed when animals have been sampled in the same place at different times (see Åkesson & Paxton 2005: Table II).

It was previously reported from interpopulation crosses that presumed genetic differences between populations of *O. labronica* were seen as variations in sex ratio differences between the P and F1 generations. The same was true of differences between reciprocal sex ratios (Åkesson & Paxton 2005). No such differences have been recorded in crosses between the five geographic strains of *O. permanae*, nor for *O. macrovifera* (of which we maintain laboratory cultures of five populations from four continents), with no indications of major genetic differences between the strains. An explanation might be anthropogenic distribution of the populations. An example has recently been recorded for gonochoristic species in Italy. After more than 100 years of dominance for *O. labronica* along the Italian coasts, another gonochoristic species has appeared as a competing species (Simonini 2002). This species is *O. japonica* that was previously recorded only from the northern Pacific. We suggest that *O. japonica* has arrived in Italy by ballast water or fouling material on large ships.

Sex determination. The genetic part of sex determination in gonochoristic *Ophryotrocha* species has been discussed by Bacci (1975) and by us in 2005. The present study does not add anything new to that discussion. Therefore we move to the environmentally mediated part of sex determination.

Bacci *et al.* (1979) coined a new expression "inducible hermaphroditism". Strains of *O. labronica* from Naples and Venice with population sex ratios of 62.3 and 52.1% respectively were used in experiments where juveniles with 6–7 chaetigers from each strain formed pairs with young females. A control group of juveniles was individually isolated. Those raised together with adult females developed into fertile males more often than could be expected due to the population sex ratios and also relative to the control group. Later, when these males were raised in isolation, a fraction of them changed sex and became fertile females. These are the inducible hermaphrodites (or secondary females) according to Bacci *et al.* (1979). They represent 25.8% (Naples strain) and 31.8% (Venice Strain) of the juveniles employed in pair formation with females. The sum of primary and secondary females come close to the population sex ratios.

In the report by Bacci *et al.* (1979) the adult influence was only tested with females. In a poster, Sella & Ramella (1988) reported similar experiments with *O. macrovifera.* They used a strain with a population sex ratio of 33%. When juveniles were isolated to form pairs with adult males for some time and then individually isolated, their adult sex ratio had decreased to 6.3%. When two juveniles were isolated with one male, the sex ratio was also decreased to 19.9%. If a male was isolated with three or more juveniles, the adult sex ratio of the juveniles was not affected. Significant changes were also obtained when three juveniles were combined with two adult males (sex ratio 29.6%), but not in the combination four or five juveniles and two males. In a

parallel series juveniles were tested with adult females, but here the sex ratios of the juveniles were not influenced in any combination. Rolando (1984) performed similar experiments with four species, *O. labronica*, *O. costlowi*, *O. robusta* and *O. macrovifera,* to search for inducible hermaphrodites. He obtained significant effects in only three out of 12 trials: in *O. robusta* with both juvenile + male and juvenile + female and in *O. labronica* with juvenile + male. No significant effect was obtained with *O. macrovifera,* a result different from that of Sella & Ramella (1988).

Germ cells. The germ cells develop floating freely in the coelom. They detach early from small, segmentally repeated gonads. In juveniles, each fertile segment contains two stem cells (gonocytes) that are located near the median genital blood vessel. These gonocytes undergo a proliferation cycle to form either oocytes with associated nurse cells or clusters of spermatocytes (Pfannenstiel & Grünig 1982, 1990). Although the authors studied *O. puerilis*, the many tendencies towards hermaphroditism in the primary gonochoristic species of the *O. labronica* group seem to justify an assumption of similar gonad formation. The nurse cell synthesises nutrients which are transported to the oocyte by an intercellular canal, a fusome (Emanuelsson 1969). The entire content of the nurse cell is exported to the oocyte which develops into a mature egg (Emanuelsson & Anehus 1985).

Fertilisation. After a period of courtship (Rolando 1981) the couple ends up side by side emitting a loose jelly into which eggs and spermatozoa are extruded (known as pseudocopulation). No nephropores or other openings to the exterior are large enough to release the germ cells. Intersegmentally repeated slits open up and the germ cells are released into the jelly. Then eggs and sperm are moved around in the jelly and have opportunities to meet each other. This phase is important as the spermatozoa are almost immotile, being aflagellate or having a short flagellar equivalent (Pfannenstiel & Grünig 1990). The characteristic tubular egg masses are formed before the surfaces of the spawn harden. Male and female cooperate in guarding the egg mass and cleaning the surfaces (Fig. 1F).

Reproductive output. The reproductive output depends on many variables. Table 2 presents fecundity figures for most of the species studied in this report. It should be noted here that the egg diameter for a species sometimes varies considerably in different populations. Therefore, the egg sizes in the systematic part and Table 1 are given as the range for a particular species. The fecundity figures in Table 2, however, are means from 12 or more egg masses of one population. The culture conditions have been the same for all species: fragmented spinach as food and temperatures ranging from 19–23ºC.

TABLE 2. Fecundity figures for select species of the *O. labronica* group. (Means from 12 or more egg masses of one population).

Species	Diameter of eggs (µm)	Mean no. of eggs/spawn	No. of chaetigers at larval release	Male ratio %
O. l. labronica	120	130	0	39
O. l. pacifica	120	85	0	31
O. costlowi, sp.nov.	125	85	0	46
O. japonica, sp.nov.	150	80	2	56
O. macrovifera, sp.nov	180	80	2	36
O. notoglandulata	125	120	0	55
O. permanae, sp.nov.	125	102	0	51
O. robusta, sp.nov.	125	200	0	54
O. rubra, sp.nov.	167	95	2	39
O. vellae, sp.nov.	110	57	0	48
O. olympica, nom.nud.	165	24	3	44
O. prolifica, nom.nud.	125	128	0	25
O. sativa, nom.nud.	120	86	0	40

When *O. labronica* was sampled from a semi-starving population, females which spawned within the first two days spawned egg masses with less than 30 eggs. In experiments with various food items, those with high protein contents like *Artemia* larvae and tissue of *Mytilus,* yielded the largest egg masses. The egg masses spawned by virginal females are usually small, increasing with the size of the female at consecutive spawnings. The temperature effect on different aspects of the reproductive output was demonstrated by Åkesson (1976).

Some variables, e.g. reproductive rate (eggs/female/day), are only suitable for intraspecific comparison as the egg sizes vary among species. Åkesson (1975) compared reproduction in four species of the *O. labronica* group: *O. macrovifera, O. robusta, O. labronica* and *O. notoglandulata.* The reproductive rate was highest in *O. labronica* and lowest in *O. macrovifera*. However, when the volume of gonadal tissue/female/day was considered, it was highest in *O. macrovifera* and lowest in *O. notoglandulata* (unpublished). We can distinguish two patterns of maternal investment among the *O. labronica* group: (1) small egg size (110–130 µm), shorter brood care, larvae released without parapodia (e.g. *O. labronica)*; and (2) larger eggs (150–180 µm), longer brood care, larvae released with 2–3 chaetigers from the egg mass (e.g. *O. macrovifera).* As the larger eggs have a higher energy content, they develop to a more mature stage before release and presumably have a better competitive ability than 0-chaetiger larvae.

Relationships. The genus *Ophryotrocha* is here considered as belonging to the family Dorvilleidae, following Eibye-Jacobsen & Kristensen (1994). The phylogeny of *Ophryotrocha* has been studied in a combined analysis of morphological, reproductive and electrophoretic characters (Pleijel & Eide 1996) and several molecular analyses (Dahlgren *et al.* 2001; Heggøy *et al.* 2007; Wiklund *et al.* 2009). The monophyly of the O. *labronica* group is supported in all of these phylogenies.

Morphologically, the *O. labronica* group can be defined by its apomorphies of dorsal single rosette glands in posterior segments (Fig. 4B, C), maxillae with distally falcate P1-forceps (Fig. 3I), bidentate P2-forceps (Fig. 5A, B) and K-forceps with right distal tip bidentate, left falcate (Fig. 5C). In addition, all species are primarily gonochoristic with all but two (perhaps three) having a diploid complement of six chromosomes. The group has a very long geological history as supported by the well-preserved fossil specimen of *O.* sp. from the Upper Cretaceous (Eriksson & Lindström 2000). The specimen is so similar to *O. labronica* investigated during a recent jaw growth study (Paxton 2004) that based on its size and degree of sclerotisation the fossil could represent a young *O. labronica* of about 10–15 chaetigers.

It has been stated that the relationships of the *O. labronica* group vary greatly between the morphological analysis and molecular studies (Thornhill et al. 2009). With respect to the study by Pleijel & Eide (1996) this is at least partially a result of uninformative characters and in some cases incorrect coding. The difficulty in establishing a phylogeny of the *O. labronica* group based on morphological characters is that the species are so exceedingly similar. During this extensive study only one phylogenetically informative morphological character could be identified. Namely, eyes medially connected by refractive crystalline platelet-bearing cells (Fig. 3C, D) or separate (Fig. 3A, B). The two eyes are medially connected in all but four species of the group (*O. japonica, O. robusta, O. rubra* and *O. olympica*, nom. nud.). In other clades of *Ophryotrocha*, the eyes are distinct, except for *O. adherens* Paavo et al. and *O. diadema* Åkesson in which the arrangement of the crystalline platelets form a different pattern. We interpret the connection of the eyes of the majority of species of the *O. labronica* group as the apomorphic state, in contrast to Pleijel & Eide (1996). The decision to code the state as apomorphic is supported by the fact that larvae and juveniles have separate eyes, and they start to become connected only when they have reached a size of about five chaetigers, indicating a transformation from a more general to a specialised character (Nelson 1978). Based on this character it appears as if *O. robusta* and *O. rubra* are the most ancestral species of the group. This is further supported by chromosome studies, which showed that *O. robusta* appeared to be quite different from all other *Ophryotrocha* species examined by Vitturi et al. (2000) and considered as having plesiomorphic characters. The phylogenetic studies also placed *O. robusta* and *O. rubra* (when included) as the most ancestral species of the *O. labronica* group (Pleijel & Eide 1996, Dahlgren et al. 2001; Heggøy et al. 2007; Wiklund et al. 2009). However, the genes of the remaining species are incompletely sampled and in need of a new molecular phylogeny study which is outside the scope of this paper.

Our species and subspecies identifications are based on results of crossing experiments following the biological species concept in the sense of Mayr (1969). Thus our interpretations are based on natural selection which may not always be in concordance with the neutral selection demonstrated in DNA sequences. Based on our crossing experiments we can state that *O. labronica* and *O. costlowi* are the two most closely related species of the *O. labronica* group. As we have reported previously, the western North Atlantic *O. costlowi* has reached sufficient genetic isolation to allow interfertility with *O. labronica labronica* (Mediterranean and eastern North Atlantic) and *O. labronica pacifica* (eastern Pacific) in one direction only, with low fecundity and low viability in both F_1 and F_2 (Åkesson & Paxton 2005).

Ophryotrocha notoglandulata from Japan is the next most closely related species to *O. labronica*. While there is total intersterility between the two species, mating was observed to be still occurring between *O. notoglandulata* and *O. labronica pacifica* (Åkesson 1984, 1994). We are here referring to our model of speciation within the *O. labronica* group where we listed six stages in the process of speciation in the group, ranging from slight changes in fecundity and sex ratio expressed in F_1 (stage 1) to no sexual interest in each other (stage 6) (Åkesson & Paxton 2005). According to this model the interactions of *O. labronica* with *O. labronica pacifica* fit stage 3, with *O. costlowi* stage 4, with *O. notoglandulata* stage 5, and with all other species of the *O. labronica* group stage 6, demonstrating that they are fully reproductively isolated.

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