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35	Abstract	<p>A sampling campaign took place in October 2011 and included 7 locations and 16 stations along the eastern coast of the island of Lanzarote (Spain). Samples yielded 61 species for a total of 96 records. Thirty-six species (27 genera and 11 families) belong to Macrodasysida while 25 species (18 genera, 7 families) to Chaetonotida. Thirty-two are known species while 29 appear to be undescribed taxa or putatively so. The finding at Lanzarote of some of the known species bear particular significance: <i>Oregodasys cirratus</i> and <i>Tetranchyroderma canariense</i> are recorded for the second time ever, while <i>Musellifer delamarei</i> and <i>Urodasys acanthostylis</i> were previously known only from the Mediterranean, and <i>Urodasys mirabilis</i> was acknowledged only for northern Europe. Furthermore, the presence of <i>Chaetonotus apechochaetus</i>, <i>C. apolemmus</i>, <i>C. siciliensis</i>, <i>Heterolepidoderma loricatum</i>, <i>Lepidodasys unicarenotus</i>, <i>Musellifer delamarei</i>, <i>Thaumastoderma mediterraneum</i>, and <i>Urodasys acanthostylis</i> strongly suggest them to be part of the temperate/warm fauna that invaded the Mediterranean basin after the Missinian crisis during the different climate eras. Of the new species, one is described as its characteristics substantially widen our knowledge of the entire genus. <i>Urodasys completus</i> sp. nov. is unique in that it possesses, among others, two testes and a sclerotic stylet. Results of a phylogenetic analysis indicated that the sequence of the evolutionary transformation that have occurred in the reproductive system of the species of <i>Urodasys</i> are likely dissimilar from the ones proposed thus far. The overall results testify the need to continue the exploration in the Canary Islands.</p>	
36	Keywords separated by ' - '	Meiofauna - Benthos - Spanish biodiversity - Canary islands - Phylogeny - Taxonomy	
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MEIOLANZA

4 **Marine gastrotrichs from Lanzarote, with a description**
5 **of a phylogenetically relevant species of *Urodasys***
6 **(Gastrotricha, Macrodasysida)**

7 **M. Antonio Todaro¹ · Agata Cesaretti¹ · Matteo Dal Zotto^{1,2}**
8

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11 **Abstract** A sampling campaign took place in October 2011
12 and included 7 locations and 16 stations along the eastern
13 coast of the island of Lanzarote (Spain). Samples yielded 61
14 species for a total of 96 records. Thirty-six species (27 genera
15 and 11 families) belong to Macrodasysida while 25 species (18
16 genera, 7 families) to Chaetonotida. Thirty-two are known
17 species while 29 appear to be undescribed taxa or putatively
18 so. The finding at Lanzarote of some of the known species
19 bear particular significance: *Oregodasys cirratus* and
20 *Tetranchyoderma canariense* are recorded for the second
21 time ever, while *Musellifer delamarei* and *Urodasys*
22 *acanthostylis* were previously known only from the
23 Mediterranean, and *Urodasys mirabilis* was acknowledged
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26 *Heterolepidoderma loricatum*, *Lepidodasys unicarenatus*,
27 *Musellifer delamarei*, *Thaumastoderma mediterraneum*, and
28 *Urodasys acanthostylis* strongly suggest them to be part of the
29 temperate/warm fauna that invaded the Mediterranean basin
30 after the Missinian crisis during the different climate eras. Of
31 the new species, one is described as its characteristics substan-
32 tially widen our knowledge of the entire genus. *Urodasys*
33 *completus* sp. nov. is unique in that it possesses, among others,
34 two testes and a sclerotic stylet. Results of a phylogenetic
35 analysis indicated that the sequence of the evolutionary

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of the species of *Urodasys* are likely dissimilar from the ones 37
proposed thus far. The overall results testify the need to con- 38
tinue the exploration in the Canary Islands. 39

Keywords Meiofauna · Benthos · Spanish biodiversity · 40
Canary islands · Phylogeny · Taxonomy 41

Introduction 42 Q1

Gastrotricha are microscopic invertebrates (0.08–3.0 mm in 43
total body length) constituting a phylum likely sister to the 44
Platyhelminthes (e.g., Struck et al. 2014; Egger et al. 2015). 45
The group is cosmopolitan and includes, as of April 2017, 826 46
species, 497 of which are marine and 329 freshwater 47
(WoRMS 2017). The phylum is divided into two orders: 48
Macrodasysida (M), mostly marine, and Chaetonotida (C), 49
common in both freshwater and marine ecosystems 50
(taxa/habitat distribution detailed in Todaro 2016 and Todaro 51 Q2
and Tongiorgi 2016; see also Kieneke and Schmidt-Rhaesa 52
2014). 53

Gastrotrichs are mainly interstitial in marine habitats, 54
whereas in freshwater they are also found as ubiquitous com- 55
ponents of the periphyton and benthos (Balsamo and Todaro 56
2002). Some freshwater genera have adapted to a semi- 57
planktonic life style, e.g., *Haltidytes*, *Stylochaeta*, 58
Kijanebalola and *Neogosseia* (e.g., Kånneby and Todaro 59
2015; Todaro et al. 2013). 60

Marine species live both intertidally and subtidally, being 61
most abundant in fine- to medium-grained sediments in crys- 62
talline waters of coastal areas (e.g., Garraffoni et al. 2016; 63
Todaro and Rocha 2004); only some species of the genus 64
Musellifer are known to inhabit deep-sea muddy substrata 65
(Hummon 1969; Leasi and Todaro 2010). In marine sandy 66

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67 bottoms, gastrotrichs typically rank third in abundance among
68 the meiofaunal taxa behind the Nematoda and the harpacticoid
69 Copepoda (e.g., density up to 364 ind./10 cm²; Todaro 1998),
70 although in several instances, they have been found to be the
Q3 71 first or the second most abundant meiofauna taxon (e.g., Coull
72 1985; Gray 1971; Hochberg 1999; Todaro et al. 1995).

73 Gastrotrichs feed on microalgae, bacteria and occasionally on
74 protists such as flagellates or foraminiferans (Kieneke and
75 Schmidt-Rhaesa 2014, and unpublished). Like most other
76 meiobenthic organisms they have a short life cycle and lack
77 larval stages useful for dispersal; consequently, marine
78 gastrotrichs spend their entire existence within the sediments.
79 Despite this life history, many species are not restricted to con-
80 fined areas; on the contrary, they seem to be widely distributed,
81 with some species being amphi-Atlantic or cosmopolitan (e.g.,
82 Todaro et al. 1995; Todaro and Rocha 2004; see also Artois et al.
83 2011). In the last decade, the widespread availability of novel
84 techniques, such as high-resolution microscopy and gene se-
85 quencing, allows for a better comparison at morphological and/
86 or genetic levels of specimens from distant areas, and have stim-
87 ulated interest in the taxonomy, phylogeny and biogeography of
88 these marine worms (e.g., Curini-Galletti et al. 2012; Hochberg
89 et al. 2014; Hummon 2011; Kieneke et al. 2012, 2013a; Kolicka
90 et al. 2015; Leasi and Todaro 2009; Schuster et al. 2017; Todaro
91 et al. 2015a). Increasing information comes especially from areas
92 of the world new or relatively new with regard to the gastrotrich
Q4 93 faunistic investigation (e.g., Pacific US: Hummon 2010a; Brazil:
Q5 94 Araujo et al. 2014; Hochberg 2014; Todaro 2012, 2013;
Q7/Q6 95 Garraffoni et al. 2016; Caribbean: Araujo et al. 2015; Atherton
Q8 96 and Hochberg 2014; Hummon 2010a, b; Kieneke et al. 2013b,
97 2015, K anneby et al. 2014, Todaro and Leasi 2013, Todaro et al.
98 2014; South Africa: Todaro et al. 2011, 2015b; Near East:
99 Hummon 2011), but, even from the well-studied Europe, recent
100 studies have brought about important novelties (e.g., Sweden:
101 Willems et al. 2009; Poland: Hummon 2008, Kolicka et al.
102 2014; Britain, Ireland, France and the Azores: Hummon 2008;
103 Italy: Dal Zotto et al. 2010; Hummon and Todaro 2009).

104 In this framework of exciting new data, it is pity that informa-
105 tion on the gastrotrich fauna from some biogeographic crucial
106 regions remains very scarce. In Europe, for example, prior to
107 investigation in Lanzarote, only 7 species have been reported in
108 print from Spain (Giere 1979; Marotta et al. 2008; Rothe and
109 Schmidt-Rhaesa 2010; Todaro et al. 2003a, b). Spain, including
110 the Canary archipelago, hosts an extreme varied fauna made up
111 of cold, temperate-cold and warm-subtropical elements (e.g.,
112 Marina et al. 2015). Consequently, a better knowledge of the
113 Spanish gastrotrich fauna could shed some light for example
114 on the origin and evolution of the Mediterranean gastrotrich as-
115 semblage, which currently appears to be one of the most diver-
116 sified in the world (Todaro et al. 2003a). The Mediterranean Sea
117 is the largest and deepest enclosed basin on Earth and is a marine
118 biodiversity hot spot (Coll et al. 2010). It has had a multifaceted
119 geological history, including isolation from the world oceans,

120 which led to its near drying out during the Messinian crisis and
121 to severe changes in sea level and salinity (Hs u 1983). The recent
122 marine biota of the Mediterranean Sea is primarily derived from
123 the Atlantic Ocean, through the Strait of Gibraltar, and includes
124 the persistent descendants of the cold, temperate, and subtropical
125 immigrants that invaded the basin over the various climate eras
126 (Coll et al. 2010). The knowledge of the gastrotrichs of Spain (at
127 large) could shed light on which of the different species that
128 currently inhabit the Mediterranean basin belong to these three
129 components (cold, temperate or subtropical).

130 The aim of this research is to assess the diversity and dis-
131 tribution of gastrotrich species along the coasts of the Canary
132 island of Lanzarote (Spain). The study is part of the 1st
133 International Workshop on Marine and Anchialine
134 Meiofauna held in Lanzarote in October 2011 and represents
135 the most extensive investigation on the Gastrotricha from
136 Spain to date. A short account of the results has been proposed
137 in Riera and Todaro (2012).

138 In a larger framework, additional information about the
139 poorly understood segment of the fauna from the
140 Macaronesia region should contribute to future debate on the
141 global biogeography of the Gastrotricha and in particular of
142 the Mediterranean fauna. Descriptions of clearly new or puta-
143 tive new taxa are beyond the scope of the present article, and
144 will be presented in forthcoming papers. However, since one
145 of the new species bears a special relevance, e.g., for the on-
146 going debate on the phylogeny of the peculiar genus
147 *Urodasys*, we provide its description here and the formal tax-
148 onomic affiliation.

149 Materials and methods

150 Sampling collection and processing

151 The meiofauna sampling campaign took place in October
152 2011 and included several locations and stations along the
153 different sides of Lanzarote (Canary Islands, Spain). The gas-
154 trotrich species reported here were found in littoral and sub-
155 littoral samples collected from seven locations and 16 stations
156 along the eastern coast of the island (Fig. 1). For the purpose
157 of the present article, a location is a locality with a name on a
158 map and/or identifiable with geographic coordinates, while
159 stations are the specific points of a location where the samples
160 were taken, in general differentiated by water depth. Littoral
161 samples were collected during low tide, by digging several
162 3- cm-deep holes at the mid-water mark, and transferring the
163 sand with a spoon to a 500-ml plastic jar. Bulk sublittoral
164 samples were taken at 1.5–35 m depth using 0.5- to 2.0-L jars
165 or plastic bags. Samples below 5 m were taken by scuba
166 diving, and the shallower samples by skin diving. In general,
167 no special permission/permits were needed to collect these
168 animals as gastrotrichs are microscopic, non-pathogenic

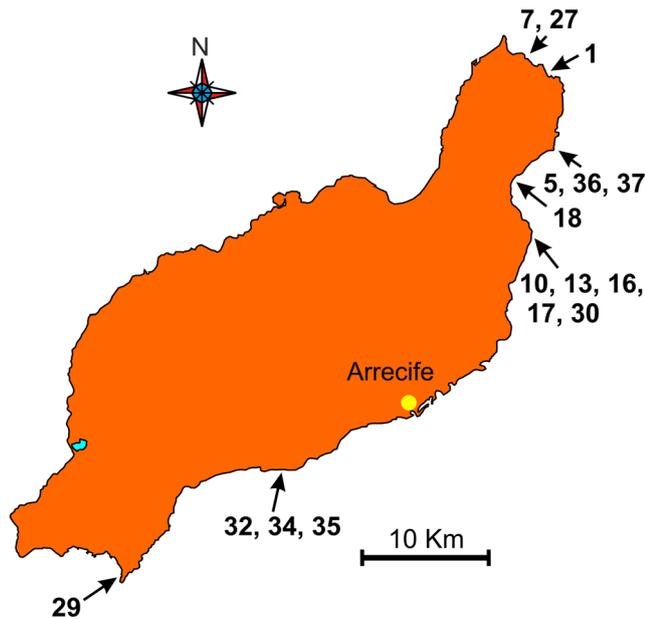


Fig. 1 Locations (and stations) along the east coast of Lanzarote (Canary Islands, Spain) where gastrotrichs were found. Playa del Caletón Blanco (1); Punta Jameos de Agua (5, 36, 37); Playa de Orzola (7, 27); Mala (10, 13, 16, 17, 30); Arrieta, playa de la Garita, (18); Playa del Papagayo (29); Puerto del Carmen, playa Chica (32, 34, 35)

169 organisms; field studies did not involve endangered species
 170 and sampling was carried out on public beaches. A permit to
 171 collect at site number 5, inside a submarine lava tube, was
 172 granted by the Government of the Canary Islands.
 173 Additional details regarding collecting dates, sampling proce-
 174 dures and characteristics of the investigated microhabitats will
 175 be provided in a forthcoming general paper; to avoid confu-
 176 sion, here the numbering of locations and stations is main-
 177 tained in accordance with the information reported in the gen-
 178 eral paper.

179 After each collecting trip, the sandy material was brought as
 180 soon as possible to the field laboratory (Aula de Naturaleza de
 181 Máguez, in Lanzarote) and processed within 1 week from col-
 182 lection; from each sampling station, up to 300 ml of sediment
 183 were processed for the gastrotrich study, in many cases sediment
 184 derived from containers shared with colleagues studying other
 185 meiobenthic organisms. Gastrotrichs were extracted from the
 186 sediment by the narcotization–decantation technique, using a
 187 sea-water isosmotic (7%) magnesium chloride solution. The
 188 fauna-containing supernatant was then poured directly into a 5-
 189 cm-diameter Petri dish and scanned for specimens under a Wild
 190 M3 dissecting microscope (Leasi and Todaro 2009).

191 **Species examination and identification**

192 When located, gastrotrichs were picked out with a micropi-
 193 pette, mounted on glass slides, and observed in vivo with
 194 Nomarski differential interference contrast optics using a
 195 Leitz Dialux 20 microscope equipped with a DS–5 M Nikon

digital camera. During observation, the animals were 196
 photographed with a DS-Fi1 Nikon digital camera and mea- 197
 sured with the Nikon NIS-F v.4.0 software. Specimens were 198
 affiliated to: (1) known species, if their morpho-metric char- 199
 acteristics matched those reported in the literature for the tax- 200
 on, (2) new species (n. sp.) if their anatomical traits appear to 201
 be clearly unique, and (3) putative new species (sp1, sp2, sp3) 202
 if the data gathered so far are not sufficient to grant their 203
 affiliation to species already described (see Tables 1, 2). As 204
 the finding of a new species of *Urodasys* brings important 205
 novelties to the vivid debate on the phylogeny of the genus, 206
 we decided to anticipate here the description and the formal 207
 affiliation of this taxon. The description of the new species 208
 follows the convention of Hummon et al. (1993), whereas the 209
 position of some morphological characteristics along the body 210
 are given in percentage units (U) of total body length mea- 211
 sured from anterior to posterior. The rationale for the key to 212
 the ecological characteristics of the species, according to 213
 Hummon et al. (1992), is as follows: frequency of a species 214
 from among a sample series (i.e., frequency of a species in 215
 samples collected in any given sampling trip): sparse, found in 216
 less than 10% of samples; occasional, found in 10–30% of 217
 samples; common, found in 30–60% of samples; usual, found 218
 in more than 60% of samples. Abundance of a species among 219
 other species of a sample: rare, less than 1% of a sample; 220
 scarce, 3–5% of a samples; numerous, 10–20% of a sample 221
 (often a sub-dominant); prevalent, more than 30% of a sample 222
 (usually dominant or co-dominant). 223

224 **Granulometric analysis**

225 The study was performed on 50–100 g of sediment for each 226
 sample following the general procedure of Buchanan (1984). 227
 Dried samples (for 24 h at 60 °C) were sieved through an 8- 228
 sieve column in an Octagon D200 test sieve shaker for 1 h. 229
 Granulometric parameters were obtained with the RYSGRAN 230
 package for R (Camargo 2006) following the method of 231
 McCammon (1962). Sediment size and sorting classes are 232
 based on Wentworth tables (Wentworth 1922).

233 **Phylogenetic analysis**

234 To shed light on the position of the new species within the 235
Urodasys phylogenetic branch, seven traits regarding the 236
 reproductive apparatus organs composition and layout, and the 237
 reproductive condition were coded in 17 taxa (Tables 3, 4). 238
 Sixteen species of *Urodasys* constituted the in-group whereas 239
Macrodasys meristocytalis Evans, 1994 was used as the out- 240
 group in order to determine character transformation within 241
 the *Urodasys* evolutionary lines. *Urodasys bucinastylis* 242
 Fregni, Faienza, Grimaldi, Tongiorgi & Balsamo, 1999, 243
U. uncinostylis Fregni, Tongiorgi & Faienza, 1998 and 244
U. toxostylus Hummon, 2011 were assumed to conform to

t1.1 **Table 1** Gastrotricha Macrodasysida, species list and distribution along the eastern coast of Lanzarote

t1.2	Taxon	Sampling station															
t1.3	MACRODASYIDA	1	5	7	10	13	16	17	18	27	29	30	32	34	35	36	37
t1.4	Dactylopodolidae																
t1.5	<i>Dactylopodola typhle</i>	+	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-
t1.6	<i>Dendrodasys</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
t1.7	Cephalodasyidae																
t1.8	<i>Cephalodasys</i> sp1	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
t1.9	<i>Mesodasys laticaudatus</i> *	+	+	-	-	+	+	+	-	-	-	-	-	-	-	-	-
t1.10	Lepidodasyidae																
t1.11	<i>Lepidodasys martini</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
t1.12	<i>Lepidodasys platyurus</i>	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
t1.13	<i>Lepidodasys unicarenotus</i>	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
t1.14	<i>Lepidodasys</i> sp1 n. sp.	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
t1.15	Macrodasysidae																
t1.16	<i>Macrodasys</i> sp1	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
t1.17	<i>Macrodasys</i> sp2	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
t1.18	<i>Macrodasys</i> sp3	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
t1.19	<i>Macrodasys</i> sp4	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
t1.20	<i>Urodasys acanthostylis</i>	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
t1.21	<i>Urodasys completus</i> sp. nov.	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-
t1.22	<i>Urodasys mirabilis</i>	+	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-
t1.23	Planodasyidae																
t1.24	<i>Crasiella</i> sp1*	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
t1.25	<i>Megadasys sterreni</i> *	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-
t1.26	Thaumastodermatidae																
t1.27	<i>Acanthodasys aculeatus</i>	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
t1.28	<i>Acanthodasys</i> sp1 n. sp.	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	+
t1.29	<i>Diplodasys</i> cf. minor	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
t1.30	<i>Diplodasys</i> sp1	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
t1.31	<i>Diplodasys</i> sp2	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-
t1.32	<i>Diplodasys</i> sp3	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
t1.33	<i>Oregodasys cirratus</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-
t1.34	<i>Oregodasys</i> sp1	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
t1.35	<i>Pseudostomella</i> sp1	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
t1.36	<i>Ptychostomella mediterranea</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
t1.37	<i>Ptychostomella</i> sp1 n. sp.	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
t1.38	<i>Tetranchyoderma canariense</i>	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-
t1.39	<i>Tetranchyoderma cirrophorum</i>	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
t1.40	<i>Tetranchyoderma</i> sp1	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
t1.41	<i>Tetranchyoderma</i> sp2 n. sp.	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+
t1.42	<i>Thaumastoderma mediterraneum</i>	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
t1.43	Turbanellidae																
t1.44	<i>Paraturbanella dorhni</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
t1.45	<i>Paraturbanella pallida</i>	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
t1.46	Incertae sedis																
t1.47	N. gen et n. sp.	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-

*Species anticipated in Riera and Todaro (2012)

t2.1 **Table 2** Gastrotricha Chaetonotida, species list and distribution along the eastern coast of Lanzarote

t2.2	Taxon	Sampling station															
t2.3	CHAETONOTIDA	1	5	7	10	13	16	17	18	27	29	30	32	34	35	36	37
t2.4	Chaetonotidae																
t2.5	<i>Aspidiophorus marinus</i>	+	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-
t2.6	<i>Aspidiophorus paramediterraneus*</i>	+	-	-	+	-	-	-	+	-	-	-	-	-	-	-	-
t2.7	<i>Aspidiophorus</i> sp1	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
t2.8	<i>Aspidiophorus</i> sp2 n. sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
t2.9	<i>Aspidiophorus</i> sp3	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
t2.10	<i>Chaetonotus apechochaetus*</i>	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
t2.11	<i>Chaetonotus apolemmus</i>	+	-	-	-	-	-	+	-	-	+	-	-	-	-	-	-
t2.12	<i>Chaetonotus dispar</i>	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-
t2.13	<i>Chaetonotus lacunosus*</i>	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
t2.14	<i>Chaetonotus neptuni</i>	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
t2.15	<i>Chaetonotus siciliensis</i>	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
t2.16	<i>Chaetonotus variosquamatus</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
t2.17	<i>Chaetonotus</i> sp1 n. sp.	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-
t2.18	<i>Chaetonotus</i> sp2	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
t2.19	<i>Halichaetonotus aculifer*</i>	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
t2.20	<i>Halichaetonotus decipiens</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
t2.21	<i>Halichaetonotus paradoxus</i>	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
t2.22	<i>Halichaetonotus</i> sp1	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
t2.23	<i>Heterolepidoderma loricatum*</i>	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
t2.24	Muselliferidae																
t2.25	<i>Musellifer delamarei</i>	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-
t2.26	Neodasyidae																
t2.27	<i>Neodasys</i> sp1	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-
t2.28	Xenotrichulidae																
t2.29	<i>Draculiciteria tessellata</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
t2.30	<i>Heteroxenotrichula pygmaea</i>	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-
t2.31	<i>Heteroxenotrichula</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
t2.32	<i>Xenotrichula punctata</i>	+	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-
t2.33	Total species (M + C) by location	17	1	2	14	6	13	4	7	1	11	2	5	1	1	1	8

*Species anticipated in Riera andand Todaro (2012)

245 the other stylet-bearing species with regard to the coded traits
 246 (see Fregni et al. 1998; Fregni et al. 1999). Phylogenetic
 247 analysis was carried out using PAUP* (Swofford 2002; v.4.0a150
 248 for 32-bit Microsoft Windows) using parsimony as the opti-
 249 mal criterion. Parsimony analyses were run using a full heu-
 250 ristic search strategy; the characters, all unordered, were
 251 equally weighted. Nodal support was assessed by a bootstrap
 252 analysis performed using 1000 replicates (heuristic search)
 253 and summarized in a 50% majority-rule consensus tree. We
 254 limited the morphological matrix to reproductive structures
 255 because they are the most conspicuous features of the group
 256 and have been the base of the previous hypothesis regarding
 257 relationships among the species of the genus (see Fregni et al.
 258 1999; Atherton and Hochberg 2014). On the other hand, we
 259 would like to stress that other the somatic characters (e.g.,
 260 regardng the external anatomy) in *Urodasys* are difficult to
 261 interpret, and either seem parsimoniously uninformative or
 262 concern a lot of meristic features demanding specific analyses,
 263 as well as the examination of many specimens, usually not
 264 available. *Macrodasys meristocytalis* was chosen as the
 265 outgroup because it summarizes the reproductive characteris-
 266 tics of the genus *Macrodasys*, which is currently systematized
 267 with *Urodasys* in the family Macrodasysidae.

Results and discussion

268

Gastrotrich diversity

269

Collection from 7 locations (16 stations/sites) along the east 270
 coast of Lanzarote yielded 61 species for a total of 96 records 271
 (species × site; Tables 3, 4). These species belonged to 27 272

Table 3 Characters and character states used in the phylogenetic analysis t3.1

Number	Characters	t3.2
1	Ovary: 0, paired; 1, single	t3.3
2	Testicle: 0, paired; 1, single; 2, absent	t3.4
3	Sperm duct: 0, paired always separated; 1, paired, converging posteriorly where they fuse on the mid-ventral plane; 2, paired, bending anteriorly where they fuse on the mid-ventral plane; 3, single; -, not applicable	t3.5
4	Male pore: 0, paired, lateral; 1, single medial; 2, single lateral; -, not applicable	t3.6
5	Caudal organ: 0, absent; 1, present	t3.7
6	Stylet: 0, absent; 1, present	t3.8
7	Reproductive condition: 0, hermaphroditic; 1, parthenogenetic	t3.9

t4.1 **Table 4** Characters matrix used in the phylogenetic analysis

t4.2	Taxa	Characters						
t4.3		1	2	3	4	5	6	7
t4.4	<i>Macrodasys meristocytalis</i>	1	0	0	0	1	0	0
t4.5	<i>U. anorektoxys</i>	0	0	2	1	0	0	0
t4.6	<i>U. elongatus</i>	0	0	2	1	0	0	0
t4.7	<i>U. mirabilis</i>	0	0	2	1	0	0	0
t4.8	<i>U. apuliensis</i>	0	0	2	1	0	0	0
t4.9	<i>U. acanthostylis</i>	0	1	3	2	1	1	0
t4.10	<i>U. bucinastylis</i>	0	1	3	2	1	1	0
t4.11	<i>U. calicostylis</i>	0	1	3	2	1	1	0
t4.12	<i>U. cornustylis</i>	0	1	3	2	1	1	0
t4.13	<i>U. nodostylis</i>	0	1	3	2	1	1	0
t4.14	<i>U. poculostylis</i>	0	1	3	2	1	1	0
t4.15	<i>U. remostylis</i>	0	1	3	2	1	1	0
t4.16	<i>U. spirostylis</i>	0	1	3	2	1	1	0
t4.17	<i>U. toxostylis</i>	0	1	3	2	1	1	0
t4.18	<i>U. uncinostylis</i>	0	1	3	2	1	1	0
t4.19	<i>U. completus</i> sp. nov.	0	0	1	1	1	1	0
t4.20	<i>U. viviparus</i>	0	2	-	-	0	-	1

273 genera and 11 families within the orders Macrodasysida (36
 274 species, 18 genera, 7 families) and Chaetonotida (25 species,
 275 9 genera, 4 families). Locations such as Mala and Playa de
 276 Caletón Blanco displayed the highest species richness with 31
 277 and 17 species, respectively.

278 Thanks to our survey the particularly minute paucitubulate
 279 gastrotrichs are reported for the first time from the Canary
 280 islands. The suborder Paucitubulatina is cosmopolitan and
 281 comprises half of all marine gastrotrichs; thus, to find some
 282 of its representatives in Lanzarote should not come as a sur-
 283 prise. In our samples, paucitubulate chaetonotidans account
 284 for some 39% of the total species (Table 2). In this,
 285 Lanzarote shares some similarities with areas of the world
 286 where gastrotrichs have been studied to a good extent and
 287 where members of the suborder account for about 40% of
 288 the total gastrotrich fauna, e.g., Italy 154 spp., 59% M and
 Q1289 41% C (Todaro et al. 2008), Belgian coast (37 spp., 62% M,
 290 38% C; Jouk et al. 1992) and Sweden (54 spp., 66% M and
 Q1291 34% C; Willems et al. 2009; Todaro et al. 2010 and unpub-
 292 lished). A higher percentage of chaetonotidans is reported for
 293 the Gulf of Mexico (45 spp., 53% M and 47% C, Todaro et al.
 294 1995) and the Caribbean island of St John (70 spp., 50% M
 295 and 50% C, Hummon et al. 2010). So far only in Greece do
 296 the chaetonotidans outnumber macrodasysidans (63 spp., 21 M
 297 and 42 C; Hummon and Roidou 1995).

298 Most of the species found during the current survey have
 299 been recorded only once or twice and consequently appear to
 300 have a restricted distribution in Lanzarote; exceptions are two
 301 chaetonotidans, *Aspidiophorus marinus* and *Chaetonotus*

apolemmus, found from north to the south of the investigated 302
 303 coastline.

304 The investigation carried out at Lanzarote increased tre- 304
 305 mendously the number of gastrotrich species and genera pre- 305
 306 viously reported from Spain, from 7 to 61 species and from 7 306
 307 to 27 genera respectively. Thirty-two are known species while 307
 308 29 appear to be new species or putatively so (Tables 1, 2). One 308
 309 such new species is described here (see below), while the 309
 310 formal affiliation of the others will be made at the end of the 310
 311 ongoing taxonomical survey and published in forthcoming 311
 312 papers along with a description of the most common species. 312

313 Of the 32 known species, *Oregodasys cirratus* and 313
 314 *Tetranchyroderma canariense* were both described from 314
 315 Tenerife (Rothe and Schmidt-Rhaesa 2010; Todaro et al. 315
 316 2003b) and so far appear to be endemic to the Canary archi- 316
 317 pelago, while the other 30 species are also present in other 317
 318 nearby geographic areas, e.g., the Mediterranean Sea 318
 319 (Todaro et al. 2003a) and/or the North European coasts (e.g., 319
 320 Dewarumez et al. 2002; Hummon and Warwick 1990; Jouk 320 /Q12
 321 et al. 1992; Remane 1927; Willems et al. 2009). More specifi- 321
 322 cally, 28 species found in Lanzarote are in common with the 322
 323 Mediterranean (*Urodasys mirabilis* and *Aspidiophorus*
 324 *marinus* are missing from the Mediterranean basin) and 22
 325 are shared with the North European coasts (*Lepidodasys*
 326 *unicarenatus*, *Thaumastoderma mediterraneum*, *Urodasys*
 327 *acanthostylis*, *Chaetonotus apechochaetus*, *C. apolemmus*,
 328 *C. siciliensis*, *Heterolepidoderma loricatum*, and *Musellifer*
 329 *delamarei* are missing from the North European coasts).

330 From a species distribution point of view, only a few re- 330
 331 cords really stand out, as the finding in Lanzarote extends the 331
 332 geographic range of some species. For instance, *Musellifer*
 333 *delamarei* and *Urodasys acanthostylis* were so far known only
 334 from the Mediterranean Sea (Italian coasts), while *Urodadys*
 335 *mirabilis* was known for the North Sea and the Atlantic coast
 336 of France. However, in a biogeographic framework involving
 337 the origin of the Mediterranean gastrotrich fauna, the contin-
 338 gent of species found also in Lanzarote but missing from the
 339 northern European regions assumes particular relevance since
 340 it makes most likely the hypothesis that sees them as part of
 341 the temperate/warm fauna that invaded the Mediterranean basin
 342 after the Missinian crisis. Further investigations should
 343 support or falsify such a hypothesis

Taxonomy 344

- Order Macrodasysida Remane, 1925 [Rao and Clausen, 1970] 345
- Family Macrodasysidae Remane, 1924 346
- Genus *Urodasys* Remane, 1926 347
- Urodasys completus* sp. nov. 348
- urn:lsid:zoobank.org:act:????? 349

350 **Examined material.** Morphological data of *Urodasys*
 351 *completus* sp. nov. is derived from six adult specimens ob-
 352 served under DIC optics. The holotype, LT = 297 μm 352

353 excluding the tail, is illustrated in Figs. 3, 4 (International
354 Code of Zoological Nomenclature, Articles 73.1.1, 73.1.4);
355 all the six physical specimens are no longer extant. Five fur-
356 ther identified specimens were fixed in alcohol and are kept in
357 the author's collection for future DNA analyses.

358 **Type locality.** The sediment sample was collected on 14
359 October 2011 from off Playa Chica, Puerto del Carmen
360 (Lanzarote; 28°50' 37"N, 13°46' 53"W). The sediment, made
361 up of shell fragments mixed with small amounts of mud, was
362 collected by A. Martínez and M. Curini Galletti at 29–31 m
363 depth inside the marine cave La Catedral (site 32, Fig. 1),
364 filling a plastic bag by hand.

365 **Etymology.** The specific epithet *completus* (Latin word for
366 “complete”, “perfect”) alludes to the reproductive system
367 composed of all the structures/organs known to occur among
368 species of the genus *Urodasys*.

369 **Diagnosis.** Body elongate, up to 297 µm in length (tail ex-
370 cluded), and rather narrow, up to 45 µm in width, flattened ven-
371 trally and vaulted dorsally; epidermic glands barely visible.
372 Cuticular covering smooth, devoided of scales and/or spines.
373 Head bluntly ovate, with sparse circumcephalic cilia but deprived
374 of pestle organs. A pair of peculiar, flexible, rod-like organs,
375 about 23 µm in length and 2.5–3 µm in diameter, are visible
376 along the dorsolateral sides of the pharyngeal region. Body width
377 relatively uniform, narrowing gradually in the hind-gut region
378 toward the elongate tail. Numerous sensory hairs of different
379 length occur around the head, others arise in 2–3 columns on
380 each lateral and dorsolateral side of the body. Ventral locomotor
381 ciliature forms a continuous field from under the head to the
382 pharyngo-intestinal junction and then continuing back to the pos-
383 terior trunk as paired bands. Anterior adhesive tubes (TbA), 3–4
384 per side, forming diagonal columns, which insert directly on the
385 body surface at some distance from the mouth. Ventral adhesive
386 tubes (TbV), absent; ventrolateral adhesive tubes (TbVL), 9 per
387 side, one along the pharyngeal region and the remaining along
388 the intestinal region. Lateral adhesive tubes (TbL), three per side,
389 two along the pharyngeal region and one along the intestinal
390 region. Dorsal adhesive tubes (TbD), and dorsolateral adhesive
391 tubes (TbDL) absent. Numerous, additional adhesive tubes are
392 distributed asymmetrically along the tail. Mouth terminal, quite
393 narrow, leading to a shallow and slightly cuticularized buccal
394 cavity; pharynx up to 40 µm long and 12 µm wide; pharyngeal
395 pores at some distance from the pharynx base, with ventrolateral
396 openings. Pharyngo-intestinal junction (PhIJ) at about U47.
397 Intestine is broadest anteriorly, narrowing to the rear; anus missing.
398 Testes bilateral. Each testis starts behind the PhIJ and extends
399 posteriorly into the sperm duct. At the rear of the frontal organ,
400 both sperm ducts fused on the mid-ventral plane, opening exter-
401 nally into a common pore, with anteriormost region posterior to
402 the PhIJ and extending as sperm ducts back to the rear of the
403 frontal organ where they fuse on the mid-ventral plane to empty
404 externally via a common pore. Mature sperm cells are about
405 20 µm long, with the anterior portion corkscrewed and the

406 posterior portion rod-like. Female gonads probably paired; left
407 ovary with oocytes maturing in a caudo-cephalic direction with
408 largest egg dorsal to the mid intestine. Frontal organ, sac-like,
409 dorsal to the intestine at about U79; rather small, ovoidal in shape
410 and completely filled with spermatozoa in individuals after cop-
411 ulation, but elongate and with a mass of spermatozoa agglutinat-
412 ed in form of a golf-club (a spermatophore?) in individuals soon
413 after copulation. A clear anatomical-functional compartmentali-
414 zation (i.e. subdivided into spermatheca and seminal receptacle
415 regions) was not observed, neither the internal nor the external
416 pore being seen. Caudal organ appearing as an oval capsule that
417 encloses a hyaline elongated bulblet on the left side and a scler-
418 otized stylet on the right side. The stylet resembles a narrow and
419 elongated mouth funnel proximally, and a curved syringe needle,
420 distally. The proximal portion of the stylet is anatomically located
421 more posterior to its distal portion.

422 **Description.** Based mostly on the adult specimen with a
423 total body length of 297 µm, excluding the tail, shown in
424 Fig. 3a. Body elongate and rather narrow, flattened ventrally
425 and vaulted dorsally; cuticular covering smooth, devoid of
426 scales and/or spines (Figs. 2a, b, 3a). Body width relatively
427 uniform from the pharynx to the anterior trunk region, increas-
428 ing slightly in the mid-gut, and then narrowing gradually in the
429 hind-gut region to the elongate tail (Figs. 2a, b, 3a). Head blunt-
430 ly ovate, with sparse circumcephalic cilia but deprived of pestle
431 organs. A pair of peculiar, flexible, rod-like organs, about
432 23 µm in length and 2.5–3 µm in diameter, are visible along
433 the pharyngeal region originating from the dorsolateral sides, at
434 U25 (Figs. 2a, b, 3a–c). Widths of head\mid-pharyngeal
435 region\PhIJ\mid-trunk\at confluence with the tail are as fol-
436 lows: 29\26\31\34\18 µm at U06\U28\U47\U63\U96, respec-
437 tively. Epidermal glands barely visible.

438 **Ciliation:** Numerous sensory hairs up to 18 µm in length
439 occur around the head, others, up to 25 µm, arise in 2–3
440 columns on each lateral and dorsolateral side of the body.
441 Ventral locomotor ciliature forms a continuous field from
442 TbA (U05) to the PhIJ (U47) then continuing back to the rear
443 of the caudal organ (U95) as paired bands (Fig. 2b).

444 **Adhesive tubes:** TbA, 3–4 per side, 6–18 µm long, forming
445 diagonal columns, which insert directly on the body surface, at
446 some distance from the oral opening from U04 to U07
447 (Fig. 2b); TbV, absent; TbVL, 9 per side, 8–10 µm long;
448 one along the pharyngeal region at U12 and the remaining
449 eight more or less evenly spaced along the intestinal region
450 (Fig. 2b); TbL, 3 per side, 6–9 µm long, two along the pha-
451 ryngeal region (at U21 and U39 respectively) and one along
452 the intestinal region at U77. TbD and TbDL apparently ab-
453 sent. Numerous, additional adhesive tubes are distributed
454 asymmetrically along the tail.

455 **Digestive tract:** Mouth terminal, quite narrow, 11 µm in
456 diameter, leading to a shallow (12 µm in length) and slightly
457 cuticularized buccal cavity (Figs. 2, 3a); pharynx is 140 µm
458 long, measured from the frontal edge, slightly increasing in

459 width from anterior (9 μm) to posterior (12 μm); pharyngeal
 460 pores, sub-basal at U41, with ventrolateral openings (Fig. 2a).
 461 Pharyngo-intestinal junction at about U47 (Fig. 2a). Intestine
 462 is broadest in front, narrowing to the rear, but lacks an anus
 463 (Figs. 2a, 3a).

464 Reproductive tract: hermaphroditic; bilateral testes with
 465 their anterior-most region just passed the PhIJ and extending
 466 as sperm ducts back to the rear toward to the frontal organ
 467 where they fuse on the mid-ventral plane and apparently empty
 468 externally via a common pore (Figs. 2a, 3d, 4; see remarks
 469 below). The right testis is slightly smaller and begins slightly
 470 posterior to the left one. Mature sperm are about 20 μm long,
 471 its anterior portion is corkscrew-shaped while the posterior
 472 portion is rod-like (Fig. 4d). Female gonads probably paired,
 473 though right ovary was not seen; left ovary showing oocytes
 474 maturing in a caudo-cephalic direction with largest egg,
 475 42 μm long and 16 μm wide, dorsal to the mid-intestine,
 476 centered at U67 (Figs. 2a, 3a). Frontal organ dorsal to the

intestine (Figs. 2a, 4b), centered at U79; in the holotypic spec-
 imens it appeared rather small, sac-like (i.e. the wall not
 muscolarised), about 18 μm long and 15 μm wide; it was
 completely filled with spermatozoa and without a clear
 anatomical-functional compartmentalization (i.e. not
 subdivided into spermatheca and seminal receptacle regions);
 neither the internal nor the external pore were observed.
 Caudal organ (at U91) appearing as an oval capsule (25 μm
 long and 16 μm wide) that encloses a hyaline elongated bulb-
 let on the left side and a sclerotized stylet on the right side
 (Figs. 2a, 4, 5). The bulblet is wider in front and narrower in
 the back; it is filled with globular masses of refringent material
 and bears a luminal continuity with the proximal portion of the
 sclerotized stylet (Figs. 2a, 5). The stylet has the proximal
 portion in the form of a narrow and elongated funnel while
 the distal portion resembles a curved syringe needle (Figs. 2a,
 4, 5). Surprising, the proximal portion of the stylet is anatom-
 ically located more posterior to its distal portion. Anterior to
 the caudal organ are two round masses of secretory material
 connected at the ventral mid-line; the appearance of this mat-
 erial is similar to the refringent droplets seen inside the bulblet
 of the caudal organ and may explain the origin of the latter;
 however, a luminal connection between the two masses and
 the caudal organ has not been observed.

Ecology. Frequency of occurrence: occasional in coarse
 sublittoral sediment (20%); abundance: prevalent (> 30% of
 a sample, dominant); in intertidal at a water depth of 29–31 m
 in coarse (0.8 phi), poorly sorted (1.49 phi) carbonate sand
 (kurtosis = 1.94; skewness = -0.05). Values of salinity and
 temperature of the interstitial water at the time of sampling
 were 33‰ and 18 °C respectively.

Variability and remarks on general morphology. The
 total body length of the measured adult specimens (i.e. showing
 a large egg and/or a stylet) ranged from 245 μm to 297 μm
 (mean = 275 μm \pm 19 SD, n = 6); maximum body width varied
 from 29 μm to 45 μm (mean = 35 μm \pm 6 SD, n = 6). The
 number and, to a lesser extent, the arrangement of the adhesive
 tubes belonging to the different series varied among the observed
 specimens; in particular, two of the animals showed four TbA per
 side where the number of TbVL ranged from 6 to 10 and TbL 6
 to 10 per side. In general, the number of these adhesive tubes
 was not strictly related to the body length, e.g., the longest specimen
 showed only 3 TbA and 9 TbVL per side, whilst the shortest had
 4 TbA and 6 TbVL per side; moreover, in some specimens, the
 lateral tubes actually seemed to originate dorsolaterally instead.
 Some differences were also noted with regard to the reproductive
 structures. More specifically, a 285- μm -long specimen showed a
 frontal organ whose morphology and content (Fig. 6a) were
 rather different from the ones described for the holotypic and
 most of the other adult specimens. In particular, in this specimen,
 the frontal organ appeared rather large and elongated in place of
 the small and roundish structure seen in other specimens; further-
 more, in place of the homogeneously distributed allosperm,

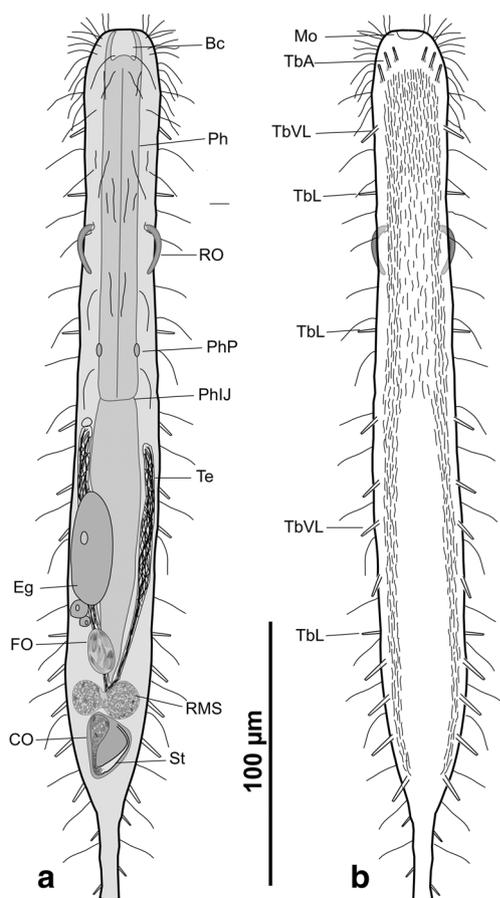
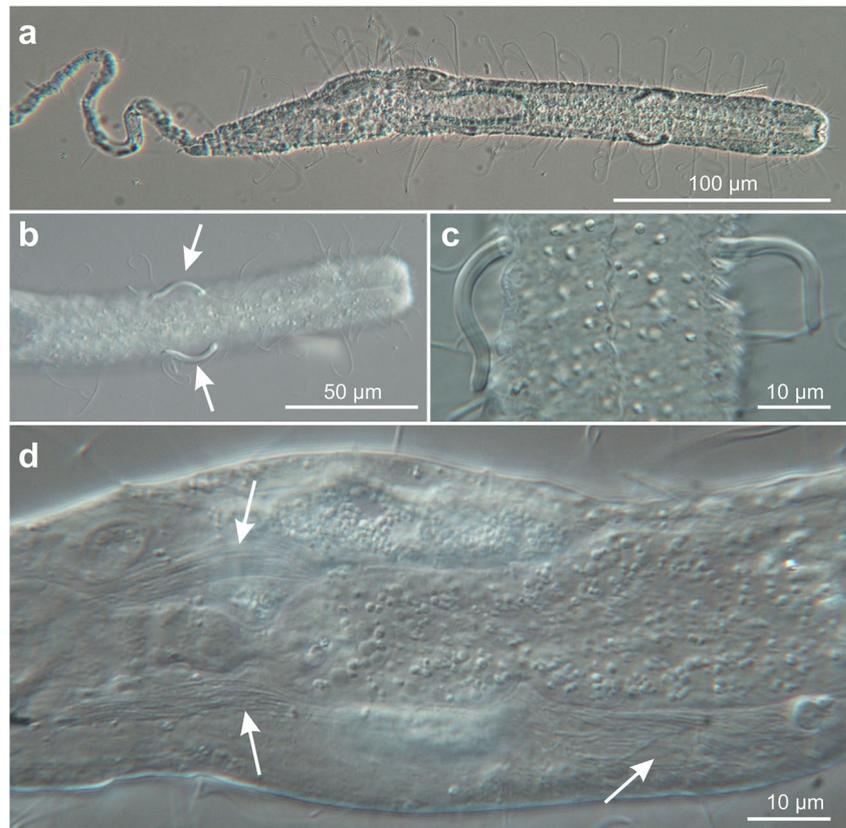


Fig. 2 Illustrations of *Urodasyus completus* sp. nov.; for clarity, the long tail has been omitted: **a** habitus as seen from the dorsal side, showing the internal anatomy with the maturing oocytes, testes, frontal- and caudal organ; **b** habitus as seen from the ventral side. Bc buccal cavity; CO caudal organ; Eg egg; FO frontal organ; Mo mouth; Ph pharynx; PhIJ pharyngo intestinal junction; PhP pharyngeal pores; RO rod-like organs; RMS round masses of secretory material; St stylet; TbA anterior adhesive tubes; TbL lateral adhesive tubes; TbVL ventrolateral adhesive tubes

Fig. 3 *Urodasys completus* sp. nov. from Lanzarote: **a** habitus; **b** anterior region showing the flexible rod-like organ (*arrows*); **c** close-up of the flexible rod-like organs; **d** internal anatomy of the mid-body region showing the paired testes (*arrows*). **a** Bright field microscopy, **b–d** DIC microscopy



530 inside it was a mass of spermatozoa agglutinated in form of a
 531 golf-club, whose head was located in the posterior region of the
 532 organ and the shaft obliquely oriented from the body midline to
 533 the left side (cf. Fig. 4c vs. Fig. 6a). Regardless of the shape, the
 534 bundle of spermatozoa recorded in the frontal organ of this spec-
 535 imen may be considered homologous to the spermatophore re-
 536 cently described for a potential new *Urodasys* species from
 537 Florida (Atherton and Hochberg 2014). In another specimen,
 538 240 μm in body length, the stylet showed additional outlets/
 539 chambers along the distal portion (Fig. 6b). Very likely, the ob-
 540 served disparities represent normal morphological variation and/
 541 or normal, time-variable aspects of the functional reproductive
 542 biology of the species, which are visible only at a certain life
 543 stage and for a short period of time. In this hypothetical frame-
 544 work, the spermatozoa of a specimen, for example, may be
 545 injected in the frontal organ of the partner as a spermatophore,
 546 like the one seen in Fig. 6a, but later on they become free from
 547 each other, hence occupying the entire lumen of the frontal organ,
 548 as shown, e.g., in Fig. 4c. Most of the sperm-carrying specimens
 549 possessed also a mature egg dorsal to the mid intestine; but,
 550 unfortunately, their ovaries were not seen. All the observed spec-
 551 imens carried the paired, flexible rod-like organs along the pha-
 552 ryngeal region, a feature that appears to be unique among
 553 Gastrotricha. Very likely, these structures represent sensorial or-
 554 gans, perhaps similar in function to the drum-stick organs found
 555 in the cephalodasyid *Pleurodasys helgolandicus* Remane, 1927

for which a sensorial function as graviceptors has recently been
 demonstrated (Marotta et al. 2008).

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Taxonomic remarks

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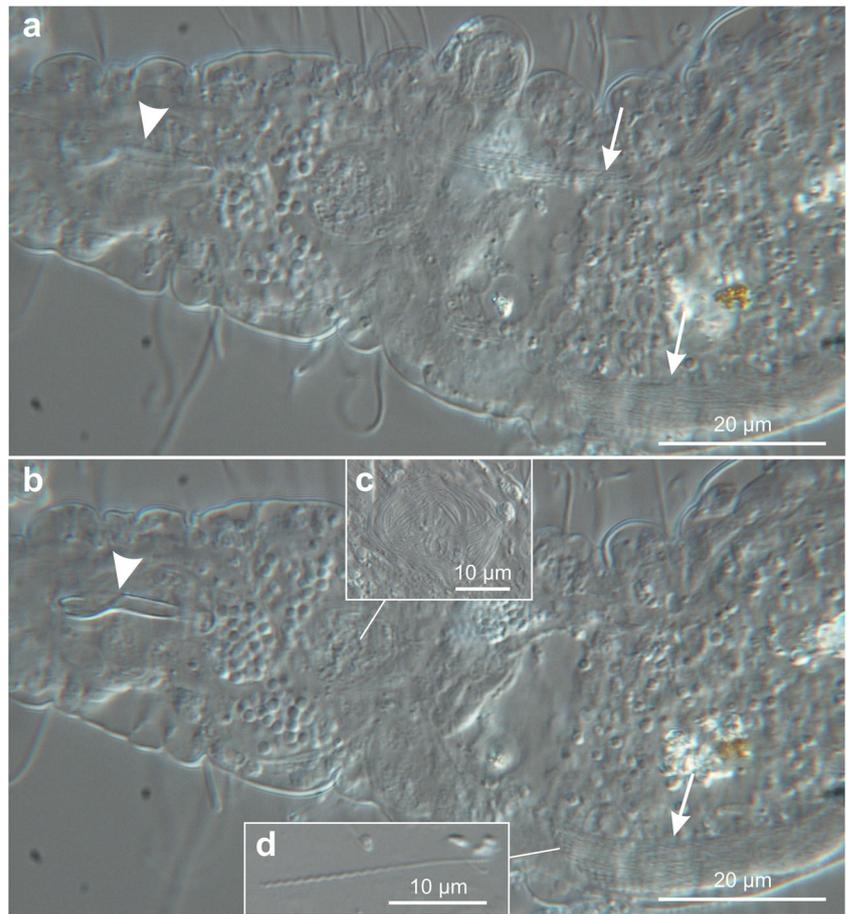
The genus *Urodasys* currently includes 15 described species
 (Atherton 2014; Hummon 2011; Hummon and Todaro 2010).
 These species can easily be subdivided into three groups
 based on their reproductive condition and presence/absence
 of various reproductive organs; in short: **Group 1**, including
 hermaphroditic species lacking a sclerotized stylet (4 spp);
Group 2, formed by hermaphroditic species possessing a
 sclerotized stylet, and **Group 3**, formed by *Urodasys*
viviparus. Specimens of this last species possess ovaries but
 lack testicles and accessory reproductive structures; they re-
 produce by parthenogenesis and, unique among Gastrotricha,
 give birth by ovoviviparity (see also Kieneke and Schmidt-
 Rhaesa 2014).

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Urodasys completus sp. nov., in virtue of its hermaphroditic
 condition and possession of a sclerotic stylet, is most similar
 to the ten species that make up the **Group 2**. The ten stylet-
 bearing species are: *U. acanthostylis* Fregni, Tongiorgi and
 Faienza 1998; *U. bucinastylis* Fregni, Faienza, Grimaldi,
 Tongiorgi and Balsamo 1999; *U. calicostylis* Schöpfer-
 Sterrer, 1974; *U. cornustylis* Schöpfer-Sterrer, 1974;

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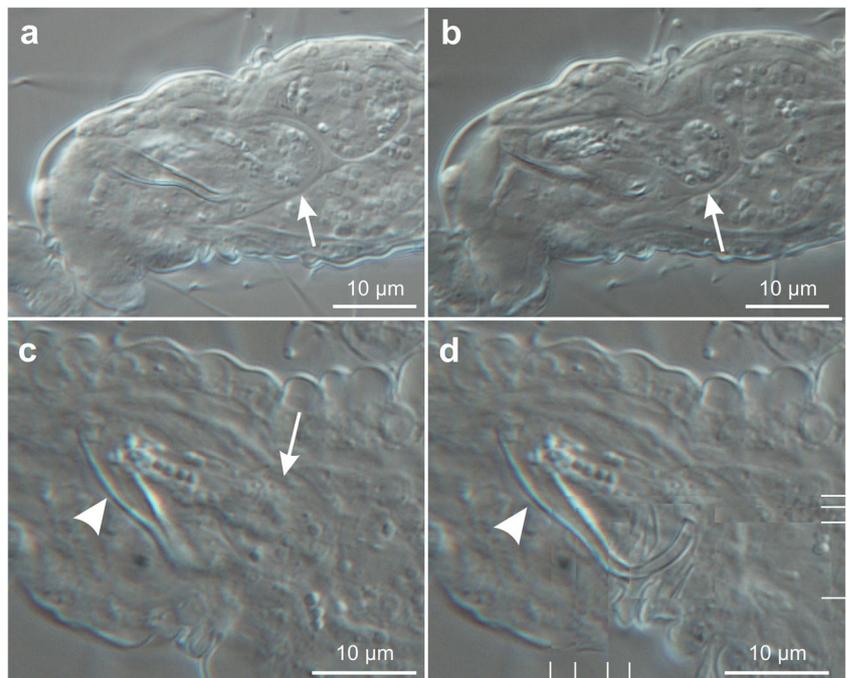
Fig. 4 *Urodasys completus* sp. nov. from Lanzarote. DIC microscopy: **a, b** internal anatomy of the posterior body region at different focal planes showing the paired testes (arrows) and the caudal organ (arrowhead); **c** close-up of the frontal organ filled with allosperm; **d** close-up of a single auto spermatozoon



579 *U. nodostylis* Schöpfer-Sterrer, 1974; *U. poculostylis*
 580 Atherton, 2014; *U. remostylis* Schöpfer-Sterrer, 1974;

U. spirostylis Schöpfer-Sterrer, 1974; *U. toxostylus* Hummon
 581 2011; and *U. uncinostylis* Fregni, Tongiorgi and Faienza 1998
 582

Fig. 5 *Urodasys completus* sp. nov. from Lanzarote. DIC microscopy: **a, b** internal anatomy of the posterior body region at different focal planes, showing the caudal organ (arrow) and its internal structures; **c** close-up of the caudal organ showing the stylet (arrowhead) and bulblet (arrow); **d** composite reconstruction of the sclerotic stylet (arrowhead); white lines indicate portions of the figures (taken at different focal planes) that contributed to the reconstruction of the entire stylet



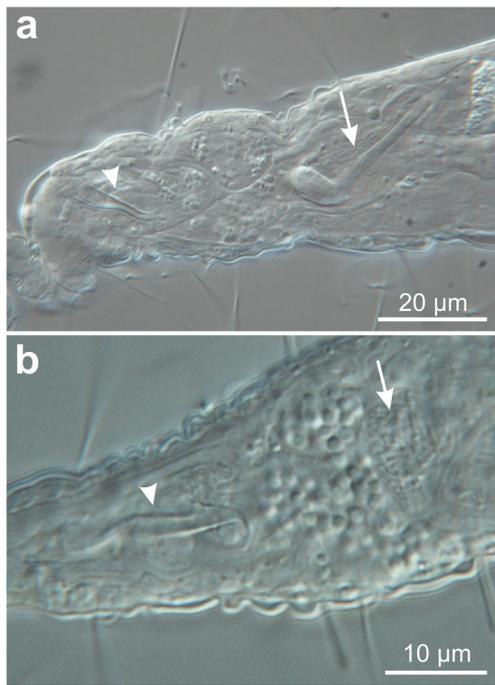


Fig. 6 *Urodasys completus* sp. nov. from Lanzarote. DIC microscopy: **a** internal anatomy of the posterior region of a mature specimen showing the stylet (*arrowhead*) and the frontal organ containing a golf-club shaped bundle of allosperm interpretable as a spermatophore (*arrow*); **b** internal anatomy of the posterior region of a different specimen showing the stylet with an additional chamber (*arrowhead*) and the frontal organ filled with homogeneously distributed allosperm. Variation borne by the stylet and the frontal organ may be interpreted as normal morphological variation and/or normal, time-variable aspects of the functional reproductive biology of the species (see text for details)

583 (see Tables 3 and 4). From all of them the new species can be
 584 easily discerned because it bears two testes, while the others
 585 have either a single testis or none altogether (*U. bucinastylis*
 586 and *U. toxostylus*). The peculiar shape of the stylet and the
 587 number and distribution of the adhesive tubes may further
 588 separate *U. completus* sp. nov. from the above mentioned taxa.
 589 Furthermore, another important diagnostic feature distin-
 590 guishes the new species from all of its congeners: the paired
 591 flexible, rod-like organs present along the pharyngeal region
 592 (e.g., Fig. 3a–c). Never before organs like these were reported
 593 among species of the genus *Urodasys*, nor among species of
 594 the entire phylum, making the new species even more unique.

595 **Phylogeny**

596 Our analysis found two most parsimonious trees, each of a
 597 length of 11 steps, whose topologies appeared extremely sim-
 598 ilar, and similar or equal to the topology of the consensus tree
 599 shown in Fig. 7. In both original trees, the species involved in
 600 the analysis appeared distributed into two main clades accord-
 601 ing the possession/lacking of a sclerotized stylet (see Tables 3
 602 and 4 for additional characters and character states). The two

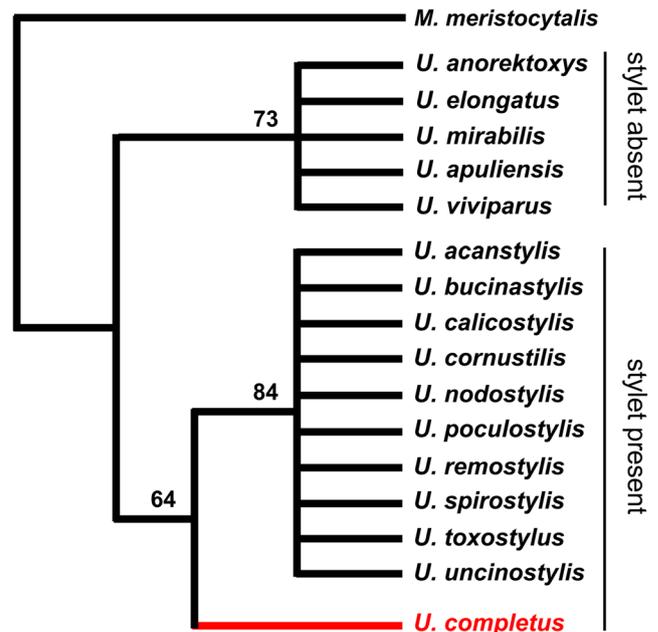


Fig. 7 Consensus tree (50% Majority-Rule) of 16 *Urodasys* species (ingroup) and 1 *Macrodasys* species (outgroup) based on 7 characters regarding the reproductive apparatus organs composition and layout, and the reproductive condition. Values at nodes represent bootstrap percentages based on 1000 replications (tree length = 11 steps; consistency index = 1.0; retention index = 1.0). *U. completus* sp. nov. (*U. comp*) is shown as an early divergent line of the branch that includes the hermaphroditic species bearing a sclerotized stylet (group 2). The parthenogenetic *Urodasys viviparus* (*U. vivi*) is shown in alliance with the hermaphroditic species lacking a sclerotized stylet (group 1). The full heuristic search found two most parsimonious trees of equal length (11 steps), which were very similar in topology. One of the trees had the same topology as the above consensus tree while the other showed *U. viviparus* as an early divergent line of the branch that included the species lacking a stylet.

603 trees also agreed in showing *Urodasys completus* sp. nov. as
 604 an early divergent line along the evolutionary branch of the
 605 stylet-bearing species, and in finding *U. viviparus* allied with
 606 the species lacking a sclerotized stylet. However, one of the
 607 trees found *U. viviparus* as an early divergent line along the
 608 evolutionary branch of the stylet-lacking species while the
 609 other tree found *U. viviparus* unresolved within this clade.
 610 Topology of the latter tree was equal to that of the consensus
 611 tree shown in Fig. 7.

612 The phylogenetic relationships among species of the genus
 613 *Urodasys* have recently been investigated based on molecular
 614 data (Atherton and Hochberg 2014). In that study, the 33 in-
 615 vestigated specimens, belonging to eight potential species,
 616 were found to be distributed in two main groups. Group 1
 617 (named clade I), including species with paired testes and ova-
 618 ries but lacking accessory sexual organs (e.g., a stylet), and
 619 Group 2, comprising the remaining species. Species belong-
 620 ing to Group 2 were subdivided into two subclasses (named
 621 clade II and clade III) according to their reproductive condi-
 622 tion and reproductive system organization. The

623 hermaphroditic, stylet-bearing species formed clade II, while
624 the parthenogenetic *U. viviparus* Wilke, 1954, represented by
625 several specimens collected in different islands of the
626 Caribbean Sea and in Brazil, formed clade III (see fig. 3 in
627 Atherton and Hochberg 2014).

628 The phylogenetic results based on a molecular marker by
629 Atherton and Hochberg (2014) were congruent with a previ-
630 ous hypothesis by Fregni et al. (1999), who, based on the
631 recognizable organization/composition of the reproductive
632 system of the species known at that time, envisioned an em-
633 pirical evolutionary scenario according to which the genus
634 *Urodasys* could be divided into two evolutionary lines. In
635 short, an evolutionary line that includes species with paired
636 gonads, but without accessory sexual organs, while the other
637 line includes species bearing a stylet. Hypotheses about the
638 reduction and/or loss of organs occurred among the species
639 included in each of the two lines were put forward in the
640 evolutionary scenario proposed by Fregni et al. (1999).
641 Furthermore, it was acknowledged that, in the depicted frame-
642 work, the parthenogenetic *Urodasys viviparus* could have
643 originated from either one of the two lineages (see Fregni
644 et al. 1999). The study by Atherton and Hochberg (2014)
645 recovered the two evolutionary lines envisioned by Fregni
646 et al. (1999), but *Urodasys viviparus* was found in a sister-
647 group relationships with the stylet-bearing species.

648 The two aforementioned studies differ at least in another
649 important point, i.e., the plesiomorphic organization of the
650 reproductive system in *Urodasys*. According to Fregni et al.
651 (1999), the ancestor of the extant *Urodasys* had paired male
652 and female gonads, a frontal organ and a caudal organ
653 furnished with a stylet. Atherton and Hochberg (2014) agreed
654 on this general set-up except that, in their hypothesized evo-
655 lution of the reproductive system within *Urodasys*, the hypo-
656 theoretical ancestor of the extant species had a caudal organ lack-
657 ing a stylet (see Fig. 4; Atherton and Hochberg 2014).

658 *Urodasys completus* sp. nov., in possessing two testes and a
659 caudal organ supplied with a sclerotized stylet, seems to match
660 the characteristics of the *Urodasys* ancestor hypothesized by
661 Fregni et al. (1999). However, the phylogenetic analysis per-
662 formed in the present study clearly shows *U. completus* sp.
663 nov. in a more derived position (Fig. 7). More specifically, the
664 new species appears as an early divergent line along the evo-
665 lutionary branch of the stylet-bearing taxa. On the other hand,
666 a quick thought at the organization of the reproductive system
667 of the new species makes it very unlikely that it could occupy
668 the basal-most position along the evolutionary tree of the ge-
669 nus *Urodasys*, at least in the way this taxon is currently rec-
670 ognized. In any case, regardless of the position that the new
671 species could occupy along the genus phylogenetic tree, its
672 traits indicate that the sequence of the evolutionary transfor-
673 mation that has occurred in the reproductive system of the
674 species of *Urodasys* is likely dissimilar from the ones pro-
675 posed by different authors thus far. Finally, we acknowledge

676 that, in contrast to the results of Atherton and Hochberg
677 (2014), in our tree, *U. viviparus* appears in alliance with the
678 stylet-lacking species. The inclusion of the new species in
679 future cladistics analysis based on molecular traits should bet-
680 ter inform on the transformation events concerning the repro-
681 ductive system that took place during the evolution of these
682 fascinating animals.

683 Conclusion

684 Lanzarote hosts a rich and diversified gastrotrich fauna as
685 testified by the fact that more than 60 species were found in
686 about 10 working days. In such a short period of time, not all
687 the potentially gastrotrich rich locations could be investigated.
688 Consequently, we anticipate that a higher number of species
689 may be discovered in the island if, in future, additional local-
690 ities, especially those on the western coast, will be
691 investigated.

692 At this time, 15% of the species found in Lanzarote appear
693 new to science; this percentage could rise to 45% if all the spec-
694 imens still under investigation prove to belong to undescribed
695 taxa. We speculate that the final figure of new species from
696 Lanzarote will be about 25–30% of the total. While these statis-
697 tics appear well below the percentage of putative new species
698 found in remote areas investigated for the first time (e.g., up to
699 80% of new species in Brazil and Kuwait; see Todaro in
700 Appeltans et al. 2012), the magnitude of new species found in
701 this small island is equally impressive considered the relatively
702 short distance of Lanzarote from the well-studied areas such as
703 the Mediterranean Sea and the North European shores (e.g.,
704 Hummon 2008; Todaro et al. 2003b).

705 Whether new to science or already known from other geo-
706 graphical regions, many of the species found in Lanzarote bear a
707 significance beyond their simple contribution to the global bio-
708 diversity of the island. For instance, *Urodasys completus* sp. nov.
709 also has a phylogenetic relevance, as its complete set of reproduc-
710 tive structures allows for better inferences about the ancestral
711 character pattern, and the possible transformations of these traits
712 occurred during the evolution of this cosmopolitan and easy to
713 identify gastrotrich genus. On the other hand, in a biogeographic
714 framework involving the origin of the Mediterranean gastrotrich
715 fauna, assumed relevant species include *Chaetonotus*
716 *apechochaetus*, *C. apolemmus*, *C. siciliensis*,
717 *Heterolepidoderma loricatum*, *Lepidodasys unicareatus*,
718 *Musellifer delamarei*, *Thaumastoderma mediterraneum*, and
719 *Urodasys acanthostylis*. The finding at Lanzarote of these species
720 lets us hypothesize that they are part of the temperate/warm fauna
721 that invaded the Mediterranean basin after the Missinian crisis,
722 during the periods in which the planet experienced a generalized
723 increase of temperatures (see “Introduction”).

724 Beside the supplementary information obtained so far on
725 the morphology and/or biology of some species, additional

726 data are expected to emerge during the taxonomic survey still
 727 ongoing and when the specimens stored for ultrastructural and
 728 DNA analyses are studied. In this regard, it is worth mention-
 729 ing that the recent ultrastructural study conducted on speci-
 730 mens of *Megadasys sterreri* found at Lanzarote contributed to
 731 the resystematization of the genus *Megadasys*, allowing its
 732 transfer to the family Planodasyidae from the original
 733 Cephalodasyidae (Guidi et al. 2014). Finally, it should be em-
 734 phasized that many species were recovered from deep sedi-
 735 ments (below 10 m water depth), usually neglected in studies
 736 on Gastrotricha, a clear indication for the future faunistic re-
 737 searches regarding these fascinating little creatures.

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