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Intersex in the gonochoristic crustacean *Tanais dulongii* (Audouin, 1826) (Peracarida: Tanaidacea: Tanaididae): a comparison of external reproductive characteristics

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Tanais dulongii (Audouin, 1826) is a small benthic crustacean with separate sexes and a marked sexual dimorphism characterized by a cephalothorax narrowed anteriorly, larger chelae (claws) and a pair of tiny genital cones in males, and ovisacs that form chambers for carrying embryos in females. Recent studies have described the existence of intersexual individuals with a cephalothorax similar to males, large chelae and ovisacs, but, due to their small size, it has not been possible to confirm the presence of genital cones under normal light microscopy. The present study analyses and compares external reproductive structures under scanning electron microscopy, of male and female *T. dulongii*, to corroborate the presence of both ovisacs and genital cones in potentially intersex individuals. The possible causes, such as hermaphroditism, environmental sex determination, parasitism, genetic aberration or endocrine-disrupting pollutants, are discussed.

Keywords: Tanaidacea; *Tanais dulongii*; intersex; genital cones; ovisacs

Introduction

Tanaidaceans are a group of more than 1200 species of small crustaceans that live from deep-water to coastal marine and freshwater environments (Blazewicz-Paszkowycz et al. 2012) and play a crucial role in food webs (Ferreira et al. 2005; Mendoza-Carranza and Vieira 2008). Reproductive potential of tanaidaceans is maximized by “unique and interesting adaptations” and a “wide range of strategies” that include separate sexes with little or marked sexual dimorphism to hermaphrodites and even parthenogenesis (Schram 1986). Hermaphroditism may be simultaneous or sequential, sometimes associated with intense male polymorphism (Heard et al. 2004; Kakui and Hiruta 2013).

Most tanaidaceans are distinctly sexually dimorphic; sexual dimorphism of Tanaididae Nobili, 1906 (= Tanaidea; see Bamber 2014) is characterized mainly by differences in shape of the cephalothorax (e.g. more narrowed anteriorly in males than in females), larger chelae (claws) and one or two tiny genital cones in males, or a variable number of structures derived from locomotory limbs in females, which form

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the ventral surface of one or two ovisacs, which hold ova during incubation (Heard et al. 2004).

Sex change in sequential hermaphrodites implies that the marsupium disappears and male genital cones appear (protogyny; Lang 1958; Bückle-Ramírez 1965; Błazewicz-Paszkowycz 2001), or *vice versa* (protandry; Wolff 1956; Heard et al. 2004; Drumm and Heard 2007). In simultaneous hermaphroditism both structures are present and functional at the same time (Larsen et al. 2011; Kakui and Hiruta 2013). Contrasting with hermaphroditism, in which transitional or simultaneous presence of primary or secondary sexual characteristics are part of the life history of populations, the term intersex may be more appropriate in cases where this event is less common or constitutes an aberration (Ford et al. 2004).

Tanais dulongii (Audouin, 1826) (Tanaidomorpha: Tanaididae) lives in tidal hard-bottom habitats generally among encrusting algae located around the world (Andersson et al. 1978; Sieg 1980; Johnson and Attramadal 1982; Holdich and Jones 1983; Hutchings et al. 1993; Perez-Ruzafa and Sanz 1993). In Mar del Plata, Argentina, *T. dulongii* populations reach densities of up to 5000 individuals/m², with a reproductive period in spring and summer, recruitment of juveniles in autumn, and the sex ratio is strongly female biased (Rumbold et al. 2012). The life cycle of *T. dulongii* includes two manca stages, followed by two to five neutrum stages in females; female sexual differentiation becomes evident during the three preparatory stages when oostegites grow to form a single or paired ovisac and oocytes develop in the ovaries (Hamers and Franke 2000). Males pass through one to three neutrum stages only, before developing genital cones and differentiated gonads (Hamers and Franke 2000).

Hermaphroditism has been reported in only one species of Tanaididae [*Sinelobus stanfordi* (Richardson 1901)] although the evidence for this phenomenon is not conclusive (Toniollo and Masunari 2007). Recently, intersex individuals with large chelae, cephalothorax narrowed anteriorly and ovisacs have been described in the Mar del Plata population of *T. dulongii* but, because of their small size, the presence of genital cones could not be confirmed with standard light microscopy (Rumbold et al. 2012). The aim of the present study was to analyse and compare external reproductive structures between male and female adults of *T. dulongii* using scanning electron microscopy, to corroborate the presence of ovisacs and genital cones in potentially intersex individuals.

Material and methods

Specimens of *T. dulongii* were collected in the intertidal La Estafeta (38°9'59.38" S, 57°38'00.37" W), located 15 km south of Mar del Plata city, Argentina. This intertidal is an open rocky shore 70 m wide when the tide recedes, characterized by the presence of numerous tide pools and a substratum formed by a consolidated sediment (loess) covered by algae, which serve as sites for feeding, breeding and shelter for a variety of invertebrates that live there (Rumbold et al. 2012).

Samples were obtained from March 2011 to March 2012. Algal patches were taken using a spatula. In the laboratory, samples were washed and organisms were sorted using a stereomicroscope. Individuals were counted and classified into three groups: males with large chelae and cephalothorax narrowed anteriorly (Figure 1A), females with small chelae, cephalothorax less narrowed and empty ovisacs

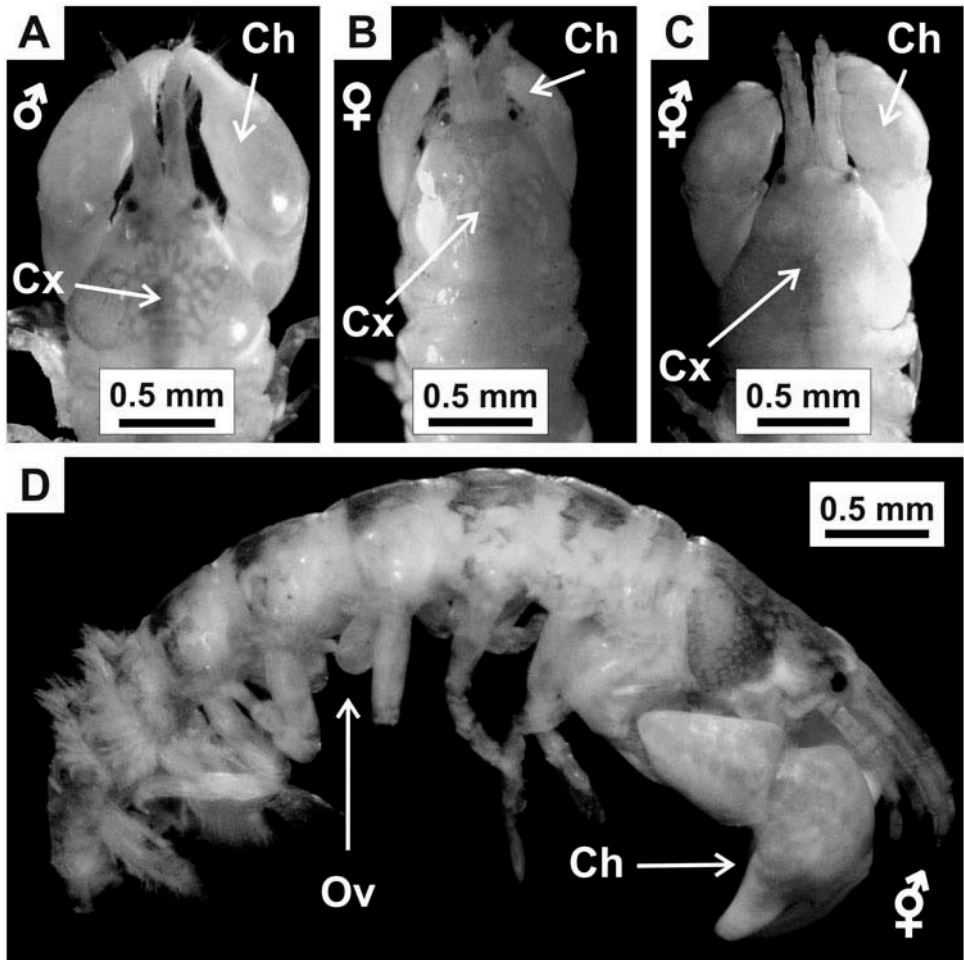


Figure 1. Light microscopy photographs of *Tanais dulongii*. Dorsal view of (A) male, (B) female and (C) intersex specimens, note the differences in size of chelae (Ch) and the shape of cephalothorax (Cx). (D) Lateral view of intersex specimen showing the presence of large chelae (Ch) and ovisacs (Ov).

(Figure 1B) and intersex individuals with large chelae, cephalothorax narrowed anteriorly and empty ovisacs (Figure 1C, D). Ovigerous females were not analysed because intersex specimens with embryos were never found. Four specimens of each group were examined using scanning electron microscopy (SEM). Chelae length (ChL) and width (ChW) of males, females and intersex specimens were measured, using a graduated eyepiece (Figure 2B) to determine size differences. All individuals were greater than 3.9 mm long, to ensure the observation and comparison of ovisacs (located on coxa of pereopod IV) and genital cones (located on ventrum of pereonite VI).

Specimens for SEM were dehydrated for 10 minutes in 75, 80, 90, 95 and 100% ethanol, then immersed for 12 hours in hexamethyldisilazane solution, mounted (all

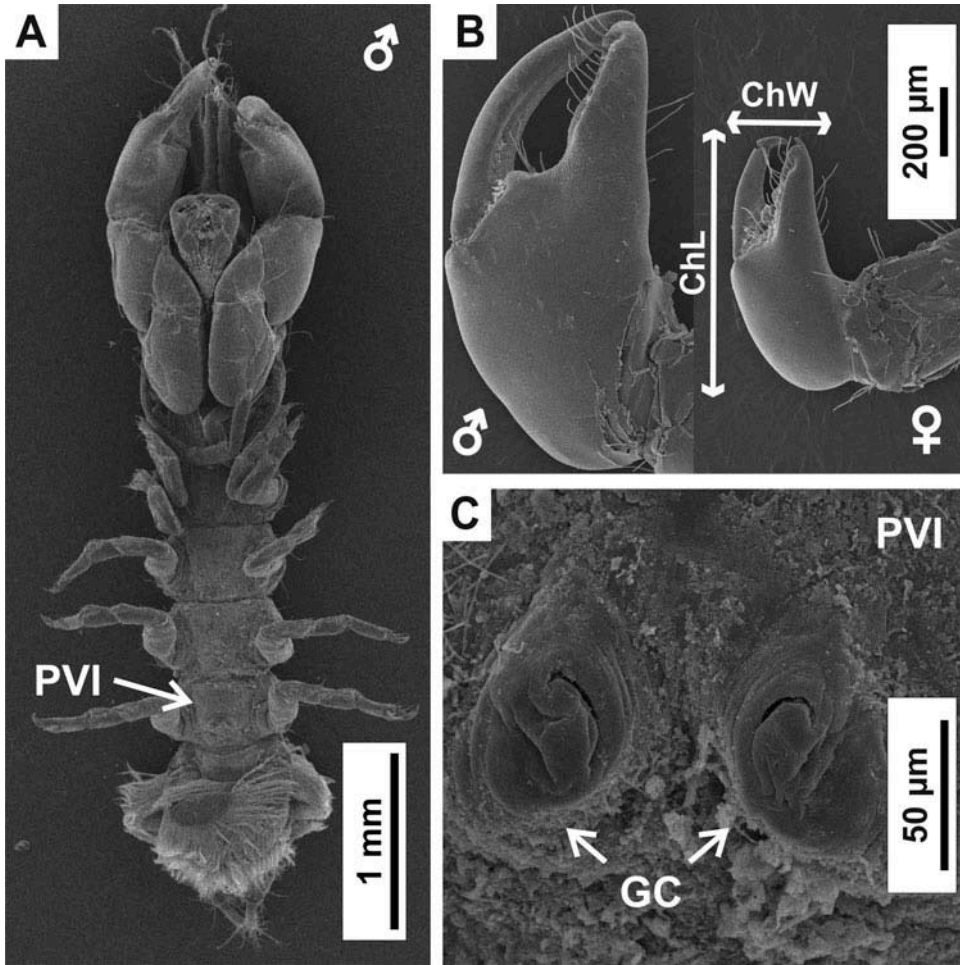


Figure 2. Scanning electron micrographs of *Tanais dulongii*. (A) Ventral view of male indicating the position of pereonite VI (PVI). (B) Lateral view of male and female chelae, note the difference in size. ChL and ChW indicate morphometric measurements of chelae length and width, respectively. (C) Magnification of pereonite VI showing the presence of genital cones (GC).

in ventral view) on specimen stubs, coated with gold-palladium in a Denton Vacuum Desk II coating unit, and examined in a JSM-6460 SEM at 15 Kv accelerating voltage (Laboratorio de Microscopía, Universidad Nacional de Mar del Plata). Denomination of morphological regions, stages and reproductive structures follows the criteria established by Hamers and Franke (2000) and Larsen (2003).

Results

During the study period, a total of 4155 individuals were collected, including 774 males (18.63%), 3377 females (81.28%) and four intersex specimens (0.1%).

The mean size of male chelae (ChL: 1.33 mm, ChW: 0.64 mm) did not differ from those of intersex individuals (ChL: 1.31 mm, ChW: 0.63 mm) and these appendages were much larger than in females (ChL: 0.75 mm, ChW: 0.25 mm). Male and intersex chelae had a wide gap between dactylus (mobile finger) and propodus (fixed finger); in addition, their dactyli were longer and markedly curved, and their propodi were more robust and supported large setae. Female chelae lacked the gap and had a straight dactylus and propodus with small setae (Figure 2B).

Males (Figure 2A) measured between 4 and 5 mm in total length and had a pair of genital cones located postero-ventrally on pereonite VI (about 0.055 mm in diameter, Figure 2C). Ovisacs or similar structures were not detected on the coxa of pereopod IV.

Females (Figure 3A) measured between 4 and 4.5 mm in total length and had a pair of large ovisacs on the coxal plates of pereopod IV (about 0.25 mm long, Figure 3B) corresponding to the second preparatory stage described by Hamers and Franke (2000). Pereonite VI had no genital cones or equivalent structures on the ventral surface (Figure 3C).

Intersex individuals (Figure 4A) ranged between 4 and 4.5 mm in total length, i.e. the same length as ovigerous females. An SEM study of the external morphology showed the presence of ovisacs on coxae of pereopod IV, also corresponding to the second preparatory stage (about 0.15 mm long, Figure 4B). Otherwise, the photomicrographs obtained from pereonite VI revealed the presence of a pair of genital cones located on the posterior end of the segment, which did not differ from those observed in normal males (about 0.045 mm in diameter, Figure 4C).

Discussion

Intersexuality occurs in many animal species (Reinboth 1975) and is widespread among crustaceans (Ford and Fernandes 2005). Its occurrence has been reported in Copepoda, Peracarida and Decapoda, often associated with hermaphroditism (Kakui and Hiruta 2013), environmental sex determination (Dunn et al. 1993; Guleer et al. 2012), parasitism (Rigaud and Juchault 1998; Kelly et al. 2004), genetic aberration (Parnes et al. 2003), or endocrine disrupting pollutants (Ford 2012). The proportion of intersexual individuals within various populations or groups is extremely diverse (e.g. Ford and Fernandes 2005). Among Peracarida, intersexuality has been intensely studied in Amphipoda and Isopoda since the seminal contributions of Charniaux-Cotton (1953) and Vandel (1947), respectively, and to a lesser degree in Mysidacea (e.g. Yamashita et al. 2001) and Tanaidacea (see Table 1 for references). However, the main causes of intersex observed in several species of tanaidaceans are still unknown.

Intersexuality may be a transient state during the processes of sexual re-differentiation (i.e. there is no all-in-one moult between the female and male stages) in sequential hermaphroditism (Rosen et al. 2010), the most common reproductive strategy in hermaphroditic tanaidaceans (Highsmith 1983; Stoner 1986; Drumm and Heard 2007). The size-advantage theory (Charnov 1982) established that this type of hermaphroditism occurs when an organism increases its fitness by being one sex when young and small, but the other sex when it gets older and larger. Protogyny would be selected when males can only mate at a large size and protandry when female fecundity is size dependent and males can mate regardless of their age or size

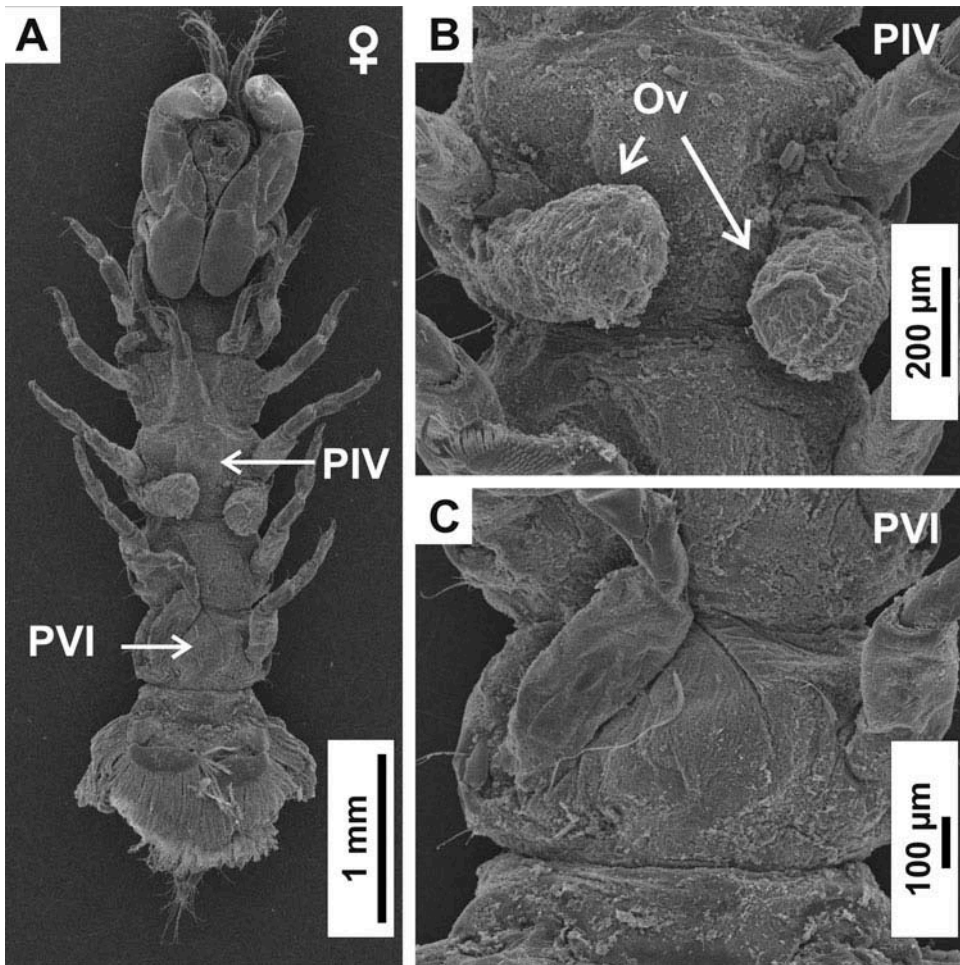


Figure 3. Scanning electron micrographs of *Tanais dulongii*. (A) Ventral view of female indicating the position of pereonite IV (PIV) and VI (PVI); (B) detail of pereonite IV showing the presence of ovisacs (Ov); (C) magnification of pereonite VI, where the lack of genital cones is clearly visible.

(Charnov 1982). Protogyny does occur in Tanaidomorpha: it has been recorded in several Paratanaoidea Lang, 1949 families, such as Paratanaidae Lang, 1949, Leptocheliidae Lang, 1974, Typhlotanaidae Sieg, 1986 and most genera of Anarthruridae Lang, 1971, associated with male polymorphism (Larsen 2001) but not in Tanaidoidea Nobili, 1906. In contrast to protogyny (Highsmith 1983; Stoner 1986), reproductive phases with male and female morphological traits may occur during sex change in protandric tanaidaceans (Lang 1968; Johnson et al. 2001). This type of hermaphroditism has been proposed for populations with larger females (Wolff 1956; Lang 1968), as in the case of the *T. dulongii* population in La Estafeta: although mean length of males is moderately larger than mean length of females (Rumbold et al. 2012), the largest individuals of this population are females.

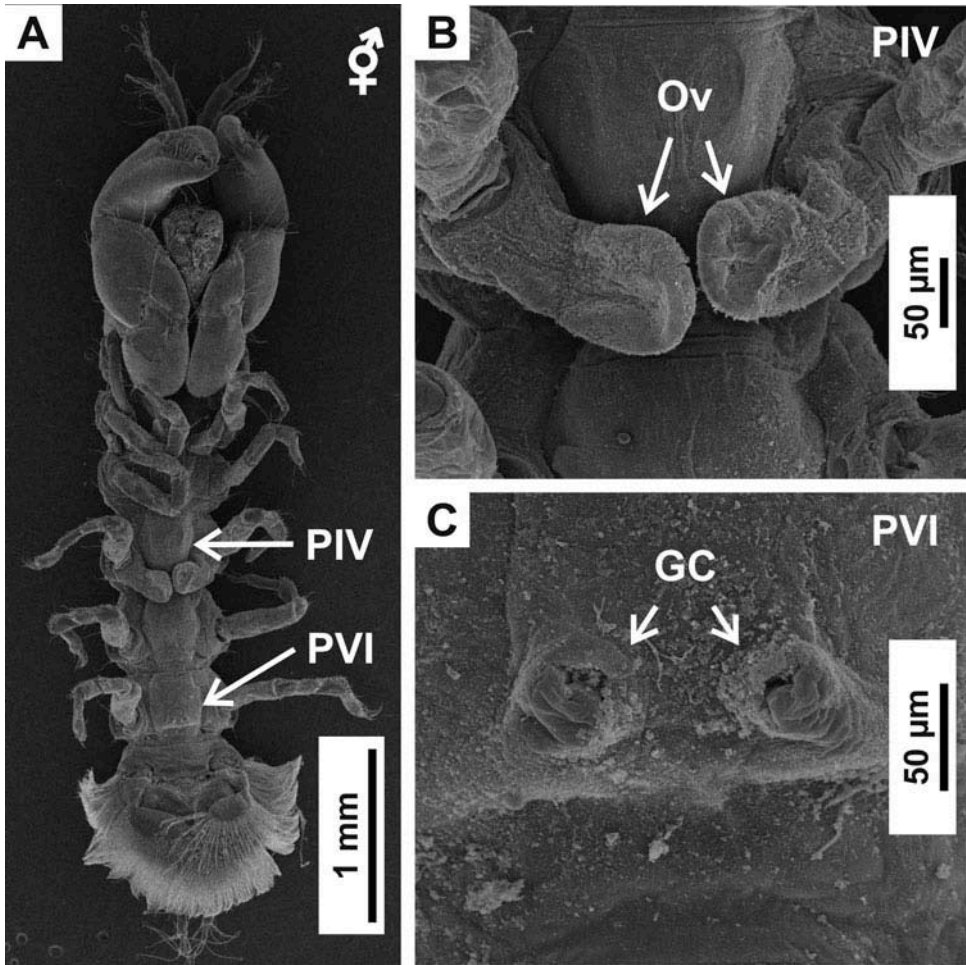


Figure 4. Scanning electron micrographs of *Tanais dulongii*. (A) Ventral view of intersex individual indicating the position of pereonite IV (PIV) and VI (PVI); (B) detail of pereonite IV showing the presence of ovisacs (Ov); (C) magnification of pereonite VI showing the presence of genital cones (GC).

However, the low number of intersex specimens found did not support this explanation.

Simultaneous hermaphroditism, on the other hand, has been proposed by taxonomists and ecologists to account for intersexuality in numerous species of tanaisidaceans (Table 1), but without histological or life history studies (Drumm and Heard 2007), except for those by Bückle-Ramírez (1965), Gardiner (1975) and Kakui and Hiruta (2013). The latter established that ovaries and testes of *Apeudes* sp. (*Apeudomorpha* Miller, 1940) could be simultaneously functional and even capable of self-fertilization. Although self-fertilization is theoretically favoured in populations with low encounter rates this may lead to increased inbreeding (Jarne and Auld 2006). So, other advantages of simultaneous hermaphrodites are related to the process of

Table 1. Occurrence of hermaphroditism and records of organisms with simultaneous male and female secondary characteristics in tanaidaceans.

Suborder/Family/Species	Type of hermaphroditism			♀/♂	Reference
	♀→♂	♂→♀	♀ + ♂		
APSEUDOMORPHA					
APSEUDIDAE					
<i>Apsedes abditospina</i>			?	x	Błażewicz-Paszkowycz and Bamber (2007)
<i>Apsedes aiseo</i>			?	x	Araújo-Silva et al. (2013)
<i>Apsedes holthuisi</i>	?				Lang (1958)
<i>Apsedes larseni</i>			?	x	Knight and Heard (2006)
<i>Apsedes noronhensis</i>			?	x	Araújo-Silva et al. (2013)
<i>Apsedes poorei</i>			?	x	Błażewicz-Paszkowycz and Bamber (2007)
<i>Apsedes quasimodo</i>				x	Błażewicz-Paszkowycz and Bamber (2012)
<i>Apsedes</i> sp.			x	x	Kakui and Hiruta (2013)
<i>Apsedes spectabilis</i>			?	x	Lang (1953)
<i>Apsedes spinosus</i>				x	Lang (1966)
<i>Apsedes talpa</i>			x	x	Larsen et al. (2011)
<i>Apsedopsis tuski</i>			?	x	Błażewicz-Paszkowycz and Bamber (2007)
<i>Fageapseudes retusifrons</i>	?		?	x	Błażewicz-Paszkowycz et al. (2011)
<i>Levitapseudes galatheae</i>				x	Lang (1968)
<i>Levitapseudes gracillimus</i>				x	Wolff (1956)
<i>Paradoxapseudes bermudeus</i>				x	Heard et al. (2004)
<i>Paradoxapseudes intermedius</i>				x	Heard et al. (2004)
KALLIAPSEUDIDAE					
<i>Mesokalliapseudes crassus</i>				x	Drumm and Heard (2007)
<i>Monokalliapseudes schubarti</i>	?				Leite et al. (2003)
PARAPSEUDIDAE					
<i>Parapseudes latifrons</i>				x	Lang (1966)

(Continued)

Table 1. (Continued).

TANAIDOMORPHA			
LEPTOCHELIIDAE			
<i>Hargeria rapax</i>	x		Modlin and Harris (1989)
<i>Heterotanaïs oerstedii</i>	x		Bückle-Ramírez (1965)
<i>Leptochelia dubia</i>	x		Highsmith (1983), Stoner (1986)
<i>Leptochelia forresti</i>	x		Stoner (1986)
<i>Leptochelia neapolitana</i>	x		Ishimaru (1984)
NOTANAIIDAE			
<i>Nototanaïs antarcticus</i>	x		Błażewicz-Paszkowycz (2001)
<i>Nototanaïs dimorphus</i>	x		Marinovic (1987)
NEOTANAIIDAE			
<i>Neotanaïs americanus</i>		?	Wolff (1956)
<i>Neotanaïs giganteus</i>		?	Lang (1968)
<i>Neotanaïs micromopher</i>	x		Gardiner (1975)
TANAIDIDAE			
<i>Sinelobus stanfordi</i>	x		Lang (1958)

Note: Abbreviations: ♀→♂, protogynous; ♂→♀, protandrous; ♀ + ♂, simultaneous; ♀/♂, record of organisms with simultaneous male and female secondary characteristics; x, recorded; ?, suggested.

cross-fertilization, in which organisms can reproduce as male or female depending which sex increases their fitness (Jarne and Auld 2006; Kakui and Hiruta 2013). The presence of ovisacs, large chelae (Rumbold et al. 2012) and genital cones (this study) may be indicators of occasional simultaneous hermaphroditism in *T. dulongii*, but histological studies are necessary to determine the maturation and functionality of testes and ovaries. In fact, hermaphroditism has no role in the *T. dulongii* life cycle (Hamers and Franke 2000) and even evidence of hermaphroditism in Tanaididae is inconclusive (Toniollo and Masunari 2007).

Recently, numerous studies have focused on the effect of industrial pollutants on crustacean intersexuality (Ford et al. 2006; Olmstead and Leblanc 2007; Pastorinho et al. 2009) and some metals can act as juvenile hormone mimics that interrupt the process of sex determination (Olmstead and Leblanc 2007). However, the studied population of *T. dulongii* lives in an area free of industrial and sewage discharges, so endocrine disruption is unlikely to occur (Rumbold et al. 2012). In addition, intersex individuals of *T. dulongii* have not been detected in highly polluted areas such as Mar del Plata harbour (approximately 3300 individuals were analysed here; Rumbold unpublished results), in which processes such as masculinization of female gastropod molluscs (i.e. imposex) caused by tributyltin have been reported in *Buccinanops monilifer* and *Adelomelon brasiliense* (Penchaszadeh et al. 2001).

Environmental sex determination is defined as the determination of sex by environmental factors during development (e.g. temperature and photoperiod) (Dunn et al. 1993; Guleer et al. 2012). In some peracarids, abrupt changes in these variables may be responsible for an incomplete sex determination, producing the occurrence of intersex specimens (Dunn et al. 1993). On the other hand, parasitism by bacteria and microsporidians is another natural cause that favours intersex in Isopoda and Amphipoda (Rigaud and Juchault 1998; Kelly et al. 2004). However, when parasitism and environmental sex determination are the main causes of intersex in species of Peracarida, the percentage of such individuals reaches values between 5% and 15% of the population (Dunn et al. 1994; Ford et al. 2004; Kelly et al. 2004; Yang et al. 2011). To date, there is no evidence for the presence of parasites in the population of *T. dulongii* at La Estafeta, and the effect of environmental factors over its sex determination is unknown.

Finally, Ginsburger-Vogel and Charniaux-Cotton (1982) and Hough et al. (1992) suggested that in populations of crustaceans where the percentage of intersex specimens is low, the presence of genetic anomalies may be the most plausible cause. This hypothesis may explain the low percentage of intersex specimens registered in the studied population of *T. dulongii* (0.1%) but not its absence in the nearby polluted area. Nevertheless, more studies on reproductive aspects (e.g. histological analysis, ontogenic development), ecology of both populations (e.g. life history, predation risk) and the effect of environmental variables (e.g. temperature, photoperiod, salinity, etc.) and parasitism are necessary to understand fully the possible causes and effects of intersex on the population of *T. dulongii* of La Estafeta.

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