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An ongoing saga: Endemic branchiobdellidans (Annelida: Clitellata) on translocated commercial North American crayfish

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Abstract

Over the last 130 years demand for crayfish has exceeded regional supplies around the world, so stocks, primarily from North America, have been imported to satisfy this need. These demands are human based and include gastronomy, sport fishing bait, food for rearing animals, educational aides, ornamentation in waterbodies, and more recently a significant increase in pet crayfish sales. The three most common commercial species from North America are *Pacifastacus leniusculus, Procambarus clarkii* and *Orconectes limosus*, although four other species are increasing in importance as they become more widely distributed. All of these crayfish in their endemic range have been reported to carry branchiobdellidan annelids. Therefore, when the crayfish are translocated, their ectosymbionts likely accompany them. Eighty-six potentially transportable branchiobdellidans are recognized in this paper, along with the distribution of six species known to have been translocated. Moreover, branchiobdellidans endemic to the translocation regions have adopted introduced crustacean hosts, which demonstrates that branchiobdellidan host species specificity is not as restrictive as many researchers believe. On the evidence to date, these translocated branchiobdellidans appear to have the same relationship and cause the same amount of damage, if any, as those on their endemic crayfish hosts. The geographical distribution of endemic branchiobdellidan—crayfish species associations are unique to each of four disjunct regions as defined by Bănărescu: Euro-Mediterranean, East Asian, western North American and eastern North American; the latter includes eastward drainages from Canada to Costa Rica.

Key words: Illegal and legal introductions, *Pacifastacus leniusculus, Procambarus clarkii, Orconectes limosus*, pet trade

Introduction

Humans have been translocating fauna and flora for hundreds of years to construct zoological gardens, and for personal and economic reasons (Hulme 2009). Among these many species, freshwater crayfish have figured in the last two categories. Clavero *et al.* (2016) presented convincing evidence that *Austropotamobius italicus* (part of the *A. pallipes* complex) was introduced into Spain in 1588 from NW Italy. The authors also showed that *A. pallipes* is common to France, England, Wales and Ireland; Grandjean *et al.* (2006) suggested it was introduced from France, possibly as early as the 12th century with subsequent translocations occurring. Currently, there are no known records of comparable movements of crayfish from one country to another or from area to area within East Asia or North America that long ago. The era of commercial intercontinental translocations of North American crayfish began in the mid-19th century with the arrival of unknown species into Italy along with crayfish plague or *Aphanomyces astaci* Schikora (Ackefors 1999). After a pause, *Orconectes immunis* (Rafinesque) was introduced into Poland in 1890, where it established a viable population (Henttonen & Huner 1999). This was followed by more translocations, legal and otherwise, of various North American species.

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The export of crayfish has always been based on human demand, but in the new era additional uses have been found which include: bait in commercial and sport fishing, food for rearing animals, educational aids, and ornamentation in waterbodies, although more recently their importance in the pet trade has increased significantly (Holdich 2002; Policar & Kozák 2015; Patoka *et al.* 2017). Many of these demands have been met by the procurement of selected North American crayfish species, which has resulted in their translocation to most parts of the world, except Australia and New Zealand. Some of the exotic crayfish species show morphological intraspecific variations that can sometimes make a positive identification difficult. This becomes more problematic when molecular sequences reveal significant differences within a morphologically described species, thus raising the possibility of a species complex or a group of cryptic species. However, as most crayfish host identifications recorded in the literature are based on older morphological keys, these are the names used in this work unless otherwise stated.

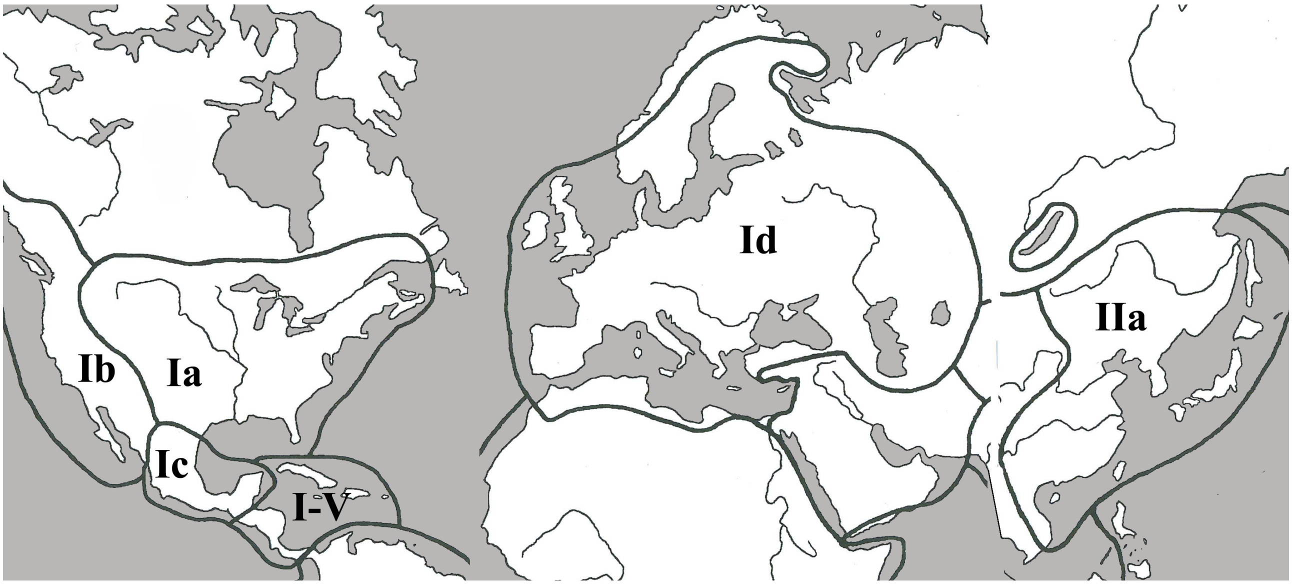

FIGURE 1. Faunal regions (the Atlantic Ocean and Central Asia are omitted) with endemic branchiobdellidans being found in the Holarctic: Ia, eastern North American subregion; Ib, western North American subregion; Ic, central Mexican subregion; Id Euro-Mediterranean subregion; I–V, Middle American/ Antillean transitional region; IIa, East Asian subregion (redrawn and modified from Bănărescu 1990: 526).

The ectosymbiotic association of branchiobdellidan annelids and their crustacean hosts was reviewed by Gelder and Williams (2015; 2016). The worms have a disjunct Holarctic distribution, with 8 genera in the Palaearctic (Gelder 2019) and 16 in the Nearctic and northern Neotropical realms (Gelder 2016, in press). Geographical and political regional descriptors used by authors are often well suited for a regional study, e.g., Central America, but become less consistent when dealing with a worldwide distribution. Therefore, this work uses the zoogeographical freshwater faunal regions and subregions proposed by Bănărescu (1990: 526) (Fig. 1). As branchiobdellidans range from France to the Ponto-Caspian Basin, "European" does not accurately reflect this distribution, but Bănărescu's Euro-Mediterranean subregion Id does. The term East Asia has been interpreted in many ways while East Asian subregion IIa encompasses all the known locations of branchiobdellidans in that area. In North America, 13 of the 16 genera live exclusively either east or west of the continental divide, with the remaining genera having species on one or other sides of the divide. While Bănărescu's western North American subregion Ib reflects the western branchiobdellidan taxa range, eastern taxa extend from Canada through the USA (Ia) and Mexico (Ic) to Costa Rica (I–V) (Fig. 1). Although these eastern components form a single sector of branchiobdellidan taxa, their hosts exhibit a transition from being almost exclusively crayfish in subregion Ia, with both crayfish and other crustaceans in subregion Ic, to non-crayfish crustaceans in region I–V. Techniques for preparing branchiobdellidans for identification are given in Gelder & Williams (2015; 2016) along with keys to the genus level. Now keys to all described species and their respective distributions are available in the multi-volume "Thorp and Covich's Freshwater Invertebrates" according to their faunal realm: Volume II, Keys to Nearctic Fauna (Gelder 2016), Volume IV, Keys to

Palaearctic Fauna, (Gelder 2019), and Volume V, Keys to Neotropical and Antarctic Fauna" (Gelder, in press). However, the reader will find an inconsistency in the taxon's rank in this series which needs to be explained. The order Branchiobdellida (Holt 1965) has been the accepted rank for the last 50 plus years and it continues to provide a pragmatic arrangement for taxonomic studies, hence the chapter in "Thorp and Covich's Freshwater Invertebrates, Ecology and General Biology", volume I was titled Branchiobdellida (Gelder & Williams 2015). In subsequent volumes editorial policy required the taxon to be raised to a subclass, Branchiobdellidea, to maintain consistency with the other clitellate taxa. However, in volume IV the subclass in the key (Thorp & Lovell 2019: 364) and chapter title (Gelder 2019: 483) is given in error as the ordinal Branchiobdellida.

Members of the Gondwanian crayfish superfamily Parastacoidea do not carry endemic branchiobdellidans, but some Australian species of *Cherax* have been introduced and cultivated in both Euro-Mediterranean and East Asian regions (Policar & Kozák 2015). To date, there are no reports of their being adopted as alternative hosts by branchiobdellidans; however, they should be considered potential hosts and a careful watch maintained for their presence. The Gondwanian analog of branchiobdellidans are temnocephalidan rhabdocoels and they are known to adopt Holarctic crayfish. Vayssière (1898) reported *Temnocephala mexicana* Vayssière, on *Procambarus digueti* Bouvier, in Mexico and they were cohabiting a host with an unidentified branchiobdellidan. More recently, Xylander (1997) collected *Temnocephala minor* Haswell, from *Astacus leptodactylus* Eschscholtz, provided by a pet reptile supply company, Exo Terra, Germany, who had in turn obtained the crayfish from Turkey. This was followed by Cuellar *et al.* (2002) reporting small numbers of *Temnocephala* sp. between March and October on *P. leniusculus* that also supported a large population of *Xironogiton victoriensis* Gelder and Hall, year-round at an aquaculture site in Spain. Cuellar *et al.* (2002) offered no explanation as to where this small temporary population of temnocephalidans could have come from, even though *Cherax destructor* Clark, had first been introduced into Spain in 1983 (Kouba *et al.* 2015: 132). Contrary to expectations, the initial translocated stock did not come from Australia, but a breeding facility in California, USA, which coincidentally is in the endemic area of the *P. leniusculus* and *X. victoriensis* association. Whether these facts are part of a fragmented story of introduction or disconnected coincidences on the ectosymbionts origins remains speculative. However, potential temnocephalidan interactions with the northern ectosymbiotic associations are not considered further in this work.

The terminology used to describe the origins and movements of symbionts and hosts in the literature has evolved, particularly over the last 50 years, to produce a number of alternate names. However, Gherardi and Holdich (1999) provided definitions and a list of synonyms that have reduced previous misunderstandings. **Endemic** (= native, indigenous and autochthonous) refers to a taxon originating and found in a particular geographical area; **exotic** (= alien, allochthonous, non-native and non-indigenous) refers to an organism introduced into an area in which it had not naturally occurred in historic times; and **translocation**, refers to the deliberate transfer of organisms for the purposes of introduction, reintroduction, or stocking.

Having covered essential background areas and terminology, this paper focuses on the actual and potential distribution of ectosymbiotic branchiobdellidan annelids through the commercial translocation of their astacoidean crayfish hosts (Gelder 2004; Gelder & Williams 2016). The histories and current distributions of crayfish involved in commercial translocations outside their endemic regions has been well documented in recent reviews (Holdich *et al.* 2009; Kawai *et al.* 2016; Kozák *et al.* 2015), so only pertinent details relevant to their branchiobdellidan ectosymbionts will be given here.

Commercial crayfish species translocated outside their endemic region

All commercial exotic crayfish species carrying branchiobdellidans currently originate from North America, with *Pacifastacus leniusculus* (Dana), from the western subregion Ib, and the remainder from the eastern sector, primarily subregion Ia (Fig. 1). The three most widespread, exotic crayfish species are, *Orconectes limosus* (Rafinesque), *P. leniusculus* and *Procambarus clarkii* (Girard), but four others are important although not so widely distributed: *Procambarus* cf. *acutus*, white river crayfish; *Orconectes immunis* (Hagen), calico crayfish; *Orconectes juvenilis* (Hagen), Kentucky river crayfish and *Orconectes virilis* (Hagen), virile crayfish (see Kouba *et al.* 2015). All of these species have been reported in Europe (Holdich *et al.* 2009), while *P. clarkii* and *P. leniusculus* account for the majority of introductions in East Asia. Initially *Orconectes rusticus*

(Girard) was report in France, but the population was later identified as *O. juvenilis* (Holdich *et al.* 2009); however, *O. rusticus* has been found in the Pacific Northwest (subregion Ib). These hosts and their reported endemic branchiobdellidans are listed in Table 1. Two other species, *Orconectes neglectus* (Faxon) and *Orconectes sanbornii* (Faxon), have also been reported from the Pacific Northwest but no mention of any branchiobdellidans was made. However, in their endemic eastern localities *Pterodrilus annulatus* Gelder, and *Pterodrilus mexicanus* Ellis, were found on *O. neglectus* and *Pterodrilus alcicornus* Moore, on *O. sanbornii*. Although many of these species are kept as pets, there are more ornate and colorful crayfish available through aquarist suppliers, some legal and others not. A web search in 2018 of North American and European aquarist catalogs (Gelder unpub. data) provided an additional 15 species of which four (*Procambarus alleni* (Faxon), *Procambarus fallax* f. *virginalis* (see Scholtz 2016: 5) *Orconectes luteus* Creaser, *Cambarus montezumae* = *Cambarellus montezumae* (Saussure)) have been reported to carry branchiobdellidans (Table 2). This number of species is increased significantly if supplies from Australia, SE Asia and the Pacific Islands are included, but as these do not have endemic branchiobdellidans, they are not considered further.

TABLE 1. Endemic branchiobdellidans recorded on commercial North America crayfish species translocated to the Palaearctic; with those already reported in Europe (▲) and East Asia (●).

Order Branchiobdellida	**Superfamily Astacoidea**								**Ref. nos**
Family Branchiobdellidae	*Pacifastacus*	*Procambarus*		*Orconectes*					
	leniusculus	*acutus*	*clarkii*	*immunis*	*juvenilis*	*limosus*	*rusticus*	*virilis*	
Branchiobdellinae									
Ankyrodrilus legaeus				**o**	**o**		**x**		**14**
Xironogiton instabilis				**x**	**x**	**x**			**17**
X. kittitasi	**x**								**17**
X. occidentalis	**x**								**10, 17**
X. victoriensis ▲●	**x**								**7, 30**
Bdellodrilinae									
Bdellodrilus illuminatus				**x**				**x**	**2, 9, 10**
Uglukodrilus hemophagus	**x**								**19, 27**
Cambarincolinae									
Cambarincola barbarae			**x**						**3, 23**
C. chirocephalus				**x**			**x**	**x**	**1, 2, 12**
C. desmissus					**x**				**12**
C. fallax			**x**					**x**	**3, 23, 28**
C. gracilis ▲	**x**								**23, 32**

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TABLE 1. (Continued)

Family Branchiobdellidae	*Pacifastacus*	*Procambarus*		*Orconectes*					
	leniusculus	*acutus*	*clarkii*	*immunis*	*juvenilis*	*limosus*	*rusticus*	*virilis*	
C. holti							**x**	**x**	**5**
C. illinoisensis								**x**	**24**
C. jamapaenesis		**x***							**16**
C. macrodontus		**x**	**x**	**x**				**x**	**1, 2, 28**
C. mesochoreus ▲●		**x**	**x**	**x**		**x**		**x**	**3, 9, 23**
C. okadai ▲●	**x**								**8, 17, 30**
C. olmecus		**x***							**16**
C. pamelae			**x**						**3, 25**
C. philadelphicus				**x**		**x**		**x**	**1, 9**
C. susanae		**x***							**16**
C. vitreus			**x**	**x**	**o**			**x**	**2, 12, 30**
Ellisodrilus clitellatus					**x**				**13**
E. durbini								**x**	**13**
Oedipodrilus anisognathus					**x**				**25**
O. macbaini				**x**			**x**	**x**	**25**
Pterodrilus alcicornus					**x**		**x**		**15**
P. cedrus					**x**		**x**	**x**	**15**
P. distichus				**x**	**x**		**x**	**o**	**15**
P. hobbsi					**x**		**x**		**4, 15**
P. missouriensis						**x**			**9**
Sathodrilus attenuatus ●	**x**								**22, 30**
S. chehalisae	**x**								**22**
S. dorfus	**x**								**20**
S. elevatus				**x**			**x**	**x**	**21**
S. inversus	**x**								**22**
S. lobatus	**x**								**20**
S. norbyi	**x**								**20**
S. prostates		**x***							**16**
S. shastae	**x**								**6, 22**
S. wardinus	**x**								**22**
Triannulata magna ▲	**x**								**10, 18**

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TABLE 1. (Continued)

Family Branchiobdellidae	*Pacifastacus*	*Procambarus*		*Orconectes*					
	leniusculus	*acutus*	*clarkii*	*immunis*	*juvenilis*	*limosus*	*rusticus*	*virilis*	
Xironodrilinae									
Xironodrilus formosus				**x**			**x**	**x**	**1, 10**
No. of species 78	**15**	**6**	**6**	**12**	**10**	**4**	**10**	**15**	

Legend: Each published association is shown by "x" and its reference(s) is given as a number with the respective citations being, (1) Ellis 1919, (2) Evans 1939, (3) Gelder 1991, (4) 1996a, (5) 1996b, (6) Gelder & Ferraguti 2001, (7) Gelder & Hall 1990, (8) Gelder & Ohtaka 2000, (9) Gelder *et al.* 2001, (10) Goodnight 1940, (12) Hoffman 1963, (13) Holt 1960, (14) 1965, (15) 1968, (16) 1973a, (17) 1974a, (18) 1974b, (19) 1977a, (20) 1977b, (21) 1978, (22) 1981a, (23) 1981b, (24) 1982, (25) 1984, (26) 1988, (27) 1989, (28) Keller 1992, (29) Lahser 1975, (30) Ohtaka *et al.* 2005, (31) Penn 1959, (32) Robinson 1954. Records from the Catalog of the National Museum of Natural History, Smithsonian Institution, Washington DC, are shown by "o". "x*" indicates these species have been recorded on *Procambarus acutus cuevachicae* Hobbs.

TABLE 2. Endemic branchiobdellidans on decorative North American crayfish listed as available through European aquarist catalogs.

Crayfish	Branchiobdellidans	References
Cambarellus montezumae	*Bdellodrilus illuminatus*	Holt, 1973a
Orconectes luteus	*Pterodrilus mexicanus*	Holt, 1968
	Pterodrilus missouriensis	Holt, 1968
	Xironodrilus formosus	Goodnight, 1940
Procambarus alleni	*Cambarincola manni*	Holt, 1973b
Procambarus fallax	*Cambarincola goodnighti*	Holt, 1973b
	Cambarincola manni	Holt, 1973b

Large scale commercial harvesting of endemic crayfish pays little or no attention to species composition. For example, populations of *P. clarkii* sometimes include small numbers of cohabiting *Procambarus acutus* (Girard). An examination of *P. acutus* by Crandall (2010a; b) found this species was composed of two different taxa that he called *P. a. acutus* and *Procambarus zonangulus* Hobbs and Hobbs. Although specimens of these two species rarely establish breeding populations when released, exceptions have been found with two populations of *P. a. acutus* (or *P. acutus*) reported in the Netherlands in 2005 (Kouba *et al.* 2015), and one at an isolated farm near Windsor in England (Almeida *et al.* 2014). Having demonstrated they can survive translocation and produce viable populations, the closely related, ornate *Procambarus acutus cuevachicae* Hobbs, from Mexico is included under *P. acutus* in Table 1. This subspecies is available through some pet trade outlets and is known to host four species of branchiobdellidans in its endemic area.

Another problematic crayfish is *Procambarus fallax* (Hagen) f. *virginalis*, the Marbled crayfish or Marmorkrebs, which was the subject of a multi-disciplinary review entitled, Section 1: Marble Crayfish—A New Model Organism for Biology, in Kawai *et al.* (2016). Although of North American origin, this new parthenogenetic form was first recognized and exploited in the mid-1990s by the aquarist trade in Germany and Austria (Souty-Grosset *et al.* 2006). Because of its attractive appearance, ability for prolific reproduction and hardiness, it is now probably the most popular pet crayfish in the world (Pârvulescu *et al.* 2017). Even though this form has been reported wild in numerous countries in Europe, Madagascar and Japan (Feria & Faulkes 2016, Kawai 2017a), none mention harboring any branchiobdellidans. Souty-Grosset *et al.* (2006: 96) stated that molecular sequences indicated *P. f.* f. *virginalis* to be closely related to *P. fallax*, the deceitful crayfish, and

Procambarus alleni (Faxon), the Florida crayfish. Both of these species are natives of Florida and Georgia, USA, where they carry branchiobdellidans, and *P. alleni* has been recorded recently in France (Table 2).

The number of crayfish species and their endemic branchiobdellidans represents a formidable list of potential invasive ectosymbionts. However, only six exotic North American branchiobdellidan species have been reported off the continent, four of them in Japan and five in Europe (Table 1). There are many reasons for branchiobdellidans dying in transit, but it appears the six species reported so far are either more resilient than most or were transported under favorable conditions. As the demand by aquarists for ornate crayfish increases, these pet species enjoy a better level of care during transportation as many suppliers guarantee them to be alive on delivery.

1. Distribution of exotic branchiobdellidans and crayfish in Eastern North America (subregion Ia, Ic and region I–V)

Although crayfish species in this sector have discrete endemic ranges, many of them have been translocated around the sector for commercial reasons. However, tracing such movements in the absence of adequate documentation is probably impossible and, fortunately, beyond the scope of this paper. No records of *Pacifastacus* species have been found to indicate their translocation into the eastern sector, and neither have there been any records of crayfish from Europe or East Asia establishing wild populations. This does not rule out the possibility that small populations of these exotic pets exist in the wild where they potentially carry any endemic branchiobdellidans or are available as alternative hosts. Although selling exotic species in aquarist shops is no longer legal in many States in the USA and Provinces in Canada, the worldwide trade in these pets continues to flourish via mail order suppliers.

2. Distribution of exotic branchiobdellidans and crayfish in Western North America (subregion Ib)

Procambarus clarkii was introduced into southern California in the 1920's (Hobbs *et al.* 1989), but an even earlier date has been suggested. A verifiable translocation of *P. clarkii* as a food source for frogs was made in 1932 near Lakeside, San Diego County, California (Riegel 1959: 46). His survey showed the crayfish populations existed from the Mexican border to north of Sacramento. Additional references of *P. clarkii* translocations into Arizona, Nevada, California, Oregon, Idaho and Utah, USA and adjacent Baja California and Sonora, Mexico, are given in Huner and Barr (1991). Although British Columbia, Canada, was not included in this range, rumors of illegal consignments from unknown locations for aquaculture were circulating in the 1990's (Gelder, unpubl. data). A survey and review of invasive crayfish in the Pacific Northwest by Larsen and Olden (2011) recorded, *O. neglectus, O. rusticus, O. sanbornii, O. virilis, P. acutus* and *P. clarkii* (see Table 1). In their endemic ranges, *O. neglectus* hosts *Pterodrilus annulatus* Gelder, and *P. mexicanus* Ellis, with *P. alcicornis* Ellis on *O. sanbornii* (Hobbs & Fitzpatrick), but neither crayfish have been reported carrying branchiobdellidans in this subregion; endemic or adopted.

Holt (1981a) identified *C. mesochoreus* on *P. clarkii* collected from Merced, Santa Barbara and Sonoma Counties in California, and subsequently (Holt 1984) transferred some of the specimens to a new species, *Cambarincola pamelae* Holt, while adding Stanislaus County to their range. A multi-species association of *C. gracilis* and *C. okadai* (= *C. montanus*) together with *C. barbarae* and *C. pamelae* was found on *P. clarkii* collected in 1960 at Solvang, Santa Barbara County, California (Holt 1981a: 683). The presence of western and eastern species indicates that *P. clarkii* had made contact with *P. leniusculus* in the recent past. Given the aggressive behavior of both species, any contact almost certainly would result in a fight and affording ample opportunity for worms to transfer to the victor to initiate a starter population. Although Holt (1981a: 680) identified *C. fallax* from one *P. clarkii* in Sonoma County, he expressed reservations about this species being in California. Gelder and Hall (1990) found *C. fallax* with *C. gracilis* and *C. okadai* cohabiting preserved *P. leniusculus* in the Royal British Columbia Museum, Victoria, Canada, that had been collected by G. C. Carl from Burdette Creek near Vancouver in 1942. Whether these specimens identified as *C. fallax* originated from an eastern host translocation or represents a very similar but new western species requires further study.

Orconectes was first recorded in California at Chic, Butte County, between 1939 and 1941 where *O. virilis* was used in the biology laboratory at Chico State College (Riegel 1959); this is about 150km north of Sacramento. Later records include Daniels (1980) finding it in the middle Pitt River around the Britton Reservoir in 1978; however, its introduction as sport fishing bait dates back to the 1960's (Maria J. Ellis unpub. data). Further north, *O. neglectus* (= *O. transfuga*) was released into the Rogue River, Jackson County, Oregon (Hobbs *et al.* 1989) probably in the 1960's. Larson and Olden (2008) collected *O. virilis* from three lakes along Puget Sound's eastern border, Washington State. The identification of crayfish in Big Lake near Mt. Vernon was subsequently corrected (Larson *et al.* 2010) to *O. sanbornii* which is endemic to the Ohio River Basin, eastern USA. Additional locations of *O. virilis* were reported at six sites on the Franklin D. Roosevelt Lake and in adjacent tributaries at Patterson, Wapato, and Moses Lakes. *Orconectes virilis*, *O. rusticus* and *P. clarkii* were found being used extensively for educational studies in Washington State schools, so finding an escaped population of *O. rusticus* is only a matter of time. In the neighboring state of Oregon, a very dense population was found in a stretch of the John Day River in the vicinity of John Day, (Olden *et al.* 2009). *Orconectes neglectus* was widespread in the Rogue River system by 1977 and believed to have been introduced following sport fishing activities (Larson & Olden 2011). To date no branchiobdellidans (Table. 1) have been reported on these exotic crayfish, but whether they failed to survive translocation, or were unable to adapt to the new habitat conditions, remain to be discovered is unknown.

3. Distribution of exotic branchiobdellidans and crayfish in the Euro-Mediterranean (subregion Id)

Europe has received the largest commercial translocation of the three main North American crayfish species along with some of their endemic branchiobdellidans (Table 1). In some areas, these exotic crayfish have been adopted successfully by local endemic branchiobdellidans showing that host specificity is less limited than many researchers believe. These two situations are dealt with separately: first, (3a) the introduced endemic associations, and second, (3b) those associations where endemic branchiobdellidans have adopted exotic hosts.

Stocks of *P. leniusculus* from the Sacramento area, California, USA, were shipped to Sweden in 1959 and released the following year. Later large-scale exportations occurred from Lakes Hennessy and Tahoe to Finland in 1967–8, and from Lake Tahoe to Sweden in 1969 (Svärdson 1995; Ackefors 1999). The latter breeding stocks were highly successful and translocations, both legally and illegally account for current populations in many western European countries including Cyprus (Holdich *et al.* 2009; Kouba *et al.* 2015). The high genetic variation found in these European populations of *P. leniusculus* is consistent with the original heterogeneous stock population created commercially in the USA, followed by multiple introductions and secondary translocations on the continent (Petrusek *et al.* 2017). Although not yet recorded from Russia, *P. leniusculus* is extending its range eastward and has already entered Slovenia and northern Croatia (Hudina *et al.* 2012).

The first introduction of *P. clarkii* into Europe consisted of shipments from Louisiana, USA, to Spain in 1973, and its subsequent history is reviewed by Kouba *et al.* (2015). These starter populations rapidly became established and thrived, and in turn loads were translocated, both legally and illegally to other areas and countries. France received its first *P. clarkii* in 1976 from translocated East African commercial stocks before being supplemented by Spanish imports in 1978 (Laurent *et al.* 1991). The species is now reported to extend from Portugal to Germany and Italy, and it is only a matter of time before its eastward expansion reaches the Caspian basin. Additional introductions within the Euro-Mediterranean region have been made into southern England, the Azores, Canaries, Sardinia, Corsica, Sicily, Cyprus (Holdich *et al.* 2009), Egypt (El Zein 2005) and Israel (Wizen *et al.* 2008). Currently, the distribution of this species can be assumed to be much greater.

In spite of *O. limosus* being introduced repeatedly into Europe over the last 120 years, there are no reports of any individuals carrying any of its endemic North American branchiobdellidans. It is included here because the species has been adopted by a number of *Branchiobdella* species. This crayfish was first introduced into Poland in 1890 with a consignment from the Delaware River, Pennsylvania, USA. Following an unsuccessful introduction into France in 1895, success followed in 1911–1913 with crayfish from New York, USA (Henttonen & Huner 1999). Records of where these crayfish were collected or how many were subsequently shipped are incomplete (Kouba *et al.* 2015; Souty-Grosset *et al.* 2006: 102). Although initially introduced for human consumption, *O. limosus* soon became an important bait for sport and commercial fishing, and accounts for its current distribution from the Pyrenees Mountains to Poland and south to Serbia and Italy; England also has viable populations of the species. Its range is enlarging as breeding populations spread eastwards along central Europe's major river systems towards the Black Sea.

a. Introduced branchiobdellidans on their endemic hosts: *Pacifastacus leniusculus* has the largest number of potential branchiobdellidan species for translocation (Table 1), with *Xironogiton victoriensis* being the most numerous and found across this host's native range (Gelder & Hall 1990; Larson & Williams 2016). The first record and study of a xironogitonid in Europe occurred on individuals from a crayfish rearing site in Drottningholm, near Stockholm, Sweden (Franzén 1962). These were identified as the eastern North American *X. instabilis* based on information then available. However, a detailed study of specimens from British Columbia, Canada, by Gelder and Hall (1990) resulted in a description of a new species, *X. victoriensis*, thereby separating it from the eastern *X. instabilis*. Although the two species are very similar morphologically, Martens *et al.* (2006) supported the validity of *X. victoriensis* and molecular sequencing has confirmed it (Williams *et al.* 2013). Without realizing this background, some researchers continue to cite the earlier incorrect name. *Cambarincola* sp. and "*X. instabilis*" were reported by Fürst (1984) in the first shipment of *P. leniusculus* to Finland from California, USA, in 1967. On termination of a 25-year study on translocated crayfish development in a small Finnish Lake, Kirjavainen and Westman (1999) found branchiobdellidans being, "either *Xironogiton instabilius* Moore or *Cambarincola* sp.". Cuellar *et al.* (2002) added a further level of confusion by calling *X. victoriensis* by its type name which Moore (1894) had placed in a different genus. Two important review publications (Minelli *et al.* 2015: 11, Longshaw 2016: 211) unfortunately ignored the corrected name of *X. victoriensis* which had already been validated as a separate species by Martens *et al.* (2006) and Williams *et al.* (2013). Additionally, and puzzling but not explained, is why Longshaw (2016) combined *X. instabilis* and *X. victoriensis*, making the former name a junior synonym contrary to the Principle of Priority as presented in Art. 23.1 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 2000). Despite these nomenclatural aberrations, *X. victoriensis* has been reported at crayfish culture sites and in the wild at: "Kőszeg: Kálvária-hegy, Gyöngyös", Hungary (Kovács & Juhász 2007); in Carinthia, Austria (Nesemann & Neubert 1999); Germany (Martens *et al.* 2006; Martens & Roos 2015), Auenbachl Creek, Bolzano Province, (Morolli & Quaglio 2002; Oberkofler *et al.* 2002; Quaglio *et al.* 2002), and Lake Brugneto, Liguria Province (Capurro *et al.* 2007), Italy; tributary streams of the Altube Erreka, Basque Province (Gelder 1999) and Ebro Basin (Oscoz *et al.* 2010; Vedia *et al.* 2014; 2016), Spain; eastern Garonne and Mayenne Basins, France (Laurent 2007; Subchev 2008; Gelder *et al.* 2012; Parpet & Gelder 2020); Wales (James *et al.* 2015); Croatia (Dražina *et al.* 2018); plus Luxembourg and Switzerland (Parpet & Gelder 2020).

Xironogiton victoriensis has been reported cohabiting with *C. gracilis* and *C. okadai* in France (Gelder *et al.* 2012; Parpet & Gelder 2020), but only with *C. okadai* in Wales (James *et al.* 2015). Initially these three species were collected from the Tarn River and its tributaries in France (Gelder *et al.* 2012) which provided the first confirmed report of a western North American *Cambarincola* species on *P. leniusculus* in Europe. Subsequent and expanded collections of *P. leniusculus* have yielded the first record of *Triannulata magna* Goodnight, in the River Seine basin in northern France (Parpet & Gelder 2020). Records of *P. leniusculus* translocations into France are sketchy but include shipments from Sweden in 1972, Lakes Tahoe and Donner, USA in 1974 (Arrignon 1996), and an unknown number of illegal shipments directly from Oregon, USA (Holdich *et al.* 2009). Which of these accounts for the three exotic branchiobdellidans being introduced will never be known. Of James *et al.*'s (2015) collections of *P. leniusculus* from mid- and south Wales, only those from the latter area yielded *C. okadai* and *X. victoriensis*, making this the first record of exotic branchiobdellidans in the UK. As this combination of exotic branchiobdellidans has only been reported in France, and the source of these crayfish was not known, it is possible that they were imported from France for culinary reasons. Support for this comes from Parpet (pers. obs.) who observed live "European crayfish", which included exotic species from unknown locations, in a French fish market. An example of host choice flexibility was demonstrated when specimens of *X. victoriensis* were observed on cohabiting *P. leniusculus* and *P. clarkii* collected from the Piedra River at Cimballa, Zaragoza, Spain. Meanwhile a population of *P. clarkii* in the Zadorra River, at Villodas, Álava, Spain, also supported *X. victoriensis* (Vedia *et al.* 2014).

Currently only one, *Cambarincola mesochoreus* Hoffman, of the six endemic branchiobdellidans reported on *P. clarkii* have been found in Europe. The first association was observed in a stream at Carmagnola, near Torino, northern Italy (Gelder *et al.* 1994), and it was rumored locally that the crayfish had been brought in illegally from France. While a recent survey (Parpet & Gelder 2020) discovered the association at a site in Southwest France.

b. Branchiobdellidans adopting exotic hosts: In spite of *O. limosus* being introduced repeatedly into Europe over the last 120+ years, there have been no reports of their carrying any of their endemic branchiobdellidans. However, it appears they are acceptable alternate hosts for some European species of *Branchiobdella*. Sympatric populations of *O. limosus* and the endemic *Au. torrentium* in a tributary to the

Steinbeck Creek, Hesse, Germany, were both found to support populations of *B. parasita* and *B. pentadonta* (Vogt 1999). *Branchiobdella* sp. and cocoons were observed in 2001 on *O. limosus* from the Świętokrzyska uplands in Poland (Dr. W. Struzynski unpub. obs.). Local anglers had told him the waterbody had contained *A. astacus* and *A. leptodactylus* a few years earlier, but it is unlikely that these anglers would have been aware of any surviving relict populations of *Astacus* species and their branchiobdellidans. Another adoption of *O. limosus* by *B. balcanica, B. hexadonta, B. parasita* and *B. pentadonta* was reported, together with their cocoons, on specimens from the River Elbe (Labe) in Obřistvi near Mělnik, Czech Republic (Czechia) (Ďuriš *et al.* 2006). After these observations were made in 2001, major flooding in the Elbe and Vltava watersheds prevented collections in 2002, and in 2003 only a few *O. limosus* were found with one carrying five *B. parasita*. Sampling at 30 sites in 2003–4 revealed some *O. limosus* but no branchiobdellidans. Bláha *et al.* (2017) collected large numbers of crayfish from two sites in the Czech Republic approximately 60km apart; a brook south of Prague and a pond west of Brno. The upper part of the brook contained *A. astacus* and the lower *O. limosus* with a narrow overlap where they cohabited. Specimens of *O. limosus* carried *B. parasita*, but those of *A. astacus* were not examined. The pond site had contained cohabiting *A. astacus* and *P. leniusculus* for over 20 years, and although the latter supported *B. parasita* and *B. pentadonta*, again specimens of *A. astacus* were not examined. Even so, this was the first report of *B. parasita* and *B. pentadonta* adopting *P. leniusculus* (Bláha *et al.* 2017). A similar displacement occurred in Estonia. In August 2018, Margo Hurt (Estonian University of Life Science, Institute of Veterinary Medicine and Animal Sciences, Tartu, Estonia; pers. com.), collected *P. leniusculus* from the Riksu Stream on Saaremaa Island, Estonia, which carried small numbers of *B. pentadonta* (identified by S. R. Gelder) on the chelae. Prior to the illegal stocking of *P. leniusculus*, Riksu Stream had a healthy population of *Astacus astacus*, but these succumbed to crayfish plague following the introduction of the exotic crayfish (M. Hurt, per. com.).

Although *C. mesochoreus* had been reported on *P. clarkii* in a stream near Torino, northern Italy (Gelder *et al.* 1994), a subsequent collection yielded *P. clarkii* without *C. mesochoreus* but populated by endemic *B. italica* and *B. parasita* from *Au. pallipes* that cohabited streams in the area (Gelder *et al.* 1999). Unfortunately, no observations were made during the interim to provide an explanation of how the change in branchiobdellidan species occurred.

4. Distribution of exotic branchiobdellidans and crayfish in East Asia (subregion IIa)

Until the early 20th century, the demand for crayfish in East Asia appears to have been met with endemic species from local suppliers. As the demand increased in Japan, individuals arranged for the North American crayfish, *P. leniusculus* and *P. clarkii* to be imported. Records show that five shipments of *P. l. leniusculus* and *P. l. trowbridgii* from Oregon, USA, between October 1926 and July 1930, were released into farm ponds across Japan (Kamita 1970). However, most introductions are believed to have survived for only a short time and no further translocations were allowed after 1930. Therefore, recent records of *P. leniusculus* in country are those that survived and spread through natural range expansions, and by deliberate or unintentional translocations (Usio *et al.* 2016). Yamaguchi (1933) stated there were no other crayfish in the area when *P. leniusculus* were released into Lake Chuzenji (=Chunzenji), Tochigi Prefecture, Honshu. More recent records show populations in the Tankai Reservoir, Shiga Prefecture, Lake Onogawa, Fukushima Prefecture (Kawai *et al.* 2004), and Akita, Gunma, Ishikawa, Nagano, Shiga and Tochigi Prefectures, all on Honshu Island, based on preserved *P. leniusculus* deposited in various academic institutions (Ohtaka *et al.* 2005). The most recent find being on an island in the Tone drainage, Chiba Prefecture, Honshu (Nakata *et al.* 2010). Specimens of *P. leniusculus* on Hokkaido Island were reported in Lake Mashu (Kawai *et al.* 2004) and are now at 12 sites indicating the crayfish's expanding range (Ohtaka *et al.* 2005; Kawai 2017a).

From the original crayfish translocation into Lake Chuzenji, a branchiobdellidan was described, *Cambarincola okadai* Yamaguchi. Unfortunately, only its external features and jaws were drawn and described, but no type specimens designated, therefore the species status was deemed *nomen inquirendum* by Holt and Opell (1993). Specimens from Washington State, USA, were subsequently described and named *Triannulata montanus* Goodnight, then Holt (1974b) transferred the species to the *Cambarincola*, where it became *C. montanus*. Professor A. Ohtaka found Yamaguchi's slide collection (Gelder & Ohtaka 2000; Ohtaka *et al.* 2020) and they recognized the original specimen from his figure, which enabled them to designate a lectotype and paralectotypes for *C. okadai*. In addition to publishing a detailed species description from the newly found specimens, *T. montanus* and *C. montanus* were designated junior synonyms.

Neseumann and Neubert (1999: 20) reported an imported *Cambarincola* in Japan but gave no details. Examinations of preserved *P. leniusculus* from various Institutions in Japan (Ohtaka *et al.* 2005) revealed *X. victoriensis* in a stream in Akashina, Nagano Prefecture and *Sathodrilus attenuatus* Holt, at Tachihiraki, Shika, Ishikawa Prefecture, both on Honshu Island; the latter species being widespread across Hokkaido.

In 1927, about 100 *P. clarkii* were shipped in a beer barrel from Louisiana, USA, to Japan (Kawai 2017b). Only 20 survived the journey and these were release into a pond to feed bullfrogs near Kamakura City, Kanagawa Prefecture (about 30km south of Tokyo). The population grew rapidly and within 20 years crayfish had been translocated to every major prefecture in Japan (Kawai & Kobayaski 2006), mainly as family aquarium pets (Hobbs *et al.* 1989). This made subsequent importations unnecessary and so after 1930 any importations made were illegal. Japanese specimens were translocated to Nanjing, China, in 1929 and started *P. clarkii*'s expansion through China, Taiwan, the Korean peninsula (Kawai & Kobayashi 2006) and to the rest of Southeast Asia (Hobbs *et al.* 1989); these were supplemented by many illegal introductions. Given the extensive legal and illegal translocations of *P. clarkii* around East Asia, it is interesting that neither *C. mesochoreus* nor any of its other endemic branchiobdellidans have been reported. However, the origin of *C. mesochoreus* on *P. clarkii* collected at two sites in suburban Tokyo (Ohtaka *et al.* 2017) is strongly suspected to be the result of escaped or released domestic pets that were recently imported into the country. It should be anticipated that other American ornate crayfish pet species will be discovered in East Asia, possibly carrying exotic branchiobdellidans.

As noted earlier, Marbled crayfish are probably the most popular pet crayfish in the world (Chucholl 2016; Pârvulescu *et al.* 2017). Eight established populations have been identified in Germany, The Netherlands, Czechia and Hungary, with 12 additional single reports extending from central Italy to western Sweden (Feria & Faulkes 2016), to which can be added the discovery of specimens in a gravel pit lake near the Drava River in Croatia (Samardžić *et al.* 2014) and the Narva River, Estonia, in 2018 (T. Timm, pers. com.). The recent record of *P. fallax* f. *virginalis* on Hokkaido and Shikoku islands in Japan is a clear reminder that exotic species continue to be introduced in spite of legislation to protect endemic species (reviewed in Kawai 2017a). Although there is little reason to believe *P. fallax* f. *virginalis* has any endemic branchiobdellidans, the chances of its being adopted by endemic worms from the introduced regions does exist. An unusual, but creative diplomatic gift of pet crayfish occurred when approximately 70 live *Cambarellus montezume patzcuarensis* Villalobos, or "Acocil", were presented to Emperor Hirohito by President Luis Echeverria of Mexican in 1972 (Kamita 1973). Kawai (2017a) provided additional details of this gift, reporting Dr. Luis Kasuga Osaka brought the crayfish to Japan where some were maintained in an aquarium in the Imperial Palace in Tokyo. The remaining specimens were divided among three aquaria and a private laboratory where the latter conducted rearing experiments; however, none of the crayfish were released into the wild.

In closing

There are only two commercial considerations when branchiobdellidans are visible on crayfish, first, live worms are considered leeches and it is "well known" by the populous that all leeches are parasites. Therefore, they must damage the crayfish and this misconception results in lowered prices at the fish market. Second, any unhealthy-looking or damage crayfish are automatically assumed to have been attacked by branchiobdellidans, even though the condition is usually due to microorganism infections or environmental conditions; however, seller and buyer visual perceptions are paramount. In reality, there have been only a few reports of a North American branchiobdellidan being an intermediate hosts for a metazoan parasite (Gelder & Williams 2015) and there is no evidence they act as vectors or paratenic hosts in translocating endemic pathogenic microorganisms. Therefore, the translocated branchiobdellidans identified so far probably have the same relationship and cause the same amount of damage, if any, as those on their endemic crayfish hosts.

In spite of the undesirability of exotic or alien branchiobdellidans and their hosts, tracking range expansions and future introductions of the worms is dependent on the alertness of a wide range of personnel in wildlife conservation, food inspection, biology teachers, and aquaculturists, as well as crustacean researchers. Keys are available (Gelder 2016, 2019, in press) for all the described species of branchiobdellidans; however, the challenge now is the accurate identifications of these ectosymbionts when found. The old approach of identifying branchiobdellidans based on host species, geographic location of capture, body size and jaw morphology is no longer acceptable as the exotic specimens are likely in a key for another realm. In addition, exotic branchiobdellidan species currently identified have been easy to recognize on their host, as they were often active and over 2.0mm long. In contrast, many of the additional, potential species listed in Tables 1 and 2 are less than 2.0mm long and about half average less than 1.0mm. Therefore, a new level of thoroughness in host examination is required that involves using a dissecting microscope, preferably while the host is still alive. An examination of the removed worms under a compound microscope will then yield information on the morphological characters, primarily the male reproductive system, required by the identification keys (Gelder & Williams 2015, 2016). Although some future reports of exotic branchiobdellidans are predictable as the host continues its range expansion, other will depend on keen eyes and serendipity.

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