

GLOBAL DISTRIBUTION OF *FABAEFORMISCANDONA SUBACUTA*: AN EXOTIC INVASIVE OSTRACODA ON THE IBERIAN PENINSULA?

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ABSTRACT

Although exotic species of Ostracoda have been recorded from various sites in Europe, none of them have a widespread European distribution. Reviews of existing literature, examination of specimens, and sampling in Spain and Japan has greatly expanded the known distribution of the candonid ostracode *Fabaeformiscandona subacuta* (Yang, 1982). We herein present new reports of its presence in mainland eastern Asia, Australia, and South America, and we review its distribution on the Iberian Peninsula. Although this species is globally widespread, we hypothesize that it is an invasive species on the Iberian Peninsula in light of the following facts: it is not known from other European countries, its known global distribution is extremely disjunct, it has not been found during palaeo-limnological investigations of European lakes, and on the Iberian Peninsula it is almost exclusively found in artificial, intensely human-impacted habitats, mostly in reservoirs and ricefields.

KEY WORDS: alien species, aquatic invasions, biogeography, *Fabaeformiscandona*, Ostracoda

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INTRODUCTION

Biological invasions in inland waters are receiving increasing attention nowadays, as they can be major threats to ecosystems and biodiversity. However, traditional invasion paradigms are basically derived from terrestrial studies, which have not been sufficiently tested for freshwater organisms (Beisel, 2001). Freshwater systems are vulnerable to invasions by non-native species for several reasons, including human-mediated introductions of exotic species (both intentional and accidental), associated environmental disturbances, and new connections with other water systems (Jażdżewski and Konopacka, 2000; van der Velde et al., 2000; Gherardi, 2007). Aquatic invertebrate invasions have generally been neglected because freshwater invasion research has mainly focussed on economically significant species, such as fishes. The American crayfish *Procambarus clarkii* (Girard, 1852) and the zebra mussel *Dreissena polymorpha* (Pallas, 1771) are exceptions to this due to their wide distributions and the significant economic losses they cause in bodies of water they have invaded.

Despite the presence of exotic freshwater ostracode species in various areas far from their sources (McKenzie and Moroni, 1986; Petkovski and Meisch, 1996; Horne and Smith, 2004; Horne et al., 2004; Garcia-Berthou et al., 2007;

Martens and Horne, 2009), little is known of their potential to invade. The lack of knowledge of the ecological impacts and biology of most exotic ostracodes, including their basic ecology and distribution, has frequently led freshwater researchers to ignore them in topical reviews, e.g., Holdich and Pöckl (2007). In Europe, the only works focusing on exotic ostracodes are those by McKenzie and Moroni (1985) and Rossi et al. (2003) in Italian rice fields, but they did not identify any exotic species that are widely distributed in water bodies other than rice fields. Data from the Iberian Peninsula indicate that exotic ostracodes may constitute a significant part of the exotic invertebrate fauna of freshwater environments, particularly in rice fields (Baltanás, 1992; Baltanás et al., 1996; García-Berthou et al., 2007).

Recently, Rueda et al. (2006) and Poquet et al. (2008) reported the ostracode *Fabaeformiscandona subacuta* (Yang, 1982; in Hou et al., 1982) [as *Fabaeformiscandona japonica* (Okubo, 1990)] from a few locations on the Iberian Peninsula, and it was considered exotic by these authors. With the present survey, we aimed to evaluate the global distribution of this ostracode to assess its status as an invasive species on the Iberian Peninsula, and to analyze its distribution and ecology in relation to habitat preferences in different areas of its geographical range. In addition, we review its taxonomy and global distribution, with a special focus on the Iberian

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Peninsula, report new data, and include taxonomic evaluations of previous records.

MATERIALS AND METHODS

We reviewed papers that reported *F. subacuta*, or its two junior synonyms: *Fabaeformiscandona sangganheensis* (Huang, 1985), and *F. japonica*. Additionally, we checked reports of *Fabaeformiscandona holzkampfi* (Hartwig, 1900), a species that closely resembles *F. subacuta*, from the Iberian Peninsula plus any other papers that include possibly doubtfully determined species of *Fabaeformiscandona* that could be assigned to *F. subacuta*. To carry out this review of papers that include *F. holzkampfi*, the “Kempf Database Ostracoda” (Kempf, 1980a, b, c, d, 1991, 1997a, b, c, d, 2002, 2006) was particularly helpful.

We checked photographs of individuals of *Fabaeformiscandona* collected in Thailand by S. Savatentalinton (initially identified as *F. cf. japonica* and confirmed as *F. subacuta* herein), and individuals collected by F. Viehberg in Germany (identified as *F. holzkampfi*). Additional samples were obtained from various previous research projects in which the authors were involved, together with new samples collected for this study from Spain and Japan. They were collected with different sampling methods, depending on their origin. Those from reservoirs were mostly taken with a sediment grab deployed from a boat, while others were taken with a hand net (100 μ S mesh size) swept through the littoral benthic zone. All were fixed with diluted ethanol in the field (30%) and later in the laboratory transferred to a higher concentration (70%). Ostracodes were picked from the samples in the laboratory with the aid of a stereomicroscope. Selected specimens were dissected and observed with light microscopy (soft parts and valves). Carapaces were photographed with scanning electron microscopy, by first coating the specimens with gold and then using a JEOL JSM-5800 LV scanning electron microscope.

RESULTS

Taxonomic Comments

Fabaeformiscandona subacuta was first described by Yang (in Hou et al., 1982) as *Candona subacuta* Yang, 1982 from specimens collected from the Neogene of China. Later, Schornikov (2004) transferred the species to the genus *Fabaeformiscandona* Krstić, 1972, and considered two other species, *Candona sangganheensis*, described by Huang (1985) from the Chinese Pleistocene, and *Fabaeformiscandona japonica*, a Recent Japanese species described by Okubo (1990), as junior synonyms.

Fabaeformiscandona holzkampfi closely resembles *F. japonica* in lateral views of the male and female carapaces and the shapes of the male fifth limbs and hemipenes. Differences include the following: the female carapace of *F. holzkampfi* has a distinctive, protruding lobe on the postero-dorsal margin of the left valve (indicated with a black triangle on Fig. 1G), a feature best seen in dorsal view (Fig. 2E, F). The female carapace of *F. holzkampfi* also lacks the small expansion on the postero-ventral area of the calcified inner lamella, a feature present in *F. subacuta* (indicated with a black triangle on Fig. 1C, D). The M-

process of the male hemipenis of *F. holzkampfi* is of similar shape to that of *F. subacuta*, but the a-lobe is smaller and more rounded than that of *F. subacuta* (Fig. 3). The h-lobe is also longer and more curved, and the b-lobe is much more angular in *F. holzkampfi*. The inner edge of the male left fifth limb palp is not bent to such an acute angle as that of *F. subacuta* (indicated with a black triangle on Fig. 3I), while the right palp is more rounded along its distal-most edge (indicated with a black triangle on Fig. 3H).

After checking accompanying drawings of soft parts, we conclude that *F. subacuta* has been misidentified as *F. holzkampfi* by Armengol (1978, as *Candona holzkampfi*), Chen (1982, as *Candona holzkampfi*), and Mezquita and Sanz-Brau (1997). Further investigations have revealed that specimens collected from Australia and identified as *F. holzkampfi* by Karanovic (2007) are also *F. subacuta* (Fig. 4), as are specimens from Thailand reported as *Fabaeformiscandona cf. japonica* (Savatentalinton and Martens, 2009) and specimens found in Colombia and reported as *Candona* sp. 1 by Torres Saldarriaga and Martínez (2010). In our revision of available papers including *F. holzkampfi*, we checked several works that had no drawings or photographs of distinctive characters (Dubowsky, 1926; Klie, 1926; Järvekiilg, 1959; Kosmal, 1968; Wouters, 1989; Fuhrman and Pietrze-niuk, 1990; Mazepova, 1990; Semenova and Sharapova, 2012) and consequently we could not ascertain whether the identifications of *F. holzkampfi* were correct or, alternatively, they actually referred to *F. subacuta*. Therefore, these findings remain doubtful. We could only confirm identifications of *F. holzkampfi* in those references that included drawings or pictures of taxonomically important features (Hartwig, 1900, 1901; Vávra, 1909; Müller, 1912; Klie, 1938; Bronshtein, 1947; Farkas, 1958; Sywula, 1974; Absolon, 1978; Györe, 1985), although it must be noted that some of them used modified drawings from previously published works, instead of original drawings of collected specimens.

An allotype individual of *C. inexpecta* (Chapman, 1963) was examined by one of us, who initially concluded that was *F. holzkampfi* (Karanovic, 2007). Further examination of the drawings of this specimen did not allow us to confirm it was *F. holzkampfi* or *F. subacuta*. It should be noted that the description of *C. inexpecta* by Chapman (1963) is confusing as it includes drawings belonging to different species of Candoninae. Collecting of more specimens from New Zealand is needed in order to clarify the taxonomy and distribution of this species.

Global and Iberian Distributions

Fabaeformiscandona subacuta was originally described by Yang (1982) as a fossil from Neogene sediments in Yancheng (Jiangsu Province, China), but was also found living in a Chinese lake (Chen, 1982, as *Candona holzkampfi*, unspecified location), and Japan (as *Candona japonica* and *F. japonica*) in the prefectures of Okayama, Fukuoka, Gunma, Shiga, and Ishikawa (Okubo, 1990, 2004; Smith and Kamiya, 2007; Smith and Janz, 2008) (Table 1, Fig. 5). It has also been found living in Korea (Lee et al., 2000, as *Fabaeformiscandona* sp. 1; Chang et al., 2012, as *F. japonica*) eastern Russia (Schornikov and Trebuchova, 2001, as *F. sangganheensis*; Schornikov, 2004; Zenina and Schornikov, 2008), Thailand (Savatentalinton and Martens, 2009, as

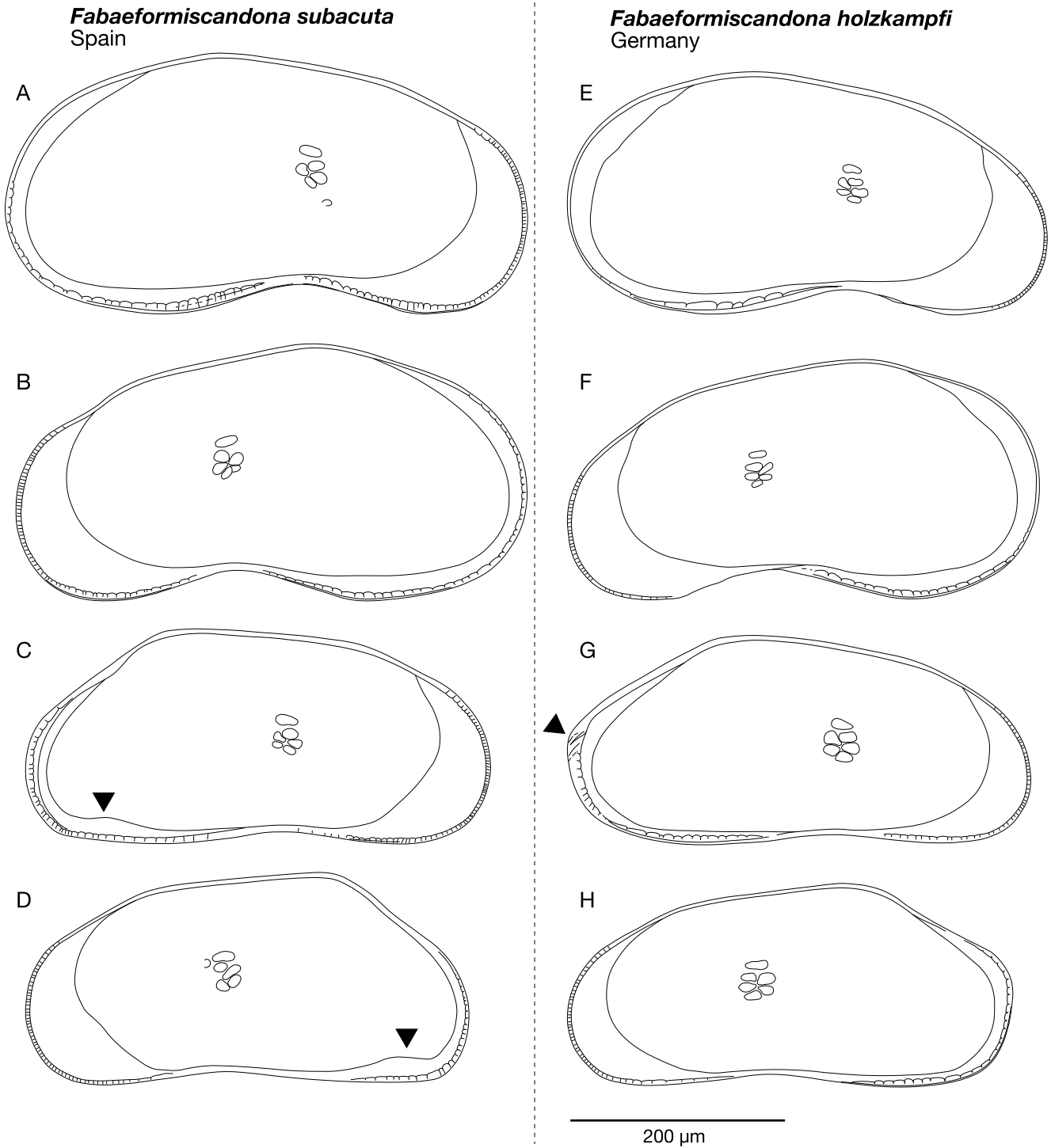


Fig. 1. *Fabaeformiscandona subacuta* (A-D) and *Fabaeformiscandona holzkampfi* (E-H). A, E, internal view of male's left valve; B, F, internal view of male's right valve; C, G, internal view of female's left valve; D, H, internal view of female's right valve.

Fabaeformiscandona cf. *japonica*), Australia (Karanovic, 2007, as *Fabaeformiscandona holzkampfi*) and Colombia (Torres Saldarriaga and Martínez, 2010, as *Candona* sp. 1). Herein, we report new localities where we have collected *F. subacuta* in Spain, Japan, China and Eastern Russia (Table 1, Fig. 5). The present Iberian distribution is only rela-

tively well-known in the Mediterranean area (Fig. 5). This is probably a consequence of the sampling effort being concentrated in eastern Spain. If more sampling is carried out over the whole Iberian Peninsula, more sites for *F. subacuta* will probably be found in different regions. Even so, it is important to note that this species has not been found in any

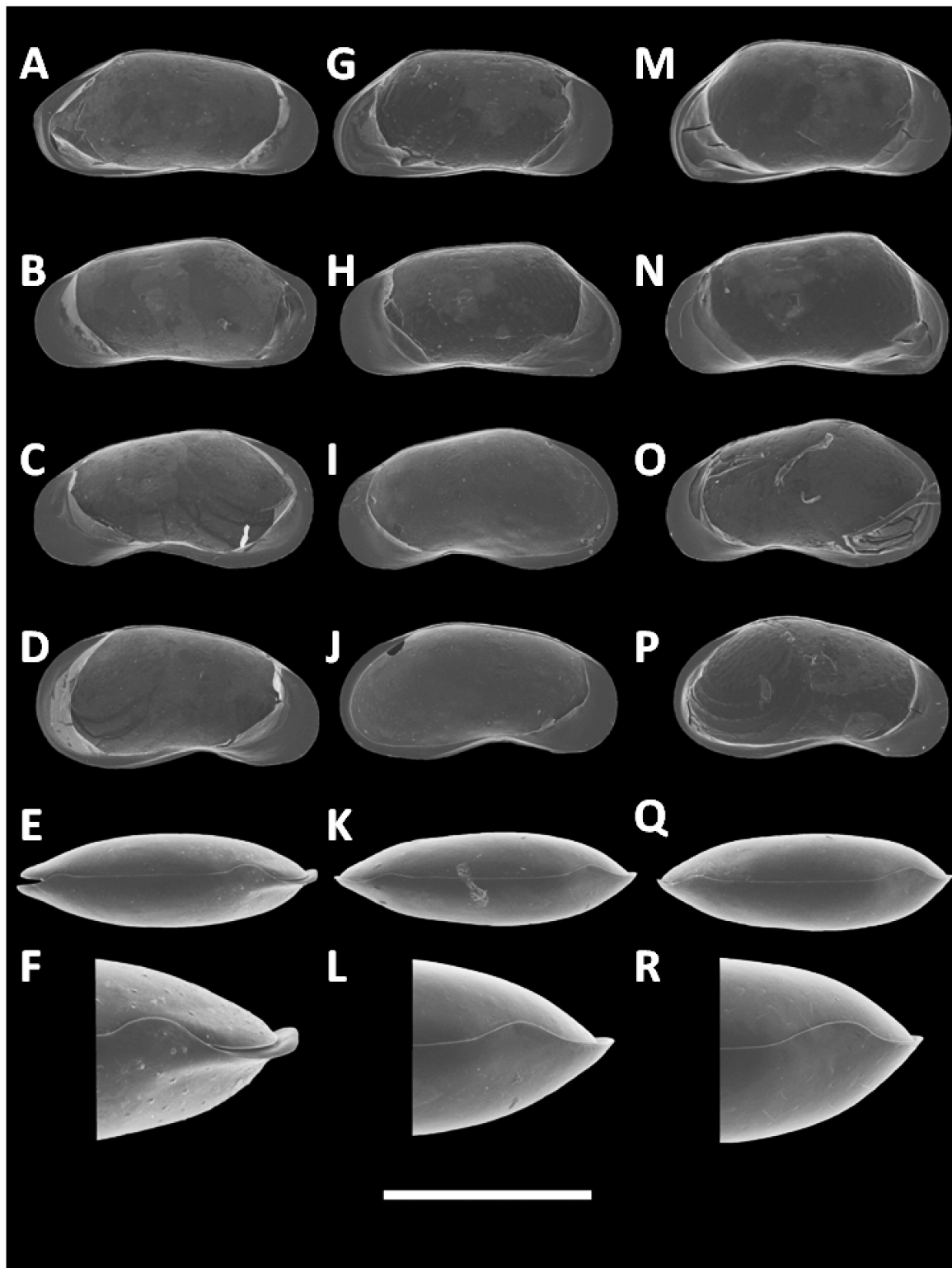


Fig. 2. SEM photographs of *Fabaeformiscandona holzkampfi* specimens from Germany (A-F) and *F. subacuta* from Spain (G-L) and Japan (M-R). A, *F. holzkampfi*, female, left valve inner view (bar = 728 μm); B, *F. holzkampfi*, female, right valve inner view (bar = 696 μm); C, *F. holzkampfi*, male, right valve inner view (bar = 743 μm); D, *F. holzkampfi*, male, left valve inner view (bar = 748 μm); E, *F. holzkampfi*, carapace of female, dorsal view (bar = 664 μm); F, *F. holzkampfi*, carapace of female, detail of postero-dorsal part (bar = 331 μm); G, *F. subacuta*, female, left valve inner view (bar = 722 μm); H, *F. subacuta*, female, right valve inner view (bar = 686 μm); I, *F. subacuta*, male, right valve inner view (bar = 810 μm); J, *F. subacuta*, male, left valve inner view (bar = 812 μm); K, *F. subacuta*, female dorsal view (bar = 645 μm); L, *F. subacuta*, carapace of female, detail of postero-dorsal part (bar = 328 μm); M, *F. subacuta*, female, left valve inner view (bar = 692 μm); N, *F. subacuta*, female, right valve inner view (bar = 658 μm); O, *F. subacuta*, male, right valve inner view (bar = 799 μm); P, *F. subacuta*, male, left valve inner view (bar = 816 μm); Q, *F. subacuta*, carapace of female, dorsal view (bar = 651 μm); R, *F. subacuta*, carapace of female, detail of postero-dorsal part (bar = 329 μm).

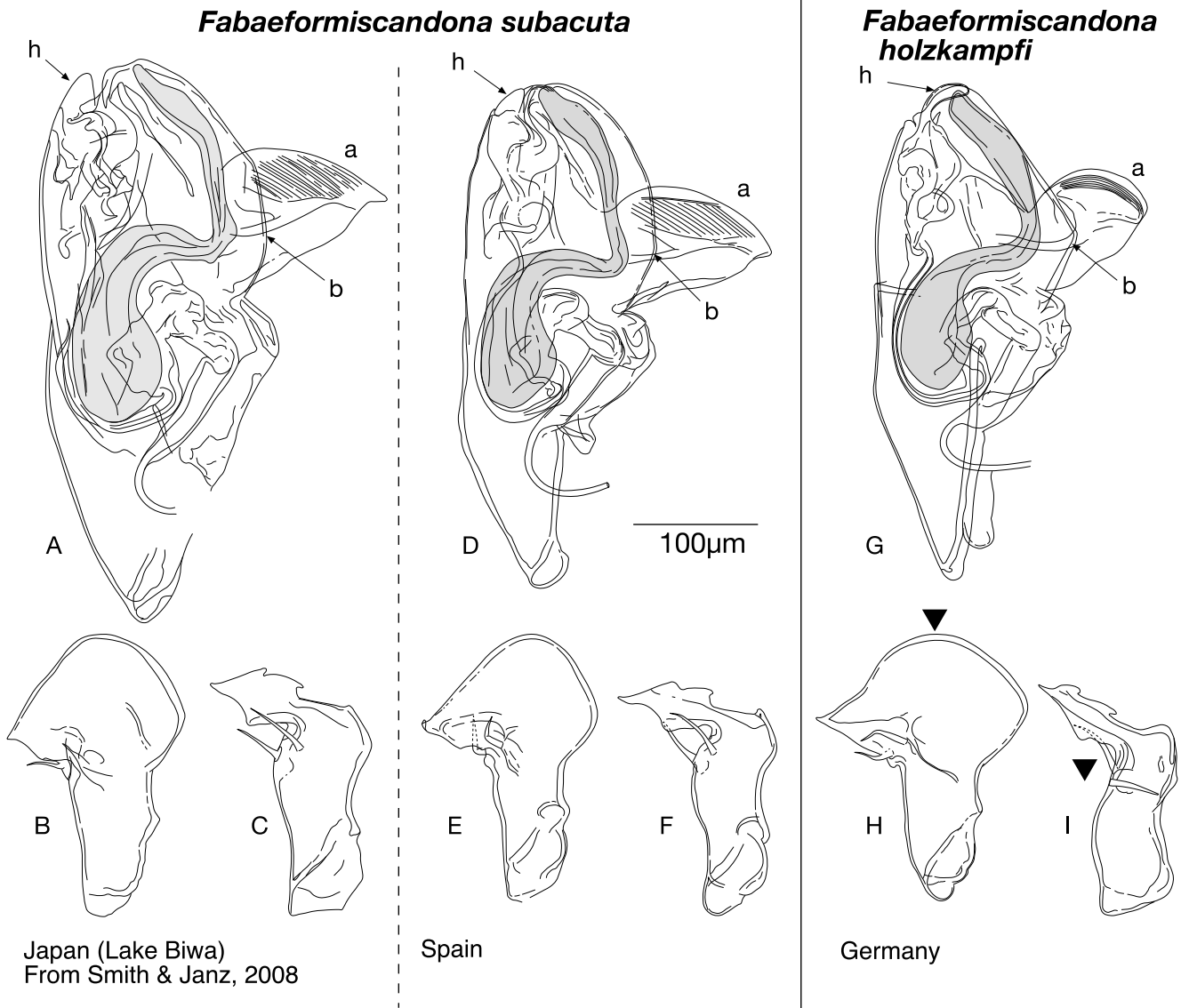


Fig. 3. *Fabaformiscandona subacuta* (A-F) and *F. holzkampfi* (G-I). A, D and G, hemipenis; B, E and H, palps of males' right fifth limbs; C, F and I, palps of males' left fifth limbs.

Pleistocene or early to mid-Holocene deposits on the Iberian Peninsula (sub-fossil valves have only been found in recent sediments of a coastal lake, l'Albufera de València; Poquet et al., 2008; as *F. japonica*), nor other locations in Europe (Griffiths, 1995). No mention of this species has been found in the literature concerning the Eurasian area between the two main groups of localities in Spain and Eastern Asia, either living or fossil.

Habitat Preferences

In Spain, *F. subacuta* seems to prefer permanent, freshwater habitats. Rice fields were the only temporary waters in which we found it, and these are usually connected to permanent water bodies, i.e., channels, reservoirs, irrigation ponds. Data on its presence in isolated sites, such as endorheic and karstic lakes or natural temporary ponds, are nearly non-existent in Spain. The other documented sites are permanent

habitats, such as reservoirs, large ponds (including oxbows) or rivers (Table 1, Fig. 5). *Fabaformiscandona subacuta* apparently prefers lentic habitats, and all of the places it has been found in Spain are connected directly to rivers or channels, or are subject to flooding. Lower reaches of rivers have not been adequately sampled for ostracods in Spain, but their similarity to reservoirs (slow water flow, planktonic communities, etc.) may make them a suitable habitat for *F. subacuta*.

With the present data on the distribution of *F. subacuta*, it is not possible to establish a clear preference for artificial or (semi-) natural water bodies, but human-modified habitats (to differing degrees) are predominant (Table 1), and it does not appear in any "pristine" environment (such as mountain lakes or well-preserved wetlands) on the Iberian Peninsula. It is usually found in sediments or detritus. It is also found in polluted areas and urban ponds, so it is probably tolerant

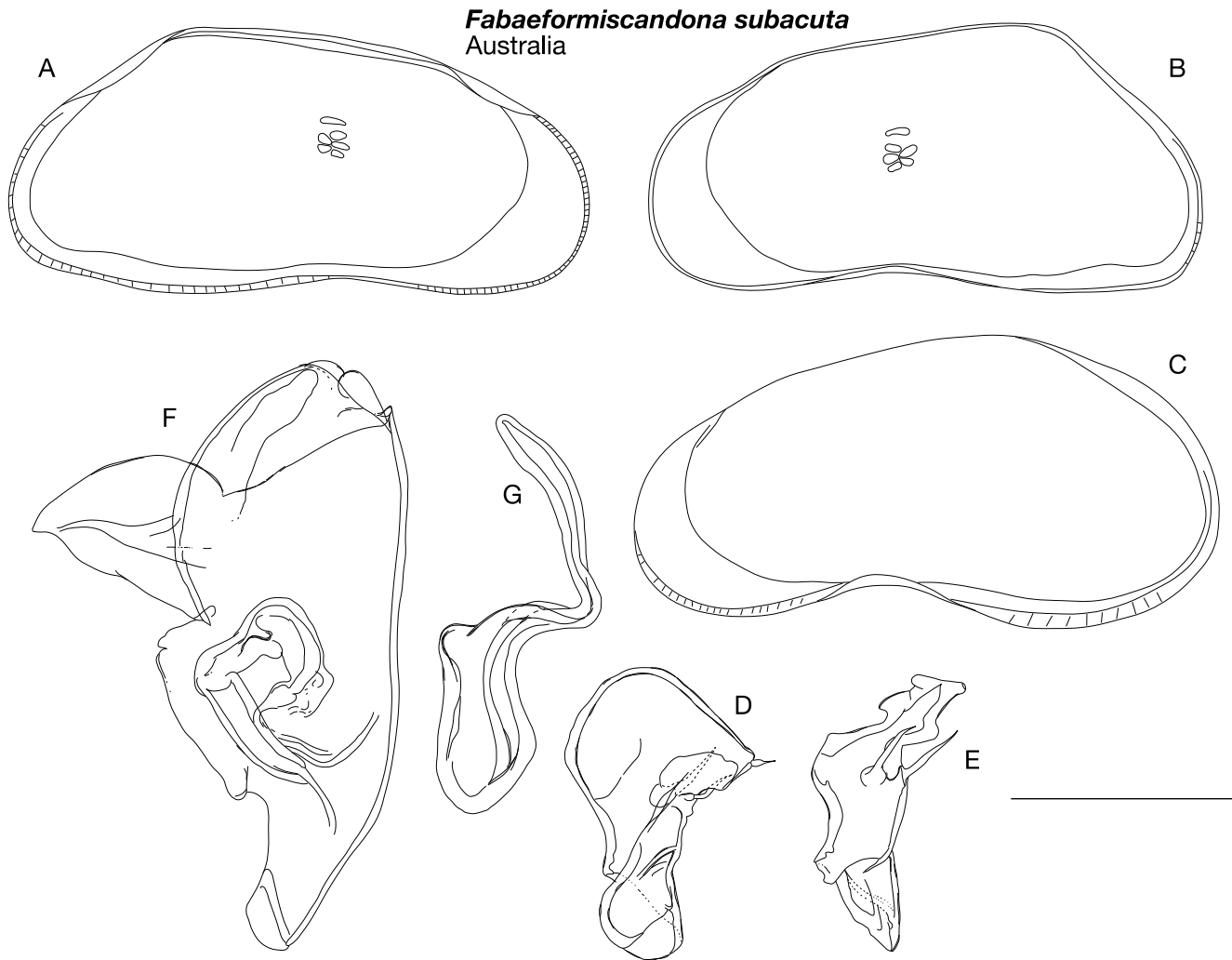


Fig. 4. *Fabaeformiscandona subacuta* (Australia). A, internal view of female's left valve; B, internal view of female's right valve; C, internal view of male's right valve; D, palp of male's right fifth limb; E, palp of male's left fifth limb; F, hemipenis; G, m-process of hemipenis. Scale bar = 410 μm for A-C, 162 μm for D-G.

of environmental conditions such as organic pollution and low oxygen levels. Physico-chemical parameters shown in Table 2 summarize the available data for the locations studied. A Mann-Whitney U test was performed in order to compare abiotic information (pH, oxygen, conductivity) for sites where living individuals were found with those where only valves have been recovered. The results show that there are no significant differences, but the number of sites with available data is still relatively low.

In Japan, *F. subacuta* is common in Lake Biwa (depths ranging from the littoral zone to 22 m), with the highest abundances found around root mats of willow trees lining the lakeshore. It is occasionally found in ricefields and in agricultural associated watercourses (Smith and Janz, 2008; this work). It has also been found in urban man-made ponds, a cave with a muddy substrate, and in a small natural stream (Smith and Kamiya, 2007; this work). The Thai specimens were collected in the Lopburi River, from a slowly flowing section with submerged macrophytes and water hyacinth (Savatenalinton and Martens, 2009). The Chinese specimens

were recorded from an unspecified lake (Chen, 1982), and ricefields, lakes (Taihu Lake) and channels in the Jiangsu Province (this work). The Korean specimens were from a coastal freshwater wetland (Lee et al., 2000), a swamp, a lotus field, small springs (Chang et al., 2012) and a ricefield (this work), and the Australian specimens were from a small stream near Perth (Karanovic, 2007).

Fabaeformiscandona subacuta is present in freshwater systems in eastern Russia (Russian Primorye), especially in the Tumen River and Lake Khanka and surrounding rivers, wetlands and rice fields (this work), both located along the border between Russia and China. It is one of the few species surviving in the polluted shore area of Lake Khanka close to Kamen-Rybolov and Astrakhana villages (Schornikov and Trebukhova, 2001). It has also been found in littoral habitats of the freshwater Lake Utinoe, with muddy sand and reeds (Zenina and Schornikov, 2008). This lake is part of the lower reaches of the Razdolnaya River, close to Amursky Bay (Sea of Japan). The northernmost location known for the species

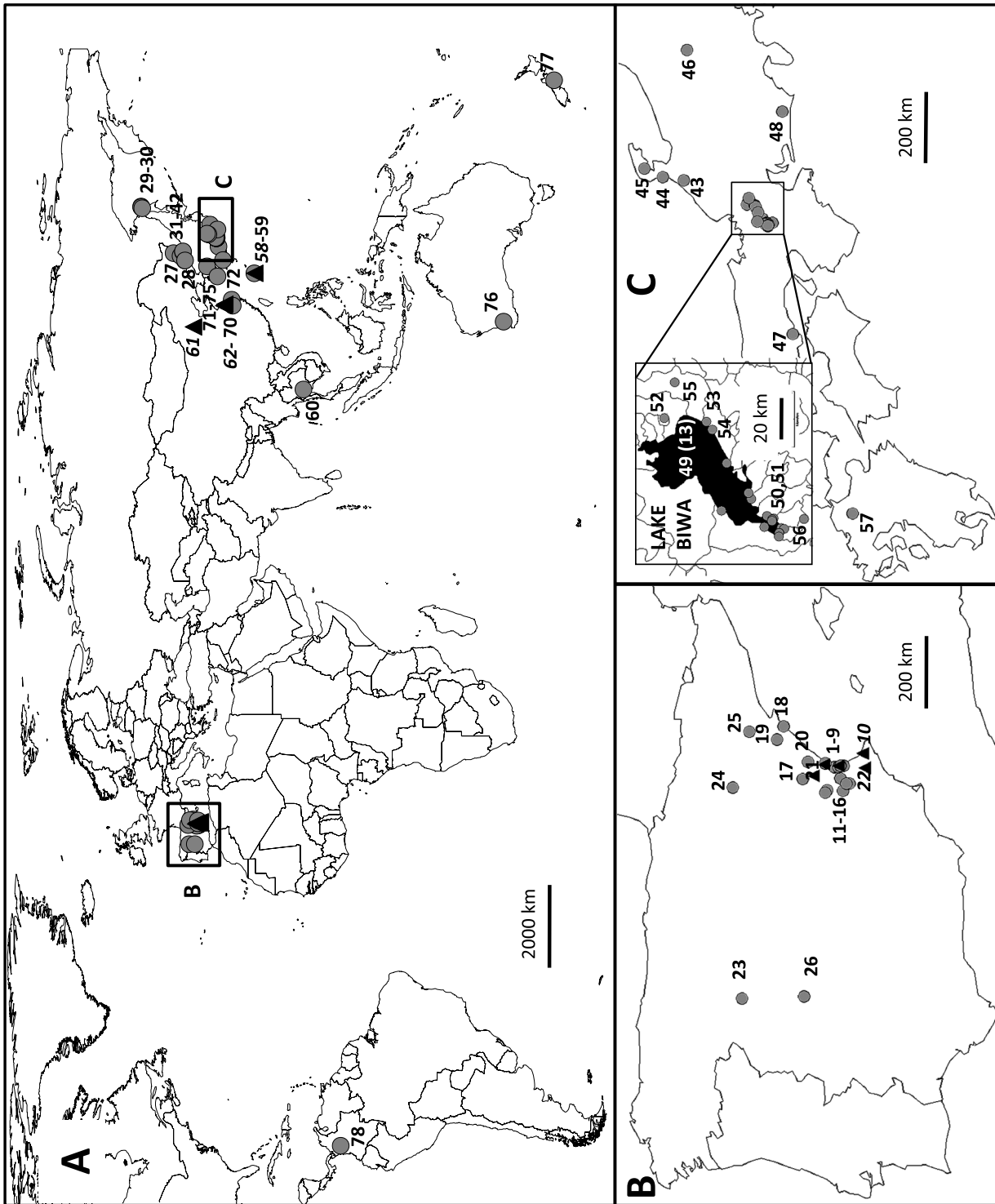


Fig. 5. A, global distribution of *Fabaeformiscandona subacuta*; B, detailed distribution in Spain; C, detailed distribution in central Japan. Numeric codes as in Table 1. Numbers in italics and black triangles refer to sites where only dead specimens (values) of *F. subacuta* have been found; regular numbers and grey circles refer to sites where live specimens of *F. subacuta* have been found in at least one sampling (see Table 1 and text for further explanations).

Table 1. World locations where *F. subacuta* has been found or cited. Prov = Province; Coun = Country; Per = Permanence (1 = permanent; 0 = temporary); Ar = Artificiality (1 = artificial or highly humanized; 0 = natural); St = status of individuals (1 = presence of living individuals; 2 = presence of only valves). Sample codes as in Fig. 5.

Code	Site	Prov	Coun	Per	Environ	Flow	Ar	St	First citation – observations
1	CAC	València	Spain	0	Pond	Lentic	1	1	This work
2	Racó de l'Olla	València	Spain	0	Pond	Lentic	1	1	This work
3	Mallada Piscina	València	Spain	1	Pond	Lentic	1	2	Rueda et al., 2006 (as <i>F. japonica</i>)
4	Baldoví	València	Spain	1	Spring	Lentic	0	1	This work
5	Albufera	València	Spain	1	Lake	Lentic	0	2	Poquet et al., 2008 (as <i>F. japonica</i>)
6	Catarroja	València	Spain	0	Ricefield	Lentic	1	1	This work
7	Catarroja SF	València	Spain	0	Ricefield	Lentic	1	1	This work
8	Cap de Terme	València	Spain	1	Wetland	Lentic	1	1	Poquet et al., 2008 (as <i>F. japonica</i>)
9	Xeresa	València	Spain	1	Wetland	Lentic	1	2	Poquet et al., 2008 (as <i>F. japonica</i>)
10	Bassa Sineu	València	Spain	1	Spring	Lentic	1	2	Zamora et al., 2005 (as <i>Fabaeformiscandona</i> sp.)
11	Chulilla	València	Spain	1	River	Lotic	0	1	Mezquita et al., 1999 (as <i>F. holzkampfi</i>)
12	Gestalgar	València	Spain	1	River	Lotic	0	1	This work
13	Magre	València	Spain	1	River	Lotic	0	1	Mezquita and Sanz-Brau, 1997 (as <i>F. holzkampfi</i>)
14	Naranjero	València	Spain	1	Reservoir	Lentic	1	1	This work
15	Escalona	València	Spain	1	Reservoir	Lentic	1	1	This work
16	Tous	València	Spain	1	Reservoir	Lentic	1	1	This work
17	Millars	València	Spain	1	River	Lotic	0	1	This work
18	Sénia	Castelló	Spain	1	River	Lotic	0	1	Escrivà, 2011 (as <i>F. japonica</i>)
19	Ulldecona	Castelló	Spain	1	Reservoir	Lentic	1	1	Escrivà, 2011 (as <i>F. japonica</i>)
20	Sitjar	Castelló	Spain	1	Reservoir	Lentic	1	1	This work
21	Regajo	Castelló	Spain	1	Reservoir	Lentic	1	2	This work
22	Beniarrés	Alacant	Spain	1	Reservoir	Lentic	1	2	This work
23	San Román	Valladolid	Spain	1	Reservoir	Lentic	1	1	Armengol, 1978 (as <i>Candona holzkampfi</i>)
24	Galacho Cartuja	Zaragoza	Spain	1	Oxbow lake	Lentic	0	1	This work
25	Ribarroja	Tarragona	Spain	1	Reservoir	Lentic	1	1	This work
26	Tiétar	Badajoz	Spain	1	River	Lotic	0	1	This work
27	Khanka Lake	Khankaisky	Russia	1	Lake	Lentic	0	1	Schornikov and Trebukhova, 2001 (as <i>F. sangganheensis</i>)
28	Tumen River Valley	Khasansky	Russia	1	River	Lentic	0	1	Schornikov and Trebukhova, 2001 (as <i>F. sangganheensis</i>)
29	Sakhalin Island	Sakhalin	Russia	1	Estuarine	Lotic	0	1	This work
30	Bolshoi Garomai River	Sakhalin	Russia	1	Oxbow	Lentic	0	1	This work
31	Bolshaya Ussurka River	Krasnoarmeysky	Russia	1	Oxbow	Lentic	0	1	This work
32	Grjaznuha River	Khankaisky	Russia	1	River	Lotic	0	1	This work
33	Mayskoe	Khankaisky	Russia	0	Ricefield	Lentic	1	1	This work
34	Kazachy Erik River Valley	Khankaisky	Russia	1	Lake	Lentic	0	1	This work
35	Vladimiro-Petrovka	Khankaisky	Russia	0	Ricefield	Lentic	1	1	This work
36	Sungach River	Spassky	Russia	1	Oxbow	Lentic	0	1	This work
37	Sungach River	Spassky	Russia	0	Drainage ditch	Lotic	1	1	This work
38	Spasovka River	Spassky	Russia	1	Oxbow	Lentic	0	2	This work
39	Novoselskoe	Spassky	Russia	1	Wetland	Lentic	0	1	This work
40	Livadyskoe Lake	Shkotovsky	Russia	1	Lake	Lentic	0	1	This work
41	Lebedinoe Lake	Shkotovsky	Russia	1	Lake	Lentic	0	1	This work
42	Utinoe Lake	Nadezhdinsky	Russia	1	Lake	Lentic	0	1	Zenina and Schornikov, 2008
43	Shinkai Pond	Ishikawa	Japan	1	Pond	Lentic	1	1	Smith and Kamiya, 2007 (as <i>F. japonica</i>)
44	Myojoji Temple	Ishikawa	Japan	0	Ricefield	Lentic	1	1	This work
45	Anamizu	Ishikawa	Japan	0	Ricefield	Lentic	1	1	This work
46	Paddy fields	Gunma	Japan	0	Ricefield	Lentic	1	1	Okubo and Ida, 1989 (as <i>Candona</i> sp.)
47	Paddy fields	Okayama	Japan	0	Ricefield	Lentic	1	1	Okubo, 1990 (as <i>Candona japonica</i>)
48	Shuchi-gum	Shizuoka	Japan	0	Irrigation ditch	Lotic	1	1	This work
49	Lake Biwa	Shiga	Japan	1	Lake	Lentic	0	1	Smith and Janz, 2008 (as <i>F. japonica</i>)
50	Oroshimo	Shiga	Japan	0	Ricefield	Lentic	1	1	This work
51	Moriyama	Shiga	Japan	0	Ricefield	Lentic	1	1	This work
52	Nagahama	Shiga	Japan	0	Ricefield	Lentic	1	1	This work
53	Hikone 1	Shiga	Japan	0	Ricefield	Lentic	1	1	This work
54	Hikone 2	Shiga	Japan	0	Ricefield	Lentic	1	1	This work
55	Ueno-Yataka stream	Shiga	Japan	1	Stream	Lotic	0	1	This work
56	Otsu	Shiga	Japan	0	Stream	Lotic	1	1	This work

Table 1. (Continued.)

Code	Site	Prov	Coun	Per	Environ	Flow	Ar	St	First citation – observations
57	<i>Paddy fields</i>	Fukuoka	Japan	0	Ricefield	Lentic	1	1	Okubo, 1990 (as <i>Candona japonica</i>)
58	<i>Gyokusendo Cave</i>	Okinawa	Japan	1	Cave stream	Lotic	0	2	This work
59	<i>Naha</i>	Okinawa	Japan	1	Pond	Lentic	1	1	This work
60	<i>Lopburi River</i>	Lopburi	Thailand	1	River	Lotic	0	1	Savatenalinton and Martens, 2009 (as <i>F. cf. japonica</i>)
61	<i>Sanggan River Valley</i>	Shanxi/Hebei	China	–	River	Lotic	0	2	Huang, 1985; Huang and Huang, 1991 (as <i>C. sangganheensis</i>), Pleistocene sediments
62	<i>Yangcheng</i>	Jiangsu	China	–	–	–	0	2	Hou et al., 1982 (as <i>C. subacuta</i>), Neogene sediments
63	<i>Chongming</i>	Jiangsu	China	0	Ricefield	Lentic	1	1	This work
64	<i>Wanggangcun</i>	Jiangsu	China	1	Channel	Lotic	1	2	This work
65	<i>Yizheng</i>	Jiangsu	China	1	Channel	Lotic	1	1	This work
66	<i>Taihu Lake</i>	Jiangsu	China	1	Lake	Lentic	0	1	This work
67	<i>Taihu Lake island</i>	Jiangsu	China	1	Pond	Lentic	0	1	This work
68	<i>Dalaba</i>	Jiangsu	China	1	Intertidal	Lentic	0	2	This work
69	<i>Duangshang</i>	Jiangsu	China	1	Intertidal	Lentic	0	2	This work
70	<i>Duangshang</i>	Jiangsu	China	1	Channel	Lotic	1	1	This work
71	<i>Yongokchon River</i>	Kangnung	S. Korea	1	River	Lotic	0	–	Lee et al., 2000 (as <i>Fabaeformiscandona</i> sp. 1)
72	<i>Chollanam Province</i>	Chollanam	S. Korea	0	Ricefield	Lotic	1	1	This work
73	<i>Upo-nup swamp</i>	Changnyeong	S. Korea	1	Wetland	Lentic	0	1	Chang et al., 2012 (as <i>F. japonica</i>)
74	<i>Daegu</i>	Gyeongsan	S. Korea	0	Lotus field	Lentic	1	1	Chang et al., 2012 (as <i>F. japonica</i>)
75	<i>Oksan-ri</i>	Gyeongju-si	S. Korea	1	Spring	Lotic	0	1	Chang et al., 2012 (as <i>F. japonica</i>)
76	<i>Marbling Brook</i>	Western Australia	Australia	0	River	Lotic	0	1	Karanovic, 2007 (as <i>F. holzkampfi</i>)
77	<i>Ashgrove Terrace</i>	Cashmere	New Zealand	–	Pond	Lentic	–	1	Chapman, 1963 (as <i>C. inexpecta</i>); Karanovic, 2007 (as <i>F. holzkampfi</i>), Dubious identification
78	<i>La Fe reservoir</i>	Antioquia	Colombia	1	Reservoir	Lentic	1	1	Torres Saldarriaga and Martínez, 2010 (as <i>Candona</i> sp. 1)

is in a wetland and an oxbow lake in Chaivo Bay, Sakhalin Island, Russia (this work).

The finding of the species in a reservoir in Colombia (La Fe Reservoir, Antioquia province) by Torres Saldarriaga and Martínez (2010), as *Candona* sp. 1, is interesting, as this type of artificially built and managed environment is one of the most common in which this species is found in Spain. In the reservoir, the species was found on a sediment substrate in shallow water, in contrast to other ostracode species found, which were commonly associated with macrophytes.

DISCUSSION

Corrected previous records of *F. subacuta* from China, Japan, Korea, Thailand, Australia, and Colombia, presented herein, greatly extend the known global distribution of this

species. The Australian (and perhaps New Zealand) and South American records are particularly significant in that they demonstrate that *F. subacuta* is not restricted to Eurasia, but is also present in the southern and western hemispheres. Additionally, new records presented herein for the Iberian Peninsula suggest that it is well established in this area.

Fabaeformiscandona subacuta has a disjunct distribution, widespread in Eastern Asia, but also found in Australia, South America, and on the Iberian Peninsula. On the Iberian Peninsula it may not be a native species, firstly because it has not been found in other European countries, either living or fossil (Griffiths, 1995; Meisch, 2000) and we didn't find it when checking many European locations where *F. holzkampfi* has been previously reported. Secondly, its widespread, but extremely disjunct global distribution in East Asia, on the Iberian Peninsula, and in Australia and

Table 2. Main limnological parameters of the locations where *F. subacuta* was found or cited in the Iberian Peninsula and in Japan. Alive = samples where living individuals were found; Dead = samples where only valves were found. Number of sites between brackets. Values are averages ± standard deviations.

Area	Status	Conductivity (mS/cm)	Dissolved oxygen (mg/l)	pH
Iberian Peninsula	Alive	1.88 ± 1.04 (10)	9.10 ± 1.91 (8)	7.90 ± 0.62 (10)
	Dead	1.94 ± 1.13 (7)	9.56 ± 3.43 (5)	8.15 ± 0.50 (7)
Japan	Alive	0.23 ± 0.07(8)	10.49 ± 5.91 (8)	8.49 ± 1.18 (8)

Colombia, suggests that it may not be native in all these regions, but has instead recently established populations outside of its area of origin. Thirdly, despite the fact that the species is present in natural environments in Asia (Chen, 1982; Smith and Janz, 2008; Zenina and Schornikov, 2008; Savatentalinton and Martens, 2009; Chang et al., 2012; this survey), its presence in natural environments in Iberia is restricted to the freshwater coastal lagoon l'Albufera de València, which is surrounded by rice fields and highly impacted by human activities. Other Iberian sites are artificial with strong human influences, e.g., rice fields and reservoirs. Fourthly, sub-fossil valves collected in recent sediments of the lagoon l'Albufera de València (Poquet et al., 2008) and living individuals collected in the 1970's in a central Iberian reservoir (Armengol, 1978) point to the presence of this species in the area for only a few decades. Other Holocene paleolimnological analyses of Spanish lakes and wetlands have not recorded this species in any older sediments (Wansard, 1997; Julià et al., 1998; Reed et al., 2001). Indeed, detailed data on the paleolimnology of the l'Albufera de València lagoon show that the species is found in sediments younger than one century (Poquet et al., 2008), but not in older sediments (Marco-Barba, 2010).

This lends support to the hypothesis that it is a recently invading, rather than a native, species on the Iberian Peninsula. Its relative widespread Eastern Asian distribution (China, Korea, Russia, Japan, and Thailand) in natural environments (lakes and rivers) may point to this region as being the origin of this species.

Presently, there are no reports of sub-recent or Pleistocene records of *F. subacuta* from Japan and Southeast Asia, but ostracode palaeolimnological studies are non-existent in both these regions, so the lack of fossil records from these areas is currently not evidence either way. In China it has been reported from Neogene and Pleistocene deposits, which is a strong additional indicator of the Asian origin of the species. Further testing of this hypothesis could come from a phylogeographic analysis of extant populations of *F. subacuta* using genetic markers, which should help determine whether Iberian (and also Colombian and Australian) populations have recently arrived in the area, (and are consequently suffering a founder effect) or they consist of relict populations from a wider past world distribution. In this way, low genetic variability would be expected if the Spanish populations were recent colonizers through one single invasion event (Sakai et al., 2007). If this was the case, further phylogeographic comparisons between Spanish and Asian populations could help determine more accurately the most likely area of origin, as has been shown with other aquatic invasive invertebrates, e.g., Kelly et al. (2006).

Exotic aquatic invertebrates can colonize new locations far away from their native ranges by different methods. Some of the most well-known invader species have been transported to their new habitats via ships' ballast water; this seems to be the case of the zebra mussel *Dreissena polymorpha*, e.g., Johnson and Padilla (1996), and, as proposed by Costa Fernandes and Leal Neto (2006), the golden mussel *Limnoperna fortunei* (Dunker, 1856). Besides ballast water, other types of in-ship transport have been recognised for many years as being important vectors of

dispersal (Myers, 1934), nowadays intensified by additional factors, such as the transportation of cargo that can harbour stagnant water. For example, shipments of car tires (Kling et al., 2007) and ornamental plants (Madon et al., 2002; Scholte et al., 2008) have been recognised as important ways for mosquito species to be transported to new locations. Some authors also hypothesise about the potential of seed-trading (especially rice seeds) as one of the main causes of long-distance ostracode dispersal (McKenzie and Moroni, 1986), although this mechanism needs to be verified with specific experimental tests.

Freshwater aquaculture has also been recognised as the cause of some worldwide invasions, such as the molluscs *Pomacea canaliculata* (Lamarck, 1822) and *Corbicula fluminea* (Müller, 1774) (Karatayev et al., 2007), and the crustaceans *Pacifastacus leniusculus* (Dana, 1852) and *Procambarus clarkii* (Holdich, 2002; Geiger et al., 2005). Non-native fish introductions, also abundant on the Iberian Peninsula (Elvira, 1995), can include small invertebrates living in the same water that is needed for their transportation. One example is the translocation of the cyclopoid copepod *Macrocyclops albidus* (Jurine, 1820). Based on haplotype studies, Karanovic and Krajicek (2012) suggested that this species was inadvertently introduced to Western Australia (the Margaret River) along with trout from North America and Europe.

Birds have been considered as efficient dispersal agents of aquatic invertebrates, including ostracods, because of propagule transport, both as mud adhered to their legs and in their feces (Figuerola and Green, 2002; Frisch et al., 2007). Long-distance dispersal by birds, as a result of the ability of some species to fly thousands of kilometres (Newton, 2008), can explain some disjunct distributions, like the presence of the ostracode *Potamocypis humilis* (Sars, 1924) in Britain, most probably originating from South African populations, as discussed by Horne and Smith (2004).

Once arrived and established, the first populations of introduced species need to spread to surrounding areas to be considered invasive. Explanations of local to mid-range dispersal mechanisms responsible need to be reviewed. Although aquatic invertebrate dispersal research has focused on non-human vectors, i.e. wind, amphibians, water birds (Bilton et al., 2001; Cáceres and Soluk, 2002; Figuerola and Green, 2002; Green et al., 2002, 2008) or even large mammals (Vanschoenwinkel et al., 2008), the human role cannot be understated (Waterkeyn et al., 2010). Dispersal can be enhanced though land management and infrastructures (Trombulak and Frissell, 2000).

Although birds can migrate long distances and be the main dispersal vector of ostracodes in some cases, it seems unlikely to be the main cause of *F. subacuta*'s presence on the Iberian Peninsula, as east-west migration routes through Eurasia are rare (Newton, 2008). We speculate that *F. subacuta* arrived on the Iberian Peninsula due to human activities, perhaps via inter-continental shipping, which has proved to be the main long-distance dispersal vector of similar freshwater species (Karatayev et al., 2007). In many areas, but especially on the Iberian Peninsula, *F. subacuta* is found in aquatic environments that are often artificially inter-connected and strongly impacted by human activities.

In particular, both reservoirs and rice fields and their associated channels are artificial habitats strongly impacted by intense human activities, and accidental or intentional faunal introductions can occur in such habitats. Ostracodes can easily spread downstream in rivers, and they are also able to colonize upstream habitats by active dispersal. Nevertheless, bird, fish or human-mediated dispersal (Vinyard, 1979; Figuerola and Green, 2002; Waterkeyn et al. 2010) could be significantly faster, especially if we take into account the high impact of invasive fishes in Spanish river basins and their human-mediated translocations (Elvira and Almodóvar, 2001) for fishing or aquacultural activities. Also, rice-field management involves some activities that could introduce exotic faunas to the environment (such as seed, soil and fertilizers transport or machinery exchange between different areas) and have been considered before as a possible dispersal mechanism for exotic ostracodes in Mediterranean environments (McKenzie and Moroni, 1986; Rossi et al., 2003).

Despite the high dispersal potential of some ostracode species via birds or humans, as discussed above, cosmopolitanism is rare in freshwater ostracodes (Martens et al., 2008). A few species, such as *Heterocypris incongruens* (Ramdohr, 1808) and *Cypridopsis vidua* (Müller, 1776), have a global distribution and inhabit both natural and artificial environments, and some other species that show inter-continental widespread distribution are commonly found in rice fields (McKenzie and Moroni, 1986; Baltanás 1992). In a recent review of non-indigenous invertebrate species naturalized in Iberian inland waters, eight out of the 45 listed species (18%) were ostracods (García-Berthou et al., 2007, based on Baltanás, 1992 and Baltanás et al., 1996), and most of these were found in rice fields.

Fabaeformiscandona subacuta is still a poorly known ostracode; its ecology remains largely unknown, and its known pattern of distribution is probably constrained by the scarce data available. A more thorough sampling effort is required in order to obtain more environmental data of the localities where it could be found. Also, a future re-sampling of Iberian sites where it has been found should be performed, as it is crucial to determine if the species is well established in those habitats or if it has colonized some sites for only a short period without establishing successful longer-term populations. Further analysis of other Mediterranean countries with suitable habitats (rice fields, reservoirs, etc.), such as Italy, southern France, and Greece, is also needed in order to determine if European populations are restricted to the Iberian Peninsula or the species is present in other areas around the Mediterranean Sea. As a conclusion, with the presently available data, we hypothesize that *F. subacuta* is an invasive species on the Iberian Peninsula, an assumption that could be tested with further research on its distribution, palaeolimnology, and phylogeography.

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