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Xyela fusca spec. nov. from Japan elucidates East Asian–North American relationships of *Xyela* (Hymenoptera, Xyelidae)

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Abstract

Morphological and genetic data indicate that *Xyela fusca* Blank, Kramp & Shinohara spec. nov. from Shikoku, Japan, plus an undescribed species from China are closely related to the Nearctic *X. bakeri* Konow, 1898. These species form the *X. bakeri* group, which is considered to be the sister clade of the Eurasian *X. julii* group. In addition to the *X. alpigena* group, the *X. bakeri* group is the second species group of *Xyela* with representatives occurring in both the Old and the New World. While *X. bakeri* is associated with *Pinus* (*Pinus*) species as the larval hosts, collection data of imagines suggest *P.* (*Strobus*) *parviflora* for *X. fusca*. This appears to be the second case, in which closely related *Xyela* species have switched hosts between species belonging to different subgenera of *Pinus*. Based on distribution data, migration of the common ancestor across Beringia appears likely, which would also have involved the change of the host subgenus. The six species of *Xyela* of Japan are keyed and new distribution data are presented. New, most northwesterly records of imagines from Yukon Territory (Canada) and field observations in Colorado and California (USA) suggest *P. contorta* as an additional larval host of *X. bakeri*.

Key words: Amphi-North Pacific disjunct distribution, biogeography, Beringia, COI barcoding, identification key, larval host plant, *Pinus*, *Strobus*

Introduction

Xyela Dalman, 1819 is the most diverse genus of Xyelidae, comprising 49 extant world species, including six recorded from Japan now (Taeger *et al.* 2010; Blank *et al.* 2013; this work). *Xyela* species are distributed in the northern Hemisphere and are coexistent with *Pinus* species (Pinaceae), which serve as the larval hosts. Females of most *Xyela* lay eggs into young staminate cones of pines with their elongate ovipositor. The larvae feed inside the growing cones on the sporophylls before the cones dry and open to release the pollen. The blooming phenology of the host and the short availability of the food source for development from eggs to mature larvae may have been a driving force for the close adaptation of *Xyela* species to particular pine species. Old World species have generally proven to be monophagous (Blank 2002; Blank *et al.* 2013). Burdick (1961) stated oligophagy for *X. bakeri* Konow, 1898, *X. minor* Norton, 1869 and *X. pini* Rohwer, 1913, but more species appear to be involved, which possibly are associated with a lower number of hosts (Blank, unpublished data). Only the Nearctic *X. gallicaulis* D.R. Smith, 1970, which causes galls in pine shoots in which the larvae feed, appears to be definitely oligophagous (Smith 1970; Yates & Smith 2009).

Imagines of *Xyela* sometimes occur in vast numbers when they swarm or run around flowers with easily accessible anthers, such as willows, oak, birch or alder (Benson 1935; Blank 2002). *Xyela* imagines usually are shorter than 5 mm (excluding the protruding ovipositor) and represent smallest forms among extant Xyelidae.

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Morphologically, they share the characteristic, long and thick synantennomere 3 with other Xyelidae, but their antennal filament is usually longer than synantennomere 3. The extant *Xyela* species are placed in the subgenus *Xyela*, in which subcosta (Sc) and radius (R) abut without interspace (Blank *et al.* 2013, fig. 4; Fig. 3B), except for the 'living fossil' *X.* (*Pinicolites*) *lata* D.R. Smith, 1990 from the western United States, in which a narrow cell is present between these veins and which has a comparatively short antennal filament (Smith 1990; Rasnitsyn 1997: figs 2–3).

Classification and identification of *Xyela* species are considerably hampered by small size of the imagines, paucity and variability of taxonomic characters, and general similarity of the species below the level of species groups. Rohwer (1910) described the first two species from Japan, *X. japonica* and *X. variegata*, from Hakone, Honshu. Keys to Japanese species were given by Takeuchi (1938), Togashi (1964) and Okutani (1982). The Japanese species were also considered in keys for the Eurasian species (Gussakovskij 1935; Blank *et al.* 2013) or the species of the World (Rasnitsyn 1965). Blank *et al.* (2005) treated the species associated with Japanese red pine, *Pinus densiflora*. Taxonomic difficulties were caused by Takeuchi (1938) and Benson (1961, 1962), who applied a very wide species concept and erroneously synonymized the East Palaearctic *X. japonica*, *X. kamtshatica* Gussakovskij, 1935 and *X. variegata* with *X. obscura* (Strobl, 1895), *X. alpigena* (Strobl, 1895) and *X. julii* (Brébisson, 1818) respectively. Actually, the latter three species are restricted to Europe or, in the case of *X. julii*, are distributed from Europe at most to the Baikal region and northern central Mongolia in the East (Blank *et al.* 2013).

Here, we provide an identification key for all *Xyela* species distributed in Japan. The most recent keys were written under a wider geographical scope (Blank *et al.* 2005, 2013). The key presented below is easier to use, because a number of similar species from outside Japan have been omitted. *Xyela japonica*, *X. kamtshatica*, *X. pumilae* Blank & Shinohara, 2013, *X. tecta* Blank & Shinohara, 2005 and *X. variegata* have already been treated in detail (Blank *et al.* 2005, 2013). Here, we include new faunistic data for those species where available. *Xyela fusca* spec. nov., described from Shikoku, provides an insight into zoogeographic relations of Eurasian and Nearctic taxa and into the evolution of larval host associations of *Xyela*.

Material and methods

Terminology and measurement. Morphological terminology generally follows Huber & Sharkey (1993) and Viitasaari (2002); surface microstructure is described following Harris (1979). The elongate and widened third antennal article, which is the ontogenetic product of the fusion of a variable number of articles, is called synantennomere 3 (Blank 2002). The combination of thinner articles following distally, is the antennal filament. Acronyms used for wing veins are explained in Figs 3A–3B, terminology of the female genitalia in Figs 3D–3F, and terminology of the penis valve in Figs 1I–1K. POL (postocellar line) denotes the shortest distance between medial edges of posterior ocelli, OOL (ocellus-ocular line) the shortest distance between lateral edge of posterior ocellus and edge of neighboring eye. POL and OOL are each taken in vertical view on measured line. Measurement of body parts has been described in detail by Blank *et al.* (2013).

The term 'monophagy' is applied in a narrow sense to species feeding on a single host species, which corresponds to '1st grade monophagy' as described by Viitasaari (2002). Species found associated with two or more host species, even although these belong to the same plant genus, are classified as oligophagous ('2nd or 3rd grade monophagy' of Viitasaari 2002).

Imaging. Digital images of the specimens were taken with a Leica DFC450C camera attached to a Leica M205 C stereomicroscope. Lighting was from a high diffuse dome illumination Leica LED5000 HDI. A grey card was used as the background and for white balance. Composite images with an extended depth of field were created using the software CombineZP (Hadley 2010). The images were processed with PhotoImpact (Ulead Systems Inc.) and assembled with CorelDraw (Corel Co.). Figures 1A–1C, 1E–1K and 2 were reproduced from Blank *et al.* (2013).

Scanning electron microscopic (SEM) investigation of two specimens of *Xyela fusca* (DEI-GISHym 5219, 5231) was performed without coating the specimens. Photos were taken with a JSM-6060LV (Jeol) microscope at 1.9–2.1 kV acceleration voltage.

Barcoding. Representatives of as many species groups of *Xyela* as possible were included in the barcoding analysis to provide genetic evidence for the placement of *X. fusca* (Table 1). Since Rasnitsyn (1965), a number of new species have been described, that do not fit smoothly into his classification, i.e., *X. gallicaulis*, *X. lata*, *X. meridionalis* Shinohara, 1983, and *X. rasnitsyni* Blank & Shinohara, 2013 (see, e.g., Rasnitsyn 1997; Blank *et al.* 2013), but COI sequences are as of yet not available for these species. The provisional names *X.* '016 China *bakeri* group', *X.* '021 USA *minor* group', *X.* '023 USA *minor* group' and *X.* '024 USA *minor* group' (Fig. 4 and Tab. 1) refer to still undescribed species, which have been identified to species-group level. For the analysis, *Macroxyela ferruginea* (Say, 1824) (GenBank accession numbers EF032211.1, KF936523.1), and two species each of *Megaxyela* Ashmead, 1898 and *Pleroneura* Konow, 1897 have been included as outgroup taxa.

Table 1 summarizes the specimens, which have been analyzed genetically. For the specimens with reference "Schmidt *et al.* (2016)", a single leg of an imago or a section from the larval trunk was submitted to the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Canada, where DNA extraction and sequencing was performed. See Schmidt *et al.* (2016) for details.

From specimens with the references "Blank *et al.* (2017)" and "this work" in Table 1, total genomic DNA was extracted from one or two legs, or from the genital capsule of a male (without mechanical disruption) using the E.Z.N.A. Tissue DNA Kit (Omega Bio-tek Inc., Norcross, USA) according to the manufacturer's protocol for tissue DNA, except some smaller modifications. Lysis time was at least 3 hours for the legs (including 850 rpm shaking) and 4 hours for the genital capsules (without shaking). Elution was performed twice with 100 µl Elution Buffer each. A partial fragment (658 bp) of the mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified by PCR using new designed barcoding primers SymF2 (5'-TTTCAACAAATCATAAARAYATTGG-3') and SymR2 (5'-TAAACTTCTGGRTGTCCAAARAATCA) (Prous *et al.* 2016). If the amplification of the 658 bp fragment failed, or was expected to fail because of low DNA quality, the region was amplified in two overlapping fragments with additional primers sym-C1-J1718 (5'-GGAGGATTTGGAAAYTGAYTAGTWCC-3') (Nyman *et al.* 2006) and C1-N1760 (5'-GGTARAAATCARAATCTTATATTAT-3') (Prous *et al.* 2011). Amplifications were performed in 15 µl reactions containing 7.5 µl of 2x Qiagen Multiplex PCR Master Mix (Qiagen, Hilden, Germany), 0.2 µM of each primer, RNase-free water and template DNA (2–3 µl). Amplification conditions were as follows: initial denaturation step at 95 °C 5 min, 38 cycles of 30 s denaturing at 95 °C, 90 s annealing at 47 °C, 1 min extension at 72 °C, followed by a final extension of 30 min at 68 °C. PCR products were purified with Exonuclease I and FastAP Thermosensitive Alkaline Phosphatase (Life Technologies, Darmstadt, Germany) and sequenced on an ABI3730XL sequencer using Big Dye v. 3.1 Terminator Kit (Thermo Fisher Scientific, Darmstadt, Germany). Sequencing was performed with the primers used for amplification. Sequences were checked, manually edited using Geneious 9.1.6 (Kearse *et al.* 2012) and aligned using BioEdit 7.2.5 (Hall 1999). All sequences have been deposited in GenBank, and the individual accession numbers are listed in Table 1. Processing included five specimens of *Xyela fusca* collected in 1981 (DEI-GISHym 5222, 5227, 30909–30911) but we finally succeeded in obtaining only a 270 bp section of the COI gene for just one specimen (5222).

A phylogenetic tree was calculated using Maximum Likelihood in MEGA7 (Kumar *et al.* 2016). The best fitting model for the analysis, the General Time Reversible model (Nei & Kumar 2000) including a discrete Gamma distribution and invariable sites (GTR+G+I), was obtained by jModelTest 2.1.7 (Darriba *et al.* 2012). The ML analysis included 1000 bootstrap replications using all sites. Bootstrap values > 50 % are shown on the ML tree next to the nodes concerned (Fig. 4). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 66 nucleotide sequences. The total of 658 positions in the final dataset was used, including 307 variable and 264 parsimony-informative positions. The number of base differences per site (p-distance) between sequences was calculated. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair.

Collection abbreviations

CNC	Canadian National Collection, Ottawa, Canada (H. Goulet)
EUMJ	Ehime University, Matsuyama, Japan (K. Konishi)
NSMT	National Museum of Nature and Science, Tsukuba, Japan
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC, USA (D.R. Smith)
YNUC	Yeungnam University, Gyeongsan, South Korea (J.-W. Lee)

TABLE 1. COI sequences of *Macroxyela*, *Megaxyela*, *Pleroneura* and *Xyela* species analyzed in this work, with classification into species groups (for *Xyela* only), unique specimen identifyer (DEI-GISHym number), deposition of voucher (coll.), length of COI-5P sequence (bp) used in ML analysis, GenBank accession number, and reference for origin of sequence. *Xyela* '016 China *bakeri* group', *Xyela* '021 USA *minor* group', *Xyela* '023 USA *minor* group' and *Xyela* '024 USA *minor* group' are provisional names referring to unidentified species classified at species group level.

Xyelidae species	DEI-GISHym	coll.	bp	GenBank	reference
Macroxyela ferruginea (Say, 1824)			658	EF032211	GenBank
Macroxyela ferruginea (Say, 1824)			658	KF936523	GenBank
Megaxyela sp. 1	18504	NSMT	658	KC974499	Schmidt *et al.* (2016), Blank *et al.* (2017)
Megaxyela sp. 2	5751	NSMT	658	KF642802	Schmidt *et al.* (2016), Blank *et al.* (2017)
Megaxyela sp. 2	5752	NSMT	658	KF642873	Schmidt *et al.* (2016), Blank *et al.* (2017)
Pleroneura coniferarum (Hartig, 1837)	15506	SDEI	658	KC977132	Schmidt *et al.* (2016)
Pleroneura piceae Shinohara & Hara, 1995	22525	SDEI	658	KY198303	this work
***Xyela alpigena* group**					
Xyela alpigena (Strobl, 1895)	4781	SDEI	627	KC976924	Schmidt *et al.* (2016)
Xyela alpigena (Strobl, 1895)	15513	SDEI	658	KC974065	Schmidt *et al.* (2016)
Xyela alpigena (Strobl, 1895)	15514	SDEI	658	KC973034	Schmidt *et al.* (2016)
Xyela alpigena (Strobl, 1895)	15655	SDEI	658	KC974218	Schmidt *et al.* (2016)
***Xyela bakeri* group**					
Xyela bakeri Konow, 1898	5244	SDEI	658	KY198304	this work
Xyela bakeri Konow, 1898	5245	SDEI	658	KY198305	this work
Xyela bakeri Konow, 1898	15670	SDEI	658	KC973150	Schmidt *et al.* (2016)
Xyela bakeri Konow, 1898	15671	SDEI	658	KC977110	Schmidt *et al.* (2016)
Xyela bakeri Konow, 1898	15672	SDEI	658	KC973190	Schmidt *et al.* (2016)
Xyela bakeri Konow, 1898	15673	SDEI	658	KC975784	Schmidt *et al.* (2016)
Xyela bakeri Konow, 1898	15679	SDEI	658	KC976771	Schmidt *et al.* (2016)
Xyela bakeri Konow, 1898	15680	SDEI	658	KC976118	Schmidt *et al.* (2016)
Xyela bakeri Konow, 1898	15681	SDEI	658	KC976761	Schmidt *et al.* (2016)
Xyela bakeri Konow, 1898	15682	SDEI	658	KC973419	Schmidt *et al.* (2016)
Xyela bakeri Konow, 1898	15683	SDEI	658	KC975576	Schmidt *et al.* (2016)
Xyela bakeri Konow, 1898	22206	SDEI	658	KY198306	this work
Xyela bakeri Konow, 1898	22208	SDEI	658	KY198307	this work
Xyela bakeri Konow, 1898	22212	SDEI	658	KY198308	this work
Xyela bakeri Konow, 1898	22214	SDEI	658	KY198309	this work
Xyela bakeri Konow, 1898	22219	SDEI	658	KY198310	this work
Xyela bakeri Konow, 1898	22224	SDEI	658	KY198311	this work
Xyela fusca spec. nov.	5222	EUMJ	270	KY198317	this work
Xyela '016 China *bakeri* group'	5749	NSMT	658	KY198327	this work
Xyela '016 China *bakeri* group'	5750	NSMT	658	KY198328	this work
Xyela '016 China *bakeri* group'	22527	NSMT	658	KY198329	this work
***Xyela brunneiceps* group**					
Xyela brunneiceps Rohwer, 1913	22185	SDEI	658	KY198312	this work

......continued on the next page

TABLE 1. (Continued)

Xyelidae species	DEI-GISHym	coll.	bp	GenBank	reference
***Xyela concava* group**					
Xyela concava Burdick, 1961	5270	SDEI	658	KY198313	this work
Xyela concava Burdick, 1961	5271	SDEI	658	KY198314	this work
***Xyela curva* group**					
Xyela curva Benson, 1938	4782	SDEI	658	JF864121	Schmidt *et al.* (2016)
Xyela curva Benson, 1938	15517	SDEI	658	KC976045	Schmidt *et al.* (2016)
Xyela curva Benson, 1938	15563	SDEI	658	KC974813	Schmidt *et al.* (2016)
Xyela occidentalis Blank & Shinohara, 2005	22306	YNUC	658	KY198326	this work
***Xyela deserti* group**					
Xyela deserti Burdick, 1961	5280	SDEI	658	KY198315	this work
Xyela deserti Burdick, 1961	5281	SDEI	658	KY198316	this work
***Xyela julii* group**					
Xyela graeca J.P.E.F. Stein, 1876	15555	SDEI	658	KC977053	Schmidt *et al.* (2016)
Xyela graeca J.P.E.F. Stein, 1876	15630	SDEI	658	KC975478	Schmidt *et al.* (2016)
Xyela graeca J.P.E.F. Stein, 1876	15636	SDEI	658	KC973519	Schmidt *et al.* (2016)
Xyela julii (Brébisson, 1818)	15504	SDEI	658	KC976112	Schmidt *et al.* (2016)
Xyela julii (Brébisson, 1818)	15510	SDEI	658	KC972746	Schmidt *et al.* (2016)
Xyela julii (Brébisson, 1818)	15511	SDEI	658	KC976641	Schmidt *et al.* (2016)
Xyela julii (Brébisson, 1818)	15524	SDEI	658	KC976096	Schmidt *et al.* (2016)
Xyela julii (Brébisson, 1818)	15562	SDEI	658	KC976309	Schmidt *et al.* (2016)
Xyela julii (Brébisson, 1818)	15641	SDEI	658	KC972985	Schmidt *et al.* (2016)
Xyela menelaus Benson, 1960	15552	SDEI	658	KC974686	Schmidt *et al.* (2016)
Xyela menelaus Benson, 1960	15558	SDEI	658	KC975395	Schmidt *et al.* (2016)
Xyela menelaus Benson, 1960	15629	SDEI	658	KC973121	Schmidt *et al.* (2016)
Xyela menelaus Benson, 1960	15637	SDEI	658	KC974375	Schmidt *et al.* (2016)
Xyela obscura (Strobl, 1895)	15515	SDEI	658	KC977073	Schmidt *et al.* (2016)
Xyela obscura (Strobl, 1895)	15516	SDEI	658	KC976669	Schmidt *et al.* (2016)
Xyela obscura (Strobl, 1895)	18741	SDEI	658	KC973270	Schmidt *et al.* (2016)
***Xyela linsleyi* group**					
Xyela linsleyi Burdick, 1961	5292	SDEI	658	KY198318	this work
Xyela linsleyi Burdick, 1961	5293	SDEI	658	KY198319	this work
***Xyela longula* group**					
Xyela longula Dalman, 1819	15657	SDEI	658	KC974742	Schmidt *et al.* (2016)
***Xyela lugdunensis* group**					
Xyela lugdunensis (Berland, 1943)	5698	SDEI	658	KF642682	Schmidt *et al.* (2016)
***Xyela minor* group**					
Xyela '021 USA *minor* group'	5305	SDEI	658	KY198320	this work
Xyela '021 USA *minor* group'	5306	SDEI	658	KY198321	this work
Xyela '023 USA *minor* group'	5322	SDEI	658	KY198322	this work
Xyela '023 USA *minor* group'	5324	SDEI	658	KY198323	this work
Xyela '024 USA *minor* group'	5329	SDEI	658	KY198324	this work
Xyela '024 USA *minor* group'	5331	SDEI	658	KY198325	this work

Results

Key to species

At genus level, *Xyela* can be identified, e.g., with the keys of Goulet (1992) and Blank (2002).

1 (a) Female 2
- (aa) Male (unknown for *X. fusca*) 7

2(1) (a) Head capsule black (brown in faded specimens) (Figs 2A, 3C), sometimes with brown spots, without yellow 3
- (aa) Head capsule yellow with brown or black pattern (Figs 2C, 2E–2F, 2I–2J) 4

3(2) (a) Ovipositor sheath straight along ventral edge (Figs 1D, 3B, 3D), 1.00–1.20 mm long, fore wing 2.80–3.10 times as long as ovipositor sheath.
- (b) Valvula 3 1.40–1.60 times as long as valvifer 2 (Figs 1D, 3D), 4.2–4.7 times as long as wide at base.
Shikoku. Larval host: supposedly *Pinus parviflora* . . . . *Xyela fusca* Blank, Kramp & Shinohara, spec. nov. ♀
- (aa) Ovipositor sheath curved ventrad (Fig. 1E), 1.65–1.90 mm long, fore wing 2.25–2.50 times as long as ovipositor sheath.
(bb) Valvula 3 1.60–1.75 times as long as valvifer 2 (Fig. 1E), 5.5–7.0 times as long as wide at base.
Honshu, Shikoku. Larval host: supposedly *Pinus densiflora*. . . . . *Xyela japonica* Rohwer, 1910 ♀

4(2) (a) Valvula 3 wedge-shaped in lateral view (Fig. 1F), dorsal and ventral outlines steadily tapering toward round tip, medial portion diamond-shaped in cross-section, width about equal in lateral and dorsal view.
(b) Pale membranous zone along ventral edge of valvula 3 extending to preapical region of valvula (Fig. 1F).
(c) Posterior claws with small subapical tooth.
Subalpine zone of Hokkaido and Honshu. Larval host: supposedly *Pinus pumila* . . . . *Xyela kamtshatica* Gussakovskij, 1935 ♀
- (aa) Valvula 3 of ovipositor sheath knife-shaped in lateral view (Figs 1A–1C), strongly compressed, medial part of valvula 3 in lateral view 3–4 times wider than combined width of both valvulae 3 in dorsal view, dorsal edge sloping down to round apex, ventral edge almost straight.
(bb) Pale membranous triangle at base of valvula 3 about as long on ventral edge as wide at base (Figs 1A–1C).
(cc) Posterior claws without subapical tooth. 5

5(4) (a) Stripes along supraantennal furrows black, separate from black longitudinal spot in middle of frons (Figs 2C).
(b) Wings brown infuscate.
Subalpine zone of Hokkaido. Larval host: supposedly *Pinus pumila*. . . . . *Xyela pumilae* Blank & Shinohara, 2013 ♀
- (aa) Stripes along supraantennal furrows at least partly brown, often very wide and fusing with medial longitudinal spot of frons (Figs 2E–2F, 2I–2J).
(bb) Wings subhyaline.
[Identification of ca 25 % of females of the following species remains ambiguous.] 6

6(5) (a) Fore wing (?2.30–)2.40–2.55 times as long as ovipositor sheath (Fig. 1B).
Honshu, Kyushu, Shikoku. Larval host: *Pinus densiflora* . . . . *Xyela tecta* Blank & Shinohara, 2005 ♀
- (aa) Fore wing 2.00–2.30(–?2.40) times as long as ovipositor sheath (Fig. 1C). Honshu, Shikoku. Larval host: *Pinus densiflora* . . . . *Xyela variegata* Rohwer, 1910 ♀

7(1) (a) Head capsule black (brown in faded specimens) (Fig. 2B), sometimes with brown spots, without yellow.
(b) Lateral lamella of valviceps vertical and wide (Fig. 1J).
Honshu, Shikoku. Larval host: supposedly *Pinus densiflora*. . . . . *Xyela japonica* Rohwer, 1910 ♂
- (aa) Head capsule yellow with brown or black pattern (e.g., Figs 2D, 2G–2H, 2K–2L).
(bb) Lateral lamella of valviceps *either* vertical and narrow (Fig. 1K) *or* oblique and wide (Figs 1G–1I) 8

8(7) (a) Posterior claws with small subapical tooth.
(b) Lateral lamella of valviceps vertical and narrow (Fig. 1K).
Subalpine zone of Hokkaido and Honshu. Larval host: supposedly *Pinus pumila*. *Xyela kamtshatica* Gussakovskij, 1935 ♂
- (aa) Posterior claws without subapical tooth.
(bb) Lateral lamella of valviceps wide and oblique (Figs 1G–1I). 9

9(8) (a) Stripes along supraantennal furrows black, separate from black longitudinal spot in middle of frons (Fig. 2D).
(b) Wings brown infuscate.
(c) Valviceps 1.55–1.60 times as long as width of medial lobe; medial lobe 1.15–1.20 times as wide as distal lobe (Fig. 1G).
Subalpine zone of Hokkaido. Larval host: *Pinus pumila*. . . . . *Xyela pumilae* Blank & Shinohara, 2013 ♂
- (aa) Stripes along supraantennal furrows at least partly brown, often very wide and fusing with medial longitudinal spot of frons (Figs 2G–2H, 2K–2L).

(bb) Wings subhyaline.
(cc) Valviceps 1.30–1.55 times as long as width of medial lobe, medial lobe 1.30–1.90 times as wide as distal lobe (Figs 1H–1I) 10

10(9) (a) Upper edge of proximal lobe of valviceps almost parallel to longitudinal axis of valviceps, straight or slightly concave, medial lobe small (Fig. 1H).
(b) Medial lobe of valviceps 1.30–1.50 times as wide as distal lobe, excision of lower edge 0.19–0.24 times as deep as width of medial lobe (Fig. 1H).
Honshu, Kyushu, Shikoku. Larval host: *Pinus densiflora* . . . . *Xyela tecta* Blank & Shinohara, 2005 ♂
\- (aa) Upper edge of proximal lobe of valviceps sloping down towards valvular stalk, more or less convex, medial lobe broad (Fig. 1I).
(bb) Medial lobe of valviceps 1.75–1.90 times as wide as distal lobe, excision of lower edge 0.12–0.15 times as deep as width of medial lobe (Fig. 1I).
Honshu, Shikoku. Larval host: *Pinus densiflora* . . . . *Xyela variegata* Rohwer, 1910 ♂

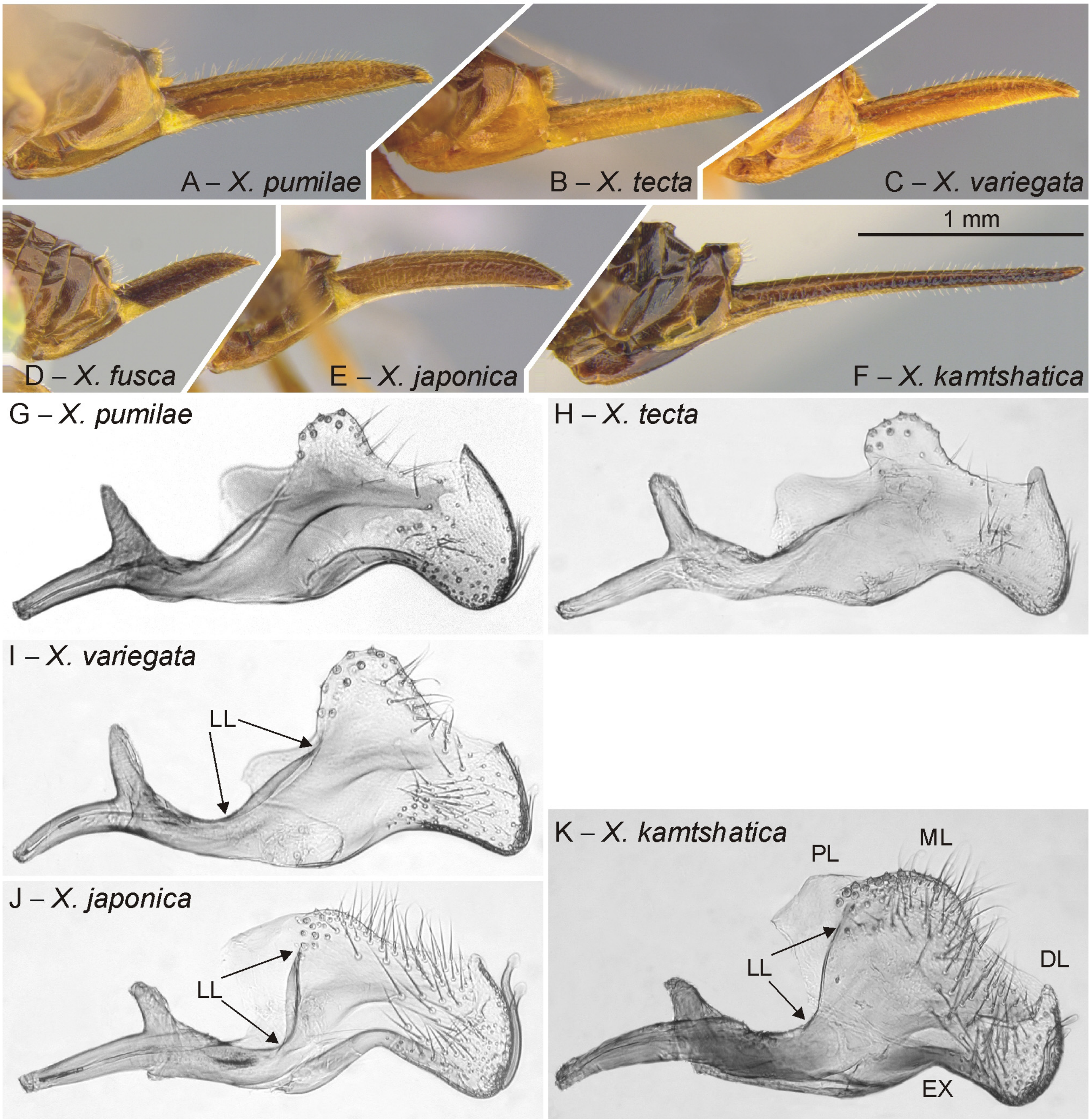

FIGURE 1. Ovipositor sheaths and penis valves of the *Xyela julii* group (*X. pumilae* [**A**, **G**], *X. tecta* [**B**, **H**], *X. variegata* [**C**, **I**]), *X. fusca* (**D**; DEI-GISHym 5231, paratype), and the *X. curva* group (*X. japonica* [**E**, **J**], *X. kamtshatica* [**F**, **K**]. The scale bar in **F** applies to **A**–**F**. Labels in **I**–**K**: EX—excision on lower edge of valviceps; DL—distal lobe of valviceps; LL—lateral lamella; ML—medial lobe; PL—proximal lobe.

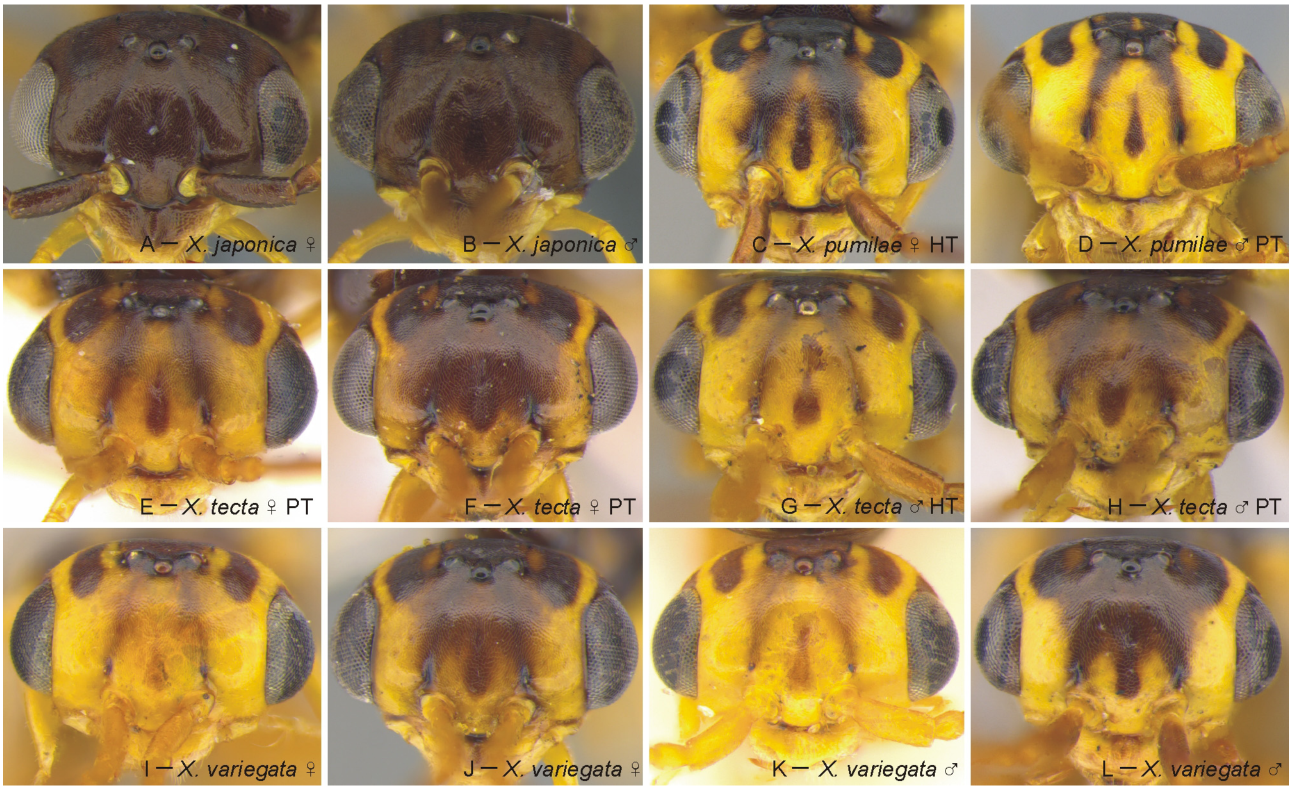

FIGURE 2. Head pattern of *Xyela japonica* (**A–B**), *X. pumilae* (**C–D**), *X. tecta* (**E–H**), *X. variegata* (**I–L**). Acronyms: HT—holotype, PT—paratype.

Species accounts

Xyela fusca Blank, Kramp & Shinohara, spec. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:3AB6F6EC-4685-4C3D-A793-4FDCE7637C93

Description. Female. Color. Head black, sometimes brown spots on vertex posterior of eye, distal edge of clypeus pale brown, labrum and mandible pale brown to white, maxillary palp pale brown (Fig. 3C). Scape, pedicel and base of synantennomere 3 brown, synantennomere 3 mostly dark brown, filament brown (Figs 3A–3B). Thorax and abdomen dorsally dark brown to black, brown ventrally, lateral parts of preapical terga, distal sterna and valvifer 2 pale brown, membranous base of valvula 3 pale brown to white, valvula 3 dark brown to black (Figs 1D, 3A–3B, 3D). Legs pale brown. Wing membrane almost hyaline, veins and pterostigma very weakly infuscated.

Morphology. Fore wing 2.9–3.7 mm long, 2.80–3.10 times as long as ovipositor sheath, vein Rs+M 110–260 µm long, 2r-m meeting vein Rs (60–)130–230 µm proximal to furcation of Rs1 and Rs2. Synantennomere 3 440–580 µm long, antennomere 4 110–140 µm long and 4.5–5.5 times as long as wide distally. Article 3 of maxillary palp 300–400 µm long, 1.35–1.60 times as long as scape and wider than synantennomere 3. OOL : POL = 1.60–1.75(–1.90) : 1. Ovipositor sheath 1.00–1.20 mm long, ventral outline straight, valvula 3 1.40–1.60 times as long as valvifer 2 and 4.2–4.7 times as long as wide at its base (Figs 1D, 3D). Valvula 3 of ovipositor compressed, pale membranous area about as long along ventral edge as basal width of valvula 3, dorsal edge of valvula 3 sloping down to narrowly rounded tip, distally with sensilla field exposed and directed caudally, bearing 3 setae (Fig. 3E). Ovipositor laterally compressed, straight (Fig. 3F). Valvula 1 with aulax terminating preapically, without preapical tooth on dorsal edge, with ca 12 oblique narrow-spaced annuli in distal half, without serrulae (Fig. 3G). Valvula 2 with smooth dorsal edge, tapering in distal 10 %, evenly sclerotized, with scattered sensilla campaniformia over most of its length, without annuli. Posterior tibia 0.65–0.85 mm long, claws with feeble subapical tooth.

Male. Unknown.

Type material. Holotype ♀: "(Shikoku) Mt. Kamegamori [33.783°N 133.200°E] Ehime Pref. 6.VI.1981 Y. Seiyama leg."; "DEI-GISHym 5219"; [red:] "Holotype *Xyela fusca* sp.n. det. S.M. Blank 2016", EUMJ. Paratypes:

37♀, same collection data, including specimens with numbers DEI-GISHym 5220–5233 and 30909–30911, EUMJ, NSMT, SDEI, USNM.

Etymology. The species name *fusca*, an adjective, was chosen to refer to the predominately infuscate head and mesonotum.

Host plant. Supposedly *Pinus parviflora* P. Siebold & Zuccarini (see Discussion).

Remarks. See Discussion for species differentiation.

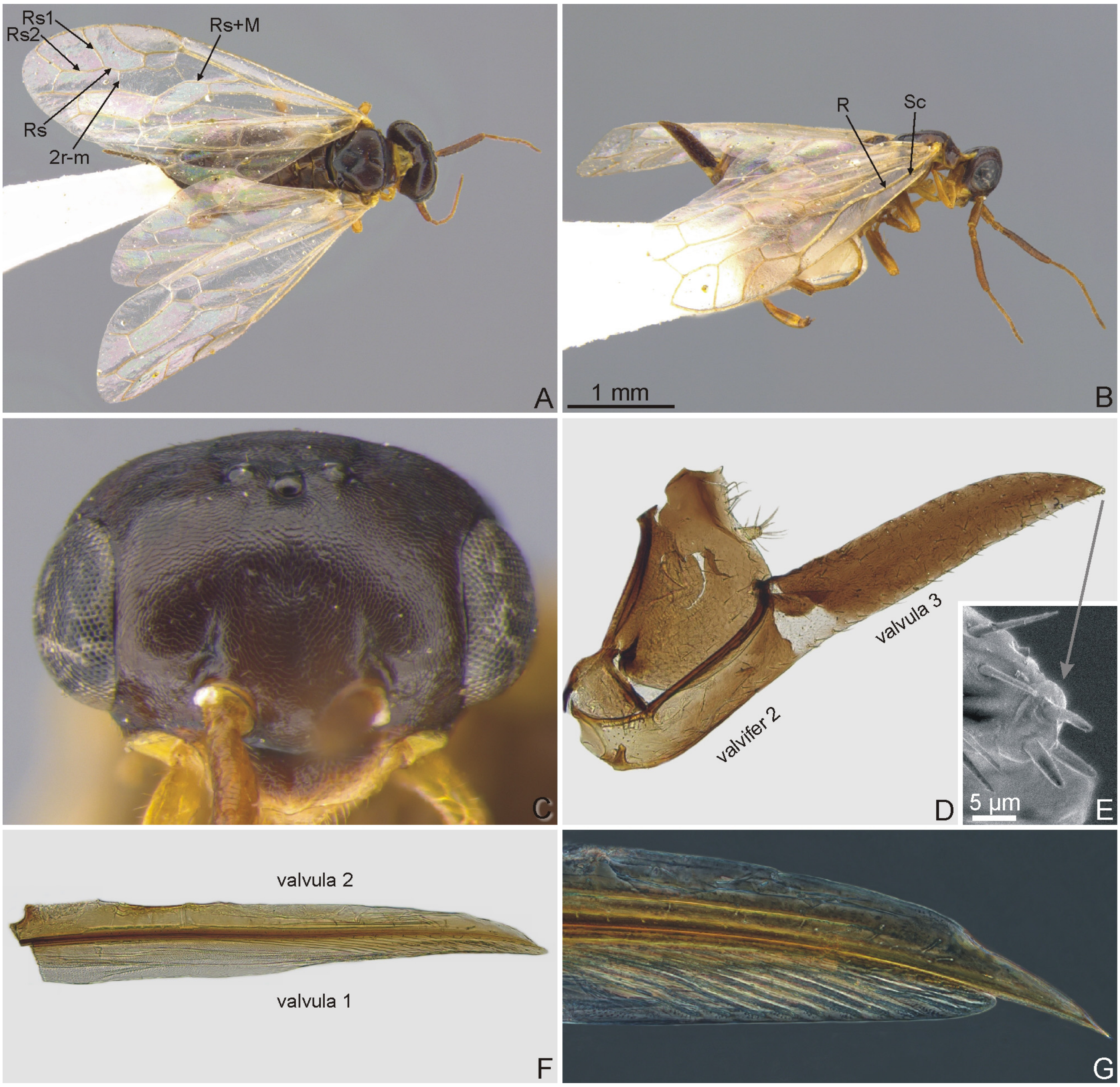

FIGURE 3. *Xyela fusca*. **A–B**) Female, dorsal and lateral views (DEI-GISHym 5219, holotype). The scale bar applies to both images **A** and **B**. **C**) Head, frontal view (5219, holotype). **D**) Ovipositor sheath, lateral (5228). **E**) Sensilla field at tip of valvula 3 (5231, SEM image of uncoated probe). **F**) Ovipositor (5222). **G**) Distal section of ovipositor (5228, phase contrast imaging).

Xyela japonica Rohwer, 1910

Xyela japonica Rohwer, 1910: 99–100, ♀, type locality: Japan, Honshu, Kanagawa Prefecture, Hakone; Takeuchi 1955: 112; Benson 1961: 171 (junior synonym of *X. obscura* (Strobl, 1895)); Blank 2002: 226–227 (removed from synonymy); Blank *et al.* 2005: 262 (identification, distribution); Yoshida, 2006: 15; Shinohara, 2013: 332; Blank *et al.* 2013: 33 (identification, distribution).

Xyela obscura: Benson 1961: 170 (senior synonym of *X. japonica*); Benson 1962: 385 (partly misidentified); Togashi, 1965: 243; Okutani, 1977: 285; Okutani 1982: 19.

Description and **type material.** Blank *et al.* (2005).

Host. Most likely *Pinus densiflora* P. Siebold & Zuccarini. The specimens from Nogutsuna Island were collected together with a series of *X. variegata*, for which *P. densiflora* is the larval host. *Xyela occidentalis*, the putatively most closely related species, is also associated with this pine species (Blank *et al.* 2005).

Distribution. Honshu (Blank *et al.* 2005; this work), Kyushu? (Takeuchi 1955), Shikoku (Okutani 1982, this work).

Records. Honshu: Ishikawa, Pref., Mt. Koshu, [136.97°E 37.38°N], 28.4.1963, 1♀, NSMT.

Shikoku: Ehime, Is[land] Nogutsuna, [33.966°N 132.691°E], 14.4.1958, leg. F. Takechi, 8♀ 2♂, EUMJ.

Remarks. Okutani (1982) gave a collection record of "*X. obscura*" from Ashizuri-misaki, Kochi Prefecture, Shikoku. The occurrence on this island is here confirmed. Takeuchi's (1955) record of *X. japonica* from Kyushu needs confirmation.

Xyela kamtshatica Gussakovskij, 1935

Xyela kamtshatica Gussakovskij, 1935: 131, 133–134, 363–364, ♀, type locality: Russia, Klyuchi, on river Kamtshatka; Takeuchi, 1938: 203 (record from Hokkaido); Togashi 1954: 12 (record from Honshu); Takeuchi, 1955: 112; Togashi 1961: 29; Benson 1961: 171 (junior synonym of *X. alpigena* (Strobl, 1895)); Rasnitsyn 1965: 503 (removed from synonymy); Okutani 1982: 19; Blank *et al.* 2013: 21 (identification, host, distribution).

Xyela alpigena: Benson 1961: 171 (senior synonym of *X. kamtshatica*); Benson 1962: 385 (partly misidentified); Togashi 1964: 51; Togashi, 1965: 243; Togashi, 1970: 7, 54; Okutani, 1977: 285.

Description and **type material.** Blank *et al.* (2013).

Host. Imagines have repeatedly been swept from *Pinus pumila* (P. Pallas) Regel (Blank *et al.* 2013; present data), but the immature stages are still unknown. Already Togashi (1964) and Okutani (1982) supposed *P. pumila* to be the host of, respectively, Japanese *X.* '*alpigena*' and *X. kamtshatica*.

Distribution. Subalpine zone of Hokkaido and Honshu (e.g., Blank *et al.* 2013; this work).

Records. Hokkaido: Daisetsuzan Mountains ["Mt. Daisetsu", 43.683°N 142.883°E], 19.7.1930, leg. Takeuchi, 1♀, NSMT; Kamishihoro-cho, south ridge of Mt. Upepesanke-yama, [43.382°N 143.099°E], 1610–1830 m altitude, 13.7.1995, leg. K. Haga, 3♀, swept from foliage *Pinus pumila*, NSMT.

Honshu: Hakusan, Kaga, Oonanjimine [a small peak on Mt. Hakusan, 36.162°N 136.766°E], 19.7.1954, leg. I. Togashi, 3♀, NSMT.

Xyela pumilae Blank & Shinohara, 2013

Xyela pumilae Blank & Shinohara in Blank *et al.* 2013: 49, ♀♂, type locality: Japan, Hokkaido, Kamikawa, Mount Piyashiri.

Description and **type material.** Blank *et al.* (2013).

Host. Imagines have repeatedly been swept from *Pinus pumila* (Blank *et al.* 2013; present data), but the immature stages are still unknown.

Distribution. Subalpine zone of Hokkaido (Blank *et al.* 2013; this work).

Records. Hokkaido: Engaru-machi, Mt Murii-dake, Tozan-one, [43.733°N 143.177°E], 1500–1876 m altitude, 3.7.2011, leg. K. Haga, 1♀, DEI-GISHym 22103, swept from *Pinus pumila* foliage, NSMT; Furano-shi, between Kumomine-yama and summit of Mt Ashibetsu-dake, [43.236°N 142.283°E], 4.7.2001 leg. K. Haga, 2♀ 3♂, swept from foliage of *Pinus pumila*, NSMT, SDEI (1♀ DEI-GISHym 22106, 1♂ DEI-GISHym 22105); Kamishihoro-cho, near summit of Mt Mikuni-yama, [43.596°N 143.147°E], 26.6.2008, leg. K. Haga, 1♀, DEI-GISHym 22104, swept from foliage of *Pinus pumila*, NSMT; Kamishihoro-cho, south ridge of Mt. Upepesanke-yama, [43.382°N 143.099°E], 1610–1830 m altitude, 13.7.1995, leg. K. Haga, 3♀, swept from foliage *Pinus pumila*, NSMT; Shimizu-cho, Mt. Memuro-dake, main peak to west peak [43.872°N 142.779°E], ca. 1700 m alt., 20.7.1999, leg. K. Haga, 1♀, swept from foliage of *Pinus pumila*, NSMT.

Remarks. The observation that two of three initially known specimens of *X. pumilae* were collected from *P. pumila* was surprising (Blank *et al.* 2013). *Xyela pumilae* is classified as belonging to the *X. julii* group, which generally has *Pinus* (*Pinus*) species as the larval hosts, while *P. pumila* is placed in *Pinus* (*Strobus*) (Eckenwalder 2009; Farjon 2010). The unusual association of *X. pumila* with *P. pumila* now seems to be corroborated by complementary collection data from five sites, where imagines were again swept from this pine species.

Xyela tecta Blank & Shinohara, 2005

Xyela tecta Blank & Shinohara in Blank *et al.* 2005: 269–271, ♀♂, type locality: Japan, Honshu, Saitama Prefecture, Akigase-koen; Blank *et al.* 2013: 52 (identification, host, distribution).

Xyela julii: Takeuchi 1938: 203–204 (partly misidentified); Takeuchi, 1955: 112; Togashi 1974: 13; Okutani, 1977: 285.

Xyela obscura: Togashi 1964: 51–52; Kondo & Miyake 1974: 100–102; Miyake & Kondo 1974: 92–95.

Description and **type material.** Blank *et al.* (2005).

Host. *Pinus densiflora* (Blank *et al.* 2005, 2013).

Distribution. Honshu (Blank *et al.* 2005), Kyushu (new record), Shikoku (new record).

Records. Kyushu: Wakasugiyama, [33.598°N 132.545°E], (Chikuzen), 10.4.1931, leg. Hiri, Fujino & Cho, 1♂, NSMT [additional 2♀ 1♂ with these collection data cannot be identified at species level since in the females the fore wing is ca 2.35 times longer than the ovipositor, and the male is missing the genital capsule].

Shikoku: Matsuyama [33.842°N 132.758°E], 21.3.1955, leg. F. Takechi, 7♀ 1♂, EUMJ; same data, 21.3.1955, 4♀, EUMJ; Ehime Prefecture, Matsuyama, Shimokarakawa Higashino ["Higashino", 33.723°N 132.736°E], 8.4.1981, leg. Y. Seiyama, 1♀, EUMJ; Nakadote near Matsuyama, Iyo, [33.807°N 132.725°E], 8.4.1953, leg. T. Yano, 3♀ 1♂, EUMJ.

Remarks. The specimens from Wakasugiyama are part of the series recorded as "*Xyela julii*" by Takeuchi (1938). The specimens collected on 21.3.1955 in Matsuyama were misidentified as *X. julii* by Togashi (1974).

Xyela variegata Rohwer, 1910

Xyela variegata Rohwer, 1910: 100, 118, ♀, type locality: Japan, Honshu, Hakone; Takeuchi 1938: 203–204 (junior synonym of *X. julii* (Brébisson, 1818)); Shinohara 2000: 295 (removed from synonymy); Naito *et al.* 2004: 6; Shinohara 2005: 229; Blank *et al.* 2005: 271 (identification, host, distribution); Yoshida 2006: 15; Shinohara 2013: 332; Blank *et al.* 2013: 54 (identification, host, distribution); Shinohara 2014: 462.

Xyela julii: Zirngiebl 1937: 348–349; Takeuchi 1938: 203–204 (senior synonym of *X. variegata*); Togashi 1964: 51–52 (misidentification?); Togashi 1974: 13; Okutani 1977: 285; Okutani 1982: 19.

Xyela obscura: Togashi 1964: 51–52; Togashi 1974: 13; Kondo & Miyake 1974: 100–102; Miyake & Kondo 1974: 92–95.

Description and **type material.** Blank *et al.* (2005).

Host. *Pinus densiflora* (Blank *et al.* 2005, 2013).

Distribution. Honshu (e.g., Blank *et al.* 2005; this work), Shikoku (new record).

Records. Honshu: Hiroshima Prefecture, Shobara, [34.857°N 133.014°E], 22.4.1981, leg. K. Maeto, 5♀, NSMT; Shimane Prefecture, Nogi-gun, Hirose town, [35.367°N 133.176°E], 10.4.1980, leg. Y. Seiyama, 1♂, EUMJ.

Shikoku: Ehime Prefecture, Matsuyama, [33.842°N 132.758°E], 21.3.1955, leg. F. Takechi, 4♀ 1♂, EUMJ; same data, 10.4.1955, 1♀, EUMJ; Ehime Prefecture, Matsuyama, Shimokarakawa Higashino ["Higashino", 33.723°N 132.736°E], 8.4.1981, leg. Y. Seiyama, 15♀ 3♂, EUMJ; Ehime Prefecture ["Iyo"], Mt. Saragamine ["Mt. Sara"], [33.721°N 132.895°E], 25.4.1953, leg. M. Miyatake, 1♀ 2♂, EUMJ; Ehime Prefecture ["Iyo"], Nakadote near Matsuyama, [33.807°N 132.725°E], 8.4.1953, leg. T. Yano, 5♀ 5♂, EUMJ; Ehime, Is[land] Nogutsuna [33.969°N 132.690°E], 14.4.1958, leg. F. Takechi, 18♀ 5♂, EUMJ;

Remarks. Specimens collected on 21.3.1955 in Matsuyama and on 14.4.1958 on Nogutsuna Island were misidentified as *Xyela julii* by Togashi (1974).

Supplementary distribution and host data for *Xyela bakeri* Konow, 1898

Records. CANADA: Yukon Territory, Watson Lake, [60.063°N 128.711°W], 28.05.1961, leg. Forest Insect Survey, 1♀ 1♂, ♀ collected from *Betula papyrifera*, CNC; Yukon Territory, Mi 780 Alaska Highway, [ca 60.199°N 132.837°W], 30.05.1961, leg. Forest Insect Survey, 1♀, CNC; Yukon Territory, Mi 901 Alaska Highway, [ca 60.815°N 135.292°W], 03.06.1961, leg. Forest Insect Survey, 1♀, CNC.

USA: California, Alpine and Tuolumne Co., Sonora Pass SW, 38.330°N 119.637°W, 2950–3050 m alt., 13.06.2007, leg. S.M. Blank, 1♀ 2♂, swept from *Salix* catkins in a stand of *P. contorta* mixed with a few *P.* (*Strobus*) *albicaulis* Engelmann, nearby *P.* (*S.*) *flexilis* E. James, SDEI, DEI-GISHym 15681–15683 (Blank *et al.* 2013); California, El Dorado Co., Placerville E 35 km, Ice House Reservoir SW 6 km, 38.797°N 120.398°W, 1600 m alt., 29.04.2013, leg. S.M. Blank, M. Hauser & C. Kutzscher, 1♀ 1♂, swept from *Salix* catkins on a pure stand of *P. ponderosa* D. Douglas ex P. Lawson & C. Lawson, SDEI, DEI-GISHym 5244–5245; Colorado, Boulder Co., Ward N, Brainard Lake Road, stop #1, 40.076°N 105.507°W, 2870 m alt., 26.05.2014, leg. S.M. Blank & C. Kutzscher, 1♀, swept from *P. contorta*, SDEI, DEI-GISHym 22224; Colorado, Larimer Co., Boulder W 7 km, Boulder Canyon Drive, stop #1, 40.006°N 105.338°W, 1830 m alt., 05.05.2014, leg. S.M. Blank & C. Kutzscher, 1♀ 1♂, swept from *Salix* catkins on a pure stand of *P. ponderosa*, SDEI, DEI-GISHym 22212–22213; Colorado, Larimer Co., Boulder WSW 15 km, Boulder Canyon Dr, stop #2, 39.990°N 105.423°W, 2300 m alt., 05.05.2014, leg. S.M. Blank & C. Kutzscher, 1♀ 1♂, swept from *Salix* catkins on a pure stand of *P. ponderosa*, SDEI, DEI-GISHym 22214–22215; Colorado, Larimer Co., Drake WNW 2 km, CR 43, 40.437°N 105.353°W, 1900 m alt., 04.05.2014, leg. S.M. Blank & C. Kutzscher, 1♀ 1♂, swept from *Salix* catkins on a pure stand of *P. ponderosa*, SDEI, DEI-GISHym 22206–22207; Colorado, Larimer Co., Glen Haven SW 3 km, Devil's Gulch Road, 40.434°N 105.463°W, 2310 m alt., 04.05.2014, leg. S.M. Blank & C. Kutzscher, 1♀ 1♂, swept from *Salix* catkins on a pure stand of *P. ponderosa*, SDEI, DEI-GISHym 22208–22209; Colorado, Teller Co., Florissant SE 5 km, Kingston Drive, 38.923°N 105.240°W, 2670 m alt., 06.05.2014, leg. S.M. Blank & C. Kutzscher, 1♀ 1♂, swept from *Salix* catkins on a pure stand of *P. ponderosa*, SDEI, DEI-GISHym 22219–22220.

See Blank *et al.* (2013) and Schmidt *et al.* (2016) for additional records from California of larvae extracted from staminate cones of *P. sabiniana* (including the specimens with DEI-GISHym 15670–15671, 15672–15673, 15679–15683).

Hosts. *Pinus contorta* (new host record), *P. ponderosa* (Burdick 1961; host record confirmed here), *P. sabiniana* (Blank *et al.* 2013).

Remarks. Burdick (1961) recorded *Xyela bakeri*, among other regions of North America, from southern Alberta and British Columbia in Canada. The additional collection data from Yukon Territory presented here are the most northwesterly for this species. The collection sites are situated close to the northern distribution limit of *Pinus contorta* (Critchfield & Little 1966).

According to Burdick (1961), *X. bakeri* "attacks many species of yellow pine", i.e., particular pine species classified as *Pinus* (*Pinus*). Our present understanding also is that *Xyela bakeri* is an oligophagous species, in contrast to most other *Xyela* species (Burdick 1961; Blank *et al.* 2013). Burdick (1961) listed several hosts also for *X. minor* Norton, 1869 and *X. pini* Rohwer, 1913, but these species require taxonomic scrutiny since more than two species appear to be involved (Blank, unpublished data). At least three pine species are hosts of *X. bakeri*, all of which belong to the section *Pinus* (*Pinus* [*Trifoliae*]) (Eckenwalder 2009; Farjon 2010). Although Burdick did not refer to *P. contorta* as a host by name, he included the range of this pine species in his map of the "expected distribution of *X. bakeri*" (Burdick 1961, map 1). The collection records listed above provide evidence, through geographic coincidence and by personal observation, that *P. contorta* is indeed a larval host in western North America. In the Yukon Territory, where four *X. bakeri* imagines were collected, *P. contorta* is the only native pine species (Critchfield & Little 1966; Mirov 1967). A female from Colorado (DEI-GISHym 22224) was swept directly from *P. contorta.* At the time of its collection, staminate cones of *P. contorta* were suitable for oviposition at this site. Two additional pine species were growing on this spot, which can be excluded as larval hosts: *P. flexilis* had too small, insufficiently developed cones, and the cones of *P. ponderosa* were already too close to blooming. Furthermore, three specimens from the Sonora Pass in California (DEI-GISHym 15681–15683) were collected next to a stand of *P. contorta* with well-developed staminate cones. At six collection sites in California and Colorado, imagines of *X. bakeri* were swept from *Salix* catkins in pure stands of *P. ponderosa* (DEI-GISHym 5244–5245, 22206–22209, 22212–22215, 22219–22220). Five larvae were extracted from cones of *P. sabiniana* in California

(DEI-GISHym 15670–15673, 15679; provisionally named *Xyela* ‘005 *P. sabiniana* sp.’ by Blank *et al.* 2013 and Schmidt *et al.* 2016). In the cladistic analysis, the COI sequences of all the adults and larvae, which were found associated with three different pine species, fall into a common tight clade indicating a single *Xyela* species (Fig. 4).

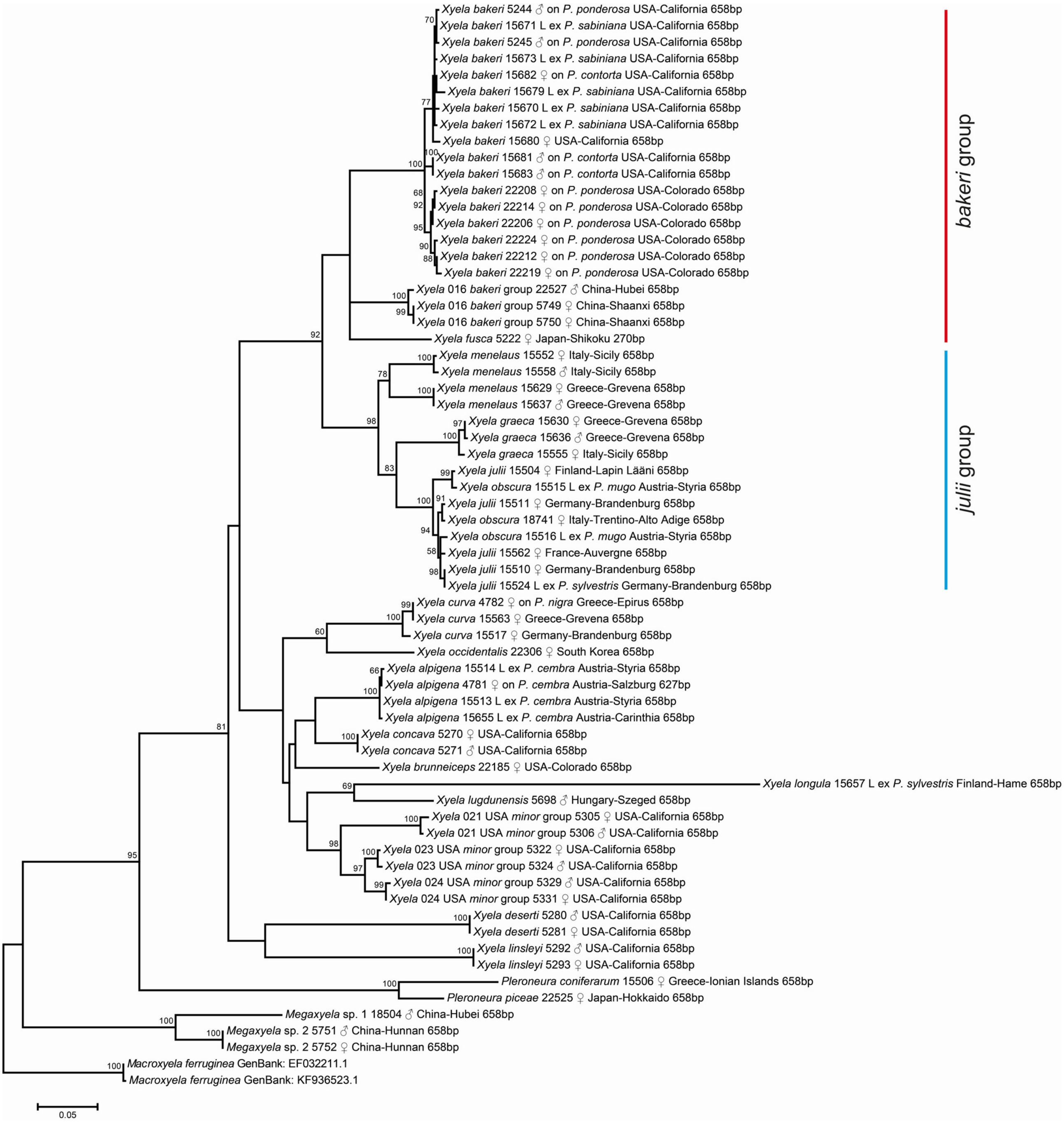

FIGURE 4. Phylogenetic hypothesis for 19 species of *Xyela* and, as outgroup taxa, five species of *Macroxyela*, *Megaxyela* and *Pleroneura* based on a maximum likelihood analysis of the barcoding section of COI. Values above branches represent maximum likelihood bootstrap clade frequencies. Each specimen is labelled as follows: “*Xyela* ...”—species name (*Xyela* ‘016 China *bakeri* group’, *Xyela* ‘021 USA *minor* group’, *Xyela* ‘023 USA *minor* group’ and *Xyela* ‘024 USA *minor* group’ are provisional names referring to unidentified species classified on species-group level); “DEI-GISHym ...”—unique specimen identifyer; “♀/♂/L”—female/male imago or larva; “ex *Pinus* …”—pine species from which larva was extracted; “USA-California …”—country and state/province of origin; “658bp/270bp”—length of sequence.

Burdick (1961) and Ebel (1966) also reported *Pinus elliottii* Engelmann, *P. palustris* P. Miller and *P. virginiana* P. Miller as larval hosts of *X. bakeri*. These host records possibly refer to different, eastern and southeastern North American species which are similar to *X. bakeri* (Blank, unpublished data).

Genetic analysis

The analysis of COI barcoding sequences included 19 *Xyela* species representing most species groups of *Xyela* (Fig. 4). Seventeen specimens identified as *X. bakeri* and three of *X.* '016 China *bakeri* group' resulted in clades supported by a bootstrap of 100 %. These two species together with a single specimen of *X. fusca* form a common, polytomous clade weakly supported by a bootstrap of only 47 %, which is here called *X. bakeri* group. Re-analysis of the data after exclusion of the only 270 bp long fragment of *X. fusca* resulted in bootstrap support of 88 % for *X. bakeri* + *X.* '016 China *bakeri* group'. *Xyela fusca* is distinguished from the other *Xyela* species by two unique sites: T at position 58 (not A) and A at position 256 (not C or T).

The *bakeri* group has the position of the sister group of the *X. julii* group supported by a bootstrap value of 92 %. Other nodes inside *Xyela* lack support except for those of the *curva* group (*curva* + *occidentalis*, 60 %), the *minor* group (*X.* '021 USA *minor* group' + (*X.* '023 USA *minor* group' + *X.* '024 USA *minor* group'), 98 %) and *X. longula* + *X. lugdunensis* (69 %). Monophyly of *Xyela* is supported by 81 %.

Discussion

Morphological discrimination and phylogenetic placement of *Xyela fusca*. Altogether, twelve species of Xyelidae occur in Japan: *Megaxyela togashii* Shinohara, 1992, *Pleroneura hikosana* Togashi, 1972, *P. itoi* Shinohara, 2016, *P. piceae* Shinohara & Hara in Shinohara, 1995, *P. subulata* Shinohara, 1995, *Xyelecia japonica* Togashi, 1972, and six species of *Xyela* (Shinohara 1992, 1995, 1998, 2016; Shinohara *et al.* 2017; Blank *et al.* 2005, 2013, 2017; this work). *Xyela fusca*, which is described here from collection material, is differentiated from the other Old World species of *Xyela* by the character combination of black head and very short, ventrally straight ovipositor. Among the Eurasian species, the head is similarly dark in *X. japonica* (from Japan) and *X. occidentalis* (from northeastern China and South Korea), and in the females of *X. heldreichii* Blank, 2013 and *X. obscura* (from Europe). The extent of brown or yellow pattern may be minimal in *X. par* Blank & Shinohara, 2005 (from South Korea) and *X. uncinatae* Blank, 2013 (from Europe). All these species have a longer ovipositor sheath than *X. fusca* (Blank *et al.* 2005, 2013). The species assigned to the *curva* group (*X. japonica*, *X. occidentalis*) are similar to *X. fusca* in the presence of a subapical tooth of the claw but disagree in the shape of the ovipositor sheath curved ventrally and the presence of a small preapical tooth on the dorsal side of valvula 1 of the ovipositor. The species associated with the *julii* group (*X. heldreichii*, *X. obscura*, *X. uncinatae*) disagree in the absence of a subapical tooth of the claw and correspond in the usually straight ovipositor and absence of a tooth on valvula 1. The *Xyela* species with the relatively shortest ovipositor sheath is *X. meridionalis*, which is restricted to Taiwan (Shinohara 1983; Blank *et al.* 2013). The head is extensively yellow in this species. The sheath is only 0.29–0.30 times as long as the fore wing (0.32–0.36 in *X. fusca*), and valvula 3 is only 0.85–0.90 times as long as valvifer 2 (1.40–1.60 in *X. fusca*) and somewhat round in cross-section in the distal 75 % of its length (compressed in *X. fusca*).

The topology obtained from the analysis of the COI barcoding sequences of 19 *Xyela* species (Fig. 4) corresponds with the assumption that the Japanese *X. fusca* and an undescribed species from China, *X.* '016 China *bakeri* group', are close to the Nearctic *X. bakeri*. The low bootstrap value of 47 % for this clade is due to the only short COI fragment (270 bp) available for *X. fusca*. But the re-analysis of 658 bp long COI sections of only *X. bakeri* and *X.* '016 China *bakeri* group' supports the monophyly of two Nearctic and East Palaearctic representatives of the *bakeri* group.

Also morphologically, *Xyela fusca* is close to the Nearctic *X. bakeri*: both share an infuscate head, a similarly short ovipositor sheath, a small subapical tooth on the claw, and the smooth dorsal side of valvula 1 lacking a preapical tooth. Additional characters of the *bakeri* group might be recognized from the penis valve, but only females of *X. fusca* are so far known. Possibly, *X. bakeri* comprises a complex of similar species, each with a more restricted host range and geographic distribution than interpreted by Burdick (1961) (Blank, unpublished data). Konow (1898) described *X. bakeri* from Colorado and Nevada. If females of *X. bakeri s.str.* from the western United States and western Canada are compared to *X. fusca*, *X. bakeri* is on average larger (fore wing 3.6–4.5 mm long in *X. bakeri* / 2.9–3.7 mm in *X. fusca*), bears an absolutely and relatively longer ovipositor sheath ([1.35–]1.50–1.90 mm / 1.00–1.20 mm; 0.38–0.44 times as long as the fore wing / 0.32–0.36), and has a wider distance between the lateral ocelli (POL : OOL = 1 : 1.15–1.45 / 1 : 1.60–1.75[–1.90]).

Rasnitsyn (1971) incorporated the *bakeri* group into the *julii* group, but we treat these sister groups as separate. The strongly protruding medial lobe of the valviceps (Blank *et al.* 2013, figs 141–152) is a unique apomorphy within *Xyela* for the *julii* group. The subapical tooth of the claw is homoplastically absent in *X. brunneiceps*, a species associated with the distantly related *alpigena* group (Blank & Kramp 2017). The very short ovipositor sheath and the black head of *X. fusca* might be regarded as derived characters present in the ancestor of the *bakeri* group, although the relative length of the sheath is a gradual character and the dark head occurs homoplastically in the *curva* group and the *julii* group. The oblique orientation of the lateral lamella of the valviceps, the comparatively low number of cone-like sensilla on the medial lobe of the valviceps and the virtual absence of the lower ergot (Burdick 1961, figs 60–61; Blank *et al.* 2013, figs 141–152) need to be reconsidered as potentially derived characters of the clade comprising *bakeri* group + *julii* group when males of *X. fusca* are found.

The potential larval host of *Xyela fusca*. The only known habitat of *Xyela fusca*, Mt. Kamegamori in Shikoku, is 1896 m high but the altitude of the collection site is not noted on the labels. According to the collector, however, the collection in June 1981 was made along the mountain trail from the car park (ca. 1650 m) to the summit (1896 m) (Seiyama, personal communication). Four pine species are native to Shikoku (Mirov 1967), but only two of them, *Pinus densiflora* and *P. parviflora*, occur on the Ishizuchi mountain range, including Mt. Kamegamori (Jinno & Yamamoto 1960). In this area, *P. densiflora* is found at lower altitudes under 1100 m (Jinno & Yamamoto 1960; Matsui, personal communication), whereas *P. parviflora* grows in higher places from 790–1700 m (Jinno & Yamamoto 1960; Sasaki 2003). Therefore, *P. parviflora* is the only likely host plant of *X. fusca*, although this host association should be confirmed by further investigation.

As opposed to the hosts of *X. bakeri s.l.*, which are all classified as *Pinus* (*Pinus*), *P. parviflora* is associated with *Pinus* (*Strobus*) (Eckenwalder 2009; Farjon 2010). After the similar case of *X. pumilae* (see Blank *et al.* 2013), *X. fusca* might represent a second instance in which a host change between *P.* (*Pinus*) and *P.* (*Strobus*) can be observed among closely related *Xyela* species.

Biogeography of the *Xyela bakeri* group. Among the species groups of *Xyela* comprising more than a single species, the *julii* and *longula* groups are restricted to Eurasia, and the *linsleyi* and *minor* groups to North America (Rasnitsyn 1965, 1971; Blank *et al.* 2013). The *alpigena* group was the only Holarctic species group so far comprising five Palaearctic and two Nearctic species. The *bakeri* group, including the Nearctic *X. bakeri*, the Japanese *X. fusca* and the Chinese *X.* '016 China *bakeri* group', now constitutes the second species group of *Xyela* with representatives in both zoogeographic realms.

Although the Eurasian fauna of *Xyela* is comparatively well known, representatives of the *bakeri* group within this realm have been found only in China (Shaanxi) and Japan (Shikoku). Thus, the migration of the common ancestor across the North Pacific landbridge Beringia appears likely – rather than across the North Atlantic De Geer or Thulean routes, which existed during the latest Cretaceous to the middle Palaeocene (Brikiatis 2014). Beringia connected North America and northern East Asia repeatedly between the Middle Triassic and the end-Pleistocene (e.g., Marincovich & Gladenkov 1999; Brikiatis 2014; Meiri *et al.* 2014).

Increases and decreases of temperature and humidity repeatedly shifted the distribution of pines northward and southward (Millar 1998). Today, pines are absent from Alaska west of 141°W (Critchfield & Little 1966; Mirov 1967). Notwithstanding, pollen and other fossil remains have been documented for Alaska and northwestern Canada since the Early Cretaceous. Among those records were *Pinus* pollen from the Early Miocene of northern Alaska, and *Pinus contorta* pollen from the pre-Pleistocene or at least the very early Pleistocene of eastern Alaska and northern Yukon (Critchfield 1985; Millar 1993, 1998). The historic presence of pines at high latitude might have provided a pathway for the dispersal of *Xyela* species across Beringia. Among xyelids, *Xyelecia japonica* Togashi, 1972 (Japan, Honshu and Shikoku) and *X. nearctica* Ross, 1932 (northwestern USA and southwestern Canada) show a similar disjunct distribution (Smith 1964; Shinohara 1998). Similar patterns have been reported for numerous animal and plant taxa, in which closely related species display an Amphi-North Pacific disjunct distribution (e.g., Kavanaugh 1986; Guo & Ricklefs 2000; Varga *et al.* 2014).

However, the spread of the ancestor of the *bakeri* group through northeastern Siberia remains ambiguous if only *Pinus* (*Pinus*) species are regarded as suitable hosts, because such pine species have not been recorded from that region. Persisting through the Pleistocene in northeastern Siberia (Kremenetski *et al.* 1998), only *Pinus* (*Strobus*) *pumila* still occurs there nowadays (Critchfield & Little 1966). If *X. fusca* actually uses *P.* (*Strobus*) *parviflora* as larval host, the migration of the ancestor across Beringia should also have involved a host shift at subgenus level.

Perspective. Seven pine species are native to Japan (Mirov 1967; Richardson & Rundel 1998; Eckenwalder 2009; Debreczy & Rácz 2011). *Xyela* species have been recorded or have been supposed only for three of these (Blank *et al.* 2005, 2013; this work): *X. tecta*, *X. variegata* and possibly *X. japonica* are associated with the Japanese red pine (*Pinus densiflora* var. *densiflora*), *X. kamtshatica* and *X. pumilae* supposedly with the dwarf stone pine (*P. pumila*), and *X. fusca* supposedly with Japanese white pine (*P. parviflora*).

No *Xyela* species have so far been reported for the four remaining Japanese pine species. *Pinus armandii* var. *amamiana* (in the islands Tanega-shima and Yaku-shima) and *P. luchuensis* (in the Ryukyu Islands) are endemic taxa with small distribution ranges in the remote South of Kyushu (Critchfield & Little 1966; Debreczy & Rácz 2011). The following two pine species are distributed in the main islands of Japan: the Japanese black pine (*P. thunbergii*) grows in Honshu, Shikoku and Kyushu predominantly along the coasts; the Korean stone pine (*P. koraiensis*) occurs in central Honshu and rarely in Shikoku at (150–)1200–2600 m a.s.l. (Critchfield & Little 1966; Mirov 1967; Debreczy & Rácz 2011). Future studies might focus on the latter two, comparatively easily accessible pine species to detect potentially undiscovered *Xyela* species in Japan.

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