



Research Article

# DNA barcoding of Japanese earwig species (Insecta, Dermaptera), with sequence diversity analyses of three species of Anisolabididae

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Academic editor: Yasen Mutafchiev

Received: 25 May 2023 | Accepted: 19 Sep 2023 | Published: 27 Sep 2023

Citation: Kamimura Y, Nishikawa M, Yamasako J (2023) DNA barcoding of Japanese earwig species (Insecta, Dermaptera), with sequence diversity analyses of three species of Anisolabididae. Biodiversity Data Journal 11: e107001. <https://doi.org/10.3897/BDJ.11.e107001>

## Abstract

Dermaptera is a polyneopteran insect order that includes more than 2,000 described species, commonly known as earwigs, that mainly inhabit tropical, subtropical and warm temperate regions. Although 40 species have been found in Japan, their distribution and habitat preferences have remained ambiguous due to sample misidentification, particularly amongst immature specimens. To overcome this problem, we sequenced and analysed the DNA barcoding region of the mitochondrial cytochrome oxidase I gene (*cox1*) of dermapteran species recorded from Japan. Including publicly available data, 72.5% of known Japanese dermapteran species were subjected to molecular identification. We extensively sampled three wingless species of subfamily Anisolabidinae (Anisolabididae): *Anisolabis maritima*, *Anisolabella marginalis* and *Euborellia pallipes*. Although these species exhibit similar habitat preferences as semi-synanthropes, *A. maritima*, a cosmopolitan species with the highest affinity to seashore, had significantly higher sequence diversity than the latter two species, which are considered endemic to East Asia. A similar trend was observed for (at least partly) winged cosmopolitan species of other families. Introgression with the congener *Anisolabis seiroides* is also suggested for *A. maritima*. Possible causes of the varying levels of sequence diversity are discussed.

## Keywords

Anisolabididae, Chelisochidae, Diplatyidae, East Asia, Forficulidae, Labiduridae, Polyneoptera, Pygidicranidae, semi-synanthropic species, Spongiphoridae, within-species sequence diversity

## Introduction

DNA barcoding, i.e. the determination of species-specific sequences of highly-variable DNA regions, is a powerful tool for species diagnosis and for discriminating closely-related species, particularly when the availability of morphological characters and/or competency of the examining researchers are limited (Hebert et al. 2003b, Armstrong and Ball 2005, Antil et al. 2023). However, its effectiveness depends on the species coverage of sequence databases. More than 2,000 species of order Dermaptera (Insecta), which are commonly known as earwigs (in English) or Hasami-mushi (in Japanese), have been reported to date (Zhang 2013, Hopkins et al. 2018). Covering environmental and climatic heterogeneity from subboreal to subtropical, 40 earwig species (i.e. ca. 2% of the worldwide species diversity) have been reported from Japan (Table 1), which represents only 0.28% of the global terrestrial area (Nishikawa 2016, Nishikawa and Naka 2019, Nishikawa 2020a, Kamimura et al. 2023). As only a few researchers study the taxonomy of this comparatively small insect order, many dermapteran samples have been misidentified by amateur scientists and non-specialised researchers, causing serious confusion and delays in evaluating the dermapteran diversity of Japan (Nishikawa 2005, Nishikawa 2013, Nishikawa 2016, Nishikawa 2020a). This is particularly true for nymphal samples, which lack many of the characteristics necessary for species diagnosis (Nishikawa 2007). For example, a nymphal dermapteran from Japan was even misidentified as an adult isopteran (Hagen 1868a, Hagen 1868b, Snyder 1916: see Kočárek and Hu (2023) for a similar confusion with Zoraptera in Taiwan).

Table 1.

List of dermapteran species recorded in Japan. Modified and updated from Nishikawa (2020a).

Family	Species	Reference	Barcoded
Diplatyidae	<i>Diplatys flavicollis</i> Shiraki, 1908		x
	<i>Paradiplatys gladiator</i> (Burr, 1905)**	Nishikawa and Naka (2019)	
Pygidicranidae	<i>Challia imamura</i> Nishikawa, 2006		x
	<i>Echinosoma akitai</i> Nishikawa, 2023	Nishikawa (2023)	

Family	Species	Reference	Barcoded
	<i>Parapsalis infernalis</i> (Burr, 1913)		x
Anisolabididae	<i>Isolabis ishigakiensis</i> Nishikawa, 2014		
	<i>Anisolabella marginalis</i> (Dohrn, 1864)		x
	<i>Anisolabella ryukyuensis</i> (Nishikawa, 1969)		x
	<i>Anisolabis boninensis</i> Nishikawa, 2013		
	<i>Anisolabis maritima</i> (Bonelli, 1832)		x
	<i>Anisolabis picea</i> Shiraki, 1906		
	<i>Anisolabis seirokui</i> Nishikawa, 2008		x
	<i>Gonolabis distincta</i> (Nishikawa, 1969)	Nishikawa (2021)	x
	<i>Gonolabis michikoeae</i> Nishikawa, 2021	Nishikawa (2021)	x
	<i>Gonolabis miyatakei</i> Nishikawa, 2021	Nishikawa (2021)	x
	<i>Euborellia annulata</i> (Fabricius, 1793)	Kamimura et al. (2023)	x*
	<i>Euborellia annulipes</i> (Lucas, 1847)		x
	<i>Euborellia pallipes</i> (Shiraki, 1906)	Kamimura et al. (2023)	x
	<i>Euborellia plebeja</i> (Dohrn, 1863)**		x*
Labiduridae	<i>Labidura riparia</i> (Pallas, 1773)		x
	<i>Nala lividipes</i> (Dufour, 1828)		x*
Spongiphoridae	<i>Chaetospania hexagonalis</i> Nishikawa, 2006		x
	<i>Labia minor</i> (Linnaeus, 1758)		x

Family	Species	Reference	Barcoded
	<i>Paralabellula curvicauda</i> (Motschulsky, 1863)		x
	<i>Spongovostox sakaii</i> Nishikawa, 2006		x
	<i>Marava arachidis</i> (Yersin, 1860)**		x*
	<i>Nesogaster lewisi</i> (de Bormans, 1903)		x
Chelisochidae	<i>Proreus simulans</i> (Stål, 1860)		x
Forficulidae	<i>Eparchus yezoensis</i> (Matsumura et Shiraki, 1905)		x
	<i>Timomenus komarowi</i> (Semenov, 1901)		
	<i>Paratimomenus flavocapitatus</i> (Shiraki, 1905)		
	<i>Anechura harmandi</i> (Burr, 1904)		x
	<i>Anechura japonica</i> (de Bormans, 1880)**		
	<i>Elaunon biparticus</i> (Kirby, 1891)		x*
	<i>Forficula auricularia</i> Linnaeus, 1758**		x*
	<i>Forficula hiromasai</i> Nishikawa, 1970		x
	<i>Forficula mikado</i> Burr, 1904		x
	<i>Forficula paratomis</i> Steinmann, 1985**		
	<i>Forficula planicollis</i> Kirby, 1891		
	<i>Forficula scudderii</i> de Bormans, 1880		
* At least one sequence is available in the Barcode of Life Data Systems (BOLD) and/or GenBank (accessed 28 March 2023) for non-Japanese samples only. Not included in the present analysis.			
**No established populations in Japan.			

Several earwig species, including many members of the subfamily Anisolabidinae (Anisolabididae), are completely wingless in all life stages or are flightless because they lack hind-wings possessing only (vestigial or complete) tegmina (Sakai 1987, Steinmann 1989a, Srivastava 2003), limiting their dispersal ability. Nevertheless, some wingless species, such as *Anisolabis maritima* (Bonelli, 1832) and *Euborellia annulipes* (Lucas, 1847) occur almost worldwide including many small continental and oceanic islands (e.g. Brindle (1969a), Brindle (1970), Kevan and Vickery (1997)), whereas others are distributed only locally. For example, both *Gonolabis michikoeae* Nishikawa, 2021 and *G. miyatakei* Nishikawa, 2021 are considered endemic to Amami-Oshima, an island (712.35 km<sup>2</sup>) in subtropical Japan (Nishikawa 2021). *Euborellia pallipes* (Shiraki, 1906) specimens have been confused with congeners, such as *Euborellia annulata* (Fabricius, 1793) (brachypterous species) and *Euborellia plebeja* (Dohrn, 1863) (winged species), which are more widely distributed (Kamimura et al. 2023). This species has sometimes been reported as *E. pallipes* (Shiraki, 1905); however, the original description was published in 1906 (Shiraki 1906). *Euborellia pallipes* is brachypterous and presently considered to occur only in East Asia (Kamimura et al. 2023), as is *Anisolabella marginalis* (Dohrn, 1864), which is a completely apterous species with credible records only from the Korean Peninsula and Japan (Nishikawa 2020a).

To overcome the problem of dermapteran species misidentification in Japan, we applied DNA barcoding to the largest possible number of dermapteran species recorded from Japan. Due to the high evolutionary rate, DNA barcode analyses can provide insights into the causes and consequences of within-species genetic diversity, in relation to habitat, life history and distribution. In this study, we performed detailed analyses of three flightless species of Anisolabidae, *Anisolabis maritima* (= *A. maritima*), *Anisolabella marginalis* (= *Al. marginalis*) and *Euborellia pallipes*, based on extensive sampling in Japan. Their sequence diversity was also compared to that of at least partly-winged earwig species, such as *Labia minor* (Linnaeus, 1758) (= *L. minor*) and *Labidura riparia* (Pallas, 1773) (= *Ld. riparia*).

## Materials and methods

### Sample collection, PCR amplification and sequencing

Dermapteran samples were collected by hand-sorting (except for *L. minor*, the foundress of the laboratory population was collected in a light trap) from various localities in Japan (Table 2). Total genomic DNA was extracted from fresh, ethanol-preserved or, in a few cases, dried samples using a DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany), according to the manufacturer's instructions. Depending on the size of the specimens, one to five legs were used for DNA extraction. Adult male samples were used whenever available. Polymerase chain reaction (PCR) amplification of the mitochondrial cytochrome c oxidase subunit I (COX1) gene region (658 bp), which is widely used in the DNA barcoding of earwigs (Matzke and Kočárek 2015, Stuart et al. 2019, Kalaentzis et al. 2021, Kočárek and Wahab 2021, Kamimura et al. 2023) and other invertebrates (Folmer et al. 1994) was performed using a T100™ thermal cycler (Bio-Rad Laboratories, Hercules, CA, USA) and primers LCO1490 and HCO2198 (Folmer et al. 1994). PCR reactions were

conducted in a 20  $\mu$ l volume containing 1  $\mu$ l each primer (10  $\mu$ M), 10  $\mu$ l 2 $\times$ PCR buffer, 4  $\mu$ l dNTPs (2 mM each), 0.4  $\mu$ l KOD FX Neo DNA polymerase (1.0 unit/ $\mu$ l; Toyobo, Osaka, Japan) and 1  $\mu$ l genomic DNA (or a total volume of 5  $\mu$ l for some samples). The PCR temperature profile consisted of 2 min at 94°C, followed by 35 cycles of 15 s at 94°C, 15 s at 51°C and 15 s at 72°C, followed by a final extension for 6 min at 72°C. For several samples, for which the primer set did not work, another set of primers (SKCOI-7 and KSCOI-2; Su et al. (2004)) was used to obtain PCR products: products by these primers largely overlapped the LCO1490–HCO2198 region. PCR reactions were conducted in a 10 or 20  $\mu$ l volume and the PCR temperature profile consisted of 2 min at 94°C, followed by 35–40 cycles of 10 s at 98°C, 30 s at 50°C and 60 s at 68°C, followed by a final extension of 8 min at 68°C. Sequencing was performed by Eurofins Genomics (Tokyo, Japan) or FASMAC (Kanagawa, Japan: for some samples). The chromatograms were checked visually and edited manually where appropriate. The sequences will be deposited in the DNA Data Bank of Japan (DDBJ), European Nucleotide Archive (ENA) and GenBank. Voucher specimens with codes starting with 2021BC were deposited in the personal collection of YK (Keio University, Japan) and those with codes starting with NARO-Dermaptera were deposited in the Insect Museum of the National Agriculture and Food Research Organization (NARO), Japan.

Table 2.

Samples analysed in the present study. See supplementary materials for further details (Suppl. material 1).

Family	Species	Code in Fig. 1 or Fig. 2	Collection site* (Location no, in Fig. 4)	DDBJ/ENA/GenBank accession no. (or BOLD sample code)
Anisolabididae	<i>Euborellia pallipes</i>	2A-01	Tokushima-Ishii [Myozai dist.]	<a href="#">LC767857</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-02	Hyogo-Takasago	<a href="#">LC715955</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-03	Fukushima-Iwaki	<a href="#">LC715956</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-04	Kagoshima-Shimokoshiki Is.	<a href="#">LC715957</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-05	Niigata-Kashiwazaki (11)	<a href="#">LC767802</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-06	Saitama-Kawagoe (7)	<a href="#">LC767827</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-07	Fukushima-Nishigo [Nishishirakawa dist.] (5)	<a href="#">LC767830</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-08	Chiba-Mobara (8)	<a href="#">LC767833</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-09	Kagoshima-Shimokoshiki Is.	<a href="#">LC767835</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-10	Fukuoka-Chikuzen Oshima Is. (13)	<a href="#">LC767851</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-11	Hyogo-Takasago	<a href="#">LC767855</a>

Family	Species	Code in Fig. 1 or Fig. 2	Collection site* (Location no, in Fig. 4)	DDBJ/ENA/GenBank accession no. (or BOLD sample code)
Anisolabididae	<i>Euborellia pallipes</i>	2A-12	Kagoshima-Shimokoshiki Is.	<a href="#">LC767864</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-13	Niigata-Joetsu (12)	<a href="#">LC767805</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-14	Miyagi-Watari [Watari dist.] (2)	<a href="#">LC767824</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-15	Shizuoka-Suruga [Shizuoka city] (9)	<a href="#">LC767817</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-16	Aichi-Gamagori (10)	<a href="#">LC767868</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-17	Fukushima-Yabuki [Yabuki dist.] (4)	<a href="#">LC767808</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-18	Shizuoka-Aoi [Shizuoka city]	<a href="#">LC715958</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-19	Tokushima-Tokushima	<a href="#">LC767837</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-20	Tokushima-Aizumi [Itano dist.] (14)	<a href="#">LC767848</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-21	Fukushima-Hirono [Futaba dist.] (3)	<a href="#">LC767821</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-22	Miyagi-Miyagino [Sendai city] (1)	<a href="#">LC767814</a>
Anisolabididae	<i>Euborellia pallipes</i>	2A-23	Ibaraki-Chikusei (6)	<a href="#">LC767811</a>
Anisolabididae	<i>Euborellia annulipes</i>	1G-01	Kagoshima-Amami Oshima Is.	<a href="#">LC731318</a>
Anisolabididae	<i>Euborellia annulipes</i>	1G-02	USA-Texas-Comal	<a href="#">HM385638</a>
Anisolabididae	<i>Euborellia annulipes</i>	1G-03	INDIA-Karnataka-Shivamogga	<a href="#">OP445698</a>
Anisolabididae	<i>Gonolabis miyatakei</i>	1G-04	Kagoshima-Amami Oshima Is.	<a href="#">LC715976</a>
Anisolabididae	<i>Gonolabis michikoe</i>	1G-05	Kagoshima-Amami Oshima Is.	<a href="#">LC715991</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-01	Kagoshima-Amami Oshima Is.	<a href="#">LC767852</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-02	USA-New York-Shirley	<a href="#">MF468287</a>

Family	Species	Code in Fig. 1 or Fig. 2	Collection site* (Location no, in Fig. 4)	DDBJ/ENA/GenBank accession no. (or BOLD sample code)
Anisolabididae	<i>Anisolabis maritima</i>	2B-03	USA-New York-Shirley	<a href="#">MF468289</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-04	USA-New York-Shirley	<a href="#">MF140524</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-05	USA-New York-Calverton	<a href="#">MT192775</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-06	Hokkaido-Otaru	<a href="#">LC767853</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-07	Niigata-Kashiwazaki (11)	<a href="#">LC767804</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-08	Niigata-Joetsu (12)	<a href="#">LC767807</a>
Anisolabididae	<i>Anisolabis seirokui</i>	2B-09	Tokushima-Ooge Is.	<a href="#">LC715961</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-10	Tokushima-Ooge Is.	<a href="#">LC715960</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-11	Tokushima-Naruto	<a href="#">LC767836</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-12	Tokushima-Naruto	<a href="#">LC767838</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-13	Tokushima-Naruto (14)	<a href="#">LC767847</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-14	Fukuoka-Chikuzen Oshima Is. (13)	<a href="#">LC767861</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-15	Ibaraki-Chikusei (6)	<a href="#">LC767819</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-16	Shizuoka-Suruga [Shizuoka city] (9)	<a href="#">LC767813</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-17	Miyagi-Miyagino [Sendai city] (1)	<a href="#">LC767816</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-18	Miyagi-Watari [Watari dist.] (2)	<a href="#">LC767826</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-19	Saitama-Kawagoe (7)	<a href="#">LC767829</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-20	Fukushima-Nishigo [Nishishirakawa dist.] (5)	<a href="#">LC767832</a>



Family	Species	Code in Fig. 1 or Fig. 2	Collection site* (Location no, in Fig. 4)	DDBJ/ENA/GenBank accession no. (or BOLD sample code)
Anisolabididae	<i>Anisolabis maritima</i>	2B-21	Chiba-Shirako [Chosei dist.]	<a href="#">LC767850</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-22	Chiba-Shirako [Chosei dist.] (8)	<a href="#">LC767858</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-23	USA-New York-Shirley	<a href="#">MF468288</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-24	USA-New York-Great South Bay	<a href="#">MZ701626</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-25	USA-New York-Great South Bay	<a href="#">MT192774</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-26	Aichi-Gamagori (10)	<a href="#">LC767834</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-27	Kochi-Toyo [Aki dist.]	<a href="#">LC767841</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-28	Fukushima-Yabuki [Yabuki dist.] (4)	<a href="#">LC767810</a>
Anisolabididae	<i>Anisolabis maritima</i>	2B-29	Fukushima-Hirono [Futaba dist.] (3)	<a href="#">LC767823</a>
Anisolabididae	<i>Anisolabis seirokui</i>	2B-30	Tokushima-Tokushima	<a href="#">LC767840</a>
Anisolabididae	<i>Gonolabis distincta</i>	1G-06	Okinawa-Naha	LC715963
Anisolabididae	<i>Gonolabis distincta</i>	1G-07	Okinawa-Naha	<a href="#">LC715982</a>
Anisolabididae	<i>Anisolabella ryukyuensis</i>	1G-08	Okinawa-Nago	<a href="#">LC715962</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-01	Niigata-Joetsu (12)	<a href="#">LC767806</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-02	Saitama-Kawagoe (7)	<a href="#">LC767828</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-03	Niigata-Kashiwazaki (11)	<a href="#">LC767803</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-04	Fukushima-Hirono [Futaba dist.] (3)	<a href="#">LC767822</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-05	Fukuoka-Chikuzen Oshima Is. (13)	<a href="#">LC767862</a>

Family	Species	Code in Fig. 1 or Fig. 2	Collection site* (Location no, in Fig. 4)	DDBJ/ENA/GenBank accession no. (or BOLD sample code)
Anisolabididae	<i>Anisolabella marginalis</i>	2C-06	Shizuoka-Suruga [Shizuoka city] (9)	<a href="#">LC767818</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-07	Miyagi-Miyagino [Sendai city] (1)	<a href="#">LC767815</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-08	Fukushima-Yabuki [Yabuki dist.] (4)	<a href="#">LC767809</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-09	Kanagawa-Midori [Yokohama city]	<a href="#">LC715980</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-10	Tokushima-Aizumi [Itano dist.] (14)	<a href="#">LC767849</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-11	Tokushima-Aizumi [Itano dist.]	<a href="#">LC767856</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-12	SOUTH KOREA-Jeollanam do-Yeosu si	<a href="#">OL663261</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-13	SOUTH KOREA-Jeollanam do-Yeosu si	<a href="#">OL663262</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-14	SOUTH KOREA-Jeollanam do-Yeosu si	<a href="#">OL663260</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-15	Fukushima-Nishigo [Nishishirakawa dist.] (5)	<a href="#">LC767831</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-16	Tokyo-Komae	<a href="#">LC715985</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-17	Ibaraki-Chikusei (6)	<a href="#">LC767812</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-18	Miyagi-Watari [Watari dist.] (2)	<a href="#">LC767825</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-19	Chiba-Oamishirasato (8)	<a href="#">LC767859</a>
Anisolabididae	<i>Anisolabella marginalis</i>	2C-20	Aichi-Gamagori (10)	<a href="#">LC767867</a>
Spongiphoridae	<i>Paralabellula curvicauda</i>	1G-09	Okinawa-Nago	<a href="#">LC767865</a>
Labiduridae	<i>Labidura riparia</i>	2D-01	Ehime-Iyo	<a href="#">LC715965</a>
Labiduridae	<i>Labidura riparia</i>	2D-02	Tokushima-Ishii [Myozai dist.]	<a href="#">LC767869</a>

Family	Species	Code in Fig. 1 or Fig. 2	Collection site* (Location no, in Fig. 4)	DDBJ/ENA/GenBank accession no. (or BOLD sample code)
Labiduridae	<i>Labidura riparia</i>	2D-03	Okinawa-Ishigaki Is.	<a href="#">LC767845</a>
Labiduridae	<i>Labidura riparia</i>	2D-04	MALAYSIA-Penang Is.	<a href="#">LC715964</a>
Labiduridae	<i>Labidura riparia</i>	2D-05	USA-California-Imperial	<a href="#">HM376335</a>
Labiduridae	<i>Labidura riparia</i>	2D-06	USA-California-Imperial	<a href="#">HM376336</a>
Labiduridae	<i>Labidura riparia</i>	2D-07	USA-California-San Diego	(UNI37133-17)
Labiduridae	<i>Labidura riparia</i>	2D-08	USA-California-Imperial	<a href="#">HM376334</a>
Labiduridae	<i>Labidura riparia</i>	2D-09	EGYPT-Alexandria-Mariot	(GMEGG330-14)
Labiduridae	<i>Labidura riparia</i>	2D-10	EGYPT-Alexandria-Mariot	(GMEGS343-14)
Labiduridae	<i>Labidura riparia</i>	2D-11	EGYPT-Alexandria-Mariot	(GMEGP026-14)
Labiduridae	<i>Labidura riparia</i>	2D-12	EGYPT-Alexandria-Mariot	(GMEGQ060-14)
Labiduridae	<i>Labidura riparia</i>	2D-13	EGYPT-Alexandria-Mariot	(GMEGP025-14)
Labiduridae	<i>Labidura riparia</i>	2D-14	EGYPT-Alexandria-Mariot	(GMEGP281-14)
Labiduridae	<i>Labidura riparia</i>	2D-15	PORTUGAL-Coimbra-Figueira da Foz	<a href="#">MT762852</a>
Labiduridae	<i>Labidura riparia</i>	2D-16	PORTUGAL-Castelo Branco-Idanha a Nova	<a href="#">MT762853</a>
Labiduridae	<i>Labidura riparia</i>	2D-17	PORTUGAL-Setubal-Sines	<a href="#">MT762842</a>
Labiduridae	<i>Labidura riparia</i>	2D-18	GEORGIA-Kakheti-Mt. Gareja	(FHDER106-16)
Labiduridae	<i>Labidura riparia</i>	2D-19	PORTUGAL-Castelo Branco-Idanha a Nova	<a href="#">MT762856</a>
Labiduridae	<i>Labidura riparia</i>	2D-20	IRAN	<a href="#">JN241998</a>
Labiduridae	<i>Labidura riparia</i>	2D-21	NORTH MACEDONIA-Valandovo	(FHDER086-16)
Labiduridae	<i>Labidura riparia</i>	2D-22	ALBANIA-Gjirokaster	(FHDER114-16)
Labiduridae	<i>Labidura riparia</i>	2D-23	BULGARIA-Sozopol	(FHDER065-16)
Labiduridae	<i>Labidura riparia</i>	2D-24	BULGARIA-Montana	(FHDER062-16)
Labiduridae	<i>Labidura riparia</i>	2D-25	BULGARIA-Montana	(FHDER061-16)
Labiduridae	<i>Labidura riparia</i>	2D-26	BULGARIA-Montana	(FHDER063-16)
Labiduridae	<i>Labidura riparia</i>	2D-27	BULGARIA-Montana	(FHDER064-16)

Family	Species	Code in Fig. 1 or Fig. 2	Collection site* (Location no, in Fig. 4)	DDBJ/ENA/GenBank accession no. (or BOLD sample code)
Spongiphoridae	<i>Nesogaster lewisi</i>	1G-10	Kanagawa-Midori [Sagamihara city]	<a href="#">LC715986</a>
Spongiphoridae	<i>Spongovostox sakaii</i>	1G-11	Kagoshima-Amami Oshima Is.	<a href="#">LC767844</a>
Spongiphoridae	<i>Chaetospania hexagonalis</i>	1G-12	Okinawa-Nago	<a href="#">LC767820</a>
Forficulidae	<i>Anechura harmandi</i>	1G-13	Akita-Kazuno	<a href="#">LC715973</a>
Forficulidae	<i>Anechura harmandi</i>	1G-14	Akita-Kitaakita	<a href="#">LC767860</a>
Forficulidae	<i>Anechura harmandi</i>	1G-15	Akita-Kitaakita	<a href="#">LC767871</a>
Forficulidae	<i>Anechura harmandi</i>	1G-16	Oita-Yufu	<a href="#">LC767854</a>
Forficulidae	<i>Anechura harmandi</i>	1G-17	Ehime-Matsuyama	<a href="#">LC767842</a>
Forficulidae	<i>Anechura harmandi</i>	1G-18	Ehime-Matsuyama	<a href="#">LC767846</a>
Pygidicranidae	<i>Challia imamura</i>	1G-19	Kagoshima-Yakushima Is.	<a href="#">LC715970</a>
Pygidicranidae	<i>Challia imamura</i>	1G-20	Kagoshima-Yakushima Is.	<a href="#">LC767872</a>
Spongiphoridae	<i>Paralabellula curvicauda</i>	1G-21	MALAYSIA-Penang-Bukit Mertajam	<a href="#">LC715972</a>
Spongiphoridae	<i>Labia minor</i>	1G-22	GREECE-Agrafa	(FHDER131-16)
Spongiphoridae	<i>Labia minor</i>	1G-23	AUSTRALIA-Western Australia-Perth	(WALPC3454-15)
Spongiphoridae	<i>Labia minor</i>	1G-24	REPUBLIC OF MALTA	<a href="#">MW323460</a>
Spongiphoridae	<i>Labia minor</i>	1G-25	NORWAY-Vestfold-Stokke	(NOORT063-12)
Spongiphoridae	<i>Labia minor</i>	1G-26	REPUBLIC OF MALTA	<a href="#">MW323457</a>
Spongiphoridae	<i>Labia minor</i>	1G-27	Hyogo-Sanda	<a href="#">LC767866</a>
Forficulidae	<i>Forficula hiromasai</i>	1G-28	Kagoshima-Amami Oshima Is.	<a href="#">LC767843</a>
Forficulidae	<i>Forficula hiromasai</i>	1G-29	Kagoshima-Amami Oshima Is.	<a href="#">LC767870</a>
Chelisochidae	<i>Proreus simulans</i>	1G-30	Kagoshima-Tokunoshima Is.	<a href="#">LC767873</a>

Family	Species	Code in Fig. 1 or Fig. 2	Collection site* (Location no, in Fig. 4)	DDBJ/ENA/GenBank accession no. (or BOLD sample code)
Chelisochidae	<i>Proreus simulans</i>	1G-31	SOUTH KOREA-detected in quarantine inspection	<a href="#">MW085283</a>
Forficulidae	<i>Eparchus yezoensis</i>	1G-32	Fukushima-Minamiaizu [Minamiaizu dist.]	<a href="#">LC715981</a>
Forficulidae	<i>Forficula mikado</i>	1G-33	Hokkaido-Rishiri Is.	<a href="#">LC767863</a>
Forficulidae	<i>Forficula mikado</i>	1G-34	Akita-Kazuno	<a href="#">LC715975</a>
Forficulidae	<i>Forficula mikado</i>	1G-35	Gifu-Takayama	<a href="#">LC767839</a>
Pygidicranidae	<i>Diplatys flavicollis</i>	1G-36	Okinawa-Iriomote Is.	<a href="#">LC715984</a>
Pygidicranidae	<i>Parapsalis infernalis</i>	1G-37	Okinawa-Nago	<a href="#">LC715974</a>
Pygidicranidae	<i>Parapsalis infernalis</i>	1G-38	Okinawa-Ogimi	<a href="#">LC715983</a>
* "Prefecture-City [or Island]" are indicated for Japanese samples. See main text for further details.				

## Sequence diversity analysis

Multiple sequence alignments were conducted using the ClustalW programme (Thompson et al. 2003) implemented in MEGA11 (Tamura et al. 2021) with the default settings. Due to the high evolutionary rates of DNA, it is generally difficult to estimate phylogenetic relationships amongst dermapteran genera, based solely on sequences of the region (Kamimura et al. 2023). Accordingly, the Maximum Likelihood (ML) tree was estimated to analyse and visualise relationships amongst closely-related species (usually congeners) and sequence diversity within species. Taking into account the uncertainty in sample identification, particularly that of Anisolabididae, we did not include sequence data that are available in the Barcode of Life Data Systems (BOLD) public repository (<https://v3.boldsystems.org/>) for non-Japanese dermapteran species. For the following species recorded from Japan, we included all sequence data for samples from foreign localities available in BOLD (accessed 28 March 2023) and those reported in Kamimura et al. (2023) for Malaysian populations: *A. maritima*, *E. annulipes*, *Ld. riparia*, *Paralabellula curvicauda* (Motschulsky, 1863) and *L. minor* and *Proreus simulans* (Stål, 1860).

The ML analysis and calculation of intraspecific genetic distances ( $p$ -distances) were performed using MEGA11. For ML analysis, the optimal nucleotide substitution model (general time-reversible model [GTR]+G+I) was determined using the Bayesian Information Criterion (BIC) and the default search algorithms and settings, which included a discrete Gamma distribution (+G) with five rate categories and an evolutionarily invariable fraction of sites (+I). As no non-dermapteran samples were added as outgroups, the resultant barcode tree was rooted by a clade of the infraorder Protodermaptera.

## Sequence diversity comparison amongst species

For *A. maritima*, *Al. marginalis* and *E. pallipes*, we analysed samples from multiple localities of Japan. To statistically compare within-species sequence diversity amongst these species, we selected 14 localities (or multiple localities within 15 km of each other), from which all three species were obtained (Table 2). For localities with multiple samples sequenced (*A. maritima* of Naruto, Tokushima Pref. and Shirako, Chiba Pref.), a single sample was randomly chosen for analysis because the sequences in each locality were identical (see Results). We calculated the mean within-species  $p$ -distance and its standard error for each species using MEGA11. The latter was estimated by bootstrapping the sequences 1,000 times. To test the differences in the mean  $p$ -distance between species, we performed a permutation test (Manly and Alberto 2021). In this analysis,  $p$ -distances were randomly shuffled amongst three species for each of 91 combinations amongst the 14 localities, using a personal script written in Python v.3.8.3 implemented with the *Numpy* v.1.23.1 package. Interspecific differences in the mean  $p$ -distance were compared amongst the 10,000-replicate permuted data (9,999 shuffled values plus one actual value) and actual values to determine the level of significance.

## Results and discussion

### PCR amplification and interspecific relationships

The universal primer set, LCO1490 and HCO2198, worked well for many dermapteran species, resulting in the amplification of 658 bp of the 5' DNA-barcoding region of the mitochondrial *cox1* gene (for [LC767869](#), [LC767870](#) and [LC767871](#), 11–135 bases of 3'-end could not be determined). Exceptions included *Challia imamurai* Nishikawa, 2006 (Pygidicranidae: partly; [LC767872](#)), *Euborellia annulipes* (Anisolabididae: all; see Kamimura et al. (2023)) and *Proreus simulans* (Chelisochidae: all; [LC767873](#)). For these samples, an alternate primer set (SKCOI-7 and KSCOI-2) was successfully applied to amplify products largely overlapping with the LCO1490-HCO2198 region. Interestingly, no consistent taxonomic bias was observed in species for which the LCO1490-HCO2198 primer set failed to work, suggesting that one or both of these primers did not match the annealing site due to the extremely high rate of molecular evolution. As a result of this work, data for this region are now available for at least one sample of 29 of 40 (72.5%) species of earwigs recorded from Japan (Table 1).

The extremely high rate of molecular evolution makes the sequenced region useful for the diagnosis and delimitation of closely-related species (Hebert et al. 2003a, Hebert et al. 2003b, Hebert et al. 2004). However, estimating deeper phylogenies (usually relationships amongst genera or deeper) is usually difficult, based solely on this region due to base substitution saturation (Folmer et al. 1994, Talavera et al. 2021) and it is true for Dermaptera (Kamimura et al. 2023). In addition, the phylogenetic relationships estimated, based on only markers of mitochondrial DNA, can be distorted by the effects of hybridisation or introgression (Funk and Omland 2003, Hebert et al. 2003b). Accordingly, interspecific relationships were not resolved (< 50% bootstrap support) in the ML barcode

tree (Fig. 1; Table 3). Although only a few representatives were sampled for each genus, monophyly was indicated for the subfamily Anisolabidinae (Anisolabididae: 54%), the genera *Anisolabis* (100%) and *Anisolabella* (97%), two species of *Gonolabis* endemic to Amami-Oshima (*G. michikoe* + *G. miyatakei*: 100%) and a clade including *Forficula mikado* Burr, 1904 + *Forficula hiromasai* Nishikawa, 1970 + *Eparchus yezoensis* (Matsumura et Shiraki, 1905) + *P. simulans* (71%). In the latter, relationships (*L. minor*, (*F. hiromasai*, (*P. simulans*, (*E. yezoensis*, *F. mikado*)))) were also suggested with weak support (55–76%) (Fig. 1).

Table 3.

Intraspecific *p*-distances for the samples collected in Japan, with the average interspecific distance to the nearest species.

Family	Species	Number of Japanese samples analysed	Intraspecific distance: Minimum–Maximum	Nearest neighbour	Average distance to nearest neighbour
Diplatyidae	<i>Diplatys flavicollis</i>	1	Not available	<i>Spongovostox sakaii</i>	0.1535
Pygidicranidae	<i>Challia imamurai</i>	2	0.0000	<i>Diplatys flavicollis</i>	0.1634
	<i>Parapsalis infernalis</i>	2	0.0046	<i>Diplatys flavicollis</i>	0.1672
Anisolabididae	<i>Anisolabella marginalis</i>	17	0.0000–0.0046	<i>Anisolabella ryukyuensis</i>	0.1208
	<i>Anisolabella ryukyuensis</i>	1	Not available	<i>Anisolabella marginalis</i>	0.1208
	<i>Anisolabis</i> spp.*	23	0.0000–0.0274	<i>Gonolabis distincta</i>	0.1454
	<i>Gonolabis distincta</i>	2	0.0091	<i>Anisolabis</i> spp.*	0.1454
	<i>Gonolabis michikoe</i>	1	Not available	<i>Gonolabis miyatakei</i>	0.0988
	<i>Gonolabis miyatakei</i>	1	Not available	<i>Gonolabis michikoe</i>	0.0988
	<i>Euborellia annulipes</i>	1	Not available	<i>Gonolabis michikoe</i>	0.1709
	<i>Euborellia pallipes</i>	23	0.0000–0.0091	<i>Anisolabis</i> spp.*	0.1595

Family	Species	Number of Japanese samples analysed	Intraspecific distance: Minimum–Maximum	Nearest neighbour	Average distance to nearest neighbour
Labiduridae	<i>Labidura riparia</i>	3	0.0077–0.0756	<i>Spongovostox sakaii</i>	0.1528
Spongiphoridae	<i>Chaetospania hexagonalis</i>	1	Not available	<i>Nesogaster lewisi</i>	0.2006
	<i>Labia minor</i>	1	Not available	<i>Forficula hiromasai</i>	0.1905
	<i>Paralabellula curvicauda</i>	1	Not available	<i>Spongovostox sakaii</i>	0.1505
	<i>Spongovostox sakaii</i>	1	Not available	<i>Nesogaster lewisi</i>	0.1383
	<i>Nesogaster lewisi</i>	1	Not available	<i>Spongovostox sakaii</i>	0.1383
Chelisochidae	<i>Proreus simulans</i>	1	Not available	<i>Eparchus yezoensis</i>	0.2000
Forficulidae	<i>Eparchus yezoensis</i>	1	Not available	<i>Proreus simulans</i>	0.2000
	<i>Anechura harmandi</i>	6	0.0000–0.0243	<i>Challia imamurai</i>	0.1995
	<i>Forficula hiromasai</i>	2	0.0243	<i>Nesogaster lewisi</i>	0.1834
	<i>Forficula mikado</i>	3	0.0106–0.0319	<i>Forficula hiromasai</i>	0.1889
* <i>Anisolabis maritima</i> and <i>Anisolabis seirokui</i>					

Interestingly, the monophyletic *Anisolabis* includes two major groups, clade B-a and B-b (Fig. 2B), each of which was supported with > 75% bootstrap value. Four samples of *A. maritima* from New York, USA, were placed within Clade B-a, two of which formed a subclade (99% support), whereas three others were placed in Clade B-b. Furthermore, two samples of *A. seirokui* from Tokushima Prefecture, Japan, were completely separated into the two major clades (blue circles, Fig. 2B), rendering *A. maritima* (orange circles, Fig. 2B) paraphyletic. In the samples of *A. maritima* from Japan, an individual from the southernmost locality (Amami-Oshima) was included in neither clade B-a nor B-b. The others were divided into the two clades, indicating geographical differentiation between Shikoku (partial) and the Sea of Japan coast of Honshu + Hokkaido + Kyushu (Clade B-a) and the Pacific coast of Honshu + Shikoku (Clade B-b). The maximum *p*-distance amongst the studied samples of *A. maritima* was 2.7%, slightly exceeding 2.0%, which is often used



to delimit insect species boundaries (Cognato 2006). However, some species exhibit remarkably high intraspecific diversity (> 5%) in the mitochondrial COI DNA sequences (up to 26.0%: Cognato (2006)), warranting further study of reproductive isolation amongst the *Anisolabis* clades.

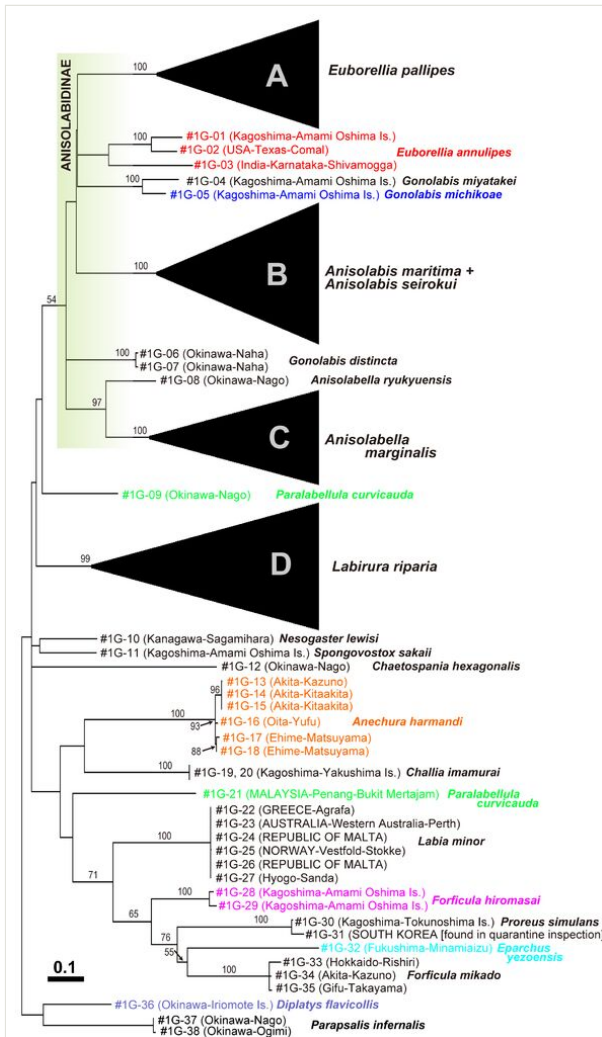


Figure 1. [doi](#)

Maximum Likelihood barcode tree constructed from mitochondrial cytochrome oxidase I gene (*cox1*) sequence data. Branch numbers indicate bootstrap values (% in 500 replicates; only values  $\geq 50\%$  are shown). Four clades (all supported with  $\geq 99\%$  bootstrap values) containing more than 20 samples (A-D) are compressed. Localities are indicated in parentheses in the format "Prefecture-City (or Island)" for samples collected in Japan. For large cities with multiple wards (or small towns within a district), the name of the ward (or town) replaces the city name, with the city or district name in brackets, where necessary. For foreign samples, the country is indicated in capital letters. A unique sample code precedes the locality. Detailed sample descriptions are provided in Table 2.

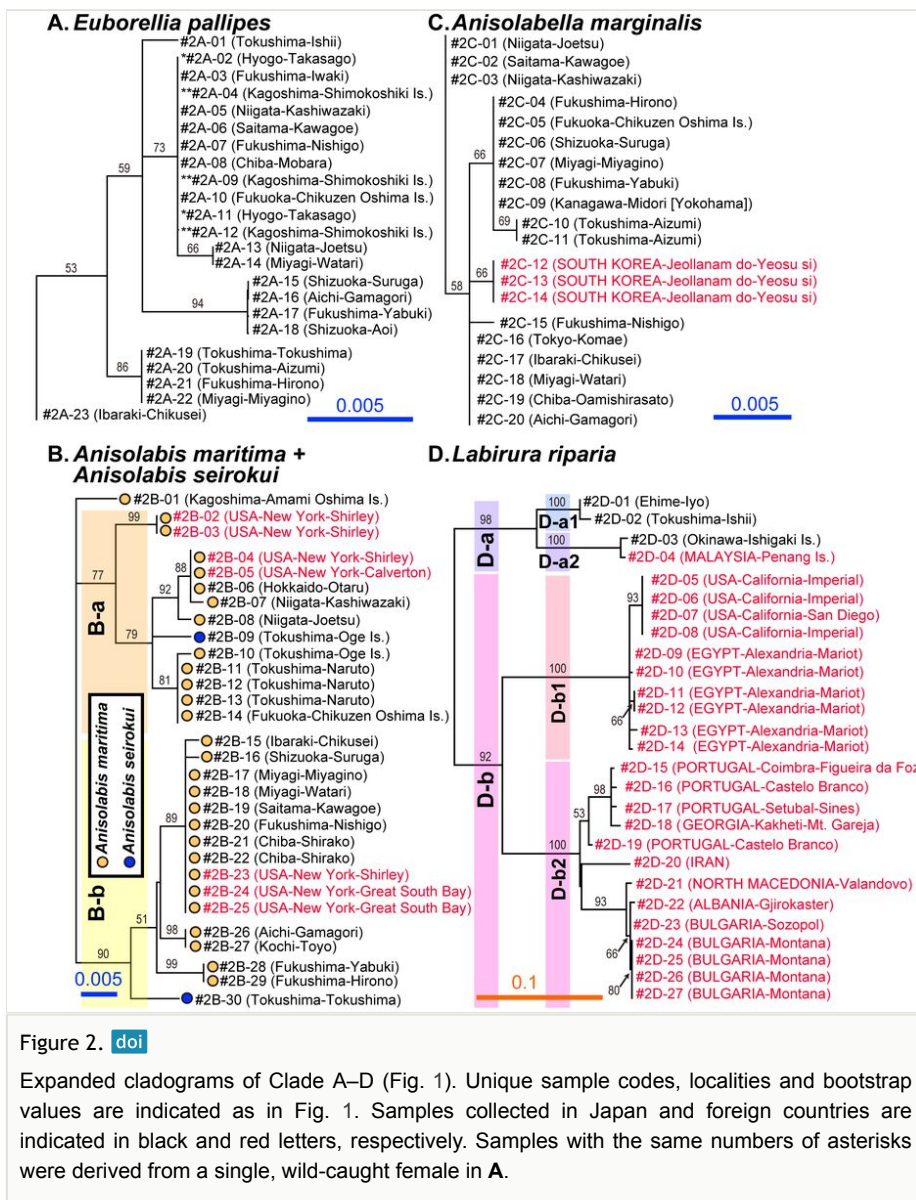


Figure 2. doi

Expanded cladograms of Clade A–D (Fig. 1). Unique sample codes, localities and bootstrap values are indicated as in Fig. 1. Samples collected in Japan and foreign countries are indicated in black and red letters, respectively. Samples with the same numbers of asterisks were derived from a single, wild-caught female in A.

*Anisolabis maritima* is a cosmopolitan species that occurs in all faunal regions, but is usually restricted to warm temperate, subtropical and tropical areas (Brindle 1969a, Sakai 1987, Steinmann 1989a, Srivastava 2003). As the species epithet suggests, this species is especially abundant under seashore debris in temperate Japan (Matsumura 1935, Tobiyaama 1985, Kamimura 2005) and foreign localities (Bennet 1904, Caudell 1913, Hebard 1917, Hincks 1947, Guppy 1950, Brindle 1969a). By contrast, *A. seirokui*, which has been recorded from Japan, the Korean Peninsula (South Korea) and Taiwan, is also a maritime species, but usually found in rocky seashores, rocky reefs or artificial marine

breakwaters (Nishikawa 2016, Nishikawa 2020a). The much more slender body shape of *A. seirokui* with its less asymmetrical, thinner male forceps (Nishikawa 2008, Nishikawa 2016) may represent an adaptation to their cryptic life in rocky environments with many narrow crevices, suggesting ecological differentiation with *A. maritima*. The observed polyphyly of *A. seirokui*, which is nested in the clades of *A. maritima*, may reflect incomplete lineage sorting after divergence of their ancestors or the results of past or present introgressions (gene flow due to hybridisation) between these incipient species (Pollard et al. 2006, Degnan and Rosenberg 2009, Fontaine et al. 2015, Mallet et al. 2016). Further sampling (especially specimens of *A. seirokui*) and analyses of multiple genes, including nuclear genes, are needed to resolve these issues.

### Intraspecific diversity

In contrast to the low power associated with constructing deeper phylogenies, the monophyly of each species with multiple samples was strongly supported with a ~ 100% bootstrap value, except for *E. annulipes*, *P. curvicauda* and the possible paraphyly of *A. maritima* (polyphyly of *A. seirokui*) (Fig. 1). For *E. annulipes*, the sequence of an Indian sample showed ca. 16–17% divergence from samples from USA and Japan, which showed 10% difference, but are undoubtedly closely related to each other (100% support).

The most notable example is the spongiphorid *P. curvicauda*: the sequence of a Japanese sample showed 17.5% difference from that of a Malaysian sample reported in Kamimura et al. (2023). Accordingly, these two samples were placed remotely in the ML barcode tree (green characters, Fig. 1). This species was originally described as *Forficesila curvicauda* by Motschulsky (1863) and is considered a cosmopolitan of tropical and subtropical regions of both the Old and New Worlds (Brindle 1969a, Steinmann 1990, Sakai 1993, Srivastava 2013, Nishikawa 2016, Nishikawa 2020a). Including *Forficesila dilaticauda* (Motschulsky, 1863), which was synonymised with *P. curvicauda* by Burr (1911), this species is known to be highly variable in the body colour, shape of male forceps and vestiture (Burr 1911, Borelli 1928, Hebard 1933b, Hincks 1947, Brindle 1971, Brindle 1973). Specimens analysed in Kamimura et al. (2023) and the present study (Fig. 3) may represent brown and black morphs, respectively. These two morphs also differ in the size of the male and female genitalia (YK, unpublished data), requiring further study.

Although reconstructed to be monophyletic, our analysis revealed that *Labidura riparia* (Labiduridae) has high sequence variation (14.4% at maximum; Figs 1, 2D), resulting in the formation of two major clades (D-a and D-b), which are subdivided into D-a1 and D-a2 and D-b1 and D-b2, respectively (Fig. 2D: all with > 90% bootstrap support). Clade D-a consists of the East and Southeast Asian samples, amongst which two individuals from Shikoku (temperate Japan) are classified in D-a1 and one from Ishigaki Island, Ryukyus (subtropical Japan) forming Clade D-a2 together with a Malaysian sample. Clades D-b1 and D-b2 make up clusters of samples from USA + Egypt and Europe to the Middle East, respectively. Although we tentatively treated all of these samples under the name *Ld. riparia* in this study, some previous authors have treated East, South and Southeast Asia and New Guinea populations as a distinct species, *Labidura japonica* (de Haan, 1842),

based on differences in external morphology (Burr 1911, Steinmann 1979, Steinmann 1989a, Steinmann 1989b). Further investigation of reproductive isolation amongst the clades using more samples from various localities will contribute to differentiating this possible species complex. In marked contrast to *Ld. riparia*, *Labia minor*, another cosmopolitan species with well-developed wings, showed extremely low sequence diversity worldwide (Figs 1, 2). Surprisingly, pairwise comparisons revealed no sequence differences (0% divergence) amongst samples collected from Greece, Malta, Australia and Japan. A sample from Norway exhibited only 0.15–0.16% divergence from the others.



Figure 3. [doi](#)

Voucher specimens (preserved in ethanol) of *Parabelbella curvicauda*. **A** 2021BCDNA40 from Malaysia (Kamimura et al. 2023); **B** 2021BCDNA57 from Japan. Scale bars: 2 mm.

In contrast to the high within-species sequence diversity observed in *A. maritima*, the other two flightless species of Anisolabididae selected for detailed analysis, *Al. marginalis* and *E. pallipes*, showed low diversity in their barcodes (Fig. 2A and C). Observed genetic diversity can depend on the geographical sampling range; however, after selecting only 14 sampling sites, from which all three species were collected, *A. maritima* still showed significantly higher sequence diversity (average  $p$ -distance of 1.34%) compared with *Al. marginalis* (0.18%; 10,000 replication permutation test,  $P = 0.0001$ ) and *E. pallipes* (0.45%;  $P = 0.0001$ ) (Fig. 4). Sequence diversity was notably low in *Al. marginalis*, significantly lower than even that of *E. pallipes* ( $P = 0.0148$ ). Though these statistical results must be interpreted with caution because of the interdependence of distance data, the standard

errors calculated directly by bootstrapping the sequence data led to a similar conclusion (Fig. 4C).

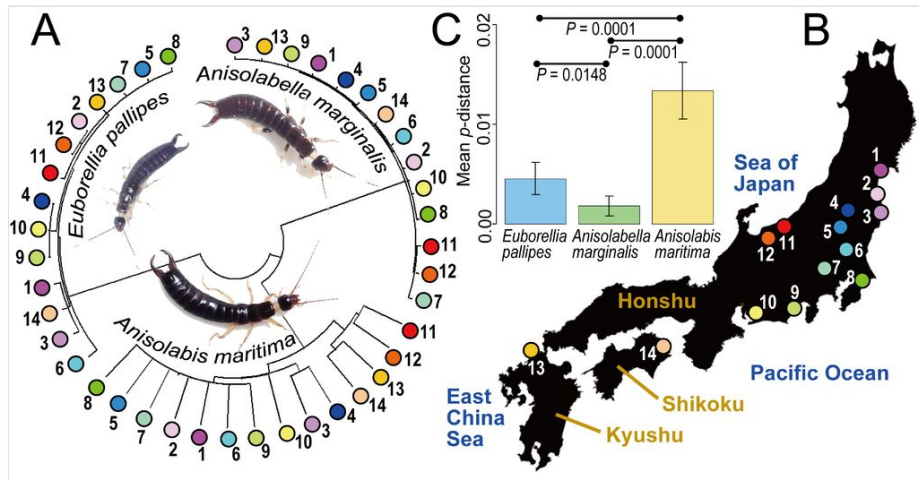


Figure 4. [doi](#)

Neighbour-joining barcode tree constructed based on uncorrected genetic distances (*p*-distances) for three anisolabid species (A; with male habitus [not scaled]), collected from 14 localities of Japan (B). Mean within-species *p*-distances are shown on the bar plot (C), with the standard errors estimated by 1,000-replication bootstrapping. Sampling points (1–14) are described in Table 2.

Although *E. pallipes* has long been confused with *E. plebeja*, a fully-winged species (see Kamimura et al. (2023) for details), these three anisolabid species are considered completely flightless (Sakai 1970, Sakai 1987, Nishikawa 2016). These semi-synanthropic species are also similar in their habitat preferences: common on the seaside, riversides, crop fields and urbanised areas in Japan (Furukawa 1965, Nishikawa 1975, Nishikawa 2016, Yamasaki 1999, Kamimura 2005). Therefore, it remains unclear why *A. maritima* shows notably higher sequence diversity than *Al. marginalis* and *E. plebeja*. Aside from the possible effects of introgression with *A. seirokui*, their wider distribution and abundance in seashore environments may be responsible for these differences. *Anisoblasis maritima* appears to be highly tolerant to high salinity (Bennet 1904) and is usually found in environments nearer to shorelines than *Al. marginalis* and *E. pallipes*. By contrast, *Al. marginalis* prefers somewhat more humid, shaded environments (Kamimura 2005). Although flightless, *A. maritima* and its allies, abundant in maritime environments, are known to readily colonise volcanic islands, possibly by debris rafting and have been found on many oceanic islands far from continents (Kevan 1965, Brindle 1968, Brindle 1969a, Brindle 1969b, Brindle 1972, Brindle 1980, Kevan and Vickery 1997, Abe 2006, Mori et al. 2020, Nishikawa 2020b). In addition, Buckel (1929) speculated on the artificial introduction of *A. maritima* to Vancouver Island, British Columbia: “They were probably introduced to Departure Bay by Japanese fishing boats, as there is a considerable trade in herrings from this point to the Orient”.

Interestingly, Kamimura et al. (2023) revealed high sequence divergence (up to 5.5%) in *E. annulata*, another circumtropical cosmopolitan that is predominantly found in seaside environments. Both *Ld. riparia* and *E. annulipes* exhibit very high sequence diversity, possibly corresponding to a complex of several cryptic species (Figs 1, 2D). The former species is also an inhabitant of open lands, especially the seaside and frequently invades new habitats (Brindle 1969a, Simberloff and Wilson 1969, Ball and Glucksman 1975, Langston and Powell 1975, Thornton et al. 2001). *Labidura riparia* is also frequently intercepted in quarantine plant inspections (personal communication by Gurney A.B. 1958, cited in Schlinger et al. (1959)). *Euborellia annulipes* is also frequent in maritime environments and has been recorded from almost all islands in the tropics or subtropics, including oceanic archipelagos (Hebard 1933a, Hebard 1933b, Kevan 1965, Brindle 1968, Brindle 1969a, Brindle 1969b, Nishikawa 1969, Brindle 1970, Brindle 1972, Brindle 1976, Brindle 1980, Kevan and Vickery 1997, Nishikawa 2020b). For *E. annulipes*, artificial transportation of living plants is also considered to contribute to their cosmopolitan distribution in warm-temperate to tropical zones worldwide and their sporadic establishment in greenhouses in colder zones (Brindle 1966, Brindle 1969a, Kocarek et al. 2015, Nishikawa 2016, Vujčić et al. 2022). Interestingly, these maritime inhabitants showed notably higher sequence diversity than *L. minor* (Fig. 1), another cosmopolitan species that flies readily with its developed wings and is attracted to light sources at night (e.g. Hebard (1917), Morse (1920), Kleinow (1966), Vickery and Kevan (1983), Vickery and Kevan (1985), Nishikawa (2016)). The high ability to colonise isolated habitats, such as oceanic islands, by the maritime species may enhance their potential for local differentiation. Sporadic long-distance transportation via ocean currents and/or human activity may contribute to stir diversified populations, resulting in their higher genetic diversity, even in small areas.

## Acknowledgements

We thank Fumio Hayashi, Mariko Shizuki, Masataka Yoshida, Seiji Morita, Shin'ichi Katada, Takeshi Miyake, Taku Tsukada and Tatsuo Hanatani for providing important samples for the present study. We also thank Tae Hwa Kang, Seo-Jin Lee, Taewoo Kim, Adriana Vella and Kazuhiko Konishi for information about the several samples. We are grateful also to Fabian Haas, Petr Kočárek and Julio C. Estrada-Álvarez for useful comments on a previous version of the manuscript. This study was partly supported by Keio Gijuku Academic Development Funds from Keio University (2021 and 2022) to YK, Grants-in-Aid for Scientific Research (KAKENHI) from the Japan Society for the Promotion of Science No. 19K06746 to YK and No. 21H02219 to JY.

## Ethics and security

Not applicable.

## Author contributions

J.Y. and M.N. conceptualised the study; M.N. and Y.K. collected animal samples; J.Y. and Y.K. performed DNA analyses; Y.K. performed statistical analyses; All authors wrote the first draft; All authors contributed to and approved the final draft of the manuscript.

## Conflicts of interest

The authors have declared that no competing interests exist.

## References

- Abe T (2006) Colonization of Nishino-shima Island by plants and arthropods 31 years after eruption. *Pacific Science* 60: 355-365. <https://doi.org/10.1353/psc.2006.0014>
- Antil S, Abraham JS, Sripoorna S, Maurya S, Dagar J, Makhija S, Bhagat P, Gupta R, Sood U, Lal R, Toteja R (2023) DNA barcoding, an effective tool for species identification: a review. *Molecular Biology Reports* 50: 761-775. <https://doi.org/10.1007/s11033-022-08015-7>
- Armstrong KF, Ball SL (2005) DNA barcodes for biosecurity: Invasive species identification. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 1813-1823. <https://doi.org/10.1098/rstb.2005.1713>
- Ball E, Glucksman J (1975) Biological colonisation of Motmot, a recently created tropical island. *Proceedings of the Royal Society of London, Series B* 190: 421-442.
- Bennet CB (1904) Earwigs (*Anisolabis maritima* Bon.). *Psyche* 11: 47-54. <https://doi.org/10.1155/1904/60136>
- Borelli A (1928) Dermaptera. In: British Museum (Natural History) (Ed.) *Insects of Samoa and other Samoan terrestrial Arthropoda. Part I Orthoptera and Dermaptera. Fasc. 1.* 1–8 pp.
- Brindle A (1966) Notes on Dermaptera in the Hamburg Museum. *Entomologische Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum Hamburg* 3: 127-141.
- Brindle A (1968) The Dermaptera of the Canary Island. *Arkiv för Zoologi* 22: 139-148.
- Brindle A (1969a) The Dermaptera of the Azores and Madeira. *Boletim do Museu Municipal do Funchal* 23: 5-24.
- Brindle A (1969b) The earwigs (Dermaptera) of the Galapagos Islands. *Entomologist's Record and Journal of Variation* 81: 331-334.
- Brindle A (1970) The Dermaptera of the Solomon Islands. *Pacific Insects* 12: 641-700.
- Brindle A (1971) The Dermaptera of the Naturhistoriska Riksmuseum Stockholm. IV. *Entomologisk Tidskrift* 92: 1-27.
- Brindle A (1972) Dermaptera. *Insects of Micronesia* 5: 97-171.
- Brindle A (1973) The Dermaptera of Africa. Part 1. *Musée Royal de l'Afrique Centrale, Tervuren, Belgique Annales* 8: 1-335.
- Brindle A (1976) Dermaptera from the Seychelles. *Revue de Zoologie Africaine* 90: 435-445.

- Brindle A (1980) The cavernicolous fauna of Hawaiian lava tubes. 12. A new species of blind troglitic earwigs (Dermaptera, Carcinophoridae), with a revision of the related surface-living earwigs of the Hawaiian Islands. *Pacific Insects* 21: 261-274.
- Buckel ER (1929) The Dermaptera of Canada. *Proceedings of the Entomological Society of British Columbia* 26: 9-21.
- Burr M (1911) *Dermaptera. Genera Insectorum*, Bruxelles 122: 1-112.
- Caudell AN (1913) Notes on Nearctic orthopterous insects 1. Non-saltatorial forms. *Proceedings of the United States National Museum* 44: 595-614. <https://doi.org/10.5479/si.00963801.44-1970.595>
- Cognato AI (2006) Standard percent DNA sequence difference for insects does not predict species boundaries. *Journal of Economic Entomology* 99: 1037-1045. <https://doi.org/10.1093/jee/99.4.1037>
- Degnan JH, Rosenberg NA (2009) Gene tree discordance, phylogenetic inference and the multispecies coalescent. *Trends in Ecology & Evolution* 24: 332-340. <https://doi.org/10.1016/j.tree.2009.01.009>
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294-299. <https://doi.org/10.1071/ZO9660275>
- Fontaine MC, Pease JB, Steele A, Waterhouse RM, Neafsey DE, Sharakhov IV, Jiang X, Hall AB, Catteruccia F, Kakani E, Mitchell SN, Wu YC, Smith HA, Love RR, Lawniczak MK, Slotman MA, Emrich SJ, Hahn MW, Besansky NJ (2015) Extensive introgression in a malaria vector species complex revealed by phylogenomics. *Science* 347: 1258524. <https://doi.org/10.1126/science.1258524>
- Funk D, Omland K (2003) Species-Level Paraphyly and Polyphyly: Frequency, Causes, and Consequences, with Insights from Animal Mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics* 34 (1): 397-423. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132421>
- Furukawa H (1965) Dermaptera. In: Furukawa H, Hasegawa H, Okutani T (Eds) *Genshoku Kontyu Hyakka Zukan* [Pictorial encyclopedia of insects in original colors]. Shueisha, Tokyo, 246–248 pp. [In Japanese].
- Guppy R (1950) Biology of *Anisolabis maritima* (Gene), the seaside earwig, on Vancouver Island. *Proceedings of the Entomological Society of British Columbia* 46: 14-18.
- Hagen H (1868a) On a wingless white ant from Japan. *Proceedings of the Boston Society of Natural History* 11: 399-400.
- Hagen H (1868b) Communication [Rectification of a paper]. *Proceedings of the Boston Society of Natural History* 12: 139-139.
- Hebard M (1917) Notes on earwigs (Dermaptera) of North America, north of the Mexican boundary. *Entomological News* 28: 311-323.
- Hebard M (1933a) Dermaptera and Orthoptera from the Society Islands. *Society Islands Insects. Pacific Entomological Survey* 6: 57-66.
- Hebard M (1933b) The Dermaptera and Orthoptera of the Marquesas Islands. *Bulletin of the Bernice P. Bishop Museum, Honolulu* 114: 105-140.
- Hebert PD, Ratnasingham S, DeWaard JR (2003a) Barcoding animal life: Cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal*



Society B: Biological Sciences 270 (Suppl 1): 96-99. <https://doi.org/10.1098/rsbl.2003.0025>

- Hebert PD, Cywinska A, Ball SL, DeWaard JR (2003b) Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biological Sciences* 270: 313-321. <https://doi.org/10.1098/rspb.2002.2218>
- Hebert PD, Penton EH, Burns JM, Janzen DH, Hallwachs W (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America* 101: 14812-14817. <https://doi.org/10.1073/pnas.0406166101>
- Hincks WD (1947) Preliminary notes on Mauritian earwigs (Dermaptera). *Annals & Magazine of Natural History* 14: 517-540. <https://doi.org/10.1080/00222934708654662>
- Hopkins H, Maehr MD, Haas F, Deem LS (2018) Dermaptera Species File. Version 5.0/5.0. <http://Dermaptera.SpeciesFile.org>. Accessed on: 2022-7-31.
- Kalaentzis K, Kazilas C, Agapakis G, Kocarek P (2021) Hidden in plain sight: First records of the alien earwig *Euborellia femoralis* (Dohrn, 1863) in Europe. *BioInvasions Records* 10: 1022-1031. <https://doi.org/10.3391/bir.2021.10.4.27>
- Kamimura Y (2005) Dermaptera. In: Ishiwata S, et al. (Ed.) *Insect Larvae of Japan*. Gakken, Tokyo, Tokyo, 48–49 pp. [In Japanese].
- Kamimura Y, Lee C-Y, Yamasako J, Nishikawa M (2023) Identification and reproductive isolation of *Euborellia* species (Insecta, Dermaptera, Anisolabididae) from East and Southeast Asia. *ZooKeys* 1146: 115-134. <https://doi.org/10.3897/zookeys.1146.98248>
- Kevan DK, Vickery VR (1997) An annotated provisional list of non-saltatorial orthopteroid insects of Micronesia, compiled mainly from the literature. *Micronesia* 30: 269-353.
- Kevan DKM (1965) The orthopteroid insects of Easter Island. *Entomologist's Record* 77: 283-286.
- Kleinow W (1966) Untersuchungen zum Flügelmechanismus der Dermapteren. *Zeitschrift für Morphologie und Ökologie der Tiere* 56: 363-416. <https://doi.org/10.1007/BF00442290>
- Kocarek P, Dvorak L, Kirstova M (2015) *Euborellia annulipes* (Dermaptera: Anisolabididae), a new alien earwig in Central European greenhouses: potential pest or beneficial inhabitant? *Applied Entomology and Zoology* 50: 201-206. <https://doi.org/10.1007/s13355-015-0322-2>
- Kočárek P, Wahab RA (2021) Termitophily documented in earwigs (Dermaptera). *Biology* 10: 1243. <https://doi.org/10.3390/biology>
- Kočárek P, Hu F-S (2023) An immature dermapteran misidentified as an adult zorapteran: The case of *Formosozoros newi* Chao & Chen, 2000. *Insects* 14: 53. <https://doi.org/10.3390/insects14010053>
- Langston RL, Powell JA (1975) The earwigs of California (Order Dermaptera). *Bulletin of the California Insect Survey* 20: 9-21.
- Mallet J, Besansky N, Hahn MW (2016) How reticulated are species? *BioEssays* 38: 140-149. <https://doi.org/10.1002/bies.201500149>
- Manly BF, Alberto JA (2021) *Randomization, bootstrap and Monte Carlo methods in biology*. 4th Edition. CRC press, New York, 358 pp.
- Matsumura S (1935) Dermaptera. 6000 illustrated insects of Japan-empire, 1931. Noe-Shoin, Tokyo, 1381–1388 pp. [In Japanese].

- Matzke D, Kočárek P (2015) Description and biology of *Euborellia arcanum* sp. nov., an alien earwig occupying greenhouses in Germany and Austria (Dermaptera: Anisolabididae). *Zootaxa* 3956: 131-139. <https://doi.org/10.11646/zootaxa.3956.1.8>
- Mori H, Kishimoto T, Terada T, Nagano H, Karube H, Kawakami K (2020) Terrestrial arthropods of Nishinoshima Island. *Ogasawara Research* 46: 95-108. [In Japanese with English summary].
- Morse AP (1920) Manual of the Orthoptera of New England, including the locusts, grasshoppers, crickets, and their allies. *Proceedings of the Boston Society of Natural History* 35: 197-556.
- Motschulsky V (1863) D'un catalogue des insectes de l'île Ceylan. *Bulletin de la Société Impériale des naturalistes de Moscou* 36: 1-153.
- Nishikawa M (1969) Notes on the Carcinophorinae of Japan and Ryukyus (Dermaptera: Carcinophoridae). *Kontyû* 37: 41-55.
- Nishikawa M (1975) Dermaptera. In: Ishihara T (Ed.) *Pictorial encyclopedia of insect III for student*. Gakken, Tokyo, 65–66 [plates], 187–383. pp. [In Japanese].
- Nishikawa M (2005) Identity of the earwig recorded as *Proreus simulans* (Dermaptera: Chelisochidae) from Watarase-Yûsuichi, Tochigi Prefecture, Japan. *Tettigonia* (7)1-8.
- Nishikawa M (2007) Identity of the earwig recorded as *Nala* (?) sp. in "Guide to Seashore Animals of Japan, Vol. II (1995)" (Dermaptera, Labiduridae). *Japanese Journal of Systematic Entomology* (13)1-5.
- Nishikawa M (2008) A new species of the genus *Anisolabis* from Japan and Korea, with notes on the nomenclatural problem of two subspecific names of *Anisolabis maritima* (Bonelli) (Dermaptera: Anisolabididae). *Insecta Matsumurana New Series* 64: 35-51.
- Nishikawa M (2013) Earwig Letters (4): The distribution of *Nesogaster lewisi* in Japan. *Battarigisu* 152: 2-12. [In Japanese].
- Nishikawa M (2016) Dermaptera. In: *Orthopterological Society of Japan (Ed.) The Standard of Polyneoptera in Japan*. Gakken, Tokyo, 170–186 pp. [In Japanese].
- Nishikawa M, Naka T (2019) A basal earwig *Paradiplatys gladiator* (Burr) (Dermaptera: Pygidicranidae) incidentally introduced into Naha city, Okinawa Prefecture, Japan. *Japanese Journal of Systematic Entomology* 25: 53-54.
- Nishikawa M (2020a) Order Dermaptera. In: *Editorial Committee of Catalogue of the Insects of Japan (Ed.) Catalogue of the Insects of Japan, Vol. 3: Polyneoptera*. Touka Shobo, Fukuoka, Japan, 56–67 pp. [In Japanese].
- Nishikawa M (2020b) Earwig Letters (11): Dermaptera of the Bonin Islands, Japan. *Battarigisu* 163: 191-196. [In Japanese].
- Nishikawa M (2021) Two new species of the genus *Gonolabis* Burr (Dermaptera: Anisolabididae) from Amami-Ôshima Island of the Ryukyus, Japan, with notes on the *Mongolabis distincta* (Nishikawa, 1969). *Japanese Journal of Systematic Entomology* 27: 212-220.
- Nishikawa M (2023) A new species of the genus *Echinosoma* (Dermaptera: Pygidicranidae) from Ishigakijima, southwestern Japan. *Japanese Journal of Systematic Entomology* 29: 173-176.
- Pollard DA, Iyer VN, Moses AM, Eisen MB (2006) Widespread discordance of gene trees with species tree in *Drosophila*: evidence for incomplete lineage sorting. *PLOS Genetics* 2: 173. <https://doi.org/10.1371/journal.pgen.0020173>
- Sakai S (1970) *Dermapterorum Catalogus Praeliminaris. I. Labiduridae and Carcinophoridae*. Daito Bunka University, Tokyo, 49 + 91 pp.

- Sakai S (1987) Dermapterorum Catalogus XIX-XX: Iconographia IV-V. Chelisochidae and Anisolabididae. Daito Bunka University, Tokyo, 1567 pp.
- Sakai S (1993) Dermapterorum Catalogus XXV: Iconographia IX. Spongiphoridae III. Daito Bunka University, Tokyo, 595 pp.
- Schlinger EI, van den Bosch R, Dietrick EJ (1959) Biological notes on the predaceous earwig *Labidura riparia* (Pallas), a recent immigrant to California [Dermaptera: Labiduridae]. Journal of Economic Entomology 52: 247-249. <https://doi.org/10.1093/jee/52.2.247>
- Shiraki T (1906) Neue Forficuliden Japans. Transactions of the Sapporo Natural History Society 1: 91-96. URL: <http://hdl.handle.net/2115/60754>
- Simberloff DS, Wilson EO (1969) Experimental zoogeography of islands: the colonization of empty islands. Ecology 50: 278-296. <https://doi.org/10.2307/1934856>
- Snyder TE (1916) Insects Injurious to Forests and Forest Products. 94. US Government Printing Office, Washington, USA, 95 pp.
- Srivastava GK (2003) Fauna of India and adjacent countries, Dermaptera part II: Anisolabioidea. Zoological Survey of India, Kolkata, India, 235 pp.
- Srivastava GK (2013) Fauna of India and the adjacent countries, Dermaptera Part III: Apachyoidea and Forficuloidea. Zoological Survey of India, Kolkata, India, 469 pp.
- Steinmann H (1979) A systematic survey of the species belonging in the genus *Labidura* Leach, 1815 (Dermaptera). Acta zoologica hungarica 25: 415-423.
- Steinmann H (1989a) Dermaptera. Catadermaptera II. Das Tierreich 105: 1-504.
- Steinmann H (1989b) World Catalogue of Dermaptera. Kluwer Academic Publishers, Dordrecht, Netherlands, 934 pp.
- Steinmann H (1990) Dermaptera. Eudermaptera I. Das Tierreich 106: 1-558.
- Stuart OP, Binns M, Umina PA, Holloway J, Severtson D, Nash M, Hedde T, Helden M, Hoffmann AA (2019) Morphological and molecular analysis of Australian earwigs (Dermaptera) points to unique species and regional endemism in the Anisolabididae family. Insects 10: 1-25. <https://doi.org/10.3390/insects10030072>
- Su ZH, Imura Y, Okamoto M, Osawa S (2004) Pattern of phylogenetic diversification of the Cycharini ground beetles in the world as deduced mainly from sequence comparisons of the mitochondrial genes. Gene 326: 43-57. <https://doi.org/10.1016/j.gene.2003.10.025>
- Talavera G, Lukhtanov V, Pierce NE, Vila R (2021) DNA Barcodes Combined with Multilocus Data of Representative Taxa Can Generate Reliable Higher-Level Phylogenies. Systematic Biology 71 (2): 382-395. <https://doi.org/10.1093/sysbio/syab038>
- Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis version 11. Molecular Biology and Evolution 38: 3022-3027. <https://doi.org/10.1093/molbev/msab120>
- Thompson J, Gibson TJ, Higgins D (2003) Multiple Sequence Alignment Using ClustalW and ClustalX. Current Protocols in Bioinformatics 00: 2.3.1-2.3.22.. <https://doi.org/10.1002/0471250953.bi0203s00>
- Thornton IW, Cook S, Edwards JS, Harrison RD, Schipper C, Shanahan M, Singadan R, Yamuna R (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VII. Overview and discussion. Journal of Biogeography 28: 1389-1408. <https://doi.org/10.1046/j.1365-2699.2001.00636.x>

- Tobiyama C (1985) Dermaptera. In: Tobiyama C, et al. (Ed.) Encyclopedia of Insect I. Sekaibunka-sha, Tokyo, 198–199 pp. [In Japanese].
- Vickery VR, Kevan DKM (1983) A monograph of the orthopteroid insects of Canada and adjacent regions. *Memoirs of the Lyman entomological Museum and Research Laboratory* 13 (1): 1-679.
- Vickery VR, Kevan DKM (1985) The insects and arachnids of Canada, Part 14: The grasshoppers, crickets, and related insects of Canada and adjacent regions. Agriculture Canada, Ottawa, Ontario, Canada, 918 pp.
- Vujić M, Vesović N, Šević M, Maričić M, Tot I (2022) A new greenhouse invader: the first report of the alien ring-legged earwig, *Euborellia annulipes* (Dermaptera, Anisolabididae) in Serbia, with the first checklist of earwigs of the country. *Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa"* 65 (2): 27-38. <https://doi.org/10.3897/travaux.63.e85829>
- Yamasaki T (1999) Dermaptera. In: Aoki J (Ed.) Pictorial Keys to Soil Animals of Japan. Tokai University Press, Hiratsuka, Japan, 811–814 (pictorial key) and p821–823 pp. [In Japanese].
- Zhang Z-Q (2013) Phylum Arthropoda. In: Zhang, Z.-Q. (Ed.) Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness (Addenda 2013). *Zootaxa* 3703: 17-26. <https://doi.org/10.11646/zootaxa.3703.1.6>

## Supplementary material

### Suppl. material 1: Table S1. Samples analysed in the present study [doi](#)

**Authors:** Yoshitaka Kamimura, Masaru Nishikawa, Junsuke Yamasako

**Data type:** Table

**Brief description:** Table summarising dermapteran samples used for the analysis of DNA barcodes.

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