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Gallancyra gen. nov. (Phthiraptera: Ischnocera), with an overview of the geographical distribution of chewing lice parasitizing chicken

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Abstract. The geographical range of the typically host-specific species of chewing lice (Phthiraptera) is often assumed to be similar to that of their hosts. We tested this assumption by reviewing the published records of twelve species of chewing lice parasitizing wild and domestic chicken, one of few bird species that occurs globally. We found that of the twelve species reviewed, eight appear to occur throughout the range of the host. This includes all the species considered to be native to wild chicken, except *Oxylipeurus dentatus* (Sugimoto, 1934). This species has only been reported from the native range of wild chicken in Southeast Asia and from parts of Central America and the Caribbean, where the host is introduced. Potentially, this discontinuous distribution is due to a low tolerance for dry environments, possibly exacerbated by competitive exclusion by *Cuclotogaster heterographus* (Nitzsch, 1866). Our examinations of *O. dentatus* also revealed that this species differs significantly from other species of *Oxylipeurus* in the male and female genitalia, head structure and chaetotaxy, and other morphological characters. We therefore here erect the monotypic genus *Gallancyra* gen. nov. for *O. dentatus*, and redescribe the type species.

Keywords. Phthiraptera, *Oxylipeurus*-complex, new genus, biogeography, domestic chicken.

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Introduction

The same species of chewing lice are often present throughout the range of a given host. For instance, Adams *et al.* (2005) found the geographical range of *Columbicola columbae* (Linnaeus, 1758) to be nearly world-wide, including areas where the host had been introduced. Similarly, *Osculonirmus limpidus* Mey, 1982, has been found in large parts of its host's range (Gustafsson & Bush 2017). However, the range of the host and the range of its lice do not always correspond completely. Clay (1976) summarized several examples of chewing louse species that appear to occur only in parts of their hosts' ranges. This includes several cases where different congeneric species of chewing lice occur in different parts of the host's range; further examples of this type of pattern have subsequently been published for many other host species (e.g., Johnson *et al.* 2002; Malenke *et al.* 2011; Gustafsson & Bush 2017).

The causes for local or regional absence of a species of chewing louse on a host are typically not known. In cases where the range of the host has expanded, either naturally or by human intervention, cases of "missing the boat" (Paterson & Gray 1997) may be common. This term describes the chance event that not all parasite species were present on the specific individuals that colonized a new area, and formed the basis for the range extension. For instance, not all louse species found in the hosts' native range have been found on introduced species in North America (Boyd 1951; Brown & Wilson 1975) and New Zealand (Paterson *et al.* 1999); though in some cases, the perceived absence of a louse species in an area may be due to insufficient sampling (e.g., Galloway & Palma 2008).

However, "missing the boat" events may be impossible to distinguish from local extinction after an introduction event ("drowning on arrival"; Paterson *et al.* 1999). Paterson *et al.* (1999) predicted that 1–2 chewing louse species would normally be lost per introduction event. Intuitively, instances of "missing the boat" should decrease with increasing numbers of introduction events, especially when introduction events may originate from different source populations. Unless there is some bias in either which species of chewing lice are present on the source population or which species of chewing lice survive the introduction event, these losses should be compensated for if multiple introduction events are involved.

Such biases may include the impact of the external environment on the population structure of chewing lice on a given host. For instance, Moyer *et al.* (2002) showed that low ambient humidity decreased both the number of lice on bird and the number of birds that were infested with lice. Ambient humidity has since been demonstrated to have an effect on chewing louse distribution also in wild birds (Bush *et al.* 2009; Malenke *et al.* 2011). Notably, Bush *et al*. (2009) showed that ambient humidity may affect different louse species differently.

Data on the presence of chewing lice on birds is normally patchy, and the true geographical range of most louse species is unknown. Most described species of chewing lice have been collected only once or a few times, often from the same region, and very few hosts have been sampled extensively for lice throughout the range of the host.

The domestic chicken, *Gallus gallus* (Linnaeus, 1758), is among the most widely distributed bird species in the world, occurring almost everywhere there are humans. Due to the economic importance of chicken, numerous surveys of infectious and parasitic diseases of chicken have been conducted, collectively covering almost all faunal regions where chicken occur (e.g., Table 1). As a result, domestic chicken has among the best-known louse faunas of any bird species. In total, 22 species of chewing lice are known from domestic chicken across the world (Table 2).

We here summarize the known distribution of several species of chewing lice with a focus on *Lipeurus dentatus* Sugimoto, 1934, hitherto placed in the genus *Oxylipeurus* Mjöberg, 1910 (Price *et al.* 2003). This species is rarely reported in the literature (Table 1), and was not included in a recent overview of the chewing lice of chicken (Khan *et al.* 2016). We redescribe and reillustrate this species here, and erect a new genus, *Gallancyra* gen. nov., based on significant morphological differences between this species and all other species of the *Oxylipeurus*-complex. We also summarize the geographical distribution of eleven other chewing louse species occurring on domestic and wild chicken, based on published records. We hope this redescription and overview will enable veterinarians and louse researchers to identify *G. dentata* gen. et comb. nov. in future surveys. This may shed some light over the discontinuous geographical distribution of this species, and over the development of differences in geographical distribution between different species of chewing lice parasitizing the same host.

Table 1 (continued on next three pages)**.** Summary of the geographical distribution of *Gallancyra dentata* (Sugimoto, 1934) gen. et comb. nov. The following published reports and checklists were consulted to establish the geographical range of twelve species of chewing lice parasitizing domestic and wild chicken. Kéler (1939) summarized the known distribution of the goniodid species at the time, and we here refer to his summary for brevity. Slides deposited at the NHMUK but not previously published are referred to with their slide identification number (NHMUKXXXXXXXXXX) and '(NHMUK)'. Locality data for specimens marked 'This study' can be found under the redescription of *G. dentata* gen. et comb. nov.

Region and country	*Gallancyra dentata* present	Source
		Afrotropical
"Africa"	No	Emerson (1956)
Algeria	No	Kéler (1939); Ilyes *et al.* (2013); Meguini *et al.* (2018)
Benin	No	Love *et al.* (2017)
Egypt	No	Hafez & Madbouly (1966); El-Aw *et al.* (2008)
Ethiopia	No	Emerson (1956); Ashenafi & Yimer (2005); Belihu *et al.* (2009); Tolossa *et al.* (2009); Mekuria & Gezahegn (2010); Amede *et al.* (2011); Tolossa & Tafesse (2013); Tamiru *et al.* (2014); Alemu *et al.* (2015); Zeryuhan & Yohannes (2015); Kebede *et al.* (2017); Mata *et al.* (2018); Serda & Abdi (2018)
Ghana	No	Aboagye *et al.* (2014)
Kenya	No	Emerson (1956); Mungube *et al.* (2008)
Liberia	No	Peters (1931); Clay (1940); Emerson (1956)
Libya	No	Gabaj *et al.* (1993); Mansur *et al.* (2019)
Malawi	No	Banda (2011)
Nigeria	No	Clay (1940); Adene & Dipeolu (1975); Fabiyi (1980, 1986, 1996); Okaeme (1988); George *et al.* (1992); Zaria *et al.* (1996); Sadiq *et al.* (2003); Ikpeze *et al.* (2008); Natala *et al.* (2009); Ekpo *et al.* (2010); Bala *et al.* (2011); Edusomwan *et al.* (2011); Usman *et al.* (2012); Odenu *et al.* (2016); Lawal *et al.* (2016, 2017); Emmanuel *et al.* (2017); Bassey & Marroh (2018); Edusomwan & Igetei (2018); Ahaotu *et al*. (2019)
Saudi Arabia	No	Aldryhim (1991); Gharsan & Elhassan (2019)
South Africa	No	Bedford (1924); Kéler (1939); Mukaratirwa & Khumalo (2012); Moyo *et al.* (2015)
Sudan	No	Kéler (1939)
Tanzania	No	Swai *et al.* (2010)
Tunisia	No	Kaboudi *et al*. (2019)
Uganda	No	Clay (1940)
Zimbabwe	No	Permin *et al.* (2002); Mukaratirwa & Hove (2009); Percy *et al.* (2012)
		Indo-Malayan
Bangladesh	No	Shanta *et al.* (2006)
Cambodia	No	Segal *et al.* (1968)[a]

Table 1 (continued)**.** Summary of the geographical distribution of *Gallancyra dentata* (Sugimoto, 1934) gen. et comb. nov.

Region and country	*Gallancyra dentata* present	Source
India	No	Kéler (1939); Clay (1940); Ansari (1946); Emerson (1956); Chopra (1968); Trivedi *et al.* (1991, 1992); Lonc *et al.* (1992); Saxena *et al.* (2004); Salam *et al.* (2009); Bhat *et al.* (2014); Mishra *et al.* (2016a, 2016b)
	Yes	This study
Indonesia	No	Kéler (1939); Clay (1940)
Laos	No	Emerson & Elbel (1957a)
	Yes	Segal *et al*. (1968)
Malaysia	No	Amin-Babjee *et al.* (1997); Rahman & Haziqah (2015); Suhaila *et al*. (2015)
	Yes	This study
Myanmar	No	Clay (1940)
Philippines	Yes	Emerson & Elbel (1957a); Manuel & Anceno (1981); Portugaliza & Bagot (2015)
“Southeast Asia”	No	Emerson (1956)
Sri Lanka	No	Clay (1940)
Taiwan	Yes	Sugimoto (1930, 1934)
Thailand	Yes	Clay (1940); Emerson & Elbel (1957a); Segal *et al*. (1968); NHMUK010682397 (NHMUK)
Vietnam	No	Clay (1940); Segal *et al*. (1968)
Nearctic		
Canada	No	Kéler (1939); Clay (1940); Emerson (1956); Thompson & Hosking (1957); Thompson (1968)
“North America”	No	Emerson (1956)
USA	No	Kéler (1939); MacCreary & Catts (1954); Emerson (1956); Murillo & Mullens (2016)
Neotropic		
Argentina	No	Kéler (1939); Ferrero *et al.* (2004)
Bahamas	No	Peters (1931); Kéler (1939)
Brazil	No	Emerson (1956); Figueiredo *et al.* (1993); Oliveira *et al.* (1999); Santos-Prezoto *et al.* (2003); Guerra *et al.* (2008); Santos *et al.* (2011)
“British West Indies”	No	Emerson (1956)
“Central America”	No	Emerson (1956)
Chile	No	González-Acuña *et al.* (2009)
Colombia	No	Marín-Gómez & Benavides-Montaño (2007)
Costa Rica	Yes	Hernandez-Divers *et al.* (2008)
Cuba	Yes	De Zayas (1941); Emerson (1956); Černy (1969)
Ecuador	No	Hernandez-Divers *et al.* (2006)
Guyana	No	Clay (1940)

Table 1 (continued)**.** Summary of the geographical distribution of *Gallancyra dentata* (Sugimoto, 1934) gen. et comb. nov.

Region and country	*Gallancyra dentata* present	Source
Mexico	No	Clay (1940); Cruz *et al.* (2013); Sánchez-Montes *et al.* (2018)
Nicaragua	Yes	Emerson (1956)
Panama	Yes	Peters (1935); Emerson (1956)
Puerto Rico	No	Emerson (1956); Maldonado-Cipriles & Miro-Mercado (1978)
	Yes	NHMUK010682387 (NHMUK)
Venezuela	No	Peters (1931); Emerson (1956); Martínez de Chirinos *et al.* (2001)
Oceania		
Australia	No	Emerson (1956); Palma & Baker (1996)
New Guinea	Yes	This study
New Zealand	No	Palma (2017)
"Various islands in Central Pacific Area"	Yes	Emerson (1956)
Palearctic		
Bulgaria	No	Preiesov (1998); Prelezov & Koinarski (2006)
China	No	Emerson (1957); Liu (1985); Arnold (2008); Wang *et al.* (2010)
Czech Republic	No	Sychra *et al.* (2008)
"Europe"	No	Emerson (1956)
Finland	No	Backlund (1934); Kéler (1939); Hackman (1994)
France	No	Séguy (1944)
Germany	No	Kéler (1939); Mey (2003)
Holland	No	Kéler (1939)
Hungary	No	Kéler (1939)
Iran	No	Rafyi *et al.* (1968); Vazirianzadeh *et al.* (2007); Eslami *et al.* (2009); Rezaei *et al.* (2016); Mirzaei *et al*. (2016)
Iraq	No	Aliraqi & Amin (2007); Abdullah & Mohammed (2013); Thamer *et al.* (2016); Al-Shaibani *et al.* (2018)
Japan	No	Kéler (1939); Matsudaira & Kaneko (1969)
Kazakhstan	No	Blagoveshtchensky (1940)
Pakistan	No	Buriro & Akbar (1978); Shahjehan & Iqbal (1995); Naheed & Adna (2004); Nadeem *et al.* (2007); Naz *et al.* (2016)
Poland	No	Kéler (1939); Lonc *et al.* (1992)
Romania	No	Clay (1940); Pisica (1985); Morariu *et al.* (2008)
Russia	No	Blagoveshtchensky (1940)
South Korea	No	Noh *et al.* (1989)
Spain	No	Martin-Mateo *et al.* (1980)

Table 1 (continued)**.** Summary of the geographical distribution of *Gallancyra dentata* (Sugimoto, 1934) gen. et comb. nov.

Region and country	*Gallancyra dentata* present	Source
Sweden	No	Kéler (1939); Jansson *et al.* (2004); Gustafsson *et al.* (2019)
Tajikistan	No	Blagoveshtchensky (1940, 1951)
Turkey	No	Mimioglu (1952); Dik *et al.* (1999); Köroglu *et al.* (1999); Aldemir (2004); Sayin Ipek & Saki (2009); Orunç & Biçek (2009); Inci *et al.* (2010); Döner & Yaman (2015)
Ukraine	No	Blagoveshtchensky (1940); Yevstafieva (2015)
United Kingdom	No	Kéler (1939); Clay (1940); Ryder (1967)

[a] Segal *et al.* (1968) also report "*Lipeurus heteroglyphus*" from several localities. No such species has ever been described, and it is unclear whether this refers to *Cuclotogaster heterographus*, *Lipeurus tropicalis*, or some other species. We have omitted these records in Fig. 2.

Fig. 1. Geographical distribution of three species of ischnoceran chewing lice parasitizing wild and domestic chicken (*Gallus* spp). Each circle is divided into three sectors, representing the three louse species: upper left = *Goniodes gigas* (Taschenberg, 1879); upper right = *Goniodes dissimilis* Denny, 1842; lower = *Goniocotes gallinae* (De Geer, 1778). Black sectors indicate that this louse species is known from this country, whereas hollow sectors indicate that we have found no published records of this species in this country. Presence of the three species of chewing lice in a country is based on the reports summarized in Table 1.

Table 2 (continued on next page)**.** Species of chewing lice reported from domestic chicken. Data sources are Emerson (1956) and Price *et al.* (2003), unless otherwise stated. Note that this list contains fewer species than that provided by Khan *et al.* (2016). This discrepancy is due to Khan *et al.* (2016) listing synonyms as separate species, and including reports of lice collected from domestic pigeons. Moreover, some species listed by Khan *et al.* (2016) are not reported in the sources they cite; these species have been excluded here.

Chewing louse species	Notes and sources
Amblycera	
Amyrsidea powelli (Bedford, 1920)	Fabiyi (1986, 1996)[a]
Amyrsidea saudiensis Alahmed *et al.*, 2017	Alahmed *et al*. (2017); presently known only from Saudi Arabia[b]
Colpocephalum turbinatum Denny, 1842	Oliveira *et al.* (1999)[c]
Menacanthus cornutus (Schömmer, 1913)	
Menacanthus longiscleritus Naz & Rizvi, 2016	Naz & Rizvi (2016); presently known only from Pakistan[d]
Menacanthus numidae (Giebel, 1874)	Séguy (1944); Martín-Mateo (1973, 1974a, 1974b); Martín-Mateo *et al*. (1980)[e]
Menacanthus pallidulus (Neumann, 1912)	
Menacanthus stramineus (Nitzsch, 1818)	
Menopon gallinae (Linnaeus, 1758)	[f]
Ischnocera	
Campanulotes compar (Burmeister, 1838)	Ferreira *et al.* (2013)[g]
Chelopistes meleagridis (Linnaeus, 1758)	Martínez de Chirinos *et al.* (2001); Meguini *et al.* (2018)[h]
Cuclotogaster heterographus (Nitzsch, 1866)	[i]
Cuclotogaster occidentalis (Tendeiro, 1954)	Fabiyi (1986, 1996)[j]
Gallancyra dentata (Sugimoto, 1934)	
Goniocotes gallinae (De Geer, 1778)	
Goniocotes maculatus (Taschenberg, 1882)	[k]
Goniocotes microthorax (Stephens, 1829)	Sychra *et al.* (2008)[l]
Goniodes dispar Burmeister, 1838	Blagoveshtchensky (1951)[m]
Goniodes dissimilis Denny, 1842	
Goniodes gigas (Taschenberg, 1879)	[n]
Lagopoecus sinensis (Sugimoto, 1930)	
Lipeurus caponis (Linnaeus, 1758)	[o]
Lipeurus tropicalis Peters, 1931	[p]

[a] The natural host of *A. powelli* is *Numida meleagris* (Linnaeus, 1758), and these lice may be established on domestic chicken only locally.

[b] First reported by Aldryhim (1991), and may represent a straggler from another bird. Specimens of the same species were also found on *Coturnix coturnix* (Linnaeus, 1758), but the species is apparently morphologically different from the *Amyrsidea* species normally found on that host.

[c] The natural host for *C. turbinatum* is *Columba livia* Gmelin, 1789. Oilveira *et al.* (1999) suggested that chicken may be an occasional natural host of *C. turbinatum*, as there was no risk of contamination during their examination. We know of no other reports of *C. turbinatum* on chicken. Martínez de Chirinos *et al.* (2001) reported

Table 2 (continued)**.** Species of chewing lice reported from domestic chicken.

Colpocephalum sp. from chicken, which presumably is also *C. turbinatum*. This host switch is likely due to hosts living in close proximity, but it is possible that *C. turbinatum* has secondarily established locally on domestic chicken.

[d] It is not clear from the original description how this species differs from other species of *Menacanthus* from the same host, as most stated differences appear to be in measurements. Measurements of both *M. longiscleritus* and the other species of the genus found on the same host are given without ranges. It is therefore not possible to establish whether the differences in dimensions are due to the small sample size. The only useful morphological character stated to be diagnostic is the length of the genital sclerite, which is twice as long in *M. longiscleritus* as in any of the other species of *Menacanthus* occurring on chicken. It is not clear whether this is sufficient to merit status as a separate species, but we tentatively accept it as valid here. It is known only from two males and one nymph collected in Pakistan. The natural host of this species may thus be some other species. Notably, sclerites of similar length are found in some species of *Menacanthus* from passeriform hosts (Price 1977), but no comparison with species parasitizing passeriform hosts were included in the original description.

[e] The natural host of *M. numidae* is *Numida meleagris*, and records from domestic chicken likely originate from stragglers among birds in mixed poultry flocks.

[f] Emerson & Elbel (1957b) reported this species from *Lophura diardi* (Bonaparte, 1856).

[g] Almost certainly stragglers, as the natural host of *C. compar* is *Columba livia* Gmelin, 1789.

[h] The natural host of *C. meleagridis* is *Meleagris gallopavo* Linnaeus, 1758, and reports of this species from domestic chicken likely originate from stragglers among birds in mixed poultry flocks.

[i] Emerson (1956) noted that this species has never been collected from wild chicken, and that the natural host is most likely some species of partridge in the genus *Alectoris* Kaup, 1829. It has recently been recorded from domestic turkey, indicating that it is capable to dispersing to new hosts (Dik *et al*. 2015).

[j] The natural host of *Cuclotogaster occidentalis* is *Pternistis bicalcarata* (Linnaeus, 1766) (Tendeiro 1958). Fabiyi (1986) found it on both domestic chicken and *Numida meleagris*.

[k] The natural host of *G. maculatus* is *Numida meleagris*, but it was originally described from domestic chicken. The only subsequent records of *G. maculatus* on domestic chicken appears to be Müller (1927) and Blagoveshchensky (1951); however, it is not clear from these publications how it was established that these lice were not *G. gallinae*. We include this species here for completeness.

[l] The natural hosts of *Goniodes microthorax* are *Perdix perdix* (Linnaeus, 1758) and *Alectoris chukar* (Gray, 1830). Sychra *et al.* (2008) found this species only on chickens that were reared in a pheasant farm, and presumed this record to be the result of straggling.

[m] *Goniodes dispar* are normally found on hosts in the genera *Alectoris* Kaup, 1829, and *Perdix* Linnaeus, 1758. Blagoveshtchensky's records may derive from misidentifications or stragglers, but may also represent a local population established on domestic chicken in Tajikistan. To our knowledge, this is the only report of *G. dispar* on domestic chicken.

[n] Emerson (1956) believed that *Goniodes gigas* originated from some species of guineafowl, as the same species is known from this host group.

[o] Reports of this species from peacock (e.g., Marniche *et al*. 2017) may represent either misidentifications, stragglers, or local host switches, and do not suggest that this is the natural host of *L. caponis*.

[p] *Lipeurus tropicalis* is also known from *Numida meleagris* (e.g., Clay 1938; Emerson 1956). Its closest relative, *Lipeurus lawrensis* Bedford, 1929, occurs exclusively on guineafowl, which suggested to Emerson (1956) that some species of guineafowl may be the natural host of *L. tropicalis*, and that this species has subsequently spread throughout chicken populations across the world.

Material and methods

All examined specimens were previously slide-mounted in Canada balsam and deposited at the Natural History Museum, London, United Kingdom (NHMUK). Specimens were examined in an Eclipse Ni (Nikon Corp., Tokyo, Japan) microscope fitted with a drawing tube. Illustrations were made by hand, scanned, and edited in GIMP (www.gimp.org). Measurements were made from live images in Evos FL Auto (Thermo Fischer Scientific, Hong Kong, China), comprising the following dimensions (all in millimeters): AW = abdominal width (at posterior end of segment V); HL = head length (at midline); HW = head width (at temples); PRW = prothoracic width; PTW = pterothoracic width; TL = total length (at midline). Terminology for morphological and setal characters (and their abbreviations) follows Gustafsson & Bush (2017): *a2* = anterior seta 2; *ads* = anterior dorsal seta; *pmes* = posterior mesosomal seta; *pst1–2* = parameral setae 1–2; *vms* = vulval marginal seta; *vss* = vulval submarginal seta. All setae mentioned in the text are marked in the figures. Host taxonomy follows Clements *et al.* (2019).

To assess the geographical range of *G. dentata* gen. et comb. nov. and other lice known from domestic chicken, we performed an extensive literature review. Searches were made primarily in Google Scholar (scholar.google.com) and on the louse literature database in Phthiraptera.info, using each of the louse species known from domestic chicken as search terms, in isolation or in combination with the search terms 'domestic chicken', 'poultry', and 'hen'. We also contacted our international network of colleagues and, in some cases, corresponding authors of publications we could not find. No attempt was made to find all published literature from before 1934, the year *Lipeurus dentatus* was described, as these are unlikely to contain identifiable references to this species. Ultimately, it is possible that not all published records could be obtained, as they were not caught in our searches. This applies particularly to reports in older journals or smaller veterinary journals that do not have digitized summaries, content lists, or abstracts, and to reports in languages other than English that do not include the scientific names of the

Fig. 2. Geographical distribution of four species of ischnoceran chewing lice parasitizing wild and domestic chicken (*Gallus* spp.). Each circle is divided into four sectors, representing the four louse species: upper left = *Lipeurus caponis* (Linnaeus, 1758); upper right = *Lipeurus tropicalis* Peters, 1931; lower left = *Cuclotogaster heterographus* (Nitzsch, 1866); lower right = *Lagopoecus sinensis* (Sugimoto, 1930). Black sectors indicate that this louse species is known from this country, whereas hollow sectors indicate that we have found no published records of this species in this country. Presence of the four species of chewing lice in a country is based on the reports summarized in Table 1.

lice we searched for. Reports published in conference proceedings or outside the scientific literature have also not been searched comprehensively.

Results

The known geographical distributions of eight species of ischnoceran chewing lice and four species of amblyceran chewing lice known from domestic chicken are summarized in Figs 1–4, based on the sources listed in Table 1. Note that these maps do not include species such as *Chelopistes meleagridis* (Linnaeus, 1758) (Meguini *et al.* 2018) or *Goniocotes microthorax* (Stephens, 1829) (Sychra *et al.* 2008) that represent stragglers originating from mixed poultry flocks. Cases where the lice appear to have been erroneously identified to genus or species level (e.g., Sadiq *et al.* 2003) are also not included.

Comparisons between specimens of *Oxylipeurus dentatus* and other lice in the genus *Oxylipeurus* indicate that this species is morphologically distinct, and very different from other species in the *Oxylipeurus*-complex. We here describe a new genus for this species, *Gallancyra* gen. nov.

Fig. 3. Geographical distribution of four species of menoponid chewing lice parasitizing wild and domestic chicken (*Gallus* spp.). Each circle is divided into four sectors, representing the four louse species: upper left = *Menacanthus cornutus* (Schömmer, 1913); upper right = *Menacanthus stramineus* (Nitzsch, 1818); lower left = *Menacanthus pallidulus* (Neumann, 1912); lower right = *Menopon gallinae* (Linnaeus, 1758). Black sectors indicate that this louse species is known from this country, whereas hollow sectors indicate that we have found no published records of this species in this country. The presence of the four species of chewing lice in a country is based on the reports summarized in Table 1. Note that the menoponid species *Amyrsidea powelli* (Bedford, 1920) appears to be established on chicken in Nigeria (Fabiyi 1986, 1996), and that *Menacanthus longiscleritus* Naz & Rizvi, 2016, has been described from chicken in Pakistan. These are not shown on the map.

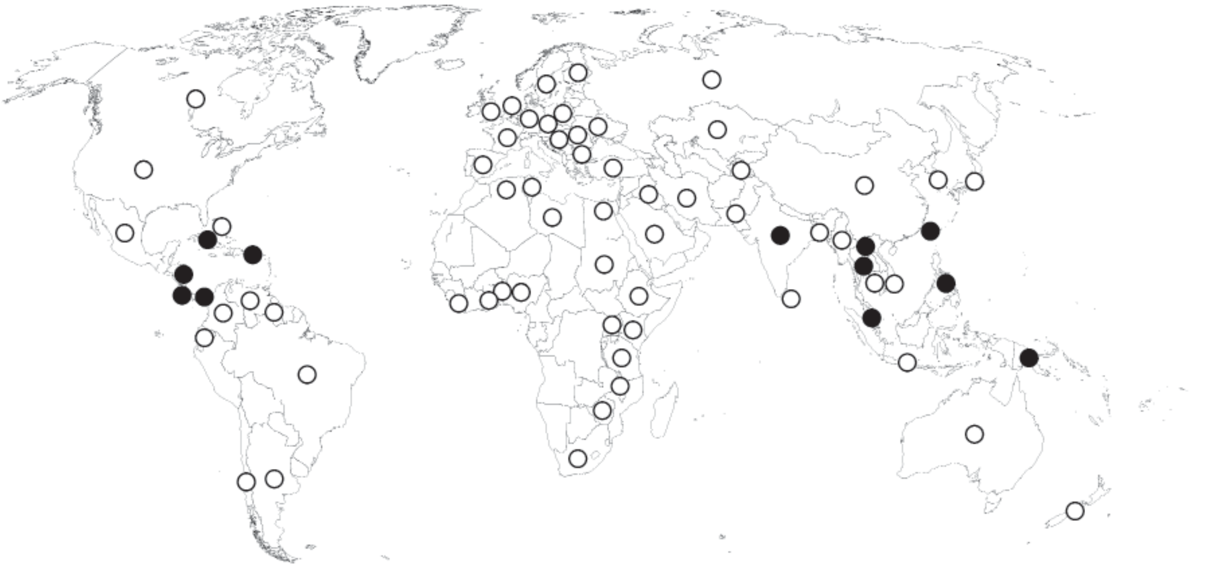


Fig. 4. Geographical distribution of the known records of *Gallancyra dentata* (Sugimoto, 1934), based on the reports cited in Table 1. Black circles indicate countries where *G. dentata* has been reported at in at least one survey, including the present report. Hollow circles indicate countries for which surveys of domestic chicken have been published, but *G. dentata* has not been found. In addition to the areas indicated on the map, Emerson (1956) reported *G. dentata* from "various islands in the Central Pacific Area", but gave no detail.

Order Phthiraptera Haeckel, 1896
Suborder Ischnocera Kellogg, 1896
Family Philopteridae Burmeister, 1838
Oxylipeurus-complex

Genus ***Gallancyra*** Gustafsson & Zou gen. nov.
urn:lsid:zoobank.org:act:7C0E09CF-B1F7-4A97-81E5-74DF2C0CD4C6
Figs 5–14

Lipeurus Nitzsch, 1818: 292 (*in partim*).
Oxylipeurus Mjöberg, 1910: 91 (*in partim*).
Reticulipeurus Kéler, 1958: 332 (*in partim*).

Type species

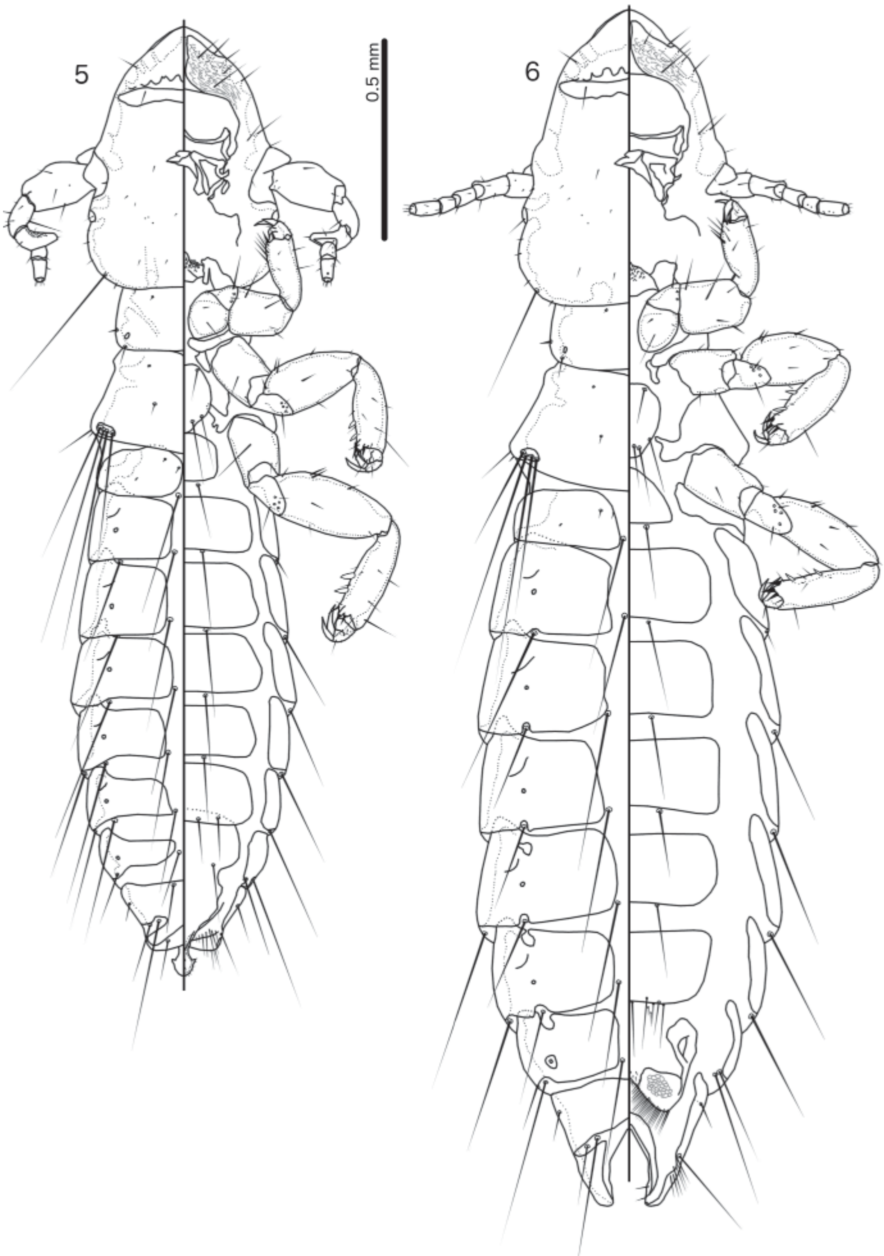
Lipeurus dentatus Sugimoto, 1934.

Diagnosis

Lipeurus dentatus was previously placed either in *Oxylipeurus* (e.g., Price *et al.* 2003) or in *Reticulipeurus* (e.g., Mey 2003). Of these two genera, *Gallancyra* is most similar to *Reticulipeurus* (see, e.g., Kéler (1958) and Gustafsson *et al*. (2020) for illustrations of most of these characters in *Reticulipeurus*, and Mey (1990) for corresponding characters in *Oxylipeurus* s. str.; see also Table 3), with which it shares the following characters: stylus extends beyond distal margin of abdomen (Fig. 7); intertergal plates absent (Figs 5–6); mesosome large, with hook-shaped antero-lateral corners, rugose distal margins, and ventral gonopore associated with transverse sclerite which bears setae laterally (Fig. 13); parameres symmetrical, at most about twice as long as mesosome, and roughly finger-shaped (Fig. 12); female subgenital plate much reduced, typically divided medially (Fig. 8); vulval opening converging medially to single, typically narrow, point, not forming convex lobes laterally (Fig. 12); post-antennal suture absent (Fig. 9).

Etymology

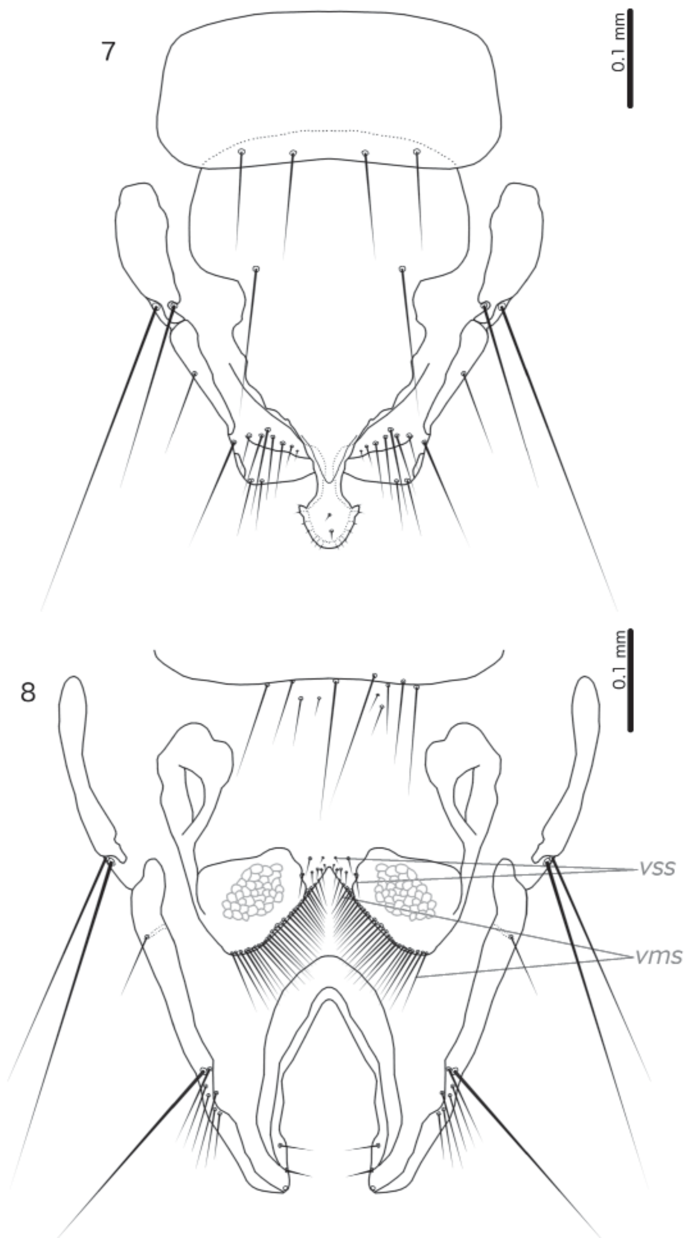
Gallancyra is constructed from the Latin name '*gallus*', for 'chicken' and the genus of the type host of the type species, and the Greek word '*ancyra*', for 'anchor'. This refers to the shape of the stylus of the male subgenital plate. The gender is feminine.



Figs 5–6. *Gallancyra dentata* (Sugimoto, 1934) gen. et comb. nov. ex *Gallus gallus* (Linnaeus, 1758) (NHMUK010682393). **5**. Habitus, ♂, dorsal and ventral view. **6**. Habitus, ♀, dorsal and ventral views. Legs II and III distorted in all examined males, here illustrated approximately, and rotated compared to how they are in the slide specimen.

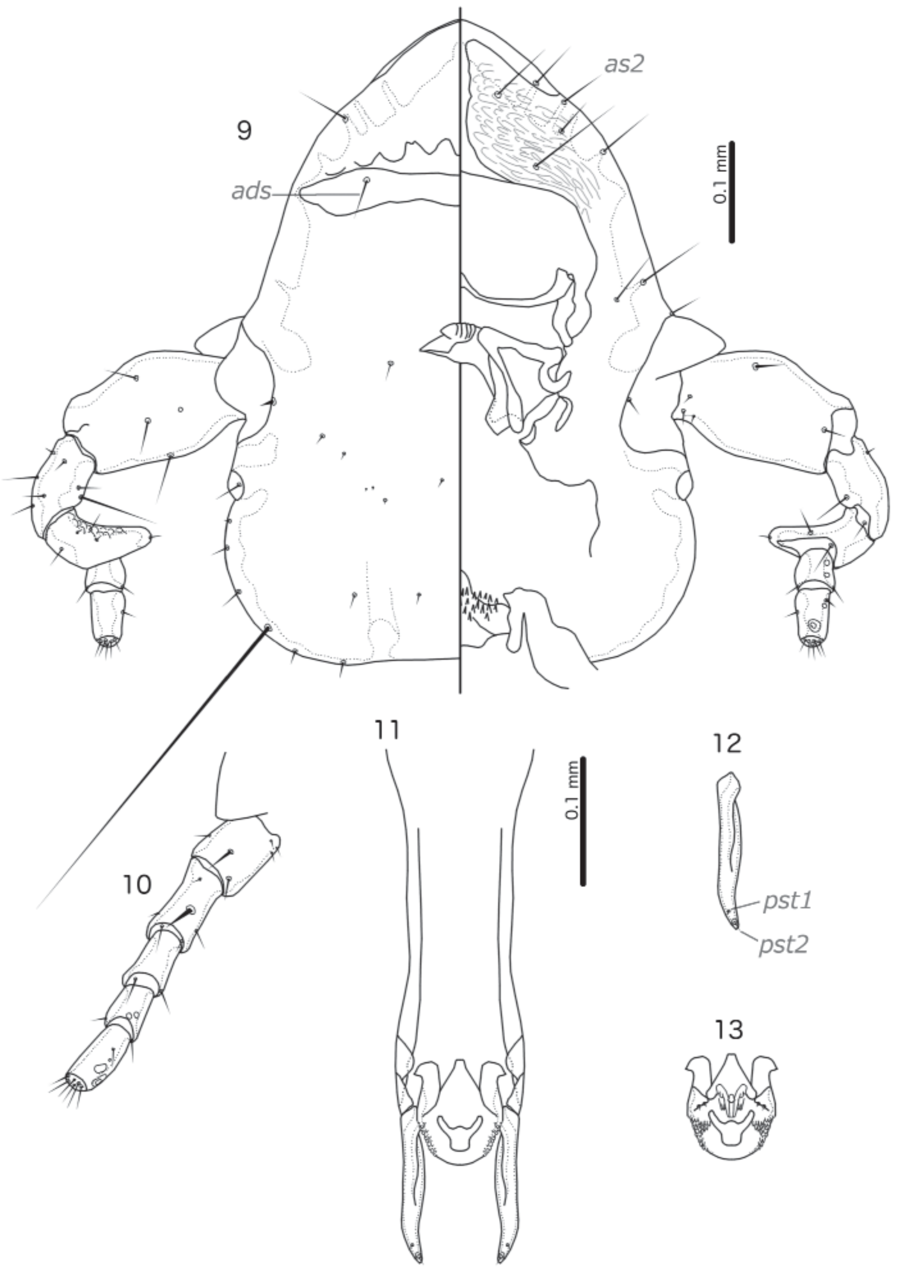
Differential diagnosis

Gallancyra gen. nov. can be separated from *Reticulipeurus* by the following characters: preantennal head pointed in *Gallancyra* gen. nov. (Fig. 9), but rounded in *Reticulipeurus*; preantennal head in *Gallancyra* gen. nov. ventrally with clypeo-labral suture that divides sclerotized section of ventral head into two lobes, and that expands in anterior end, seemingly making ventral side of frons hyaline (Fig. 9), but without any clypeo-labral suture and with no ventral hyaline region in *Reticulipeurus*; tergopleurites with clear reticulation at least laterally on some segments in *Reticulipeurus*, but without clear reticulation in *Gallancyra* gen. nov. (Figs 5–6); stylus arising from distal margin and with protruding section expanded into anchor-shape in *Gallancyra* gen. nov. (Fig. 7), but arising subterminally and with protruding section not or only little expanded, and never anchor-shaped in *Reticulipeurus*; rugose section of distal mesosome



Figs 7–8. *Gallancyra dentata* (Sugimoto, 1934) gen. et comb. nov. ex *Gallus gallus* (Linnaeus, 1758) (NHMUK010682393). **7**. Male subgenital plate and terminal end of abdomen, ventral view. **8**. Female subgenital plate and terminal end of abdomen, ventral view. Abbreviations: *vms* = vulval marginal setae; *vss* = vulval submarginal setae.

limited to lateral margins and expanding medially in anterior end in *Gallancyra* gen. nov. (Fig. 13), but typically limited to distal margin and not expanded in anterior end in *Reticulipeurus*; sclerotized plate present on distal mesosome in *Gallancyra* gen. nov. (Fig. 13), but absent in *Reticulipeurus*; *pst1–2* placed close-together subterminally, and both with visible microsetae in *Gallancyra* gen. nov. (Fig. 12), but *pst1* is a sensillus and typically placed well proximal of *pst2* in *Reticulipeurus*; subvulval sclerites present in *Reticulipeurus*, but absent in *Gallancyra* gen. nov. (Fig. 8).



Figs 9–13. *Gallancyra dentata* (Sugimoto, 1934) gen. et comb. nov. ex *Gallus gallus* (Linnaeus, 1758) (NHMUK010682393). **9**. Male head, dorsal and ventral views. **10**. Female antenna, ventral view. **11**. Male genitalia, dorsal view. **12**. Male paramere, dorsal view. **13**. Male mesosome, ventral view. Female antenna at same scale as male head. Abbreviations: *ads* = anterior dorsal seta; *as2* = anterior seta 2; *pst1–2* = parameral setae 1–2. All genitalic component drawn at same scale.

Table 3. Morphological comparison of *Gallancyra* gen. nov., *Reticulipeurus* Kéler, 1958 and *Oxylipeurus* Mjöberg, 1910. Note that genitalia of *Oxylipeurus* s. str. are hard to homologize with those of other genera in the complex based on published illustrations (e.g., Mey 1990). In particular, the mesosome of species in this genus appears to be much reduced and fused to the basal apodeme.

Characters	*Gallancyra* gen. nov.	*Reticulipeurus* Kéler, 1958	*Oxylipeurus* s. str. Mjöberg, 1910
Frons	Pointed	Rounded	Pointed or rounded
Hyaline margin	Prominent ventrally	Absent	Absent
Ventral carina	Medianly interrupted	Medianly continuous	Medianly continuous
Post-antennal suture	Absent	Absent	Present
Reticulation of tergopleurites	Absent	Present but variable in extent	Absent
Intertergal plates	Absent	Absent	Present
Stylus position	Arising terminally	Arising subterminally	Arising terminally
Stylus length	Reaching beyond distal margin of abdomen	Reaching beyond distal margin of abdomen	Not reaching distal margin of abdomen
Stylus shape	Anchor-shaped	More or less equal in width throughout	Short and blunt
Female subgenital plate	Much reduced, divided medianly	Much reduced, divided or continuous medianly	Not reduced, medianly continuous
Vulval margin	Without lateral lobes	Without lateral lobes	With lateral lobes
Subvulval plates	Absent	Present	Unknown? [1]
Mesosome	Large, anterior ends hook-shaped	Large, anterior ends hook-shaped	Much reduced, may be absent
Rugose areas	Mainly lateral	Across all or most of distal margin	Absent
Distal sclerotized plate of mesosome	Present	Absent	Absent
Gonopore	With transverse sclerite bearing setae	With transverse sclerite bearing setae	Much reduced
Parameres	Symmetrical, roughly finger-shaped	Symmetrical, roughly finger-shaped	Asymmetrical, roughly triangular
pst1–2	Close together subterminally, both microsetae	Separated, *pst1* typically sensillus	Unknown? [1]

[1] This character is not clearly visible in the illustrations of Mey (1990), and we have not examined any specimens belonging to any species of *Oxylipeurus* s. str.

The structure of the preantennal head (Fig. 9) and the stylus (Fig. 7) of *Gallancyra dentata* gen. et comb. nov. are unique within the *Oxylipeurus*-complex and, to the extent of our knowledge, the entire Ischnocera. These two characters should separate *Gallancyra* gen. nov. from all other genera of ischnoceran chewing lice.

Description

Both sexes

Head overall trapezoidal, widening posteriorly, but with frons triangularly extended into medial point (Fig. 9). Hyaline margin seemingly present as very narrow translucent band near frons; this is not visible in all examined specimens, and in many cases differs between sides of the same specimen. Marginal carina uninterrupted, but displaced dorsally anterior to *as2*; most preantennal setae with clear attendant canals going through the marginal carina. Internal thickenings present anterior to *ads*, varying in extent among specimens. Dorsal preantennal suture present, enveloping aperture of *ads*, and approaching but not reaching lateral margins of head. Ventrally, head capsule appears to be hyaline medially and anteriorly, with sclerotized sections densely decorated with semi-reticulated pattern. Ventral carina not clearly visible. Head and antennal chaetotaxy as in Fig. 9. Preantennal nodi large, bulging. Antennae sexually dimorphic (Figs 9–10). Pre-and postocular nodi present. Occipital carinae not visible. Temporal carinae visible only in posterior section, connecting to bulbous nodi. Gular plate diffuse, approximately as in Fig. 9; area around gular plate with conspicuous spiculate thickenings.

Thoracic segments and chaetotaxy as in Figs 5–6. Pronotum and pteronotum each medially continuous. Meso- and metanota fused into single plate. Metepisterna broad, medial end with finger-like extension that may reach pteronotum. Legs and leg chaetotaxy as in Fig. 14; anterior setae of trochanters II–III may be present, but not visible in examined species as legs are distorted. At least two setae on medial margin of tibiae II–III appear to be hyaline and larger than other setae (illustrated as hollow). Abdominal segments and chaetotaxy as in Figs 5–6. Tergopleurites II–VIII medially divided, tergopleurite IX+X medially continuous. Internal thickening of antero-lateral corners of tergopleurites present on segments III–VII. Sternal plates present on segments II–VII.

Male

Antennae as in Fig. 9; scape, pedicel, and flagellomere I expanded compared to female; flagellomere I with thumb-like extension and rugose medial surface. Subgenital plate seemingly protruding internally to sternal plate VII (Fig. 7). Stylus arises from distal margin of subgenital plate and reaches beyond distal margin of abdomen; distal section of stylus expanded, with lateral margins extended into small “hooks” in anterior end. Basal apodeme slender, lateral margins slightly concave, anterior end diffuse (Fig. 11). Mesosome with antero-lateral sclerotized hook-shaped extensions, distally with rounded margin and rugose area only laterally (Fig. 13). Gonoporal complex small compared to mesosome. Sclerotized plate with arched antero-lateral extensions. Parameres as in Fig. 12; *pst1–2* both microsetae.

Female

Antennae as in Fig. 10. Distal end of abdomen as in Fig. 8. Subgenital plate divided medially, with conspicuous honey-comb reticulation in central parts. Vulval margin deeply concave. Most distal anal seta apparently modified to sensilla, as only alveoli are visible in examined specimens.

Host distribution

Presently only known from hosts in the genus *Gallus* Brisson, 1760. This genus is closely related to the genus *Bambusicola* Gould, 1836 (Armstrong *et al.* 2001; Dyke *et al.* 2003; Kimball & Braun 2008; Wang *et al.* 2013), but no species of the *Oxylipeurus*-complex lice are known from hosts in the genus *Bambusicola*.

Geographical range

See Table 1 and Fig. 4; primarily the Indo-Malayan region and Central America, but also known from New Guinea, the Caribbean, and islands in the Central Pacific. Seemingly absent over large parts of the host's (introduced) range, but may be overlooked.

Remarks

Złotorzycka (1966) considered the species here placed in *Gallancyra* gen. nov. to belong in *Oxylipeurus* s. str., but did not justify this placement other than by reference to published illustrations. Presumably her judgement was based on the presence of an anteriorly pointed head in both *Gallancyra dentata* gen. et comb. nov. and species of *Oxylipeurus*, whereas other genera in the complex generally have rounded preantennal heads. Comparing *G. dentata* gen. et comb. nov. to more recent illustrations of *Oxylipeurus* s. str. (e.g., Mey 1990) shows that, apart from the pointed head, there are few morphological similarities between the two genera. For instance, *Oxylipeurus* s. str. has intertergal plates, medially continuous tergopleurites VII–VIII, a post-antennal suture, much reduced and highly modified male genitalia, and a small, distally blunt, stylus.

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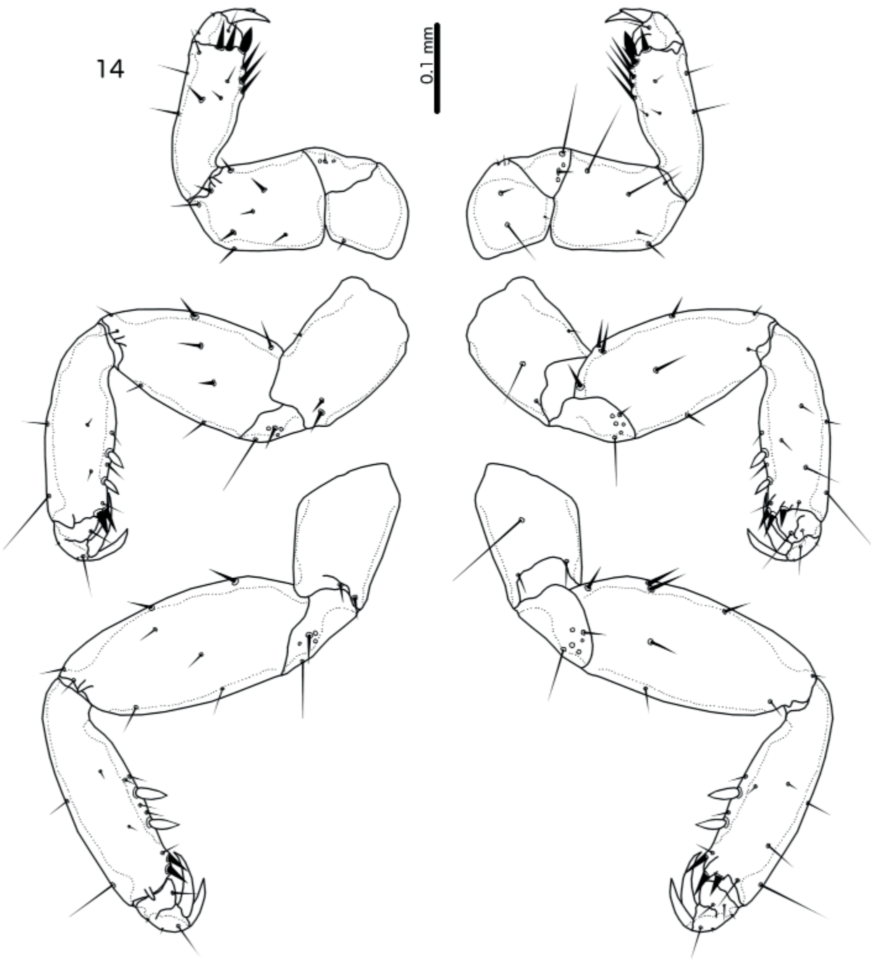

Fig. 14. *Gallancyra dentata* (Sugimoto, 1934) gen. et comb. nov. ex *Gallus gallus* (Linnaeus, 1758) (NHMUK010682393). Male legs I–III, dorsal and ventral views. Legs II and III distorted in all examined males, and here illustrated approximately; note that marginal and near-marginal setae (marked with small black circles) are illustrated on both dorsal and ventral side, as their exact placement is difficult to establish due to the distortion of the legs. Some setae on tibiae II–III appear hyaline in examined specimens, and have here been illustrated as hollow.

Gallancyra dentata (Sugimoto, 1934) gen. et comb. nov.

Lipeurus dentatus Sugimoto, 1934: 2, figs 1–11 + 2 unnumbered photos.
Lipeurus angularis Peters, 1935: 101, figs 1–3.

Oxylipeurus dentatus – Clay, 1938: 181.
Reticulipeurus dentatus (Sugimoto, 1935) [sic] – Mey 2003: 90.

Type host

Gallus gallus (Linnaeus, 1758) – Red Junglefowl (domestic chicken).

Other hosts

Gallus gallus murghi Robinsson & Kloss, 1920; *Gallus gallus spadiceus* (Bonnaterre, 1790) (Emerson & Elbel 1956: 382); *Gallus lafayettii* Lesson, 1831 (Price *et al.* 2003: 203) – Sri Lanka Junglefowl. "[S]everal of the wild chickens of Southeast Asia" (Emerson 1956: 78).

Type locality

Taiwan.

Material examined

Non-type material
Ex *Gallus gallus murghi*

INDIA • 1 ♂, 2 ♀♀; Sikkim; Jan. 1922; R. Meinertzhagen, 345; NHMUK010682390; NHMUK.

Ex *Gallus gallus* ssp.

PAPUA NEW GUINEA • 2 ♀♀; Central District, Kapogere Area; Apr. 1971; I.L. Owen leg.; 1192/71; Brit.Mus. 1971-292; NHMUK010682394; NHMUK.

MALAYSIA • 1 ♀; Trengganu; 1968; A. Mustaffa leg.; Brit. Mus. 1968-292; NHMUK010682389 • 2 ♂♂, 3 ♀♀; Trengganu; Jun. 1969; A. Mustaffa leg.; Brit. Mus. 1969-396; NHMUK010682393; NHMUK.

Description

Both sexes
See genus description; below are listed only details of those characters typically variable among species in the *Oxylipeurus*-complex.

Male
Proximal mesosome extended into rather trapezoidal structure that overlaps with distal section of basal apodeme (Fig. 13); this section is rather diffuse in specimens, and has here been illustrated approximately. Antero-lateral sections of mesosome elongated hook-shaped, more intensely sclerotized than trapezoidal section. Distal mesosome gently rounded, with rugose areas limited to lateral margins; rugose section expands medially in anterior end. Sclerotized plate present in central part of distal mesosome, with arched antero-lateral extensions on each side. Gonopore slender, not reaching distal half of mesosome. A single tube situated on each side of gonopore, which may terminate in sensilla, but no such sensillae visible in examined specimens. Two *pmes* microsetae visible on each side lateral to gonopore. Parameres slender, without distinct head; *pst1–2* as in Fig. 12, both subterminal microsetae. Measurements (n = 3, except TL and PTW where n = 2); TL = 2.22–2.32; HL = 0.63–064; HW = 0.44–0.46; PRW = 0.32–0.35; PTW = 0.44–0.46; AW = 0.53–0.62.

Female

Vulval margin with 20–32 *vms* on each side, and 11–15 *vss* gathered in the central section. In both sets of setae, lateral setae are longer than medial setae. Measurements (n = 8); TL = 2.54–2.84; HL = 0.70–0.74; HW = 0.51–0.55; PRW = 0.36–0.42; PTW = 0.52–0.59; AW = 0.69–0.75.

Remarks

Peters (1935), Clay (1938), Emerson (1956) and Price *et al.* (2003) all list "*Lipeurus denticlypeus* Sugimoto, 1934" as a synonym or potential synonym of *O. dentatus*. Clay (1938: 181) noted that the change in name is only in the reprint, not in the published version of the manuscript. As such, it has never been published, and is at best considered a manuscript name, with no nomenclatorial existence.

Moreover, the translation of this manuscript is usually given as "On a new species of Mallophaga, *Lipeurus denticlypeatus* n. sp., from the Formosan fowl" (e.g., Price *et al.* 2003). The original Japanese title does not include either the name of the louse, the name of the host, or the origin of the specimens. It roughly translates to "Additional information on the head lice of domestic birds". No information on the location on Sugimoto's type specimens appears to be included in the original description, and the location of the holotype is unknown. As we have no evidence that it has been destroyed or lost, we here do not select a neotype for *L. dentatus*.

A single examined male of *G. dentata* gen. et comb. nov. from *Gallus gallus murghi* has a larger head with a blunter preantennal area than males from *G. g. gallus*, but heads of females from the two host subspecies are near identical. Other characters are largely indistinguishable between specimens from the two host subspecies, but the male genitalia of the single male from *G. g. murghi* are destroyed and partially obscured by gut content, and cannot be compared adequately. As so few specimens have been examined from either host subspecies, and the natural variation is thus not known, we presently do not consider these differences to be significant, until a large series of specimens have been examined. We therefore consider specimens from both host subspecies to be conspecific.

Discussion

The extensive introductions of domestic chicken into almost all parts of the world make this species an ideal model for examining the effect of the external environment on the parasite fauna of a bird. Moreover, the economic importance of domestic chicken has led to many surveys of their ectoparasite fauna (Table 1), in contrast to the often very limited geographical data known for lice on most wild birds. We have summarized the known geographical ranges of all species of chewing lice occurring on domestic chicken (Figs 1–4; Table 1). Below, we discuss these ranges and the possible limitations to them, for each species of chewing louse known from domestic chicken.

Chewing lice presumably native to chicken

Emerson (1956) considered only six chewing louse species (*Goniocotes gallinae* (De Geer, 1778), *Goniodes dissimilis* Denny, 1842, *Lipeurus caponis* (Linnaeus, 1758), *Menacanthus pallidulus* (Neumann, 1912), *Menopon gallinae* (Linnaeus, 1758), *Gallancyra dentata* gen. et comb. nov.) as definitely having chicken as their natural host, based on records from non-domesticated hosts in Southeast Asia. A seventh species, *Menacanthus cornutus* (Schömmer, 1913), he considered doubtful, as he had only examined a single specimen from a wild chicken from Southeast Asia. This species has also been recorded from turkey (Camacho-Escobar *et al.* 2014).

Of the six louse species Emerson (1956) presumed to be native to chicken, four (*G. gallinae*, *G. dissimilis*, *L. caponis* and *M. gallinae*) appear to be near global in their distribution (Figs 1–3), with no obvious gaps in their distribution that cannot be explained by the patchiness of sampling efforts. All four species appear to occur in both drier and more humid habitats, and in both colder and warmer areas. However, Fabiyi (1996) reported that *G. dissimilis* and *M. gallinae* are absent in areas with short humid season, perhaps mirroring the environmental conditions in the native range of chicken. In the same study, *L. caponis* and *G. gallinae* showed no preference for areas with either short or long humid season. Trivedi *et al.* (1992) stated that the highest prevalence of *L. caponis* was during periods with slightly lower temperatures, whereas the other four species increased during periods of higher temperature.

Menacanthus pallidulus is reported less often than the others in surveys. Fabiyi (1996) reported that this species is absent in areas with a shorter humid season, which may explain its absence in some areas. However, *M. pallidulus* does not seem to be common on the host. Do Carmo Rezende *et al.* (2016) found *M. pallidulus* in only 3.7% of the examined chickens, a prevalence less than half that of *M. cornutus* and *M. stramineus* (Nitzsch, 1818) in the same study. Similarly, only 30 of almost 25000 lice collected from chicken by Ilyes *et al.* (2013) were identified as *M. pallidulus*. However, the records shown in Fig. 3 span most of the range of domestic chicken. It is absent in most of Sub-Saharan Africa, but this may be an artifact of sampling, as it is present in Nigeria, the country with the highest number of surveys (Table 1). More data are needed before the true range of *M. pallidulus* can be approximated.

By contrast, *Gallancyra dentata* gen. et comb. nov. has a very limited distribution (Fig. 4), which is split between the native range of chicken (Southeast Asia), New Guinea and Central Pacific Islands (Emerson 1956) as well as parts of Central America and the Caribbean. All these areas are tropical and Hohorst (1939) listed *G. dentata* gen. et comb. nov. under "Tropical species".

Gallancyra dentata gen. et comb. nov. is rarely reported in the literature. In a recent review of louse infestation in domestic chicken, the species was not even included (Khan *et al.* 2016), which may indicate how poorly known *G. dentata* gen. et comb. nov. is. However, it should be noted that details of how lice were identified are not always given in the published literature and the reliability of some records may be doubtful. This is especially the case for those species that are reported in anomalous regions of the host's body. For instance, lice in the genus *Lipeurus* are normally reported from the wings and tail of the host (e.g., Trivedi *et al.* 1991; Gabaj *et al.* 1993; Ilyes *et al.* 2013), but sometimes reported exclusively from the host's head (Santos-Prezoto *et al.* 2003). Both *Cuclotogaster heterographus* and *Gallancyra dentata* gen. et comb. nov. are normally collected from the host's head (e.g., Peters 1935; Emerson 1956; Gabaj *et al.* 1993). It is therefore possible that some records of *Lipeurus* from the head of the hosts are misidentifications of either of these two species. It is also possible that *Lipeurus* records from the host's head are the result of the Drost effect (Eichler 1970), the observation that after the host dies, lice typically abandon their natural microhabitats and move to the host's head. Greater care in reporting how chewing louse specimens were identified, and how the Drost-effect was prevented is needed.

Nevertheless, in large areas of the host's introduced range, this lack of records is likely genuine. For instance, the most densely surveyed countries in Africa are Nigeria and Ethiopia, with 20 and 12 published surveys of domestic chicken lice, respectively. No specimens of *G. dentata* gen. et comb. nov. have been reported, despite collectively covering several thousand chickens. Similarly, no specimens of this louse species have been found in numerous surveys of chicken in Turkey, Iran, and Pakistan (Table 1); the specimens from Sikkim we examined appear to be the first record of this species from India, despite at least nine surveys having been conducted.

Chewing lice originating from other hosts

Apart from occasional stragglers recorded from domestic chicken kept in mixed poultry flocks (Table 2; *Campanulotes compar* (Burmeister, 1838), *Chelopistes meleagridis* (Linnaeus, 1758), *Colpocephalum turbinatum* Denny, 1842, *Goniodes microthorax* (Stephens, 1829)), several species of ischnoceran lice on chicken are suspected to have originated from other hosts and subsequently become widely established. Two recently described species (*Menacanthus longiscleritus* Naz & Rizvi, 2016 and *Amyrsidea saudiensis* Alahmed *et al*., 2017) are not discussed further here, as both are only known from their type localities, and it cannot be excluded that they represent stragglers from different host species.

The most common sources of presumed non-native lice found on chicken are guineafowl (Numididae). Of the 22 species of chewing lice reported from domestic chicken, five species are also known from at least some species of guineafowl (*Amyrsidea powelli* (Bedford, 1920), *Menacanthus numidae* (Giebel, 1874), *Goniocotes maculatus* (Taschenberg, 1882), *Goniodes gigas* (Taschenberg, 1879), *Lipeurus tropicalis* Peters, 1931). Of these, only *G. gigas* and *L. tropicalis* appear to be widely distributed outside the native range of guineafowl (Figs 1–2). Of the remaining three species, *A. powelli* has been reported from Nigeria (Fabiyi 1986), *M. numidae* from South Africa (Bedford 1924), France (Séguy 1944) and Spain (Martin Mateo 1973, 1974; Martin Mateo *et al.* 1980), and apart from the original description of *G. maculatus*, the only subsequent report from domestic chicken appears to be from Poland (Müller 1927); however, the identification of this record is dubious as no details are given.

Lipeurus tropicalis appears to be limited to tropical areas in Africa, the Neotropics, and the Indian subcontinent (Fig. 2). This may suggest that some environmental factors are limiting its range. Arora & Chopra (1957) and Saxena & Agarwal (1982) have both reported that lower temperatures may impact the life span, egg-laying rate, and morphogenesis inside the egg of *L. tropicalis*, with the optimal temperature being 30–40˚C, and the optimal relative humidity 80–85%, with decreasing temperatures decreasing both life span and daily egg-laying rate. Agarwal & Saxena (1979) showed that these two factors had a clear impact on population size of *L. tropicalis* over the year. These two factors may be the reason *L. tropicalis* is absent in parts of the world where the temperature or humidity are more disadvantageous than in India. However, Fabiyi (1996) did not find any pattern of preference for different climatic zones in Nigerian *L. tropicalis*.

In contrast, *Goniodes gigas* occurs as far north as Sweden, and has been found on every larger landmass in the world (Tabel 1; Fig. 1). Buriro & Akbar (1978) suggested that *G. gigas* is highly adaptable to different climatic zones, but also stated that the species appeared to prefer drier habitats. Fabiyi (1996) only found *G. gigas* in areas with a short humid season, suggesting that *G. gigas* may prefer drier climates. This may seem counter-intuitive, as chewing lice obtain all their water from the air, using a specialized water-uptake system (Rudolph 1983). However, similar biogeographical patterns are known from lice in the genus *Brueelia*, which may also occur primarily in areas with low ambient humidity (Bush *et al.* 2009). Notably, Conci (1956) managed to raise *G. gigas* in temperature and humidity conditions similar to those mentioned above for *L. tropicalis*. As shown in Fig. 1, *G. gigas* is known across a large range of ambient humidities and temperatures, and may be very adaptable. However, many records are from domestic chicken in poultry farms indoors, which may skew the distributional data.

Emerson (1956) noted that the closest relatives of *Cuclotogaster heterographus* (Nitzsch [in Giebel], 1866) all occur on *Alectoris* Kaup, 1829 partridges around the Mediterranean. Other species of *Cuclotogaster* Carriker, 1936 are also primarily found on primarily dry-land hosts such as francolins (Tendeiro 1958; Price *et al.* 2003), suggesting that lice in this genus are also adapted to lower humidities. Based on this observation, Emerson (1956) suggested that the original host of *C. heterographus* might not be chicken, but some species of *Alectoris* partridge. All the subspecies of *C. heterographus* described by Clay (1938) from partridges are today treated as separate species (Price *et al.* 2003), but no thorough revision of the genus has been published. Conci (1952) found that the optimal temperature for survival of *C. heterographus* was 35.5–36.5˚C. The geographical range of *C. heterographus* appears to be global (Fig. 2), but reports from the Neotropics, Sub-Saharan Africa, and the native Southeast Asian range of chicken are rare. Fabiyi (1996) found Nigerian chicken to be parasitized by the closely related *Cuclotogaster occidentalis* (Tendeiro, 1954), which likely originates from some species of francolin.

Menacanthus stramineus has been found from several subspecies of wild turkey (Emerson 1956), which is likely the natural host of this louse species. Emerson (1956) stated that the species has never been found on any other wild host species, and that it readily transfers from one host to another in mixed poultry flocks. DeVaney *et al.* (1980) showed that this dispersal can occur very rapidly. Emerson (1956) assumed that this species was global in range. Fabiyi (1986, 1996) found no specimens in Nigeria, but the species has been reported from Nigeria, e.g., by Okaeme (1988). The overall range of this species spans almost the entire range of chicken (Fig. 3), and its absence in some regions may be due to patchiness in distribution, or low numbers of sampled birds. Notably, *M. stramineus* has also locally established itself on other hosts, such as *Numida melagris* (Linnaeus, 1758) (Okaeme 1988) and *Pavo cristatus* Linnaeus, 1758 (Nasser *et al.* 2015).

Lagopoecus sinensis (Sugimoto, 1930) was not included in the key of lice from domestic chicken by Emerson (1956), but has been reported from chicken in China and Taiwan at least three times (Sugimoto 1930; Emerson 1957; Arnold 2008) and never from any other host species. This may suggest that chicken is a natural host of this louse species, but Arnold (2008) stated that he could not separate this species reliably from *Lagopoecus colchicus* Emerson, 1949. Potentially, all records of this species may originate from stragglers from some pheasant species, but more research is needed.

Possibility of competitive exclusion

The rarity of *G. dentata* gen. et comb. nov. is peculiar, especially considering the discontinuous range of the species (Fig. 4), and the otherwise near-global range of most other species of ischnoceran chewing lice presumed to be native to chicken. Moreover, the fact that chewing louse species presumed to be native to guineafowl or turkey have not only become established on domestic chicken, but in some cases spread throughout the range of domesticated chicken, makes the absence of *G. dentata* gen. et comb. nov. from large parts of the host's range even more puzzling. Why has this louse species failed to capitalize on the huge range expansion of domestic chicken?

No data are available for the preferred environmental humidity or temperature of *G. dentata* gen. et comb. nov., but the known distribution suggests that the species cannot survive outside the warm and humid areas of the tropics. A few other species in the *Oxylipeurus*-complex are known from Africa (Ledger 1980), but the group otherwise occurs world-wide (Price *et al.* 2003). Overall, species in the *Oxylipeurus*-complex are typically absent from galliforms hosts that occur primarily in drier areas, but appear to occur on almost all groups of galliforms in the more humid parts of Southeast Asia (Price *et al.* 2003).

Notably, *G. dentata* gen. et comb. nov. occurs on the head of the host (Peters 1935), a microhabitat preference it shares with another chewing louse species known from chicken: *Cuclotogaster heterographus* (e.g., Hafez & Madbouly 1966; Murillo & Mullens 2016). Lice in the genus *Cuclotogaster* are common in Africa and other drier areas of the world (Ledger 1980; Price *et al.* 2003). Fabiyi (1996) found that *Cuclotogaster occidentalis* was entirely absent in areas of Nigeria with a long humid season. Even if most chewing lice are dependent on extracting water vapour from the air to survive, species of lice adapted to or thriving in very dry environments are known (Carillo *et al.* 2007; Bush *et al.* 2009).

Together, this suggests that *G. dentata* gen. et comb. nov. may be adapted to more humid areas, whereas *C. heterographus* is adapted to drier areas. If both species compete for the same resources (head feathers), this may give each species an advantage over the other depending on the external environment. Competition between different louse species on the same host is poorly known, but has been shown to occur in pigeons (Bush & Malenke 2008). In one documented case, the competition between two congeneric louse species on the same host species is mediated by ambient humidity, with one species being better adapted to drier areas and the other to more humid areas (Malenke *et al.* 2011).

Direct competition between *C. heterographus* and *G. dentata* gen. et comb. nov. has not been demonstrated, but would explain the geographical distribution patterns of both species. Most reports of *C. heterographus* are from drier areas, such as the Middle East or the northern half of Africa, but the species is largely absent from the native range of wild chicken in Southeast Asia, and from Central America and the Caribbean, where *G. dentata* gen. et comb. nov. is established (Table 1; Figs 2, 4). In contrast, *G. dentata* gen. et comb. nov. is absent from the Middle East and all of Africa, where *C. heterographus* is frequently reported. The absence of *G. dentata* gen. et comb. nov. in, e.g., more humid areas of South America and Africa may be due to underreporting, or to unknown factors that limit its spread. More surveys are needed to establish whether *G. dentata* gen. et comb. nov. is circumtropical, or actually absent from these areas.

Conclusions

Due to the large number of published surveys of chewing lice on chicken, it is possible to outline the geographical range of these louse species. Some louse species appear to occur throughout the range of the host, including some species that likely originated from other host species. In contrast, other species of chewing lice show very limited geographical ranges. This may in some cases be affected by differences in the external environment, or by competition between chewing louse species occupying the same microhabitat on the bird.

The distribution records summarized here are more extensive and more complete than for any other bird-louse association. Moreover, much research has been performed to establish the environmental factors that influence life histories and survival of chewing lice on chicken. However, more detailed surveys of wild and domestic chicken across the tropics are sorely needed. In particular, more data is needed from more humid parts of Africa, as well as from drier areas in the outskirts of the native range of chicken, such as parts of China and India. More data are also needed from humid areas within the natural range of chicken, such as Myanmar, India and Indonesia, as well as from other host subspecies and other species of *Gallus* Brisson, 1760. We hope that the redescription and illustrations provided here will aid future efforts to understand the range and evolutionary history of *Gallancyra dentata* gen. et comb. nov.

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