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

Daniel R. GUSTAFSSON1,* & Fasheng ZOU2

1 Institute of Applied Biological Resources, Xingang West Road 105, Haizhu District, Guangzhou, 510260, Guangdong, China.
2 Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Guangdong, China.

*Corresponding author: kotatsu@fripost.org
Email: zoufs@giabr.gd.cn

1 urn:lsid:zoobank.org:author:8D918E7D-07D5-49F4-A8D2-85682F00200C
2 urn:lsid:zoobank.org:author:A0E4F4A7-CF40-4524-AAAE-60D0AD845479

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 (NHMUKXXXXXXXXX) 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 & Gezahen (2010); Amede et al. (2011); Tolossa & Tafesse (2013); Tamiru et al. (2014); Alemu et al. (2015); Zeryuhan & Yohana (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) |

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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) |
| Indonesia          | Yes                         | This study |
| Laos               | No                          | Clay (1940) |
| Malaysia           | No                          | Emerson & Elbel (1957a); Amin-Babjee *et al.* (1997); Rahman & Haziqah (2015); Suhaila *et al.* (2015) |
| Myanmar            | Yes                         | This study |
| Philippines        | Yes                         | Clay (1940); Emerson & Elbel (1957a); Manuel & Anceno (1981); Portugaliza & Bagot (2015) |
| “Southeast Asia”   | No                          | Emerson (1956) |
| Sri Lanka          | No                          | Clay (1940) |
| Taiwan             | Yes                         | Clay (1940); Emerson & Elbel (1957a); Segal *et al.* (1968); NHMUK010682397 (NHMUK) |
| 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) |
| **Neotropica**     |                             |         |
| 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); Prelesov & 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                           | Alrazi & 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                           | Burirko & 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                        | Blagoveshtensky (1940, 1951) |
| Turkey             | No                        | Mimioglu (1952); Dik et al. (1999); Koroškoglu et al. (1999); Aldemir (2004); Sayin Ipek & Saki (2009); Orunç & Bićek (2009); Inci et al. (2010); Dönör & Yaman (2015) |
| Ukraine            | No                        | Blagoveshtensky (1940); Yevstafieva (2015) |
| United Kingdom     | No                        | Kéler (1939); Clay (1940); Ryder (1967) |

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

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

<sup>b</sup> 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.

<sup>c</sup> 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 *Cuculotogaster 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 Blagoveshtchensky (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). Syehra *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; \( \text{ads} \) = anterior dorsal seta; \( \text{pmes} \) = posterior mesosomal seta; \( \text{pst}1–2 \) = parameral setae 1–2; \( \text{vms} \) = vulval marginal seta; \( \text{vss} \) = 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 (\textit{Gallus} spp.). Each circle is divided into four sectors, representing the four louse species: upper left = \textit{Lipeurus caponis} (Linnaeus, 1758); upper right = \textit{Lipeurus tropicalis} Peters, 1931; lower left = \textit{Cuclotogaster heterographus} (Nitzsch, 1866); lower right = \textit{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 ambllyceran 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 meleagris* (Linnaeus, 1758) (Meguini et al. 2018) or *Goniocotes microthorax* (Stephens, 1829) (Syhara 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* (Schömer, 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.
Order Phthiraptera Haeckel, 1896
Suborder Ischnocera Kellogg, 1896
Family Philopteridae Burmeister, 1838
Oxylipeurus-complex

Genus **Gallancyra** Gustafsson & Zou gen. nov.

*Oxylipeurus* 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; as^2_2 = 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 | Much reduced, divided          | Not reduced, medianly continuous   |
|                                  | medianly               | or continuous medianly         |                                    |
| Vulval margin                     | Without lateral lobes  | Without lateral lobes           | With lateral lobes                  |
| Subvulval plates                  | Absent                 | Present                        | Unknown? 1                         |
| Mesosome                          | Large, anterior ends   | Large, anterior ends            | Much reduced, may be               |
|                                  | hook-shaped            | hook-shaped                     | absent                             |
| Rugose areas                      | Mainly lateral         | Across all or most of           | Absent                             |
|                                  |                        | distal margin                  |                                    |
| Distal sclerotized plate of mesosome | Present               | Absent                         | Absent                             |
| Gonopore                          | With transverse sclerite bearing setae | With transverse sclerite bearing setae | Much reduced                      |
| Parameres                         | Symmetrical, roughly   | Symmetrical, roughly            | Asymmetrical, roughly              |
|                                  | finger-shaped          | finger-shaped                   | triangular                         |
| pst1–2                            | Close together         | Separated, *pst1*               | Unknown? 1                         |
|                                  | subterminally, both    | typically sensillus             |                                    |
|                                  | microsetae             |                                 |                                    |

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. 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.

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] – Moy 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; psst1–2 as in Fig. 12, both subterminal microsetae. Measurements (n = 3, except TL and PTW where n = 2); TL = 2.22–2.32; HL = 0.63–0.64; 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 of 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 (Schömer, 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 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). Buririo & 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 Carrriker, 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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