

New Pleistocene bird fossils in Taiwan reveal unexpected seabirds in East Asia

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The island of Taiwan, with its diverse microclimates and key position on the East Asian-Australasian Flyway, attracts numerous bird enthusiasts due to its diverse avian fauna. Nevertheless, due to the scarcity of fossil records, there is a significant knowledge gap between modern and ancient avifaunas in Taiwan. Currently, there is only a single described Pleistocene fossil; it is attributed to Phasianidae. To address this gap, this study describes two new bird fossils, a left humerus and a left tibiotarsus, and discusses them in detail herein. The fossils were collected from the Liuchungchi Formation (Early Pleistocene, 1.95–1.35 Ma) in Niubu, Chiayi, southwestern Taiwan, which represents a neritic environment. The fossils are identified as from species of Gaviidae (loons), with the humerus belonging to an undetermined species of *Gavia* and the tibiotarsus to *Gavia stellata*. Loons are seabirds that are primarily distributed in high- and middle latitudes of the Northern Hemisphere. In addition, these birds are extremely rare in modern Taiwan: records are scarce and most are limited to northern and northeastern Taiwan since the 1860s, indicating that the modern *Gavia* birds only occasionally visit Taiwan. All known Pleistocene fossils of species of *Gavia* from the northern West Pacific come from Japan. The Taiwan fossils of *Gavia* provide valuable bird evolutionary and paleobiogeographic information for the subtropical West Pacific and may imply the presence of a distinct avifauna in the region during the Early Pleistocene.

Key words: Aves, *Gavia*, loon, seabird, Early Pleistocene, Taiwan.

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Introduction

Seabirds inhabit marine environments and forage for fish, squid and krill as their primary diet. They are diverse, with some species also distributed to freshwater environments (BirdLife International 2023; Mayr 2022; Tyrberg 1998). They play a vital role in indicating the health of marine habitats due to their high trophic level and long-distance flights to locate ideal foraging habitats (Croxford et al. 1999, 2012; Piatt et al. 2007; Parsons et al. 2008). Therefore, oceanographic dynamics at geological scales have driven the evolution and distribution of seabirds (Warheit 1992; Block et al. 2011; Clay et al. 2017; Drummond et al. 2021). The Pacific Ocean and surrounding coasts have supported a high diversity of seabirds through the Cenozoic (BirdLife International 2023). Based on fossil records, seabirds appear to have evolved and diversified in the North Pacific

region early in the Eocene and Oligocene, and continued to thrive during the Miocene and Pliocene. Examples include Charadriiformes (Miller 1931), Gaviiformes (Olson and Rasmussen 2001), Procellariiformes (Mayr 2015; Mayr and Goedert 2017), and pterodromids, flightless wing-propelled divers in Suliformes (Goedert 1988; Olson and Hasegawa 1996; Kimura et al. 1998; Goedert and Cornish 2002; Sakurai et al. 2008; Dyke et al. 2011; Mayr et al. 2015; Mayr and Goedert 2018, 2022; Ohashi and Hasegawa 2020). During the Pleistocene, the fossil records of seabirds become more diversified with modern lineages, but most are restricted to the Northeast Pacific (Miller 1914, 1925, 1930; Howard 1936, 1949, 1958; Guthrie 1992, 2005; Collins et al. 2018). In the Northwest Pacific, diverse Pleistocene seabird faunas have been reported from Japan (Hasegawa et al. 1988; Watanabe and Matsuoka 2015; Watanabe et al. 2016, 2018a, b, 2020; Matsuoka and Hasegawa 2018; Aotsuka et

al. 2022), and a few examples come from Russia (Harington 1978; Tyrberg 1998).

Taiwan is a subtropical island (~20° N) in the Northwest Pacific where many seabirds can be found (Xiao and Li 2022). Though well-known for its diverse modern avifauna, little is known about its ancient birds due to the extreme rarity of bird fossils. The Western Foothills of Taiwan has several fossil localities that sample mainly marine sedimentary environments, making it challenging to discover bird fossils (Lin et al. 2021). The only published bird fossil record to date is a phasianid tarsometatarsus from the Middle Pleistocene of southern Taiwan (Tsai and Mayr 2021).

Recently, two previously undescribed Early Pleistocene bird fossils from southwest Taiwan were found in the Chiayi Municipal Museum. This paper aims to describe these specimens in detail by comparing their morphology with modern specimens and investigate their correspondence with the whole avifauna in the Pleistocene of the Northwest Pacific.

Institutional abbreviations.—CMM, Chiayi Municipal Museum, Chiayi, Taiwan; NHMUK, Natural History Museum, Tring, UK; YIO, Yamashina Institute for Ornithology, Abiko, Chiba, Japan.

Geological setting

The fossils were collected from Niubu, Chiayi, southwest Taiwan (Fig. 1). The Niubu area is renowned for its rich deposits of marine fossils (Hu 1989; Tao 1993; Hu and Tao 1996, 2004; Xue 2004; Buckeridge et al. 2018; Lin et al. 2018, 2022); some terrestrial mammalian fossils and fragments of carbonized woods are also known (Xue 2004). The locality is along the Bazhang River where the Liuchungchi Formation is widely exposed (Lin et al. 2022: figs. 1, 2). The Liuchungchi Formation is composed of light gray muddy siltstone intercalated with dark gray shale or sandy shale, and the depositional environment sequence reflects a shoreface environment from offshore transition zone to inner offshore (Chang 2008; Chen 2016). Because the exact stratigraphic localities of the fossil specimens (Fig. 2) are uncertain, we conducted a pilot nannofossil analysis to constrain the age of the two fossils. Approximately 20 mg of sediments on the surfaces of the fossils and inside each of the shafts were removed. Then two sediment subsamples for each bird fossil were prepared and investigated for nannofossils using polarized light microscopy (Zeiss Axioscope Microscope), following the procedures of Gartner (1969). However, no nannofossils were found in any of the samples. A previous calcareous nannofossil biostratigraphic analysis of the southern Liuchungchi Formation identified the first appearance datum (FAD) *Gephyrocapsa oceanica* (~1.7 Ma) and the last appearance datum (LAD) *Discoaster brouweri* (~1.95 Ma) events (Chi 1980; Huang and Ting 1981), but a biostratigraphic study of the northern Liuchungchi Formation, where Niubu is located, has not been conducted. Chen et al. (2011)

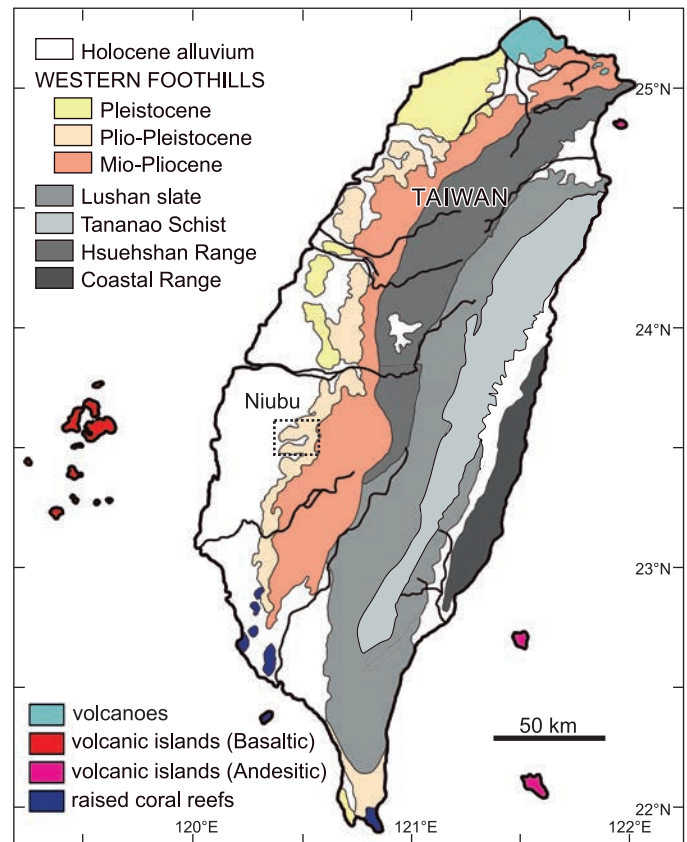


Fig. 1. Geological setting of Taiwan area and Niubu area; the locality of the two bird fossils is marked with rectangle (modified after Lin et al. 2022).

studied both paleomagnetic and sequence stratigraphic data of the whole Liuchungchi Formation and constrained the age of the formation to 1.90–1.35 Ma. Therefore, we use the gross age 1.95–1.35 Ma for our fossils (Fig. 3).

Material and methods

The fossils were collected during the 1980s–2000s by the private collector Wen-Ji Xue, who then donated them to the Chiayi Municipal Museum (CMM), Chiayi, Taiwan. The fossils have been cataloged under CMM 2123 and CMM 2124. The two bird fossils are the well-preserved distal ends of a left humerus and a left tibiotarsus, respectively (Fig. 2).

To uncover the bone morphology covered by the sediments, computed tomography (CT) was applied on the bird fossils using SkyScan 1276 (Bruker microCT, Kontich, Belgium) at the Taiwan Mouse Clinic, Academia Sinica and Taiwan Animal Consortium, Taiwan. The voltage, current, and scan resolution of X-ray source were set to 100 kV, 200 μ A, and 20.5 μ m, respectively. The filters Al and Cu were used. After scanning was completed, the image processing algorithms following Wang et al. (2015) were applied to the 3D raw images to build the 3D models. The widths and depths of the bird fossils were obtained by using calipers while avoiding broken surfaces. The measurements of

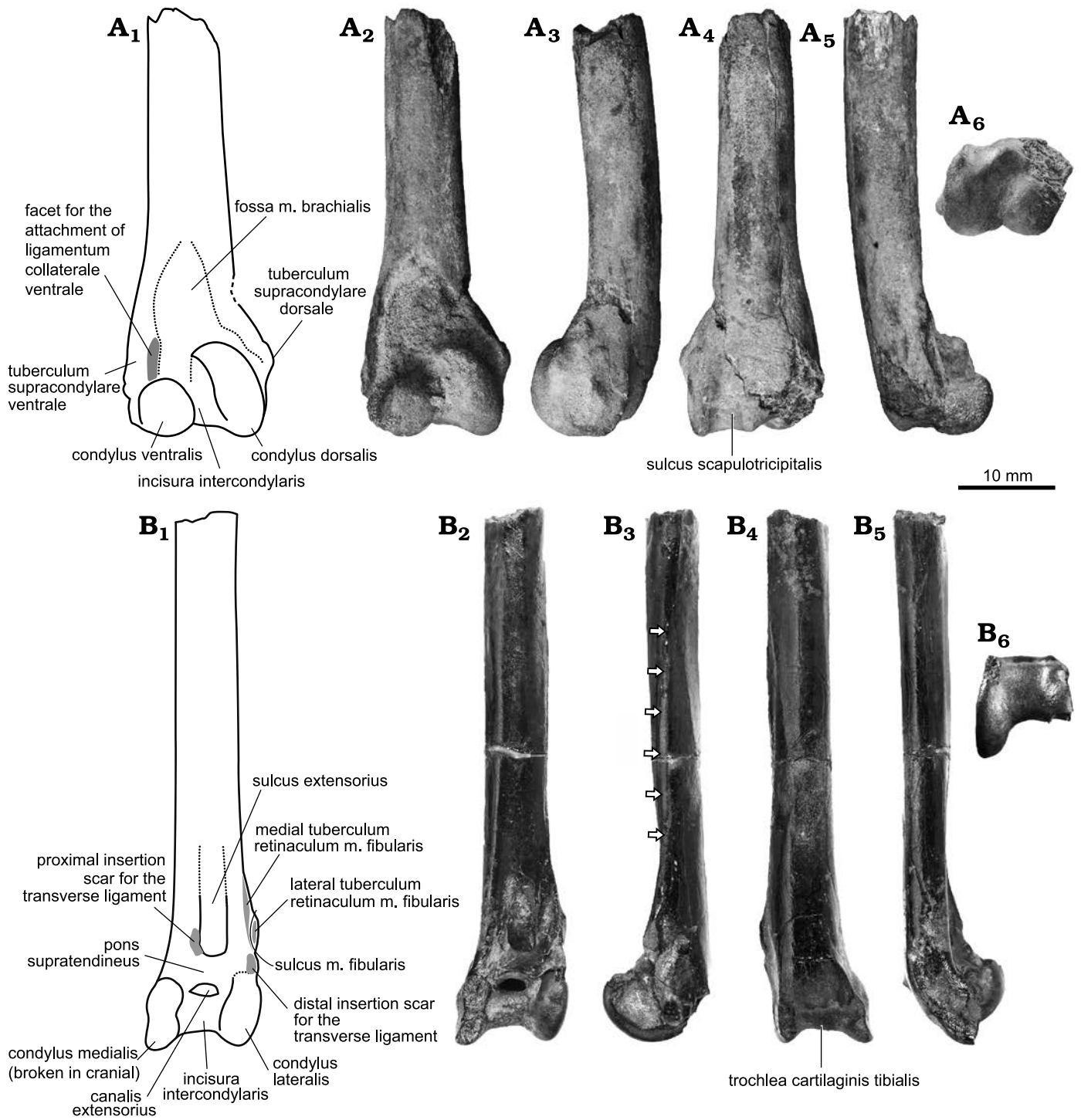


Fig. 2. The fossils of gaviid seabirds from Niubu, Chiayi, Taiwan, Liuchungchi Formation, Lower Pleistocene. **A.** *Gavia* sp., CMM 2123, distal left humerus in cranial (A₁, A₂), dorsal (A₃), caudal (A₄), ventral (A₅), and distal (A₆) views. **B.** *Gavia stellata* (Pontoppidan, 1763), CMM 2124, distal left tibiotarsus in cranial (B₁, B₂), lateral (B₃), caudal (B₄), medial (B₅), and distal (B₆) views. Arrows highlight the articular scar for the distal fibula.

CMM 2123 include: (i) the dorsoventral length of the shaft from the cranial view as the shaft width; (ii) the cranio-caudal length from the dorsal view of the shaft as the shaft depth; (iii) the length between the ventrodistal face of the condylus ventralis and the dorsodistal face of the condylus dorsalis from the cranial view as the distal width; (iv) the maximal craniocaudal length of the condylus dorsalis from

the dorsal view as the distal depth. The measurements of CMM 2124 include: (i) the mediolateral length of the shaft from the cranial view as the shaft width; (ii) the cranio-caudal length from the lateral view of the shaft as the shaft depth; (iii) the length between the medial face of the condylus medialis and the lateral face of the condylus lateralis from the cranial view as the distal width; (iv) the maximal

craniocaudal length of the condylus lateralis from the lateral view as the distal depth.

To compare the size variations, the measurements of modern specimens preserved in the Yamashina Institute for Ornithology, Abiko, Chiba, Japan (YIO) were obtained using the same criteria as those of the fossil specimens (see above). For *Gavia immer* (Brünnich, 1764), a species not from the West Pacific and not found in YIO, the measurements were obtained from the images of the specimens from the Natural History Museum, Tring, UK (photos courtesy of Junya Watanabe) with a scale bar by using Adobe Photoshop (v. 24.1.1) and its Ruler Tool. Though it was not ideal to obtain measurements from photos, the scale bar was located close to the bone to minimize the measurement error and the obtained data are sufficient to show that the fossils were considerably smaller than the specimens in the imaged sample. The anatomical nomenclature follows Baumel and Witmer (1993).

Systematic palaeontology

Aves Linnaeus, 1758

Order Gaviiformes Wetmore and Miller, 1926

Family Gaviidae Allen, 1897 (Gray, 1840)

Genus *Gavia* Forster, 1788

Type species: Gavia immer (Brünnich, 1764); Recent, North America.

Gavia sp.

Figs. 2A, 4A.

Material.—CMM 2123 left humerus, Bazhang River, Niubu area, Taiwan; Liuchungchi Formation (Fig. 3); 1.95–1.35 Ma.

Measurements.—See Table 1.

Description.—The shaft of the distal left humerus CMM 2123 is stout and rounded in cross section, and is notched craniodorsally proximal to the tuberculum supracondylare dorsale. Distally, the shaft forms an angle of 150° with re-

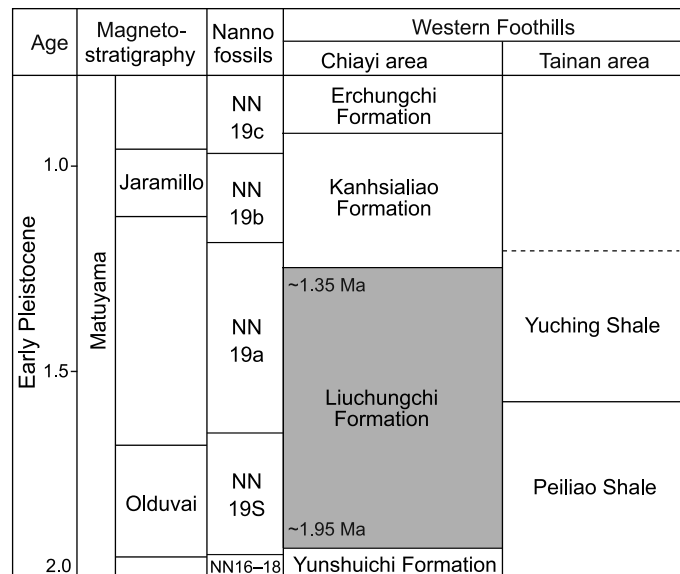


Fig. 3. Stratigraphy of the Western Foothills of southern Taiwan (modified after Chen 2016; Lin et al. 2021). Grey block highlights the Liuchungchi Formation, wherein the bird fossils were found. Only the Early Pleistocene of southern Taiwan is shown.

spect to the proximal side of the tuberculum supracondylare dorsale. The tuberculum supracondylare dorsale is dorsally prominent and proximodistally overlaps the condylus dorsalis such that the apex is located distal to the most proximal part of the condyle; the sharp and elevated apex extends smoothly to the shaft. The fossa m. brachialis is shallow, proximally elongate, and has its narrow proximal end close to the ventral margin of the fossil, making the fossa remarkably broad. The non-elevated tuberculum supracondylare ventrale is elongated and narrow, and has a narrow proximal margin close to the fossa m. brachialis. The facet where the ligamentum collaterale ventrale attaches to the tuberculum supracondylare ventrale is poorly defined, and slight ventral expansion distally. The proximal end of the facet lies only slightly proximal to the level of the proximal apex of the condylus dorsalis. The

Table 1. Measurements (in mm) of the fossils and modern Gaviidae. Number in the parentheses denotes sample size. The order of modern Gaviidae follows the taxonomy established by Sprengelmeyer (2014). The measurements of *Gavia immer* were obtained from photos taken by Junya Watanabe. Abbreviations: D, depth; W, width.

| Measurement | CMM 2123 | CMM 2124 | <i>Gavia stellata</i> | | <i>Gavia arctica</i> | | <i>Gavia pacifica</i> | | <i>Gavia adamsii</i> | | <i>Gavia immer</i> | |
|--------------------|----------|----------|-----------------------|----------|----------------------|----------|-----------------------|-----------|----------------------|----------|--------------------|----------|
| | | | Range | Mean | Range | Mean | Range | Mean | Range | Mean | Range | Mean |
| Humerus | | | | | | | | | | | | |
| shaft W | 8.5 | NA | 6.9–7.9 | 7.4 (4) | 8.1–9.2 | 8.6 (7) | 7.3–9.4 | 8.3 (14) | 11.2–11.2 | 11.2 (1) | 8.8–11.6 | 10.5 (6) |
| shaft D | 7.9 | NA | 5.3–6.8 | 5.9 (4) | 5.7–7.4 | 6.4 (7) | 5.6–7.8 | 6.4 (14) | 8.0–8.0 | 8.0 (1) | 7.2–8.7 | 8.3 (6) |
| distal W | 13.8 | NA | 11.0–12.0 | 11.6 (4) | 12.3–13.9 | 13.1 (7) | 11.5–13.4 | 12.6 (14) | 17.0–17.0 | 17.0 (1) | 15.0–18.0 | 16.7 (6) |
| distal D | 11.0 | NA | 8.2–9.7 | 8.9 (4) | 9.8–11.1 | 10.5 (7) | 9.3–10.6 | 10.0 (14) | 13.9–13.9 | 13.9 (1) | 11.8–15.0 | 13.6 (6) |
| shaft W/distal W | 0.6 | NA | 0.6–0.7 | 0.6 (4) | 0.6–0.7 | 0.7 (7) | 0.6–0.7 | 0.7 (14) | 0.7–0.7 | 0.7 (1) | 0.6–0.7 | 0.6 (6) |
| Tibiotarsus | | | | | | | | | | | | |
| shaft W | NA | 6.9 | 7.9–9.1 | 8.5 (4) | 7.0–8.3 | 7.6 (7) | 6.6–9.1 | 7.5 (11) | 9.4–9.5 | 9.4 (2) | 8.9–11.1 | 9.9 (6) |
| shaft D | NA | 4.8 | 4.6–5.5 | 5.2 (4) | 4.4–5.8 | 5.2 (7) | 4.6–6.6 | 5.2 (11) | 6.4–7.4 | 6.9 (2) | 6.0–6.5 | 6.2 (6) |
| distal W | NA | 12.0 | 10.6–12.3 | 11.6 (4) | 12.1–13.1 | 12.7 (7) | 11.8–13.8 | 12.3 (11) | 15.3–15.8 | 15.5 (2) | 14.0–17.9 | 16.4 (6) |
| distal D | NA | 12.0 | 11.6–13.0 | 12.2 (4) | 12.5–14.1 | 13.1 (7) | 11.2–13.8 | 12.4 (11) | 16.4–16.7 | 16.6 (2) | 14.2–17.3 | 15.5 (6) |
| shaft W/distal W | NA | 0.5 | 0.7–0.8 | 0.7 (4) | 0.5–0.6 | 0.6 (7) | 0.6–0.7 | 0.6 (11) | 0.6–0.6 | 0.6 (2) | 0.6–0.6 | 0.6 (6) |

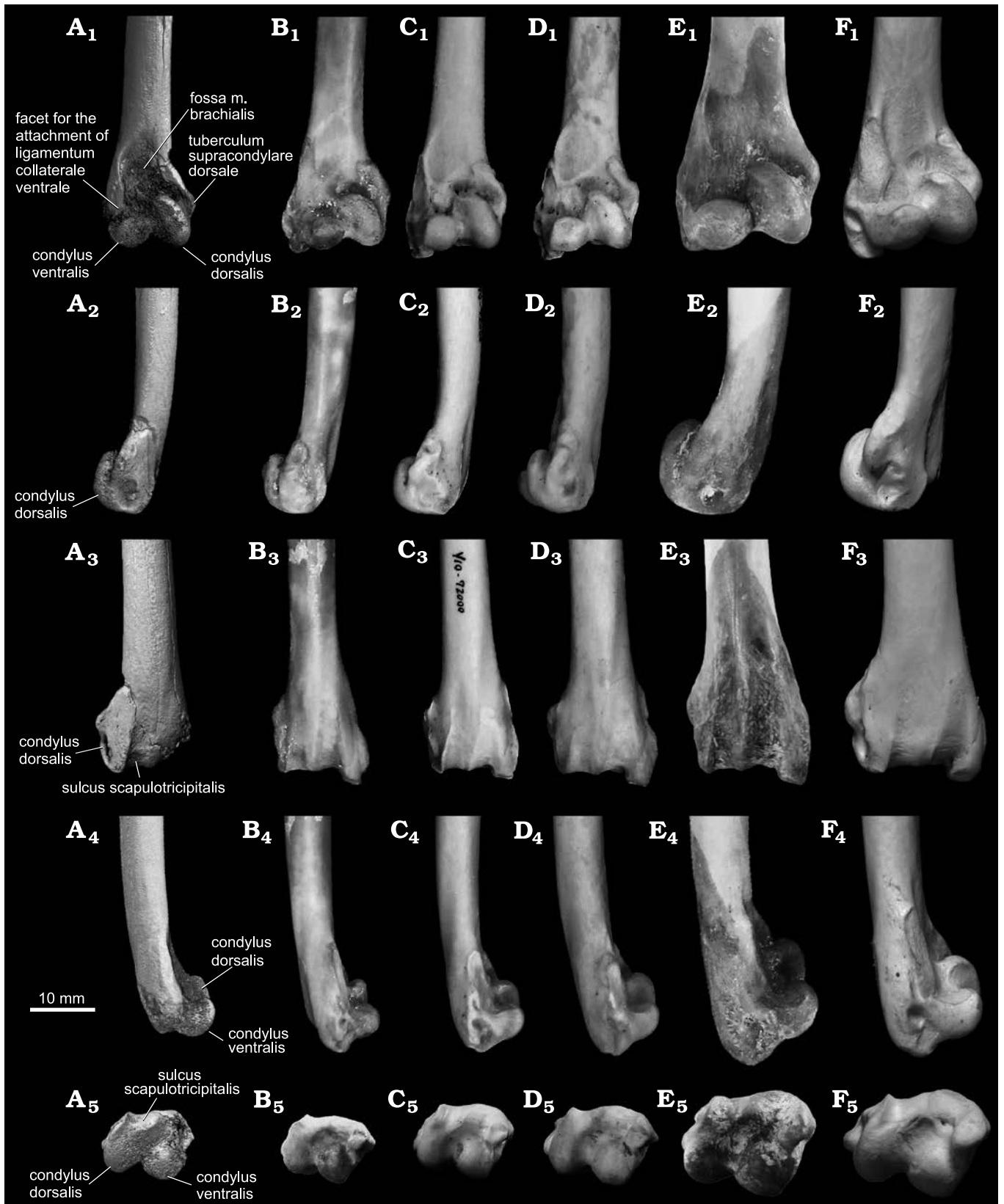


Fig. 4. The humeri of the fossil gaviid seabird *Gavia* sp. (A) and modern Gaviidae (B–F) in cranial (A₁–F₁), dorsal (A₂–F₂), caudal (A₃–F₃), ventral (A₄–F₄), and distal (A₅–F₅) views. **A.** CMM 2123 from Niubu, Chiayi, Taiwan, Liuchungchi Formation, Lower Pleistocene. **B.** *Gavia stellata* (Pontoppidan, 1763) (YIO 79598). **C.** *Gavia arctica* (Linnaeus, 1758) (YIO 72000). **D.** *Gavia pacifica* (Lawrence, 1858) (YIO 64763). **E.** *Gavia adamsii* (G.R. Gray, 1859) (YIO 63205). **F.** *Gavia immer* (Brünnich, 1764) (NHMUK S/1987.13.1). The images of CMM 2123 were obtained from CT. The image order of modern Gaviidae follows the taxonomy established by Sprengelmeyer (2014) and the photos of *G. immer* are courtesy of Junya Watanabe.

condylus ventralis is rounded with a proximodistal length about half of the condylus dorsalis. The two condyli are separated by a narrow incisura intercondylaris. On the caudal side, the sulcus scapulo-tricipitalis is well-defined and deep, with the two margins slightly converging proximally, and the processus flexorius is missing (Figs. 2, 4A₃).

Remarks.—CMM 2123 is referred to *Gavia* based on (i) broad fossa m. brachialis that comes close to the medial margin proximally, (ii) the elongate, narrow, and non-elevated tuberculum supracondylare ventrale, (iii) pronounced dorsally projected tuberculum supracondylare dorsale, and (iv) shaft notched craniodorsally proximally-adjacent to the tuberculum supracondylare dorsale. CMM 2123 represents an adult as displayed by the smooth surface, and the two condyli and processes with clear shapes as displayed in the modern adult specimens (Fig. 4). In addition, CMM 2123 shares the following qualitative features with humeri of modern *Gavia adamsii* (G.R. Gray, 1859): the relatively sharp (in cranial aspect) apex of tuberculum supracondylare dorsale, the smooth dorsal surface on the proximal side of tuberculum supracondylare dorsale, narrow (less than half width of the tuberculum) and non-elevated proximal end of the facet for the attachment of ligamentum collaterale ventrale on the tuberculum supracondylare ventrale, and the sulcus scapulo-tricipitalis with deep distal end and slightly proximally converged margins (Figs. 2, 4). However, the fossil humerus is rather smaller than those of the examined *G. adamsii* specimens, and is also relative larger than the examined *G. stellata* (Pontoppidan, 1763) specimens (Fig. 4B, E; Table 1). This excludes the possibility of identifying the humerus as either *Gavia adamsii* or *G. stellata*. *Gavia artica* (Linnaeus, 1758) (Fig. 4C) and *Gavia pacifica* (Lawrence, 1858) (Fig. 4D), while of similar size to the fossil (Table 1), differ by having larger facets for the attachment of ligamentum collaterale ventrale on the tuberculum supracondylare ventrale, having prominent scars for the palmar branch of m. extensor carpi radialis that interrupt the dorsal profile proximal to the apex of the tuberculum supracondylare dorsale, and a much shallower sulcus scapulo-tricipitalis; *G. immer* (Fig. 4F) is larger, and has a much more massive facet for the attachment of ligamentum collaterale ventrale on the tuberculum supracondylare ventrale that more greatly separates the fossa brachialis from the ventral shaft facies, a prominent scar for the palmar branch of m. extensor carpi radialis that interrupts the dorsal profile proximal to the apex of the tuberculum supracondylare dorsale, a less rounded condylus ventralis, and a much broader sulcus scapulo-tricipitalis that is bound ventrally by a lower ridge.

Gavia stellata (Pontoppidan, 1763)

Figs. 2B, 5A.

Material.—CMM 2124 tibiotarsus, Bazhang River, Niubu area, Taiwan; Liuchungchi Formation (Fig. 3); 1.95–1.35 Ma.

Measurements.—See Table 1.

Description.—The shaft of the tibiotarsus CMM 2124 is slightly compressed craniocaudally with an oval cross sec-

tion, and the distal end expands medially, with and the condylus medialis extending slightly further distally than the condylus lateralis. The articular scar for the distal fibula is, most proximally, on the lateral side of the shaft. It distally locates increasingly cranially and terminates near the proximal end of the medial tuberculum retinaculum m. fibularis. The medial tuberculum retinaculum m. fibularis is more elevated cranially and extends farther proximally than its lateral counterpart, which is prominent laterally, projecting slightly further laterally than the condylus lateralis. Proximally, both tubercula converge cranially, and distally, they converge laterally, which makes the sulcus m. fibularis shallow. The sulcus m. fibularis sits between the tubercula and faces slightly laterally. Distally, the sulcus m. fibularis passes caudally to a small lateral prominence at the distal end of the lateral tuberculum retinaculum m. fibularis. The medial tuberculum extends distally to join a small narrow laterally-facing crest and hence to the condylus lateralis at its proximolateral point. The effect of this is that proximally the sulcus m. fibularis is enclosed by medial and lateral tubercula, but at the level of the proximal margin of the pons supratendineus, the sulcus passes onto the lateral shaft facies. A distinct sulcus sits adjacent to the proximal end of condylus lateralis and is bounded laterally by the distal end of the medial tuberculum retinaculum m. fibularis. This sulcus is interpreted as the distolateral insertion scar of the transverse ligament. The pons supratendineus is wide proximodistally, and its proximomedial side has a rounded and elevated insertion scar, for the proximomedial insertion of the transverse ligament. The canalis extensorius is centered on the shaft and opens widely proximodistally between the condyli, and is close to the condylus medialis.

Remarks.—The fossil tibiotarsus displays several characteristics that are typical of *Gavia*: (i) parallel condyli that are proximodistally shorter than the distal width of the bone and are medially inclined distally, (ii) proximally-elevated medial and laterally-projected lateral tuberculi retinaculum m. fibularis, with a shallow sulcus m. fibularis in-between, (iii) a proximodistally wide pons supratendineus, (iv) a rounded scar abutting the proximomedial margin of the pons supratendineus for the proximomedial insertion of the transverse ligament, (v) a pit sits beside the end of the thin ridge immediately proximal to the condylus lateralis for the distolateral insertion of the transverse ligament, (vi) a wide opening of the canalis extensorius which is aligned proximodistally between the condyli (not proximal to the condyli) and is medially close to the condylus medialis, and (vii) a proximodistally short incisura intercondylaris with respect to the adjacent condyli. The fossil is similar to *G. stellata*, especially regarding the fact that the caudomedial margin of the condylus medialis lacks a caudomedially prominent rounded projection as seen in all the other modern gaviids compared (Fig. 5). This characteristic clearly separates the fossil and *G. stellata* from the other extant species of Gaviidae. While the mediolateral width of the shaft with respect to the distal end of the fossil in the cranial view seems to be smaller than

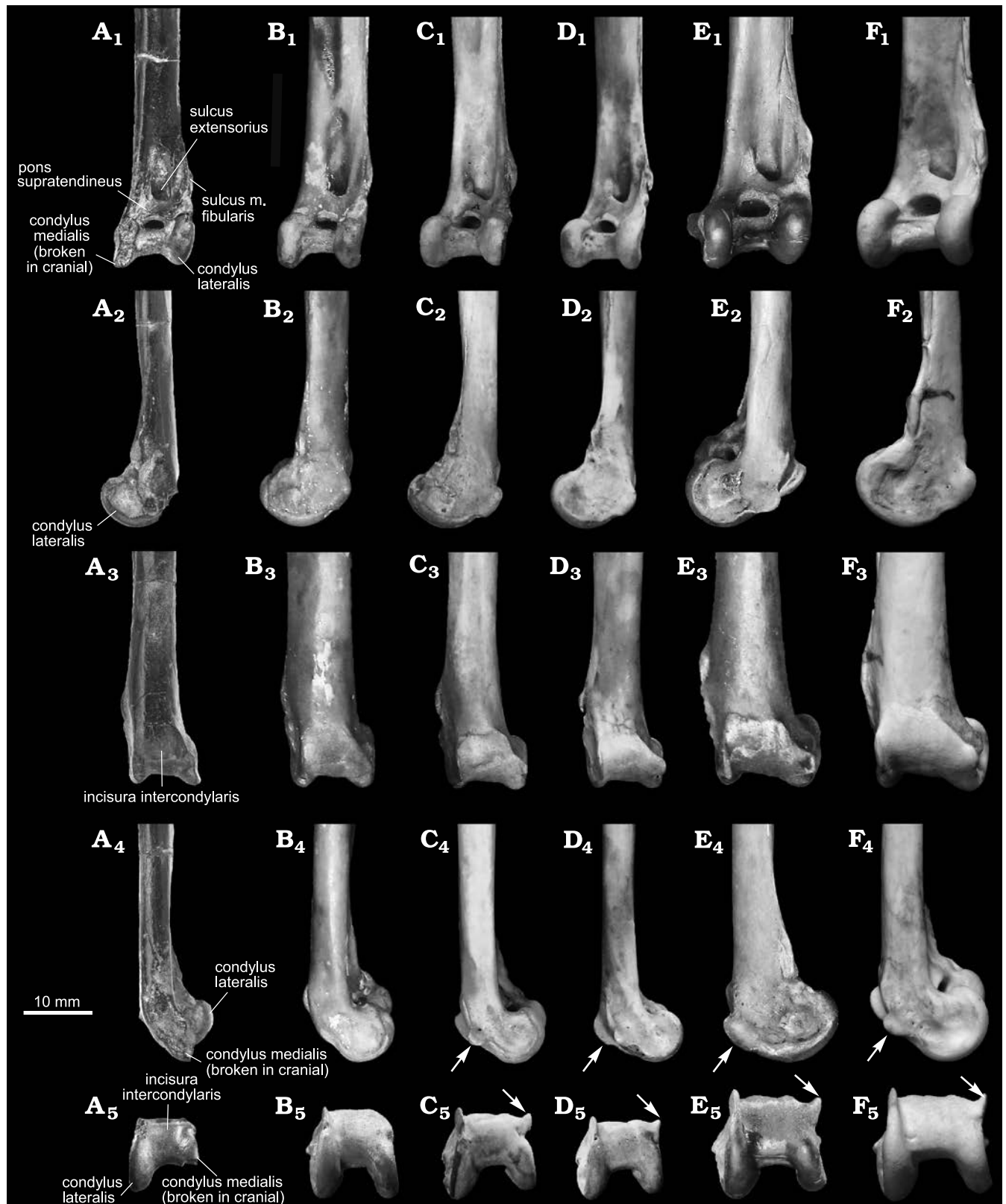


Fig. 5. Tibiotarsi of the fossil gaviid seabird *Gavia stellata* (Pontoppidan, 1763) (A) and modern Gaviidae (B–F), in cranial (A₁–F₁), lateral (A₂–F₂), caudal (A₃–F₃), medial (A₄–F₄), and distal (A₅–F₅) views. A. CMM 2124 from Niubu, Chiayi, Taiwan, Liuchungchi Formation, Lower Pleistocene. B. *Gavia stellata* (Pontoppidan, 1763) (YIO 79598). C. *Gavia arctica* (Linnaeus, 1758) (YIO 79597). D. *Gavia pacifica* (Lawrence, 1858) (YIO 60621). E. *Gavia adamsii* (G.R. Gray, 1859) (YIO 74354); F. *Gavia immer* (Brünnich, 1764) (NHMUK S/1987.13.1). Arrows on C₄–F₄ and C₅–F₅ indicate the caudomedial process present in these taxa that is lacking in *G. stellata*. The image order of modern Gaviidae follows the taxonomy established by Sprengelmeyer (2014) and the photos of *G. immer* are courtesy of Junya Watanabe.

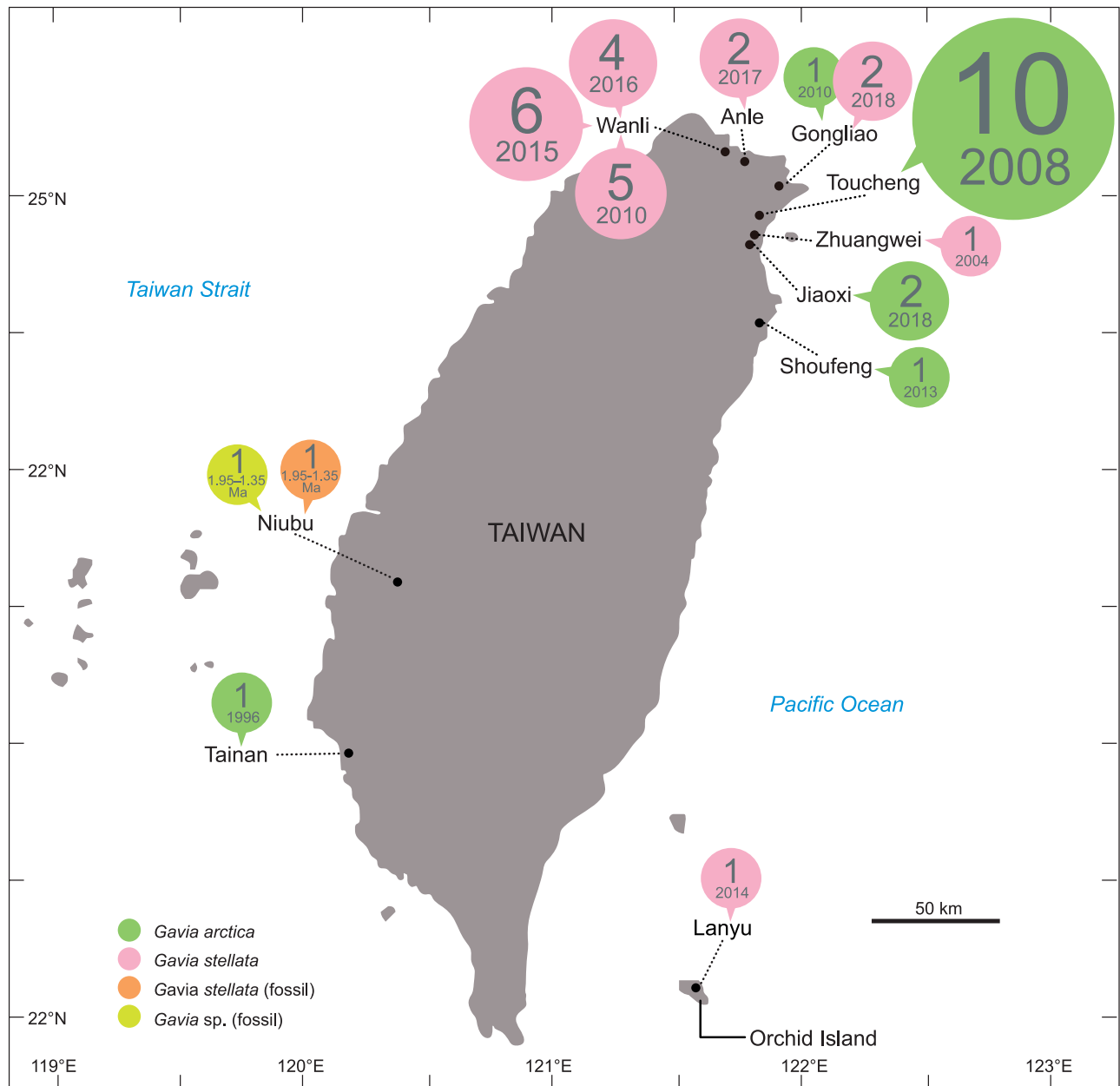


Fig. 6. Records of Gaviidae in Taiwan. The records are displayed as the number of occurrences (1–10) and dates (year or Ma). Records between 1861–1862 and between 1970–1971 are not included because the accurate localities are not accessible. See SOM 1: table S2 for details.

G. stellata (see Table 1), we think this disparity falls within intraspecific scope and, therefore, we prefer to identify the fossil as *G. stellata* (Table 1).

Discussion

Ecology of gaviids and paleoenvironmental interpretation.—The Gaviidae (loons), the modern representatives of Gaviiformes, include five species: *Gavia stellata*, *G. arctica*, *G. pacifica*, *G. adamsii*, and *G. immer* (HBW and BirdLife International 2022), all of which are migratory seabirds that are entirely limited to the Northern Hemisphere. They mate and breed near mid- and high-latitude lakes during the sum-

mer, and migrate south in the winter, when they predominantly stay at sea or near sea coasts. Fishes are their main diet, but crustaceans, mollusks, worms, and plants are also common (BirdLife International 2023). In the Northwest Pacific, all species of *Gavia* except *G. immer* are distributed around most islands and along the coastlines of the Asian continent but not in Taiwan, where the subtropical-tropical climate at 20° N is not suitable for them. During the past 160 years, only two *Gavia* species, *G. arctica* and *G. stellata*, have been rare occasional visitors to mainly the northeastern parts of Taiwan (Fig. 6; SOM 1: table S2, Supplementary Online Material available at http://app.pan.pl/SOM/app68-Wu_etal_SOM.pdf) (Swinhoe 1863; Yen 1984; Chu 1996; Chao 2006; National Taiwan Museum 2023; Taiwan Biodiversity

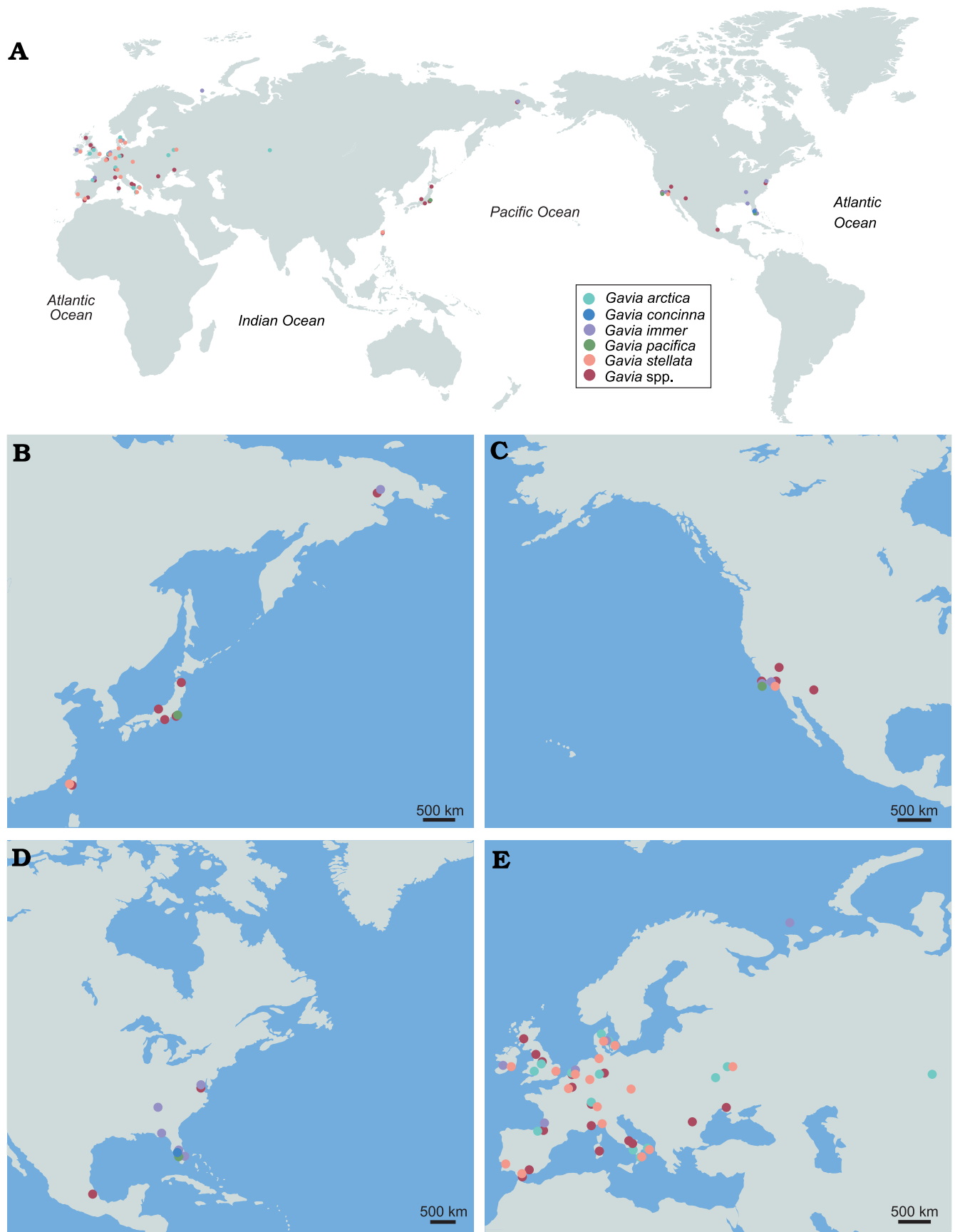


Fig. 7. Distribution of Pleistocene records of Gaviidae. **A**. The distribution around the world. Regional distribution in the Northwest Pacific (**B**), the Northeast Pacific (**C**), the Northwest Atlantic (**D**), and the Northeast Atlantic (**E**). Taxa with uncertainty are grouped into *Gavia* spp. See SOM 1: table S3 for details.

Network 2023). Only two seabird fossils have been found in the Liuchungchi Formation and it seems unlikely that a species as rare as modern gaviids are in the region today would be represented in such a meagre fossil record. By this reasoning, the fossils likely represent a greater abundance of gaviids in the region in the Early Pleistocene. This in turn suggests that the two fossil *Gavia* species were deposited during a cooler climate interval during the oscillation of glacial-interglacial periods (Lisiecki and Raymo 2005; Huybers 2006; Liautaud et al. 2020; Vaucher et al. 2021). If so, this suggests that the Early Pleistocene paleo-avifauna in southwestern Taiwan included regular visitors of species of *Gavia* reflecting a period when the Gaviidae expanded their distribution south to the subtropical Northwest Pacific during the relatively cold time of the Early Pleistocene. The change in oceanic currents associated with cooler glacial period climate, e.g., the Kuroshio Current in the Northwest Pacific, may have brought upwellings that supported both marine and coastal ecosystems in the ancient Taiwan Strait. This hypothesis is supported by a highly diverse fossil record of rays, sharks and bony fishes during the Early Pleistocene in the Liuchungchi Formation (Lin et al. 2018, 2021, 2022).

Fossil gaviids in Taiwan and their significance to the gaviid records in the Pleistocene.—The humerus CMM 2123 we identify as an indeterminate species of *Gavia* is smaller than the few modern specimens of *G. adamsii* we compared it to, but is more similar in qualitative features to this modern species than it is to any other modern *Gavia* species. These observations may be explained by three possible reasons. First, the specimen represent the small end of a larger size range than our samples of modern *G. adamsii* represents; however modern measurements of birds do not support this (Uher-Koch et al. 2020; US Fish & Wildlife Service 2023). Second, the fossil derives from birds in the Early Pleistocene population that consisted of smaller individuals than their modern counterparts. Third, this fossil represents an extinct sister-species to *G. adamsii*, characterized by the same qualitative features and smaller size. Resolution of this issue will require further fossils. The fossil records of *G. adamsii* are quite scarce, restricted to the North Pacific, and all come from the Holocene (Friedmann 1934a, b, 1935, 1941). In contrast, *G. stellata* has numerous Pleistocene fossil records from Europe, Asia and the Northeast Pacific (Fig. 7, SOM 1: table S3). The relative abundance of fossil records for *G. stellata* and *G. adamsii* is consistent with their modern distribution, as the former is widely distributed in mid- and high-latitude areas, whereas the latter is mainly found in a narrower zone in coastal regions of high-latitude areas (BirdLife International 2023). Most Pleistocene gaviid records are restricted to mid- and high-latitude regions of the Northern Hemisphere, and a few records from low-latitudes are from Mexico (Corona Martínez 2009) and Florida (Brodkorb 1953, 1963; Woolfenden 1959; Emslie 1995, 1998) (Fig. 7). The gaviid fossils from Taiwan provide another low-latitude occurrence, the first for the Pacific.

Conclusions

The two fossil species of *Gavia* from Taiwan, *G. stellata*, and an indeterminate species, are the first Pleistocene records of Gaviidae in the subtropical Northwest Pacific. They not only suggest a southern expansion of Pleistocene Gaviidae populations in the Northwest Pacific, but also hint at a distinct Pleistocene paleoavifauna in southern Taiwan, where the current subtropical climate is not suitable for Gaviidae. Therefore, the climate may have been colder when the two birds were alive in the Early Pleistocene, and the ancient Taiwan Strait may have been more productive and supported seabirds like Gaviidae and the greater diversity of fish evidenced by fossils. One of the two fossils is a species of *Gavia* which is much smaller than *G. adamsii*, yet similar in morphological features. To solve the taxonomic implications of the size disparity between it and *G. adamsii* requires more fossil remains.

Authors' contributions

SMW and CHL conceived and designed the project and wrote the paper. SMW collected the data. THW and SMW worked on the taxonomic identification. CKC conducted the biostratigraphy study. All authors edited the manuscript.

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