Historically transposed flipper pairs in a mounted plesiosaurian skeleton

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Received: 31 August 2021 / Accepted: 17 February 2022 / Published online: 15 April 2022
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Abstract
Plesiosaurs evolved four wing-like flippers that are morphologically similar to each other and were most likely used in underwater flight. Plesiosaurs have been the subject of a long research history as well as a long history of misidentifications and misinterpretations, especially transposition of parts of or entire fore- and hind flippers. We identified the transposed fore- and hind flippers in a mounted Cryptoclidus eurymerus specimen (GPIT-PV-30092) on display in the Paleontological Collection of Tübingen University. It is likely that the fore- and hind flippers were accidentally transposed when the skeleton was mounted, although, amongst plesiosaurs, the fore- and hind flippers of Cryptoclidus eurymerus are some of the least similar-looking ones. This occurred either during a remounting of the skeleton from a free-standing armature on the ground to a freely “flying” skeleton hanging from the ceiling, or after a research project conducted on the specimen in the 1970s. We summarize osteological characteristics that can be used to correctly identify fore- and hind flippers of this species, and for better future assessment of the plesiosaurs locomotory system.

Keywords Transposed flippers · Underwater flight · Locomotion · Research history · Preparation · Curation

Introduction
Since the emergence of paleontology as a scientific discipline, plesiosaurs have been found, recovered, studied, and reconstructed (e.g., de la Beche and Conybeare 1821; Owen 1840; Meyer 1855). Plesiosauria (Sauropterygia) is a secondarily aquatic clade situated within Diapsida (Neenan et al. 2013) that inhabited mostly marine environments (Kear et al. 2006) across the globe, from the Late Triassic (Winrich et al. 2017) through to the end of the Cretaceous (Vincent et al. 2013). Among plesiosaurs, two body forms evolved repeatedly and convergently: plesiosauromorph and pliosauromorph. The former morphotype is recognized by its relatively small head and a long neck, while the latter is characterized by a large head and a relatively short neck (Benson and Druckenmiller 2014).

All plesiosaurs had two hydrofoil-like flipper pairs that, osteologically, are almost identical in their appearance (Robinson 1975, 1977; Caldwell 1997) (Fig. 1a, c, d–h, Fig. 2a). In the pectoral girdle, the clavicle was much reduced, as was the dorsal projection of the scapula (Godfrey 1984). Most of the scapula was positioned anteroventrally on the plesiosaurian thorax. The coracoids were also positioned ventrally and were much enlarged in comparison to other Sauropterygia (i.e., placodonts, nothosaurs, pachypleurosau-saur, and plesiosaurs) (Storrs 1993) (Fig. 2a, b). In the pelvic girdle, the clavicle was much reduced, as was the dorsal projection of the pubis and ischium (Godfrey 1984). The pubis and ischium were positioned ventrally and flat on the belly. The pubis was much enlarged in comparison to other sauropterygians (Storrs 1993) (Fig. 2a, c). Closely spaced gastralia covered
Fig. 1 Plesiosaur exhibition at the Paleontological Collection, Tübingen University, Germany. a Peloneustes philarchicus (GPIT-PV-30091, syn. PV 17870 and GPIT/RE/3182; University archives) in 1920 and b in the current exhibition (picture by Valentin Marquardt 2020). c Liopleurodon ferox (left) (GPIT-PV-30093, syn. PV 17998 and GPIT/RE/3184), Peloneustes philarchicus (right bottom), and Cryptoclidus eurymerus (GPIT-PV-30092; syn. PV 17933 and GPIT/RE/3183) (right top) (picture by Valentin Marquardt 2020). d Cryptoclidus eurymerus (foreground, to the left; Peloneustes philarchicus to the right side behind Cryptoclidus eurymerus) on exhibition, around 1964 (Augusta and Burian 1964) and e around 1905, to the right side in the foreground, in the middle Peloneustes philarchicus is found and Liopleurodon ferox in the background (Koken 1905b). All three taxa at the Paleontological Collection, University of Tübingen. Note the traditional rowing position of the flippers in these historical mountings. f Excerpt from the old catalogue (Petrefaktenverzeichnis; PV) noting the acquisition of Cryptoclidus eurymerus with the old collection number PV 17933
the belly in between the pectoral and the pelvic girdle (Storr 1993) (Fig. 1a).

In the evolutionary history of Tetrapoda, plesiosaurians evolved a unique locomotory apparatus with four hydrofoils. All other paraxial swimming tetrapods with hydrofoil-like limbs—sea turtles and penguins—have only one pair (Robinson 1975). How plesiosaurians swim with two flipper pairs is still an area of active research. Williston (1914), Watson (1924), Tarlo (1958), Araújo and Correia (2015), and Araújo et al. (2015) interpreted plesiosaurians as rowers. Williston’s (1914) and Watson’s (1924) work probably greatly influenced the appearance of historical mounts of plesiosaurian skeletons, e.g., *Peloneustes philarchicus* (Fig. 1a, b) and *Liopleurodon ferox* (Fig. 1c), both exhibited at the Paleontological Collection, University of Tübingen (acronym: GPIT, for the former Geologisch-Paläontologisches Institut Tübingen). Later, it was proposed that plesiosaurians swam like sea lions. This means that plesiosaurians were partially rowing and were partially underwater flying during one limb cycle (Godfrey 1984; Lingham-Soliar 2000; Liu et al. 2015). Today, the general consensus is that plesiosaurians were underwater flyers (Fig. 3d), based on the hydrofoil shape of the flipper, and the anatomy of the glenoid and acetabulum (see e.g., Robinson (1975, 1977), Lingham-Soliar (2000), Carpenter et al. (2010), Liu et al. (2015), Muscutt et al. (2017), Krahl (2021) and Krahl and Witzel (2021)).

Almost as old as the earliest studies of plesiosaurians is the history of errors when interpreting, reconstructing, and mounting parts of plesiosaurians. In 1868, Edward Drinker Cope (1840–1897) famously presented a reconstruction of *Elasmosaurus platyurus* in which he placed the skull at the end of the tail. This contributed to his personal feud with Othniel Charles Marsh (1831–1899) and stuck to him as an anecdote and as part of the history of paleontology to this day (Davidson 2002). This was followed by several authors who mistakenly identified plesiosaurian bones of the pelvic girdle as bones of the pectoral girdle or the other way around (Hector 1874; Brown 1913, 1958, 1959). Tarlo (1958) even based plesiosaurian foreflipper muscle reconstructions and erected a novel genus (‘*Stretosaurus*’) (Tarlo 1959) based on a misidentified ilium, which he identified as a scapula. Smith (2007a) provided a redescriptions of *Cryptoclidus* (“*Apractocephalus*”) *aldingeri* (MGHU 28378 from the Geologisk Museum in Copenhagen, Denmark) which was originally described by Tübingen curator Friedrich von Huene (1875–1969). Smith (2007a) showed that von Huene (1935) misidentified the plesiosaurian remains, like E. D. Cope did, in reverse. Consequently, the originally described tail, pelvic girdle bones, and fragmental femur were redescribed as posterior cervical vertebrae, pectoral girdle bones, and a fragmental humerus (Smith 2007a). A cast of another plesiosaurian specimen, *Rhomaleosaurus cramponi* in the Bath Royal Literary and Scientific Institute, also contains an anatomical error in the mount: the forelimbs and hind limbs have been transposed (Smith 2007b).

**Curational history and observations on the Tübingen *Cryptoclidus eurymerus* specimen**

Here we report on a historical mount of a plesiosaurian skeleton with its foreflippers mounted in the position of the hind flippers, and its hind flippers mounted in the position of the foreflippers. The specimen, *Cryptoclidus eurymerus* (GPIT-PV-30092; syn. PV 17933 and GPIT/RE/3183), is displayed in the exhibition of the Paleontological Collection of Tübingen University (Figs. 1c and 2a). The plesiosaurian remains were originally found, recovered, prepared, and mounted by Alfred Nicholson Leedsm in Peterborough (Cambridgeshire, UK), and were collected from the Oxford Clay Formation (Callovian, Middle Jurassic around 1900). Leedsm amassed large collections from these deposits, which were sold or donated in batches and dispersed across several European institutions (Leedsm 1956; Noè 2009). Fossil dealer Bernard Stürtz from Bonn, Germany, bought this *Cryptoclidus eurymerus* skeleton from Leedsm in 1904. Brown (1981) provided a thorough systematic diagnosis for *C. eurymerus*, and GPIT-PV-30092 possesses the following diagnostic postcranial characteristics for the genus: about 55 presacral vertebrae, of which usually 32 are cervical; the cervical vertebrae have relatively amphicoelous centra, the length of which very rarely exceeds the height; and the width across the posterior cornua of the coracoids exceeds the interglenoid width (in osteologically mature individuals) by up to 40%. The specimen can also be more precisely referred to *C. eurymerus* based on the following diagnostic characters for the species as defined by Brown (1981): the humerus is greatly expanded distally by an anterior expansion of the portion bearing the radial facet; the radius is enlarged by the anterior expansion of the portion bearing the humeral facet causing the anterior margin to describe a sigmoid curve; and the ulna is much wider than long. The *C. eurymerus* skeleton was then bought by maecenas Friedrich Glimpf from Mannheim, Germany, and gifted to the Tübingen collection, as mentioned in the museum’s inventory catalogue (Universitätsarchiv Tübingen (Tübingen University Archive) UAT: Petrefactenverzeichnis 1897–1935, folio page 16; Fig. 1f), on the occasion of its new opening in 1904/1905 (not documented to the day) (Koken 1904, 1905a, b). A picture of the specimen taken in 1905 shows it mounted on an armature on the ground, with its four limbs swept back in a rowing position (Fig. 1e). This orientation of the limbs, relative to the body, is beyond the biologically possible ranges (Liu et al. 2015). The first skeleton mountings by Friedrich
von Huene, who became reknown for the modularity of his mountings (Buzdogan 2021; Werneburg 2021), are from around 1919 (von Huene 1919). It is highly unlikely that in 1904 the mounting of that skeleton was made by the young scientist von Huene (curator from 1927 to 1948; see Werneburg 2021), but rather by the Stürtz-company, which delivered the skeleton together with the complete steel girdle and limb scaffolds were screwed together; arrows mark screws that fix the bones on the steel scaffold. g Anterior section (therefore the frame in c is smaller than this picture due to the perspective) of the humerus enlarged, depicting foreflipper muscle insertions; S H ANT = musculus scapulohumeralis anterior, and PEC = musculus pectoralis, as described by Robinson (1975).

As the fore- and hind flippers look very similar in plesiosaurs (Fig. 1a–c), which is known because of numerous articulated specimens that have been found, it can be difficult to distinguish between them. Contrastingly, in C. eurymerus the humerus and femur are relatively easy to distinguish in non-juvenile specimens (Brown 1981). The humerus and femur are both hammer-shaped. Both long bones are proximally round in cross-section and become dorsoventrally flattened towards the mid-length of the bone and therefore oval in cross section. The distal ends are dorsoventrally flattened and expanded anteroposteriorly. The humerus is more expanded or broader in anteroposterior direction than the femur (compare Fig. 3c to a, b). The humerus and femur are anterodistally curved convex and posterodistally curved concave. On the dorsal side of the humerus is a tuberosity expanding from posteroproximally to anterodistally (Fig. 3c). Similarly, on the dorsal femur is a trochanter that expands from posteroproximally to anterodistally (Figs. 2a and 3a, b). In proximal view, the tuberosity of the humerus is positioned posterodorsal to the humerus head, whereas in the femur the equivalent trochanter is positioned dorsal and directly above the femoral head. This way, one can tell the humerus and femur apart and determine whether it is a left or right long bone (Andrews 1910; Brown 1981). This differing position of the tuberosity/trochanter occurs in all plesiosaurian taxa and therefore provides a way to differentiate between the fore- and hind limbs in plesiosaurs in general, when this part of the propodial is preserved.

In early sauropterygians, the radius, ulna, tibia, and fibula are hour-glass-shaped (compare to e.g., Rieppel 2000). In later plesiosaurs, these bones become dorsoventrally depressed polygonal discs. In adult C. eurymerus, the radius is larger than ulna, tibia, and fibula (Andrews 1910). The contact areas of the radius to the humerus and ulna curves from anteroproximal to posteroproximal to posterodistal. The distal articulation surface is a relatively straight line. On the anterior side, the radius bulges slightly anteriorly and then continues straight directed slightly posteriorly and distally. Contrastingly, the proximal and posterior articulation surface of the tibia is rather straight. Anteriorly and distally, the tibia is round. The radius has a markedly different shape compared to the tibia (Fig. 3a, b). Ulna and fibula almost look like a triangle with the hypenuse lying proximally adjacent to the humerus respectively the femur (Andrews 1910; Fig. 3a, b). The other carpals and tarsals are difficult to identify if found isolated due to ontogenetic and preservational differences. Therefore, one can conclude confidently, that at least humerus, radius, and ulna of both foreflippers as well as femur, tibia, and fibula of both hind flippers have been swapped in the historic mounting in Tübingen. It appears likely that the whole flippers were mounted correctly, and then they were mistakenly transposed when they were mounted onto the specimen.

**Discussion and conclusion**

The question arises, how and when did the fore- and hind flippers of the Tübingen Cryptoclidus specimen become transposed? In photographs taken in 1905 (Fig. 1e) and pre-1964 (Fig. 1d) the fore- and hind flippers are clearly visible and mounted in the correct positions. In 1964, the Cryptoclidus mount that was originally standing on the ground (Fig. 1d, e) was rebuilt and suspended from the ceiling, as it appears in the exhibition today (Figs. 1c and 2a; ‘annual reports of the institute’: stored at University Archive Tübingen, UAT signature: 678/593; personal communication Frank Westphal 2021). The remounting seems likely to be the occasion when the flipper transposition took place (see below).

We found old stickers marking the insertion points of muscles on the humerus and femur (Fig. 2d, g). These may be associated with the muscle reconstructions made by Jane Ann Robinson, who was a visiting scientist in the collection in the early 1970s, conducting part of her doctoral thesis (UAT signature: 678/593). Robinson wrote thorough and groundbreaking papers on plesiosaurian locomotion, in which she included muscle reconstructions and comparisons to functionally analogous extant tetrapods (Robinson 1975, 1977). She concluded that plesiosaurs were most likely underwater flyers and not rowers. This greatly influenced
our current research on extinct secondary aquatic reptiles and the way plesiosaurians are depicted in life restorations (Figs. 1c, 2a, 3d). Robinson has been the only researcher to argue that the dorsal humerus and femur side have to point into the anterior direction due to the configuration of the articulation surfaces of the shoulder and hip joints (Robinson 1975). Because of this 90° rotation of humerus and femur, many proximally inserting humerus and femur muscles are displaced by 90°, too. In Fig. 2d and g, it can be seen that musculus pectoralis (= PEC) of the foreflipper and musculus adductores (= AD) of the hind flipper insert anteriorly into the plesiosaurian long bones. Usually, these muscles insert ventrally into humerus and femur in extant Sauropsida (Walker 1973; Russel and Bauer 2008; Meers 2003). This configuration of stickers representing muscle attachments found on the plesiosaurian skeleton, today, is identical with the muscle reconstructions published by Robinson (1975, fig. 19b and fig. 21b). She clearly knew which flipper pair was the foreflipper and which was the hind flipper, because she reconstructed forelimb muscles onto the foreflipper and hind limb muscles onto the hind flipper in Cryptoclidus.

Robinson (1975) did not mention that the limbs were transposed in the Tübingen specimen, which could mean that the flippers were transposed after her study. It is more likely, however, that this preparatory artifact was simply not worth mentioning in her purely anatomical analysis. The bones are firmly fixed to the steel scaffold by porous steel pins that usually break off when unmounting particular bones and have to be welded on for secondary mounting (Fig. 2f). In the Cryptoclidus specimen, no welded joints are visible in the respective steel pins. On the other hand, the limbs as a whole could have been removed by Robinson, as the stiff
limb scaffolds are only screwed to the girdle scaffolds at one point each (Fig. 2e). When screwing back to the girdles, the fore- and hind limbs could have been transposed, although we assume this is rather unlikely by following reason: A replacement of the wire ropes that hold the specimen on the ceiling took place in November 2013 by current preparator Henrik Stöhr (unpublished chronicle of the collection). He informed us in 2021 that each single steel rope was replaced by a newer one. One wire rope per limb was present already in the original mounting as they are crucial to ensure the stability of the whole suspended specimen. As such, it is very unlikely that Robinson unmounted the whole limbs risking a fatal damage to the suspended plesiosaurian, and unmounting the specimen was not necessary for her purposes. As such, it seems most plausible that the confusion between the fore- and hind flippers was already present prior to Robinson’s work on the specimen.

It is likely that von Huene, who was active in the institute until his death in 1969, supervised the mounting of the hanging Cryptoclidus specimen in 1964 and that the flipper transposition took place on this occasion. He did so for many mounted skeletons after his retirement in 1948 (Hölder 1953, 1977). The technicians at the time were Wilhelm Wetzel (1902–1983; preparator: 1922–1967), Friedrich Kern (born 1912; mechanist: 1950–1975), and Hans Luginsland (*1948, preparator: 1963–2013) (see Werneburg (2021)). As mentioned above, von Huene (1935) had previously confused the vertebrae of another ‘Cryptoclidus’ species, like Cope, probably followed by the misidentification of the fore- and hind flippers. So, the transposed flippers of the hanging Tübingen specimen perhaps happened under his advice and direction. However, at this time von Huene was very busy (Turner 2009; Maisch 2014), so perhaps he only provided general instructions for construction of the specimen at the beginning of the project and did not check the mounting at every step.

It is noteworthy that the Cryptoclidus mount as it appears today seems to be posed in an underwater flight gait rather than a rowing gait. A rowing gate in the forelimb is usually implied by (a) a downward/ventrally angled humerus and femur, (b) flippers that are swept backwards, and (c) a humerus and femur that are often rotated significantly along their length axis. (a) and (b) can be seen in Tübingen in the Liopleurodon ferox und Peloneustes philarchus mounting (Fig. 1c) and the old mounting of Cryptoclidus eurymerus (Fig. 1d). (c) can be observed in Peloneustes philarchus (Fig. 1b, c). This is because a rowing stroke is mostly characterized by an anteroposterior plane of flipper movement and an approximately 90° limb rotation which is often performed at the body midline or below. Contrastingly during underwater flight, the flippers are mainly moved through the dorsoventral plane and the rotation along the humeral/femoral length axis is less than 90° (Rivera et al. 2013).
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