



Historically transposed flipper pairs in a mounted plesiosaurian skeleton

Anna Krahl¹ · Adam S. Smith² · Ingmar Werneburg^{1,3}

Received: 31 August 2021 / Accepted: 17 February 2022 / Published online: 15 April 2022
© The Author(s) 2022

Abstract

Plesiosaurians evolved four wing-like flippers that are morphologically similar to each other and were most likely used in underwater flight. Plesiosaurians 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 plesiosaurians, 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 plesiosaurian locomotory system.

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

Introduction

Since the emergence of paleontology as a scientific discipline, plesiosaurians 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

(Wintrich et al. 2017) through to the end of the Cretaceous (Vincent et al. 2013). Among plesiosaurians, 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 plesiosaurians 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, pachypleurosaurs, and pistosaurs) (Storrs 1993) (Fig. 2a, b). In the pelvic girdle, the dorsally projecting ilium was much reduced in size in comparison to other sauropterygians, comparable to the scapular blade (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 gastralria covered

Handling Editor: Walter Joyce.

✉ Anna Krahl
anna.krahl@uni-tuebingen.de

✉ Ingmar Werneburg
ingmar.werneburg@senckenberg.de

¹ Fachbereich Geowissenschaften der Universität Tübingen, Paläontologische Sammlung, Hölderlinstraße 12, 72074 Tübingen, Germany

² Nottingham Natural History Museum, Wollaton Hall, Nottingham NG8 2AE, UK

³ Senckenberg Center for Human Evolution and Palaeoenvironment an der Universität Tübingen, Sigwartstraße 10, 72076 Tübingen, Germany



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 philar-*

chus 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 philarchus* 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 (Storrs 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 swam 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 (1931–1899) 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; Tarlo 1958, 1959). Tarlo (1958) even based plesiosaurian foreflipper muscle reconstructions on and erected a novel genus ('*Stretosaurus*') (Tarlo 1959) based on a misidentified ilium, which he identified as a scapula. Smith (2007a) provided a redescription of *Cryptoclidus* ("*Apractocleidus*") *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 re-described as posterior cervical vertebrae, pectoral girdle bones, and a fragmental humerus (Smith 2007a). A cast of another plesiosaurian specimen, *Rhomaleosaurus cramptoni* 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).

Curatorial 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 Leeds in Peterborough (Cambridgeshire, UK), and were collected from the Oxford Clay Formation (Callovian, Middle Jurassic around 1900). Leeds amassed large collections from these deposits, which were sold or donated in batches and dispersed across several European institutions (Leeds 1956; Noè 2009). Fossil dealer Bernard Stürtz from Bonn, Germany, bought this *Cryptoclidus eurymerus* skeleton from Leeds 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

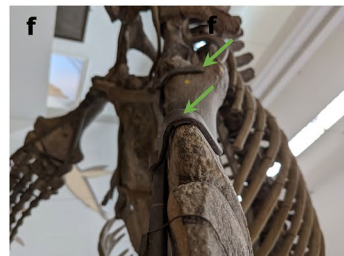
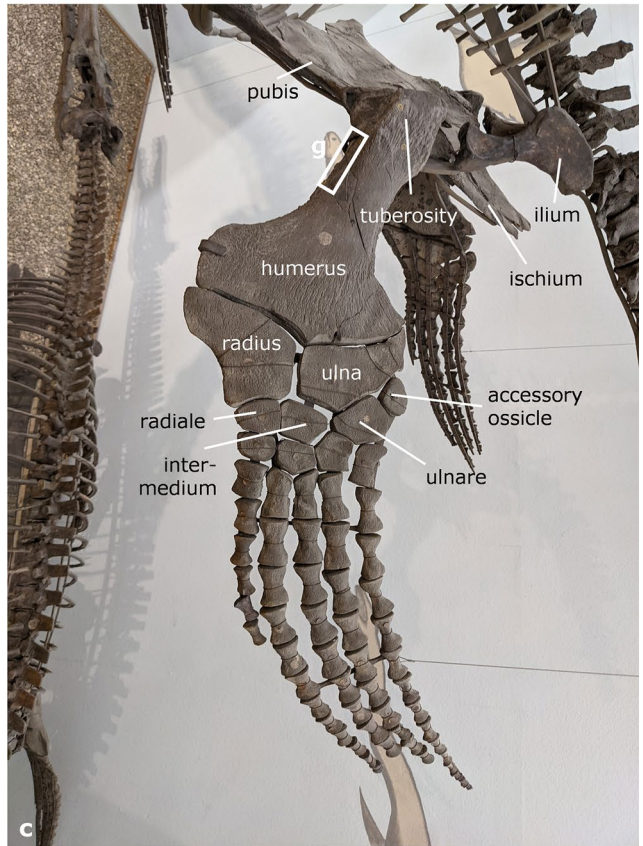
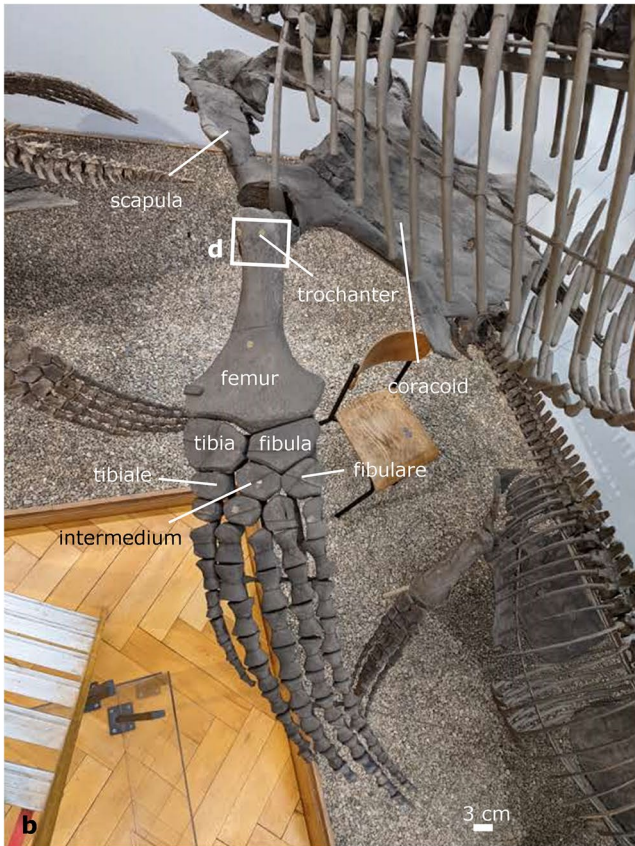
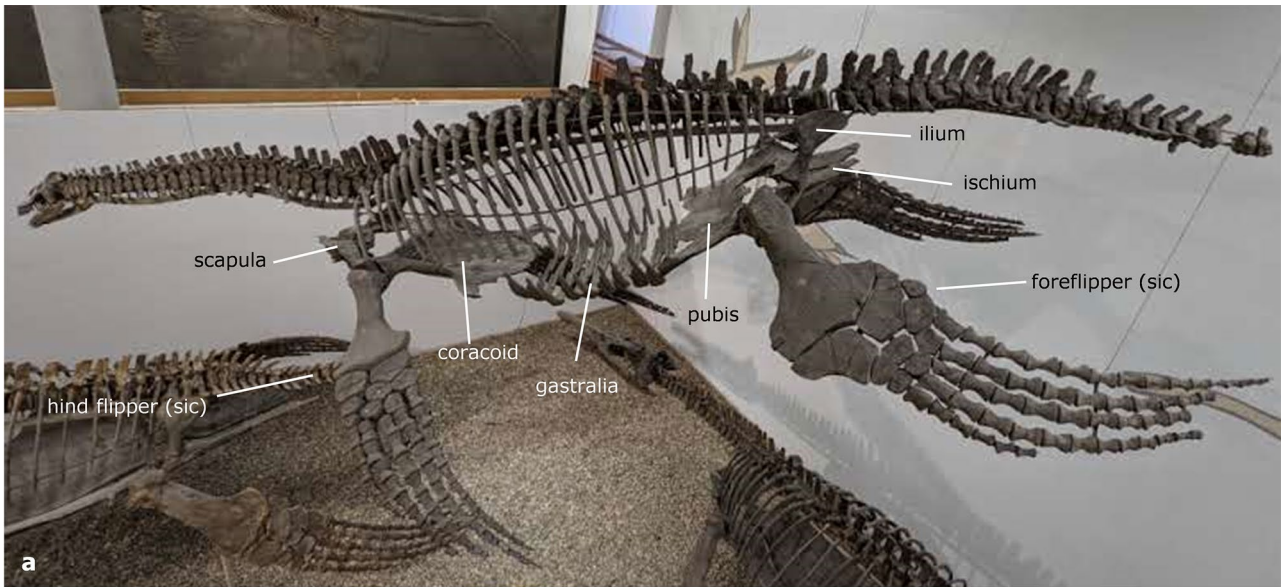


Fig. 2 *Cryptoclidus eurymerus* anatomy. **a** Overview of the current display of *Cryptoclidus* (GPIT-PV-30092), Paleontological Collection, Tübingen University, approximately 6 m in length. **b** Left hind flipper in the position of the foreflipper. **c** Left foreflipper in the position of the hind flipper. **d** Anterodorsal section of femur enlarged, showing stickers with notes of Robinson identifying hind limb muscle attachments (AD=musculus adductors and PIFI=musculus puboischiofemoralis internus and P=possibly the pubic portion of this muscle as described by Robinson (1975)). **e** Girdle and limb scaffolds are screwed together; arrows mark screws **f** steel pins 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)

von Huene, who became reknown for the modularity of his mountings (Buzdogán 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 likely delivered the skeleton together with the complete steel armature, because the exhibition with the plesiosaurians on display was opened shortly after (Koken 1904, 1905a, b), and it would have been too little time to organize such complex mountings in Tübingen.

As the fore- and hind flippers look very similar in plesiosaurians (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 podial is preserved.

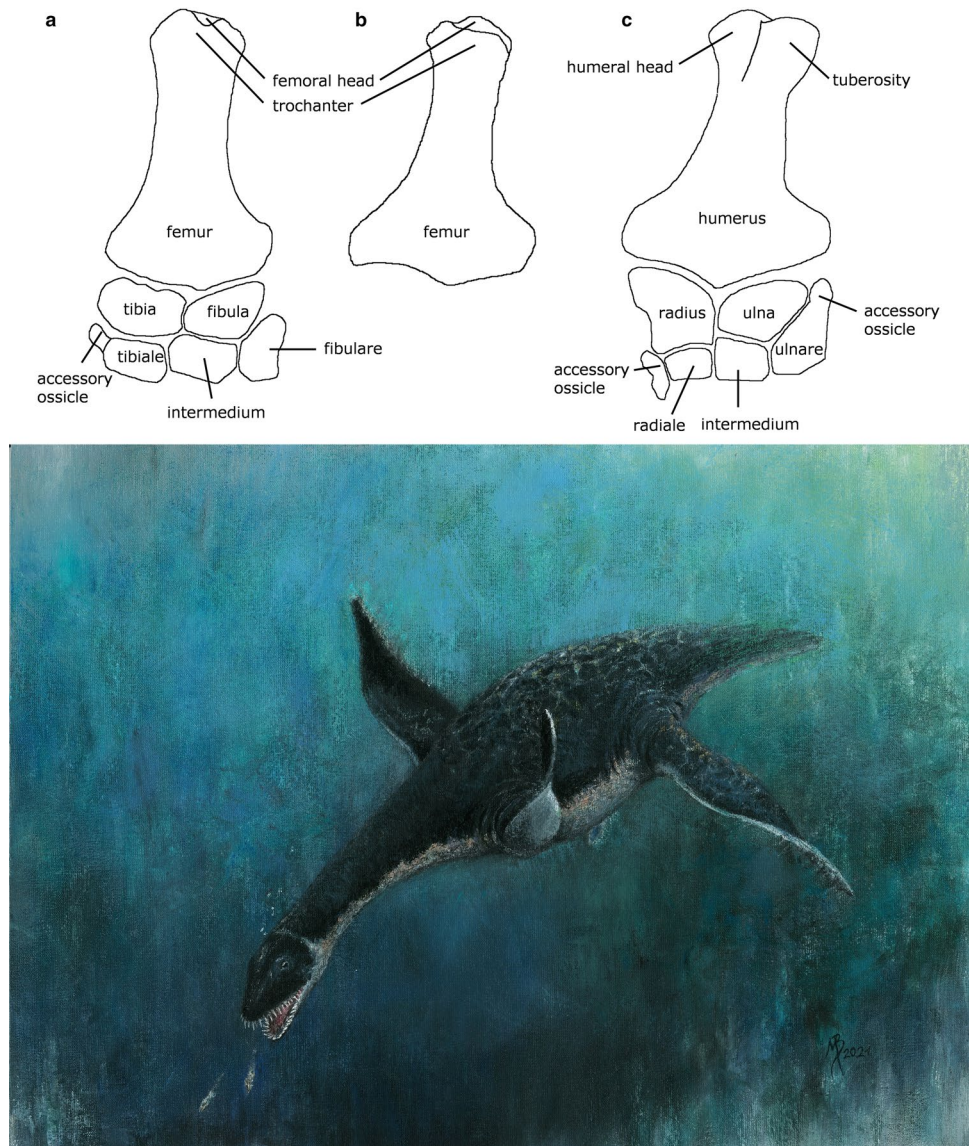
In early sauropterygians, the radius, ulna, tibia, and fibula are hour-glass-shaped (compare to e.g., Rieppel 2000). In later plesiosaurians, these bones become dorsoventrally depressed polygonal discs. In adult *C. eurymerus*, the radius is larger than ulna, tibia, and fibula (Andrews 1910). The contact 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 proximally 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 hypotenuse 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 plesiosaurians were most likely underwater flyers and not rowers. This greatly influenced

Fig. 3 *Cryptoclidus eurymerus* fore- and hind flipper osteology. **a** Part of the left hind flipper of *Cryptoclidus*, redrawn from Andrews (1910). **b** Left femur of *Cryptoclidus* that resembles the one of GPIT-PV-30092, redrawn from Andrews (1910). **c** Part of the right foreflipper of *Cryptoclidus*, redrawn and mirrored from Andrews (1910). **d** *Cryptoclidus eurymerus* (GPIT-PV-30092) life reconstruction (GPIT-PV-113559) showing underwater flight and flipper twisting based on Krahl (2021) and Krahl and Witzel (2021) by paleoartist Marcus Burkhardt



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 gait in plesiosaurs 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).

This is observable in the current mounting of *Cryptoclidus eurymerus* (Figs. 1c and 2d). The depiction of underwater flight is surprising because, firstly, usually plesiosaurs were depicted as rowers before 1975 (see above and Fig. 1a–e) and, secondly, the skeletal remounting appears to predate, by eleven years, the seminal work of Robinson on an underwater flight in plesiosaurs (Robinson 1975). One can speculate now, that the vision for underwater flight in plesiosaurs was first manifested in the remounting of a now underwater flying *Cryptoclidus eurymerus* in 1964 by Friedrich von Huene and then followed and underpinned by the scientific work of Robinson (1975, 1977) or that Robinson had even been inspired by the remounted skeleton. Von Huene is known to have prepared visionary skeletal reconstructions in natural, i.e. biological postures. As shown by his reprint collection (stored in the institute's library in Tübingen; Turner 2009), he also read biological papers dealing with muscle-bone associations. One of his publications, 'A biological museum mounting of *Placodus* [another sauropterygian] in Tübingen' (translated by us) (von Huene 1949), had a holistic conceptualization in mind that inspired skeletal preparation worldwide (Buzdogán 2021; Werneburg 2021). This modern method of skeletal mounting even enabled a higher salary ranking for the institute's technician Friedrich ("Fritz") Kern, who was, at the time, the expert of this method and even advanced it over the years (UAT signature: 193/2446).

Acknowledgements We would like to thank preparator Henrik Stöhr from the Paleontological Collection of Universität Tübingen for discussion. Special thanks go to Marcus Burkhardt for the beautiful life reconstruction of *Cryptoclidus eurymerus*. We are thankful to Lene L. Delsett, Peggy Vincent, and one anonymous reviewer for their comments that led to an improved manuscript. The former and the current Editor-in-Chief M. Reich and M. Rasser as well as Handling Editor W. Joyce are thanked.

Author contributions AK and IW wrote the manuscript and provided figures. ASS improved the text and helped with discussion.

Funding Open Access funding enabled and organized by Projekt DEAL. I.W. is supported by Deutsche Forschungsgemeinschafts DFG-grant WE 5440/6-1.

Declarations

Conflict of interest All authors declare they have no competing interests.

Availability of data and material Not applicable.

Code availability Not applicable.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication All authors have read the final version of the manuscript and agree with its publication.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Andrews, C.W. 1910. *A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay, Part I*. London: British Museum (Natural History).
- Araújo, R., and F. Correia. 2015. Soft-tissue anatomy of the plesiosaur pectoral girdle inferred from basal Eosauropterygia taxa and the extant phylogenetic bracket. *Palaeontologica Electronica* 18 (1): 1–32.
- Araújo, R., M.J. Polcyn, A.S. Schulp, O. Mateus, L.L. Jacobs, A. Olímpio Goncalves, and M.-L. Morais. 2015. A new elasmosauroid from the early Maastrichtian of Angola and the implications of girdle morphology on swimming style in plesiosaurs. *Netherlands Journal of Geosciences - Geologie en Mijnbouw* 94 (1): 109–120. <https://doi.org/10.1017/njg.2014.44>.
- Augusta, J., and Z. Burian. 1964. *Prehistoric Sea Monsters*, 1–64. London: P. Hamlyn.
- Benson, R.B.J., and P.S. Druckenmiller. 2014. Faunal turnover of marine tetrapods during the Jurassic–Cretaceous transition. *Biological Reviews* 89: 1–23.
- Brown, B. 1913. A new plesiosaur, *Leurospondylus*, from the Edmonton Cretaceous of Alberta. *Bulletin of the American Museum of Natural History* 32: 605–661.
- Brown, D.S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bulletin of the British Museum of Natural History (geological Series)* 35 (4): 253–347.
- Buzdógan, A. 2021. 1927/28 *Stahleckeria*—Ursprung der Säugetiere. In *Aus der Tiefenzeit—Die Paläontologische Sammlung der Eberhard Karls Universität Tübingen*, ed. E. Seidl, E. Bierende, and I. Werneburg, 414–431. Tübingen: Publikationen der Universität Tübingen.
- Caldwell, M.W. 1997. Limb osteology and ossification patterns in *Cryptoclidus* (Reptilia: Plesiosauroidea) with a review of sauropterygian limbs. *Journal of Vertebrate Paleontology* 17 (2): 295–307.
- Carpenter, K., F. Sanders, B. Reed, J. Reed, and P. Larson. 2010. Plesiosaur swimming as interpreted from skeletal analysis and experimental results. *Transactions of the Kansas Academy of Science* 113 (1/2): 1–34.
- Davidson, J.P. 2002. Bonehead mistakes: the background in scientific literature and illustrations for Edward Drinker Cope's first restoration of *Elasmosaurus platyrus*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 152: 215–240.
- de la Beche, H.T., and W.D. Conybeare. 1821. Notice of the discovery of a new fossil animal, forming a link between the *Ichthyosaurus* and crocodile, together with general remarks on the osteology of the ichthyosaurs. *Transactions of the Geological Society of London, Series 1* (5): 559–594.
- Godfrey, S.J. 1984. Plesiosaur subaqueous locomotion: a reappraisal. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1984 (11): 661–672.
- Hector, J. 1874. On the fossil reptiles of New Zealand. *Transactions of the New Zealand Institute* 6: 333–358.
- Hölder, H. 1953. *Zeugen der Urzeit; Ein Rundgang durch das Universitätsmuseum für Geologie und Paläontologie*. Tübingen: Attempto Verlag (museum brochure).
- Hölder, H. 1977. Geschichte der Geologie und Paläontologie an der Universität Tübingen. In *Mineralogie, Geologie und Paläontologie an der Universität Tübingen von den Anfängen bis zur Gegenwart (Contubernium, 20)*, ed. W. Engelhardt and H. Hölder, 87–292. Germany: Tübingen.
- Kear, B.P., N.I. Schroeder, and M.S. Lee. 2006. An archaic crested plesiosaur in opal from the Lower Cretaceous high-latitude deposits of Australia. *Biology Letters* 2 (4): 615–619.
- Koken, E. 1904. Das Geologisch-Mineralogische Institut in Tübingen. *Centralblatt für Mineralogie, Geologie und Paläontologie* 1904: 673–693.
- Koken, E. 1905a. *Das Geologisch-Mineralogische Institut in Tübingen mit 3 Planskizzen*, 1–21. Stuttgart: Schweizerbartsche Verlagsbuchhandlung.
- Koken, E. 1905b. *Führer durch die Sammlungen des Geologisch-Mineralogischen Instituts*, 1–110. Stuttgart: Schweizerbartsche Verlagsbuchhandlung.
- Krahl, A. 2021. The locomotory apparatus and paraxial swimming in fossil and living marine reptiles: comparing Nothosauroida, Plesiosauria, and Chelonioidea. *PalZ*. <https://doi.org/10.1007/s12542-021-00563-w>.
- Krahl, A., and U. Witzel. 2021. Foreflipper and hindflipper muscle reconstructions of *Cryptoclidus eurymerus* in comparison to functional analogues: introduction of a myological mechanism for flipper twisting. *PeerJ* 9: e12537. <https://doi.org/10.7717/peerj.12537>.
- Leeds, E.T. 1956. *The Leeds Collection of Fossil Reptiles from the Oxford Clay of Peterborough*. Oxford: Blackwell.
- Lingham-Soliar, T. 2000. Plesiosaur locomotion: is the four-wing problem real or merely an atheoretical exercise? *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 217 (1): 45–87.
- Liu, S., A.S. Smith, Y. Gu, J. Tan, C.K. Liu, and G. Turk. 2015. Computer simulations imply forelimb-dominated underwater flight in plesiosaurs. *PLoS Computational Biology* 11 (12): e1004605. <https://doi.org/10.1371/journal.pcbi.1004605>.
- Maisch, M. 2014. Bedeutende Paläontologen—Friedrich von Huene (1875–1969). *Fossilien* 1: 32–37.
- Meers, M.B. 2003. Crocodylian forelimb musculature and its relevance to Archosauria. *The Anatomical Record* 274 (2): 891–916.
- Muscott, L.E., G. Dyke, G.D. Weymouth, D. Naish, C. Palmer, and B. Ganapathisubramani. 2017. The four-flipper swimming method of plesiosaurs enabled efficient and effective locomotion. *Proceedings of the Royal Society B* 284 (1861): 20170951. <https://doi.org/10.1098/rspb.2017.0951>.
- Neenan, J.M., N. Klein, and T.M. Scheyer. 2013. European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. *Nature Communications* 4: 1621. <https://doi.org/10.1038/ncomms2633>.
- Noè, L. 2009. The Alfred Leeds Collection of fossil vertebrates; past present and future. *NatSCA News* 17: 10–13.
- Owen, R. 1840. Report on British fossil reptiles. *Report of the Ninth Meeting of the British Association for the Advancement of Science* 9: 43–126.
- Rieppel, O. 2000. Sauropterygia I: Placodontia, Pachypleurosauria, Nothosauroida, Pistosauroida. In *Encyclopedia of Paleoherpetology*, vol. 12A, ed. P. Wellnhofer, 1–134. München: Pfeil.

- Rivera, A.R.V., G. Rivera, and R.W. Blob. 2013. Forelimb kinematics during swimming in the pig-nosed turtle, *Carettochelys insculpta*, compared with other turtle taxa: rowing versus flapping, convergence versus intermediacy. *The Journal of Experimental Biology* 216 (Pt. 4): 668–680. <https://doi.org/10.1242/jeb.079715>.
- Robinson, J.A. 1975. The locomotion of plesiosaurs. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 149: 286–332.
- Robinson, J.A. 1977. Intracorporal force transmission in plesiosaurs. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 153: 86–128.
- Russell, A.P., and A.M. Bauer. 2008. The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates. In *Biology of the Reptilia*, vol. 21, ed. C. Gans and T.S. Parsons, 1–465. New York: Academic Press.
- Smith, A.S. 2007a. The back-to-front-plesiosaur *Cryptocleidus (Apractocleidus) aldingerae* from the Kimmeridgian of Milne Land, Greenland. *Bulletin of the Geological Society of Denmark* 55: 1–7.
- Smith, A.S. 2007b. *Anatomy and Systematics of the Rhomaleosauridae (Sauropterygia: Plesiosauria)*. PhD thesis. University College Dublin, p. 278.
- Storrs, G.W. 1993. Function and phylogeny in sauropterygian (Diapsida) evolution. *American Journal of Science* 293: 63–90.
- Tarlo, L.B. 1958. The scapula of *Pliosaurus macromeris* Phillips. *Palaeontology* 1 (3): 193–199.
- Tarlo, L.B. 1959. *Stretosaurus* gen. nov., a giant pliosaur from the Kimmeridge Clay. *Palaeontology* 2 (1): 39–55.
- Turner, S. 2009. Reverent and exemplary: ‘Dinosaur man’ Friedrich von Huene (1875–1969). *Geological Society, London, Special Publications* 310: 223–243.
- Vincent, P., N. Bardet, A. Houssaye, M. Amaghazaz, and S. Meslouh. 2013. New plesiosaur specimens from the Maastrichtian phosphates of Morocco and their implications for the ecology of the latest Cretaceous marine apex predators. *Gondwana Research* 24 (2): 796–805.
- von Huene, F. 1919. Bilder aus der paläontologischen Universitäts-Sammlung in Tübingen. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg* 1–3: 177–184.
- von Huene, F. 1935. Ein Plesiosaurier-Rest aus Grönländischem Oberem Jura. *Kommissionen for Videnskabelige Undersøgelser I Grønland* 99 (4): 1–11.
- von Huene, F. 1949. Eine biologische Museumsaufstellung von *Placodus* in Tübingen. *Neues Jahrbuch Für Mineralogie, Geologie Und Palaeontologie* 1–3: 76–80.
- von Meyer, H. 1855. *Zur Fauna der Vorwelt. Die Saurier des Muschelkalkes mit Rücksicht auf die Saurier aus buntem Sandstein und Keuper*. Frankfurt am Main: Heinrich Keller.
- Walker, W.F. 1973. The locomotor apparatus of Testudines. In *Biology of Reptilia*, vol. 4, ed. C. Gans and T.S. Parsons, 1–100. New York: Academic Press.
- Watson, D.M.S. 1924. The elasmosaurid shoulder-girdle and fore-limb. *Proceedings of the Zoological Society of London* 58: 885–917.
- Werneburg, I. 2021. Ein Stück Kulturgeschichte. Zur Entwicklung der Paläontologischen Sammlung in Tübingen. In *Aus der Tiefenzeit—Die Paläontologische Sammlung der Eberhard Karls Universität Tübingen*, ed. E. Seidl, E. Bierende, and I. Werneburg, 30–63. Tübingen: Publikationen des Museums der Universität Tübingen.
- Williston, S.W. 1914. *Water Reptiles of the Past and Present*. Chicago: University of Chicago Press.
- Wintrich, T., S. Hayashi, A. Houssaye, Y. Nakajima, and P.M. Sander. 2017. A Triassic plesiosaur skeleton and bone histology inform on evolution of a unique body plan. *Science Advances* 3 (12): e1701144. <https://doi.org/10.1126/sciadv.1701144>.