Plesiosaurs from Svalbard

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Contents

Abstract: A re-description and a re-classification is made for the plesiosaur specimen PMO A 27745 previously identified in 1962 as *Tricleidus svalbardensis* Persson.

In all probability the fossil is from the Slottsmøya Member of the Agardhfjellet Formation and was collected at the entrance to Sassenfjorden, Svalbard. Its age is Volgian. Study of the material, in reference to the current taxonomy of the Plesiosauria which acknowledges the Polycotylidae as part of the Plesiosauria, suggests that it may belong to the Tricleidia of the Superfamily Cryptocleidoidea. A cladistic analysis of related taxa places *Tricleidus svalbardensis* in a close relationship with *Polycotylus*, *Dolichorhynchops* and *Tricleidus*. The distal part of the fossil is preserved, from the pelvic girdle backwards with dorsal, sacral, and caudal vertebrae present, along with two ischia, two pubes and two flippers of which the right is almost complete. Some rib fragments are also preserved.

A catalogue has been made of all available Jurassic and Cretaceous marine vertebrate material from Svalbard containing three plesiosaur propodials and epipodials, a plesiosaur ilium, a large ichthyosaurian humerus and a few plesiosaur teeth.

Introduction

This master thesis describes a Tricleidian plesiosaur collected from the Agardhfjellet Formation on Svalbard in 1931. In 1962 the specimen, comprising the distal half, from the pelvis and back, was briefly described by Per Ove Persson then of the University of Lund in Sweden and designated the holotype of a new species, *Tricleidus svalbardensis*.

Persson (1962) assigned the specimen to this genus based mainly on features of the proximal bones in its hind limbs. However, much has changed since regarding plesiosaur classification and a new thorough examination and description of the material was necessary.

In addition to a re-description and re-interpretation of the plesiosaur specimen mentioned above a quick look will be taken on other miscellaneous material from Svalbard, in the collection at the Geological Museum of Oslo. Most of this latter material, with the exception of many solitary vertebrae and phalanges, is beyond recognition. However, a few interesting pieces have been found such as plesiosaur teeth, an almost complete plesiosaur ilium, a plesiosaur propodial with a more or less complete autopodium, and lastly what appears to be a very large ichthyosaurian humerus.

I will also discuss aspects of the taxonomic chaos surrounding the Plesiosauria and also look at the functional anatomy of the plesiosaurs. In the latter, features of the plesiosaur body structure, especially those of the flippers, associated with aquatic life will be compared with today's aquatic air-breathers, the Cetaceans, as well as the ichthyosaurs.

The fossil history of the Plesiosauria

The order Plesiosauria, meaning "near-lizard", are not dinosaurs but contemporary sea-reptiles or tetrapods that dominated the Mesozoic seas, especially in the Jurassic and the Cretaceous.

The earliest remains of the group are of isolated bones from the Middle Triassic (Anisian) of Germany, but the first complete and articulated specimens comes from the Lower Jurassic of Lyme Regis, Dorset, and the Bristol region of England.

De la Beche & Conybeare (1821), created the genus *Plesiosauria* on the basis of miscellaneous and unidentified material from the Lyme Regis region in England. This reconstruction was criticised at the time because it was based on isolated and disarticulated material. However, in December 1823 in the Lower Lias (Sinemurian) near Lyme Regis, an 18 year old girl Mary Anning (1799-1847), found the first ever complete skeleton of this new reptile group, which confirmed Conybeare's conclusion about a new species (Torrens 1995; Taylor & Torrens 1987).

One year later in 1824, this skeleton provided Conybeare with the material with which he made the first specific description of a plesiosaur, the type species *Plesiosaurus dolichodeirus* (Conybeare 1824) (Fig. 1). This specimen is housed at the Natural History Museum in London (NHM) and is now recognised as the type species for the genus.

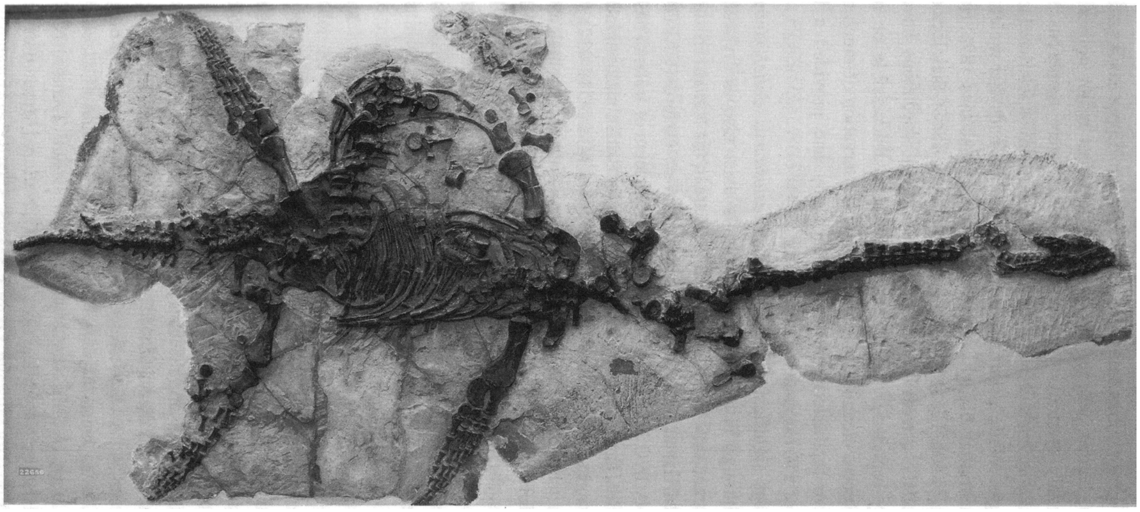


Fig. 1: Dorsal view of the holotype *Plesiosaurus dolichodeirus*, BMNH 22656, from the Lower Jurassic of Dorset, England (from Storrs 1997).

Even though the limestones in Lyme Regis in Dorset have produced many of the most important plesiosaur specimens known, it is not the only place where these fossil reptiles are found. Fossil plesiosaurs, both long and short-necked, have been found on virtually every continent, from geographically separated countries and areas such as Europe, Japan, Australia, USA, South-America, Africa and the South-pole. Because of this worldwide distribution plesiosaurs are regarded as a cosmopolitan group of which some members lived, at least parts of their life, in the open ocean.

An interesting point regarding the geographical distribution of plesiosaurs is that the Jurassic forms are found mainly in the Northern Hemisphere, and it is not until the Late Jurassic - Early Cretaceous that we find these animals in the southern hemisphere (Persson 1963; Bartholomai 1966; Gasparini & Spalleti 1993; Gasparini 1997).

Whether this north - south trend has any specific evolutionary meaning is not possible to say. It could also be the result of early Mesozoic strata lacking in these parts of the world, or that the fossils are there but, as yet, simply have not been found.

Plesiosaurs evolved from being small, relatively inconspicuous marine reptiles in the Triassic and early Jurassic, to become feared predators of enormous size in the late Jurassic and the Cretaceous. Some large fossil specimens formerly described as *Liopleurodon ferox* (Sauvage 1873), now considered spec. indet., was as much as 25 meters in length and weighing over 20 tons, making it one of the largest and most colossal marine predators ever to have existed (Fig.2).

Fig. 2: Probably one of the largest marine reptiles ever to exist, *Liopleurodon ferox* (Haines 2000).

Taxonomical history of the Plesiosauria

Since the time of Conybeare's description in (1824) and later Owen (1840, 1865), relatively little has been done regarding classification and clarifying of the anatomy of the group Plesiosauria and other marine reptiles, at least compared to the work done on dinosaurs.

The marine reptiles as a group have long suffered from being overshadowed by the dinosaurs. This is a little strange as it was one of the first reptile-groups to be found, and long before the first dinosaur fossil was recognized. This has, as Glenn Storrs (1997) puts it, reduced the taxon to a wastebasket for problematic material dating from the Rhaetian to the Maastrichtian.

However, one important thing to keep in mind is that the discovery of the marine reptiles during the late eighteenth century and the early nineteenth century was a major contribution to the development of vertebrate palaeontology as a science (Taylor 1997).

Even though there is still a great lack in understanding the phylogeny of the order Plesiosauria, attempts have been made in recent years, and work is currently being done by several researchers to place the group, with all its families and genera, into a systematic relationship. Plesiosaur relationships have been studied recently by Brown & Cruickshank (1994), Carpenter (1997) and O'Keefe (2001) among others.

The traditional view was, and still is although a few changes have been made, to divide the order Plesiosauria into two superfamilies, the short-necked Pliosauroidea and the long-necked

Plesiosauroidea (Andrews 1910, 1913; Welles 1943, 1952; Tarlo 1960; Persson 1963; Brown 1981).

In the early attempts of classification, plesiosaur taxonomy was mainly based on morphometric characters relating to body proportions, such as relative skull length, neck length, lengths of the ischium/pubis, scapula/coracoid, and the relative length of the humerus and femur, etc. These characters are very homoplastic in the Plesiosauria, meaning that they are subject to a high level of convergence, and have in the past inevitably led to genera and species being placed in wrong clades. A good example of this is the traditional placing of the short-necked Polycotylidae within the Pliosauroidea.

Based on morphometric characters polycotylids look very similar to plesiosaurs with a "pliosauromorph" body plan. However when comparing characters from the skull between animals within these two groups marked differences are found and it is obvious that the Polycotylidae should be part of the Plesiosauroidea.

The close kinship found between some short and long-necked plesiosaurs is the latest in a line of discoveries in plesiosaur taxonomy. This has led to the idea that the long-necked plesiosaurs of the Cretaceous, such as elasmosaurs, perhaps are more related to Jurassic short-necked taxa than they are to long-necked taxa from the same period. This will inevitably mean that the pliosauromorph and plesiosauromorph body plan has evolved more than once.

The early taxonomic work done by Andrews (1910, 1913), Welles (1943, 1952), and Tarlo 1960) is now under drastic modification because of this new theory which states that there is a link between the Cretaceous long-necked plesiosaurs (elasmosaurs) and the short-necked pliosaurs.

One of the first to break with the traditional morphometric classification scheme was Carpenter (1997) and later also Bardet (1998) who challenged the monophyly of the superfamily Pliosauroidea. However credit must also be given to Williston, who as early as 1907 suggested that the short neck in pliosaurs might have evolved at least twice.

An obvious reason why there is such a difficulty in establishing a solid taxonomic scheme for plesiosaurs and other fossils is that you cannot rely on sophisticated DNA analysis for an accurate species or genera specification. The next best thing has been shown to be the use of the posterior parts of the animals` skull. The area around the temporal fenestra and the posterior palate are especially important in plesiosaurs.

The reason for this is that the skull, as an anatomical structure, is much less susceptible to complete convergence as a result of being less affected by stimuli from the environment than morphometric characters (Carpenter 1997; Bakker 1993; O'Keefe 2001).

Plesiosaur flippers as an example are so devoid of complexity that very minor convergent selection between different species could in theory produce nearly identical patterns and thus be of no use in taxonomical classification.

Just consider such evolutionary separated and unrelated animal groups as the dolphins, whales, plesiosaurs, and the ichthyosaurs which still share a very similar limb structure as a result of adaptation to a similar habitat. Their skulls on the other hand are very different and possess several individual synapomorphic features.

Structural differences between specimens now known to be of purely ontogenetic character were in the past used in taxonomy to produce new lineages and groups. This led to an overabundance of now rejected generic and specific names, which again led to many alternative schemes of classification.

Brown (1981), and later Cruickshank (1994) and O'Keefe (2001) went from only using morphometric characters to also include the more stable characters of the skull in their phylogenetic work. In doing so they greatly diminished the problem related to ontogenetic features.

In his review of Upper Jurassic plesiosaurs, Brown (1981) discussed the use of thirty-eight plesiosaur characters used by taxonomists in classification. Fifteen of these, seven being skull characters, were regarded as important in distinguishing phyletic lineages.

Recently, O'Keefe (2001, 2002) has made a cladistic analysis of the Plesiosauria where the superfamily Pliosauroidea was found to be polyphyletic due to the inclusion of the Polycotylidae. To test the result he conducted parsimony analysis on his data set with the constraint of Pliosauridae and Polycotylidae being a monophyletic clade. This resulted in two most parsimonious trees with tree lengths of 447, which were fifteen steps longer than the result from his original analysis (see Fig. 3). The large increase in tree length indicates the polyphyly of the traditional Pliosauroidea. The Polycotylidae were formerly thought to be Cretaceous pliosaurs but is now, based on synapomorphies in the skull, found to be more closely related to the long-necked elasmosaurs and should therefore be placed within the Plesiosauroidea and not the Pliosauroidea.

Within the superfamily Plesiosauroidea there are several families of which three or sometimes four are of higher importance. How many families one operates with usually depends on the author, and the numbers vary. In this thesis I will follow the latest work done by Carpenter (1997) and especially O'Keefe (2001) where four main families are identified within the Plesiosauroidea. These are the Cryptoclididae*,* Polycotylidae*,* Cimoliasauridae, and the Elasmosauridae.

The single genus *Plesiosaurus* is here made the sister-group and out-group to all other "plesiosauromorphs" – any plesiosaur with a short head and a long neck.
For a full overview of the phylogenetic relationship of the Plesiosauria see Fig.3 which shows the strict consensus tree, the unique tree that contains only those groups that occur in all rival cladograms (Kitching et al. 2000), computed from the twelve most parsimonious trees.

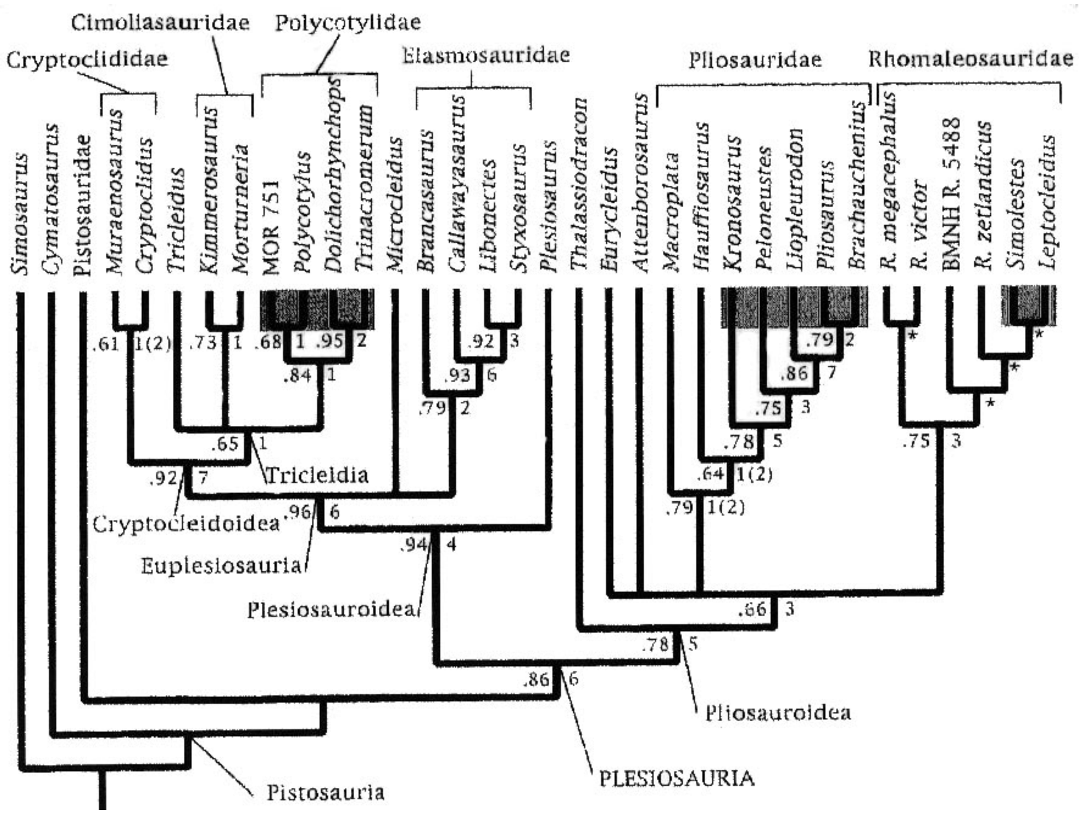


Fig. 3: Phylogenetic relationships of the Plesiosauria. Shown is the strict consensus of twelve most parsimonious trees with a length of 432. Numbers to the left of nodes are bootstrap values; those to the right are decay indices. Numbers in parentheses are the support for a given node after morphometric characters were removed. Stars mark nodes with less than 50 % bootstrap support and a decay indice of one (Taken from O'Keefe 2001).

The above tree was the result of 34 taxa being scored for 166 morphological characters using *Simosaurus*, *Cymatosaurus*, and Pistosauridae as outgroup taxa. According to O'Keefe (2001) there are two large groups within the Plesiosauroidea consisting of the well-supported Elasmosauridae, and the Cryptocleidoidea. The latter clade is a larger group consisting of two subclades, the Cryptoclididae and the Tricleidia.

Tricleidia is a new taxon defined by O'Keefe (2001) to include the Polycotylidae, the Cimoliasauridae, and *Tricleidus* while the Cryptoclididae comprises *Muraenosaurus* and *Cryptoclidus*.

The placing of *Muraenosaurus* in this clade and not within the traditional Elasmosauridae as done by Andrews (1910) and Brown (1981), suggests that the long neck and small head evolved independently in *Muraenosaurus* (O'Keefe 2001).

Bakker (1993) argued that the Cretaceous long-necked elasmosaurs along with the short-necked pliosaurs both were derived from an Upper Jurassic short-necked plesiosaur and not as traditionally believed from one of the dominant long-necked clades. Bakker based this on the sharing of a specialised palate (covering of the basicranium by the pterygoids) by Cretaceous pliosaurids, elasmosaurids, and Jurassic pliosaurs.

He also argued that the Jurassic long-necked plesiosaurs died out at the Jurassic-Cretaceous extinction, leaving only the short-necked pliosaurs as probable ancestors of the Cretaceous elasmosaurs (Bakker 1993). This view degrades the long and short-necked clades to mere ecological configurations attained independently by several waves of iterative evolution.

However, O'Keefe (2001) found support for a division of the Plesiosauria into the Plesiosauroidea and Pliosauroidea, although with a reorganisation of some of the families and the recognition of a new clade, the Tricleidia, as well as a new taxon, the Euplesiosauria.

It is important to note however that this division is solely based on shared synapomorphic characters and has nothing to do with neck length or head size.

Carpenter (1997) came to a similar conclusion as Bakker (1993) when he compared the skulls of two Cretaceous plesiosaurs from the Western Interior basin, USA.

By examining synapomorphies of the skull he found that the long-necked *Libonectes morgani* and the short-necked *Dolichorhynchops osborni*, both from the Upper Cretaceous, shared a common ancestor. However, Carpenter (1997) argued that Bakker (1993) had been wrong about the palatal condition in *L. morgani* and *D. osborni*, which obviously was more similar to that found in Jurassic long-necked plesiosaurs and not short necked as stated by Bakker (1993). The essential synapomorphic features in these taxa included the presence of a vomeronasal fenestra, expansion of the pterygoids into plates beneath the braincase, and loss of both pineal foramen and stapes.

Carpenter (1997) therefore operates with an alternative phylogenetic scheme similar to that of O'Keefe (2001), where the short-necked Cretaceous polycotylids are the sister-group to long-necked elasmosaurids (see Fig.4).

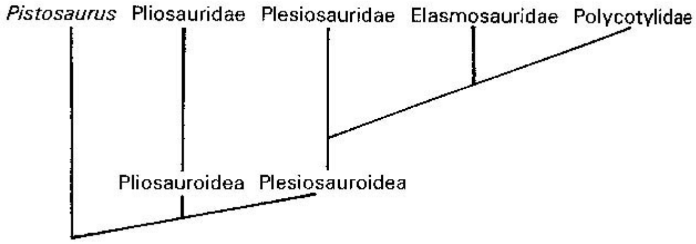


Fig. 4: An alternative cladogram with the placing of the Polycotylidae within the Family Plesiosauroidea (from Carpenter 1997).

Summarising the statements from above one can in short conclude with the following. The large headed and short-necked polycotylids have not descended from the short-necked pliosaurs of the Jurassic as previously believed. Instead synapomorphic characters of the skull have shown the group to be more related to the long-necked groups of the Upper Jurassic such as *Cryptclidus*, *Muraenosaurus*, *Microcleidus*, and *Tricleidus* (Carpenter 1997; O'Keefe 2001). The short neck has appeared independently at least twice in the Plesiosauria and the term pliosaur referring to any short-necked plesiosaur should be abandoned to avoid any phyletic implications (Carpenter 1997). The long neck or large head in plesiosaurs should be seen as mere ecological adaptations within a clade rather than evolutionary related features to be used in taxonomic classification.

Most researchers today operate with six main families within the order Plesiosauria, of which four are of the long-necked type and two, the Pliosauridae and Rhomaleosauridae, has a short neck and a relatively big skull (Carroll 1988; O'Keefe 2001). Some believe that pliosaurs are much more diverse than this and that it should be split into several families.
Within these six groups there are of course many genera and species, none of which are mentioned here since the systematic relationship between many of these groups is still under revision.

Origin of the Plesiosaurs

The origin of the group Plesiosauria, and from what type of land reptile the plesiosaurs are descended, is somewhat blurred as they seem to have both primitive and advanced features. Moreover, the plesiosaurs do not fit into any of the three basic amniotic groups – the Anapsida, the Synapsida, or the Diapsida, defined on the number of temporal openings or fenestrae in the side of the skull of amniotes.

The Anapsida has no opening and includes the earliest reptiles, *Hylomonus* and *Paleothyris*, as well as the modern day turtles, whilst the Synapsida has one temporal opening in the lower part of the skull, surrounded by the squamosum, jugal and postorbital dermal bones. This group comprises the early mammal-like reptiles, such as the pelycosaurs and the therapsids, and the true mammals.
The Diapsida has two openings in the skull. The lower opening is the same as in the Synapsids, and the second lies dorsally, surrounded by the squamosum, postorbital and the parietale. This group includes the dinosaurs, crocodiles and the birds (see Fig.5 for a view of dermal bones and temporal openings in the skull of reptiles).

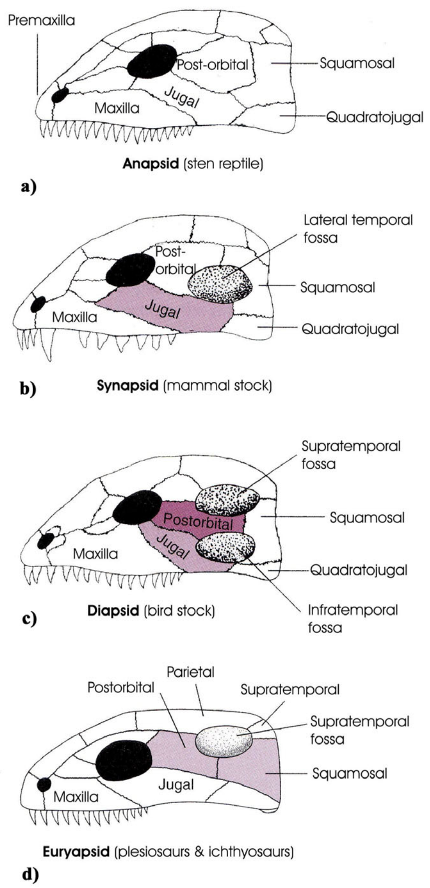


Fig. 5: Dermal bones in reptiles. A: anapsida (stem reptile); B: synapsida (mammal stock); C: diapsida (bird stock) and D: euryapsida (ichthyosaur and plesiosaur stock) (from Kent & Millor 1997).

The plesiosaurs and their relatives, the pistosaurs and nothosaurs alongside the placodonts, collectively called the Sauropterygia (Rieppel 2000) all have one opening in the skull like the

Synapsids. The only problem is that it is located dorsally and not ventrally making it difficult to ascertain the exact taxonomic position of these animals.

However, most researchers view the sea-reptiles as part of the diapsid stock, only modified later to only have one upper opening. This relationship with the diapsids is demonstrated by similarities seen in the skulls of early diapsids such as *Claudiosaurus* with that of nothosaurs (Carroll 1985). Members of this modified version of the Diapsida was first grouped together by Williston (1925) on the basis of a single upper temporal fenestra, under the name "Synaptosauria" which correctly included the Sauropterygia and the Placodonts. This was however later changed to Euryapsida by Colbert (1955), a term supported by Romer (1956) which also included the Permian diapsid *Araeoscelis*. Due to lack of certainty regarding its monophyly the term "Euryapsida" has fallen into disuse although Merck (1997), after performing a cladistic analysis on all "euryapsids", believes the group to be a monophyletic clade.

Today the close relationship between placodonts and other sauropterygians are no longer in doubt thanks to work done by Carroll & Gaskill (1985) and later by Rieppel, who made an exhaustive phylogenetic revision of stem-group sauropterygians (Rieppel 1989, 1994, 1998, 1999, 2000; Rieppel & Wild 1996). The Sauropterygia is now classified as crown-group diapsids (Rieppel 2000).

The Diapsida has been divided into two major clades termed the Lepidosauromorpha and the Archosauromorpha. The first group comprises the modern lizards, snakes, and sphenodonts, while the second group includes the dinosaurs, crocodiles and the birds.

Rieppel (1993) argues that lepidosauromorpha also includes the Sauropterygia and Ichthyopterygia, both of which independently lost their lower temporal opening. He also concludes that the Sauropterygia share some lepidosauromorphian characters, such as a thyroid fenestra in the pelvis and absence of the supratemporal bone in the skull (Benton 2000).

Carroll (1985) places the ichthyosaurs within the archosauria, and refers to some specimens found in China from the Lower Triassic which are described as having two temporal openings and therefore more related to the dinosaurs and other diapsids (Carroll 1985, p.146).

Contrary to Rieppel (1993, 2000) Merck (1997) found the Sauropterygia to be positioned at the base of the archosauromorph lineage.

Although the phylogenetic relationship of the Sauropterygia among crown-group diapsids still remains debatable, its status as a subclade of either the Lepidosauromorpha or Archosauromorpha seems no longer in doubt (Rieppel 2000).

The following taxonomic relationship of the major diapsid groups and the plesiosaurs is based upon the work of several researchers, including Evans (1988), Laurin (1991), Carpenter (1997), Rieppel (1993, 1997, 1998, 2000), Rieppel & Hagdorn (1997), Benton (2000), O'Keefe (2001) and Rieppel, Sander & Storrs (2002).

Systematics:

Class Reptilia
Subclass Diapsida (Osborn 1903)
Infraclass Archosauromorpha
Infraclass Lepidosauromorpha
(Division Euryapsida)
Superorder Ichthyopterygia
Superorder Sauropterygia (Owen 1860)
Order Placodontia (Cope 1871)
Order Eosauropterygia (Rieppel 1994)
Suborder Eusauropterygia (Tschanz 1989)
Infraorder Nothosauroidea (Baur 1889)
Infraorder Pistosauroidea (Baur 1887)
Superfamily Pistosauria (Baur 1887)
(Family) Plesiosauria (de Blainville 1835)
(Subfamily) Plesiosauroidea (Welles 1943)
(Infrafamily) Plesiosauridae (Gray 1825)
(Infrafamily) Elasmosauridae (Cope 1871)
(Infrafamily) Cryptoclididae (Williston 1925)
(Infrafamily) Polycotylidae (Williston 1908)
(Infrafamily) Cimoliasauridae (Delair 1959)
(Subfamily) Pliosauroidea (Welles 1943)
(Infrafamily) Pliosauridae (Seeley 1874)
(Infrafamily) Rhomaleosauridae (Kuhn 1961)

In Rieppel's view the placodonts are found to be the sister-group of the Eosauropterygia, a monophyletic group including the Pachypleurosauria, Nothosauria, and the Pistosauroidea (Rieppel 1994a). *Pachypleurosaurus* is also the sister-taxon, or out-group of the Eusauropterygia (Tschanz 1989), a monophyletic taxon including the Nothosauroidea and the Pistosauroidea. The latter group includes the Plesiosauria (O'Keefe 2001; Rieppel 1997, 2000) (see Fig. 6).

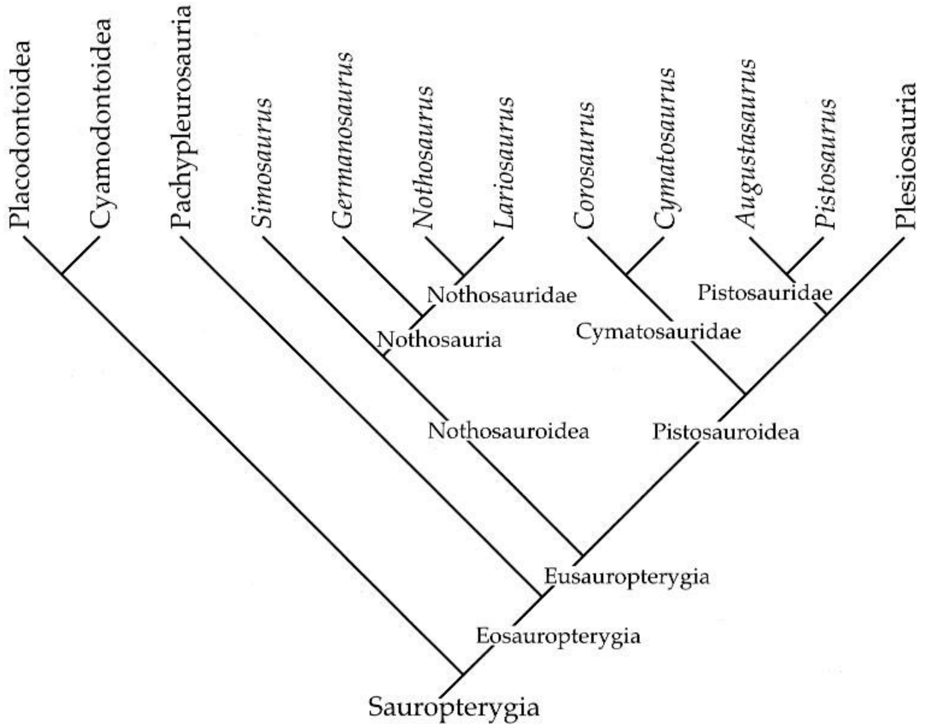


Fig. 6: Cladogram showing the phylogenetic interrelationships within Triassic stem-group Sauropterygia. Note that plesiosaurs are placed within the sauropterygia, and have close affinities with the pistosaurs. (from Rieppel 2000).

For a more detailed study on the diagnosis and definitions within stem-group Sauropterygia, see Rieppel (2000).

Today it is generally accepted that the plesiosaurs at least are closely related to the pistosaurs, which have a similar bodyoutline, but with less functionally developed limbs for a life in water (see Fig.7).

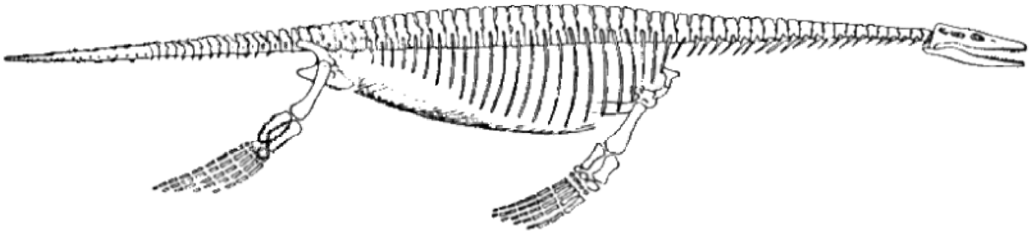


Fig. 7: The anatomical structure of a pistosaur. Note the very plesiosaur-like body outline but primitive limb structure, as seen in the longer epipodials (from von Huene 1948) http://www.grinpach.cl/pistosaurus.gif

Pachypleurosauria, a generally small eosauropterygian from the Middle Triassic (Carroll 1988), also resemble the plesiosaurs in that their limbs, especially the epipodials, are reduced relative to primitive terrestrial reptiles. The limbs are however not highly modified for aquatic propulsion, and their skull still remains plesiomorphic. Ossification of the girdles and the mesopodials (carpals/tarsals) are greatly reduced making movement on land difficult for these animals.
The external nostrils are also placed back away from the tip of the snout in Pachypleurosaurs although the head is still relatively short (Fig.8). As we will see later, this points toward an intermediate condition of aquatic adaptaion.

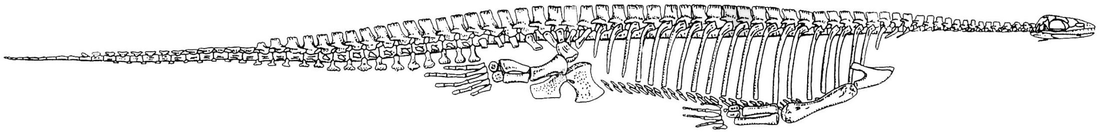


Fig. 8: *Pachypleurosaurus* showing its key features; relatively short head, long epipodials, and short phalanges (from Carroll 1988).

There is some controversy as to the taxonomic position of the Pachypleurosauria as some see it as part of the nothosauria and others see it as a separate clade.
The nothosauria as a group has long been seen as a one of the closest relatives to the plesiosaurs. This relationship however seems to be contradicted by the structure of the palate in these two groups. The palate of plesiosaurs is less specialised than that of nothosaurs in the retention of

interpterygoid vacuities. Within nothosaurs the palate is greatly modified relative to more primitive diapsids as well as plesiosaurs with the complete closure of palatal vacuities (Fig. 9). This suggests that the plesiosaurs may have evolved from a more primitive diapsid rather than from any of the well-known nothosaurs (Carroll 1988).

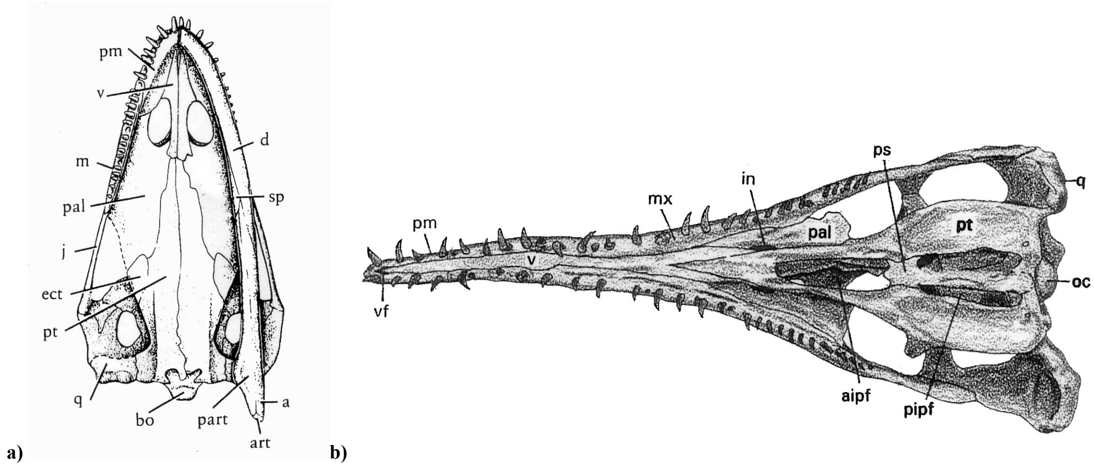


Fig. 9: Palate of (a) pachypleurosaurus (from Carroll 1988), and (b) *Dolichorynchops osborni* (plesiosaur) (from Carpenter 1997). Note the interpterygoid fenestra marked "aipf" and "pipf" on *D. osborni*, which are lacking in pachypleurosaurus (from Carpenter 1997).

Pistosaurus from the Middle Triassic was originally described as a nothosaur but is now placed within the infraorder Pistosauroidea (Rieppel 2000). Pistosauroidea retains a more primitive pattern of the palate, and might be a good candidate for the link between the nothosaurs and plesiosaurs (see Fig. 6 for a view of the relationship between plesiosaurs and pistosaurs).

In all Sauropterygians the pterygoids extend backwards to the posterior margin of the basicranium, concealing the para-basisphenoid and basioccipital, except in *Pistosaurus*, *Augustasaurus* (Pistosauridae), and the Plesiosauria which secondarily developed interpterygoid vacuities (Rieppel 2000) (see Fig.10).

This reappearance of anterior and posterior interpterygoid vacuities in plesiosaurs is correlated with a general trend of reduced ossification in the skeleton, a feature common to many aquatic tetrapods (Storrs 1991; Romer 1956).

Other features connecting plesiosaurs with the Pistosauroidea are loss of the quadratojugal, which is present in all other basal sauropterygians, and the possession of a suture between the maxilla and squamosum, a suture that excludes the jugal from the ventral skull roof. In *Simosaurus* and other nothosaur-grade sauropterygians the jugal enters the ventral skull margin (O'Keefe 2001).

All sauropterygians including the plesiosaurs have a large thyroid fenstra in the pelvis, the obturator foramen however which primitively is present in the pubis of sauropterygians is lost in plesiosaurs, *Cymatosaurus* (pistosaur), and *Lariosaurus* (nothosaur).

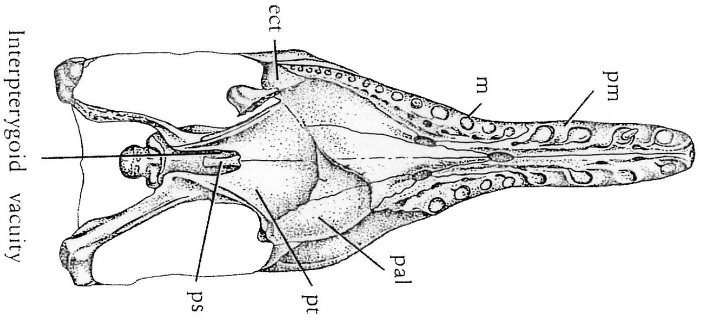


Fig. 10: The palate of *Pistosaurus*. Note the interpterygoid vacuity indicating affinities with the plesiosaurs (from Carroll 1988).

As mentioned earlier there is still some debate as to whether the Sauropterygia belongs to the Archosauromorpha or the Lepidosauromorpha, however the majority of researchers seem to prefer a Lepidosaurian heritage.

The Lepidosauromorpha retained the primitive sinusoidal mode of locomotion and lateral movement of the trunk, a walking mode like that seen in modern lepidosaurs such as snakes and crocodiles.

Leoidosauromorphs stand in marked contrast to the archosauromorphs which developed a stiff trunk and eventually upright posture.

Advanced members of the lepidosaurs, like the plesiosaurs and pliosaurs who relied on their flippers for propulsion, also developed a stiff trunk like the dinosaurs. This stiffening was a result of the plesiosaurs mode of locomotion, which did not rely on the primitive lateral undulation of the trunk, as this would have had a negative effect on oxygen storage in their lungs. Every animal with a sprawling gait and thus a sideways undulation of the trunk has problems running and breathing at the same time. This is what Cowen (2001) has called ”Carriers Constraint”, after Carrier (1987) who connected styles of terrestrial locomotion with air breathing and metabolic level.

I will briefly return to this topic when discussing the functionality of the limbs in plesiosaurs as it has greatly affected their way of locomotion.

The order Plesiosauria existed from the Late Early Triassic (Olenekian) to the end of the Cretaceous where they suffered the same fate as the dinosaurs, as casualties of the end-Cretaceous mass extinction (Romer 1966). They were most likely shallow water dwellers although the pliosaurs might have had the body-structure to venture further into deep-ocean to hunt.
During their time-span of approximately 243 million years, they became one of the dominant predators, alongside the Ichthyosauria, the Cretaceous Mosasauria and the sharks of the Mesozoic seas.

About adaptation to the sea

Every species will strive to adapt itself to its surroundings, or if possible, escape hostile environments. They will do this consciously or by instinct to survive and transfer their genes to the next generation. This is to ensure, as Darwin (1859) stated in his book ”On the o*rigin of species*”, that favoured races or traits are preserved and passed on to the next generation.

Among living and extinct aquatic air-breathers there are certain features that are very characteristic for marine life. Some of these features such as an elongated skull with long and slender jaws and external nostrils situated far back on the skull to facilitate breathing are seen in the Cetaceans. However, some researchers argue that the external nostrils in plesiosaurs were used for smelling and had nothing to do with breathing. One of the reasons for this is because their secondary palate was not fully developed. The position of the external nostrils in plesiosaurs therefore had nothing to do with simplifying breathing at the surface (Cruickshank et al. 1991).
Most marine animals also have a relatively short neck, an advantage for swift movements under water. A long neck found in many Upper Jurassic and especially Cretaceous plesiosaurs would actually have a negative effect on movement (McGowan 1999).
Animals well adapted for a life in the sea seem to have a short neck and a well-developed tail fin for locomotion. The latter has developed at the expense of the hind limbs. This obviously is not the case with plesiosaurs such as the long-necked elasmosaurs that have very long necks, a small inconspicuous tail and large flippers for propulsion. In this regard plesiosaurs seem to go against every rule for aquatic adaptation. The short-necked types like *Euryclidus*, Pliosaurs and Rhomaleosaurs on the other hand seem to be better suited for an aquatic life with their longer heads and more streamlined body.

All of the above modifications are significant with regards to aquatic adaptation, but the major changes in marine air-breathers are still seen in the limbs. No other part of the body has so different functions on land and in the sea.

The femur and the humerus are always very short in those animals that have a well-developed propelling tail (Halstead 1989). This is clearly seen in whales and dolphins, but also in the Mesozoic ichthyosaurs which are all good swimmers.

Sea lions and walruses, which to a lesser degree are adapted to a life in the sea, have retained their hind limbs as well as their front-limbs, though these are all modified as flippers. In addition their heads are shorter with more anteriorly situated nostrils. This is a bodyplan similar to that seen in the plesiosaurs, with longer femurs and humeri (Fig. 11) to make up for the power-loss these animals experience for not having an effective tail for propulsion. Larger propodials increase the surface area of the flippers, and hence the power in each retraction gets higher.

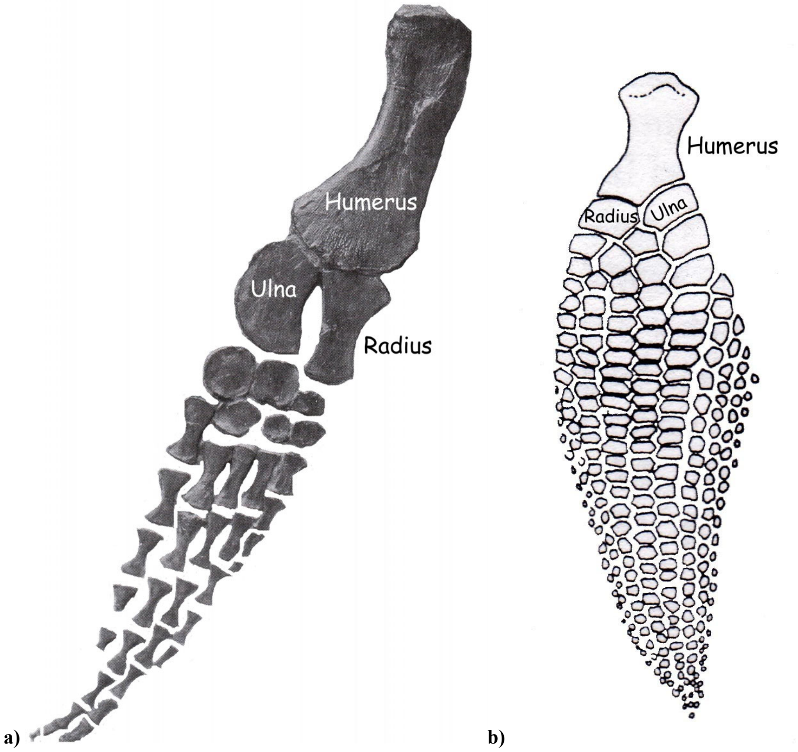


Fig. 11: Plesiosaurs (a) need longer propodials to compensate for the lack of tailpropulsion. Ichthyosaurs (b) who have well developed tail fins have shorter propodials (Carroll 1985).

When the plesiosaurs returned to the sea sometime in the late Permian or early Triassic they had to change their way of life drastically. They had to change to compete with the already existing animals in the sea, who over millions of years had adapted themselves nearly to perfection for a life in the ocean.

The plesiosaurs had two possibilities of modifying their limbs, they could either loose them (at least the hind ones) and replace them with a tailfin-equivalent as the Cetaceans did, or modify them into some sort of propulsive organ. The plesiosaurs obviously did the latter.

A gradual change in limb bones is clearly seen from early semi-aquatic diapsids such as placodonts and nothosaurs up to the plesiosaurs (Williston 1914).

Plesiosaurs, together with the marine turtles and *placodonts*, are the only reptiles that did not use lateral undulation of the trunk and tail for their primary means of aquatic locomotion.

As mentioned earlier the trunk became very stiff in plesiosaurs making the primitive *lepidosaurian* type of propulsion impossible (Cowen 2001). Instead they developed a limb-dominated swimming mode. No other animal, living or extinct has the same system of movement or body-plan as the plesiosaurs, with four highly specialised flippers, a rigid trunk and a short tail.

If the propodials are long and powerful in these animals the opposite can be said about the next pair of bones in the limb, the radius/ulna in the front limb and tibia/fibula in the hind limb (Fig. 12).

As mentioned earlier, these bones (called epipodials) are in most other animals long and slender, especially in running or jumping forms, but in aquatic animals they tend to shorten in length.

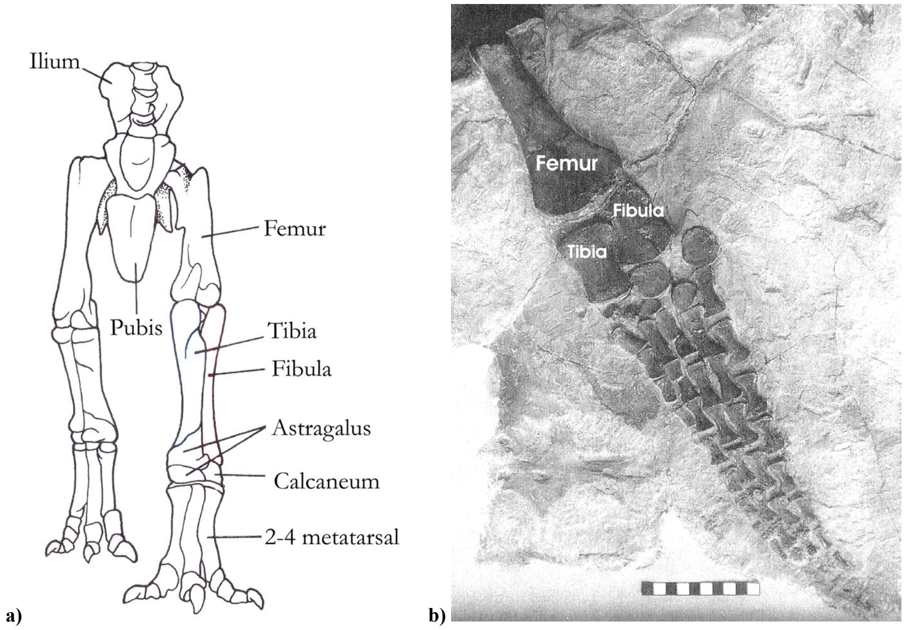


Fig. 12: Notice the length- difference between the long tibia and fibula of *Tyrannosaurus rex* (a) (from Benton 2000), with those of *Plesiosaurus dolichodeirus* (b) (from Storrs 1997). This shortening of the epipodials in plesiosaurs is a result of perichondral bone loss from the shafts of these, once so long bones. This shortening allows a more powerful propulsive force for each retraction of the sculls. Scale bar = 10 cm.

This shortening of the epipodials is a result of changes in, or rather loss of perichondral bone from the shafts of long bones (Caldwell 1997). Bone development starts with the formation of cartilage, which in turn starts off with the ossification of a bounding membrane (perichondrium).

Perichondrium is the first step in cartilage formation and forms the outer layer of the cartilage element. The inner layer, which ossifies at a later stage, is called endochondrium (Kent & Miller 1997) and is differentiated from perchondrium by the nature of its alignment relative to various axes of the cartilage element (Wolpert & Tickle 1993).

In the development of long bones there is a certain pattern of orientation between perichondrium and endochondrium where the cells are oriented at right angles to each other.

In contrast, the cartilage cells in short bones such as carpals and tarsals fail to form symmetrical patterns and there is no differentiation between perichondral and endochondral tissue

Rooney et al. (1984) found that perichondrium, which initiates cartilage formation imposes a mechanical and physical constraint on growth of the endochondrium by being the first to emerge and also the outermost element. In other words the perichondrium controls the growth and hence the form of the epipodials. Any change in the development of perichondral bone will therefore influence the morphology of the whole cartilage and eventually the bone itself.

In carpals and tarsals (mesopodials), which are much shorter elements with irregular to polygonal shapes, a differentiated perichondrium is not observed during chondrogenesis. It is likely that the forms of these smaller bones are related to the absence of perichondrial tissue (Caldwell 1997).

Caldwell (1997) argues that if the perichondrium is important in determining the shape of an element, alterations to its development will affect the shape of a bone and thus in time its function (Fig. 13).

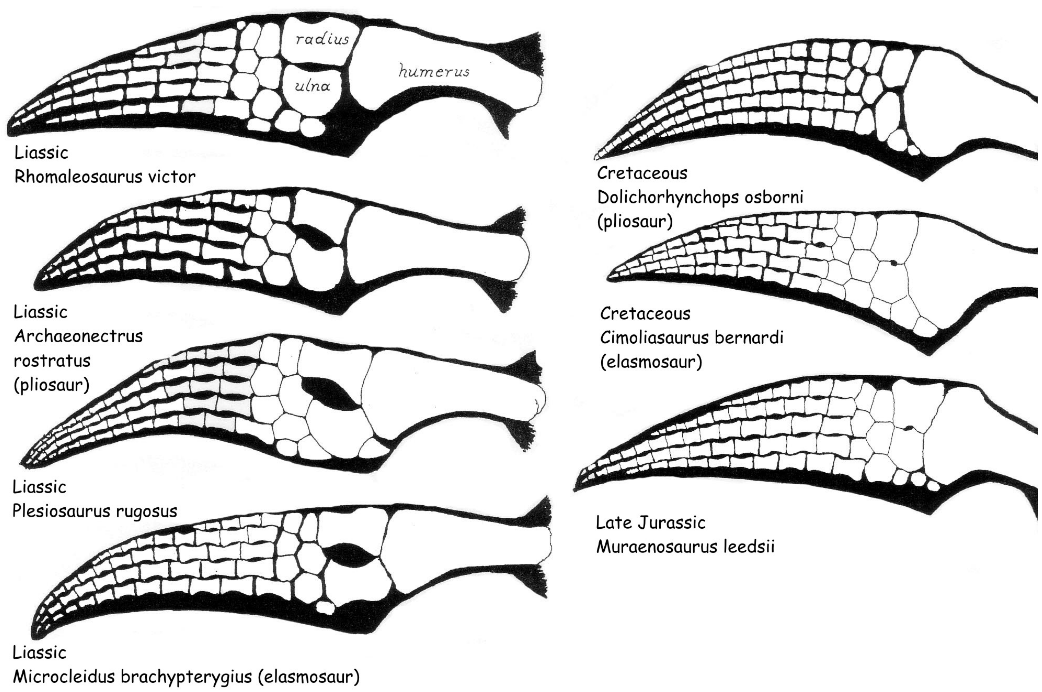


Fig. 13: Diagram showing a dorsal view of the left front sculls of different plesiosaurs. Those on the left side are early Jurassic in age, and show the more elongate radius and ulna. The three on the right which are much shorter and compact are Cretaceous in age. The shortening of the epipodials is due to alterations or loss of perichondrium from long bone elements (from Bakker 1993).

Loss of perichondral bone from the shafts of epipodial elements in plesiosaurs, is probably a major reason why the plesiosaurs in time developed flippers.

Comparing epipodial elements in plesiosaurs with that of early terrestrial diapsids such as the Younginiformes, Caldwell (1997) found that perichondral bone loss in plesiosaurs is first observed on the proximal and distal margins of the ulna and fibula in Lower Jurassic taxa.

In geologically later species the loss is confined to all margins of the ulna/radius, and fibula/tibia. This shortening of the forearm/leg bones is seen as an adaptation to life in the sea, and the degree of shortening can tell us something about the degree of adaptation.

Material & Methods

Historical information regarding the fossil specimen A 27745

In the spring of 2001 the plesiosaur material, PMO A 27745 from the Agardhfjellet Formation, was removed from its mounted display at the Palaentological museum, University of Oslo, and the surrounding matrix in the display-cabinet was thoroughly examined for other possible pieces of the fossil (Fig. 14).

Many broken and indefinable pieces were found along with a few more complete elements, such as small pieces belonging to the phalanges and what looks like part of a rib.

Before the fossil was removed from its display cabinet pictures were taken and a grid pattern of simple thread and some nails was made to ensure that the original position of the material was preserved. All of the pieces were checked to see if any were in need of repairing and glued accordingly. In this process a few modifications regarding the position and articulation of a few pieces was conducted. Details on the latter are mentioned below.

All of the pieces were given a separate collection number from 0 to 231. Exceptions are 6 unnumbered bags of miscellaneous material collected from the matrix after the specimen was removed. These bags are labelled according to where in the cabinet grid pattern the material was found.

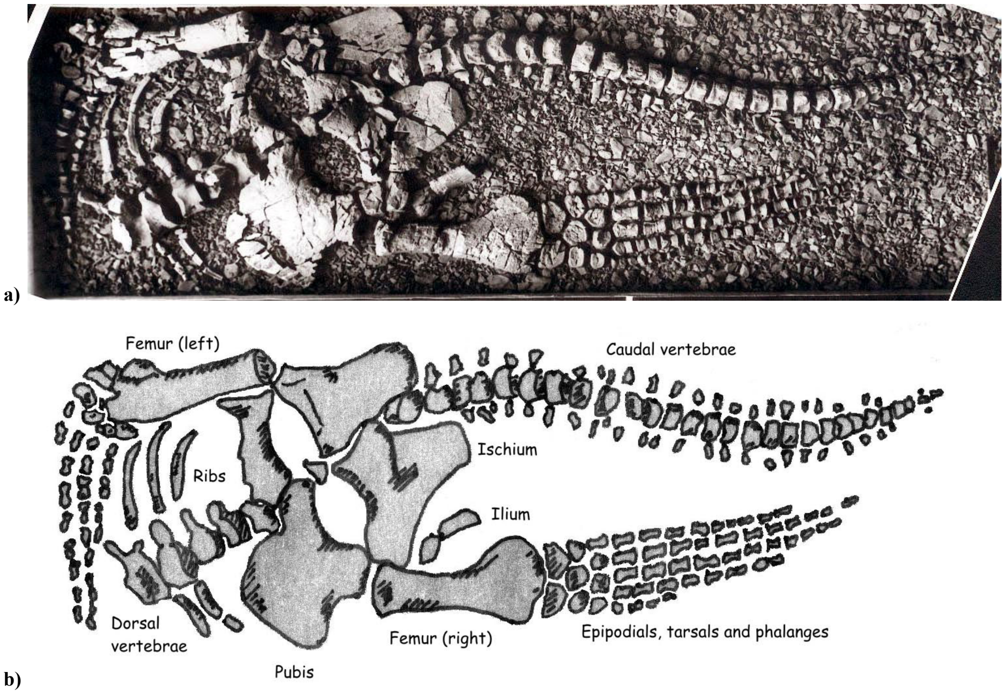


Fig. 14: Picture of the plesiosaur specimen in its mounted display at the Palaeontological museum in Oslo (a) (PMO: A 27745). Below is a drawing of the specimen with an explanation on what is seen (b).

A few minor changes have been made to the order of reconstructing the skeleton including repositioning of some of the pieces in the left epipodial region and articulation of a few new pieces also in the left limb and pelvis region. Among the most important changes is the unification of the two pieces making up the acetabulum for the left femur (pieces 150 & 153), and the assembly of a nearly complete intermedium and fifth metatarsal also from the left limb (Figs. 29 and 30).

Very little information was previously available regarding the age of the fossil and where it was found other than a label stating "*Jurassic? The mouth of Sassenfjorden, West-spitsbergen*" (Persson 1962). The specimen was apparently found by accident embedded in a dark grey shaly matrix by three American physicians, Dr. Freeze, Dr. Maller, and Dr. Paul who were on Svalbard in 1931 studying the Spanish influenza (Persson 1962; Heintz 1964) (Fig. 15).

Fig. 15: Picture of the three American physicians together with two locals over the partly buried fossil (Photo taken by Aasgaard 1931).

The remains of the skeleton were found partly covered by matrix in a dark shale representing anoxic conditions (Dypvik 1980; 1985) and grouped together in such a way that leaves no doubt that they represent one individual plesiosaur.

After excavating the fossil the remains were shipped to the mainland and arrived at the Palaeontological museum in Oslo to be mounted as originally found by Professor L. Størmer.

Persson (1962) argued that the age of the specimen must have been somewhere between the Oxfordian and the Neocomian and Heintz (1964) without providing evidence, states that it was found on Diabasodden, on the south side of Isfjorden. However, I have been able to extrapolate the age; geological horizon and geographical area in which the fossil was found based mainly on information obtained from Persson (1962), Heintz (1964) and Dallmann (1999). Thus I conclude that the fossil must have been found in the Agardhfjellet Formation (Parker 1967) and most likely in the Slottsmøya Member (Dypvik et. al 1991) north-west of Janusfjellet and hence be of Volgian age (Fig. 16).

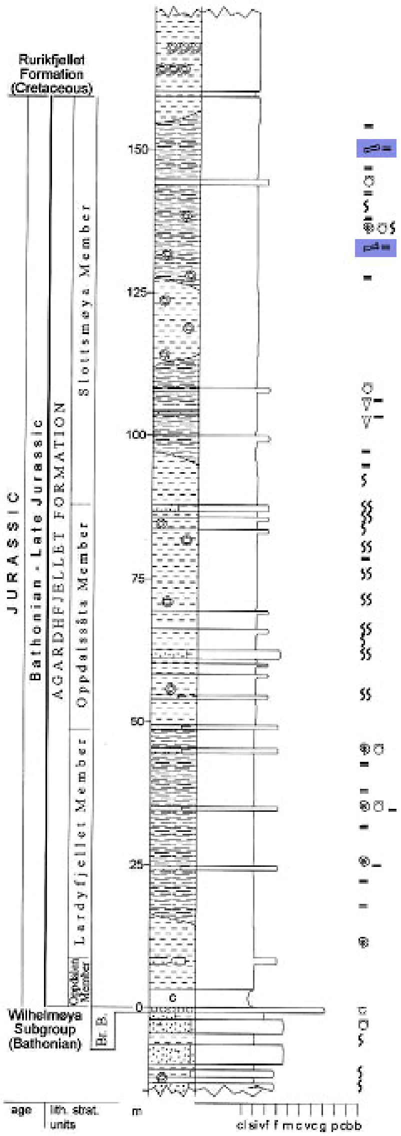


Fig. 16: Stratigraphic sectoion of the Agardhfjellet Formation. The "bone" symbol in the Slottsmøya Member (in blue) represents plesiosaurian fossil remains (from Dallmann 1999).

The reason for this is the fact that the specimen is from the Jurassic and that it was found somewhere in the area around the entrance to Sassenfjorden. A geological map of this area (see Fig. 17) indicates that it must have been found somewhere in the Agardhfjellet Formation on the south side of the northwest-southeast trending fault, as this is the only Jurassic strata in this area.
The Slottsmøya Member of the Agardhfjellet Formation is also known to have produced many plesiosaur remains throughout the years.
According to Dallmann (1999) the Member is of a depositional age dating Late Jurassic (Volgian) in age.

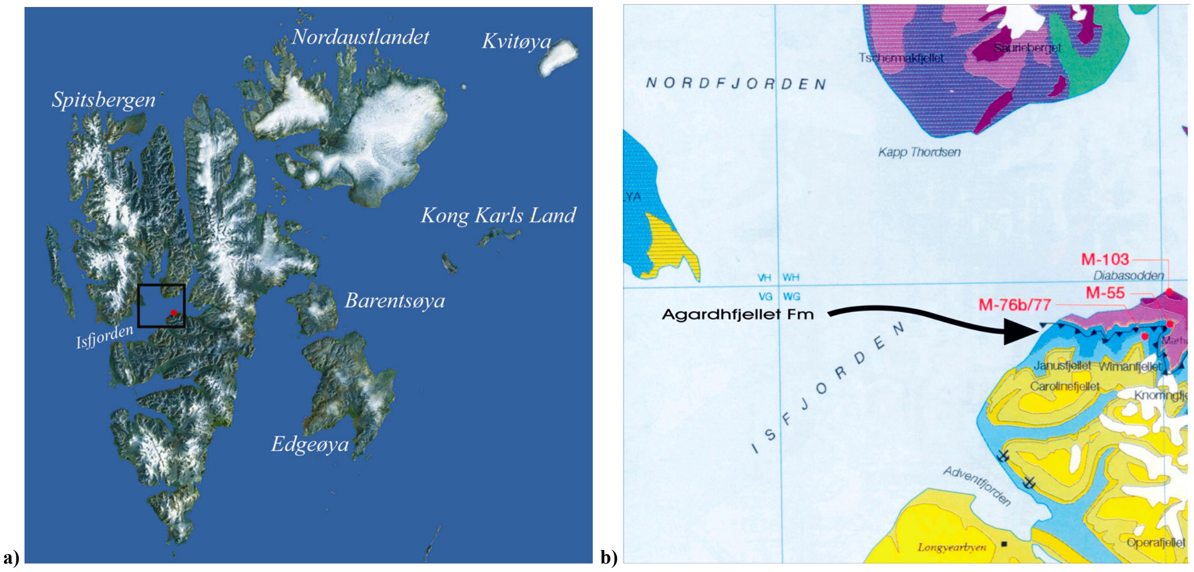


Fig. 17: A: Picture of Svalbard with the locality where the specimen was found marked as a red dot. B: Close up geological view showing Isfjorden and the entrance to Sassenfjorden. The darker blue colour below the fault-line represents the Agardhfjellet Formation (Dallmann 1999).

In contrast to mainland Norway, Svalbard, situated between 74° and 81° north and 10° and 34° east, has large areas of exposed Mesozoic rocks. Plesiosaurian remains from these rocks have been recorded as early as 1914 when Wiman published a description of a vertebral centrum found south of Deltaneset on Janusfjellet (Wiman 1914).
Discoveries and descriptions of marine reptiles however, date back as early as 1864 when Nordenskiold discovered a number of fragmentary ichthyosaurian specimens from the Triassic (Merriam 1911). In 1873 E. Hulke provived the first description of two species of ichthyosaurs from Svalbard (Heintz 1964) and since then more fossils of marine reptiles, mainly of ichthyosaurs and plesiosaurs have been discovered along with tracks from dinosaurs. This makes Svalbard an exiting area for future palaeontological discoveries.

Description of the specimen PMO A 27745

PMO. A 27745: The material constitutes the distal half of a plesiosaur from the pelvis and back, (see Fig. 18) containing these preserved parts: 38 vertebrae, some rib fragments, a relatively large part of the pelvic girdle, and both hind limbs, the right being the best preserved. For a complete list of the material refer to Table 1.

There are a total of 231 numbered pieces along with a few unnumbered fragmentary pieces from the partly crushed left epipodial and autopodial-region. Some of the pieces from the autopodial-region have been partly put together after numbering, such as the intermedium, the fifth metatarsal, and part of the second distal tarsal. The bones in this area have been compared to those of the right limb and repositioned in the best way possible as to resemble the true morphology of the region. However, so many of the bones are missing and the material is in such a badly preserved state that error is bound to occur.

After removing the specimen, the display cabinet was divided into 29 rows which all were thoroughly examined for additional material. This material was put in six separate bags and labelled as miscellaneous material.

The length of the preserved fossil material is about 2.25 meters. The length of the entire animal is difficult to ascertain as much depends on the length of the neck, which varies greatly among different species. Using Cryptocleidus as a reference frame, Persson (1962) came up with an estimated guess on somewhere around 6.2 meters for the whole animal.

The way in which the fossil specimen PMO. A 27745 was found and the arrangement of the bones more than suggests that the described material from Sassenfjorden belong to a single individual. The white coating found on the left femur, the pubis and other smaller parts like the phalanges, a few vertebrae and rib-fragments are also indicative of this (see Figs. 24a & 26a).

Due to the cold climate in which the fossil was found much of the material have inevitably suffered from frost action (congelifraction) causing the material to crack and split. Aside from this the fossil is in a relatively good state of preservation.

Systematic Paleontology

Class Reptilia
Infraclass Lepidosauromorpha
Superorder Sauropterygia (Owen 1860)
Suborder Eusauropterygia (Tschanz 1989)
Infraorder Pistosauroidea (Baur 1887)
Superfamily Pistosauria (Baur 1887)
Plesiosauria (de Blainville 1835)
Plesiosauroidea (Welles 1943)
Cryptocleidoidea (Williston 1925)
Gen. et sp. indet.

After the fairly recent inclusion of the Plesiosauria within the Superfamily Pistosauria a problem has arisen concerning the taxonomic level of the clades within the Pistosauria. Should we for example still think of the Plesiosauroidea and the Cryptocleidoidea as two separate Superfamilies within the Superfamily Pistosauria? As a result of these problems I have decided not to specify the taxonomic level of the clades within the Pistosauria.

The above taxonomy is based on the work done by Rieppel (2000) and O'Keefe (2001). In his work on Sauropterygians Rieppel (2000) only goes as far as saying that the Plesiosauria is a part of the monophyletic Superfamily Pistosauria (Baur 1887-90). The most reliable and comprehensive taxonomy of the plesiosauria comes from O'Keefe (2001, 2002) who made a cladistic analysis of the Plesiosauria scoring 34 taxa against 166 characters. The result of his work can be seen in Fig. 3.

List of material

Table 1: material comprising the fossil specimen A 27745.

Specimen number	Anatomical part
1.	Last caudal vertebrae
2.	↓
3.	.
4.	.
5.	.
6.	.

7.	.
8.	.
9.	.
10.	.
11.	.
12.	.
13.	.
14.	↓
15.	↓
16.	.
17.	.
18.	.
19.	.
20.	.
21.	.
22.	.
23.	.
24.	.
25.	.
26.	.
27.	.
28.	↓
29.	First caudal vertebrae
30.	Last sacral vertebrae
31.	Dorsal neural-spine, vertebrae 1
32.	Dorsal neural-spine, vertebrae 2
33.	↓
34.	.
35.	.
36.	.
37.	.
38.	.
39.	.
40.	.
41.	.
42.	.
43.	.
44.	.
45.	.
46.	.
47.	.
48.	.

49.	.
50.	.
51.	.
52.	.
53.	.
54.	.
55.	.
56.	↓
57.	Dorsal neural-spine, vertebrae 27
58.	Ventral chevron bones, vertebrae 1
59.	↓
60.	.
61.	.
62.	.
63.	.
64.	.
65.	.
66.	.
67.	.
68.	.
69.	.
70.	.
71.	.
72.	.
73.	.
74.	.
75.	.
76.	.
77.	.
78.	.
79.	.
80.	.
81.	.
82.	.
83.	↓
84.	Ventral chevron bones, vertebrae 29/30
85.	Right limb: Fifth digit-first phalang, starting distally.
86.	↓
87.	.
88.	.
89.	.
90.	.

91.	↓
92.	Last phalang on the fifth digit
93.	Fifth metatarsal
94.	Fibulare
95.	Fourth digit-first phalang, starting distally
96.	↓
97.	.
98.	.
99.	↓
100.	.
101.	.
102.	.
103.	.
104.	.
105.	↓
106.	Last phalang on the fourth digit
107.	Fourth metatarsal
108.	Third distal tarsal
109.	Intermedium
110.	Third digit-first phalang, starting distally
111.	↓
112.	.
113.	.
114.	.
115.	.
116.	.
117.	.
118.	.
119.	.
120.	↓
121.	Last phalang on the third digit
122.	Third metatarsal
123.	Second distal tarsal
124.	Second digit-first phalang, starting distally
125.	↓
126.	.
127.	.
128.	.
129.	.
130.	.
131.	↓
132.	Last phalang on the second digit

133.	Second metatarsal
134.	First digit-first phalang, starting distally
135.	↓
136.	.
137.	Last phalang on the first digit
138.	First metatarsal
139.	First distal tarsal
140.	Tibiale
141.	Tibia
142.	Fibula
143.	Right femur
144.	Left ischim
145.	↓
146.	.
147.	.
148.	.
149.	.
150.	.
151.	.
152.	.
153.	.
154.	.
155.	Right ischium
156.	↓
157.	.
158.	.
159.	.
160.	.
161.	.
162.	.
163.	Right ilium
164.	.
165.	Left pubis
166.	↓
167.	.
168.	.
169.	.
170.	Sacral vertebrae
171.	↓
172.	First sacral vertebrae
173.	Right pubis
174.	↓

175.	.
176.	.
177.	.
178.	.
179.	Miscellaneous material from the right pubis
180.	Last dorsal vertebrae
181.	Neural spine
182.	Dorsal vertebrae
183.	Dorsal vertebrae
184.	Neural spine
185.	Dorsal vertebrae
186.	Neural spine attached to vertebrae 187
187.	Dorsal vertebrae
188.	Rib fragment above the dorsals
189.	↓
190.	.
191.	.
192.	.
193.	.
194.	.
195.	.
196.	.
197.	.
198.	Rib fragment below the dorsals
199.	↓
200.	.
201.	.
202.	.
203.	.
204.	.
205.	Left femur
206.	Part of the left femur
207.	Fifth digit first phalang
208.	Fourth metatarsal
209.	Part of the second metatarsal
210.	Fourth digit fourth phalang?
211.	Fourth digit, fifth phalang?
212.	Fourth digit, sixth phalang?
213.	Fourth digit, part of the first phalang?
214.	Third digit, part of the fourth phalang?
215.	Third digit, first or second phalang
216.	Second digit, part of the third phalang?

217.	Fourth digit, eight phalang?
218.	Second digit, part of the sixth phalang?
219.	Third digit, part of the eight phalang?
220.	Fourth digit, seventh phalang?
221.	Third digit, part of the fifth phalang?
222.	Second digit, part of the fifth phalang?
223.	First digit, part of the first phalang?
224.	Second digit, part of the third phalang?
225.	Part of the fist metatarsal
226.	Second digit, part of the second phalang?
227.	Fifth digit, part of the fourth phalang?
228.	Fifth digit, second phalang
229.	Fourth digit, last part of the first phalang? (229+213)
230.	Third metatarsal
231.	Miscellaneous material from the left limb epipodial region

In the following section a general description is provided for the vertebrae, ribs, pelvic girdle, and limbs of specimen P.M.O. A 27445. This is followed by a more detailed discussion of some of the more important bones from these regions.

Vertebrae

One change has been made from the original material on the foremost vertebra. The single process which was thought to be a transverse process belonging to the second foremost vertebra (Collection number 185) was found to be the missing transverse process on the foremost vertebra (Collection number 187).

A total of 38 centra are preserved which can be divided into the following groups: dorsals, sacrals, and caudals (Fig. 18).

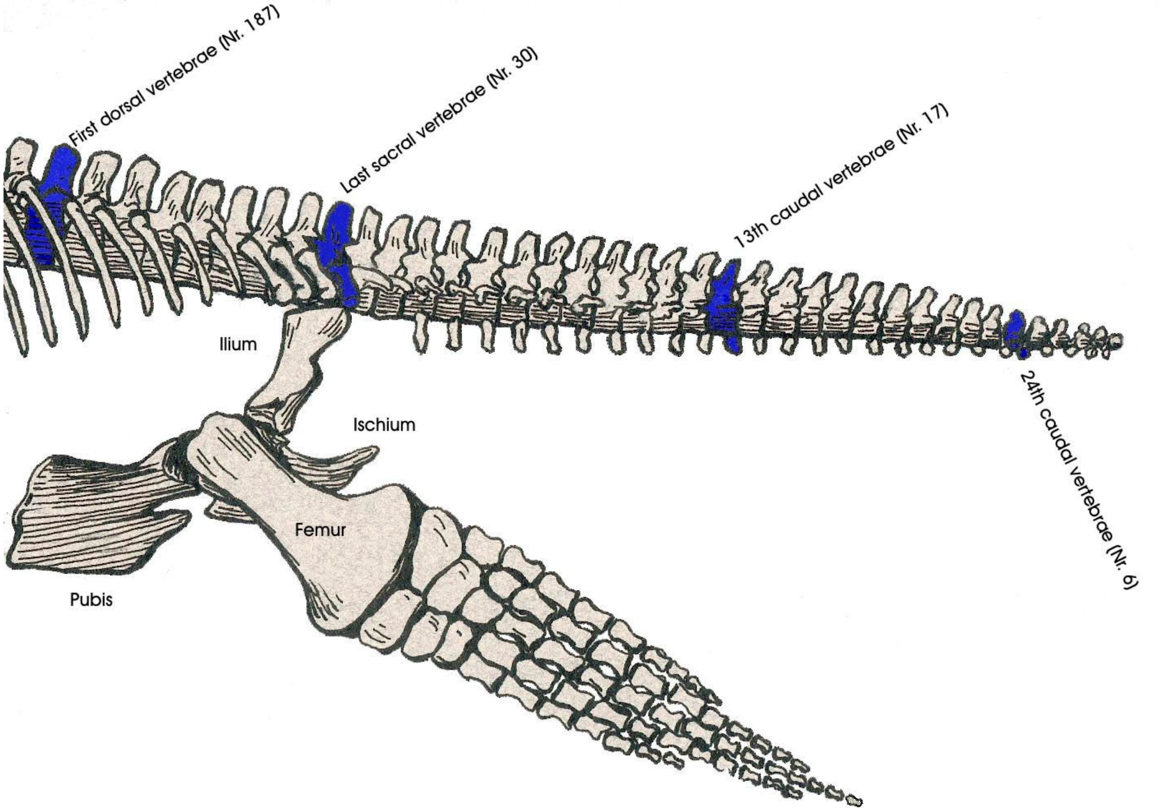


Fig. 18: The preserved material of the fossil specimen. The first dorsal, last sacral and one middle and one posterior caudal vertebrae are highlighted and will be studied in detail below. Other pieces to be examined are also shown.

The first five centra are dorsals, where the transverse process is located on the neural arch. The first dorsal centrum is the only one with articulated transverse processes. Two other solitary unarticulated processes are found in this region.

The number of sacral vertebrae is harder to estimate as the material in this region is more weathered. However, four centra show signs of the transverse process originating from what looks like the centrum and neural arch area.

The next two centra are almost impossible to place, but as the usual number of sacrals in plesiosaurs are three or four (Williston, 1914) it is most likely that they are the first caudals. The number of sacral vertebrae in today's reptiles, birds and opossums are two, so it would be relatively safe to say that the remaining 29 vertebrae are caudals. The last 27 at least show clear signs of being caudals, having the facets for rib articulation on the centrum only.

The centra become smaller posteriorly through successive dorsal, sacral and caudal vertebrae. Likewise their shape changes from nearly circular in outline to a more oval shape. This trend can also be manifested in height to width ratio, which changes from nearly 1 (circular) to less than 1 (oval).

However, this trend seems to diminish towards the last few caudals where the height and width-ratio of the centra becomes closer to 1, or even larger than 1, meaning that height exceeds width. This trend starts at vertebrae number 8 and continues throughout the last caudals, reaching positive height to width ratios at number 4.

All of the vertebrae lack fused ribs and neural spines and only the three foremost have residues of the neural arch attached to the centrum. However, all vertebrae have smaller parts of the lower neural arch fused to the centrum.

The best-preserved vertebra is the first dorsal which has a nearly complete neural arch and two transverse processes for articulation with the ribs (see Fig. 20).

For future references material found above and below the vertebral column was after study stored in plastic bags which was then numbered according to their respective vertebrae. This means that there are two bag sets for each vertebra, one containing the dorsal material and one the ventral material.

Most of this material is fragmentary and beyond identification other than it represents dorsal neural-spine and ventral chevron-bone pieces as well as a few transverse processes.

In some of the material found dorsal to the trunk such as bag number 053 (vertebra 023) and bag 055 (vertebra 025) part of the posterior zygapophysis seems to be preserved on the neural-spine (Fig. 19).

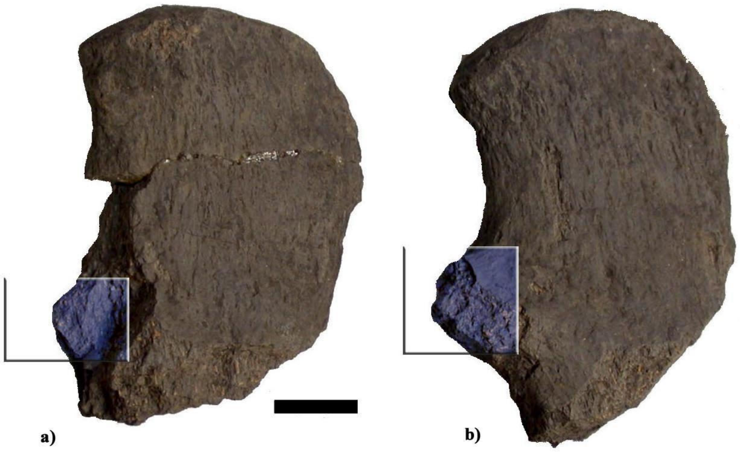


Fig 19: From left to right, neural spines belonging to (a) the 5th and (b) 7th caudal vertebrae respectively. Note the posterior zygapophysis marked in blue (PMO: A 27745- Collection number 23 & 25 respectively). Scale bar = 1 cm

Most vertebrae are in a fairly good condition, except the sacrals and the first three or four caudals. The following description is selective and restricted to the best preserved from each region of the preserved trunk.

The first dorsal vertebra (Collection Number. 187) (Fig. 20): This is almost complete, lacking only the neural spine and smaller parts of the centrum. The articular surface of the centrum is nearly circular in outline and biconcave/amphicelous. The centrum also displays concavity when seen from the sides and from below, giving it a sharp and well-defined edge.
The length, width, and height of the centrum, is 6.2 cm, 8.2 cm, and 8.6 cm respectively, measured from the anterior end at its centre. In posterior view the width of the centrum is a little larger, measuring 8.6 cm, making the centrum widen from front to back like a wedge. The neural canal measures 4 cm. in height and 1.5 cm in width, being a little broader at the bottom. The inner surface of the neural canal is very smooth but with a prominent ridge on the left inner wall.

Fig. 20: First dorsal vertebra shown in (a) lateral and (b) anterior view. The ridge inside the neural canal can be seen in the picture on the right as a bulb in the middle of the canal on the right hand side (PMO: A 27745-Collection number 187). Scale bar = 5 cm.

There are no clear signs of the zygapophysis on the vertebra, except maybe some relics on the posterior side just above the neural canal.

The lengths of the transverse processes are approximately 10.5 cm, the distal part being the thickest, measuring 4.5 cm in width.

What looks like a nutritive foramen is located on the right side of the centra, a little ventrad in an area with small grooves. The foramen on the other side is missing because of the lack of the left-ventral side of the centra.

4th sacral vertbra (Collection number. 30) (Fig. 21): Only half the centrum remains, of what looks to be the right side, and the articular surfaces are both weathered with the outer surface missing.

As with the first dorsal, the articular surfaces as well as the lateral and ventral sides are all biconcave giving the centrum a well-defined edge. However, this is not as prominent as that seen in the first dorsal because of more weathering on the edges.
A small part of the neural canal floor is present along with the facet for the right transverse process. This facet, which is oval in outline and situated in a nearly vertical manner, is relatively deep with two conspicuous concavities at its centre. The size of the facet for the transverse process is 3.7 cm and 1.6 cm respectively.

a) b)

Fig. 21: The last sacral vertebra shown in (a) anterior and (b) lateral view. The drawing (c) below shows the vertebrae in anterior view with the preserved piece in grey (PMO: A27745-Collection number 30). Scale bar = 5 cm.

A few irregularities are also seen just below the facet, which most likely are some sort of nutritive foramina or perhaps markings from articulation with the pelvic girdle and the ilium. Reconstruction of the bone allowed for the length, width, and height to be measured which was 5.0 cm, 8.0 cm, and 7.2 cm respectively.

From the caudal region I will describe two vertebrae, one from the middle region (number 17) and one from the posterior region (number 6).

13th caudal vertebra (Collection number 17) (Fig. 22): The centrum is a little broader than high, 7.1 cm to 6.0 cm respectively, and has a length of approximately 4.2 cm. As with the dorsal vertebrae these measurements are taken from the anterior end where the width of the articulation surface is a little smaller than on the posterior end, where the width is 7.7 cm. This is a feature seen in most of the caudals except the posterior ones and causes the centra to be a little more elliptical in outline in posterior view. Other than this the anterior and posterior surfaces are similar in appearance and are both biconcave.

The facet for the left transverse process measures 3.0 and 2.4 cm, taking the long and short axis respectively. The facet is easily recognisable and is tilted somewhat downwards at the posterior end. The facet on the right side is more weathered and therefore not as pronounced.

From below, the centrum has a sub-rectangular concavity with two laterally placed, low longitudinal ridges, one on each side of the foramina for nutritive vessels. These ridges are mentioned by Welles (1943) as one of the distinctive characters of dolichodiran plesiosaurs. One of the nutritive foramina is clearly visible towards the centre of the vertebra, while the second one is lacking because of a crack passing through the centrum.

The four sub-triangular chevron facets are preserved and easily recognisable. They are situated one on each end of the ventral transverse ridges.

Why there are four facets and not two is because the chevron bone articulates with a facet which is shared between this centrum and the one in front and behind. This is a feature that starts in the seventeenth vertebra and continues throughout the rest of the caudals. In the caudals anterior to number 17 there are only two chevron facets situated on the posterior end of the centrum.

Only a small part of the neural canal floor is preserved due a crack going through the centrum. A small part of the left neural-arch wall no more than 1 cm high is also preserved.

a) **b)**

Fig. 22: The 13th caudal vertebra from the middle caudal region shown in (a) anterior and (b) lateral view (PMO: A 27745-Collection number 17). Scale bar = 5 cm.

24th caudal vertebrae (Collection number 6) (Fig. 23): The width, height, and length of the vertebrae is 5.0 cm, 4.5 cm, and 3.3 cm, respectively. The centrum is biconcave but not as much as in the dorsals and anterior caudals.

The anterior side of the centrum is best preserved with few cracks. Seen in antero-posterior view the centrum widens in the dorsal direction, giving it a shape somewhat like an inverted triangle. The reason for this is that the ventral part of the centrum seems to be a little compressed laterally.

The facets for the small caudal ribs, or rather the facets for the transverse processes, are prominent and situated a little more anteriorly on the centrum compared to the dorsals and anterior caudals. The long-axis of the facet measures 2.0 cm in length and the width perpendicular to the long axis is about 1.2 cm.

Below the rib facets there is a marked semicircular concavity on both sides with a well-developed rim. Ventrally the centrum is also concave with the same longitudinal crests on its lateral sides as mentioned in number 016, although much more pronounced.

Situated on the end of these crests are the four chevron-facets, the two posterior being the largest.

The nutritive foramina have most likely coalesced to form one hole situated a little towards the anterior end of the centrum.

Dorsally the neural canal floor is missing and only two tiny longitudinal ridges are left of the neural arch.

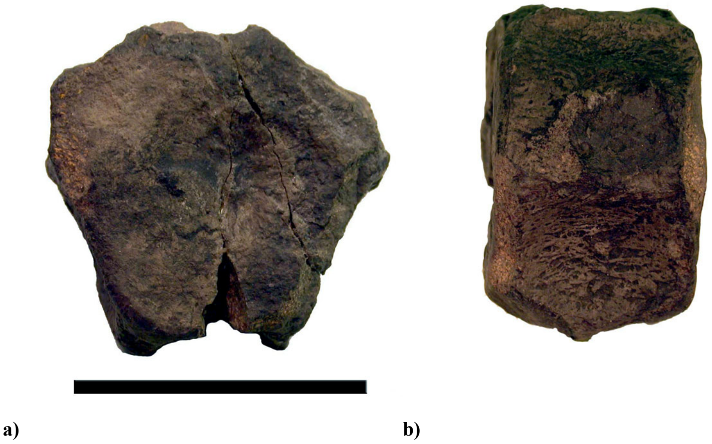


Fig. 23: The 21 caudal vertebra shown in (a) anterior and (b) lateral view (PMO: A 27745- Collection number 6). Scale bar = 5 cm.

Ribs (Fig. 24)

Only five incomplete ribs were originally preserved, all found in the anterior region of the fossil above and below the first five dorsals. They are slender and dorso-ventrally flattened or rod-shaped and most of them show clear muscle-scar lineations especially towards the articulation facets.

The three ribs above the dorsal vertebrae are in a relatively good state of preservation although not complete. The two posterior ribs have parts of their articulation site with the transverse processes intact.

In the first of these, number 192, the actual articulation facet for connection with the transverse process is present.

Fig. 24: A total of five fragmented ribs are preserved. The two white (a + b) were located below the dorsal centra while the three grey ribs (c + d + e) were located above (PMO: A 27745- Collection number 188-204). Scale bar = 5 cm.

The thickness and width is the same throughout the rib and features from below a lunar-shaped concavity extending up the rib. In the second rib, number 188, the articulation area is a much larger element, almost twice the size to that seen in number 192, which also has a lateral bend to it at the proximal end. The actual articulation facet with the transverse process in this latter rib element is missing.

The two ventral ribs are very fragmentary but show the same overall features as those found in the dorsal ribs. Rib number 201 from the anterior ventral rib contains part of the articulation facet with the transverse process which is somewhat square-shaped. The overall shape of this rib-element is a little different from that seen in the other ribs, it is not dorso-ventrally flattened but rather has a more stocky shape to it. The two ventral ribs are also covered with a white coating containing Carbonate-fluorapatite $[Ca_5(PO_4,CO_3)_3F]$, Braunite $[Mn^{2+}Mn_6^{3+}Sio_{12}]$, and Fluorapatite $[Ca_5(PO_4)_3F]$. This is the same coating mentioned earlier also covering part of the right pelvis, left limb and some vertebrae (Fig. 25).

A small unnumbered fragment of what looks like part of a rib-fragment was found lying beside vertebrae number 23.

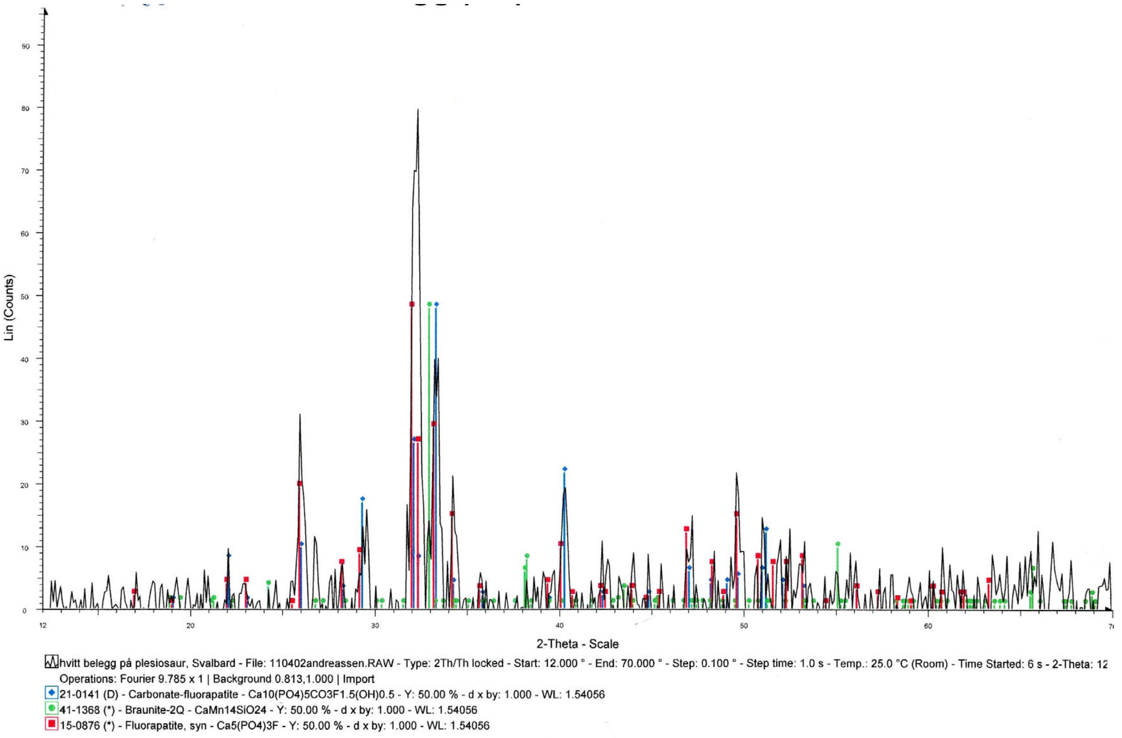


Fig. 25: Graphical illustration showing the constituents of the white coating found on different pieces of the specimen. The different minerals are colour coded; blue-Carbonate-fluorapatite, green-Braunite, and red-Fluorapatite.

Pelvic girdle (Fig. 26)

The left and right pubis and ischia, as well as the right ilium constitute the preserved parts of the pelvic girdle. The left side is severely weathered and much of the material is missing. The right side however is in a relatively good state of preservation and is described in detail below.

Although not complete, the right pubis is the largest single piece of the pelvic girdle.

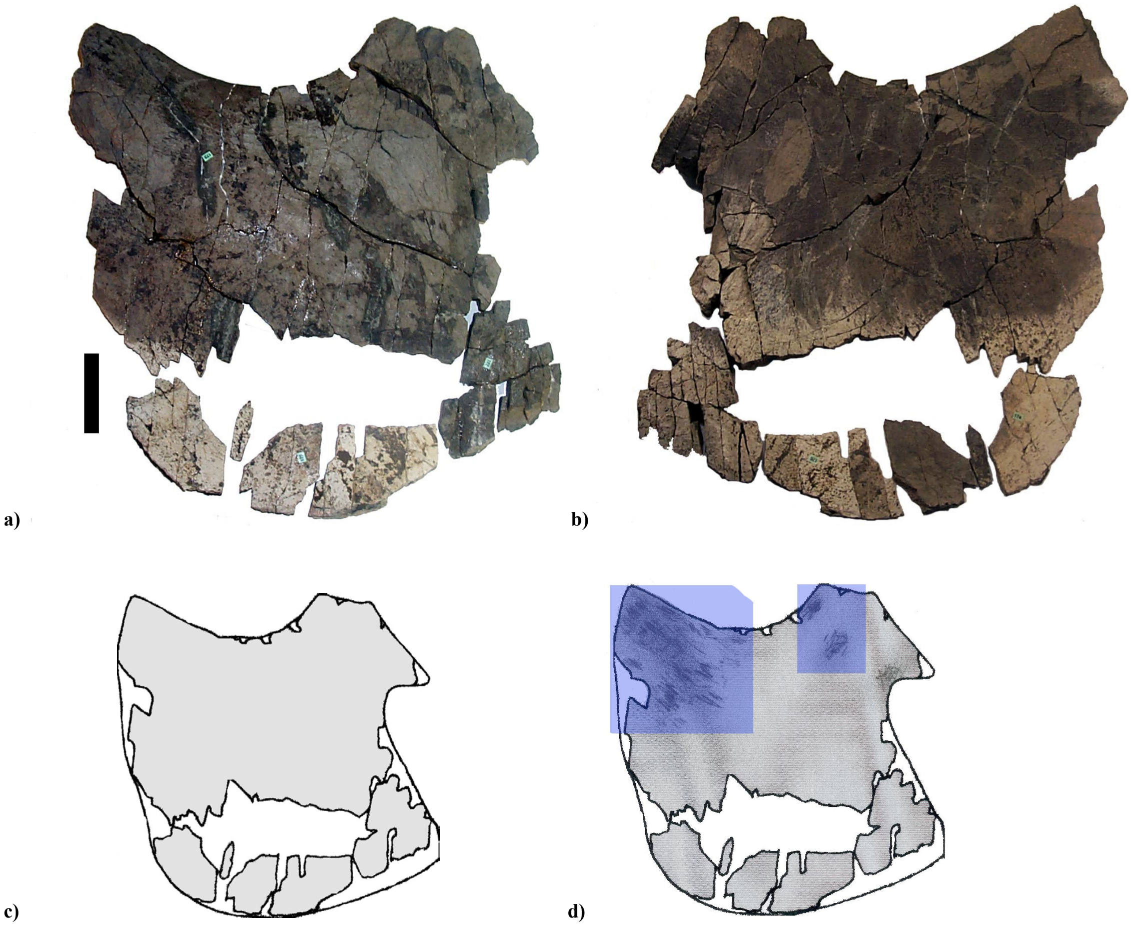


Fig. 26: The right pubis of PMO A 27745 exposed in (a) ventral and (b) dorsal view, the scale is 10 cm. A drawing of the pubis in ventral view (c) with the preserved pieces in grey and a sketch of the areas with the most pronounced muscle scars (in ventral view) (d) is shown below (PMO: A 27745- Collection number 173-178). Scale bar = 5 cm.

The anterior part is partly broken and the exact shape is difficult to ascertain as the entire outer rim of the bone is missing. This is probably due to the rim having been capped in cartilage.

The length and width of the remaining pubis measures 28 cm and 31.5 cm respectively. It thickens posteriorly and to some extent also towards the acetabulum where it articulates with the femur. In dorsal view the pubis is slightly concave from front to back and displays several rugosities and striations especially towards the posterior end where the markings seem to follow the outer rim of the bone. These markings are most likely muscle scars.

In a depression, situated anteriorly and to the left towards the left pubis, another accumulation of muscle scars is seen.

The ventral side is a little more worn but clear markings after muscle attachment is nonetheless visible at much the same places as those seen in dorsal view.

The articulation facet with the femur is almost complete save for the missing outermost rim. It has a width of 9.8 cm and a height of 5.6 cm. This concave facet is continuous with the smaller symphysial border with the right ischium, which measures 6.0 cm in width and 4.4 cm in height. The height of this latter facet diminishes towards the obturator fenestrae and was measured close to the acetabulum.

The facet for articulation with the left pubis is also preserved although a small dorsal part is missing. This facet measures 7.3 cm in width and 4.5 cm in height.

The right ischium is partly crushed and composed of several separate pieces. However some, such as the articulation sites with the femur and the left ischium together with the posterior part, are in a relatively good state of preservation. The length and width of the ischium is 32.8 and 30.6 cm respectively (Fig. 27).

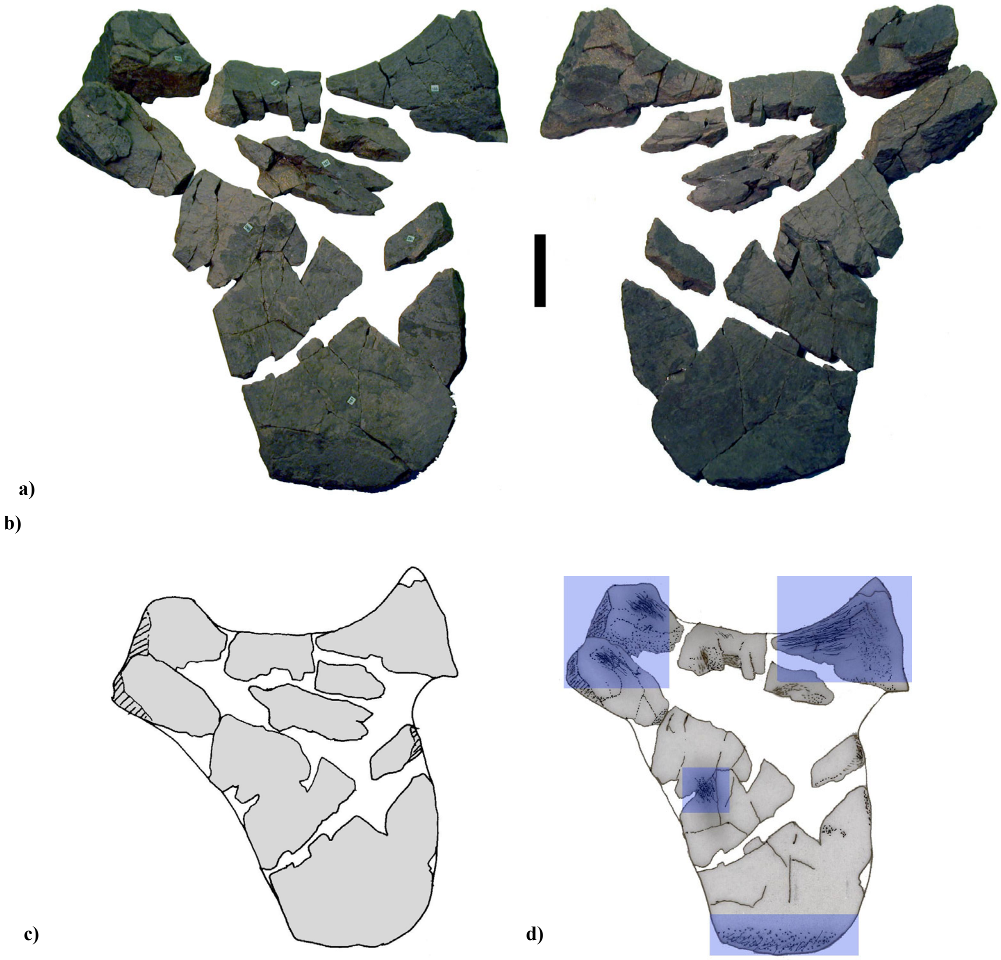


Fig. 27: The right ischium exposed in both (a) ventral and (b) dorsal view. A drawing of the ischium in ventral view with the preserved pieces in grey (c) and a sketch of the areas with the most pronounced muscle scars (d) is shown below (PMO: A 27745- Collection number 155-162). Scale bar = 5 cm.

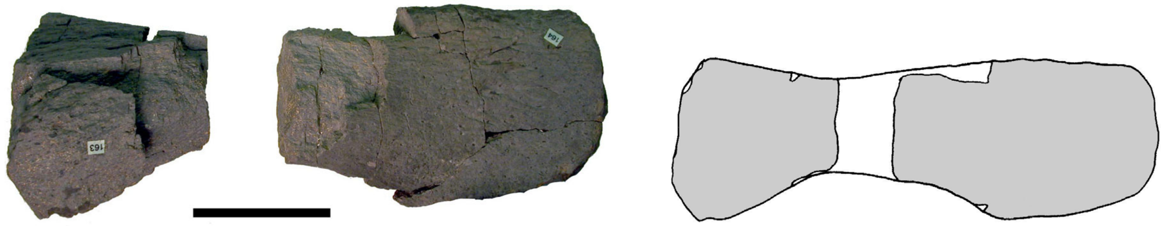
The articulation sites with the right pubis, right femur, and right ilium are present and relatively well-preserved. The heights and widths for these respective facets are 6.0 & 6.7 cm, 7.3 & 8.2 cm, and 6.1 & 7.4 cm.

An almost complete facet for the articulation with the left ischium is also preserved with a height and width of 7.0 and 11.4 cm respectively.

The posterior edge of the ischium is almost completely straight and has a peculiar downward bend to it when seen in ventral view.

Muscle scars are clearly visible especially in two regions, around the area of the femur/ilium attachment and around the attachment site with the left ischium.

The right ilium is a rod like element preserved in two pieces. The largest is a flat and broad element that attaches to the sacral vertebrae of the trunk. The other is the head of the ilium and articulates with the ischium and pelvis. A piece of the ilium, which should have made up the intermediate part, is missing. The exact length is therefore difficult to estimate, but approximately 20 cm is reasonable (Fig. 28).



a) **b)**

Fig. 28: The right ilium (a). The drawing of the ilium (b) shows the preserved parts highlighted (PMO: A 27745- Collection number 163 & 164). Scale bar = 5 cm.

Both pieces show clear muscle scar markings although they perhaps are a little more prominent on the head than on the distal end. Scars on the distal end of the ilium imply that a connection of some sort indeed was present between the pelvic girdle and the trunk. Whether this was sufficient to support the weight of the animal on land is difficult to say.

Limbs

Both hind limbs are preserved, the right being the best preserved and most complete, while the left is badly weathered and lacking a few elements of the epipodial and autopodial-region (ankle and digits).

It has been possible to partly restore some of the disarticulated material of the left limb such as the fifth metatarsal and the intermedium as well as what could be part of the second metatarsal. The remaining pieces making up the left epipodial and autopodial region are too fragmentary to be restored fully.

A few changes have been made with regards to the position of the bones in the autopodium of the left limb by comparing the left and right limbs.

In addition to the femur, the left limb comprises thirty-two numbered pieces and seven unnumbered clusters of bone-fragments. The latter have been placed within the epipodial and autopodial region as part of the tibia, fibula, tibiale, fibulare, and the first, second, and third distal tarsal. This grouping was mainly done on the basis of bone-thickness and general morphology of the fragmented material. One bone-cluster in particular, placed as the tibiale, is also a good candidate for either the tibia or ulna.

Three previously undescribed elements of the left limb, the intermedium, fifth metatarsal, and what is most likely the top part of the second metatarsal are here described.
The intermedium measures 6.5 cm in width, 5.5 cm in height, and approximately 1.5 cm in thickness. It is almost complete save for a few missing elements in the centre and towards the articulation with the tibiale. The bone is very similar, both in size and general morphology, to that of the right-limb intermedium (Fig. 29).

a) **b)**

Fig. 29: The partly restored intermedium of the left limb (a). The drawing (b) on the right shows the complete intermedium with the preserved parts highlighted (PMO: A 27745- Collection number 231). Scale bar = 5 cm.

The fifth metatarsal has a height, width, and thickness of approximately 6 cm, 3 cm, and 2.2 cm respectively. It was made by combining the proximal part of what was originally thought to be the fifth metatarsal with a new part found among the digits of the left limb (Fig. 30).

Fig. 30: The new fifth metatarsal of the left limb. The distal part is new with regards to how the specimen first was laid out (PMO: A 27745- Collection number 232). Scale bar = 1 cm.

The second metatarsal of the left limb came to light when fitting the distal residual part of the original fifth metatarsal with an inconspicuous fragment found in the epipodial region of the left limb (Fig. 31). The bone has the characteristic square-shaped head such as seen on the equivalent element of the right limb.

Fig. 31: The new second metatarsal of the left limb(PMO: A 27745- Collection number 209). Scale bar = 1 cm.

With the exception of a few missing phalanges the right limb is almost complete.
The femur articulates distally with only two elements, the tibia and fibula (Fig. 32), which in turn articulates with three elements, the tibiale, intermedium, and fibulare.
The tibia articulates distally with the tibiale and intermedium while the fibula articulates with the intermedium and fibulare.

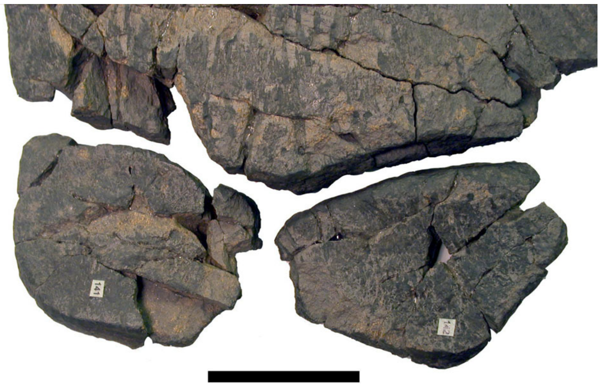


Fig. 32: The tibia and fibula of the right limb seen in ventral view (PMO: A 27745- Collection number 141 & 142). Scale bar = 5 cm.

In the third row there are four elements, the distal tarsals d_1, d_2, and d_3 as well as the fifth metatarsal, m_5. The tibiale articulates distally mainly with the first distal tarsal (d_1) but also touches the corner of the second distal tarsal (d_2). The intermedium has articulation facets for both d_2 and d_3 but not d_1. The fifth metatarsal (m_5) articulates with the fibulare only (Fig. 33).

Fig. 33: The right femur seen in (a) ventral and (b) distal view (PMO: A 27745-Collection number 143). Scale bar = 10 cm.

In the fourth row, the remaining four metatarsals are located as well as the first bone of the fifth digit. The first distal tarsal (d_1) articulates distally with two elements, the first and second metatarsal (m_1 & m_2). The second distal tarsal (d_2) also articulates distally with two elements, the second and third metatarsal (m_2 & m_3). The third distal tarsal (d_3) and the fifth metatarsal (m_5) however articulate with only one element distally, the fourth metatarsal (m_4) and the phalang from the fifth digit respectively.

The number of preserved phalanges in the digits I - IV are 4-9-12-12 and 8 respectively.

Discussion and systematics

Due to the incomplete skeleton available and especially the lack of the skull plus the chaotic taxonomic history of the order Plesiosauria, it is very difficult to assign the specimen to a known genus or species. However certain morphological features present allow for some conclusions to be drawn.

Before comparing the fossil material with that of other contemporary specimens I will briefly mention some of the general misconceptions in plesiosaur taxonomy and also refer to the interpretations and conclusions presented by Persson (1962).

Since its inception the Order Plesiosauria has suffered from taxonomic chaos because assigned genera and species have been erected on the basis of insufficient material or because ontogenetic variations have been misinterpreted as synapomorphies. Strong ontogenetic variability of the plesiosaur skeleton is seen in the proportions and forms of the vertebrae, especially the centra, and in the girdle bones, commonly found as fossils (Godefroit 1995; Bardet & Godefroit 1995; Carpenter 1996, 1999).

In the early nineteenth century little was known of the now well established taxonomic concept which identifies the skull as one of the most important regions exhibiting apomorphic characters. The regions around the temporal fenestra and the palate are especially important in plesiosaurs.

The reason why the skull is a more reliable feature of use in taxonomy is because cranial features and the atlas-axis complex are much more evolutionary stable than postcranial features, and hence are much less susceptible to convergence (Carpenter 1997).

Many of the characters used in early classifications are very homoplastic within the Plesiosauria, meaning that they are very susceptible to convergence and hence of no real taxonomic value.

However, of late extensive revisions of the Sauropterygia (e.g. Storrs 1991, 1993; Rieppel 1999, 2000; Rieppel & Wild 1996) and the order Plesiosauria (Brown 1981, 1993; Brown & Cruickshank 1994; Bardet 1998; Storrs 1997; O'Keefe, 2001, 2002) have significantly improved our knowledge of the phylogeny of the marine reptiles.

In describing *Tricleidus svalbardensis*, Persson (1962) based most of his work on the characteristic shape of the ischia and the epipodials of the right hind limb, from where he argued that the fossil showed close affinities with in particular two genera, *Tricleidus*

Andrews 1909 and *Apractocleidus* Smellie 1915. The latter has since been recognised as a synonym of *Cryptoclidus* Phillips 1871 by Brown (1981).

Based on features of the ischia, Persson (1962) compared the present material with that of the type specimen *Cryptoclidus eurymerus*. However there were some minor differences between the two, regarding the posterior border of the ischia, which is almost straight in the Svalbard-specimen and curved in *C. eurymerus*. Other differences can be seen in the hind limbs where in *C. eurymerus* the femur has a more concave anterior end and also a more expanded distal end.

Following the work by Smellie (1915, 1916) on *Apractocleidus teretipes* (= *Cryptoclidus eurymerus*), Persson (1962) identified yet another difference based on the number of elements associated with the distal articulation of the femur. According to Smellie (1916, p.625) the femur of his *A. teretipes* (= *C. eurymerus*) articulated with four elements distally whereas the present specimen articulates with the tibia and fibula only. For this reason Persson (1962) compared the Svalbard material with *Tricleidus seeleyi* as this was the only form with a similar hind limb. Persson (1962) used the above information to eliminate *Cryptoclidus* as a possible name for the present specimen.

It is now known however, that *C. eurymerus* only has two epipodial elements and therefore can not be excluded as a taxonomically related clade on the terms set by Smellie (1916).

Tricleidus seeleyi is the type species of the genus and was described in detail by Andrews (1909) and later by Brown (1981). It is part of the Leeds collection (R 3539) consisting of disarticulated material of most of the skull together with half the postcranial skeleton.

Other material includes one pectoral girdle and humerus of an adult (NMW. 19.96.G7) and the right humerus of an adult (H.M.G. V.1800), both from the Oxford Clay in the area around Peterborough.

The diagnosis for the genus is largely based on features of the skull, teeth and some elements of the pectoral girdle. This makes the process of comparing it with the Svalbard-specimen, where only the distal parts from the pelvis and back are preserved, difficult.

In the following section the Svalbard material is compared with three of the following five known contemporary genera, *Cryptoclidus*, *Muraenosaurus*, *Tricleidus, Colymbosaurus,* and *Kimmerosaurus*.

Material of *Kimmerosaurus* only consists of an incomplete skull and 11 teeth, while *Colymbosaurus* has articular facets for three epipodials on the distal end of the femur and therefore clearly is not related to the Svalbard-specimen.

Persson's (1962) attempts of classifying the Svalbard material is fairly accurate, but it has simply been surpassed as the result of more thorough analysis of early plesiosaur material leading to the recognition of new clades and to the establishment of previously unknown relationships between taxa within the Plesiosauria.

Especially data based on the postcranial characters as used by O'Keefe (2001), Rieppel (1997), and Brown (1981) are particularly relevant here.
Data for Jurassic plesiosaurs found in the cladistic analysis by Bardet, Godefroit & Sciau (1999) and especially that of O'Keefe (2001) has been important in helping to provide the cladistic scheme shown here (Fig. 34).

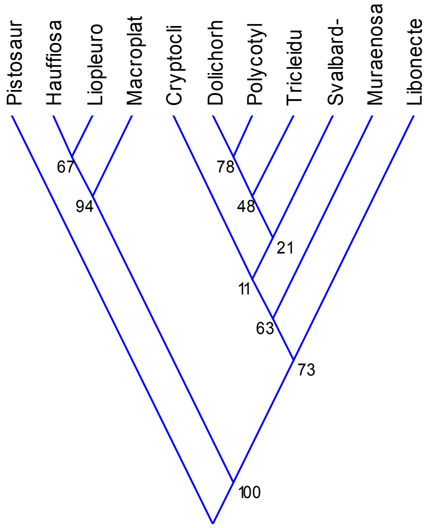


Fig. 34: Tentative phylogenetic relationship between the Svalbard specimen and 10 other well known Upper Jurassic taxa. The fossil was scored against 166 characters taken from O'Keefe's cladistic analysis of plesiosaurs (O'Keefe 2001). The matrix yielded 7 most parsimonious trees with a tree-length of 192 steps. All clades have a Bremer support of 1 (Bremer 1994). From left to right the taxa above are: *Pistosaurus*, *Hauffiosaurus*, *Liopleurodon*, *Macroplata*, *Cryptoclidus*, *Dolichorhynchops*, *Polycotylus*, *Tricleidus*, the current specimen, *Muraenosaurus*, and *Libonectes*.

O'Keefe (2001) has provided the most recent cladistic analysis of the Plesiosauria in which he scored 34 taxa against 166 morphological characters where the primitive state was set to zero and polarity was determined using outgroup comparison. Of these 166 characters, 107 concerned the skull whereas only 59 were postcranial. Only 21 of the postcranial characters were applicable to the Svalbard specimen, which has been compared with 10 taxa taken from O'Keffe (2001).

In the resulting matrix only 4 of the postcranial characters were informative, the 17 residuary were either found in all or only one taxa thus being of no taxonomical importance. The 4 informative characters (3, 130, 146, and 161) concern relative length of ischium/pubis, lateral compression of neural spines, presence/absence of median pelvic bar, and epipodial morphology (O'Keefe 2001).

Parsimony analysis of the data matrix using Fitch-optimisation (Fitch 1971) and branch-and-bound search yielded 7 most parsimonious trees, each with a tree length of 192.

The strict consensus tree computed from these trees is shown in Fig. 34. For a look at the seven most parsimonious trees along with a 50 % majority rule consensus tree, refer to the appendix 1 page 99.

The Svalbard-specimen is located in a clade comprising *Muraenosaurus*, *Cryptoclidus*, *Tricleidus*, *Polycotylus*, *Dolichorhynchops* and *Libonectes*. All of these taxa except *Libonectes,* which is an elasmosaur, are part of the group Cryptocleidoidea as defined by O'Keefe (2001) (see Fig.3).

That the specimen was found to be part of the Cryptocleidoidea is not surprising and rather expected as it also displays very similar morphological features to taxa within this group. However, with only 4 of the characters being informative this taxonomical position is rather tentative.

Based on the three ontogenetic stages defined by Brown (1981) "juveniles, "adults, and "old adults" it appears that the present specimen is an adult or at least a young adult. This is based on the general size of the bones as well as the observation that the neural arches, where well enough preserved, are fused to the centra, and to the shape of the pelvic bones. The pubis and ischia of juvenile plesiosaurs lack a continuous symphysial border and are usually only connected medially. This often results in the characteristic hatchet-shaped ischia typical of juvenile plesiosaurs, a feature absent on the present material.

Establishing an approximate age to the fossil is important with regards to classification because it enables us to use some features, such as those of the limbs and pelvis, in classification if the animal is fully-grown.

Taxonomical comparison

Although diagnostic characters confirming assignment to the superfamily Cryptocleidoidea are lacking there are certain morphological features that link the present material to contemporary specimens within that group. These are: *Muraenosaurus*, *Cryptoclidus* and *Tricleidus*.

Femur: This is very similar to that of contemporary genera, such as *Muraenosaurus*, *Cryptoclidus*, and *Tricleidus*. It shows some similarities to *M. leedsii* (holotype: R. 2421) seen in the small convex bulb on the distal end of the femur separating a right and left facet for the articulation with the tibia and fibula. This convexity however is perhaps a little more pronounced in both *T.seeleyi* (holotype: R 3539) and *C.eurymerus* (neotype: R 2860). The Svalbard-specimen also has a much more inwardly curved anterior distal end of the femur as well as a sharper bend on the posterior distal end than does *M.leedsii*.

As far as overall size goes the Svalbard-specimen has a much larger femur, almost double the size, compared to the holotypes of the three taxa mentioned above. With regards to the general appearance of the femur the specimen would have to be placed closest to *Tricleidus*. Some differences worth mentioning are first of all the already mentioned difference in size, the Svalbard-specimen having an almost twice as large femur (41cm compared to 21cm in *T. seeleyii* (R. 3539)). Because both specimen most likely are a fully-grown animals, judging by the vertebrae and the pelvic/pectoral girdle, this big size difference undoubtedly point toward a more distant relationship between the two species.

When this is said it is important to note that the specimen has a large femur when compared to most taxa. Of the plesiosaur fossils described by Andrews (1910) where the femur is preserved the range in length goes from approximately 16 cm up to a maximum length of 35.7 cm measured in *M. leedsii* (R.2861).

The only contemporary taxa I have come across to have approximately the same length as the Svalbard-specimen is *Colymbosaurus trochanterius* (41 cm) (Owen 1840) described by Brown (1981). Besides the similar length of the femur however these taxa are rather different.

The second thing is a minor difference on the anterior distal end of the femur where *Tricleidus seeleyii* seem to be a little more convex just before the articulation with the tibia.

An example of how difficult it is to use the femur in plesiosaur classification is understood when you see that the form and shape of the bone actually can be quite different between specimens referred to the same species. This is easily seen when comparing the femur of two *Muraenosaurus* of the species *leedsii*, R. 2678 and R. 2421 from the Leeds collection Andrews (1910: fig. 10 plate 4 & fig.12 plate 5) which clearly look rather different.
This obviously makes it difficult to classify the specimen based on the shape of the femur.

Epipodials: As with the femur these elements are similar to those of contemporary taxa.
The tibia is virtually identical to that found in Cryptoclidus, and to a lesser degree that in Tricleidus and Muraenosaurus. The tibia of Cryptoclidus shares a similar sharp edge on the anterior side close to the femur. If you look at Tricleidus and Muraenosaurus you see that the tibia lacks this edge and actually is much more concave leaving a small wedge on the anterior side of the limb between the femur and the tibia.
With regards to the fibula Tricleidus and Cryptoclidus are the ones that stand out in terms of similarity. They both share the triangular-shape seen in the Svalbard-specimen, with one end being relatively squeezed together and the other more pulled apart in a proximal-distally point of view. In terms of general appearance the fibula of Tricleidus is perhaps the most similar. However, taking into account the huge difference in size between the fibula of Tricleidus and the Svalbard-specimen, the latter being almost double the size, Tricleidus looses a point to Cryptoclidus, which is a little larger.

Pelvis: As in all plesiosaurs the pelvic girdle is composed of the three usual bones, ilium, pubis, and ischium. Although similar to that of other plesiosaurs the pelvis of the Svalbard-specimen displays a few characteristic features most of which are found in the ischium.
The ischium is maybe the single one piece of bone that separates the specimen from other well-known taxa of the Upper Jurassic. What makes this piece so special is its symmetrical display when seen in antero-posterior view, its relatively straight posterior border, and its length.
The ischium can in an anterior-posterior view be divided into a right and left part that are extraordinary similar when compared to the ischia of other plesiosaurs. Typical for most other taxa is that the posterior plate of the ischial bone is somewhat shifted towards the symphysial border (left when looking at a right ischium and right when looking at a left ischium). This is clearly seen in the ischia of the type specimen R. 2421 and the younger R. 2428, both of which belong to the Muraenosaurus leedsii.

Going from the acetabulum and backwards in the Svalbard-specimen the ischia almost immediately begins to bend, making a gently concave continuous outer border. In contrast the two specimens mentioned above has a much more laterally progressing border before it bends off towards the posterior end. This results in the latter species having a much more pronounced head on their acetabular side of the ischium than is the case with the Svalbard-specimen. The other conspicuous features seen in the ischium are the almost straight posterior border and its relatively long length.

For reasons mentioned above most other plesiosaurs tend to have a more pointy posterior end to the ischium. In plesiosaurs belonging to the long-necked small-headed guild the ischium is usually also a much shorter and smaller element than the pubis. A long ischium is a conspicuous feature found in the pliosaurian body-type together with the large head and short neck. This body type evolved in three plesiosaur clades: the Rhomaleosauridae, Pliosauridae and Polycotylidae

The Cretaceous Polycotylidae is, as mentioned before, found to be in a closer relationship with the long-necked plesiosaurs of the Upper Jurassic and therefore placed within the Tricleidia.

Based on these similarities with the polycotylids with regards to the ischium and the fact that the Svalbard-specimen was found to be in a close evolutionary relationship to taxa within the Cryptocleidoidea (refer to Fig. 3 and 34) I would tentatively refer the specimen to the family Tricleidia within the Cryptocleidoidea.

Remember that Persson (1962) defined the specimen as *Tricleidus svalbardensis* and that *Tricleidus* at that time was part of the Family Elasmosauridae. However, according to O'Keefe (2001) the Tricleidia is a separate clade comprising the Polycotylidae and the Cimoliasauridae as well as the genus *Tricleidus*.

O'Keefe (2001, 2002) argues that the placing of the Polycotylidae within the Tricleidia shows that the pliosauromorph body type of the polycotylids is derived from a *Tricleidus*-like ancestor. Further he says that *Tricleidus* possesses several synapomorphies linking it with the short-necked plesiosaurids, which explains the close relationship it has with the Polycotylidae. These synapomorphies include the presence of posterior medial processes of the pterygoids, reduced basioccipital tubers, a median contact between the basioccipital and parasphenoid, and the presence of a third distinct articulation on the propodials for a supernumery ossification in the epipodial row. Traits shared by all short-necked plesiosauroids.

That *Tricleidus* as defined by O'Keefe (2001) share synapomorphies with the short-necked plesiosaurs is quite interesting as the Svalbard-specimen also shows a feature typical for short-necked types, seen in its relatively long ischium.

However, the third articulation facet on the propodials as mentioned by O'Keefe (2001) is not present in the hind limb of the Svalbard-specimen and everything suggests that it only had two elements in the epipodial row.

A hypothetical suggestion is then whether the Svalbard-specimen maybe is an intermediate specimen between Upper Jurassic long-necked plesiosaurs and short-necked plesiosaurs of the Cretaceous. But without synapomorphies of the skull it is impossible to conclude whether or not this specimen is in fact closely related to the short-necked plesiosaurs.

On how plesiosaurs used their flippers in propulsion

How plesiosaurs used their flippers in locomotion has long puzzled palaeontologists and a number of theories have been proposed.

Watson (1924) believed the two pairs of flippers were used as oars, moved back and forth in the water. This view was later replaced with a new theory in which the limbs were said to be used more like a birds wing, beating up and down in the water (Tarlo 1958; Robinson 1975). In this scenario the four limbs were treated as identical structures. But this new theory of a four-winged plesiosaur did not last, and the reason was the clearly inadequate musculature for the upward recovery stroke in the hind flippers (Lingham-Soliar 2000).

Robinson (1975) has received a lot of criticism for her theory about the upstroke propulsive force in the plesiosaur flippers. Especially Tarsitano & Riess (1982) and Frey & Riess (1991) have stressed that the power-stroke was on the downbeat, and that the recovery stroke was passive. This is also consistent with the nature of the elements of the girdles (Halstead 1989; Godfrey 1984).

Today it is commonly agreed that the anterior flippers, which have a more crescent shape, as in a swallows wings, are dynamically more efficient for propulsion than the posterior sculls which are more straight. Lingham-Soliar (2000) sees the plesiosaurs as with a front-wheeled drive engine, the front flippers producing thrust and lift, whereas the hind flippers are more passive, serving as steering and manoeuvring organs.

But in order for the anterior sculls to function effectively they must be used symmetrically rather than alternatively (Carroll 1985, p. 153). This has to do with not loosing oxygen due to sideways undulation of the thorax. Asymmetrical movement of the flippers would bend the thorax sideways and compress the lungs, depleting them of oxygen. As mentioned earlier this problem is also seen in modern lizards and amphibians, where the backbone bends to the right and left respectively for each stride, compressing the lungs as it does so. Running and breathing at the same time is therefore impossible in these animals (Cowen 2001).

This problem called ”Carrier’s constraint”, after Carrier (1987), has been solved in most land vertebrates by evolving erect stance. Plesiosaurs solved the problem by stiffening their backbone and synchronising the front and hind flippers, the front ones going up while the hind ones go down, and vice versa. This also causes a dorso-ventral undulation of the body, actually reducing the drag of the water (Halstead 1989 & McGowan 1999).

An interesting point regarding the front and hind flippers in plesiosaurs is the size difference seen between short-necked and long-necked morphotypes. The relatively better adapted short-necked plesiosaurs actually have slightly larger hind limbs whereas the long-necked plesiosaurs have longer front limbs (Bakker 1993). This is most likely a result of the different life-modes and hunting tactics these two groups displayed, the short-necked being active predatory hunters for other marine animals whereas the long-necked plesiosaur used ambush tactics on schools of fish. This view is supported by O'Keefe (2001) who studied the aspect ratios (ARs) of plesiosaur flippers and compared the results with the AR found in birds, bats and aircrafts. He concluded that short-necked taxa were specialized for manoeuvrability and pursuit, whereas long-necked taxa were specialized for efficiency and cruising. This difference in hunting and prey preferences is also supported by their different tooth morphology, where the long-necked plesiosaurs have slender cone shaped teeth used primarily for piercing fish and the short-necked have more curved and robust teeth with coarse longitudinal ridges used for cutting (Massare 1987).

In the current specimen there is of course no way to establish the size difference between the front and hind limbs as only the latter is preserved. With a femur measuring 42 cm in length however the specimen is found within a group comprising such taxa as *Attenborosaurus* (BMNH R.1339-femur: 38 cm), *Peloneustes* (BMNH R.3318-femur: 40 cm), *Rhomaleosaurus megacephalus* (LEICS G221.1851-femur: 40 cm) and *Trinacromerum* (SM 3025- femur: 43 cm). All of these taxa except *Trinacromerum* which is part of the Polycotylidae, are found within the short-necked Pliosauroidea. As reference contemporary long-necked taxa such as *Muraenosaurua* (BMNH R.2863), *Tricleidus* (BMNH R.3539) and *Cryptoclidus* (BMNH R.2860) have femur lengths of 29.5 cm, 21cm and 25.5 cm respectively. This strengthens the suggestion that the current specimen could be related to the short-necked pliosauromorphs or the Polycotylidae.

Jurassic and Cretaceous marine vertebrate fossils from Svalbard in the collection of the Geological Museum, Oslo

This material consists of fragmentary specimens collected in the past by various people from different parts of Svalbard. For the most part the location and stratigraphical age is not known except for a few boxes labelled "Sassenfjorden, Jurassic ?".
Where possible the age and location is provided in the following list. If not otherwise stated the material belongs to the Plesiosauria.

One previously unnumbered specimen listed as a plesiosaur femur probably belongs to an ichthyosaur (Fig. 35).

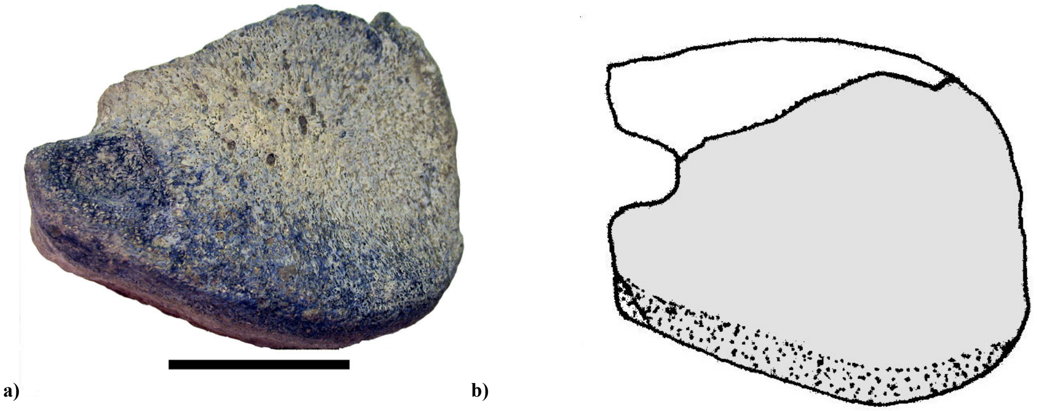


Fig. 35: A: an almost complete ichthyosaurian humerus seen in dorsal view. B: drawing showing the complete humerus with the preserved piece in grey (PMO: 203.512). Scale bar = 5 cm.

76-ME 10: Location: Helvetiafjellet Fm. Svalbard. Age: Early Cretaceous (Barremian).
This material was found in 1976 and constitutes a propodial, most likely a femur, with some of its epipodial and autopodial elements. In addition there is also one vertebrae, several fragmented rib pieces, 145 in all, and 8 phalanges. A diagram showing the limb material and the relative position of the constituent pieces is seen below Fig. 36).
A note found together with the material states that it was found in the "Ginkgo", presumably this is the Ginkgo-Schichten. Ginkgo-Schichten is now an abandoned lithostratigraphic unit name which correlates with the upper part of the Helvetiafjellet Formation (M-89) (Dallmann

1999). The material was also stated to be of Jurassic age, the real age is instead Early Cretaceous (Barremian).

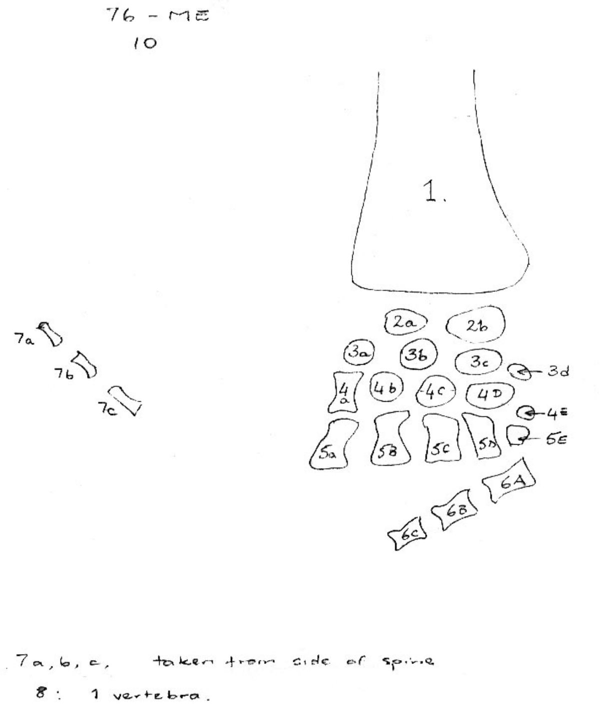


Fig. 36: The material comprising ME 10. This sketch was found with the material and shows the original posture of the bones.

Number 1: 8 pieces that when fitted together made up a complete plesiosaur propodial, possibly a femur (Fig. 37).

Number 2: Contains two pieces, 2a and 2b, the first of which most likely is an intermedium, whereas the latter probably is a fibula.

Number 3: Four pieces, 3a-3d, which most likely constitutes the tarsals/carpals.

Number 4: 4a is most likely the fifth metatarsal whereas the other four pieces (4b-4e) are distal tarsals/carpals.

Number 5: These are the remaining four metatarsals/carpals in addition to a somewhat crescent-moon shaped tarsal/carpal element.

Number 6: Three phalanges, a, b, and c.

Number 7: Three phalanges, a, b, and c which is stated to have been taken from the spine area.

Number 8: This is the single vertebrae of which only the centrum is preserved. The rib facets are on the centrum only and the nutritive foramina are situated fairly close together on its ventral side, both features of cervical vertebrae. Based on overall shape and the closeness of the nutritive foramina it is probably one of the mid or last cervicals.

Fig. 37: Possibly a right femur belonging to a *Leptocleidus* Andrews 1922 seen in (a) ventral and (b) distal view (ME 10-1). Scale bar = 10 cm.

76-ME 12: Location: Agardhfjellet Fm. Svalbard. Age: Jurassic.

This material was found and collected at the same time as ME 10 and comprises material of the autopodial region together with two partially complete propodials.

There are five large bags labelled A, B, C, D, and E each of which contain all the pieces within a vertical line of its digit. "A" comprises digit one, "B" digit two and so forth until digit five. Several other pieces were found, amongst them three epipodials of which one looks to be a fibula, one bone looks very similar to a metatarsal bone perhaps the second.

Of the two propodials, which both seem to be humeri and possibly cryptoclidian in origin, one is larger and also more complete (see Fig. 38).

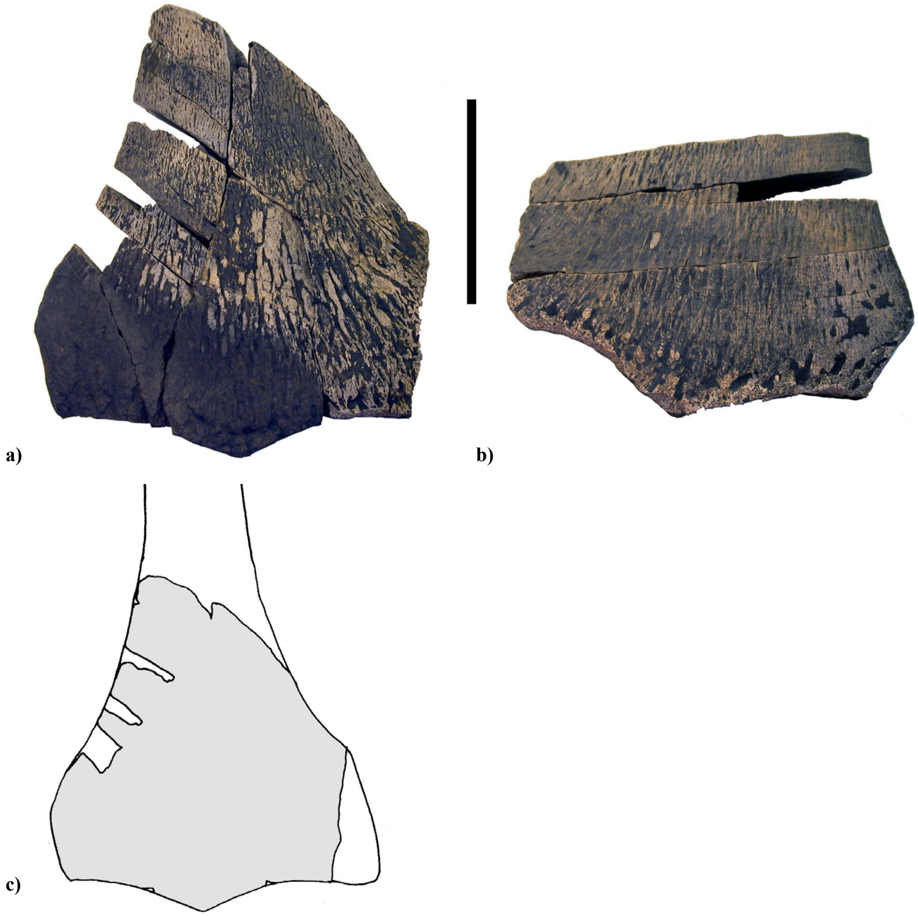


Fig. 38: The two humeri of a possible Crytoclidid plesiosaur (a + b). Below (c) is a drawing of the humerus on the left showing the preserved pieces in grey (76-ME 12). Scale bar = 10 cm.

A few other miscellaneous pieces making out parts of a third propodial, some rib fragments and some epipodial elements were also found.
A diagram showing the material and their relative positions is seen below (Fig. 39).

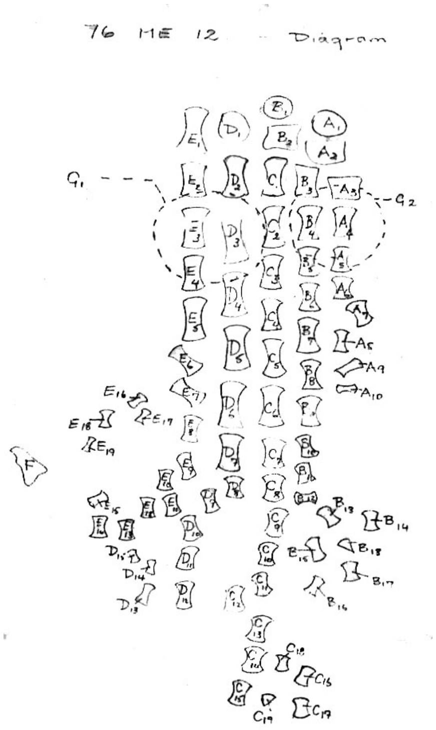


Fig. 39: The material comprising ME 12. The sketch shows the original posture of the bones.

A: a1: epipodial element, possibly a tibiale.
a2: first distal tarsal/carpal.
a3: first metatarsal/carpal.
a4-a12: phalanges of the first digit.

B: b1: epipodial element.
b2: second distal tarsal/carpal.
b3: second metatarsal/carpal.
b4-b18: phalanges of the second digit.

C: c1: Most likely the third metatarsal/carpal.
c2-c19: phalanges of the third digit.
D: d1: third distal tarsal/carpal.
d2: fourth metatarsal/carpal.

d3-d15: phalanges of the fourth digit.

E: e1: Fifth metatarsal/carpal.

e2:-e19: phalanges of the fifth digit.

e20: maybe part of a transverse process. This piece is not marked on the diagram.

G: g1: This was originally 6 fragments found in the area marked G1 on the diagram (see fig. 39). After some effort these pieces have been arranged and interpreted as being a flattened dorsal vertebra (Fig. 40). Much of the outline is preserved and a depression on the ventral side looks like a nutritive foramina. The two jagged peaks on the dorsal side are the beginnings of the outer walls of the neural arch.

g2: Three pieces fit together to give a similar appearance to g1. However, it is not clear whether this is a vertebra.

Fig. 40: The flattened vertebra in anterior view (ME 12-G1).

Nr.132.126: Location: Svalbard. Age: unknown.

Rod shaped element collected by Ø. Lauritsen in 1992 and stated to be a plesiosaur fragment. My belief is that this is an ichthyosaurian bone possibly part of a dentary.

Nr.132.127: Location: Svalbard. Age: unknown.

Part of the same rod shaped element as mentioned above.

Nr.132.128: Location: Svalbard, Sticky Creep Formation. Age: Triassic.

One half of a large ichthyosaurian humerus. Collected by Ø. Lauritsen in 1992 on the "Kongressfjellet" north of Longyearbyen.

Nr.132.129: Location: Svalbard. Age: unknown.

Bone fragment collected by Lauritsen. If this is a plesiosaurian bone it would have to be some sort of epipodial element. Most plesiosaurian epipodials however are more polygonal in shape and not oval as is the case here. An alternative guess is thus that this is an ichthyosaurian epipodial.

Nr.132.130: Location: Svalbard, Sticky Creep Formation. Age: Triassic.

Second half of the ichthyosaurian humerus mentioned above in Nr. 132.128. (see Fig. 49).

Nr. 132.131: Location: Svalbard. Age: unknown.

Part of a plesiosaurian or ichthyosaurian epipodial element. Collected by Lauritsen.

Nr. 132.132: Location: Svalbard. Age: unknown.

Plesiosaurian or ichthyosaurian epipodial element collected by Lauritsen.

Nr. 132.133: Location: Svalbard. Age: unknown.

Part of a rod shaped bone stated to be from a plesiosaur. As with the other rod shaped elements mentioned above I believe this to be part of an ichthyosaurian jaw (dentale).

Nr. 132.135: Location: Svalbard. Age: unknown.

Same rod shaped element as above possibly from an ichthyosaur jaw

Nr. A 27333: Location & Age unknown.

Part of a propodial shaft.

Nr. A 27348: Location & Age unknown.

The head of the propodial shaft mentioned above (A 27333).

Nr. A 27415: Location: Spitsbergen. Age: unknown.

117 rib fragments.

Nr. A 27424: Location: Spitsbergen. Age: unknown.

74 bone fragments.

Nr. A 27435: Location: Section 6, Spitsbergen. Age: unknown.

6 bone fragments of which one looks like the distal part of an ilium.

Nr. A 27464: Location: Spitsbergen. Age: unknown.

27 rib fragments.

Nr. A 27468: Location: Spitsbergen. Age: unknown.

28 rib fragments in addition to one complete phalang and a small part of a vertebrae centrum.

Nr. A 27468: Location: Spitsbergen. Age: unknown.
One anterior cervical vertebra in addition to 11 bone fragments. This material has been given the same number as another collection of plesiosaur rib pieces.

Nr. A 27471: Location: Spitsbergen. Age: unknown.
98 bone fragments, mostly of ribs and transverse processes.

Nr. A 27479: Location: Spitsbergen. Age: unknown.
Approximately 45 bone fragments possibly of a propodial together with several smaller bone fragments.

Nr. A 27488: Location: Spitsbergen. Age: unknown.
261 bone fragments.

Nr. A 27492: Location: Spitsbergen. Age: unknown.
Part of a propodial shaft.

Nr. A 27499: Location: Spitsbergen. Age: unknown.
Part of a propodial head, my guess is that of a femur although this is difficult to say for certain.

Nr. A 27522: Location: Svalbard. Age: unknown
9 bone fragments of unknown origin.

Nr. A 27526: Location: Spitsbergen. Age: unknown.
Most likely part of a plesiosaur propodial.

Nr. A 27531: Location: Spitsbergen. Age: unknown.
Bone fragment, most likely part of a propodial or girdle.

Nr. A 27533: Location: Spitsbergen. Age: unknown.
Most likely part of a plesiosaur propodial.

Nr. A 27535: Location: Spitsbergen. Age: unknown.
10 bone pieces therein one transverse process and one neural spine.

Nr. A 27543: Age and location unknown.
6 bone fragments of uncertain origin.

Nr. A 27543: [A 27549- 551] Location: Spitsbergen, section 6. Age: unknown.
Same number as the box above containing three separately numbered pieces. A 27549: Most likely part of a girdle, perhaps a pubis; A 27550: posterior part of a pubis; A 27551: anterior part of a

pubis, could be part of A 27550.

Nr. A 32222: Location: Spitsbergen. Age: unknown.
20 bone fragments of which 4 can be identified as phalanges. The remaining pieces are impossible to diagnose.

Nr. A 32291: Location: Spitsbergen. Age: unknown.
11 bone fragments of uncertain origin. A label with the number 5 was also present.

Nr. A 32343: Location: Spitsbergen. Age: unknown.
100 bone fragments.

Nr. A 32363: Location: Spitsbergen. Age: unknown.
34 rib fragments.

Nr. A 32364: Location: Spitsbergen. Age: unknown.
18 bone fragments of uncertain origin. A label with the number 5 was found within the box.

Nr. A 32373: Age and location unknown.
40 bone-fragments, most likely of vertebrae.

Nr. A 32577: Location: Spitsbergen. Age: unknown.
11 bone fragments of which 7 can be identified as ribs.
The single largest piece is perhaps part of a propodial head or part of a facet either from the shoulder or pelvic girdle. A label with the number 1 was found in the box.

Nr. A 35680: Location: Spitsbergen. Age: unknown.
32 bone fragments, possibly of vertebrae. A brownish rod-like structure was found in one of the pieces which may be filled nutritive foramina. A chemical analysis was conducted on the mineral filling of the nutritive foramina and which turned out to be ferriferous (Fig. 41).

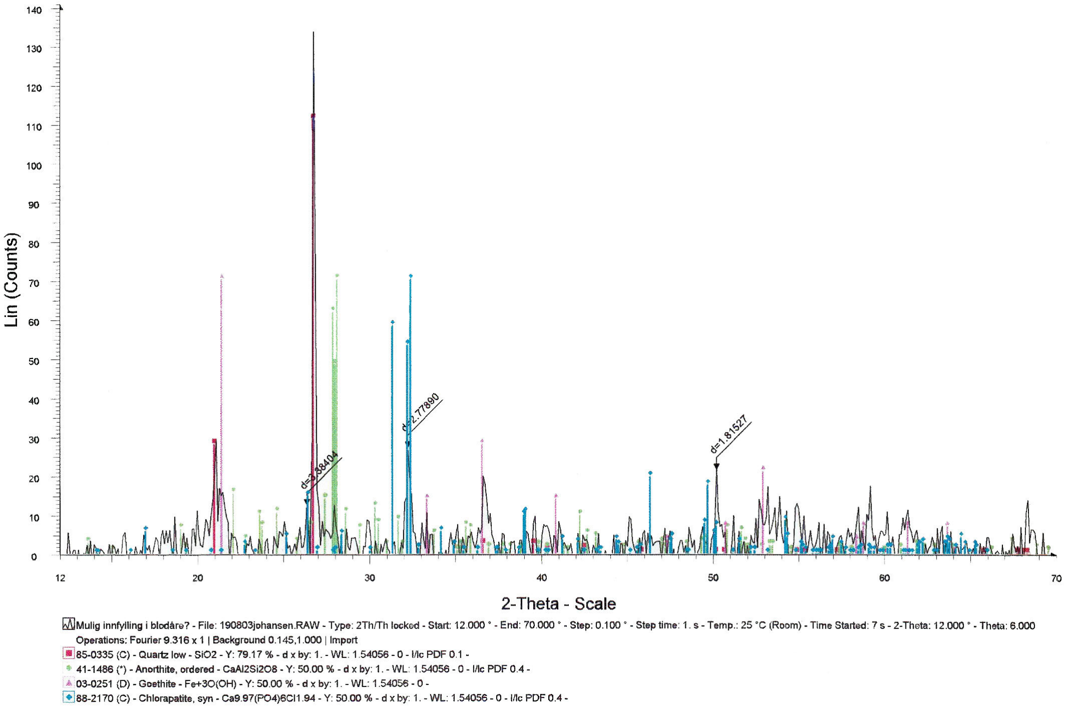


Fig. 41: Graphical representation of the iron filling found in the nutritive foramina of a plesiosaur centrum. The different minerals are colour coded; red- Quarts, green- Anorthite, pink- Goethite, and blue- Chlorapatite.

Nr. A 35681: Location: Spitsbergen. Age: unknown.

33 bone fragments together with a note with the number 6.

Nr. A 35682: Location: Spitsbergen. Age: unknown.

20 bone fragments of uncertain origin.

Nr. A 35683: Location: Spitsbergen. Age: unknown.

113 bone fragments of different origin. Most of the material is sedimentary rock containing fossilised brachiopods possibly of *Thecidea* and are thus not bone material. A few smaller pieces however contain the porous structure typical of bone but whether they are plesiosaurian or not is impossible to tell.

Nr. A 35684: Location: Spitsbergen. Age: unknown.

250 rib fragments.

Nr. A 35685: Location: Spitsbergen. Age: unknown.

85 bone fragments some of which are possibly from a plesiosaur. However, some of the pieces are lacking the porous structure typical for plesiosaur bone and seem to be containing pieces of smaller fossils.

Nr. A 35686: Location: Spitsbergen. Age: unknown.

34 bone fragments possibly of vertebrae. Two of the pieces contain brown/red rod like structures which lie at right angles to the vertebrae tissue. As mentioned above this could be filled nutritive foramina.

Nr. A 35687: Location: Spitsbergen. Age: unknown.

72 bone fragments, possibly of vertebrae. More pieces containing the reddish brown rods. In one of the smaller pieces there are two vertical rods (in ref. to tissue growth) situated close together that penetrate the outer edge of the bone which adds to the probability that these indeed are casts of nutritive foramina.

Nr. A 35688: Location: Spitsbergen. Age: unknown.

255 bone fragments of uncertain origin.

Nr. A 35689: Location: Spitsbergen. Age: unknown.

20 bone fragments possibly from the epipodial region. One piece seems to be part of a rib. A label with the number 6 was found among the material.

Nr. A 35690: Location: Spitsbergen. Age: unknown.

27 bone fragments, most of which possibly are pieces of vertebrae. One of the pieces can easily be identified as being either a posterior pectoral vertebrae or a sacral vertebrae due to the positioning of the nutritive foramina and the diapophysis (Fig. 42). Two labels each with the number 5 written on it was found together with the material.

Fig. 42: Pectoral or sacral vertebrae from Svalbard. Age and locality unknown (PMO: A 35690). Scale bar = 5 cm.

Nr. A 35691: Location: Spitsbergen. Age: unknown.
30 bone fragments, most of which are identifiable as vertebrae.
One piece is a possible girdle fragment.

Nr. A 35692: Location: Spitsbergen. Age: unknown.
51 rib fragments.

Nr. A 35693: Location Sassenfjorden Section 2, Spitsbergen. Age Jurassic?
11 plesiosaur bone pieces which seem to be of the girdle and epipodial region. Three pieces can be identified; one is part of an ilium head, the two others are epipodial elements one of which is a possible fibula (Fig. 43).

Fig. 43: Three plesiosaur pieces found in box A 35693 identified as being an a) ilium head, b) a possible fibula and c) one epipodial element (PMO: A 35693). Scale bar = 5 cm.

Nr. A 35694: Location: Sassenfjorden Section 6, Spitsbergen. Age: Jurassic?
13 bone pieces of articulated and interlocking phalanges. The longest piece measures about 20 cm in length and consists of two whole phalanges together with two halves (Fig. 44).

Fig. 44: Interlocking plesiosaurian phalanges (PMO: A 35694). Scale bar = 5 cm.

Nr. A 35696: Location: Sassenfjorden. Age: Jurassic?

199 bone fragments most of which are impossible to identify. A few pieces however can be identified as vertebrae and ribs. One piece deserves extra attention as it contains plesiosaur teeth most likely from a small-headed plesiosaur. There are four teeth physically present, the most complete measuring 3 cm in length with easily recognisable ridges running along the tooth. Of the others only the broken end is showing as the rest is concealed in matrix. In addition there is also an easily recognisable imprint of a tooth lying right next to the largest tooth (see Fig. 48).

Nr. A 35697: Location: Sassenfjorden Section 9, Spitsbergen. Age: Jurassic?

53 bone fragments of mostly transverse processes but also a few pieces of the vertebrae centrum as well. One of the larger pieces looks like a possible part of an ilium.

Nr. A 35698: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?

16 vertebrae bone fragments.

Nr. A 35699: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?

110 bone fragments, where four or five pieces can be identified as possible ribs.

Nr. A 35700: Location: Sassenfjorden section 6, Spitsbergen. Age: Jurassic?

42 rib fragments.

Nr. A 35701: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
161 bone fragments of uncertain origin.

Nr. A 35702: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
24 bone fragments possibly of ribs and/or the head of a transverse process. The latter could as well be the top of a neural spine.

Nr. A 35703: Location: Sassenfjorden Section 9, Spitsbergen. Age: Jurassic?
46 bone fragments of plesiosaurian diapophysis.

Nr. A 35704: Location: Sassenfjorden Spitsbergen. Age: Jurassic?
53 bone fragments. Most can be identified as rib pieces while one or two possibly are part of vertebrae diapophysis.

Nr. A 35705: Location Sassenfjorden Spitsbergen. Age Jurassic?
51 bone fragments. Two notes saying “Tale part one” and “Tale part two” was found in the box. Whether the pieces indeed are caudal vertebrae is difficult to say.

Nr. A 35706: Location: Sassenfjorden Section 7, Spitsbergen. Age: Jurassic?
186 bone fragments.

Nr. A 35707: Location: Sassenfjorden Section 9, Spitsbergen. Age: Jurassic?
65 bone fragments of mostly plesiosaurian origin. Some of the pieces however can be identified as containing brachiopods and are not plesiosaur material. This particular material was collected during the Norwegian Spitsbergen-expedition from 1909-1910 under Isachsen.

Nr. A 35708: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
37 rib fragments.

Nr. A 35709: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
48 bone fragments. One piece can be identified as a possible neural spine or maybe a transverse process. A second piece is possibly part of a propodial head.

Nr. A 35710: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
9 bone fragments of uncertain origin. Collected during the norwegian Spitsbergen expedition led by Isachsen in 1909-1910.

Nr. A 35711: Location: Sassenfjorden Spitsbergen. Age: Jurassic?
23 bone fragments. The three largest pieces are most likely part of a girdle, possibly a pubis. The remaining pieces are rib fragments.

Nr. A 35712: Location: Sassenfjorden, Section 6 Spitsbergen. Age: Jurassic?
28 bone fragments in which two can be identified as vertebrae, possibly caudals.

Nr. A 35713: Location: Sassenfjorden Spitsbergen. Age: Jurassic?
17 rib fragments.

Nr. A 35714: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
39 fragments of phalanges and epipodials.

Nr. A 35715: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
19 vertebrae fragments. A series of three ossified vertebrae can be identified as caudals due to the nutritive foramina present on the ventral side of the centrum and the location of the diapophysis on the lateral side of the centrum. Two other vertebrae are most likely caudals based on the position of the diapophysial facets. One vertebrae is probably a cervical due to the nutritive foramina on the ventral side being relatively close (Fig. 45).

Fig. 45: Some of the vertebrae belonging to A 35715. From top to bottom: (a) the three ossified caudals and (b + c) two possible caudal vertebrae together with (c) one cervical vertebra all seen in dorsal view (PMO: A 35715).

Nr. A 35716: Location: Sassenfjorden Spitsbergen. Age: Jurassic.
8 vertebrae bone fragments.

Nr. A 35717: Location: Sassenfjorden, Section 4 Spitsbergen. Age: Jurassic?
130 bone fragments of uncertain origin.

Nr. A 35718: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
31 bone fragments of what looks to be mostly vertebrae.

Nr. A 35719: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
19 bone fragments, most of which are transverse processes.

Nr. A 35720: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
28 bone fragments most likely of vertebrae.

Nr. A 35721: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
11 bone fragments. One piece seems to be part of a rib.

Nr. A 35722: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
19 bone fragments which is a mixture of transverse processes and rib pieces.

Nr. A 35723: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
26 bone fragments of unknown origin.

Nr. A 35724: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
39 vertebrae fragments.

Nr. A 35725: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
Most likely a weathered transverse process from a plesiosaur.

Nr. A 35726: Location: Sassenfjorden, Section 6 Spitsbergen. Age: Jurassic?
32 bone fragments where a few rib pieces, possibly some girdle pieces and a peculiar piece that could be a girdle element or maybe part of a jaw (Fig. 46).

Fig. 46: An 11 cm long bone which is either part of a plesiosaur jaw or a weathered part of a girdle element (PMO: A 35726).

Nr. A 35727: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
150 rib fragments.

Nr. A 35728: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
13 plesiosaur bone fragments of what looks to be vertebrae.

Nr. A 35729 - 31: Location: Sassenfjorden, Section 8 Spitsbergen. Age: Jurassic?
3 dorsal vertebrae.

Nr. A 35732 – 37: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
6 vertebrae pieces, three of which seem to be dorsals.

Nr. A 35738: Location: Sassenfjorden, Spitsbergen Age: Jurassic?
15 pieces of which four can be identified as being part of a caudal vertebra. The residual eleven pieces are difficult to diagnose and contain different sized fossil impressions of mostly molluscs.

Nr. A 35739: Location: Spitsbergen, Section 6 & 8? Age: unknown.
33 bone fragments of uncertain origin. One epipodial element, some phalanges, and a girdle piece can be distinguished.

Nr. A 35740: Location: Sassenfjorden, Svalbard. Age: Jurassic?
56 bone fragments of which most are beyond recognition. One piece looks to be a chevron bone and a larger element has a possible chevron fragment attached to it.

Nr. A 35741: Location: Sassenfjorden, Section 8 Svalbard. Age: Jurassic.
124 bone fragments both large and small. All except maybe one or two pieces, which look like part of a propodium, are impossible to diagnose.

Nr. A 35743: Location: Sassenfjorden, Svalbard. Age: Jurassic.
20 bone fragments most of which are beyond recognition. Two pieces are possible to diagnose, one being the distal part of a transverse process, the other a small part of a rib.

Nr. A 35744: Location: Sassenfjorden, Svalbard. Age: Jurassic?
23 bone fragments of mostly vertebrae.

Nr. A 35745: Location: Sassenfjorden, Svalbard. Age: Jurassic?
28 bone fragments of uncertain origin.

Nr. A 35746: Location: Sassenfjorden, Section 9 Spitsbergen. Age: Jurassic?
24 bone fragments a few of which can be distinguished as possible rib elements.

Nr. A 35747: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?

70 bone fragments of unknown origin.

Nr. A 35748: Location: Sassenfjorden, Svalbard. Age: Jurassic.

Three pieces of what could be part of ribs or chevrons.

Nr. A 35749: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?

15 bone fragments in addition to a note saying “box nr. 4” was present. Bone tissue is clearly seen in all pieces.

Nr. A 35750: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?

8 bone fragments. Two seem to be part of transverse processes from a vertebra.

Nr. A 35751: Location: Sassenfjorden, Svalbard. Age: Jurassic.

32 fragments including parts of a transverse process and possibly part of a neural spine.

Nr. A 35752: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?

Part of a girdle, most likely a pubis with the femur articulation facet intact.

Nr. A 35753: Location: Sassenfjorden, Svalbard. Age: Jurassic.

28 bone fragments possibly part of a propodial or girdle. Some of the pieces are water worn and are smooth + polished.

Nr. A 35753: Location: Sassenfjorden, Svalbard. Age: Jurassic.

20 bone fragments mostly of phalanges.

Nr. A 35755: Location: Sassenfjorden, Section 1. South & north, Svalbard. Age: Jurassic.

24 pieces of what seems to be chevron bones.

Nr. A 35756: Location: Sassenfjorden, Svalbard. Age: Jurassic.

Ten bone fragments, three of which are beyond recognition. The two largest pieces are most likely part of an acetabulum or glenoid fossa. Compared to the acetabulum of A 27745, which was found in the same area, they could be part of the acetabulum of a pubis.

The remaining material consists of part of an epipodial, the proximal end of a rib, a small caudal vertebrae and part of a propodial. Based on age, location, colour and the glue used in reconstruction I believe this latter piece to be part of the left femur of A 27745 (Fig. 47).

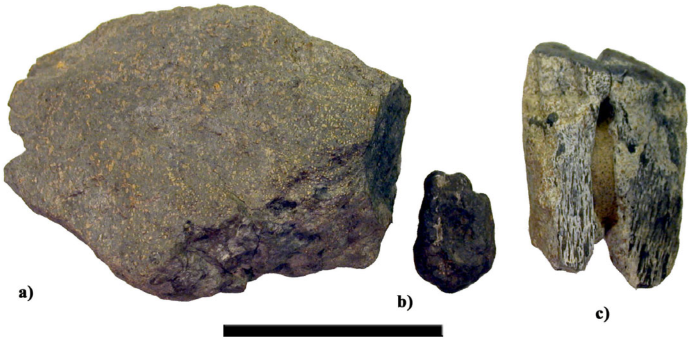


Fig. 47: A possible acetabulum or glenoid fossa from a plesiosaur (a), together with (b) a small caudal vertebra and (c) what looks like a piece of the left femur of A 27745 (PMO: A 35756).

Nr. A 35757: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
54 rib fragments.

Nr. A 35758: Location: Sassenfjorden, Spitsbergen. Age: Jurassic.
29 bone fragments, possibly chevron bones or pieces from the autopodial region.

Nr. A 35759: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
14 bone fragments of unknown origin.

Nr. A 35760: Location Sassenfjorden Spitsbergen. Age: Jurassic?
14 bone fragments of unknown origin.

Nr. A 35761: Location: Sassenfjorden Spitsbergen. Age: Jurassic?
Stated to be a posterior cervical vertebra, which is partly confirmed by the distance between the ventral nutritive foramina and the position of the rib facets on the centrum. However, nutritive foramina are also similarly separated in caudals but since the ventral side is partly destroyed it is difficult to confirm any possible chevron facets. Based on the position of the rib facets which are relatively high on the centrum I would ascribe this vertebrae to be an anterior caudal. On cervicals the rib facets are usually quite low or ventrally situated.

Nr. A 35762 – 773: Location: Spitsbergen, Sassenfjorden. Age: Jurassic?
Caudal vertebrae. Vertebra 35770 was missing from the material.

Nr. A 35774: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?

24 vertebrae bone fragments.

Nr. A 35775: Location: Sassenfjorden, Section 6 Spitsbergen. Age: Jurassic?
13 bone fragments of which three can be identified as being ribs

Nr. A 35776: Location: Sassenfjorden, Section 6 Spitsbergen. Age: Jurassic?
An almost complete ilium measuring 18.5 cm in length. The head is scarred as a result of muscle attachment (see Fig. 50).

Nr. A 35777: Location: Sassenfjorden Spitsbergen. Age: Jurassic?
25 fragments of mostly phalanges and possibly a few pieces of small epipodial elements.

Nr. A 35778: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
35 bone fragments of unknown origin.

Nr. A 35779: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
52 bone fragments. Two of the pieces can be identified as being a neural spine and a possible chevron bone.

Nr. A 35780: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
25 bone fragments possibly from the autopodial region.
A note with the number 1 was also found in the box.

Nr. A 35777-35780: Very fragmentary pieces of unknown origin. Location and age not mentioned.

Nr. A 35781: Location: Sassenfjorden, Spitsbergen. Age: Jurassic?
22 bone fragments. Most likely plesiosaur ribs.

Nr. A 35782: Location; Sassenfjorden, Spitsbergen. Age: Jurassic?
24 bone fragments of uncertain origin.

In addition to the many centra, ribs and phalanges that were found, a few pieces of some significance are worth mentioning. These are plesiosaurian teeth, a large ichthyosaurian humerus, an almost complete ilium, and a propodial together with a more or less complete mesopodium.

Teeth (Fig. 48)

There are a total of 5 teeth, all situated in a relatively small piece of rock. One is clearly visible and displays a 3.4 cm ridged and slender tooth most likely belonging to a longnecked plesiosaur. The other teeth are partially covered by matrix, but it seems that only a small part of the tooth tip is present. A tooth imprint measuring 3 cm, is also preserved.

A bone fragment is also present in the rock matrix, which could be part of the animals' jaw or some other indefinable skull piece.

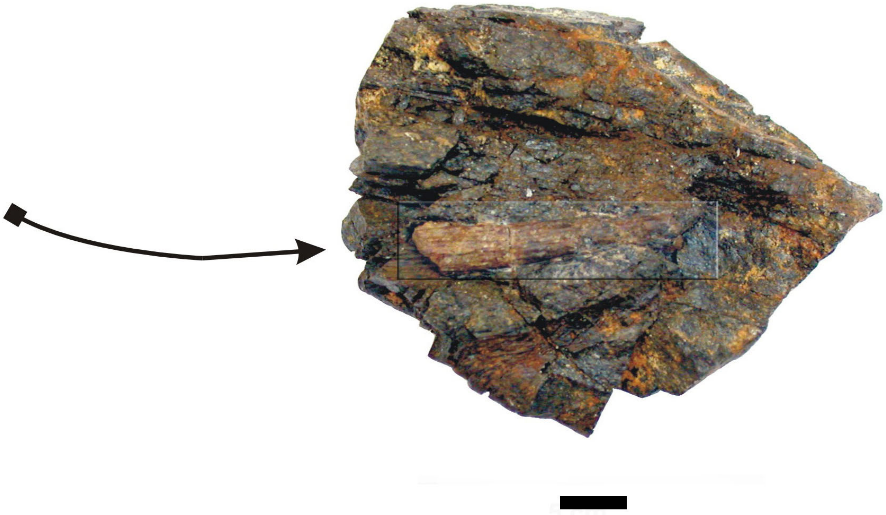


Fig. 48: The first teeth from a plesiosaur found on Svalbard. Only one of a total of six teeth is visible in addition to an imprint seen just below. The other teeth are covered by matrix. The remains of the largest tooth measures 3 cm in length (PMO: A 35696). Diameter of the coin is 1.8 cm. Scale bar = 1 cm.

Humerus (Fig. 49)

The ichthyosaurian humerus was first thought to be a very large plesiosaur epipodial element, possibly a primitive ulna. However, having had the age of the specimen confirmed as being early Triassic by the collector Ø. Lauritzen (Lauritzen, pers. comm. 2003) R. Forrest and Ryosuke Motani (pers. comm. 2003) were able to confirm that it is in fact a humerus of a large ichthyosaur, possibly *Shastosaurus*.

The bone measures 18 cm in length and 17 cm in width, indicating that the animal was large and at least 10 m long.

Fig. 49: Large ichthyosaurian humerus found together with the plesiosaurian material (PMO: 132.128 & 132.130). Scale bar = 10 cm.

Ilium (Fig. 50)

A wel- preserved ilium with only a small part in the middle missing. It measures 18.5 cm in length and probably belonged to a primitive plesiosaur. Compared to the ilium of the specimen under revision it is a much smaller and delicate bone with a less developed distal end.

Fig. 50: Almost complete plesiosaur ilium (PMO: A 35776). Scale bar = 5 cm.

Summary and conclusions

The plesiosaur specimen PMO A 27745 previously assigned to the genus *Tricleidus* and given the specific name *svalbardensis* is found to be part of the clade Cryptocleidoidea and is tentatively assigned to the Tricleidia as defined by O'Keefe in 2001. Within this latter group the specimen seems to fall somewhere in between the genus *Tricleidus* and the short necked Polycotylids and could therefore be an intermediate between long-necked and short-necked plesiosaurs. Bear in mind however that the Polycotylidae, with secondarily derived short necks, are a part of the Plesiosauroidea.

The specimen was found partly embedded in a dark grey shale-stone at the entrance to Sassenfjorden north of Longyearbyen. Stratigraphically this is in the Agardhfjellet Formation and most likely in the Slottsmøya Member.

The fossil was found to be Upper Jurassic in age, more precisely from the Volgian.

Its most salient features are:

- A relatively long ischium.

- The straight posterior ischial border.

- A triangular shaped fibula.

- A small convex area on the anterior distal end of the femur.

Most of the material comprising the miscellaneous marine material from Svalbard is very fragmentary and consists mostly of vertebrae, phalanges and smaller pieces from the girdles. Some interesting pieces however are worth mentioning:

- The first ever teeth from a plesiosaur found on Svalbard.

- One complete femur possibly belonging to a *Leptocleidus*.

- Two humeri of which only the distal parts are preserved. They most likely belong to a *Cryptoclidus*.
- An almost complete plesiosaur ilium.
- One large humerus belonging to an ichthyosaur.

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Appendix 1

Parsimony analysis of Table 2-data matrix with PAST version 1.20

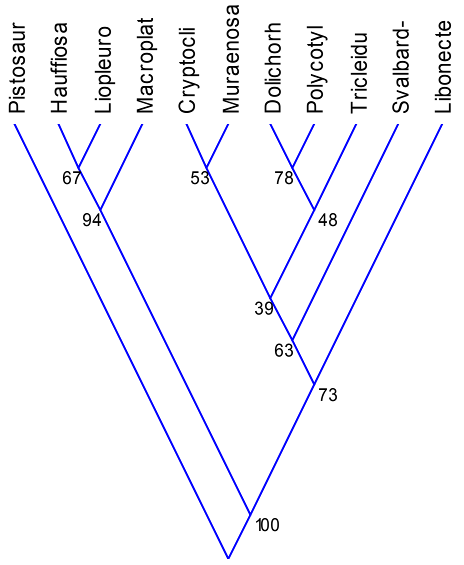
11 taxa, 166 characters.

Analysis settings:

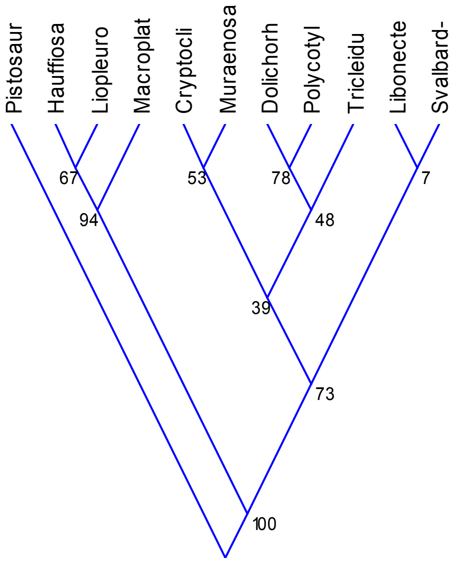
Fitch (unordered) characters, branch-and-bound search.
1000 bootstrap replicates.

Results:

7 most parsimonious trees (length 192), with bootstrap values, consistency index (CI) and retention index (RI):



CI=0.76, RI=0.96



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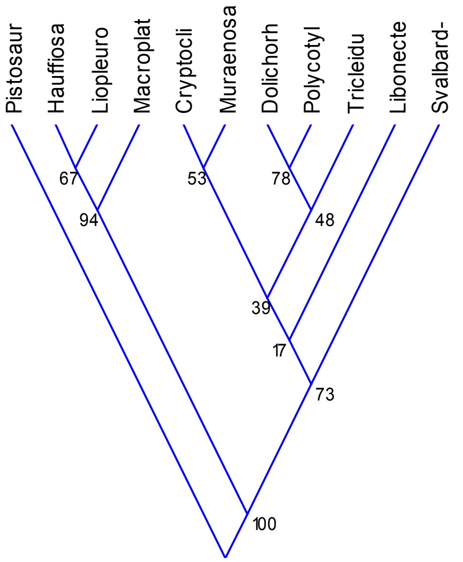

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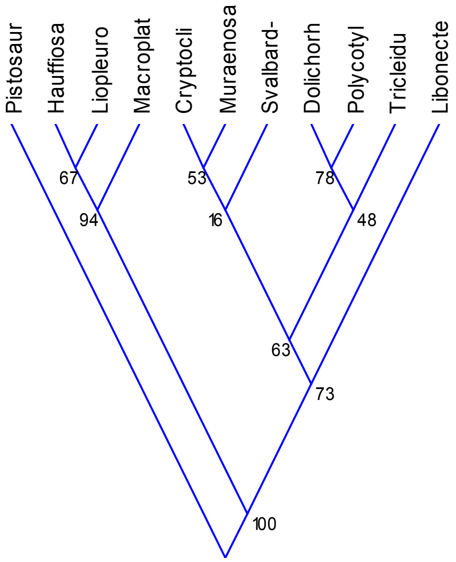

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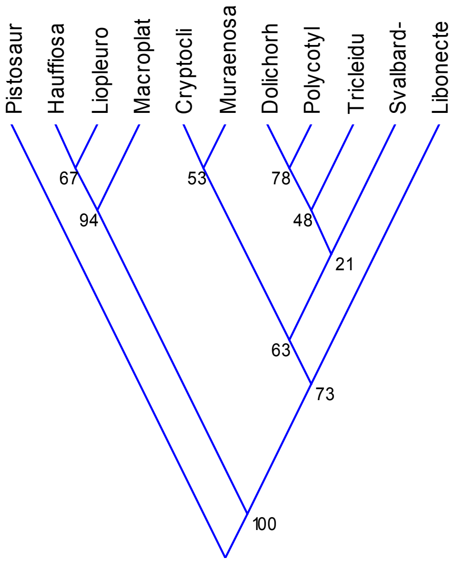

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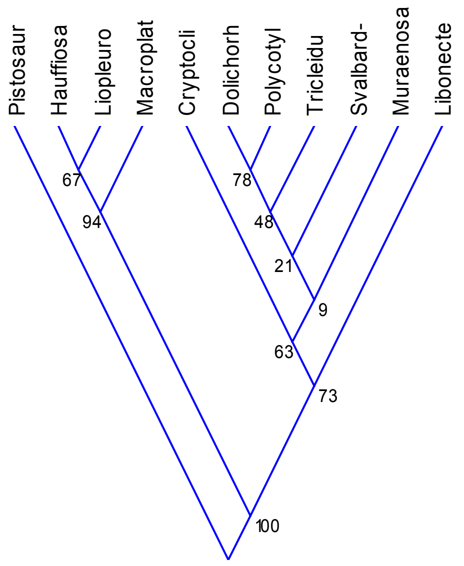

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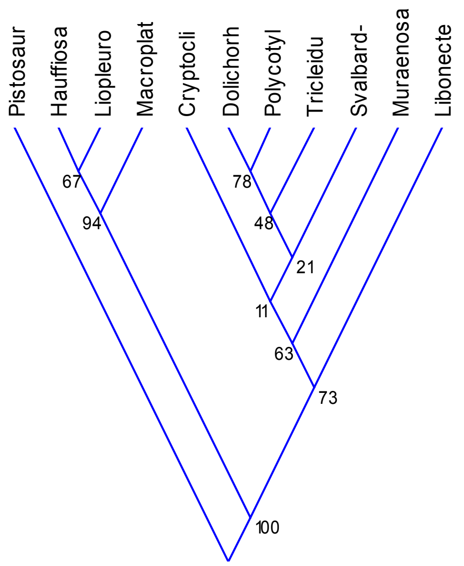
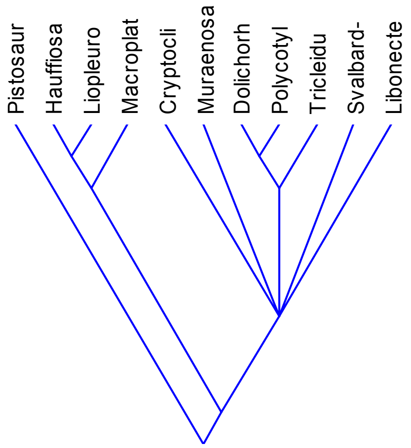
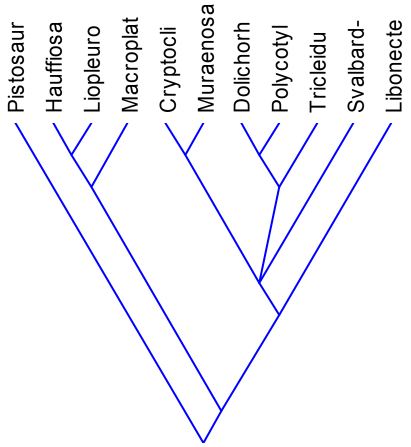


CI=0.77, RI=0.96

Strict consensus tree:

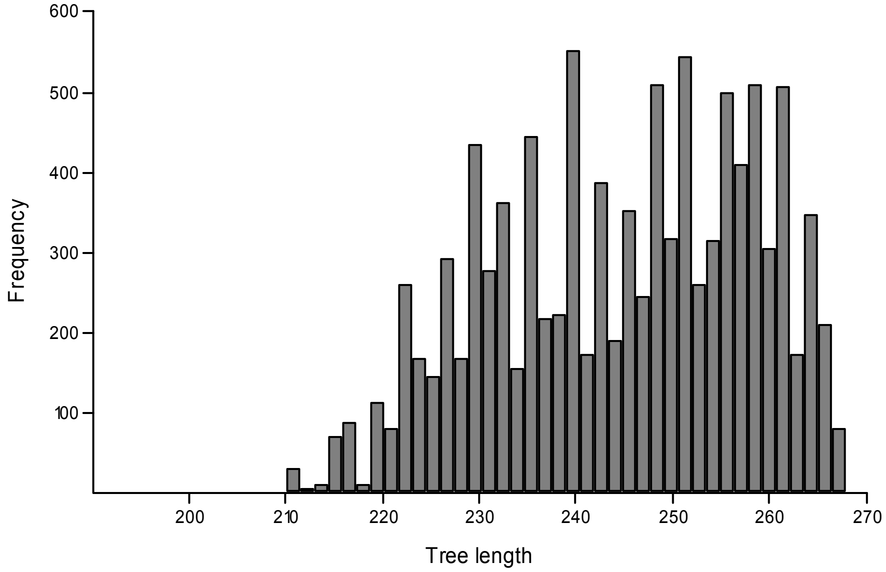


50% majority rule consensus tree:



All clades retained in strict consensus tree have Bremer support of 1 (low support).

Distribution of tree lengths:



Appendix 2

Character matrix for the cladistic analysis of the current specimen

Character	*Character description*	*States/coding*
1	Relative skull length	Primitive (0), large (1), small (2)
2	Relative neck length	Primitive (0), long (1), short (2)
*3**	Relative length of ischium/pubis	Subequal (0), ischium longer (1), pubis longer (2)
4	Relative length of ischium/pubis	Subequal (0), coracoid longer (1)
5	Relative length of humerus/femur	Subequal (0), humerus longer (1), femur longer (2)
6	Preorbital and postorbital skull length	Subequal (0), preorbital longer (1), shorter (2)
7	Fin aspect ratio	High (0), low (1)
8	Elongate rostrum	Absent (0), premaxilla only (1), very long incl. Maxilla (2), elongate and hoop-like/unconstr. (3)
9	Constricted snout	Unconstricted (0), constr. at maxilla/premaxilla suture (1), second constriction in maxilla (3)
10	Temporal emargination	Present (0), absent (1)
11	Dorso-medial process of premaxilla	Contacts frontal (0), cont. parietal at pineal foramen (1), cont. anterior extens. of parietale (2)
12	Premaxilla/external naris contact	Present (0), absent (1)
13	Dorsal median foramen	Absent (0), present (1)
14	Frontals paired/fused in adults	Paired (0), fused (1)
15	Parietals paired/fused in adult	Paired (0), fused posteriorly (1), fused (2)
16	Frontal with/without distinct postero-lateral process	Without process (0), with proc. (1)
17	Postorbital bar	Both po and pof have orbital contact (0), frontal/po suture excludes pof from orbit margin (1)
18	Frontal enters margin of temporal fenestra	Does not (0), does narrowly (1)
19	Frontal contacts external naris	Does contact (0), does not contact (1)
20	Pineal foramen location	Middle of parietal (0), anterior (1)
21	Pineal foramen bordered anteriorly by frontals on dorsal skull surface	Not bordered by frontal (0), bordered (1)
22	Prefrontal present/absent	Present (0), absent (1)
23	Accessory fenestra above orbits	Absent (0), present (1)
24	Frontal process projects into orbit	Absent (0), present (1)
25	Parietal skull table	Relatively broad (0), constricted (1), sagittal crest (2)
26	Squamosal produces long, thin process covering quadrate laterally	No medial process (0), medial process and socket-like squamosal (1)
27	Squamosal dorsal process	No suture (0), meet in arch at midline (1)
28	Squamosal/postorbital contact	Contact (0), no contact (1)
29	Jugal/squamosal contact	No contact (0), contact (1)
30	Jugal extends anteriorly along ventral orbit margin	Anterior margin (0), middle of orbit (1), restricyed to posterior margin (2)
31	Jugal contacts orbit margin	Contacts orbit (0), excluded by po/m contact (1)
32	Jugal/prefrontal suture anterior to orbit	Absent (0), present (1)
33	Jugal forms narrow bar between orbit and temporal emargination	Does not (0), does(1)

34	Quadratojugal	Present (0), absent (1)
35	Nasal	Not reduced (0), reduced (1), absent (2)
36	Location of nasal relative to external naris	Behind external naris (0), in front of external naris (1)
37	Distinct grooves anterior to external naris	Absent (0), present (1)
38	Nasal enters margin of external naris	Do enter (0), do not enter (1)
39	Prefrontal contacts margin of external naris	No contact (0), contact (1)
40	Prefrontal and postfrontal exclude frontal from dorsal orbit margin	Frontal excluded (0), frontal enters margin (1)
41	Maxilla/squamosal contact	No contact (0), contact (1), expanded posterior flange (2)
42	Exoccipital participates in formation of occipital condyle	Do not participate (0), do participate (1)
43	Occipital condyle morpholgy	Hemispherical with groove (0), short with no groove (1)
44	Paraoccipital process/formation of posttemporal fossa margin	No process/occiput plate-like (0), rod-shaped process (1)
45	Distinct squamosal notch for articulation of paraoccipital process	Without notch (0), with notch (1)
46	Paraoccipital process morphology	Gracile (0), robust (1)
47	Paraoccipita process articulation	Squamosal exclusively (0), quadrate excl. (1), both squamosal and quadrate (2)
48	Ventral extent of paraoccipital process	Does not extend ventral to occipital condyle (0), extends past condyle (1)
49	Nature of paraoccipital process/quadrate pterygoid flange contact	No contact (0), contact at lateral articul. only (1), long contact along bodies of process (2)
50	Quadrate flange of pterygoid/quadrate articulation	Quadrate only (0), quadrate and squamosal (1)
51	Quadrate produces distinct process for articulation with pterygoid flange	Process absent (0), present (1)
52	Dorsal wing of epipterygoid	Broad/columnar (0), reduced (1)
53	Epipterygoid dorsal process contacts parietal	Contact (0), no contact (1)
54	Quadrate embayed/dished-shaped anteriorly	Massive quadrate (0), dished anteriorly (1)
55	Posterior bulb formed by squamosals	Absent (0), present (1)
56	Supraoccipital morpholgy	Round (0), median process (1)
57	Shape of the quadrate pterygoid flange	Curved with raised lat. margin (0), straight and narrowing (1), sigmoid with rolled lat. marg. (2)
58	Squared lappet of pterygoid underlies quadrate pterygoid flange	No squared lappet (0), squared lappet (1)
59	Supraoccipital depth/ sigmoid suture	Shallow (0), deep antero-posteriorly/sigmoid suture with exoccipital and prootic (1)
60	Anterior interpterygoid vacuity	Absent (0), slit-like (1), broad with round ends (2)
61	Posterior interpterygoid vacuity	Absent (0), present (1)
62	Pterygoids meet posterior to posterior interpterygoid vacuity	Pterugoids do not meet (0), pterygoids meet (1), meet but are covered by parasphen. proc. (2)
63	Pterygoids meet beteween anterior and posterior interpterygoid vacuities	Do not meet between vacuities (0), do meet (1)
64	Basioccipital exposed posteroir to posterior pterygoid suture	Exposed (0), not exposed (1)
65	Ectopte. reaches medially to lateral margin of posterior interpt. vacuities	Does not (0), does (1)
66	Columnar ectoptrygoid contacts postorbital bar	No contact (0), contact (1)
67	Dished pterygoids	Absent (0), present (1)
68	Posterior pterygoid/parasphenoid contact	Absent (0), present (1)
69	Ectopter. and pter. form lateral flanges ventro-lateral to post. ptery. vacuity	Not form flanges (0), flanges (1), meet in short dished contact at midline (2), broad cont. (3)
70	Parasphenoid morpholgy	Long, tapering anteriorly (0), short and blunt (1)
71	Parasphenoid keel	Not keeled (0), sharp keel (1), keeled anteriorly (2)

72	Parasphenoid exposure anterior to posterior interptrygoid vacuities	Anterior parasphenoid not exposed on palate surface (0), exposed via extension of posterior interpterygoid vacuities (1), exposed with lateral pterygoid sutures (2)
73	Psession of cristae ventrolaterales	Present (0), absent (1)
74	Parasphenoid/basioccipital contact on midline	Absent (0), present (1)
75	Possession of basal articulation	Present (0), absent (1)
76	Basioccipital tubers reduced	Not reduced (0), reduced /tuber facets confluent with basisphenoid articulation (1)
77	Jugal has small exposure on palate surface	No exposure (0), exposure (1)
78	Lateral palatal fenestration bordered by palatine and pterygoid	Absent (0), present (1)
79	Palatine/internal naris	Palatine enters internal naris border (0), excluded by vomer/maxilla contact (1)
80	Palatines approachclosely or meet at midline	Do not meet (0), close approach or meet at midline (1)
81	Premaxilla/anteriorborder of internal naris	Premaxilla enters anterior border (0), is excluded by vomer/maxilla contact (1)
82	Sub-orbital fenestration	Absent (0), present (1)
83	Vomers extend far posterior to internal nares on midline	Do not (0), extend posterior and meet pterygoids in wide interdigitating suture (1)
84	Prominent pterygoid flange/ectopterygoid boss	Absent (0), present (1)
85	Ectopterygoid boss has wide contact with jugal/squamosal	Contact absent (0), contacts jugal (1)
86	Bowed maxilla	Absent (0), present (1)
87	Meckelian canal open anteriorly	Not open (0), open (1)
88	Vental mandibular ridge/pedestal-like symphysis	No ridge (0), ridge (1)
89	Mandibular symphysis	Short (0), somewhat enforced (1), scooplike (2), long (3)
90	Splenial participates in symphysis	Does not participate (0), does participate (1), angulars extend past symphysis (2)
91	Lingual mandibular fenestra	Absent (0), present (1)
92	Morphology of dentary/angular-surangular suture	Angular projects forward of surangular in lateral view (0), surangularanterior process (1)
93	Coronoid	Present (0), absent (1)
94	Long lingual coronoid process	Absent (0), present (1)
95	Coronoid exposed on lateral jaw surface	No exposure (0), exposure (1)
96	Prearticular	Present (0), absent (1)
97	Prearticular shelf/groove	Absent (0), present (1)
98	Jaw articulation in relation to tooth row	Above or at colinnear with tooth row (0), lower that tooth row (1)
99	Diastema at maxilla/premaxilla suture	Absent (0), present (1)
100	First tooth after diastema	Large (0), reduced (1)
101	Premaxilla and dentary fangs	Absent (0), present (1)
102	One or two caniniform teeth on maxilla	Present (1), absent (0)
103	Tooth form	Gracile, small root, narrow, no wear (0), robust, large root, wear (1), very small/needle-like (2)
104	Teeth round or with reinforced planar face	Round (0), planar face (1)
105	Longitudinal striations on teeth	Striations all around (0), lingual only (1), none (2)
106	Number of premaxillary teeth	5 (0), 6 (1), 7(2), greater than 7 (3)
107	Maxillary teeth	Less than twenty (0), twenty to thirty (1), many more than thirty (2)
108	Number of axis rib heads	2 (0), 1(1)
109	Articulation of axis rib	Broad articulation with atlas centrum and/or other elements (0), head confined to axis centrum (1)

110	Atlas/axis morphology	No lateral exposure of atlas centrum on cup face (0), lat. exp. (1), no lat. exp. but atlas & axis intercentra exclude atlas centrum ventrally (2)
111	Number of cervical vertebrae	Primitive (0), increased (1), reduced (2), greater than 50 (3)
112	Proportions of cervical centra	Length equal to height (0), length greater than height (1), length less than height (2)
113	Distinct change in zygapophyseal angle along cervical column	No change in angle (0), change (1)
114	Ventral keel on cervical vertebrae	Absent (0), present (1)
115	Lateral ridge on anterior cervical vertebrae in adults	Absent (0), present (1)
116	Binocular shaped anterior cervical centra	Absent (0), present (1)
117	Number of cervical rib heads	2 (0), 1 (1)
118	Ventral foramina in cervical vertebrae	Absent (0), present (1)
119	Foramina subcentralia reduced and lateral	Medial and large (0), lateral and reduced (1)
120	Width of cervical zygapophysis	Wider than centrum (0), subequal with centrum (1), more narrow than centrum (2)
121	Posterior articulation for succeeding neural spine, cervical vertebrae	Absent (0), present (1)
122	Cervical rib articu. greatly elongate/cervical ribs expanded and blade-like	Circular/subcircular (0), elongate (1)
123	Anterior process of cervical ribs	Present (0), absent (1)
124	Anterior neural flange on cervical neural spines	Absent (0), present (1)
125	Neural spines, cervical vertebrae	Angled backward (0), not angled (1)
*126**	Distal end of transverse processes, dorsal vertebrae	No diameter increase (0), thickened (1)
*127**	Dorsal neural arch height	Subequal to centrum height (0), shorter than centrum height (1)
128	Zygosphene/zygantrum articulation	Present (0), absent (1)
*129**	Height of neural spines, dorsal vertebrae	Low (0), low and rugose (1), high (2)
*130**	Lateral compr. of neural spines, dorsal and cervical vertebrae	Not compressed (0), compressed and blade-like (1)
131	Interclavicle posterior process	Present (0), absent (1)
132	Dorsal process of scapula	Tapers to blunt tip (0), ventrally expanded posteriorly
133	Presence of clavicles and interclavicles	Present (0), interclavicle absent (1), both absent (2)
134	Clavicle median symphysis	Symphysis (0), seperated by interclavicle (1) meet only behind notch (2)
135	Scapulae meet in anterior median symphysis	Separated by clav./interclav. (0), meet medially but leave notch for dermal elements (1), meet in long symphysis with no notch (2)
136	Anterior intrascapular fenestra	Absent (0), present (1)
137	Longitudinal pectoral bar	Absent (0), formed by clavicle & coracoid (1), formed by scapulae & coracoid (2)
138	Supracoracoid foramen/notch	Present (0), absent (1)
139	Coracoid shape	Rounded contours/not plate-like (0), expanded median symphysis (1)
140	Median coracoid perforations	Absent (0), present (1)
141	Posterior coracoid extension with deep median embayment	Absent (0), present (1)
142	Postero-lateral coracoid wings	Absent (0), present (1)
*143**	Contact between ilium and pubis	Present (0), absent (1)
*144**	Pubis ventral (medial) margin	Conve? (1), concave (0)
*145**	Large ventral pubo-ischiatic plate	Absent (0), present (1)
*146**	Median pelvic bar	Absent (0), present (1)
*147**	Thyroid fenestra closed or open i nadult	Closed (0), open (1)
*148**	Obturator foramen	Absent (0), present (1)
*149**	Iliac blade	Well-developed (0), reduced (1)

150	Angled humerus	Absent (1), present (0)
*151**	Expanded distal propodials with dorsal trochanter/tuberosity	Absent (0), present (1)
152	Distal end of humerus has two distinct planes in adult	Absent (0), present (1)
153	Distinct facet on distal humerus for supernumery ossification	Absent (0), present (1)
*154**	Gracile or massive propodials	Gracile/constricted (0), massive (1)
*155**	Relative elongation of propodials	Not elongate (0), elongate with narrow distal head (1)
156	Deltopectoral crest	Present (0), absent (1)
157	Ulnar shape	narrow (0), or broad distally (1)
158	Distinctly lunate ulna	Absent (0), present (1)
*159**	Internal trochanter	Well-developed (0), reduced (1)
*160**	Inter-trochanteric fossa	Deep (0), distinct but reduced (1), rudimentary or absent (2)
*161**	Epipodial morphology	Longer than broad (0), equal or broader than long (1)
162	Supernumery ossifications, forelimb	None (0), epipodial row/pisiform (1), propodial (2), both (3)
*163**	Fifth metapodial	In line with rest of metapodial row (0), shifted into distal mesopodial row (1)
*164**	Hyperphalangy	No increase (2-3-4-5-3) (0), hyperphalangy present (1)
*165**	Interlocking distal phalanges anterior to fifth phalangeal row	Absent (0), present (1)
166	Median gastral rib element	Always one lateral process (0), may have two lateral processes (1)

Matrix of character scoring

The first taxa is the outgroup. Inapplicable/unknown characters are coded ? Ancestral condition is generally coded "0"

Taxon

Character	*Pistosaurus*	*Cryptoclidus*	*Dolichorhynchops*	*Hauffiosaurus*	*Libonectes*	*Liopleurodon*	*Macroplata*	*Muraenosaurus*	*Polycotylus*	*Tricleidus*	*Svalbard-specimen*
1	0	2	1	1	2	1	1	2	?	2	?
2	0	0	2	1	2	1	1	2	?	2	?
*3**	?	0	1	2	?	1	2	0	1	?	1
4	1	1	1	1	0	1	1	1	1	1	?
5	?	2	0	0	?	1	0	2	0	0	?
6	0	0	1	1	0	1	1	0	?	2	?
7	?	1	1	0	0	1	0	1	1	1	?
8	1	0	2	2	0	2	2	0	?	0	?
9	0	0	0	1	0	2	0	0	?	0	?
10	0	0	0	0	0	0	0	0	?	0	?
11	0	0	1	?	2	1	?	0	?	0	?
12	?	0	0	?	0	1	1	0	?	0	?
13	0	0	0	?	0	0	0	0	?	0	?
14	0	0	?	?	?	?	?	0	?	0	?
15	1	?	?	?	?	?	0	?	?	?	?
16	1	0	0	?	?	0	0	0	?	?	?
17	0	0	0	?	1	0	?	0	?	?	?
18	1	0	0	?	?	0	?	0	?	0	?
19	?	1	?	?	?	1	0	0	?	?	?
20	1	1	1	?	1	1	1	1	?	1	?
21	0	1	0	?	1	0	0	1	?	0	?
22	0	0	0	?	0	0	0	?	?	0	?
23	0	0	0	?	0	0	0	0	?	0	?
24	0	0	1	?	?	0	0	0	?	0	?
25	2	2	2	?	2	2	2	2	?	2	?
26	0	1	1	?	1	0	0	1	?	1	?
27	1	1	1	?	?	1	1	1	?	1	?
28	0	0	0	?	1	0	?	0	?	?	?
29	1	1	1	1	1	1	1	1	?	1	?
30	1	2	2	?	2	0	0	2	?	2	?
31	0	0	0	?	0	0	0	0	?	0	?
32	0	0	0	?	0	1	1	0	?	0	?
33	0	1	0	0	0	0	0	?	?	1	?
34	?	1	1	1	1	1	1	?	?	1	?
35	1	2	2	?	2	1	1	?	?	2	?

36	0	?	?	?	?	0	0	?	?	?	?
37	0	0	0	?	0	0	1	0	?	0	?
38	1	?	?	?	?	0	0	?	?	?	?
39	0	1	1	?	1	0	0	?	?	?	?
40	1	1	1	?	1	0	?	1	?	1	?
41	0	0	2	0	?	0	?	?	?	0	?
42	?	1	0	?	0	0	0	0	?	0	?
43	?	1	0	1	0	1	1	1	?	0	?
44	1	1	1	?	1	1	1	1	?	1	?
45	?	?	1	?	1	0	1	?	?	1	?
46	?	0	0	?	0	1	0	0	?	0	?
47	?	1	1	?	2	0	0	?	?	1	?
48	?	0	1	?	0	0	0	0	?	1	?
49	?	0	1	?	1	1	0	?	?	0	?
50	?	?	0	0	1	1	0	?	?	0	?
51	?	0	0	0	1	0	0	?	?	0	?
52	1	?	0	?	1	0	?	?	?	?	?
53	?	?	0	?	?	1	0	?	?	?	?
54	0	1	1	1	0	1	?	1	?	1	?
55	0	0	0	?	0	1	1	0	?	0	?
56	?	1	1	?	1	?	?	?	?	?	?
57	?	1	1	?	1	0	?	1	?	?	?
58	?	1	1	2	1	2	1	1	?	1	?
59	0	0	0	0	1	0	0	0	?	0	?
60	0	2	2	0	0	1	0	2	?	2	?
61	1	1	1	1	1	1	1	1	?	1	?
62	0	0	2	1	2	1	0	0	?	0	?
63	?	0	0	1	0	1	1	0	?	0	?
64	?	?	0	0	0	0	?	?	0	?	?
65	0	0	0	1	0	0	?	0	?	0	?
66	?	1	1	0	1	0	?	1	?	1	?
67	0	0	1	0	0	0	0	0	?	0	?
68	0	0	1	0	0	0	0	0	?	1	?
69	0	0	0	2	0	3	0	0	?	0	?
70	?	1	1	0	0	0	0	1	?	1	?
71	1	0	0	2	1	2	2	0	?	0	?
72	0	2	2	2	2	2	2	1	?	2	?
73	?	1	1	?	1	?	0	1	1	1	?
74	0	0	1	0	?	0	0	0	1	1	?
75	?	0	0	?	0	?	?	0	?	0	?
76	?	0	1	0	0	0	0	0	?	1	?
77	0	0	0	0	0	0	?	0	?	?	?
78	0	0	0	0	?	1	?	0	?	?	?
79	0	0	0	0	0	1	0	1	?	?	?
80	0	0	0	0	0	1	0	0	?	0	?
81	0	?	1	1	1	1	1	0	?	0	?
82	0	0	0	0	0	1	?	0	?	?	?
83	0	0	0	1	1	1	1	1	?	0	?

84	1	0	0	1	0	1	0	0	?	0	?
85	?	?	?	1	?	1	?	?	?	?	?
86	0	0	0	0	?	0	0	0	?	0	?
87	?	1	?	?	1	1	0	1	?	1	?
88	?	0	0	0	0	0	0	0	0	0	?
89	1	0	3	3	1	2	3	0	?	0	?
90	?	0	2	1	0	1	1	0	?	0	?
91	?	0	0	0	1	0	?	0	0	0	?
92	?	0	0	?	0	1	1	0	?	0	?
93	?	0	0	?	`0	0	?	0	0	0	?
94	?	0	0	?	0	1	?	0	0	0	?
95	?	1	1	?	0	0	?	1	1	?	?
96	?	0	0	?	0	0	0	0	0	0	?
97	?	1	1	0	0	0	0	1	1	1	?
98	?	0	1	0	1	0	0	0	1	1	?
99	0	0	0	1	0	1	?	0	?	0	?
100	?	?	?	1	?	1	?	?	?	?	?
101	1	0	0	0	0	0	0	0	?	0	?
102	0	0	0	0	1	0	0	0	?	0	?
103	?	0	0	0	0	1	0	0	1	0	?
104	0	0	0	0	0	0	0	0	0	0	?
105	?	0	?	?	?	1	0	0	?	0	?
106	0	1	0	2	0	0	?	0	?	0	?
107	0	0	0	1	0	1	1	0	?	?	?
108	?	1	1	?	1	?	0	1	1	1	?
109	?	0	1	?	?	?	?	0	1	?	?
110	?	1	2	?	0	?	0	1	2	1	?
111	0	0	2	0	3	2	0	1	2	0	?
112	0	0	2	0	1	2	0	1	2	0	?
113	0	1	1	0	1	0	?	0	0	1	?
114	0	0	?	?	?	0	1	0	?	0	?
115	0	0	0	0	1	0	0	0	0	0	?
116	0	0	0	0	1	0	0	?	0	0	?
117	0	1	1	0	1	0	0	1	1	1	?
118	1	1	1	?	1	1	1	1	1	1	?
119	0	0	0	0	0	1	0	0	0	0	?
120	1	2	2	2	2	2	2	2	1	2	?
121	1	0	1	?	1	1	0	1	1	1	?
122	0	1	0	0	1	0	0	1	0	0	?
123	0	1	?	?	?	1	?	1	?	1	?
124	0	1	1	?	0	0	0	1	1	1	?
125	0,1	1	1	?	1	0	0	1	1	1	?
126*	1	1	1	?	?	1	?	1	1	1	1
127*	0	1	1	1	1	1	1	1	1	1	1
128	0	1	1	1	1	1	1	1	1	1	1
129*	1	2	2	?	?	2	0	2	2	2	2
130*	0	1	0	0	1	0	0	1	0	0	1
131	?	?	?	?	?	?	?	?	?	0	?

132	1	0	0	0	0	0	?	0	0	0	?
133	0	0	0	?	0	?	?	0	0	0	?
134	?	0	2	?	0	?	?	1	2	2	?
135	0	1	0	0	2	0	?	1	0	1	?
136	0	1	1	0	0	?	?	1	1	0	?
137	0	2	1	?	2	?	?	2	1	2	?
138	1	1	1	1	1	1	?	1	1	1	?
139	1	1	1	1	1	1	1	1	1	1	?
140	?	0	1	0	?	0	?	0	1	0	?
141	0	0	0	0	1	0	?	0	?	0	?
142	0	1	1	1	1	1	?	1	?	1	?
*143**	0	1	1	1	?	1	1	1	1	1	1
*144**	?	1	1	1	?	1	1	1	1	1	1
*145**	1	1	1	1	?	1	1	1	1	1	1
*146**	?	0	0	?	?	1	1	0	0	0	?
*147**	?	1	1	1	?	1	1	1	1	1	1
*148**	1	1	1	1	?	1	1	1	1	1	1
*149**	1	1	1	?	?	1	?	1	1	?	1
150	0	1	1	1	?	1	1	1	1	1	?
*151**	0	1	1	1	?	1	1	1	1	1	1
152	?	1	1	0	?	0	0	1	1	1	?
153	0	0	0	0	?	0	0	1	1	1	?
*154**	?	0	0	0	?	0	0	0	0	0	0
*155**	?	0	0	0	?	0	0	0	0	0	0
156	1	1	1	1	?	1	1	1	1	1	?
157	1	1	1	1	?	1	1	1	1	1	?
158	0	0	0	1	?	0	?	0	0	0	?
*159**	1	1	1	1	?	1	1	1	1	1	1
*160**	?	2	2	2	?	2	2	2	2	2	2
*161**	0	1	1	0	?	1	0	1	1	1	1
162	0	1	3	2	?	0	?	1	3	2	?
*163**	0	1	1	1	?	1	?	1	1	1	1
*164**	?	1	1	1	?	1	1	1	1	1	1
*165**	?	0	1	0	?	0	?	0	?	?	?
166	0	0	?	0	?	0	?	0	0	0	?

*Modified from O'Keefe (2001). * Characters that are applicable to the Svalbard-specimen.*