

FIRST COMPLETE FOREFIN OF THE ICHTHYOSAUR *GRIPPIA LONGIROSTRIS* FROM THE TRIASSIC OF SPITSBERGEN

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ABSTRACT. A new and nearly complete forefin has been discovered on a slab containing a specimen of the ichthyosaur *Grippia longirostris*. It is the only well-articulated forefin of this poorly known species, and is one of the most complete forefins known for the earliest ichthyosaurs from the Lower Triassic (Spathian). Contrary to the proposals of previous authors, the terminal phalanges did not support 'hooves'. The forefin resembles that of *Utatusaurus hataii*, another Spathian ichthyosaur, but is more derived, sharing four synapomorphies with *Mixosaurus cornalianus*, a slightly younger ichthyosaur from the Middle Triassic. Ichthyosaurian forefins, described from British Columbia and assigned to *Grippia*, lack at least two of these synapomorphies, and thus do not belong to this genus. A 'partial hindfin' of *Grippia*, also from British Columbia, is similar to the new forefin, casting doubt on its identification as a hindfin.

THE earliest ichthyosaur species are found in the Lower Triassic (Spathian; Callaway and Massare 1989), with *Grippia longirostris* from Spitsbergen (Wiman 1929, 1933) the first to have been described. Although additional Spathian genera, including *Chaohusaurus* Young and Dong, 1972, *Utatusaurus* Shikama, Kamei and Murata, 1978 and *Chensaurus* Mazin, Suteethorn, Buffetaut, Jaeger, and Helmcke-Ingavat, 1991 (= *Anhuisaurus* Chen, 1985, which was preoccupied), have subsequently been described, studies of early ichthyosaurs have been biased towards *G. longirostris* (Mazin 1981, 1982, 1986; Callaway 1989; Massare and Callaway 1990). However, this species is known only from fragmentary materials (Wiman 1933; Mazin 1981; Motani 1997a), which restricted previous authors to speculative reconstructions of the skull and the forefin. Because the understanding of basal forms is important to phylogenetic systematics, the incompleteness of *G. longirostris* has been a major impediment to the study of ichthyosaurian evolution.

Forefins are among the most informative structures for ichthyosaurian systematics (McGowan 1991), but are poorly known for *Grippia longirostris*. Wiman's (1929) first description of the species was based upon one specimen, a skull with mandibles, but lacking the snout. Preserved between the mandibular rami was an isolated, key-hole-shaped fin element, which Wiman (1929) believed was an ungual phalanx. A later expedition to Spitsbergen brought back additional specimens (Wiman 1933), but none was complete. The best preserved forefin material comprised the proximal part of a fin, complete as far as the level of the distal carpals (Wiman 1933, nodule 8); the other specimens were mainly composed of isolated elements. In the absence of a complete forelimb, Wiman (1933) maintained his earlier claim for ungual phalanges, arguing that *G. longirostris* retained a limb that was not as well adapted to the aquatic environment as the fins of later ichthyosaurs. Almost half a century later and without any additional material, Mazin (1981) published a reconstruction of the forelimb of *G. longirostris*, in which, following Wiman's (1929) supposition, he depicted a limb with a 'hoof' at the tip of each digit. Mazin (1986) further argued that *G. longirostris* was more primitive than *Utatusaurus hataii*, another Spathian ichthyosaur, based on the supposed possession of fewer adaptations in the forelimbs for an aquatic lifestyle.

A close examination of Wiman's (1933) nodule 8 revealed an undescribed humerus, lying beside the described one. The subject of the present paper is to report a new, well-articulated forefin discovered distal to this humerus.

MATERIALS AND METHODS

Abbreviations used for the institutions are: BMNH, Natural History Museum, London; PMU, Paleontologiska Museet, Uppsala Universitet, Uppsala, Sweden; and RTMP, Royal Tyrrell Museum of Paleontology, Drumheller, Alberta. The principal specimen described in this study, which Wiman (1933) called nodule 8, is now registered as PMU R472. Reference is also made to specimens of *Grippia longirostris*, including PMU R447, R449, R453, R456, and R474 (nodules 11, 5, 7, 15, and 9 respectively, of Wiman 1933). Localities for the specimens are summarized in Wiman (1933). Canadian specimens referred to *Grippia* (Brinkman *et al.* 1992) include RTMP 89.127.3, 89.127.12, and 89.128.5, and were also examined. Hindfins of *Mixosaurus cornalianus* (BMNH R5702) and *M. nordenskiöldii* (PMU R158) were used for comparison.

Only the middle part of PMU R472, where the new fin is located, was prepared, to preserve as much of this historically important specimen as possible. Preparation was performed under a binocular microscope, using an airscriber and mounted needles. Acid preparation, using 10 per cent. acetic acid, proved unsuccessful. A CT-scanner (General Electric Advantage Hispeed) was used to locate the hidden forefin before preparation. Scans with a thickness of 1 mm were made at 1 mm intervals, and used to reconstruct the two-dimensional image of the hidden forefin on a computer. This image was utilized during the preparation process, in order to reduce the risk of damaging the bones.

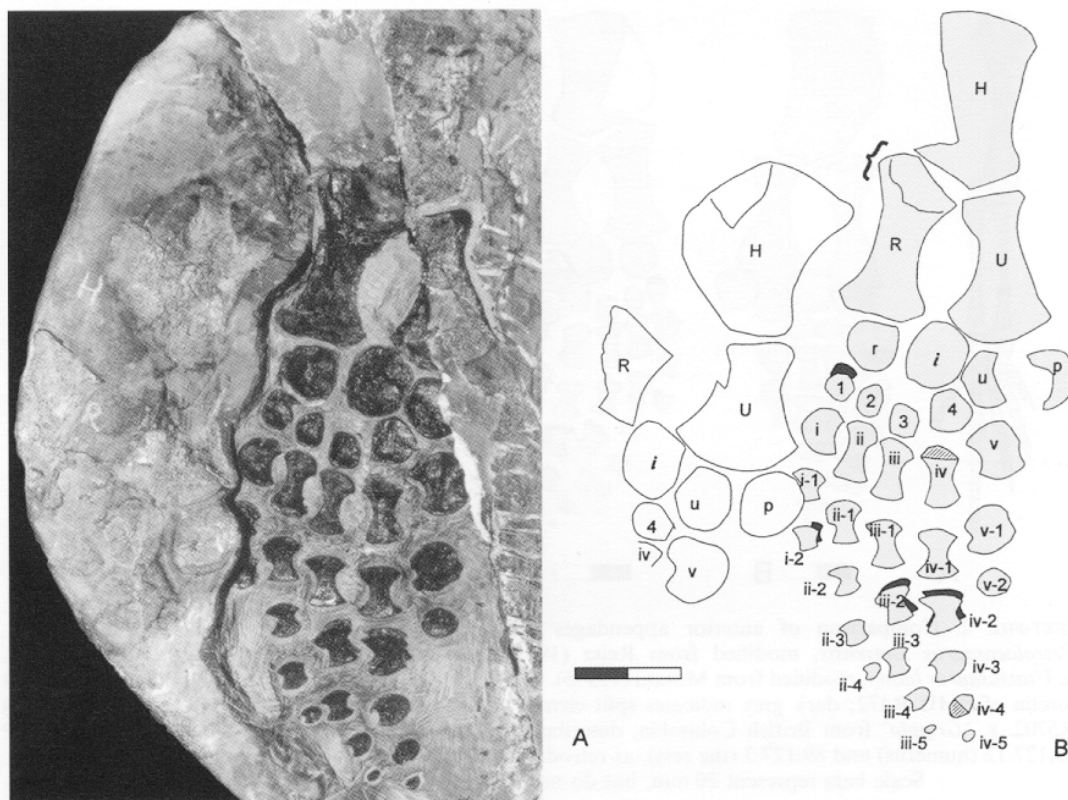
DESCRIPTION

A partial forefin, originally exposed along the circular edge of PMU R472 (Text-fig. 1), was figured by Wiman (1933, pl. 2, fig. 2). The bones are weathered, some badly, and the distal part of the fin is not preserved. The newly discovered forefin is located on the right side of this fin (Text-fig. 1). The humerus, radius, ulna, pisiform, and fifth metacarpal were also partially exposed, and suffered from the same weathering that damaged the other fin. The pisiform and the fifth metacarpal have been further damaged by a crack which runs through the middle of the slab (Text-fig. 1); this has been filled with plaster, probably during Wiman's study. The two forefins are nearly equal in size, and are associated with an articulated vertebral column and gastralia: thus they most probably belong to the same individual. The new forefin underlies the original one, with the gastralia lying in between them. Because the leading edges of both forefins are towards the left-hand side, the newly exposed one is interpreted as the right forefin, visible in the ventral view, whilst the other is the left forefin, exposed dorsally.

The description in the following paragraphs is based on the right forefin of PMU R472, unless otherwise stated. The forefin is pentadactyl, with a preserved phalangeal formula of 2-4-5-5-2. Distal elements may be missing from digits one, two and five, but, judging from the small size of the preserved bones, this probably does not amount to more than one element per digit. The fifth phalanges of digits three and four are so small that they are likely to be the terminal elements. If this is correct, then there were no more than five phalangeal ossifications in any of the digits. This does not preclude the possibility, however, of further unossified phalanges distal to the ossified elements. All manual elements are well spaced from each other, in contrast to the forefin of *Utatusaurus* where elements are more closely packed (Motani 1997b).

Both humeri of PMU R472 are badly eroded, and only their outlines can be observed. The humerus is as wide as it is long (Text-fig. 1), largely due to a well-developed articular facet for the radius, and a bony flange anterior to the shaft. Wiman (1933) figured two variations for the anterior flange on the humerus of *Grippia longirostris*: one is well developed (PMU R474), and the other is narrow (PMU R447 and R453). However, in PMU R447 and R453, bones are preserved as natural moulds, and the moulds of the humeri are incomplete anteriorly, suggesting that only the posterior parts of the anterior flanges are preserved. It is likely therefore that the narrow variation is an artefact of preservation, and that the well-developed flange represents the true morphology. Mazin's (1981) reconstruction seems to be based on PMU R447, without considering the incompleteness of the specimen, and is too slender.

The proximal part of the radius was exposed, and has been weathered away. However, its impression is preserved as a natural mould, enabling a reasonably accurate reconstruction of the outline. The radius is similar to that depicted by Wiman (1933) for PMU R449, although Wiman's figure is upside down (i.e. the distal end is at the top). There is a prominence proximally, anterior to the articular facet for the humerus (indicated by the 'bracket' symbol in Text-fig. 1), as in *Utatusaurus* (Motani 1997b), but this prominence is entirely absent from Mazin's (1981) reconstruction. The ulna is also similar to that of *Utatusaurus*, in that it

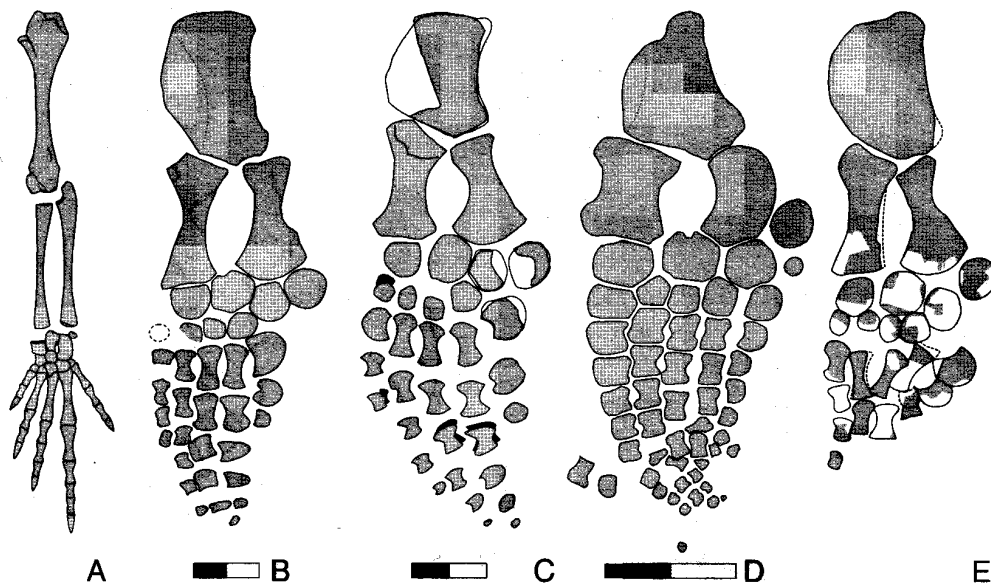


TEXT-FIG. 1. *Grippia longirostris* Wiman, 1929; PMU R472. A, a photograph of the area containing fin elements. B, identification of each element. The partial left forefin (white) was originally exposed, and was described by Wiman (1933). The newly discovered right forefin (light grey) is nearly complete. The left ulna seems to be broken, and is therefore shorter than the right one. Some elements have been split into dorsal and ventral plates, which have slipped with respect to each other (black). Hatched areas represent the indentation described in the text, and dashed lines are reconstructions of the missing parts. The bracket symbol indicates the antero-proximal prominence of the radius. Abbreviations: H, humerus; R, radius; U, ulna; *i*, intermedium; *p*, pisiform; *r*, radiale; *u*, ulnare; 1-4, distal carpals; *i*-*v*, metacarpals; *i*1-*v*2, phalanges. Scale bar represents 20 mm.

expands distally into a fan-shape (Text-fig. 2). The articular facet for the humerus is wider than that of the humerus for the ulna, again resembling *Utatusaurus*. The only ulna depicted by Wiman (1933) was the left one of PMU R472, which is 23 per cent. shorter than the newly exposed right one. The left ulna appears to be broken in the middle, and it seems likely that this accounts for the observed shortness. Both radius and ulna are more robust than those of *Utatusaurus* (Text-fig. 2).

There are four proximal carpals, all of similar size, although the intermedium is slightly larger than the others (Text-fig. 1). The outline of each element resembles the corresponding carpal of *Utatusaurus*; thus the pisiform is oval, the ulnare is somewhat pentagonal, but with a rounded distal margin, the intermedium is elongated, and the radiale has a straight proximal margin (Text-fig. 2B-C). Four distal carpals are present, and support the first four digits. The fourth one is the largest, but its diameter is only about half that of the proximal carpals (Text-fig. 1). Mazin (1986) claimed that the distal carpals were equal in size to the proximal carpals, but this is not evident in any of the specimens. All carpals are well separated from each other, indicating the osteological immaturity of the individual.

Two forms of metacarpals are recognizable: normal (second to fourth) and lunate (the first and fifth). The normal form resembles the cylindrical phalanges of other amniotes, but is flattened. The extremities of these



TEXT-FIG. 2. Comparison of anterior appendages of early ichthyosaurs and a primitive diapsid. A, *Petrolacosaurus kansensis*, modified from Reisz (1981); the elbow and wrist joints are disarticulated. B, *Utatusaurus hataii*, modified from Motani (1997b). C, *Grippia longirostris*, a composite of the right and left forefin of PMU R472; dark grey indicates split elements. D, *Mixosaurus cornalianus*, drawn from BMNH R5702. E, '*Grippia*' from British Columbia, described by Brinkman *et al.* (1992); a composite of RTMP 89.127.12 (humerus) and 89.127.3 (the rest), as retrodeformed according to the method of Motani (in press). Scale bars represent 20 mm, but do not apply to A and E (composite figures).

metacarpals are markedly expanded, indicating a degree of osteological maturity for this individual, although this is contrary to the immaturity indicated by the well-spaced carpals and phalanges. The lunate metacarpals occur along the anterior and posterior margins of the fin, with their concave sides facing inwards, towards the longitudinal axis. This type of metacarpal may derive from the normal type through the lack of perichondral ossification along the side of the bone facing the fin margin (Caldwell in press), resulting in the convexity of the bone on that side. The fifth metacarpal is located more proximally than in *U. hataii*, and, with further growth, it would have contacted the ulnare.

The phalanges are similar to the metacarpals in that there are normal and lunate forms, and the latter occur near the margins of the fin. However, in addition to these two forms, there is a third form that is entirely oval, and occurs toward the distal end of the fin (e.g. the fourth and fifth phalanges of the fourth digit; see Text-fig. 1B). This oval form, which entirely lacks perichondral ossification, is not known in *Utatusaurus* (Motani 1997b), but is commonly observed towards the tip of the fins in later ichthyosaurs (McGowan 1991, fig. 4). There are no traces of unguis phalanges, contrary to Wiman's (1929, 1933) supposition which was followed by Mazin (1981, 1986). Wiman's supposed unguis phalanx is probably a proximal phalanx, because some of these elements are also key-hole shaped (e.g. the second phalanx of the third digit; see Text-fig. 1B). The fourth phalanx of the fourth digit is deeply grooved antero-ventrally, and although this may appear to be mechanical damage caused during preparation, it is natural (Text-fig. 1B, hatched). The fourth metacarpal is also naturally indented at the proximal end (Text-fig. 1B, hatched).

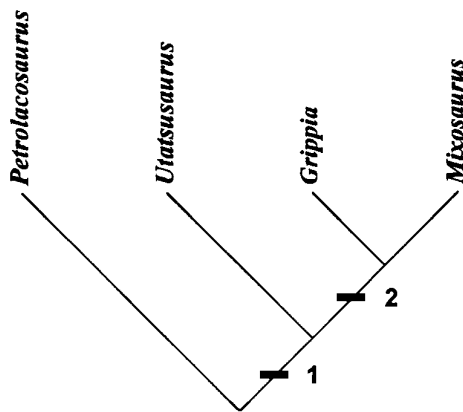
The second phalanges of digits one, three and four show an unusual feature: they have been split into dorsal and ventral plates, and the two plates have slipped with respect to each other (Text-fig. 1B, elements in black). The dorsal plates are located proximal to their ventral counterparts, and exhibit a spongy inner structure. These elements are constricted in the middle, but the margins along the constrictions are sharply edged, instead of being smooth and round as in the shafts of metacarpals. It is possible that the constricted parts of these phalanges were associated with little perichondral bone, leading to a weak bond between the dorsal and ventral

plates. A similar slippage occurs in the first distal carpal, suggesting that the ossification patterns may have been similar in this element. The dorsal and ventral plates are almost identically shaped in all displaced elements, and the spongy structure is not covered by a secondary ossification; therefore, the slippage was probably a post-mortem phenomenon. All four elements were probably dislocated by the same force, because the direction and magnitude of the slippage is nearly uniform among the elements. One possible explanation is that the deposition of the dead animal rotated the horizontal forefin in a parasagittal direction, pulling the dorsal connective tissues proximally while pushing the ventral ones distally, creating shearing stress inside the fin and splitting some elements along mechanically weak planes.

DISCUSSION

An important question concerns the osteological maturity of PMU R472. Johnson (1977) pointed out four forefin features that indicate osteological immaturity in the Upper Liassic ichthyosaur *Stenopterygius*: (1) humeral head incompletely ossified; (2) rough surface of the humeral shaft; (3) proximal elements not well packed; and (4) absence of notched elements on the leading-edge (only applicable to those species whose adults have notched elements). Features 1 and 2 are probably useful for *Grippia longirostris*, but not applicable to PMU R472 due to the poor preservation of the humeri. Feature 4 is not applicable to *G. longirostris*, because notched elements are absent from the leading edge. This only leaves feature 3, and since proximal elements are well spaced from each other in PMU R472, the specimen probably represents an immature individual. Immaturity of PMU R472 is further supported by the fact that the specimen has the smallest humerus of all the referred specimens of *G. longirostris*. Although size is not always a good indicator of osteological maturity, the humerus of PMU R472 is much shorter than the largest known humerus (PMU R474), being about 63 per cent. of the latter. Also, the vertebrae of PMU 472 are only half the size of those in the largest vertebral series (PMU R456). Moreover, the well spaced phalanges suggest that the ossification of the epiphyses was incomplete, thus the expanded extremities of the metacarpals and phalanges reflect the shape of the diaphyses rather than that of the epiphyses. I therefore conclude that PMU R472 is osteologically immature, and that the well-expanded extremities of the metacarpals and phalanges do not necessarily indicate maturity.

A second question is whether the forefin of *Grippia* is more plesiomorphic than that of *Utatusaurus*, as suggested by previous authors although based on incomplete information. To address this question, the pectoral limbs of these two genera were compared with those of *Petrolacosaurus kansensis* (the earliest known diapsid, from the Upper Carboniferous; Text-fig. 2A) and *Mixosaurus cornalianus*, a Middle Triassic ichthyosaur (Text-fig. 2D). *P. kansensis* was used as the outgroup because ichthyosaurs are probably diapsids (Massare and Callaway 1990). The monophyly of *U. hataii*, *G. longirostris*, and *M. cornalianus* is established by at least five forelimb features that are absent in *P. kansensis*: (1) anterior flange on the humerus; (2) lunate fifth metacarpal; (3) flattened limb elements; (4) hyperphalangy in the second and third digits; and (5) antero-proximal prominence of the radius. *G. longirostris* and *M. cornalianus* share the following features that are absent in *U. hataii* and *P. kansensis*: (1) round distal elements (i.e. the occurrence of phalanges without perichondral ossification); (2) lunate first metacarpal (i.e. loss of perichondral ossification on the leading edge of the first metacarpal); (3) humerus with a large articular facet for the radius, resulting in the prominent distal expansion of the bone; and (4) manus clearly longer than the combined length of the propodial and epipodials. Although no complete first metacarpal is known for *U. hataii*, it is obviously not lunate, judging from the preserved remains in the holotype. On the other hand, there are no obvious derived character states shared by *U. hataii* and *M. cornalianus* that are not present in *P. kansensis* or *G. longirostris*. In addition, *U. hataii* and *G. longirostris* do not share any derived character state that is absent in *M. cornalianus* and *P. kansensis*. Therefore, by a simple three-taxon comparison, *G. longirostris* forms a clade with *M. cornalianus*, and *U. hataii* is the sister group of this clade (Text-fig. 3). This was confirmed by analysing the data matrix in Table 1 (last four characters only, since the first five are cladistically uninformative), using the exhaustive search option of PAUP 3.1.1 (Swofford 1993) which resulted in a single most parsimonious tree (tree length = 4, retention index = 1.0). Clearly a larger scale



TEXT-FIG. 3. Preliminary phylogenetic hypotheses for early ichthyosaurs, based on forefin features. The cladogram contains *Utatusaurus hataii*, *Grippia longirostris*, and *Mixosaurus cornalianus* as early ichthyosaurs, with *Petrolacosaurus kansensis* as the outgroup. The numbered internodes are characterized by the following synapomorphies: 1, anterior flange on the humerus; lunate fifth metacarpal; flattened fin elements; hyperphalangy in the second and third digits; antero-proximal prominence on the radius; 2, lunate first metacarpal; rounded distal forefin elements; humerus with an expanded articular facet for the radius; manus longer than the humerus and epipodials combined. See text for discussion.

TABLE 1. The character matrix used in the discussion.

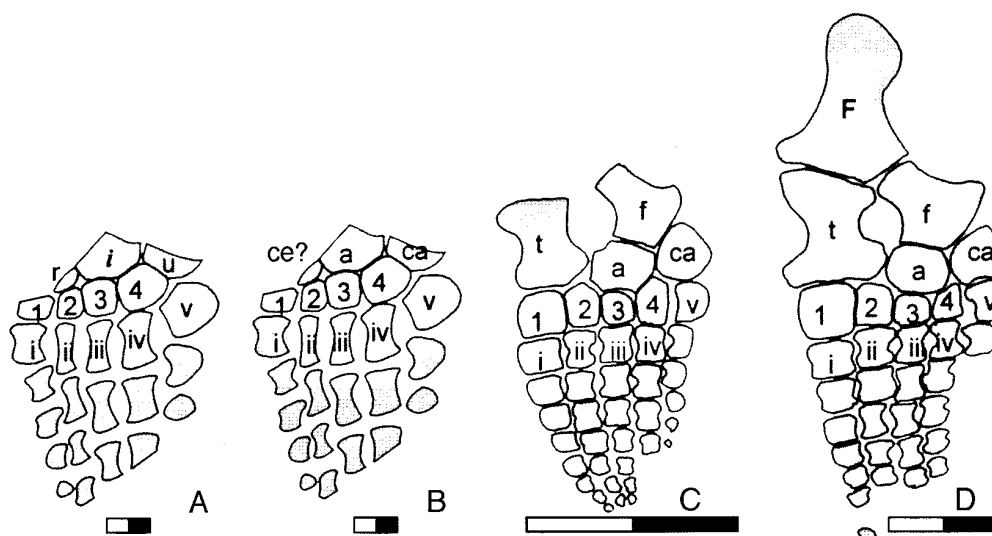
The character states were coded in the following manner.

1. Anterior flange of the humerus: (0) absent; (1) present.
2. Antero-proximal prominence of the radius: (0) absent; (1) present.
3. Fifth metacarpal: (0) cylindrical, with complete perichondral bone sheath; (1) lunate, with posterior perichondral bone absent.
4. Limb elements: (0) not flattened; (1) flattened.
5. Hyperphalangy: (0) absent; (1) present.
6. Distal end of the humerus: (0) similar size to the proximal end; (1) well expanded, with a large articular facet for the radius.
7. First metacarpal: (0) cylindrical, with complete perichondral bone sheath; (1) lunate, with anterior perichondral bone absent.
8. Combined length of propodial and epipodial: (0) longer than manual length; (1) shorter than manual length.
9. Distal manual elements: (0) with perichondral bone; (1) round, without perichondral bone.

Taxon	123456789
<i>Petrolacosaurus</i>	000000000
<i>Utatusaurus</i>	111110000
<i>Grippia</i>	111111111
<i>Mixosaurus</i>	111111111

cladistic analysis that involves other characters from the rest of the skeleton, as well as other ichthyosaur species, is required. Little is known about these early ichthyosaurs, however, hence such an analysis will necessitate extensive studies of these forms, and is beyond the scope of the present paper.

Now that details of the forefin osteology have been established for *Grippia*, it is possible to assess some problematical fin specimens from the Lower Triassic. Thus a third question concerns the identity of incomplete forefins (RTMP 89.127.3 and 89.127.12) from the Lower Triassic of British Columbia, described by Brinkman *et al.* (1992) as belonging to the monotypic genus *Grippia*. Brinkman *et al.* (1992) referred these specimens to *Grippia* on the basis of six features, five of which were first used by Mazin (1986). I show elsewhere (Motani in press) that these specimens were tectonically deformed, and linear retrodeformation of images of the forefins, calibrated against measurements of the vertebral centra, revealed somewhat wider shapes than originally described. I also argue that none of the six features was useful for the taxonomic identification of the British



TEXT-FIG. 4. Fins of Triassic ichthyosaurs. Because of its similarity to the newly reported forefin of *Grippia* (Text-fig. 1), RTMP 89.128.5 can be reasonably identified as a forefin (A), although it was originally described as the hindfin, assuming the presence of the centrale (B). The hindfins of *Mixosaurus cornalianus* (C, based on BMNH R5702) and *M. nordenskiöldii* (D, based on PMU R185), which are the oldest known articulated hindfins of ichthyosaurs, lack the centrale. See text for discussion. Scale bars represent 20 mm.

Columbia fins (Motani in press). Now that the new forefin of *G. longirostris* is available, it is possible to extend this taxonomic discussion. The ichthyosaur represented by RTMP 89.127.3 and 89.127.12 has a first metacarpal that is not lunate, and a humerus that is not distally expanded (Text-fig. 2E). Therefore, this species lacks synapomorphies that unite *G. longirostris* and *M. cornalianus* (Text-fig. 3A). Whether this species had oval phalanges, or whether the manus was large, is unknown, due to poor preservation. In addition, there seem to be no derived character states shared uniquely by *Grippia* and this species. I therefore conclude that these specimens cannot be referred to *Grippia*. The forefin of the British Columbian ichthyosaur resembles that of *U. hataii* in many respects, but is much smaller than the latter. Small ichthyosaurs of similar size to the British Columbian specimens have been reported from the Lower Triassic of China (Young and Dong 1972; Chen 1985; Motani *et al.* 1996), and examination of these taxa may help to resolve the taxonomic identification of the specimens from British Columbia.

Brinkman *et al.* (1992) described another incomplete fin of an ichthyosaur from the Lower Triassic of British Columbia (RTMP 89.128.5), referring to it as a hindfin. The propodial and epipodial elements are not preserved in this supposed hindfin, and the proximal mesopodials are incomplete (Text-fig. 4A–B), causing much difficulty in determining whether it is a pectoral or pelvic fin. Brinkman *et al.* (1992) identified the fin as a hindfin because they found the arrangement of the proximal mesopodials to be similar to that in the hindlimbs of primitive diapsids. However, the new forefin of *Grippia* casts doubt on this identification: the mesopodial arrangements in this forefin and the BC fin are so similar to each other that the BC fin can be reasonably interpreted as a pectoral fin (Text-fig. 4A). On the other hand, the interpretation of the BC fin as a pelvic fin (Text-fig. 4B) postulates the presence of a centrale in this limb, which has yet to be confirmed for any ichthyosaur. For example, in the oldest known articulated hindfins of ichthyosaurs, represented by *Mixosaurus* from the Middle Triassic (Text-fig. 4C–D), the centrale is clearly absent. Many derived ichthyosaurs from the Jurassic have three elements distal to the epipodials, one of which may be identified as the centrale (Caldwell in press). However, some *Stenopterygius* even have three elements in the

epipodial row of the hindfin, suggesting a breakdown of the usual limb-developmental pattern, and the presence of a mechanism to increase the number of proximal elements. Hence, further study is necessary before the homology of the hindfin elements of derived ichthyosaurs from the Jurassic can be established. For these reasons, I conclude that there is insufficient justification for identifying the BC fin as the hindfin.

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