A PRIMITIVE ICHTHYOSAUR FROM THE LOWER TRIASSIC OF BRITISH COLUMBIA, CANADA

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ABSTRACT. The primitive ichthyosaur, *Grippia* cf. *G. longirostris* occurs in Lower Triassic beds near Wapiti Lake, British Columbia. The material includes a well-preserved forelimb and a partial foot, and allows for a new interpretation of the homologies of the elements of the carpus and tarsus. Four distal carpals and five metacarpals are present in the hand, the element previously identified as the fifth distal carpal being reidentified as the fifth metacarpal. Similarly, the proximal element of the fifth digit in the foot is reidentified as the fifth metatarsal. The tarsus includes three proximal elements which are identified as an astragalus, calcaneum and centrale, four distal carpals, and five metatarsals. The centrale is lost in later ichthyosaurs. The early evolution of ichthyosaur paddles is reviewed.

CALLAWAY and Brinkman (1989) reported the presence of a primitive ichthyosaur of uncertain affinities in the Lower Triassic Vega Phroso Siltstone Member of the Sulphur Mountain Formation. The only specimen available at that time consisted of disarticulated remains including ribs, a single centrum, and limb elements thought to be from the fore-limb. The ribs and vertebra were mixosaurian, but the presence of an elongate epipodial and circular, plate-like carpal elements indicated that it was more primitive than any known mixosaur. Also, the large size of some of the possible carpal elements raised the possibility that more than one individual was present in this material.

Recently collected specimens from the Lower Triassic Vega–Phroso Siltstone Member show that this material is referable to *Grippia*, although it may be specifically distinct from *G. longirostris*, the only known species of the genus. Well-preserved partial postcranial skeletons document the structure of the presacral vertebral column in this genus and provide a basis for considering the homologies of the tarsal elements in primitive ichthyosaurs and the early evolution of the ichthyosaur hind-paddle. All specimens are housed in the collections of the Royal Tyrrell Museum of Palaeontology (TMP).

SYSTEMATIC PALAEONTOLOGY

Order ICHTHYOPTERYGIA Owen, 1860

Genus GRIPPIA Wiman, 1929

Type species. Grippia longirostris Wiman, 1929.

Distribution. Lower Triassic of Spitsbergen and British Columbia.

Grippia cf. *G. longirostris* Wiman, 1929

Text-figs 1–5

1929 *Grippia longirostris* Wiman, p. 186, fig. 2.
1933 *Grippia longirostris* Wiman; Wiman, pp. 1–19, pl. 1–2, figs 3–4.
1972 *Mixosaurus longirostris* (Wiman); McGowan, pp. 4–5.
1976 *Mixosaurus longirostris* (Wiman); McGowan, pp. 680–681.
1981 *Grippia longirostris* Wiman; Mazin, pp. 317–340.
1986 *Grippia longirostris* Wiman; Mazin, pp. 314–318.

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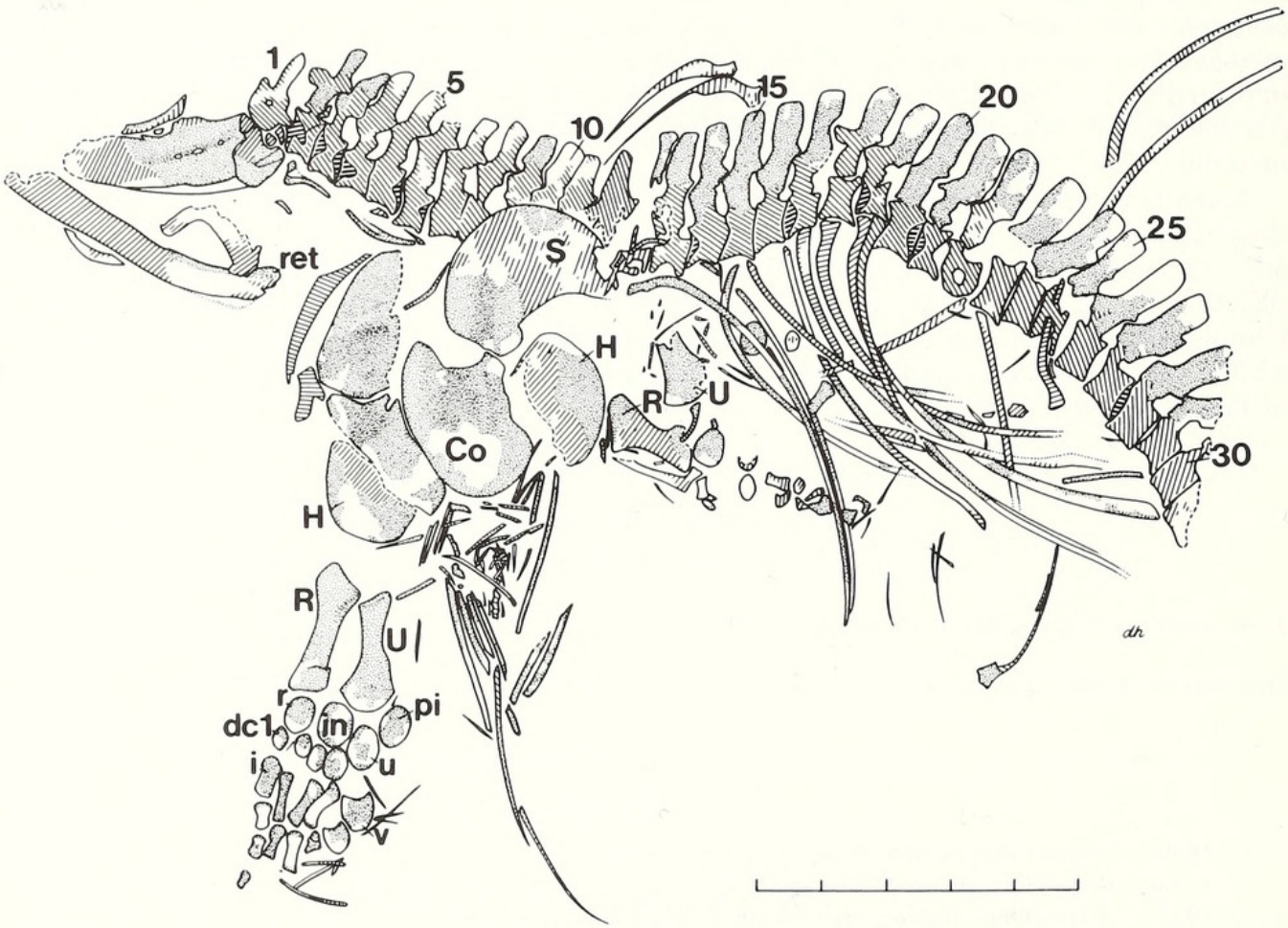
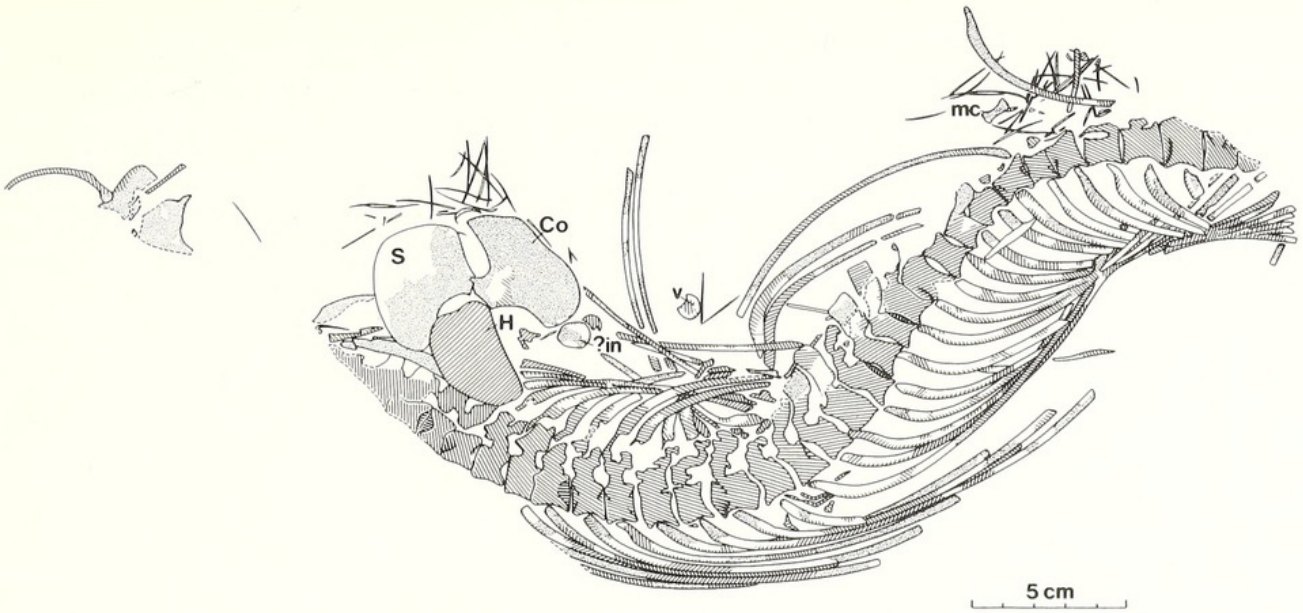
Referred specimens. TMP 89.127.3, a partial skeleton of a single individual including the posterior end of both lower jaws, impression of cheek region of skull, and front part of postcranial skeleton, from south end of cirque designated as D locality; TMP 89.128.5, partial hind limb including most of tarsus, five metatarsals, basal three phalanges of digits one and two, basal two phalanges of digits three to five, and traces of soft tissue, from locality A; TMP 86.152.12, disarticulated remains including ribs, a single (?) dorsal centrum, and elements of the forelimb including ?humerus, radius, and carpal elements, and (?) proximal tarsals, from locality A; TMP 89.127.12, a partial skeleton of a single individual including fragments of posterior end of skull, much of the dorsal region of the presacral vertebral column with ribs of left side in articulation and ribs of right side partially disarticulated, articulated right scapula, coracoid and humerus, and scattered elements of the carpus and metacarpus, from the central portion of D cirque.

Horizon and locality. All specimens are from two localities south-east of Wapiti Lake in east-central British Columbia. Locality A is 54° 31′ 35″ N, 120° 44′ 10″ W; and Locality D is 54° 31′ 10″ N, 120° 43′ 19″ W. All specimens are from the Lower to Middle Triassic Sulphur Mountain Formation. TMP 89.127.3, TMP 89.128.5, and TMP 86.152.12 are from the Vega–Phroso Member of the Sulphur Mountain Formation and are Early Triassic in age. The exact horizon of TMP 89.127.12 within the Sulphur Mountain Formation is unknown.

Description. Both TMP 89.127.3 (Text-fig. 1) and TMP 89.127.12 (Text-fig. 2) were originally preserved with the skull, but in both cases, only fragments remain. TMP 89.127.3 includes impressions of the cheek region and the posterior end of both lower jaws. Like that of *Grippia*, the cheek region was relatively long and had a distinct emargination. Sutures cannot be identified. Fragments of the posterior end of the skull on specimen TMP 89.127.12 could not be identified with certainty, but may include the lateral edge of the upper temporal opening. The posterior ends of the lower jaws are preserved in TMP 89.127.3. A short retroarticular process was present.



TEXT-FIG. 1. *Grippia* cf. *G. longirostris*, TMP 89.127.3. Abbreviations: Co, coracoid; dc1, first distal carpal; H, humerus; in, intermedium; pi, pisiform; R, radius; r, radiale; ret, retroarticular process; S, scapula; U, ulna, u, ulnare; i–v, first to fifth metacarpals; 1–30, vertebrae number one to thirty. Scale bar is 50 mm.



TEXT-FIG. 2. *Grippia* cf. *G. longirostris*, TMP 89.127.12. Abbreviations: Co, coracoid; dc, distal carpal; H, humerus; ?in, intermedium; S, scapula; v, fifth metacarpal.

Thirty-one vertebrae are present in specimen TMP 89.127.3. The first of these is located just posterior to the cranial elements, so may be one of the first three vertebrae. Except for the first and twenty-second vertebrae, which have rotated 90°, all are preserved in articulation and are seen in lateral view. Thirty-two vertebrae, all from the dorsal series, are preserved in specimen TMP 89.127.12. The first seventeen of these are seen in lateral view, vertebrae number eighteen to thirty are seen in dorso-lateral view, and the last two are again seen in lateral view. Although the complete length of the vertebral column is unknown, these two specimens demonstrate that *Grippia* cf. *G. longirostris* had a long snake-like body.

The shortest vertebrae are the cervicals. The length of the centra increases posteriorly along the column, although both specimens show that at their maximum length, the dorsal vertebrae are higher than they are long (Table 1). Thus the proportions of the centra of *Grippia* cf. *G. longirostris* differ from those of *Grippia longirostris* and other Lower Triassic ichthyosaurs, such as *Utatsusaurus hataii* and *Chaohusaurus geishanensis* where some of the vertebrae in the cervical and anterior dorsal region are as long as, or longer than, they are high (Yang and Dong 1972; Shikama *et al.* 1978; Mazin 1981). The third and twenty-first centra in specimen TMP 89.127.3 are preserved in medial cross section, and the twenty-second vertebra in end view. These centra show that the vertebrae are deeply amphicoelous.

The neural arches and spines are clearly visible in lateral view along most of the preserved section of the vertebral column in TMP 89.127.3. Neural arches are preserved along most of the vertebral column of TMP 89.127.12 but only four complete neural spines are present. All four are from the posterior half of the column. As in the dorsal vertebrae of *Grippia longirostris* (Wiman 1933, pl. 1, fig. 9) the neural spines are relatively short and the neural arches are high. The neural arch is highest at the anterior end of the dorsal series and gradually decreases in height posteriorly. The height of the neural spine increases relative to the height of the neural arch, but their combined height does not change relative to the height of the centrum. The width of the neural spine measured antero-posteriorly increases posteriorly along the column. In specimen TMP 89.127.3, the antero-posterior width of the neural spine of the second vertebra is about three-quarters of the length of the centrum, and at the posterior end of the column, the width of the spine is only slightly less than the length of the centrum. The antero-posterior width of the complete neural spines of TMP 89.127.12 is also only slightly less than the length of the centrum.

One cervical rib is present in TMP 89.127.3. This is a short, double-headed rib located next to the second vertebra. Many of the dorsal ribs in specimen TMP 89.127.12 are complete and are preserved in articulation with the vertebral column. These ribs are similar to those of *Mixosaurus* in being long, having a strongly curved proximal third and a nearly straight distal two-thirds. These proportions suggest that *Grippia* cf. *G. longirostris* had a deep, laterally-compressed body. One displaced right rib located near the posterior end of the vertebral column is shorter and more evenly curved. This rib must have come from near the posterior end of the dorsal series, and suggests that the preserved section of vertebral column nearly reaches the sacral region. The

TABLE 1. Measurements of vertebrae of TMP 89.127.3. All measurements are in mm. The length of the centrum is measured at its base and its height is measured at its anterior end; the height of the neural arch is measured from the dorsal edge of the posterior end of the centrum to the postzygapophysis; the height of the neural spine is measured from the postzygapophysis to the tip of the spine.

Vertebra	Length of centrum	Height of centrum	Height of neural arch	Height of neural spine	Width of neural spine
2	4·3	6·2	6·5	5·6	—
3	4·3	6·8	5·7	6·8	2·5
4	4·4	7·4	4·5	7·0	—
5	4·7	6·9	5·0	6·5	3·2
6	6·2	6·7	6·2	6·2	3·0
7	4·5	7·3	7·0	6·3	3·0
8	5·0	7·6	—	6·4	—
9	—	—	6·7	6·7	3·0
10	—	—	6·5	7·6	3·0
11	—	—	—	—	—
12	—	—	—	7·8	—
13	4·8	6·0	6·6	7·8	3·7
14	4·6	5·2	7·0	7·7	4·2
15	5·7	6·7	7·0	8·4	4·0
16	4·5	6·6	7·4	8·6	4·5
17	4·9	6·7	7·3	7·6	4·2
18	5·3	6·7	—	8·2	4·4
19	—	—	—	9·7	5·2
20	5·5	7·5	6·5	10·6	5·2
21	5·3	7·9	5·7	9·4	5·2
22	—	—	—	10·8	5·3
23	5·5	8·5	5·6	10·9	5·7
24	5·8	—	5·8	10·3	5·5
25	—	—	5·6	10·1	—
26	6·1	7·4	5·8	10·2	—
27	6·2	7·2	6·0	10·4	5·7
28	5·8	7·6	5·5	—	—
29	5·7	7·2	—	—	—
30	5·6	6·3	—	—	—

proximal end of four dorsal ribs in specimen TMP 89.127.3 are visible. These are preserved approximately in place adjacent to the twelfth, eighteenth, nineteenth and twenty-second vertebrae, and are all single-headed.

Scattered gastralia are present in TMP 89.127.3. They are generally ichthyosaurian in shape, although their arrangement is uncertain.

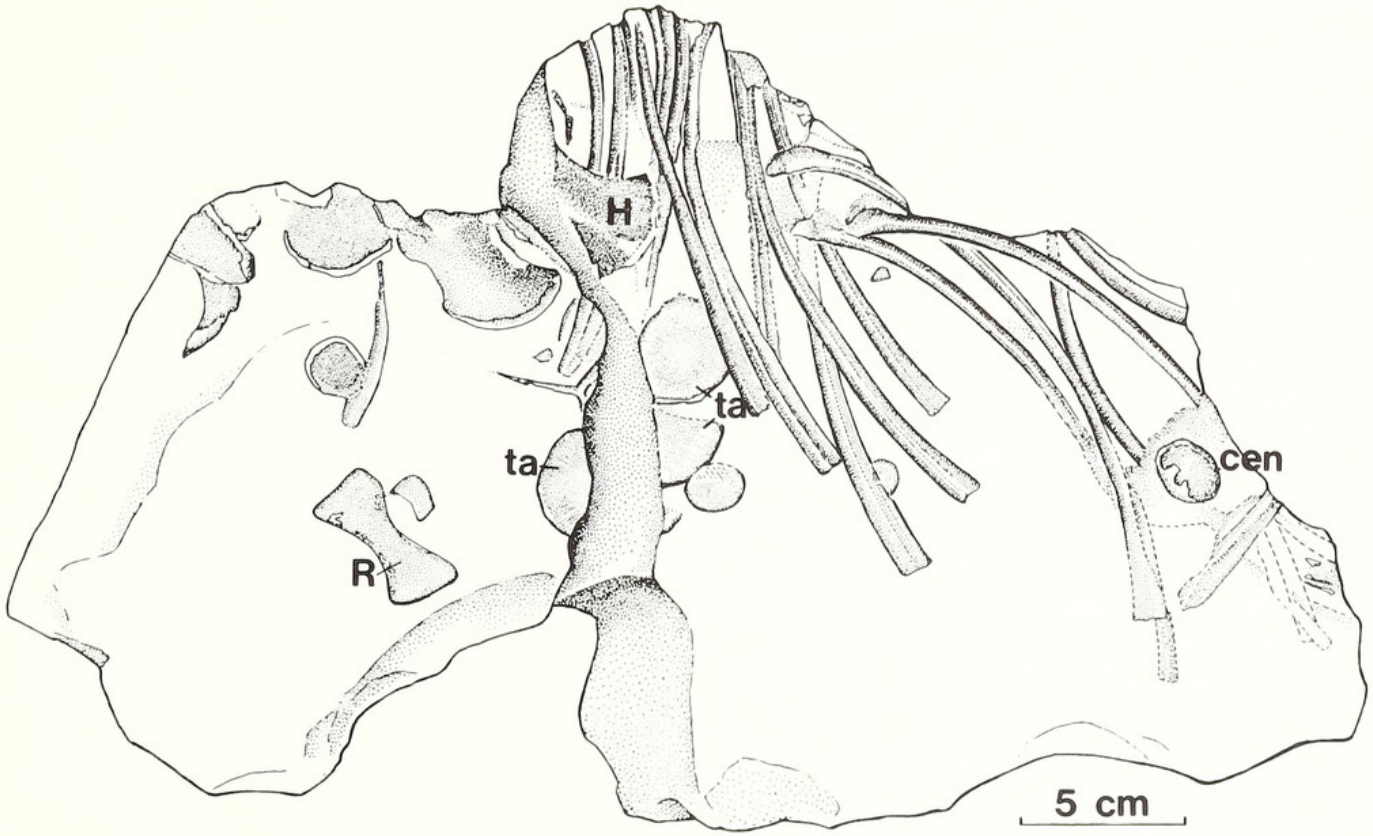
The left scapula and coracoid are complete in specimen TMP 89.127.3, and the right are partly visible. A clavicle and interclavicle are visible anterior to the right scapula, but these are seen in cross-section, so their shape is uncertain. A nearly complete right scapula and coracoid are preserved in TMP 89.127.12.

The shoulder girdle is mixosaurian in its general shape. The coracoid has a greatly expanded ventral plate that narrows to a short peduncle laterally. This peduncle forms both the coracoid portion of the glenoid and the articular surface for the scapula. The scapula has a greatly expanded blade. The ventral edge of the blade is separated from the coracoid, contact between the two elements being restricted to the peduncle of the coracoid.

Both right and left humeri of TMP 89.127.3 are represented by their distal ends and a complete right humerus is present in TMP 89.127.12. These confirm that the element in TMP 86.152.12 tentatively identified as a humerus by Callaway and Brinkman (1989) was correctly identified (Text-fig. 3). The humerus is similar to that of *Grippia longirostris* and *Utatsusaurus hataii* in general shape but is more elongate than in those genera. In TMP 89.127.2, the width/length ratio is 0·64, while in *Utatsusaurus hataii* this is 0·70, and in *Grippia*

longirostris it is 0·79 (Mazin 1986). The distal articular surfaces can be divided into distinct radial and ulnar portions. The angle between these two portions is 145°, intermediate between that of *Utatsusaurus hataii* (152°), and *Grippia longirostris* (133°) (Mazin 1986).

The radius, as in *Grippia longirostris* and *Utatsusaurus hataii*, is elongate and has expanded proximal and distal ends. The right radius is well preserved in specimen TMP 89.127.3, and, based on this element, the epipodial preserved in specimen TMP 86.152.12 can be identified as a radius (Text-fig. 3). Surprisingly, the left radius in TMP 89.127.3 is shorter and more robust than the right. In general proportions, the radius is similar to *G. longirostris* rather than *U. hataii*, in that the angle between the proximal articular surface and the shaft of the bone is 56° in both the right radius of TMP 89.127.3 and the radius of TMP 86.152.12 and 67° in the left radius of TMP 89.127.3. The corresponding angle in *G. longirostris* is 57° and in *U. hataii* it is 84° (Mazin 1986).



TEXT-FIG. 3. *Grippia* cf. *G. longirostris*, TMP 86.152.12. Abbreviations: cen, centrum; H, humerus; R, radius; ta, tarsal element.

The right ulna is well preserved and the distal end of the left is present in TMP 89.127.3. As with the radius, this is an elongate bone with expanded ends. The distal end is much more expanded than the proximal, and bears distinct articular surfaces for the intermedium, ulnare, and pisiform. The inner (radiad) border of the ulna is more strongly concave than the external border, giving the element an asymmetrical shape.

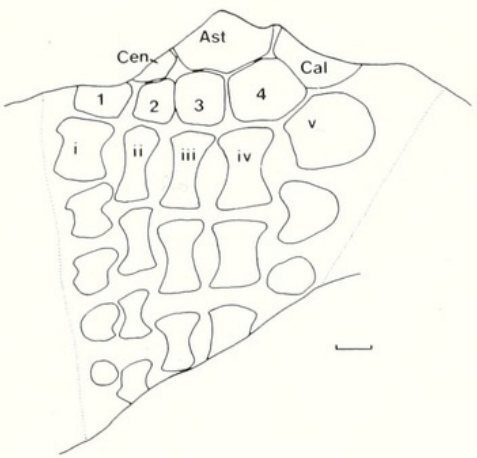
The right carpus is preserved in articulation in TMP 89.127.3. The carpus in TMP 89.127.12 is represented by two of the proximal elements, the fifth metacarpal, and an unidentified metacarpal or proximal phalanx. Specimen TMP 86.152.12 includes several elements that were identified as carpal elements by Callaway and Brinkman (1989). However, some of these are much larger relative to the size of the radius than in specimen TMP 89.27.3, and are reidentified as proximal tarsals (Text-fig. 3).

All the elements of the carpus are plate-like. As in *Grippia longirostris* and *Utatsusaurus hataii* the four proximal elements are the radiale, intermedium, ulnare, and pisiform. The intermedium is the largest of these, the remaining three are subequal in size. As in ichthyosaurs generally, the centrale are absent. The four distal elements are identified as the first to fourth distal carpals. The first three are subequal in size and are distinctly smaller than the fourth. The second articulates between the radiale and intermedium, and the fourth articulates between the intermedium and ulnare. The distal carpals are all smaller than the proximal carpal bones.

The first to fourth metacarpals are elongate, slender bones. The fifth metacarpal is a broad, hook-shaped element with an extensive distal articular surface and without a lateral notch. The identification of this element as the fifth metacarpal, rather than the fifth distal carpal, is based primarily on its large size relative to the fourth distal carpal. In primitive reptiles with five distal carpals, the fifth distal carpal is the smallest of these elements. Also, generally the fifth distal carpal is lost before the fifth metacarpal.

The basal three phalanges of the first toe are present. All of these are longer than broad, although the differences in length and breadth decreases distally along the toe. The proximal two elements have a distinct shaft and expanded ends. The third is subrectangular in shape and shows only slightly expanded ends. The second and third digits are represented only by their basal phalanges. These are elongate elements, over half the length of their respective metacarpals and with broadly expanded proximal ends. The basal phalanx of the fifth digit is overlain by the fifth toe. The fifth toe is represented by the basal two phalanges. The first of these is a short, wide element with a broadly concave internal border and a tight notch on the external border. The second phalanx is incompletely preserved but appears to have been a subcircular element.

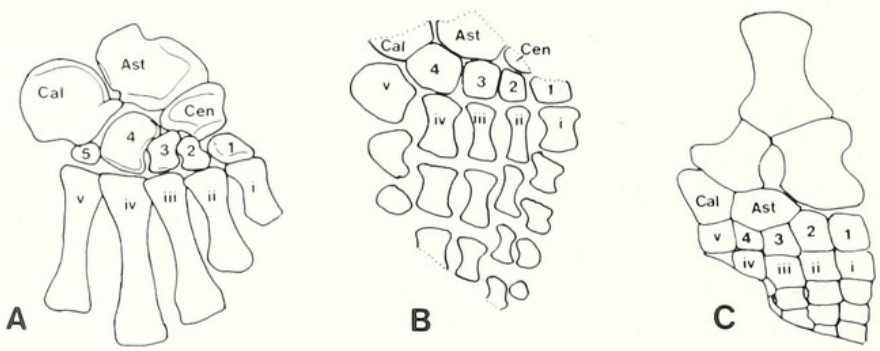
A partial hind-limb is present in specimen TMP 89.128.5 (Text-fig. 4). Three large proximal tarsal elements are incompletely preserved but appear to match some of the elements in TMP 86.152.12 that were previously identified as large carpal elements. Thus these elements are reidentified as the three proximal tarsal elements (Text-fig. 4).



TEXT-FIG. 4. *Grippia* cf. *G. longirostris*; TMP 89.128.5; partial hind limb. Abbreviations: Ast, astragalus; Cal, calcaneum; Cen, centrale; i–v, first to fifth metatarsals; 1–4, first to fourth distal tarsals. Scale bar is 10 mm.

The tarsal elements and phalanges of TMP 89.128.5 are undisturbed, and traces of soft tissue preserved as a faint bluish stain show the extent of the fin. In contrast to the carpus of TMP 89.127.3, the elements of the tarsus of TMP 89.128.5 are closely articulated. This difference is interpreted as a developmental feature associated with the larger size of TMP 89.128.5.

The relative size and position of the elements in the tarsus compares closely with the elements of the tarsus in primitive diapsids (Text-fig. 5A), so despite the incomplete preservation of the three proximal elements, they can be identified as the astragalus, calcaneum and centrale. The astragalus and calcaneum, when complete,



TEXT-FIG. 5. Comparison of the tarsus in primitive diapsid reptiles and early ichthyosaurs. A, *Galesphyrus* from Carroll (1976). B, *Grippia* cf. *G. longirostris*, drawn from TMP 89.128.5. C, *Mixosaurus nordenskioldii*, drawn from TMP 89.126.5. Not to scale. Abbreviations: Ast, astragalus; Cal, calcaneum; Cen, centrale; i–v, first to fifth metatarsals; 1–5, first to fifth distal tarsals.

would have been the largest elements in the tarsus. The centrale lies between the astragalus and first three distal tarsals. The fourth distal tarsal is the largest of the distal tarsals and lies between, and distal to, the astragalus and calcaneum. The first three distal tarsals are subequal in size, but, as typical in primitive reptiles with a separate centrale, the second is slightly smaller than the first and third.

Five metatarsals are present. The first four are hourglass-shaped. The first is short and broad, its proximal width and length being subequal. The second to fourth are longer. These show an increase in width with the fourth being the widest. The fifth metatarsal is a short, broad, plate-like element. It articulates with the disto-lateral edge of the fourth distal tarsal.

All phalanges are flattened, apparently naturally so. Four phalanges are preserved in the first digit, three in the second, and two in the third to fifth digits. The phalanges of the first digit show a transition from hour-glass-shaped to circular. The phalanges of the second to fourth digits are all hourglass-shaped. As with the metatarsals, the phalanges of the second digit are the narrowest, and the phalanges of the fourth digit are the widest. The basal phalanges of the fifth digit is bean-shaped, the second is circular. There is a tendency for the phalanges of the first three digits to form an interlocking structure, with the phalanges of the more medial digits tending to lie lateral to the joints between the corresponding elements of the more lateral digits. This is also the case for the arrangement of the phalanges of the fourth and fifth digits.

Traces of the soft tissue show that the fin was gently tapered. The anterior (leading) edge of the fin is located adjacent to the anterior edge of its bony support. The posterior (trailing) edge extends distal to the posterior edge of the bony support. The presence of unsupported tissue on the distal edge of the fin is a feature that was considered by Robinson (1975) to be typical of fins that are used for underwater flying. Thus although the tarsus and phalanges of *Grippia* cf. *G. longirostris* are morphologically distinct, the hind-limb was functionally specialized for use as a hydrofoil.

Comparisons. Three Lower Triassic ichthyosaurs are well represented by postcranial skeletal material. These are *Utatsusaurus hataii* from Japan (Shikama *et al.* 1978), *Grippia longirostris* from Spitsbergen (Wiman 1929; Mazin 1981), and *Chaohusaurus geishanensis* from China (Yang and Dong 1972). The material described here differs from *Chaohusaurus* and is similar to *G. longirostris* and *U. hataii* in the shape of the humerus and in the presence of a pisiform. The humerus of *Chaohusaurus*, like that of the members of the Shastasauridae and Jurassic ichthyosaurs, has concave pre- and postaxial borders. *G. longirostris*, *U. hataii*, and the Wapiti Lake taxon have a flange on the anterior edge of the humerus giving the element a convex anterior margin. This structure is also seen in *Mixosaurus* and *Omphalosaurus*, and has been interpreted as a primitive ichthyosaurian character because of its wide distribution in primitive ichthyosaurs (Mazin 1986). The presence of a pisiform is a primitive feature in tetrapods, and its absence in *Chaohusaurus* can be interpreted as a derived feature, possibly linking that genus with the Shastasauridae which are characterized in part by the development of a very narrow pectoral fin.

Both *Utatsusaurus hataii* and *Grippia longirostris* are represented by well-preserved forelimb material, and Mazin (1986) has shown that these forelimbs differ in several features. In general, where they differ, the British Columbia specimens conform closely to *G. longirostris* (Table 2). The similarity in the shape of the radius and ulna is particularly striking, and the British Columbia material is referred to the genus *Grippia* on the basis of these similarities.

The British Columbia material differs from *Grippia longirostris* in features of the vertebrae, humerus, carpus, and metatarsus. The cervical vertebrae of the British Columbia taxon are more derived than those of *G. longirostris* in being shorter than they are high. Three cervical vertebrae are known in *G. longirostris* (Wiman 1929; Mazin 1981). All of these have centra that are longer than they are high. The presence of longer cervical centra can be interpreted as a more primitive condition.

The humerus of TMP 89.127.12 differs from that of *Grippia longirostris* in being longer relative to its width and in that the angle formed by the radial and ulnar articular surfaces of the humerus is intermediate between that of *G. longirostris* and *Utatsusaurus hataii* (Table 2). The presence of a relatively longer humerus is probably a primitive feature. The difference in the angle formed by the radial and ulnare articular surfaces is of uncertain polarity.

The carpus of TMP 89.127.3 differs from that of *Grippia longirostris* as reconstructed by Mazin (1986), in that the first three distal carpals are about half the size of the fourth distal carpal, rather

TABLE 2. Comparison of the pectoral limbs of Lower Triassic ichthyosaurs.

	Grippia longirostris	*Utatsusaurus hataii*	*Grippia* cf. *G. longirostris*
Width/length ratio of the humerus	0·79	0·70	0·64
Angle between articular surface for the radius and ulna	133°	152°	145°
Angle formed between proximal articular surface and general axis of radius	57°	84°	56–67°
Ulna shape	Asymmetrical	Symmetrical	Asymmetrical
Size of distal carpals relative to the size of the proximal carpals	Equal	Less than half	Less than half
Basal phalanges of fourth digit	—	Broader than long	Longer than broad

than being subequal in size. The condition seen in *G. longirostris* was thought to be primitive by Mazin (1986). If correct, this would suggest that the Wapiti Lake material should be assigned to *Utatsusaurus*, which also has a fourth distal carpal that is much larger than the first three. However, primitive diapsids typically have a fourth distal carpal that is large relative to the first three, so the presence of these proportions is better considered to be a primitive feature. Thus if correctly reconstructed, *G. longirostris* would be autapomorphic in the proportions of the distal carpals.

The metatarsus of the British Columbia taxon differs from that of *Grippia longirostris* as reconstructed by Mazin (1981) in that the elements are strongly dorso-ventrally flattened, rather than cylindrical and in the shape of the first and fifth metatarsals. The first is short and wide compared to the second to fourth. In *G. longirostris*, the first four metatarsals are of subequal length. The fifth metatarsal is derived in being a short, hook-shaped element. The element identified as the fifth metatarsal of *G. longirostris* by Mazin (1981) is elongate and cylindrical. In all these features, the metatarsus of the Wapiti Lake taxon can be interpreted as derived relative to *G. longirostris*.

Thus, although the British Columbia material can be identified as *Grippia* on the basis of the similarities in the forelimb, it is not easily referable to *Grippia longirostris*. Of particular note are the differences in the cervical vertebrae and metatarsus which suggest that the new specimens are from a taxon that is derived relative to *G. longirostris*. However, we do not recognize a new species since the skull, which is the best known part of the skeleton of *G. longirostris*, is largely unrepresented in the British Columbia material, and the vertebral column and pelvic limb, which are well known in the Canadian specimens, are incompletely represented in *G. longirostris*. Thus the British Columbia material is referred to as *Grippia* cf. *G. longirostris* at present.

EARLY EVOLUTION OF THE ICHTHYOSAUR PADDLES

Since the limb material of *Grippia* cf. *G. longirostris* provides a much better understanding of the structure of the limbs in that genus, it is possible to reconsider the early evolution of the ichthyosaur limb. The forelimb of *Grippia* cf. *G. longirostris* is slightly more primitive than that of *Utatsusaurus hataii* in that more of the basal phalanges remain distinct. In *Utatsusaurus hataii*, all the basal phalanges are short, nearly square elements, while in *Grippia* cf. *G. longirostris*, the basal phalanges of the first three digits are much longer than they are wide. Thus *Grippia* cf. *G. longirostris* can be placed at the base of a morphological series showing increased specialization of the fore-limb of ichthyosaurs to form a paddle. This sequence shows that the external and distal elements of the hand were the first to lose their phalanx-like character, and that the most central and proximal phalanges (the basal phalanges of the second and third digits) were the last. *Grippia* and

Utatsusaurus share the loss of the centrale. Whether this is related to the development of aquatic specializations of the limb is uncertain.

The tarsus of *Grippia* cf. *G. longirostris* is the most primitive ichthyosaur tarsus known in that it retains three proximal tarsals and in that the elements of the metatarsus and pes are elongate. Previously the most primitive well-known ichthyosaur tarsus was that of *Mixosaurus* (Text-fig. 5C). The paddle of *Mixosaurus* is primitive relative to other known Triassic ichthyosaur pelvic limbs in that the tibia and fibula retained distinct shafts and were separated from one another (Appleby 1979). However, as in more derived ichthyosaurs and in contrast to *Grippia* cf. *G. longirostris*, the elements of the tarsus and metatarsus in *Mixosaurus* have largely lost their individuality. This has made the homologies of the elements of the ichthyosaur paddle difficult to identify. The three proximal tarsals cannot be the tibiale, intermedium and fibulare. As pointed out by Romer (1956, p. 401), primitive reptiles did not have a distinct intermedium, that element having been incorporated into the astragalus (Peabody 1951).

Callaway (1989) suggested that the two large proximal elements in the mixosaur tarsus were the astragalus and calcaneum, that the centrale was lost, and that the five elements distal to the astragalus and calcaneum were distal tarsals one to five. This proposal largely brought the tarsus of primitive ichthyosaurs in line with that of primitive reptiles, but it was unusual compared to diapsid reptiles in the presence of a large fifth distal tarsal. This was one of the few features that contradicted the hypothesis that ichthyosaurs were derived from diapsid reptiles, a hypothesis that otherwise seems consistent with the morphology of early ichthyosaurs and primitive diapsid reptiles (Tarsitano 1983; Callaway 1989).

The paddle of *Grippia* cf. *G. longirostris* confirms Callaway's (1989) interpretation that the two large proximal elements are the astragalus and calcaneum and that the centrale is lost in the mixosaur tarsus. However, according to the homologies presented here, the tarsus of *Grippia* has four, rather than five, distal tarsals. Based on this, the basal element of the fifth digit in the *Mixosaurus* foot is reidentified as a fifth metatarsal. This reinterpretation removed one of the major obstacles to the hypothesis that ichthyosaurs originated from diapsid reptiles.

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