PHYLOGENY OF THE ICHTHYOSAURIA (AMNIOTA: REPTILIA) WITH SPECIAL REFERENCE TO TRIASSIC FORMS

by

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ABSTRACT

PHYLOGENY OF THE ICHTHYOSAURIA (AMNIOTA: REPTILIA) WITH SPECIAL REFERENCE TO TRIASSIC FORMS

Doctor of Philosophy, 1997

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The interrelationships among Triassic ichthyosaurs have been poorly understood due to the lack of knowledge regarding their basic osteologies, especially that of the earliest forms from the Spathian (Lower Triassic). These earliest ichthyosaurs represent relatively new additions to our knowledge, most of them having been found during the last 25 years. Reexaminations of Utatsusaurus, Grippia, Chaohusaurus (Early Triassic), Parvinatator (Early or Middle Triassic), and of Mixosaurus (Middle Triassic), reveals many previously unrecognized features of the skull, dentition, and forefin. This new knowledge, together with preliminary examinations of other Triassic ichthyosaurs, enables a comprehensive comparison among Triassic ichthyosaurs, for the first time.

A phylogenetic hypothesis for Triassic ichthyosaurs is proposed, based on cladistic analyses of osteological characters, again for the first time. The monophyly of the Order Ichthyosauria, which was previously never questioned although never explicitly stated, is established based on at least nine characters that unambiguously define the basal node of the Order. Early Triassic ichthyosaurs (including Parvinatator) form the stem group of the

Ichthyosauria, while all others form a crown-group clade, the Euichthyosauria. This taxon is further divided into two large clades, the Shastasauriformes and Ichthyosauriformes. The former includes Cymbospondylus and Shastasaurus, and their most recent common ancestor, while the latter comprises the Mixosauroidea and Ichthyosauroidea, and their most recent common ancestor. Toretocnemus and Californosaurus, which have long been considered as shastasaurids, are shown to be ichthyosauroids. Cymbospondylus and Ichthyosaurus, as previously designated, appeared paraphyletic on the cladogram, therefore two new generic names are proposed to solve the problem.

Omphalosaurus is considered non-ichthyosaurian, because none of the ichthyosaurian synapomorphies are known for this genus, while it shows several sauropterygian features. The taxonomy of Pessopteryx should be reconsidered.

Tectonic deformation has remarkably distorted the original morphologies of some of the specimens studied, namely all specimens of Parvinatator and some specimens of Utatsusaurus. A method is devised to retrodeform the images of these specimens, using a personal computer. This method is unique for incorporating matrix algebra, thus simplifying the calculation process, while enabling the statistical selection of best solution.

DEDICATION

To my father, Kensuke Motani,

who, as a child, survived the bombing of Toyama city in 1945,

which took his parents' lives,

and raised his sons with devoted love.

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I have to thank so many people for where I stand today, but I will keep it shorter than I really want. As a Japanese who was brought up in Japan, I came to Canada at the age of 24, to study ichthyosaurs with Dr. Chris McGowan, who became my academic father as soon as I landed at Pearson International Airport. Chris started his parental care by securing my life in Canada: he gave me a place to live and food to eat, then made me learn English conversation and writing. Socially, he treated me as if I were his son, and all of these made me feel at home in this foreign country, which in turn made it possible to concentrate on my study. Needless to say, Chris was also very helpful in academic aspects. Every piece of his knowledge on ichthyosaurs, which indeed constitutes the world's largest database on this subject, was always available to me. Yet, he let me plan and carry out my own research, and when asked, gave appropriate criticisms to my methods and interpretations.

The members of my graduate committee, Drs. Hans-Dieter Sues and Robert Reisz, were always available for discussion when needed, and gave me very useful suggestions. Hans also made available rare literature from his private collections. The teaching staff of ZOO 1462 (Advanced application of phylogenetics), namely Drs. Bob Murphy and Doug Currie, and Kevin Doyle (TA), provided stimulating environment when studying phylogenetic systematics, while not forcing any particular philosophy on me.

Drs. Mike Caldwell and Betsy Nicholls kindly made available their manuscripts in press. Dr. Don Brinkman gave permission to reproduce a figure in his publication, and also provided photographs for my research. I thank Drs. Jean-Michel Mazin, Olivier Rieppel, Martin Sander, and Rupert Wild for discussions regarding the biology of ichthyosaurs, and the status of Omphalosaurus. Dr. Wild also sent me a copy of a paper on an Omphalosaurus specimen from Austria, which is difficult to obtain in Toronto. For their useful comments on the submitted chapters, I thank Drs. Alan Baker, Jack M. Callaway, R. A. Cooper, Nigel C. Hughes, Mike A. Taylor, and Paul. W. Webb.

Drs. Kei Mori (IGPS), Solweig Stuenes (PMU), and Angela Milner (BMNH) kindly loaned specimens of Utatsusaurus hataii (IGPS 95941, 95942), Grippia longirostris (PMU R443, 444, 472), and Mixosaurus cornalianus (BMNH R5702) respectively, with permissions for preparation. Without their generosity, this study never could have been conducted. Dr. Itaru Hayami (Kanagawa University and University of Tokyo), who was my advisor at the University of Tokyo, kindly borrowed the specimens of Utatsusaurus on my behalf. Dr. Nachio Minoura (HUG) allowed me to study undescribed specimens of Utatsusaurus, which he was studying himself. Dr. Tomida (NSM) provided me with the casts of these specimens. He also provided extensive help when I was perparing to study abroad.

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Ian Morrison taught me preparation techniques. He, Ted Ecclestone, Brian Iwama, Tim Fedak, Raoul Bain, and Ian Nicklin were always helpful in the preparation lab of the ROM. Catherine Skrabec, Joan Burke, and Sheila Freeman made sure various official documents were taken care of, without which I could not have survived.

My parents, Junko and Kensuke Motani, always believed in their son's potential, and gave him his education, financial support, and love, the thought of which makes me speechless. My brothers, Shunsuke and Kosuke, shared their interests—in computers and dinosaurs, respectively, when I was growing up.

Finally, I cannot possibly thank my wife, Yoko, enough. She was always there when I needed her, and made everything worthwhile.

Institutional abbreviations are: **BGRB**, Bundesanstalt für Geowissenschaften und Rohstoffe, Aussenstelle Berlin; **BMNH**, Natural History Museum, London; **HUG**, Hokkaido University, Department of Geology, Sapporo; **IGPS**, Institute for Geology and Paleontology, Tohoku University, Sendai; **IVPP**, Institute for Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing; **MNB**, Museum für Naturkunde, Berlin; **MNHN**, Institut de Paléontologie du Muséum National d'Histoire Naturelle, Paris; **NSM**, National Science Museum, Tokyo; **PMO**, Paleontologisk Museum, Universitetet i Oslo; **PMU**, Paleontologiska Museet, Uppsala Universtet; **ROM**, Royal Ontario Museum, Toronto; **RTMP**, Royal Tyrrell Museum of Paleontology, Drumheller; **SMC**, Sedgwick Museum, Universtiy of Cambridge; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart; **UCMP**, University of California, Museum of Paleontology, Berkeley.

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GENERAL INTRODUCTION

INTRODUCTION TO THE ICHTHYOSAURIA

Ichthyosaurs are extinct marine reptiles that are often referred to as "reptilian analogues of dolphins" , because advanced forms evolved thunniform (i.e., tuna-like) body shapes. Their fossil record ranges from the Lower Triassic (Callaway and Massare, 1989) to the Upper Cretaceous (Baird, 1984), and 25 genera and 53 species are currently considered valid in the literature (McGowan, 1972, 1974a, b, 1976, 1979, 1991, 1994a, 1995, 1996a, b, c; Callaway and Massare, 1989; Sander, 1989; Mazin et al., 1991; Nicholls and Brinkman, 1995). The first 40 million years of ichthyosaurian evolution, during the Triassic period, is poorly known because Triassic fossils are not only rare but also inadequately studied. In fact, most major references for Middle and Late Triassic ichthyosaurs were written in the early 1900s (e.g., Merriam, 1902, 1903, 1908, 1910; Repossi, 1902; Wiman, 1910; von Huene, 1916), and have not been critically revised since then. Early Triassic ichthyosaurs, which are the earliest forms known, are relatively new additions to our knowledge of ichthyosaurs: most of them were discovered during the past quarter of this century (Young and Dong, 1972; Shikama et al., 1978; Mazin, 1981; Chen, 1985; Callaway and Brinkman, 1989; Brinkman et al., 1992). Even the first description, which was of Grippia longirostris (Wiman, 1929, 1933), was given more than a century after the first description of Jurassic species (Conybeare, 1822). These earliest ichthyosaurs are important because they are most likely basal, but their world-wide distribution, which includes China and Japan, has hampered comparative studies. The only comparative work was done by Mazin (1981, 1986), who, instead of improving our knowledge, confused the descriptions in the literature through a series of misinterpretations of the fossils (Motani 1996, 1997, in press).

The lack of knowledge regarding the early forms has been the major impediment to phylogenetic studies of the Ichthyosauria. The Ichthyosauria has been assumed to be a monophyletic group, but the characters defining the Order were never explicitly stated. They are most likely diapsids (Tarsitano, 1982; Massare and Callaway, 1990; Caldwell, 1996), but no consensus has been reached regarding their position within the Diapsida (Callaway, 1989; Massare and Callaway, 1990; Caldwell, 1996). Most phylogenetic studies of basal diapsids purposely omit ichthyosaurs from the data matrix (Gauthier, 1984; Benton, 1985; Evans, 1988; Rieppel, 1994), because characteristics of basal ichthyosaurs are not well known. The interrelationships of the ichthyosaurian species is also poorly understood. The only cladistic study of the Order, conducted by Mazin (1982), merely presented a cladogram with selected features plotted on it, without even giving a data matrix. His hypothesis largely relied on dental characters, which were incorrectly interpreted (Motani, 1996, 1997, in press). Therefore, no reasonable phylogenetic hypothesis is currently available for ichthyosaurs.

One of the reasons Triassic ichthyosaurs are so poorly understood is that their specimens, unlike later ones, are often badly distorted through tectonic deformation. Therefore proper description of their true morphologies is only possible after the retrodeformation of their images. However, such retrodeformation processes are usually ignored by vertebrate paleontologists, resulting in inaccurate description of the shape of the original animals. For example, two Canadian specimens were described by Brinkman et al. (1992) and Nicholls and Brinkman (1995) as being unusual for their unequally sized forefins and elongated carpals. However, such abnormalities can be explained as artifacts of tectonic deformation.

Retrodeformation of fossil images has been studied by invertebrate paleontologists (e.g., Lake, 1943; Hughes and Jell, 1992) and structural geologists (e.g., Ramsay and Huber, 1983; Cooper, 1990) but these traditional approaches require either a subjective drawing process, or complicated computations. Therefore it is important to introduce retrodeformation techniques to vertebrate paleontology, and to simplify the methodology by taking advantage of recent advancement in personal computer technologies.

OBJECTIVES

This dissertation constitutes the first attempt to clarify the phylogeny of Triassic ichthyosaurs, using cladistic methodologies. Two minor objectives are: 1) to develop a computerized method for the retrodeformation of tectonically distorted fossils; and 2) to reconsider the conditions for the use of the standard allometric growth equation.

DISSERTATION ORGANIZATION

The first step of the present study was to reexamine the specimens of various Triassic ichthyosaurs in person, to make a comprehensive comparisons among them for the first time. Nine countries were visited in Asia, Europe, and North America to examine 26 major ichthyosaur collections. Many specimens, especially those of Early Triassic ichthyosaurs, required redescription, because of the poor quality of the original publications.

This dissertation is presented as a series of 12 separate manuscripts, which will be (or have been) submitted for publication, and one appendix. Each chapter ends with its own literature citation. Chapters 1 to 11 are dedicated to basic studies, such as description, interpretation, and analysis of anatomical structures. These eleven chapters, together with three publications from my master's study (Motani, 1996, 1997, in press), form the basis for the cladistic analysis of Triassic ichthyosaurs, reported in the 12th chapter. A mathematically elaborated methodology for retrodeforming tectonically distorted fossils is proposed in Chapter 2. The limitation of the standard allometric equation for embryonic studies is discussed in Chapter 5; an alternative equation is proposed. The appendix summarizes my view regarding the probabilistic justification of character-step parsimony methods of phylogeny reconstruction. This appendix was added because the views I share with many molecular systematists are still questioned among vertebrate paleontologist.

Chapter 1 is in press in a book volume (reprinted with permission from Callaway/Nicholls, Ancient Marine Reptiles copyright [1997] Academic Press [http://www.apnet.com].), while Chapters 2 to 4 are in review by journals. Chapter 11 was published from Nature (reprinted with permission from Nature [382:347-8] copyright [1996] Macmillan Magazines Ltd.). I have co-authors for those chapters describing Chinese fossils, namely Chapters 4, 5, 11: non-Chinese paleontologists have to have a Chinese co-author to publish on Chinese specimens. The following is a list of the chapters that have been published, accepted, or which are in review.

Chapter 1	Ancient Marine Reptiles (Academic Press)	in press.
Chapter 2	Lethaia	in review.
Chapter 3	Palaeontology	in review.
Chapter 4	Journal of Paleontology	in review.
Chapter 11	Nature	382:347-8 (1996).

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CHAPTER

1

TOOTH IMPLANTATION AND REPLACEMENT IN ICHTHYOSAURS

ABSTRACT

It has been known since Owen's time that the teeth of post-Triassic ichthyosaurs are implanted in a dental groove. This condition was believed to have been derived from the thecodont condition of Triassic ichthyosaurs, as exemplified by Mixosaurus cornalianus from the Middle Triassic. However, a literature survey, and an examination of Triassic ichthyosaurs, reveals that this derivation is unlikely. The occurrence of deep alveoli is only known in Shonisaurus (Upper Triassic), and possibly also in Cymbospondylus (Middle Triassic). In the most complete specimen of Shastasaurus, a dental groove is present. Dental sockets exists in the posterior dentition of Phalarodon, but they are associated with a shallow dental groove, at least in the anterior portion of the maxilla. In M. cornalianus sockets are present only in the maxilla, dental grooves occurring elsewhere. The geologically oldest taxa, namely Grippia longirostris and Utatsusaurus hataii, have dental grooves, at least in the mandible, and the implantation is subthecodont, which is primitive for amniotes. Thus, presence of deep sockets is derived rather than primitive for ichthyosaurs, and the dental groove in post-Triassic ichthyosaurs is likely to be homologous to that of the subthecodont condition. Replacement teeth always occur outside the pulp cavities in ichthyosaurs, and this may be synapomorphic for the Order.

INTRODUCTION

The fossil record of the Ichthyosauria ranges from the Smithian of the Lower Triassic (Callaway and Massare, 1989b) to the Cenomanian of the Upper Cretaceous (Baird, 1984). While Jurassic ichthyosaurs are quite abundant and well preserved, Triassic ones are comparably rare and poorly preserved. Consequently, our knowledge of ichthyosaurian biology is largely biased toward Jurassic forms, and little is known about their evolution during the Triassic.

One of the common features of post-Triassic ichthyosaurs is that their teeth are set in a longitudinal groove, which is often referred to as a "dental groove", in the upper and lower jaw margins. It has been suggested that the dental groove evolved from the thecodont condition found in some of the Triassic forms, such as Mixosaurus cornalianus (Merriam, 1908; Peyer, 1968; Mazin, 1983). Mazin (1983) coined the term "aulacodont" for the dental implantation in post-Triassic ichthyosaurs, defining it as a derivative of thecodont implantation. However, a recent study of the mandibular dentitions of Utatsusaurus hataii and Grippia longirostris -- the most primitive ichthyosaurs from the Lower Triassic-- established the occurrence of a dental groove (Motani, 1996, 1997). Thus, a reconsideration of the evolution of the ichthyosaurian dental groove is required.

When discussing dental implantation in ichthyosaurs, it is important to recognize that two kinds of implantation may occur within the same jaw ramus depending on position. Therefore it is useful to divide the dentition into four parts when describing tooth implantation, namely, the maxillary, premaxillary, anterior dentary, and posterior dentary dentitions. However, published descriptions are scarcely available for all four parts, not only because complete jaw material is rare, but also because most authors did not pay attention to the change in dental implantation within a given jaw ramus. Before discussing the evolution of the dental groove, a review of the geological history of various dental implantations among ichthyosaur species is necessary. Although a similar review has already been undertaken by Mazin (1983), he did not consider the occurrence of more than one kind of dental implantation within an individual, leading to some misunderstanding of the true situation.

MATERIALS AND METHODS

The abbreviations used for the institutions are as follows: BMNH- Natural History Museum, London; IGPS- Institute of Geology and Paleontology, Tohoku University, Sendai; PMU- Paleontologiska Museet, Uppsala Universitet, Uppsala, Sweden; UCMP- University of California, Museum of Paleontology, Berkeley. The specimens with the prefix of SVT are stored in MNHN (Institut de Paléontologie du Muséum National d'Histoire Naturelle, Paris, France).

Tooth implantation and replacement in ichthyosaurs was reviewed based on a literature survey and upon examination of some specimens. Specimens examined are: *Utatsusaurus hataii*- IGPS 95941 and 95942; *Grippia longirostris*- PMU R445 and R449, SVT 201 and 202; *Mixosaurus cornalianus*- BMNH R5702. Described specimens of *Pessosaurus polaris*, *Mixosaurus nordenskioeldii*, *Himalayasaurus tibetensis*, and *Shastasaurus neoscapularis* were also examined to verify the descriptions in the literature.

TERMINOLOGY

The terminology for tooth implantation in amniotes varies among authors, leading to confusion, therefore it is important to clarify the usage in the present paper. I essentially follow Romer (1956) and Edmund (1969), and recognize five basic types, namely acrodonty, pleurodonty, subthecodonty, ankylosed thecodonty, thecodonty (Fig. 1-1). The term aulacodonty (Mazin, 1983) is employed for the implantation in post-Triassic ichthyosaurs, but without the evolutionary implication that was originally intended. Other terms are either synonymous with, or variation upon, these five basic patterns.

Acrodonty

Definition-- The teeth are ankylosed to the jaw bone (Miles and Poole, 1967). A dental groove or a socket is absent, and the teeth are fixed to the margin of the jaw.

Example-- Some lizards, and Sphenodon. Not known in ichthyosaurs.

Pleurodonty

Definition-- There is no proper socket, and the teeth are ankylosed to the surface of the jaw bones. A longitudinal dental groove with a high labial and low lingual wall may exist (Romer, 1956), or the lingual wall is lost (Edmund, 1969). I follow Romer's definition and consider that the loss of the lingual wall is not a necessary condition for pleurodonty. The teeth are mainly attached to the lingual side of the labial wall, while they may also be attached to the bottom of the dental groove.

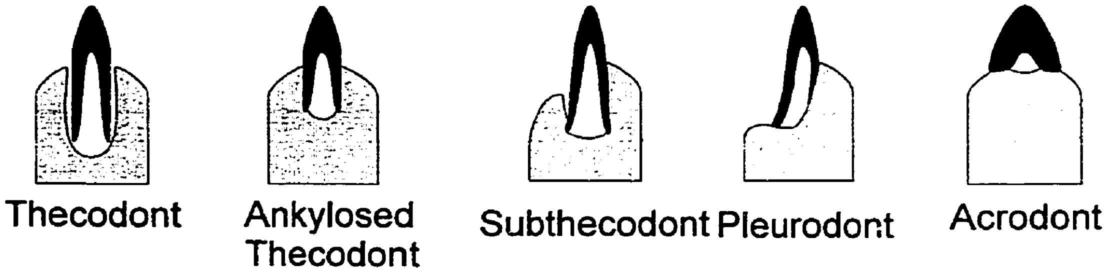
Example-- Varanid and iguanid lizards.

Ankylosed thecodonty

Definition-- The teeth are set in sockets, which can be deep, up to a depth of about the height of the crown (Edmund, 1969). The surrounding bone of the sockets is ankylosed to the teeth. Edmund (1969) pointed out that ankylosed thecodonty merges with subthecodonty because they can only be distinguished by the relative depth of the socket. Although it is difficult to set a

Figure 1-1. Five major types of tooth implantation in amniotes.

Five major types of tooth implantation, and several variations of them, are recognized in amniotes. After Romer (1956) and Edmund (1960).


Thecodont
Ankylosed Thecodont
Subthecodont
Pleurodont
Acrodont

clear line between the two, ankylosed thecodonty can be distinguished from subthecodonty by the absence of the dental groove in the former.

Example-- Maxillary teeth of Mixosaurus comalianus.

Subthecodonty

Definition-- Teeth are set in shallow sockets arranged at the bottom of a longitudinal dental groove with high labial and low lingual walls (Romer, 1956). Reduction of the lingual wall would result in the formation of a lingual shelf, as described for Petrolacosaurus (Reisz, 1981), but this is interpreted here as a variation of a dental groove. "Prothecodont" (Peyer, 1968), "protothecodont" (Edmund, 1969), and "pleurothecodont" (Wild, 1973) are synonymous with subthecodont, and are accordingly not used here, to avoid confusion. The word "prothecodont" was also used by Wild (1973) in a sense which resembles that for "ankylosed thecodont" of Edmund (1969), but because this usage is confusing, it is not employed here.

Example-- Most early amniotes, including Paleothyris, Petrolacosaurus. Other tetrapods, such as Seymouria, also have this implantation.

Thecodonty

Definition-- Teeth are set in sockets which are deeper than the height of the tooth crowns. There is no ankylosis between the teeth and the jaw bone, and the teeth are fixed to the jaw bone by fibrous organic connective tissue. The roots of the teeth are cylindrical.

Example-- Crocodilians and many other archosaurs; mammals.

Aulacodonty

Definition-- Mazin (1983) described the tooth implantation seen in post-Triassic ichthyosaurs as "aulacodonty", defining this as a derivative of thecodonty. However, as will be discussed later, the ichthyosaurian dental groove is not necessarily derived from the thecodont condition, therefore this term is used here without evolutionary implication. The teeth are set in a longitudinal dental groove along the jaw margin, and there is no proper socket. Whether the teeth are ankylosed to the jaw bone is not well established in the literature. Mazin (1983) noted that the fixation is of a non-mineralized type, but did not provide any evidence. (Should the fixation prove to be of an ankylosis type with a shallow socket, aulacodonty would become a junior synonym for subthecodonty.)

Example-- post-Triassic ichthyosaurs, such as Ichthyosaurus.

Labial pleurodonty

Rieppel (1978) explained that this term is used for pleurodont implantation where only the labial side of the tooth is in contact with the labial wall of the jaw; the lingual part of the tooth rests on a horizontal bony shelf that extends lingually from the bottom of the labial wall. He used this term to distinguish the complete pleurodonty seen in platynoan lizards from the implantation of many other lizards. However, in many cases the labial wall of the dental groove gradually shifts to the horizontal shelf toward the bottom, hence it is very difficult to set a clear line between the labial wall and the shelf. Because pleurodonty and labial pleurodonty cannot always be distinguished, I follow Romer (1956) in considering labial pleurodonty as a variation of pleurodonty. Pleuroacrodonty (subacrodonty) of Wild (1973) may be similar to labial pleurodonty.

Pleuroacrodonty

See labial pleurodonty.

Pleurothecodonty

See subthecodonty.

Prothecodonty

See subthecodonty.

Protothecodonty

See subthecodonty.

Subacrodonty

See labial pleurodonty.

Subpleurodonty

The definition of subpleurodonty is not well established. Smith (1958) used this term to describe pleurodont implantation with the varanid type of tooth replacement (sensu Edmund, 1960), where replacement teeth occur in the interdental positions. Dong (1972) used this term for the implantation in an Upper Triassic ichthyosaur, Himalayasaurus tibetensis, which is essentially pleurodont but "the jaw bone joins the roots of the teeth [translation]". Presch (1974) used this term for the implantation in some teiid lizards, such as Dracaena guianensis, where the pleurodont teeth are covered with extensive bone of attachment at their bases. Smith's (1958) "subpleurodont" is synonymous with pleurodont, because the only difference is the mode of replacement, which should not be considered in the terminology for tooth implantation. The usages of Dong (1972) and Presch (1974) are similar: in both cases, pleurodont implantation is strengthened by the well developed bone of attachment. However, it is difficult to set a clear line between pleurodonty and subpleurodonty, because there is an intermediate state. For example, in the rhinoceros iguana, Cyclura cornuta (ROM R1154), the bone of attachment is better developed than in typical pleurodonty in varanid lizards, but it covers the roots only partially. Therefore, subpleurodonty is considered to be a variation of pleurodonty.

TOOTH IMPLANTATION AND REPLACEMENT IN ICHTHYOSAURS

Early Triassic Forms

Grippia longirostris Wiman 1929

Known Parts-- Maxillary, posterior part of the mandibular, and posteriormost part of the premaxillary dentitions.

Implantation-- Wiman (1929) stated that dental implantation in Grippia longirostris is pleurodont, as in Recent varanid lizards. However, Wiman (1933) revised his previous description, and redescribed the teeth as being set in shallow sockets. Mazin (1983) described the dental implantation of the species as ankylosed thecodont, without specifying the part of the dentition. I have shown that implantation is subthecodont, at least in the posterior part of the mandible (Motani, 1997).

Replacement-- The arrangement of the maxillary teeth suggests that a replacement tooth occurs disto-lingual of a functional tooth, and migrates toward the latter to replace it. (Motani, 1997)

Utatsusaurus hataii Shikama, Kamei and Murata 1978

Known Parts-- Mandibular dentition.

Implantation-- The mandibular dentition is pleurodont at the anterior tip, gradually changing to subthecodont posteriorly (Motani, 1996). The teeth are well fused to the labial wall of the dental groove all along the jaw.

Replacement-- A replacement tooth appears disto-lingual of a functional tooth, and migrates toward the latter to replace it (Motani, 1996). Formation of the resorption cavity in the functional tooth is not known.

Utatsusaurus sp. Nicholls and Brinkman (1993)

Known Parts-- Maxillary, premaxillary, and partial mandibular dentitions.

Implantation-- Nicholls and Brinkman (1993) reported that implantation is subthecodont, without specifying the position.

Replacement-- Unknown.

Middle Triassic Forms

Cymbospondylus petrinus Leidy 1886

Known Parts-- All parts of the dentition

Implantation-- Merriam (1908) described that the teeth of Cymbospondylus petrinus are set in distinct pits, at least in part of the mandible. He figured three cross-sections of the mandibular teeth in horizontal, transverse, or disto-mesial sections (Merriam, 1908: figs. 10 - 12). In the transverse section, it is seen that the bottom of the tooth is ankylosed to the bottom of the socket, while the upper part of the tooth is clearly free from the wall of the socket. This ankylosis at the bottom of the root is confirmed in the horizontal section, where the folded root of a mature tooth (i.e. the one associated with a replacement tooth) is shown. This implantation might be called thecodont if it were not for the ankylosis at the bottom of the socket and for the folding of the root. It also differs from ankylosed thecodont in that the ankylosis is restricted to the bottom of the socket. Therefore, tooth implantation in C. petrinus is tentatively termed here as ichthyosaurian thecodonty.

Replacement--Judging from Merriam's (1908; fig. 10) figure, tooth replacement in C. petrinus is similar to that in sauropterygians, such as nothosaurs (Edmund, 1960): a replacement tooth occurs in its own crypt, located lingual of a functional tooth.

Mixosaurus atavus (Quenstedt, 1852)

Known Parts-- Maxillary and mandibular dentitions.

Implantation-- Fraas (1891, p. 38) noted that the teeth of M. atavus are fixed to the bone, although they are arranged in a common groove. Huene (1916, p. 4) redescribed the dentition of the species, and stated that the teeth are set in a groove, with rudimentary bony septa between the bottom portions of the roots. Tooth implantation is therefore probably subthecodont. Huene (1916, pl. 3, fig. 7) illustrated a cross-section of an isolated jaw fragment, with a tooth which is unusual for having a long and tapering root that curves as it tapers. However, no such root morphology is known in other ichthyosaurs, and the jaw rami of other specimens of M. atavus are too shallow compared to the crown height to accommodate such a long root.

Replacement-- Unknown.

Mixosaurus cornalianus (Bassani 1886)

Known Parts-- All parts of the dentition.

Implantation-- Repposi (1902) gave a good description of the dental implantation of Mixosaurus cornalianus: maxillary teeth are set in alveoli, while a dental groove is present elsewhere. He noted that the groove becomes very narrow between the teeth in the premaxilla and dentary, and gave a clear figure. However, Besmer (1947) could not find the dental groove in the premaxilla, and stated that the teeth are set in distinct pits in the upper jaw while they are set in a groove in the mandible. The dental groove is known at least in the premaxillae of some mixosaur specimens from Tessin. Therefore, tooth implantation is probably subthecodont in the mandible and in the anterior part of the upper jaw, but becomes ankylosed thecodont posteriorly in the upper jaw, through the reduction of the dental groove.

Merriam (1908) briefly noted that the teeth are set in distinct pits in M. cornalianus, but did not specify the relative position in the dentition. Because he examined the same specimen as Repposi's (1902), I interpret that his comment was based on the maxillary teeth. Merriam (1910) described tooth implantation in early ichthyosaurs, including M. cornalianus, as being thecodont but his usage of the term is incorrect. Peyer (1968), referring to Besmer (1947), noted that the teeth of M. cornalianus are set in distinct alveoli. He provided a radiograph quoted from Besmer (1947) to show the presence of sockets (Peyer, 1968, pl. 62b). However, this radiograph was taken through the mandible of a large ichthyosaur from Tessin which does not belong to the genus Mixosaurus, and this ichthyosaur has a pleurodont implantation (Besmer, 1947). Therefore, Peyer's comment is irrelevant to Mixosaurus.

Replacement-- Unknown.

Mixosaurus nordenskioeldii (Hulke 1873)

Known Parts-- Maxillary and premaxillary dentitions.

Implantation-- Wiman (1910, p. 130) noted that the teeth are set in "more or less separated alveoli". However, judging from his figure (Wiman, 1910, pl. 5, fig. 8), there seems to be a dental groove anteriorly in the upper jaw, therefore tooth implantation is probably subthecodont in this region. It is possible that tooth implantation in the upper jaw is similar to that in M. cornalianus, where the subthecodont implantation in the anterior region becomes ankylosed thecodont posteriorly, through the reduction of the dental groove.

Replacement-- Unknown.

Note-- I was informed that this species is being assigned to Phalarodon in a paper in press, which I have yet to consult (Nicholls et al., in press).

Pessosaurus polaris (Hulke 1873)

Known Parts-- Jaw fragments of uncertain position.

Implantation-- Wiman (1910) described that the teeth are loosely set in a groove. Judging from his figures (Wiman, 1910, pl. 7, fig. 7 and pl. 10, fig. 28), the root is expanded and folded, as Mazin (1983) mentioned, therefore subthecodont implantation is likely.

Replacement-- Wiman's figure (1910, pl. 10, fig. 28) shows a small tooth between a pair of mature teeth shifted to one side of the dental groove. This small tooth is probably a replacement tooth, and this side of the groove (top in his figure) is possibly lingual, because the dental lamina is located lingually in amniotes. A replacement tooth occurs outside the pulp cavity, possibly disto-lingual of each functional tooth: replacement teeth may move from distal to mesial in other ichthyosaurs, but never from mesial to distal.

Phalarodon fraasi (Merriam 1910)

Known Parts-- Maxillary and posterior mandibular dentitions.

Implantation-- According to Merriam (1910), the posterior teeth are set in sockets in both upper and lower jaws, and the bones of the sockets surround the roots very closely. He noted that the sockets are located at the bottom of a shallow longitudinal groove, at least anteriorly in the upper jaw. The roots are associated with vertical grooves, and the presence of cementum is not established. The sockets cannot be very deep, judging from the depth of the jaws. Although bony fixation is not described, tight sockets and the vertical grooves on the roots are indicative of fixation by bony tissue. The presence of shallow sockets and of a dental groove suggests subthecodont implantation, at least anteriorly in the upper jaw. A dental groove is absent posteriorly, and implantation is therefore ankylosed thecodont. This arrangement of tooth implantation in the upper jaw is similar to that in M. cornalianus. Implantation is certainly not thecodont sensu strico.

Replacement-- Merriam (1910) described two tooth rows per maxilla, one row comprising smaller teeth than the other. P. fraasi has very robust posterior teeth, for which a durophagous diet has been proposed (Merriam, 1910). In the Recent durophagous lizard Dracaena guianensis, which similarly has robust posterior teeth, two tooth rows per maxilla are reported for young individuals (Dalrymple, 1979). The lingual tooth row of the maxilla of D. guianensis comprises replacement teeth for the labial row, and these are larger than the functional teeth: in this lizard species, tooth size, rather than tooth number, increases as it grows. A similar replacement pattern is possible for P. fraasi, or replacement never occurred and the tooth rows were continuously added as in Captorhinus aguti.

Note-- I was informed that this species is being sysnonymized with P. nordenskioeldii in a paper in press (Nicholls et al., in press).

Late Triassic Forms

Himalayasaurus tibetensis Dong 1972

Known Parts-- Almost all parts of the dentition.

Implantation-- Dong (1972) stated that the upper and lower jaws of Himalayasaurus tibetensis have different dental implantations. He called the condition in the lower jaw pleurodont, and that in the upper jaw subpleurodont, a variation of pleurodont with an extensive bone of attachment covering the root.

Replacement-- Unknown.

Note-- I was informed that this species is being declared a nomen dubium in a paper in press (Lucas and González-Léon, in press).

Merriamia zitteli (Merriam 1903)

Known Parts-- Maxillary and posterior mandibular dentitions.

Implantation-- Merriam (1903) described the teeth as set in an open groove, with no evidence of bony partitions between the teeth. The teeth are numerous and closely packed, at least in the posterior portion of the jaw. Merriam figured a transverse-section of the jaw, where a loose dental groove is seen. Therefore, tooth implantation seems to be similar to that described for post-Triassic ichthyosaurs.

Replacement-- Unknown.

Shastasaurus neoscapularis McGowan 1994

Known Parts: All parts of the dentition

Implantation-- McGowan (1994) described the teeth of Shastasaurus neoscapularis as being set in dental grooves. The holotype of the species has the only complete dentition of the genus. Although Merriam (1908) mentioned that Shastasaurus had a dental groove, there was no substantial support for this statement, as Callaway and Massare (1989a) noted. S. neoscapularis establishes the presence of dental grooves in Shastasaurus for the first time. The teeth are numerous and closely packed posteriorly, and the implantation seems to be similar to that described for post-Triassic ichthyosaurs (aulacodonty).

Replacement-- Unknown.

Shonisaurus popularis Camp 1976

Known Parts: All parts of the dentition

Implantation-- Camp (1980) figured and described deep alveoli for the mandibular dentition of Shonisaurus popularis; implantation in the upper jaw was figured for the premaxilla but was not mentioned in the text. The root, which is much longer than the crown, is folded and there is a gap between the teeth and the wall of the socket. According to Camp, the cementum covers the roots as a thin coating and fills the necks of the alveoli. Judging from his figure (Camp, 1980, fig. 23), there is possibly a bony fixation between the bottom of the root and the socket. This implantation would be described as thecodont if it were not for the folding of the root, the possible bony fixation at the bottom, and the cementum filling the neck of the alveolus. Because tooth implantation in Cymbospondylus petrinus is similar to this condition, tooth implantation in S. popularis is tentatively described as ichthyosaurian thecodonty. The teeth are well spaced.

Replacement-- Camp noted that replacement teeth occur in pockets lying against the roots of old teeth. Camp's figure (1980, fig. 2A) depicts two small crypts just beside alveoli, being partially connected to the latter. Their occurrence is similar to that of the replacement teeth in Cymbospondylus petrinus, and to those of sauropterygians. These two crypts are on the same side of the dental row, and, although Camp did not specify the lingual direction in his figure, this side is likely to be lingual, considering the position of the dental lamina.

UCMP 27141 (? Shonisaurus) Callaway and Massare 1989

Known Parts-- Posterior part of the upper and lower dentitions.

Implantation-- Callaway and Massare (1989a) described how the teeth of UCMP 27141 are set in clearly defined sockets. They did not discuss whether the fixation is bony or not. The teeth are well spaced.

Replacement-- Unknown.

Comment--Callaway and Massare (1989a) assigned UCMP 27141 to Shastasaurus altispinus Merriam 1902, based on features of the dorsal vertebrae and podial elements. However, these features are also known for Shonisaurus, a contemporary of Shastasaurus (compare Callaway and Massare, 1989a, figs 5 and 6 to Camp, 1980, figs 29-30 and 50, respectively). Other features of this specimen, namely the teeth set in deep sockets and the premaxilla excluding the nasal from the external naris, have yet to be confirmed in other specimens of Shastasaurus; the former character is known for both Shonisaurus and Cymbospondylus, and the latter for Cymbospondylus. According to Camp's (1980) description, the nasal region of Shonisaurus is represented by inadequate materials, so the reconstruction of this region is speculative. The identification of the specimen as Shastasaurus altispinus is therefore not well established, and it is possible that the specimen may be referable to Shonisaurus, or a new species related to the genus.

Triassic incertae sedis

Thaisaurus chonglakmanii Mazin et al. 1991

Known Parts-- Partial premaxillary and partial mandibular dentitions.

Implantation-- Mazin et al. (1991) stated that the teeth are set in incomplete alveoli without ossified transverse septa, and are tightly fused to the bone. The root is smooth-walled, which is exceptional for ichthyosaurs.

Replacement-- Unknown.

Comment-- Mazin et al. stated that the specimens are from the Lower Triassic, based on the elongated podial elements. However, elongated podial elements are known from other levels of the Triassic, too. Moreover, the age should be determined by evidence independent of the material that is being described. Because associated ammonoids were identified as being Triassic (Mazin et al., 1991), the age of this species is regarded here as Triassic without further subdivision

Post-Triassic Forms

The presence of a dental groove is well established for post-Triassic ichthyosaurs. For example, a dental groove has been described for Platypterygius compylodon from the Cretaceous (Owen, 1851), Ophthalmosaurus icenicus from the Middle and Upper Jurassic (Andrews, 1910), Ichthyosaurus quadriscissus and I. acutirostris from the Upper Liassic (Besmer, 1947), and for Ichthyosaurus sp. from the Lower Liassic (Sollas, 1916). However, tooth implantation is not described for many other post-Triassic ichthyosaurs.

One exception to this mode of implantation has been depicted by Mazin (1988), who described the presence of bony partitions between the posterior maxillary teeth of a partial ichthyosaurian skull from the Toarcian of France. Although this skull was previously identified as Ichthyosaurus tenuirostris, it lacks the diagnostic features, such as the long, slender snout and a well constricted humeral shaft, hence the identification is questionable (McGowan pers. comm.). Moreover, I. tenuirostris is so far known from the Rhaetian to Sinemurian, and not from the Toarcian. Because the anterior part of the skull is missing, only the most posterior two tooth positions are preserved in the figured maxilla, and these are located in a very shallow longitudinal groove (Mazin, 1988; pl. 3a). This longitudinal groove seems to be identical to the dental groove described for the maxilla of Ichthyosaurus (McGowan, 1973), which becomes shallow and wide posteriorly. In Mazin's (1988) specimen, the bony partitions between the tooth positions seem to be incomplete, forming a bar rather than a wall (Mazin, 1983). Tooth implantation in the maxilla of post-Triassic ichthyosaurs has not been well documented, therefore it is possible that the teeth are located in pits at the bottom of the dental groove in the most posterior part, where the dental groove is shallow. Sollas (1916), who made serial cross-sections of the skull of Ichthyosaurus sp. for every 1 mm, did not describe a bony partition between each pair of maxillary teeth. However, it is possible that 1 mm is not fine enough to detect a thin partition.

Tooth replacement in Jurassic ichthyosaurs was described by Edmund (1960). The replacement tooth emerges disto-lingual of each functional tooth, outside the pulp cavity, then moves mesio-labially to replace the functional tooth. A resorption cavity is formed in each functional tooth, allowing the replacement tooth to enter the pulp cavity.

DISCUSSION

Many authors, such as Merriam (1908, 1910), Edinger (1934), Peyer (1968), and Mazin (1983), have stressed that the teeth of Triassic ichthyosaurs are set in sockets, and Merriam and Mazin both applied the term thecodont to this condition. Their arguments are largely based on the condition in Mixosaurus. However, as I have shown, tooth implantation in Mixosaurus has been incorrectly interpreted by these authors, and there is no thecodonty in this genus. My compilation of described tooth implantation of ichthyosaurs shows that dental grooves are more dominant in Triassic ichthyosaurs than deep alveoli (Table 1-2). The only ichthyosaurs without dental grooves are those with ichthyosaurian thecodonty, which slightly differs from the thecodonty of archosaurs for having folded roots and possibly a bony fixation with the bottom of the sockets. Ichthyosaurian thecodonty is only reported for some of the large species from the Middle to Upper Triassic, namely Cymbospondylus petrinus and Shonisaurus popularis, and for UCMP 27141, which probably belongs to Shonisaurus as discussed earlier in this paper.

It is likely that the subthecodont implantation of the oldest ichthyosaurs, such as Utatsusaurus hataii, is ancestral for the group, because subthecodonty is common among early amniotes. Accordingly, the presence of a dental groove, a shallow socket, and bony fixation seems to be plesiomorphic for the Ichthyosauria. The absence of a dental groove in Cymbospondylus and in Shonisaurus is therefore probably a derived character, assuming that ichthyosaurs are monophyletic. This shared derived character may establish the monophyly of the Subfamily Cymbospondylinae Callaway 1989, which was originally designated as a paraphyletic group.

Tooth implantation in ichthyosaurs has three essential elements, namely a dental groove, sockets, and bony fixation. Depending on how the character states for these three are combined, four types of tooth implantation are recognizable, which I refer to as the subthecodont, ankylosed thecodont, aulacodont, and ichthyosaurian thecodont types. The taxonomic distribution of various tooth implantation is summarized in Table 1-1. A brief summary of the features of each type is given in Table 1-2 and Fig. 1-2, while stratigraphical distribution is summarized in Table 1-3.

Table 1-1. Described tooth implantation of various ichthyosaurs.

Descriptions in the literature are compiled for tooth implantation of ichthyosaurs, and are interpreted according to the terminology defined in the text.

EPOCH	TAXON	REFERENCE	Upper Jaw		Lower Jaw	
			Premaxillary	Maxillary	Anterior	Posterior
	Jurassic and Cretaceous ichthyosaurs general	see Text	dental groove			
L. Jurassic	Ichthyosaur from Normandy	Mazin, 1988	?	socket	?	
U. Triassic	*Himalayasaurus tibetensis*	Dong, 1972	subpleurodont		pleurodont	
	Merriamia zitteli	Merriam, 1903	groove			
	UCPM 27141 (? *Shonisaurus*)	Callaway and Massare, 1989	socket			
	Shastasaurus neoscapularis	McGowan, 1994	groove		groove	
	Shonisaurus popularis	Camp, 1980	socket			
		Figure	socket	?	socket	
M. Triassic	*Cymbospondylus petrinus*	Merriam, 1908	?		socket	
	Mixosaurus atavus	Fraas, 1891	groove and shallow socket			
		Huene, 1916	groove and rudimentary socket			
	Mixosaurus cornalianus	Repposi, 1902	groove	socket	groove	
		Besmer, 1947	socket	socket	groove	
	Mixosaurus nordenskioeldii	Wiman, 1910	more or less separated alveoli (=subthecodont?)			
		Figure	subthecodont			
	Phalarodon fraasi	Merriam, 1910	subthecodont?	socket	?	socket
	Pessosaurus polaris	Wiman, 1910	groove			
	Large ichthyosaur from Tessin	Besmer, 1947	?		pleurodont	
L. Triassic	*Grippia longirostris*	Wiman, 1929	pleurodont			
		Wiman, 1933	shallow alveoli (=suthecodont?)			
		Mazin, 1981	fused to the bone (=subthecodont?)			
		Mazin, 1983	thecodont			
		Motani, 1994	?		?	subthecodont
	Utatsusaurus hataii	Motani, 1994	?		pleurodont	subthecodont

Table 1-2. Features of the four types of tooth implantation in ichthyosaurs.

	Dental Groove		Sockets		Root	Taxonomic Distribution
	Anterior	Posterior	Anterior	Posterior		
Subthecodont Type	Y	Y	Shallow	Shallow	Expanded	*Grippia, Utatsusaurus, Pessosaurus*
Ankylosed Thecodont Type	Y	N	Shallow	Moderate	Straight	*Mixosaurus, Phalarodon*
Ichthyosaurian Thecodont Type	N	N	Deep	Deep	Straight	*Cymbospondylus, Shonisaurus*
Aulacodont Type	Y	Y	None	None	Straight	*Merriamia, Shastasaurus, post-Triassic species*

Figure 1-2. Four types of tooth implantation in ichthyosaurs.

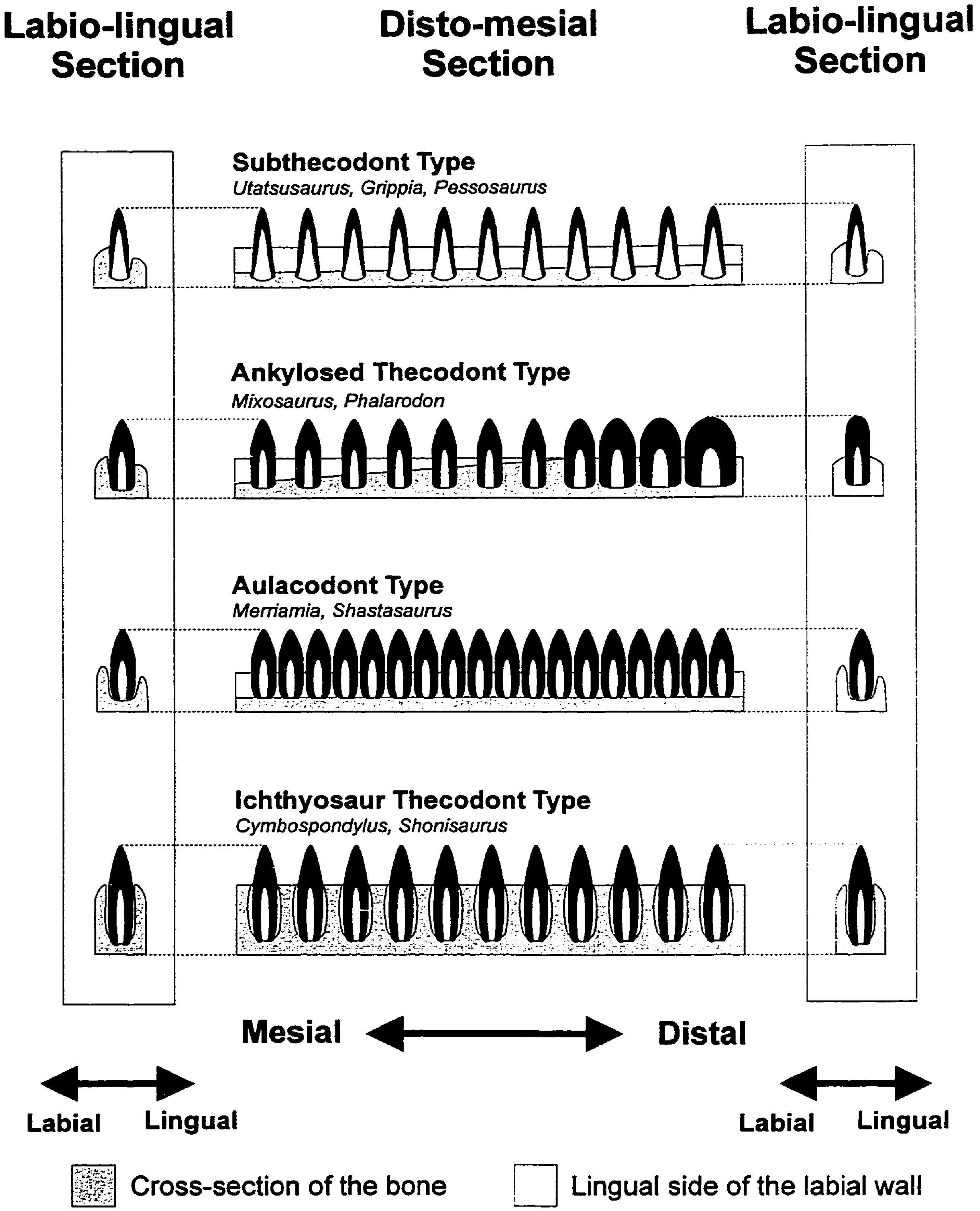

Labio-lingual Section
Disto-mesial Section
Labio-lingual Section
Subthecodont Type
Utatsusaurus, Grippia, Pessosaurus
Ankylosed Thecodont Type
Mixosaurus, Phalarodon
Aulacodont Type
Merriamia, Shastasaurus
Ichthyosaur Thecodont Type
Cymbospondylus, Shonisaurus
Mesial
Distal
Labial
Lingual
Labial
Lingual
Cross-section of the bone
Lingual side of the labial wall

Table 1-3. Stratigraphical distribution of the four types of tooth implantation in ichthyosaurs.

	Stratigraphical Distribution							
	L. Triassic		M. Triassic		U. Triassic			post-Triassic
	...	Spathian	Anisian	Ladinian	Carnian	Norian	Rhaet.	
Subthecodont Type		■	■	■				
Ankylosed Thecodont Type			■	■				
Aulacodont Type					■	■	■	■
Ichthyosaurian Thecodont Type			■	■	■			

Subthecodont Type

Taxonomic Distribution: Utatsusaurus, Grippia, and Pessosaurus

Stratigraphical Distribution: Lower to Middle Triassic

Description: Dental groove is present for the entire tooth-bearing portion of the jaw margin. The teeth are set in shallow sockets located at the bottom of the dental groove to which they are fused. The root of the tooth is expanded, the pulp cavity is open and the walls of the root are folded.

Ankylosed Thecodont Type

Taxonomic Distribution: Mixosaurus and Phalarodon

Stratigraphical Distribution: Middle Triassic

Description: Dental groove is present anteriorly, shallowing posteriorly, and may be absent in the most posterior region. The teeth are usually set in shallow sockets, but posteriorly, where the dental groove is absent, the sockets may be as deep as the height of the crowns. The roots are not very much expanded, and are straight in many cases. The sockets fit tightly to the roots, and fixation is probably bony.

Aulacodont Type

Taxonomic Distribution: Merriamia, Shastasaurus, possibly Himalayasaurus, and post-Triassic ichthyosaurs.

Stratigraphical Distribution: Upper Triassic to Cretaceous.

Description: The teeth are set in a common dental groove which forms the margin of the tooth-bearing portions of the jaws. The teeth may fit inside the groove tightly or loosely, and there is no complete bony partitions between the teeth. Bony fixation may be present at the bottom of the groove, but this is not well established in the literature. The roots of the teeth are not expanded but are straight.

Ichthyosaurian thecodont Type

Taxonomic Distribution: Cymbospondylus and Shonisaurus

Stratigraphical Distribution: Middle to Upper Triassic.

Description: Dental groove is absent and the teeth are set in deep sockets which are deeper than the height of the crowns. Teeth seems to be fused to the bottom of the socket, therefore implantation is not truly thecodont, although there is a gap between the wall of the socket and the tooth. The roots of the teeth are not expanded. Replacement teeth occur in their own crypts, located lingual of the socket of functional teeth.

Although Mazin (1983) suggested that the dental grooves of post-Triassic ichthyosaurs were derived from the thecodont condition in Triassic ichthyosaurs, this is not necessary because the dental groove is probably plesiomorphic for ichthyosaurs. The aulacodont condition could be derived from either the subthecodont or ankylosed thecodont types. The non-expanded root of post-Triassic ichthyosaurs is probably a derived character, but whether this character is homologous with that of the ichthyosaurian thecodont condition cannot be established without a comprehensive phylogenetic analysis of the Ichthyosauria.

The ankylosed thecodont type of implantation can easily be derived from the subthecodont condition, through a strengthening of the tooth fixation in the posterior region of the dentition. All ichthyosaurs with the ankylosed thecodont type of implantation have varying degrees of differentiation in their dentition, more robust teeth being located in the posterior region than in the anterior region, therefore there is a functional advantage for a stronger fixation of the posterior teeth. The tendency of the posterior teeth toward being more strongly fixed to the bone than the anterior teeth is also seen in the upper jaw of an ichthyosaur from the Toarcian of France (Mazin, 1988), and in the mandible of Utatsusaurus (Motani, 1996). This is reasonable on functional grounds: the stress resulting from the adduction of the jaw is higher in the posterior portion of the dentition, hence stronger attachment of the teeth is functionally adaptive.

Fraas (1889) noted that the presence of both a groove and of sockets in M. atavus is very similar to the condition in young crocodilians, but the conditions are not the same. In young individuals of some crocodilians, such as Alligator mississipiensis, dental grooves occur posteriorly because ossification of interalveolar bony septa, which starts anteriorly in the jaw ramus, is still incomplete in this region. In M. atavus, dental grooves are present anteriorly, while posterior teeth are set in independent alveoli.

Peyer (1968) stated that Triassic ichthyosaurs, which he collectively called "mixosaurs", have slight or no folding of the roots. This statement is largely based on Besmer (1947), who figured cross-sections of the teeth of Mixosaurus cornalianus without the folding of the dentine wall, but this is the only example of ichthyosaurian teeth lacking deep folding of the dentine wall (plicidentine). However, plicidentine is reported even for Early Triassic ichthyosaurs, i.e., Grippia longirostris (Mazin, 1981: fig. 7b) and isolated teeth from Spitsbergen (Wiman, 1910: pl. 10, figs. 24-27). It is possible that Besmer's (1947) cross-sections were taken at a higher level than the plicated part of the dentine. However, since plicidentine in Grippia is only reported for the bulbous maxillary teeth, it is necessary to cross-section the teeth of Utatsusaurus, which shows less functional adaptation than those of Grippia, before concluding whether plicidentine is a universal feature among ichthyosaurs. Unfortunately, scarcity of material prevents such a destructive study (Motani, 1996).

All ichthyosaurs have replacement teeth that occur outside the pulp cavity. Although this may be an important synapomorphy for the Order, it has to be tested against a reasonable hypothesis for the ichthyosaurian relationship to other amniotes. Formation of a resorption cavity in the functional tooth that is being replaced is only reported for Jurassic ichthyosaurs, therefore it is probably a derived feature.

SUMMARY

Four essential types of dental implantation are recognized for ichthyosaurs, namely the subthecodont , ankylosed thecodont , ichthyosaurian thecodont , and aulacodont types. The subthecodont type, as exemplified by the oldest ichthyosaurs such as Utatsusaurus, is common among early amniotes, therefore subthecodonty is probably plesiomorphic for ichthyosaurs. Some authors described Mixosaurus and Phalarodon as having thecodont implantation, but they actually possess dental grooves anteriorly and ankylosed thecodont implantation posteriorly, therefore they are categorized as being of the ankylosed thecodont type. The ichthyosaurian thecodont type is rare, and has only been described for Shonisaurus and Cymbospondylus. The aulacodont type, which is the commonest, is dominant among post-Triassic ichthyosaurs, as well as in Late Triassic species. The previously proposed derivation of the aulacodont type from the thecodont type is not necessarily so, because the presence of a dental groove is probably plesiomorphic for ichthyosaurs. Replacement teeth always occur outside the pulp cavities in ichthyosaurs, and this feature may be an important synapomorphy of the group.

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CHAPTER

2

NEW TECHNIQUE FOR RETRODEFORMING TECTONICALLY DEFORMED FOSSILS, WITH EXAMPLES FOR ICHTHYOSAURIAN SPECIMEN

ABSTRACT

A new technique is devised to retrodeform two-dimensional images of tectonically deformed fossils. As opposed to traditional methods that try to find the strain ellipse directly, the present method calculates the two-by-two matrix that represents the retrodeformation first, using simple algebra. This method is widely applicable to various kinds of deformed fossil specimens, including isolated ones, as long as at least two sets of measurements, each set comprising dimensions or angles that were equal to each other prior to tectonic deformation, are available. Application of this method to ichthyosaurian specimens from the Lower Triassic of British Columbia, formerly assigned to the genus Grippia, reveals that the fins of the specimens are wider than previously described, invalidating the ratios and angles that were used for taxonomic arguments. It is not possible to assign the specimens either to Grippia or Utatsusaurus, based on available information.

INTRODUCTION

One of the major impediments to the accurate description of fossil organisms is the tectonic deformation they have undergone. Because such diagenetic modification of the original morphology can lead to taxonomic shortcomings (Cooper 1990; Hughes and Jell 1992), it is important to try to restore the original shape of the material.

As well summarized by Cooper (1990), the published methods for retrodeforming tectonically distorted fossils are designed to restore the two-dimensional images of fossils on the bedding plane, assuming that the deformation is homogeneous within the area being analyzed. The methods utilize measurements of fossils to determine the strain ellipse, the axes of which represent the direction and proportion of the distortion that has occurred. The strain ellipse can be found either graphically (Wellman 1962; Cooper 1990), or by calculating the extensions in various directions (Ramsay and Huber 1983). There are two kinds of measurements that are used: a set of deformed angles which had been equal to one another prior to the distortion (Lake 1943; Sdzuy 1966; Wellman 1962; Cooper 1990; Rushton and Smith 1993), and a set of deformed vectors that had had the same magnitude before being distorted (Hills and Thomas 1944; Cooper 1990). The former will be referred to as deformed equi-angles in the following sections, and the latter as deformed equi-dimensions. The former contains a special case where the angle in question is a right angle, and this kind of data will be referred to as deformed right angles (Cooper 1990).

Although these methods are well established, they require either at least two deformed right angles, three deformed equi-angles, or three deformed equi-dimensions. Such measurements are not always available within an area that is small enough to assume a homogeneous deformation. This is probably one of the reasons why only certain kinds of fossils, such as trilobites, graptolites, belemnites, and crinoids, had been used for the purpose.

In the present paper, I will describe a more generally applicable methodology for retrodeforming distorted fossils. The method is unique in first calculating the two-by-two matrix that represents the retrodeformation process, rather than trying to find the strain ellipse directly. No more than two sets of deformed equi-dimensions are required, therefore it is applicable to a wider range of specimens than previous methods are. I will give an example by applying the method to flattened fossils of a marine reptile (Ichthyosauria). As will be shown, the taxonomy of the specimens was based upon false features formed by tectonic deformation along the bedding plane.

MATERIALS

Abbreviations for the institutions are: IGPS: Institute for Geology and Palaeontology, Tohoku University, Sendai; PMU: Paleontologiska Museet, Uppsala Universitet, Uppsala, Sweden; TMP: Royal Tyrrell Museum of Palaeontology, Alberta.

The materials for the present study are partial ichthyosaurian skeletons referred to Grippia (TMP 89.127.3 and 89.127.12) from the Vega-Phroso Member (Lower Triassic) of the Sulphur Mountain Formation, British Columbia, Canada (Brinkman et al. 1992). The two specimens were collected from the same locality and show similar osteological features, and were therefore considered to represent the same species (Brinkman et al. 1992). TMP 89.127.3 has a well preserved forefin, but both humeri are incomplete. TMP 89.127.12, a larger individual, has a complete humerus, but the rest of the forefin is scattered. Therefore, the description of the forefin of the animal was based on these two specimens (Brinkman et al. 1992). My analysis is based on photographs of the two specimens, kindly provided by Don Brinkman.

Both specimens are compressed into thin sheets of bone along the bedding plane. Brinkman et al. (1992) noted that the right and left radii of TMP 89.127.3, which were preserved with their longitudinal axes approximately perpendicular to each other, differ in length and shape, but the reason for this inequality was unknown. Another unusual feature of the specimen is the shape of vertebral centra. In compressed ichthyosaurian specimens, the centra appear as rectangles in the circumferential view, while in the present specimen, they appear as parallelograms. This is also true for TMP. 89.127.12, suggesting that both specimens have undergone diagenetic distortion in all three dimensions, which altered the shape of the bones along the bedding plane.

Comparative measurements were taken from the specimens of Utatsusaurus hataii (IGPS 95941 and 95942), and of Grippia longirostris (PMU R449, R453, and R472).

METHODS

Model of Deformation

Assumptions.—The following assumptions were made based on my observations of the specimens.

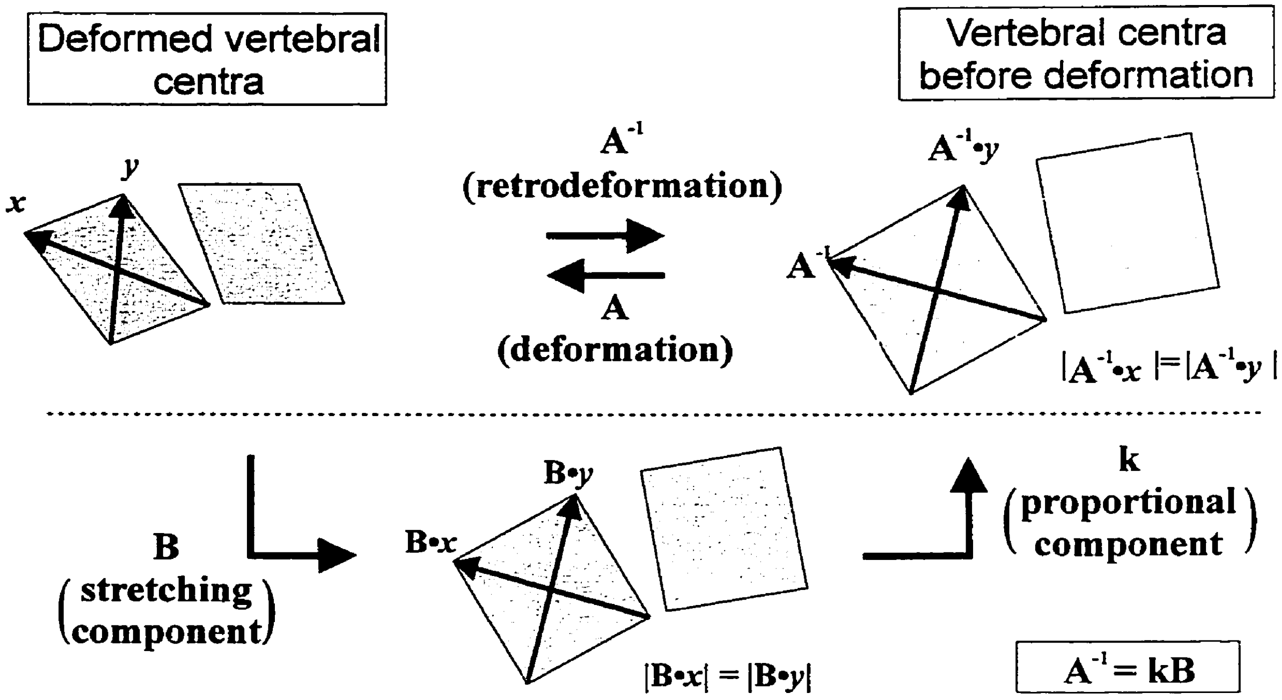
1) The deformation is homogeneous within the area being analyzed because originally parallel lines appear parallel. Therefore, the deformation along the plane can be modeled by a two-dimensional linear transformation, represented by a two-by-two matrix.

2) The right and left radii were deposited from the same aspect, so that their images on the bedding plane were identical (or symmetrical) prior to the deformation.

3) The vertebral centra were approximately cylindrical, and the images of their dorsal and posterior margins on the bedding plane were perpendicular to each other before the deformation.

Figure 2-1. Matrices involved in the method section, and the transformations they represent.

True retrodeformation, defined by A-1, is not possible for the reason explained in the text. A-1 can be expressed as A-1 = kB, k representing the proportional component of the true retrodeformation and B the stretching component. It is possible to restore the original proportion by finding one of many Bs.


Deformed vertebral centra
Vertebral centra before deformation
x
y
A^{-1}
(retrodeformation)
A
(deformation)
$A^{-1}{\bullet}y$
A^{-1}
$|A^{-1}{\bullet}x| = |A^{-1}{\bullet}y|$
B
(stretching component)
$B{\bullet}y$
$B{\bullet}x$
$|B{\bullet}x| = |B{\bullet}y|$
k
(proportional component)
$A^{-1} = kB$

Why true retrodeformation is impossible.—Let **A** be a two-by-two matrix that represents the deformation of a fossil along the bedding plane, then the retrodeformation of the fossil in question can be performed by finding its reverse matrix $\mathbf{A^{-1}}$, which defines the retrodeformation process (Fig. 2-1, above). $\mathbf{A^{-1}}$ can be expressed as

$$A^{-1} = \begin{pmatrix} a & b \\ c & d \end{pmatrix},$$

where a, b, c, and d are real numbers. Therefore, these four components have to be found in order to be able to restore the original shape of the fossil.

Measurements of the specimen are used to calculate the values of the components a, b, c, and d. Let **x** and **y** be the vectors representing a set of deformed equi-dimensions (e.g., two diagonals of the parallelogram component of the centra). Because **x** and **y** had equal magnitudes before the tectonic deformation, they give one equation:

$$|A^{-1} \cdot x| = |A^{-1} \cdot y|. \tag{1}$$

Four sets of such equi-dimensions therefore give four such equations, and because there are only four unknown numbers (i.e., a, b, c, and d), it may appear as if it is possible to solve the simultaneous equations. This, however, is not the case. Equation (1) is based on the similarity alone, while the true retrodeformation may contain proportional component that do not affect the similarity of the image (Fig. 2-1). Therefore information provided by equation (1) is inadequate for finding the proportional component. This means that even when four equations derived from equation (1) are available, information contained in them partially overlap, so the information content equals to when having two such equations. Therefore it is not possible to find $\mathbf{A^{-1}}$ solely based on deformed equi-dimensions.

Restoring only the proportion.--Because the tectonic deformations dealt with here are simple strains, $\mathbf{A}^{-1}$ also represents a simple strain. Therefore, the mapping represented by $\mathbf{A}^{-1}$ is a simple stretching or compression of the image into two orthogonal directions on the observation plane. This means that the mapping does not involve any rotation, and the eigenvectors of $\mathbf{A}^{-1}$ are at a right angle to each other. For the eigenvectors of $\mathbf{A}^{-1}$ to be perpendicular with each other, it is necessary and sufficient that

$$(A^{-1})^T = A^{-1},$$

where $\mathbf{X}^T$ stands for the transposed matrix of $\mathbf{X}$. Therefore $\mathbf{A}^{-1}$ is expressed as

$$A^{-1} = \begin{pmatrix} a & b \\ b & d \end{pmatrix} \tag{2}$$

where a, b, and d are real numbers. It is still impossible to find $\mathbf{A}^{-1}$ based on equi-dimensions, but it is possible to restore the original proportion of the image by finding the matrix **B** in the equation

$$A^{-1} = k \cdot B\ ,$$

where **k** is a real number that defines the proportional transformation and **B** is a matrix that defines the stretching of the image (Fig. 2-1, below). For a given $\mathbf{A}^{-1}$, there are many possible combinations of **ks** and **Bs**, but it suffices to find one of such **Bs** for the purpose of the proportion restoration. For example, by finding appropriate **k**, **B** can be expressed as

$$B = \begin{pmatrix} a' & \pm 1 \\ \pm 1 & d' \end{pmatrix},\ a' \cdot d' > 0 \tag{3}$$

or

$$B = \begin{pmatrix} \pm 1 & 0 \\ 0 & d' \end{pmatrix}, \qquad (4)$$

The condition a'·d'>0 was added because natural deformation cannot possibly convert one fossil into its mirror image. Equation (4) can only be used when the directions of the eigenvectors (i.e., direction of the axes of the strain ellipse) are known, and Lake's (1943) study corresponds to this case. However, such a priori knowledge of those directions is often unavailable, although rough estimates may be given based on slaty cleavage, hence I will use equation (3), which is more generally applicable, in the following sections. Because **B** restores the original proportion,

$$|B \cdot x| = |B \cdot y| \qquad (5)$$

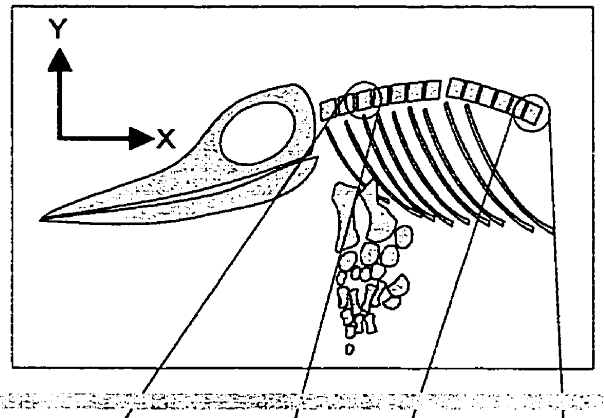
where **x** and **y** are a set of deformed equi-dimensions. **B** has two unknown components in equation (3), and these can be calculated from two sets of vectors satisfying equation (5), defining two simultaneous equations with two unknown numbers.

Calculation and image manipulation.—A Step by step example for the actual calculation and image manipulation is depicted in Fig. 2-2-2. The first step is to capture the image by an image scanner. Once the image is captured as a bitmap, X and Y axes can be arbitrarily set to the horizontal and vertical axes of the bitmap (Fig.2-2, step 1). Vectors for equi-dimensions are then measured as x and y components (Fig. 2-2, step 2). With these measurements and the equations (3) and (5), it is possible to find two **B**s (Fig. 2-2, step 3).

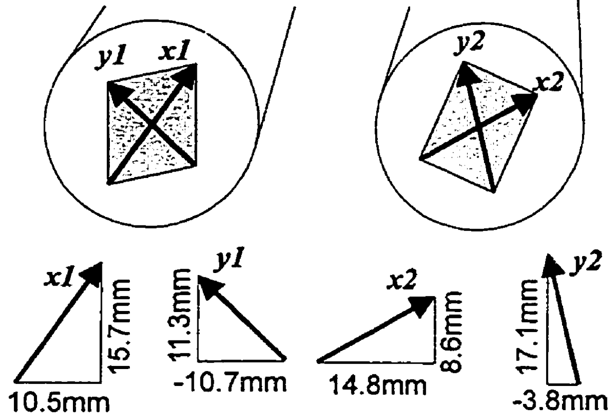
Figure 2-2. Step by step example of the actual application of the method presented in the text.

A schematic image of ichthyosaur fossil, linearly deformed in a computer, is used as the material, and its original proportion is restored by the method described in the text. The second **B** found in the step 3 has negative eigenvalues, and while such **B** can restore the proportion just as well as those with positive eigenvalues, it is difficult to interpret it in terms of a natural process.

Step 1: Scan the image, set the axes



Step 2: Take measurements



$$x1=\begin{pmatrix}10.5\\15.7\end{pmatrix}\ y1=\begin{pmatrix}-10.7\\11.3\end{pmatrix}\ x2=\begin{pmatrix}14.8\\8.6\end{pmatrix}\ y2=\begin{pmatrix}-3.8\\17.1\end{pmatrix}$$

Step 3: Finding matrix B

Given

$$\begin{cases}|B\bullet x1|=|B\bullet y1|\\|B\bullet x2|=|B\bullet y2|\end{cases},\quad B=\begin{pmatrix}a' & \pm1\\ \pm1 & d'\end{pmatrix}$$

Then

$$B=\begin{pmatrix}13.3 & -1\\ -1 & 11.1\end{pmatrix}\quad B'=\begin{pmatrix}-13.3 & 1\\ 1 & -11.1\end{pmatrix}$$

Step 4: Eigenvalues and vectors for B

$$e1=\begin{pmatrix}0.933\\-0.358\end{pmatrix}\quad eigenvalue1=13.7$$

$$e2=\begin{pmatrix}0.358\\0.933\end{pmatrix}\quad eigenvalue2=10.7$$

Step 5: Stretch ratio and angle

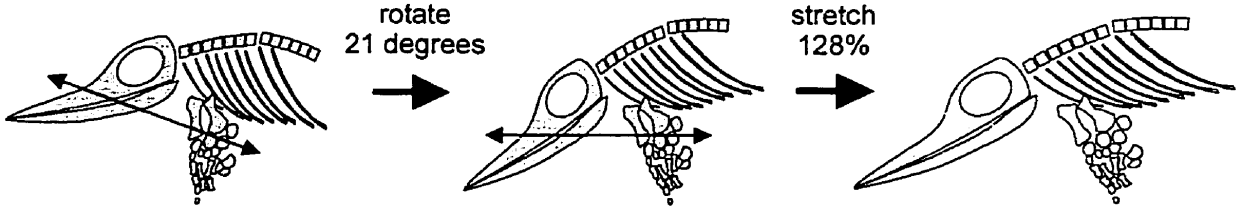
e1 is angled to the x axis at:

$$\operatorname{atan}\left(\frac{-0.358}{0.933}\right)=-21.0°$$

The image should be stretched in the direction of e1 by the factor of:

$$\frac{eigenvalue\ 1}{eigenvalue\ 2}\ x\ 100 = 128\%$$

Step 6: Rotate and stretch the image



This step 3 can be readily performed by mathematical computer software, without expanding the matrix expression (e.g., by using solve block of Mathcad). Once **B** is found, its eigenvectors and eigenvalues can be calculated (Fig. 2-2, step 4), again using computer software. One of the **B**s has positive eigenvalues, while the other has negative ones, and both equally restore the original proportion. However, it is difficult to interpret the latter type as a reversal of a natural process: negative eigenvalues reverse the direction along the two eigenvectors, which results in a 180 degree rotation of the image. Therefore, it is more reasonable to proceed with the **B** with positive eigenvalues.

There is only one pair of originally orthogonal directions that retain their perpendicular relationship after a linear transformation (Ramsay and Huber 1983), and, in the present model, these are parallel to the eigenvectors of **B.** Therefore, reconstruction of the original proportion can be realized by stretching the image in the direction of one of the eigenvectors, by the factor specified by the ratio of eigenvalues (Fig. 2-2, steps 5). Such transformation may differ from the one defined by **B** in the size of the resulting image, but this difference does not affect the restoration of the proportions.

Most graphical software only allows horizontal or vertical stretching, therefore it is first necessary to rotate the image into the appropriate direction. This is done by making eigenvectors parallel to the horizontal and vertical directions of the bitmap (Fig. 2-2, step 6). Finally, the proportion of the image can be restored by stretching it according to the result of the step 5 (Fig. 2-2, step6).

When there are more than two sets of measurements for one specimen, there are two possible procedure to find a single most suitable restoration process: 1) find **B** for every possible combination of the measurement sets, then average the direction and magnitude of stretching that each **B** represents; 2) instead of dealing with two sets at a time, put all available data into the calculation when solving simultaneous equations in the step 3, then find a matrix **B** that minimizes the discrepancy among the data. The latter procedure can be performed using computer software (e.g., Minerr function of Mathcad), and is probably superior to the former, because the former method does not consider all available information simultaneously, which possibly leads to inaccuracy. Therefore, the results from the latter method will be used for the image restoration in the following sections.

APPLICATION TO REAL SPECIMENS

Measurements

Measurements were taken using CorelDraw 5.0, based on the scanned images of the photographs of the specimens. The photographs were scanned as 256-color bitmaps, at the resolution of 600 dpi, using HP Scanjet IIcx. Mathcad 5.0 Plus for Windows performed all the calculations, and the proportion of the image was modified using CorelDraw 5.0.

Four vertebral centra were measured for TMP 89.127.3, and three for TMP. 89.127.12; poor preservation prevented other bones from being included in the analysis. For each centrum, dorsal and posterior margins were measured as vectors, while the vectors connecting the two reference points were recorded for the radii. Vectors representing the dorsal and posterior margins of the centra were converted into their sum and difference, because the latter two are equal to the vectors for the diagonals of the centra (**x** and **y** in Fig. 2-1). The number of data is more than required for the present methodology, which needs only two sets of such measurements per specimen, but additional measurements would increase the accuracy of the results. There are six ways to choose two sets from the four, and three ways from three, therefore **B** was calculated for each of the six (TMP 89.127.3) and three (TMP 89.127.12) combinations. Also, a single **B** that minimizes the discrepancy among measurements was obtained by using the Minerr function of Mathcad.

For simplicity, I will describe each transformation obtained by a vector that is parallel to the eigenvector of **B** in the first quadrant, and whose magnitude is specified by the eigenvalue for that eigenvector divided by the other eigenvalue. That is, the transformation represented by **B** is proportional to stretching the image by the factor specified by the magnitude of this vector, in the direction parallel to this vector.

Results

TMP 89.127.3.—Six transformations were obtained for the six combinations, and the average of the six transformations is represented by a vector that forms the angle of 84.0 degrees anti-clockwise from the x axis, and whose magnitude is 0.775. The Minerr function of Mathcad found a transformation that slightly differs from the above result: it is directed 79.7 degrees anti-clockwise from the x axis, and its magnitude is 0.749. The retrodeformed images of the specimen, based on the latter result, are depicted in Figs. 3A and 4D.

TMP 89.127.12.—Three matrices were obtained for three combinations, and the average of the three is represented by a vector with a direction of 82.7 degrees anti-clockwise from the x axis, and a magnitude of 1.15. The Minerr function of Mathcad found a transformation with exactly the same specification: stretch the image 115 percent in the direction 82.7 degrees anti-clockwise from the x axis. The retrodeformed images of the specimen are given in Fig. 2-3B and 4B.

Discussion

In Fig.2-3, the shapes of the two radii of TMP 89.127.3 became similar to each other, and the vertebral centra of the two specimens appear more rectangular than before, although some of them still appear as parallelograms. The scapulae of the two specimens, which had different shapes prior to retrodeformation, have similar shapes in the retrodeformed images; the same is also true for the coracoids. These observations lend biological support to the accuracy of the retrodeformations. There is a noticeable difference in the length/width ratio of the forefins before and after the retrodeformation (Fig. 2-4).

It is common among published studies of fossil retrodeformations that the results for various measurements from the same slab slightly disagree with one another, as in the present study. In many studies, such variations are compensated for by arbitrarily drawing a best-fit strain ellipse through the distribution of points (Wellman 1962; Cooper 1990). The present method has an advantage over such a subjective technique because of the objectivity in selecting a single transformation.

Two reasons have been suggested for the occurrence of variation in the results: biological variation originally contained in the material (Cooper 1990) and differential deformation between fossils and matrix (Ramsay and Huber 1983). Both kinds of error are probably involved in the present study. For example, the vertebral centra may not appear strictly rectangular due to biological variation. Also, the present skeletons contains large areas of matrix filling the space unoccupied by the bones. This uneven distribution of bones and matrix may have decreased the homogeneity of the strain, due to different physical properties of the two materials involved.

Figure 2-3. Retrodeformed images of (A) TMP 89.127.3 and (B) 89.127.12.

The ellipse and circle in the lower right corner of each image indicate the transformation involved in the retrodeformation. The ellipse is the strain ellipse of the tectonic deformation that altered the specimen into the present state, with the directions of arbitrarily chosen x and y axes indicated by two perpendicular lines. The circle resulted from the retrodeformation of the strain ellipse, and the coordinate axes are no longer orthogonal in the former. Note that the two radii in A are similarly shaped. No scale is available due to the nature of the retrodeformation method (see text). Co: coracoid; H: humerus; R: radius; S: scapula; U: ulna; dc1: distal carpal 1; in: intermedium; mc: unidentified metacarpal; pi: pisiform; r: radiale; u: ulnare; i: metacarpal 1; v: metacarpal 5; 1-30: vertebral column. Modified from Brinkman et al. (1992).

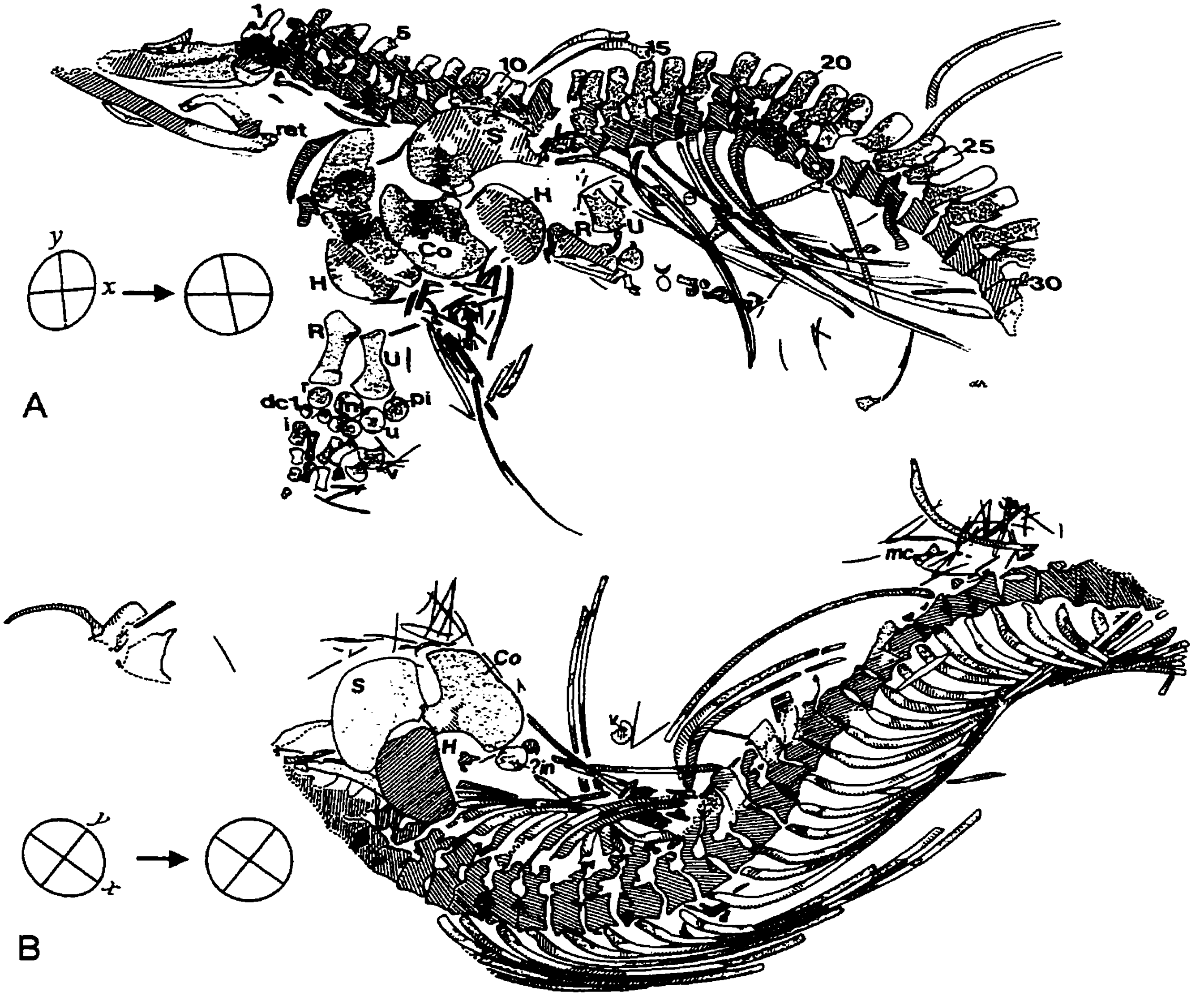

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Figure 2-4. The humerus of TMP 89.127.12 (A and B) and the left forefin of TMP 89.127.3 (C and D), before (A and C) and after (B and D) retrodeformation.

Note that the forefin elements are wider in B and D than in A and C, and the proximal articular facets of the radius and ulna are less steeply angled with respect to the longitudinal axes of the elements. No scales are available for B and D, due to the nature of the retrodeformation method (see text). See Fig. 2-3 for the identification of the bones.


A
B
C
D

TAXONOMIC IMPLICATION

The taxonomy of the specimens was based upon six features of the forefin (Brinkman et al. 1992, table 2), the only diagnostic structure preserved. The forefins of the present specimens resemble those of two Early Triassic ichthyosaurs, Grippia longirostris from Spitsbergen and Utatsusaurus hataii from Japan, and Brinkman et al. (1992) tried to determine the closest affinity. Five of these features were also used by Mazin (1986), when attempting to distinguish between the forefins of G. longirostris and U. hataii. Brinkman et al. (1992) found that their material closely matches G. longirostris in two of the six features (viz., the angle formed by the proximal end of the radius, and the symmetry of the ulna), while matching U. hataii in two others (viz., width/length ratio of the humerus, and the relative size of the distal carpals compared to the proximal carpals). The remaining two features (viz., shape of the distal end of the humerus and that of the basal phalanges) were considered to be of no taxonomic significance. They found that the similarities between the epipodials of these materials and of G. longirostris were "striking", and accordingly referred the specimens to Grippia. However, some of these features are artifacts of tectonic deformation, as shown below.

I have re-measured all of these features for G. longirostris and U. hataii, and found that the values listed by Mazin (1986) are unreliable. This is probably because the specimens of U. hataii were only incompletely prepared at the time when Mazin examined the material (Motani 1996, in press). Moreover, the published figure of the forefin of G. longirostris (Mazin 1981, fig. 11), with which Mazin's (1986) measurements agree well, is incorrect. According to my examination of prepared specimens, none of the features seem to be useful in distinguishing between the two species (Table 2-1). Forefin measurements taken from the retrodeformed images of the present specimens do not indicate a clear resemblance to either G. longirostris or

U. hataii (Table 2-1). I conclude that it is not possible to determine the affinity of the present specimens on these features.

Table 2-1. Corrected data for the features previously used for distinguishing between Grippia longirostris and Utatsusaurus hataii.

The data have been replaced from Brinkman et al. (1992:table 2), based on observations and measurements of the actual specimens of G. longirostris and U. hataii, and of retrodeformed images of the present specimens. There seems to be no taxonomic structure in the data, invalidating the proposed affinity of the present specimens to G. longirostris. Two values separated by a comma indicate measurements from different specimens of the same species.

	Grippia longirostris	*Utatsusaurus hataii*	Present Specimens
Width/length ratio of the humerus	0.67	0.60, 0.62	0.70
Angle between articular surfaces for the radius and ulna	126°	138°	146°
Angle formed between proximal articular surface and general axis of radius	64°	79°	61°
Ulna shape	Asymmetrical	Asymmetrical	Asymmetrical
Size of distal carpals relative to the size of the proximal carpals	Less than half	Less than half	Less than half
Basal phalanges of fourth digit	Longer than broad	Longer than broad	Longer than broad

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CHAPTER 3 THE FIRST COMPLETE FOREFIN OF GRIPPIA LONGIROSTRIS DISCOVERED FROM AN HISTORICAL SPECIMEN

ABSTRACT

A new and nearly complete forefin was discovered in the slab containing one of the referred specimens of Grippia longirostris (Ichthyosauria). 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 speculation of previous authors, the terminal phalanges are not ungual. The forefin resembles that of Utatsusaurus hataii, another Spathian ichthyosaur, but is more derived, sharing four synapomorphies with Mixosaurus cornalianus, a slightly younger ichthyosaur from the Middle Triassic. The ichthyosaurian forefins described from British Columbia as belonging to Grippia, lack at least two of these synapomorphies, and therefore cannot be assigned to this genus. The partial hindfin of Grippia, also described from British Columbia, shares the topology of the new forefin, and its identification as a hindfin is questioned.

INTRODUCTION

The earliest ichthyosaur species occur from the Spathian of the Lower Triassic (Callaway and Massare, 1989), and Grippia longirostris from Spitsbergen (Wiman, 1929, 1933) was the first to be described from that stage. Although three additional Spathian genera, namely Chaohusaurus (Young and Dong, 1972), Utatsusaurus (Shikama et al., 1978), and Chensaurus (Anhuisaurus of Chen [1985] was preoccupied, so Mazin et al., [1991] changed the generic name]), have been described since, the studies of early ichthyosaurs have been biased towards G. longirostris (Mazin, 1981, 1982, 1986; Callaway 1989; Massare and Callaway 1990). However, the species is only known from fragmentary materials (Wiman, 1933; Mazin, 1981; Motani, 1997), which led the previous authors to rely upon 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 the major impediment to the study of ichthyosaurian evolution.

Forefins are among the most informative structures for ichthyosaurian systematics, but they are poorly known for Grippia longirostris. Wiman's (1929) first description of the species was based upon one specimen, a skull that lacks the snout. Preserved between the mandibular rami of this skull was an isolated, key-hole shaped fin element, which Wiman (1929) believed was an ungual phalanx similar to that of hadrosaurs. A later expedition to Spitsbergen brought back additional specimens (Wiman, 1933), but none were 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 comprised mostly isolated elements. In the absence of a complete forelimb, Wiman (1933) maintained his previous speculation on ungual phalanges, arguing that G. longirostris retained a limb that was not as well adapted to aquatic environment as were 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. He depicted a limb with a hoof at the tip of each digit, following Wiman's (1929) speculation. Mazin (1986) further argued that G. longirostris was more primitive than Utatsusaurus hataii, another Spathian ichthyosaur, based on the supposed possession of less aquatically adapted forelimbs.

A close examination of Wiman's (1933) nodule 8 revealed a second humerus, undescribed by Wiman (1933), lying beside the original one. It was likely that the rest of this second forefin was preserved within the slab. This was confirmed using medical CT-scanning, after conventional radiography failed, probably because the bones are thin and less dense than the surrounding matrix, resulting in poor contrast. The new forefin was subsequently exposed by mechanical preparation, and its description is the subject of the present paper.

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 primary specimen for the present study, which Wiman (1933) called nodule 8, is now registered as PMU R472. References are also made to the other specimens of Grippia longirostris, namely 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), namely RTMP 89.127.3, 89.127.12, and 89.128.5, were also examined.

Only the middle part of PMU R472, where the second fin is located, was prepared, to preserve as much of this historical specimen as possible. Preparation was performed under a binocular microscope, using an airscriber and mounted needles. Acid preparation, using 10 percent acetic acid, proved unsuccessful. A CT-scanner (General Electric Advantage Hispeed) was used to locate the hidden forefin before the preparation. Scans were made every 1 mm, with a thickness of 1 mm, and the image of the hidden forefin was reconstructed two-dimensionally by computer, based on these scans. The image obtained was referred to during preparation to reduce the risk of damaging the bones.

DESCRIPTION

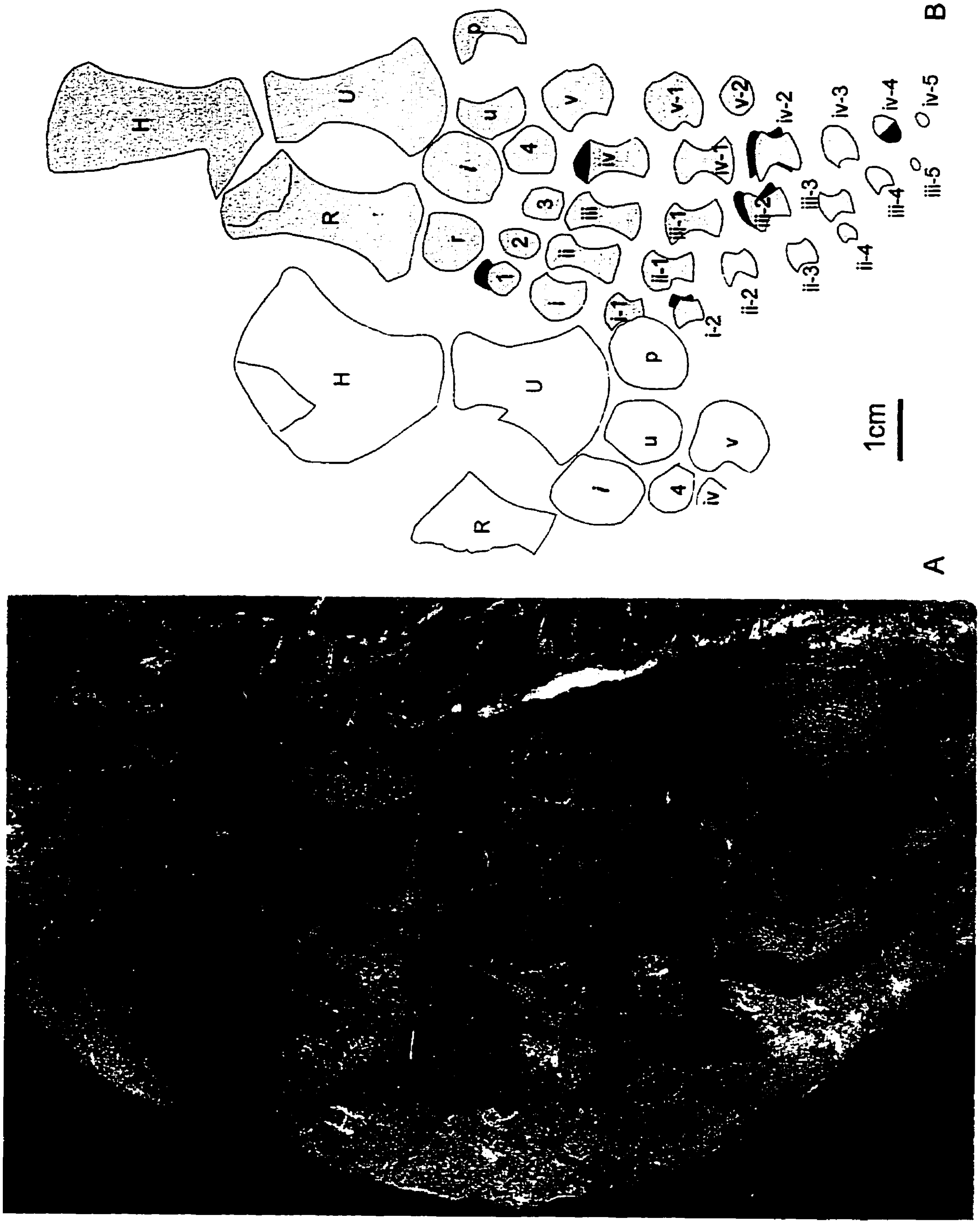
A partial forefin was originally exposed along the circular edge of PMU R472 (Fig. 3-1), and figured by Wiman (1933, pl. 2, fig. 2). The bones are weathered, some badly, and the distal part of the fin is not preserved. The newly discovered forefin is located on the right side of this fin (Fig. 3-1), with its humerus, radius, ulna, pisiform, and the fifth metacarpal having being partially exposed naturally, and subjected to the same weathering that damaged the other fin. The pisiform and the fifth metacarpal are further damaged by a crack running through the middle of the slab (Fig. 3-1), which had 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, therefore they most likely 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 in ventral view, while the other is the left forefin exposed dorsally.

The descriptions in the following paragraphs are based on the right forefin of PMU R472, unless otherwise noted. The forefin is pentadactyl, with the preserved phalangeal formula of 2-4-5-5-2. Distal elements could be missing from digits one, two, and five, but probably not more than one element per digit, judging from the small sizes of the preserved ones. The fifth phalanges of digits three and four are so small that they are likely to be the terminal ones. Therefore there were no more than five phalangeal ossifications in any of the digits. This, however, does not preclude the possibility that unossified phalanges existed distally. All manal elements are well spaced from each other, in contrast to the forefin of Utatsusaurus.

Both humeri of PMU R472 are badly eroded, and only the outline can be observed. The humerus is as wide as it is long (Fig. 3-1), largely due to a well-developed articular facet for the

Figure 3-1. Grippia longirostris, 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 gray) 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 (dark gray). Black areas represent the indentation described in text, and dashed lines are reconstructions of the missing parts. Abbreviations: H, humerus; R, radius; U, ulna; i, intermedium; p, pisiform; r, radiale; u, ulnare; 1-4, distal carpals; i-v, metacarpals; i1-v2, phalanges. Natural size.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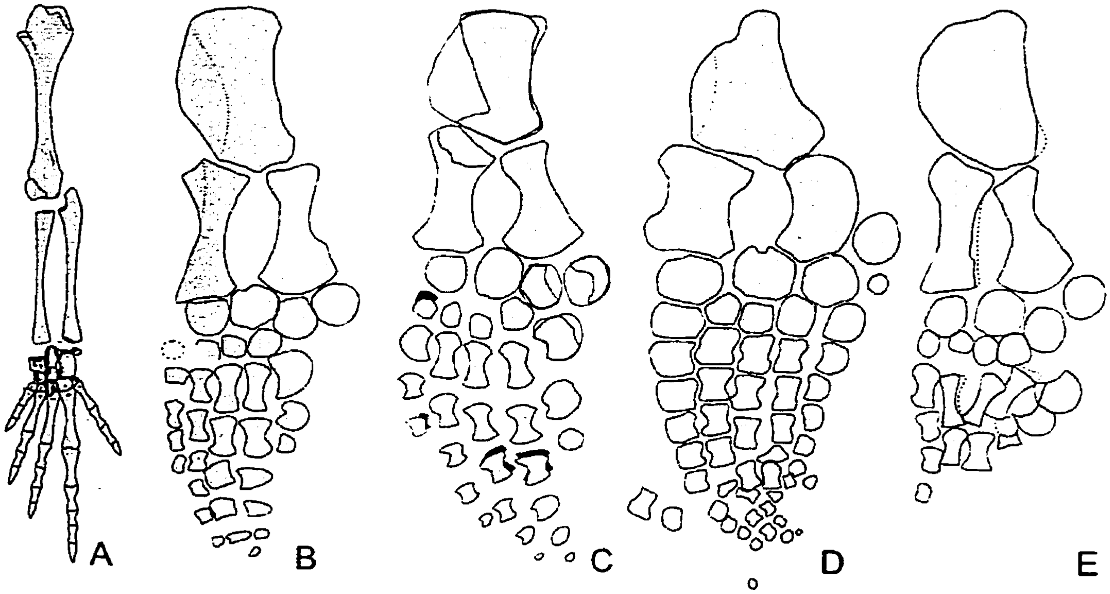
radius, and a bony flange anterior to the shaft. Wiman (1933) figured two types of anterior flanges for Grippia longirostris, one is well developed (PMU R474), and the other is narrow (PMU R447 and R453). In PMU R447 and R453, the bones are preserved as natural molds, and the molds of the humeri are incomplete anteriorly, suggesting that the humeri did have well-developed anterior flanges, as in PMU R472 and R474. Mazin's (1981) reconstruction seems to be based on PMU R447, without considering the incompleteness of the specimen, and is therefore too slender.

The proximal part of the radius, which was originally exposed, has been weathered away. However, its impression is preserved as a natural mold, enabling a reasonable reconstruction of its outline. The radius is similarly shaped as the one depicted by Wiman (1933) for PMU R449, although Wiman's figure is upside down (i.e., the distal end up). There is a prominence proximally, anterior to the articular facet for the humerus (Fig. 3-1, bracket), as in Utatsusaurus (Motani, in press). This prominence is entirely absent from Mazin's (1981) reconstruction. The ulna is also similar to that of Utatsusaurus, in that it expands distally into a fan shape (Fig. 3-2). The articular facet of the ulna for the humerus is wider than that of the humerus for the ulna, again resembling Utatsusaurus. The only ulna depicted by Wiman (1933) was the left one of PMU R472, which is 23 percent shorter than the newly exposed right one. The left ulna seems to be broken in the middle, and it is likely that this breakage resulted in the observed shortness. Both radius and ulna are more robust than in Utatsusaurus (Fig. 3-2).

There are four proximal carpals, all of which are similarly sized, but the intermedium is slightly larger than the others (Fig. 3-1). The outline of each element resembles that of Utatsusaurus, thus the pisiform is oval, the ulnare is somewhat pentagonal but with a rounded

Figure. 3-2. A 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, Utatsusaurus hataii, modified from Motani (in press). C, Grippia longirostris, a composite of the right and left forefin of PMU R472; dark gray for 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 undeformed according to the method described in Chapter 2. Not to scale.


A
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E

distal margin, the intermedium is elongated, and the radiale has a straight proximal margin (Fig. 3-2B, C). Four distal carpals are present, supporting the first four digits. The fourth one is the largest of the four, but its diameter is only about half that of the proximal carpals (Fig. 3-1). Mazin (1986) claimed that the distal carpals are approximately the same size as the proximal ones are, but no such evidence exists in any of the specimens. All carpals are well separated from each other, suggesting osteological immaturity of the individual.

Two types of metacarpals are recognizable: lunate ones (the first and fifth) and normal ones (the second to fourth). The normal ones resemble the cylindrical phalanges of many other amniotes, but are flattened. The extremities of these metacarpals are well expanded, which may suggest that the epiphyses are at lease partially ossified. This suggests the osteological maturity of the individual, which is contrary to the well-spaced carpals and phalanges. The lunate metacarpals occur along the anterior and posterior margins of the fin, with their concave sides facing towards its longitudinal axis. This type could derive from the normal type through the loss 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 compared to U. hataii, and it would have contacted the ulnare with further growth.

The phalanges are similar to the metacarpals in that there are lunate and normal types, and that the lunate type occurs near the margins of the fin. However, in addition to these two types, there is a third type that is entirely oval, and which appears toward the distal end of the fin (e.g., the fourth and fifth phalanges of the fourth digit; see Fig. 3-1B). This oval type, which entirely lacks perichondral ossification, is not known in Utatsusaurus (Motani, in press), but is commonly observed in later ichthyosaurs, towards the tip of the fins (McGowan 1991, fig. 4). These oval phalanges seem to have no perichondral ossification. There is no trace of an ungual phalanx, contrary to Wiman's (1929, 1933) speculation, as followed by Mazin (1981,1986). Wiman's supposed ungual phalanx is probably a proximal phalanx, because some of those elements are also key-hole shaped (e.g., the second phalanx of the third digit; see Fig. 3-1B). The fourth phalanx of the fourth digit is deeply grooved antero-ventrally, and although this may seem like a mechanical breakage during the preparation, it is natural. The fourth metacarpal is also naturally indented at the proximal end.

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 (Fig. 3-1B, elements in dark gray). There the dorsal plates are located relatively proximal to their ventral counterparts, revealing 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 the metacarpals. It is possible that the constricted parts of these phalanges are associated with little perichondral bone, leading to a weak bond between the dorsal and ventral plates. A similar slipping occurs in the first distal carpal, suggesting that its ossification patterns may have been similar. The dorsal and ventral plates are almost identically shaped in all slipped elements, and the spongy structure is not covered by a secondary ossification, therefore the slipping was probably a post-mortem phenomenon. All four elements were probably dislocated by the same force, because the directions and the magnitudes of the slipping are nearly uniform among the elements. One possible interpretation is that the deposition of the dead animal rotated the horizontal forefin into the vertical position, which pulled the dorsal connective tissues proximally while pushing the ventral ones distally, causing a shearing inside the fin that split some elements with mechanically weak planes. This, however, is speculative.

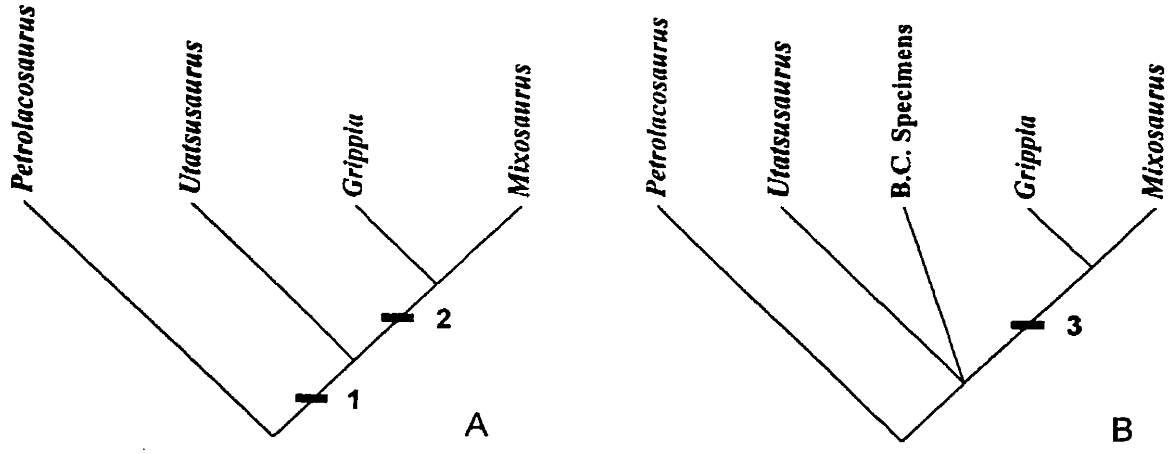
DISCUSSION

The first question concerns whether PMU R472 represents an osteologically immature individual. Johnson (1977) pointed out four forefin features that indicate osteological immaturity in Stenopterygius, an Upper Liassic ichthyosaurs: 1) humeral head incompletely ossified, 2) rough surface of the humeral shaft, 3) proximal elements not well packed, and 4) absence of notched elements in the first digit (in applicable species). 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 in the first digit are known only in Late Triassic and later ichthyosaurs. This only leaves feature 3, which indicates that PMU R472 is immature. 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 remarkably shorter than the largest known humerus (PMU R474), being about 63 percent of the latter. Also, the vertebrae of PMU R472 are nearly half the size of those in the largest vertebral series (PMU R456). Moreover, well spaced phalanges suggest that the ossification of the epiphyses is incomplete, therefore the expanded extremities of the metacarpals and phalanges reflect the shape of the diaphyses rather than that of the epiphyses. Therefore, I conclude that PMU R472 is osteologically immature, and that the well-expanded extremities of the metacarpals and phalanges do not necessarily indicate maturity.

The second question is which of Grippia longirostris and Utatsusaurus hataii has the more derived forefin. To address this question, these two pectoral limbs were compared with those of Petrolacosaurus kansensis (the earliest diapsid, from the Pennsylvanian) and Mixosaurus cornalianus (Middle Triassic ichthyosaur; Fig. 3-2D). P. kansensis was used as the outgroup because ichthyosaurs are most likely diapsids (Massare and Callaway, 1990). The monophyly of U. hataii, G. longirostris, and M. cornalianus is established by at least five features of the pectoral limb: 1) anterior flange of 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 elements present distally (i.e., occurrence of phalanges without perichondral ossification); 2) first metacarpal lunate (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 distally expanded shape of the bone; and 4) manus clearly longer than the propodial and epipodials combined. Although no complete first metacarpal is known for U. hataii, it is obviously not lunate, judging from the preserved part in the holotype. On the other hand, there are no obvious traits shared between U. hataii and M. cornalianus that are not present in P. kansensis or G. longirostris. Also, U. hataii and G. longirostris do not share any traits that are absent in M. cornalianus and P. kansensis. Therefore, by a simple three-taxon statement, it is likely that G. longirostris forms a clade with M. cornalianus, and U. hataii is the sister group of this clade (Fig. 3-3A). It is desirable to conduct a larger scale cladistic analysis that involves other characters from the rest of the skeleton, as well as including other ichthyosaur species. However, very little is known about these early ichthyosaurs, and such an analysis requires extensive primary study of these forms, which is beyond the scope of the present paper.

Figure. 3-3. Preliminary phylogenetic hypotheses for early ichthyosaurs, based on the forefin features.

A, cladogram for Utatsusaurus hataii, Grippia longirostris, and Mixosaurus cornalianus, with Petrolacosaurus kansensis as the outgroup. B, The unnamed species represented by the forefins from British Columbia was added to A, revealing that the assignment of this species to Grippia (Brinkman et al., 1992) is inappropriate. The numbered internodes are characterized by the following synapomorphies: 1, anterior flange of the humerus; lunate fifth metacarpal; flattened fin elements; hyperphalangy in the second and third digits; antero-proximal prominence of 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; 3, lunate first metacarpal; humerus with an expanded articular facet for the radius. See text for discussion.


Petrolacosaurus
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3
B

The third question concerns the identity of the forefin materials from the Lower Triassic of British Columbia, described by Brinkman et al. (1992) as belonging to the monotypic genus Grippia (RTMP 89.127.3 and 89.127.12). Brinkman et al. (1992) referred the specimens to Grippia based on the examination of six features, five of which are from Mazin (1986). I have shown elsewhere that these specimens were tectonically distorted, and linear undeformation of the images of the forefins, based on measurements of the vertebral centra, revealed somewhat wider shapes than originally described (Chapter 2). I also showed that none of the six features were taxonomically significant for resolving the affinity of the British Columbia fins (Chapter 2). Now that the new forefin of G. longirostris is available, it is possible to continue this taxonomic discussion. The species represented by RTMP 89.127.3 and 89.127.12 has: 1) first metacarpal that is not lunate, and 2) humerus that is not distally expanded (Fig. 3-2E). Therefore this species lacks the synapomorphies for G. longirostris and M. cornalianus, hence it cannot be referred to Grippia (Fig. 3-3B). Whether it had oval phalanges, or whether the manus was large, is unknown due to poor preservation distally. The forefin of this species resembles that of U. hataii in many respects, but it is much smaller. There are similarly small ichthyosaurs reported from the Lower Triassic of China (Young and Dong 1972; Chen 1985; Motani et al. 1996), and examination of these specimens is necessary before resolving the present taxonomic problem.

Brinkman et al. (1992) described a partial ichthyosaurian fin from the Lower Triassic of British Columbia (RTMP 89.128.5), referring to it as a hindfin. This fin, however, is more likely a forefin, or at least it is impossible to identify it as a hindfin. The propodial and epipodial elements are not preserved in this specimen, and the proximal mesopodials are incomplete, making it difficult to determine whether it is pectoral or pelvic. The fin is very similar to the forefin of Utatsusaurus hataii, but differs from it in that the fifth metapodial is located more proximally, almost contacting the proximal mesopodial elements. The new forefin of Grippia longirostris (PMU R472), however, has the fifth metapodial located in a similar position as in RTMP 89.128.5, and even though the element does not contact the proximal mesopodial elements, it would have if its growth had continued (PMU R472 is immature, while RTMP 89.128.5 is large, and with well-packed mesopodial elements, suggesting osteological maturity [Brinkman et al., 1992]). Therefore the position of the fifth metapodial cannot be used as a criterion for distinguishing between the forefin and hindfin. This new interpretation suggests that RTMP 89.128.5 is a forefin. Furthermore, identification of RTMP 89.128.5 as a hindfin postulates the presence of the pes centrale (Brinkman et al., 1992), which is clearly lacking in Mixosaurus, a slightly younger ichthyosaur from the Middle Triassic.

SUMMARY

Study of a nearly complete forefin of Grippia longirostris, discovered from the slab containing one of the referred specimens, presents the following conclusions.

1) The preserved phalangeal formula is 2-4-5-5-2, and the true formula is probably less than 3-5-5-5-3, therefore there are no more than five phalangeal ossifications per digit.
2) There is no ungual phalanx at the tip of each digit, and Wiman's (1929, 1933) supposed ungual phalanx is most likely a proximal one.
3) The forefin belongs to an immature individual, because the proximal carpals are well spaced, and the size of the humerus is much smaller than the largest humerus known for the species.

4) The forefin is more derived than that of Utatsusaurus hataii, in that perichondral ossification is lost along the anterior margin of the first metacarpal; oval phalanges without perichondral bone exist towards the tip; the humerus is distally expanded due to a large articular facet for the radius; and the manus is large, occupying more than half of the entire fin.

5) Lower Triassic ichthyosaurian forefins from British Columbia, which were assigned to Grippia by Brinkman et al. (1992), cannot be assigned to this genus.

6) The ichthyosaurian hindfin described by Brinkman et al. (1992) is more likely a forefin, or at least cannot be positively identified as a hindfin.

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CHAPTER 4 THE FOREFIN OF CHENSAURUS CHAOXIANENSIS (ICHTHYOSAURIA) SHOWS DELAYED MESOPODIAL OSSIFICATION

ABSTRACT

The hitherto poorly known forefin of Chensaurus chaoxianensis (Ichthyosauria) is redescribed, based on the holotype and two new specimens. The humerus resembles that of Utatsusaurus hataii, but is distinctive in having an emargination in the middle of the anterior margin. The anteroproximal prominence of the radius is well developed, unlike that of other ichthyosaurs. All three specimens have five metacarpals and many phalanges, but only three carpals, which are identified as the ulnare, intermedium, and the fourth distal carpal. These specimens show, for the first time, that delayed mesopodial ossification occurred in ichthyosaurs, at least in the earliest stage of their evolution. Delay in mesopodial ossification is common among diapsids but absent in Jurassic ichthyosaurs, and therefore it was lost during the evolution of the Ichthyosauria. The osteogenic developmental axis appears to have continued into the fourth digit, as in other amniotes. The ossification pattern provides conclusive evidence supporting the suggestion made by some authors that the basal element of the fifth digit in Early Triassic ichthyosaurs is a metacarpal, rather than a carpal.

INTRODUCTION

Ichthyosaurian limbs are usually referred to as fins because of their appearance. This aquatic adaptation involved an extensive modification of limb bones, therefore it is difficult to compare ichthyosaurian limbs with those of terrestrial amniotes. In advanced Jurassic forms, such as Stenopterygius and Ichthyosaurus, the epipodial, mesopodial, and metapodial elements are all similarly shaped, obscuring the distinction among these three areas (McGowan, 1972;Johnson, 1977;Caldwell, in press a). On the other hand, the earliest ichthyosaurs from the Lower Triassic (Spathian), such as Utatsusaurus, have distinctively shaped mesopodial elements arranged as in some terrestrial diapsids (Brinkman et al., 1992; Motani, in press).

It is known for diapsids that the mesopodial region usually becomes ossified later than the other areas of the limb (Rieppel, 1992a,b,c,1993; Caldwell, 1994). Caldwell (in press a, b) recently discussed the mesopodial development in ichthyosaurs for the first time, reporting that there is no delay in the mesopodial ossification, at least not for Stenopterygius, from the Lower Jurassic. Whether the lack of delayed mesopodial ossification is unique to advanced ichthyosaurs like Stenopterygius, or whether it is common to all ichthyosaurs was not known, because no juvenile specimens had been reported from the Lower Triassic.

Reexamination of the holotype of Chensaurus chaoxianensis revealed that the forefins of the specimen, which were poorly described, showed some juvenile features. Unfortunately the forefins are only half complete, therefore the entire forefin morphology has to be described from other specimens. Additional ichthyosaurian specimens have been collected from the type locality of C. chaoxianensis, and nearby quarries, since the study of Chen (1985), one of which was briefly reported by Motani et al. (1996). Among the undescribed material are two nearly complete forefins that are suitable for descriptive studies. The purpose of the present paper is threefold: 1) redescribe the holotype forefin of C. chaoxianensis to clarify the diagnostic features; 2) describe new and well preserved forefins that are identified as C. chaoxianensis based on these diagnostic features; and 3) discuss the juvenile features in these forefins.

MATERIALS AND METHODS

The abbreviations used for the institutions are as follows: AGM- Anhui Geological Museum, Hefei, China; IGPS- Institute of Geology and Paleontology, Tohoku University, Sendai; and IVPP- Institute for Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing.

The holotype of *Chensaurus chaoxianensis* (Chen) 1985 is stored at AGM, and retains the field number given by Chen (1985), P45-H85-25. The generic name was given by Mazin et al. (1991) as a replacement for *Anhuisaurus* of Chen (1985), which was preoccupied. The new forefins are a part of the ichthyosaurian fossil collection made by Hailu You during 1991. They are registered at IVPP, and are numbered IVPP V11361 and V11362. IVPP V11361 is preserved in a gray limestone slab, while IVPP V11362 is in a brown mudstone slab. Although the rock types are different, they are from the same biostratigraphical zone of the type locality of *Chensaurus chaoxianensis*, located at Majia-Shan, Chao County, Anhui Province, P.R. China. More detailed stratigraphical information can be found in Chen (1985).

The specimens used for comparisons are IGPS 95941 and 95942, the holotype and one of the paratypes of *Utatsusaurus hataii* Shikama, Kamei, and Murata 1978. The holotype of *U. hataii* is not fully mature (Motani, in press), but is more mature than IVPP V11361 and V11362. Measurements were taken using digital calipers, and recorded to the nearest 0.1 mm.

DIAGNOSTIC FEATURES OF THE HOLOTYPE

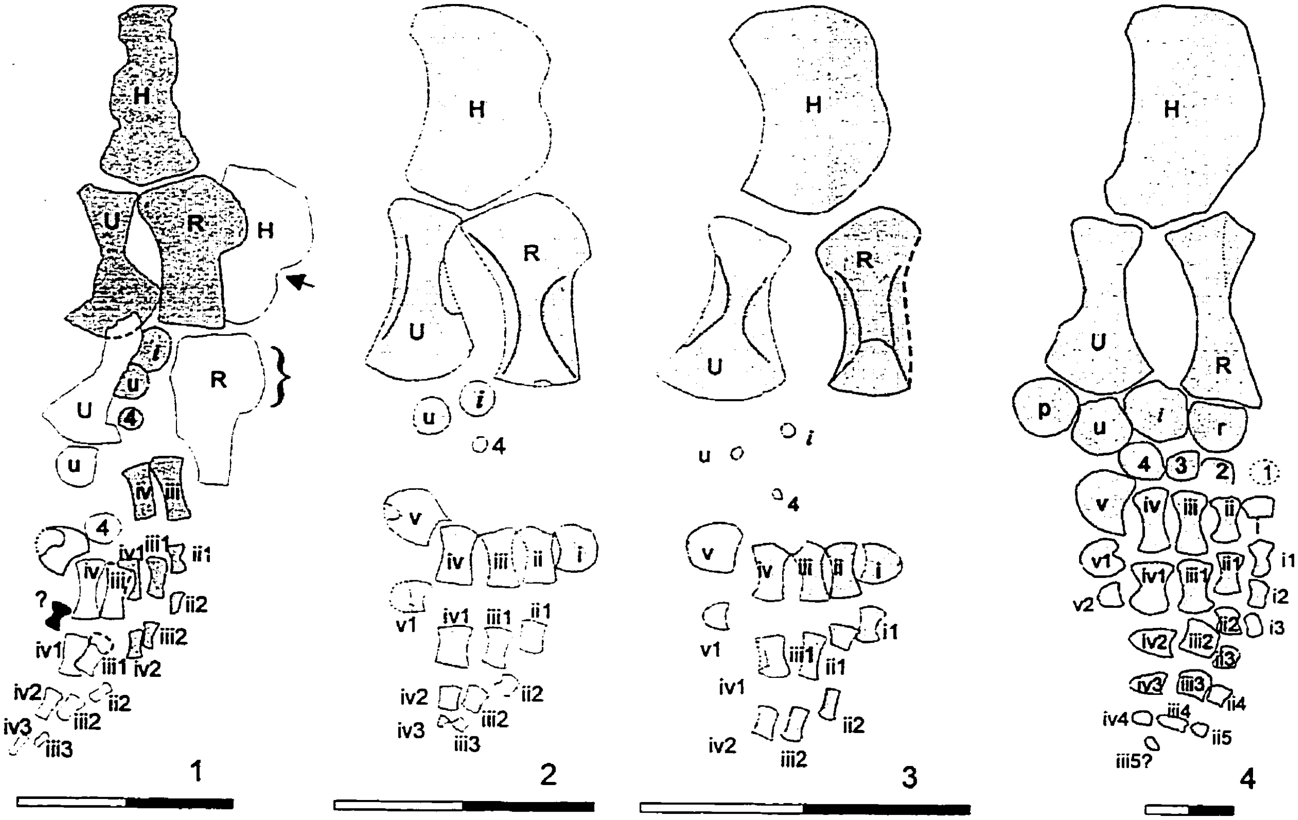
The forefin of *Chensaurus chaoxianensis* was poorly described by Chen (1985), and his descriptions or plates do not supply sufficient information for making subsequent identifications. It is therefore necessary to redescribe the forefins of the holotype of C. chaoxianensis first, to clarify the diagnostic features of this species.

Although the areas around the forefins show some chisel marks, no detailed preparation seems to have been conducted on the holotype since its discovery. Two incomplete forefins are preserved, lying nearly parallel to each other. The right forefin overlies the left one (Fig. 4-1A), but because it is shifted proximally relative to the latter, elements of one fin can be readily distinguished from those of the other. The identification of each element is given in Fig. 4-1A. No more than three carpals per forefin are present, and their small size suggests that not all carpals were ossified when the animal died. However, the possibility remains that the absence of some of the carpals is due to preservational bias, considering the incompleteness of the forefins.

The leading and trailing edges of the forefins are very poorly preserved, with obvious breaks in many places. The extreme example of this damage is the right humerus, which appears as a long and narrow structure because the anterior and posterior parts are missing (Fig. 4-1A). Fortunately, the left humerus is not damaged, although it is concealed by the overlying right radius posteriorly (Fig. 4-1A). Judging from what is exposed, the humerus seems to be of a common Early Triassic type that has an anterior flange (Wiman, 1933; Brinkman et al., 1992; Motani, in press). The anterior flange of this species, however, has one distinctive feature that is not known in any other Early Triassic ichthyosaur: an emargination in the middle of the anterior margin (Fig. 4-1A, arrow). Chen (1985) described the humerus as having two expanded ends, which seems to be based on the broken right humerus. The radius is also similar to that of other Early Triassic ichthyosaurs, in that there is an anteroproximal

Figure 4-1. Forefins of *Chensaurus chaoxianensis* and *Utatsusaurus hataii*.

A, forefins of the holotype of *C. chaoxianensis* (AGM P45-H85-25); B, left forefin of IVPP V11362 (*C. chaoxianensis*), in ventral view; C, right forefin of IVPP V11361 (*C. chaoxianensis*), in dorsal view; D, forefin of *U. hataii* (laterally inverted from Motani [in press]). Abbreviations are: H, humerus; R, radius; U, ulna; *i*, intermedium; u, ulnare; 4, fourth distal carpal ; i-v, metacarpals; i1-v2, phalanges. Bar scale is two centimeters long. In Fig. 4-1A, the right forefin is colored in light gray, the left in white. The element in dark gray is unidentified. Arrow indicates the position of the notch in the anterior flange of the left humerus. Right bracket indicates the well developed anteroproximal prominence of the left radius.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prominence (Motani, in press). However, this prominence is very well developed in C. chaoxianensis, with a long and round anteroproximal margin, unlike that in Utatsusaurus hataii (Fig. 4-1D) or in Grippia longirostris (Chapter 3). Therefore there are two diagnostic features for the forefin of Chensaurus chaoxianensis: 1) notch in the middle of the anterior flange of the humerus; and 2) well developed anteroproximal prominence of the radius with a long and curved anteroproximal margin. These two features are also present in C. faciles, whose forefin is distinguished from that of C. chaoxianensis mainly by its smaller size. The erection of C. faciles was largely based on size: Chen (1985) estimated that C. chaoxianensis is approximately 60 percent larger than C. faciles in body length, and about twice as large in forefin length. Size difference alone, however, is not taxonomically significant in the better studied ichthyosaurs from the Jurassic (McGowan, 1974a,1974b,1979), therefore the validity of the species C. faciles is in doubt. Moreover, the discrepancy between the body and forefin lengths of the two species likely indicates a growth series, where the forefin shows a positive allometry. It is beyond the scope of the present paper to discuss the taxonomy of C. faciles further, because such a study would involve a reexamination of yet another species from the same geographical area, Chaohusaurus geishanensis (Young and Dong, 1972). Therefore the two species are tentatively distinguished based on size differences, as originally proposed by Chen (1985).

ADDITIONAL SPECIMENS

Both IVPP V11361 and V11362 possess the two diagnostic forefin features of Chensaurus chaoxianensis given above. They are also from the type locality of C. chaoxianensis. The forefins are similar in size to that of the holotype of C. chaoxianensis, therefore it is reasonable to assign the specimens to this species, rather than to C. faciles.

General Account.—The bones are compressed in both specimens, and minimum preparation has been conducted since their discovery. There is a preservational problem that could obscure the true forefin morphology. When the animal was first exposed, many of its bones were broken into two or more pieces, being disposed onto two separate slabs. As a result, the shape of a bone on one slab does not necessarily correspond to that of its counter part on the other slab. In the case of IVPP V11362, for which the counter slab is not preserved, special attention has to be paid so as not to interpret a break line as the natural outline of a bone.

IVPP V11362 comprises a partial skeleton, extending from the posterior part of the skull to the anterior dorsal region. The left forefin is preserved from the ventral aspect (Figs. 4-1B, 4-2A), and is articulated with the shoulder girdle. IVPP V11361 comprises the mid-dorsal region and a forefin, which is probably the right one in dorsal view (Fig. 4-1C, 2B). The specimen is disposed on the main and the counter slabs. The humerus of IVPP V11362 is approximately 30 percent longer than that of V11361 (Table 4-1). Both specimens have incompletely ossified mesopodial regions, suggesting osteological immaturity. Measurements are summarized in Table 4-1.

Humerus.—The humerus is completely exposed in both specimens (Fig. 4-2), and resembles that of Utatsusaurus hataii in having an anterior flange, a concave posterior margin, and a tuberosity in the middle part of the shaft (Motani, in press). However, the previously mentioned notch is present on the margin of the anterior flange, marking a striking difference from U. hataii. This notched area does not appear to be of perichondral bone, because its surface striations are not parallel with the shaft of the humerus (Fig. 4-2A). Therefore the notch may become lost as the animal grows. Another striking difference between the humeri of

Figure 4-2. Chensaurus chaoxianensis, photographs of the forefins of the new specimens.

A, the left forefin of IVPP V11362; B, the right forefin of IVPP V11361. Bar scale is one centimeter.


1
2
1 cm

Table 4-1. Measurements of the propodial, epipodial, and mesopodial elements of IVPP V11362 and IVPP V11361.

In millimeters.

	IVPP V11362		IVPP V11361	
	Max. Diam.	Min. Diam.	Max. Diam.	Min. Diam.
Ulnare	3.5	2.9	1.2	1.0
Intermedium	3.2	2.9	1.9	1.8
Dist.Carpal 4	1.5	1.4	1.3	1.0
	Length	Width	Length	Width
Humerus	16.7	11.2	12.8	10.1
Ulna	15.1	8.3	11.1	7.9
Radius	15.9	9.8	12.1	7.7

C. chaoxianensis and of U. hataii is size: the humerus of IGPS 95941 (U. hataii) is more than 2.5 times longer than that of IVPP V11362 (C. chaoxianensis) (Fig. 4-1). Although this may be explained by growth, further discussion requires a comprehensive and quantitative study. The head is not well developed, and the shaft surface is rough (Fig. 4-2) as in young individuals of Stenopterygius (Johnson, 1977). This suggests that the criteria proposed by Johnson (1977) for judging the relative age of Stenopterygius are also useful for Early Triassic ichthyosaurs. The deltopectoral crest is recognizable, but is not well developed.

Radius and ulna.—The ulna has a wide, fan-shaped distal end (Fig. 4-2), which is typical of Early Triassic ichthyosaurs, such as Utatsusaurus hataii (Motani, in press) and Grippia longirostris (Chapter 3). The radius is similar to that of U. hataii, but is more robust. The anteroproximal prominence of the radius is very well developed, with a long and round anteroproximal margin. As previously mentioned, this is in contrast to the poorly developed one in U. hataii, which has a straight margin anteroproximally (Motani, in press). Both radius and ulna are associated with weak but clear ridges on the surface (Figs. 4-1, 4-2). The nature of these lines is unknown, but they may be related to the ossification process.

Carpals.—There are only three carpals in IVPP V11361 and V11362, clearly showing delayed mesopodial ossification. The elements are identified as the ulnare, intermedium, and the fourth distal carpal, based on topology. Ossification is probably more advanced in the latter specimen, the relative size of each element, compared to the epipodials, being larger than in the former specimen (Table 4-1). The ulnare is the largest of the three in IVPP V11362, but it is slightly smaller than the intermedium in V11361.

Metacarpals.—Five metacarpals are present in both specimens. The first and fifth ones are lunate, while the second to fourth are flattened cylinders. The two lunate metacarpals are not well preserved in IVPP V11362, and they look as if they are constricted in the middle. However, this is due to the breakage of the bones when the slabs were separated (the fifth metacarpal of IVPP V11361 also appears constricted on one of the slabs, but it is lunate on the counter slab). The second to fourth metacarpals are short, compared to those of Utatsusaurus hataii, and the extremities are not very much expanded, indicating that their diaphyses are incompletely ossified.

Phalanges.—The phalanges resemble the metacarpals in that there are lunate and flattened-cylinder types. The lunate type occurs in the fifth digit, which has only one phalanx in each specimen. This bone is clearly broken in IVPP V11362, but the impression of a lunate outline can bee seen. The preserved phalangeal formula is 0-2-3-3-1 for IVPP V11362, and 1-2-2-2-1 for V11361. These low phalangeal counts are most likely due to osteological immaturity of the individuals, although the lack of phalanges in the first digit of IVPP V11362 is possibly due to its loss during the preservation, because a phalanx exists in a more immature individual (i.e., IVPP V11361).

DISCUSSION

The delay in mesopodial ossification seen in AGM P45-H85-25, IVPP V11362 and V11361 shows, for the first time, that ichthyosaurs primitively retained this feature. Such delay has been observed for living (Rieppel, 1992a,b,c,1993) and Permian (Caldwell, 1994) diapsids. Because it is absent in Stenopterygius (Caldwell, in press a), this limb ossification pattern must have been lost during the ichthyosaurian evolution, but when? Caldwell (1994) suggested that the delay in mesopodial ossification may be related to the difference in the timing in perichondral and endochondral ossifications. He also mentioned that the lack of ossification delay in the mesopodial of Jurassic ichthyosaurs is possibly related to the lack of perichondral ossification in every element (Caldwell, in press b). Late Triassic and later ichthyosaurs, including Stenopterygius, all have mesopodials that are similar in shape to the metapodials, while all Early Triassic ichthyosaurs and Mixosaurus, and possibly Cymbospondylus, have distinctively shaped mesopodial elements. Considering Caldwell's (in press b) accounts on perichondral ossification, it is possible that only those ichthyosaurs belonging to the latter group (i.e., Early Triassic ichthyosaurs, Mixosaurus, and Cymbospondylus) retained delayed mesopodial ossification. At present, it has not been established that the Late Triassic and later ichthyosaurs are monophyletic, and the loss of delayed mesopodial ossification may have taken place twice or more during ichthyosaurian evolution.

The first three carpals to ossify in Chensaurus chaoxianensis, namely the ulnare, intermedium, and the fourth distal carpal, are the same as in many Permian diapsids (Caldwell, 1994). Therefore it is likely that the primary axis (Shubin and Alberch, 1986) continues distally into the fourth digit, as in other tetrapods. Caldwell (in press a) suggested that the primary axis can be recognized by extended ossification in the forefin of Stenopterygius, but this criterion is not useful in Early Triassic ichthyosaurs: the second digit has no fewer elements than the third or fourth digits in Utatsusaurus (Motani, in press). It was therefore impossible to identify the osteogenic developmental axis for Early Triassic ichthyosaurs before.

There has been much confusion in the identification of carpals and metacarpals of Early Triassic ichthyosaurs (e.g., Shikama et al., 1978;Mazin, 1986), but a consensus has been reached, at least for the carpals (Carroll, 1987;Brinkman et al., 1992;Nicholls and Brinkman, 1995;Motani, in press). The most controversial element is the one that forms the base of the fifth digit, which lies in between the distal carpal and metacarpal rows of the other digits (Fig.

4-1). The element is shifted toward the distal carpal row in Grippia longirostris (Wiman, 1933), but toward the metacarpal row in Utatsusaurus hataii (Shikama et al., 1978;Motani in press). It is lunate unlike typical metacarpals, but it is at least twice as large as any distal carpal. Shikama et al. (1978) and Mazin (1986) described this element as one of the distal carpals, but Brinkman et al. (1992) identified it as the fifth metacarpal, arguing that the fifth distal carpal was absent. They gave two reasons for their identification: 1) the fifth distal carpal, when present, is the smallest of all carpals, unlike this element, and 2) the fifth distal carpal generally become lost earlier than the fifth metacarpal. These two distinctions are reasonable but not definitive, and more substantial evidence is required. The juvenile fins reported here supply conclusive evidence to the identification of the element. In these specimens, the controversial element shows no delay in its ossification process while the carpals belonging to the same forefins do, therefore it cannot be a mesopodial element. Accordingly, the element is identified as the fifth metacarpal, as first suggested by Brinkman et al. (1992).

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CHAPTER

5

GROWTH SERIES IN CHAOHUSAURUS GEISHANENSIS (ICHTHYOSAURIA), WITH A NOTE ON THE ALLOMETRIC EQUATION

ABSTRACT

Three of the six earliest ichthyosaurs, namely, Chaohusaurus geishanensis, Chensaurus chaoxianensis, and Chensaurus faciles, occur sympatrically in the Lower Triassic (Spathian) of the Chaohu area, Anhui Province, China. A reexamination of the three holotypes, and two referred specimens, indicates that they form a growth series. The features originally used to distinguish between the three species are either growth related or false, and the specimens therefore should be assigned to one species, Chaohusaurus geishanensis Young and Dong 1972. The forefin of this species shows a strongly positive allometry, leading to the unusually large forefin in the largest specimen (the holotype). The lunate fin elements, which commonly occur in the first and fifth digits of Early Triassic ichthyosaurs, first become ossified as biconcave elements, as in other metacarpals and phalanges. The standard allometric equation overestimates the allometric coefficient when used for analyzing the relative growth of the carpals relative to the body because the carpals start their ossification late. An alternative and more inclusive equation, which compensates for the initial size difference, is therefore proposed.

INTRODUCTION

The earliest ichthyosaurs occur from the Spathian of the Lower Triassic (Callaway and Massare, 1989). They possess transitional features between land vertebrates and derived ichthyosaurs (Motani et al., 1996), and are therefore important to the study of ichthyosaurian evolution. However, our knowledge of Spathian ichthyosaurs is very limited, because of the lack of data. Two major factors have been the cause of this deficiency: 1) scarcity of material and 2) scattered distribution of specimens throughout the Northern Hemisphere that deterred comparative studies. Increasing interest in these forms, however, is changing the situation: the specimen number has been doubled over the last 15 years, and detailed comparisons are being made, at least between two major species, Grippia longirostris and Utatsusaurus hataii (Motani, 1996, 1997, in press, Chapter 3). Nevertheless, Spathian ichthyosaurs from other localities are still poorly known, and their reexamination is long overdue.

There are four major localities for Spathian ichthyosaurs: Spitsbergen (Wiman, 1929,1933; Mazin, 1981); Anhui, China (Young and Dong, 1972; Chen, 1985; Motani et al., 1996); Miyagi, Japan (Shikama et al., 1978); and British Columbia (Brinkman et al., 1992;Nicholls and Brinkman, 1993). The most productive of the four is probably Anhui Province, which has yielded articulated specimens assigned to three species, namely Chaohusaurus geishanensis Young and Dong 1972, Chensaurus chaoxianensis (Chen) 1985, and Chensaurus faciles (Chen) 1985. These three are considerably smaller than Grippia longirostris or Utatsusaurus hataii, but there are also size differences among the three: Chensaurus faciles is the smallest, Chensaurus chaoxianensis is intermediate, and Chaohusaurus geishanensis is the largest. I showed in Chapter 4 that the specimens assigned to Chensaurus chaoxianensis are immature, raising a question regarding the validity of the existing taxonomy. The purpose of the present paper is to establish the synonymy among the three species by showing that the specimens assigned to them actually form a growth series.

MATERIALS AND METHODS

The abbreviations for institutions are: AGM- Anhui Geological Museum, Hefei, China; IGPS- Institute of Geology and Paleontology, Tohoku University, Sendai, Japan; IVPP- Institute for Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; WCRAI- Wuwei Cultural Relic Administrative Institute, Wuwei, China.

The specimens examined are: AGM P45-H85-25, the holotype of Chensaurus chaoxianensis; AGM P45-H85-20, the holotype of Chensaurus faciles; a cast of IVPP V4001, the holotype of Chaohusaurus geishanensis (IVPP V4001 is currently stored at the Anhui Provincial Museum, and was unavailable to this study); IVPP V11361 and V11362, specimens described in Chapter 4; IGPS 95941, the holotype of Utatsusaurus hataii. For AGM P45-H85-25, the measurements were taken from the right forefin, which is better preserved than the left one: the other specimens only preserve one forefin each.

Measurements were taken using digital calipers and recorded to the nearest 0.1 mm. Size was calculated by measuring two adjacent vertebral centra in the anterior dorsal region, within three to seven vertebral counts from the shoulder girdle. The length of one centrum was calculated by averaging the measurements. This averaging process, however, was not possible for IVPP V11362, due to poor preservation of the vertebral column, so the measurement for this specimen is based on a single impression of a centrum.

Statistical analyses were conducted on Mathcad 5.0 Plus. CorelDraw 5.0 was used to generate figures, in the same manner as in Motani (in press).

TEST OF GROWTH SERIES

The forefins of the five Chinese specimens examined range from a very small juvenile form to a well ossified adult, and, intuitively, they seem to form a growth series (Fig. 5-1). However it is necessary to test if this observed allometric growth is statistically significant. Unfortunately, all five specimens are incomplete, and it is therefore impossible to obtain commonly used standard measurements, such as body, trunk, or skull lengths. This necessitates the use of an alternative standard measurement, the length of the vertebral centrum. Because the vertebral count to the caudal fin is not age dependent in postembryonic ichthyosaurs (McGowan, 1974a,b,1979;R.M. personal observation), it is reasonable for the trunk length to grow isometrically to the centrum length. Incidentally, the length of the vertebral centrum is known to grow isometrically to the trunk length at least in Alligator mississippiensis (Dodson, 1975). However, it is important to note that the lengths of centra may vary within the individual, depending on its position, so measurements have to be taken from the same body region for every specimens. I used the anterior dorsal region because at least one centrum is known for this area in all specimens (see Materials and Methods).

In Fig. 5-2A, a double logarithmic graph of the humerus length against the centrum length is plotted for four specimens formerly assigned to Chensaurus, and for the holotypes of Chaohusaurus geishanensis and Utatsusaurus hataii. The type of Chaohusaurus geishanensis seems to form a line with the specimens assigned to Chensaurus, while the type of U. hataii is a distant outlier. Therefore it is likely that the type of Chaohusaurus and the specimens formerly assigned to Chensaurus together represent a growth series, to which the type of U. hataii does not belong. An analysis of correlation among the five Chinese specimens for the same characters reveals that the correlation coefficient for the underlying population is estimated

Figure 5-1. Chaohusaurus geishanensis, growth series of the forefin.

A, AGM P45-H85-20, the holotype of Chensaurus faciles; B, IVPP V11361; C, IVPP V11362; D, AGM P45-H85-25, the holotype of Chensaurus chaoxianensis, left forefin; E, right forefin of the same; F, IVPP V4001, the holotype of Chaohusaurus geishanensis. For comparative purposes, the fins are depicted as the right ones in ventral view. B-E, modified from Chapter 4. F, drawn from the cast of IVPP V4001. Natural size (the scale is two centimeters in total).

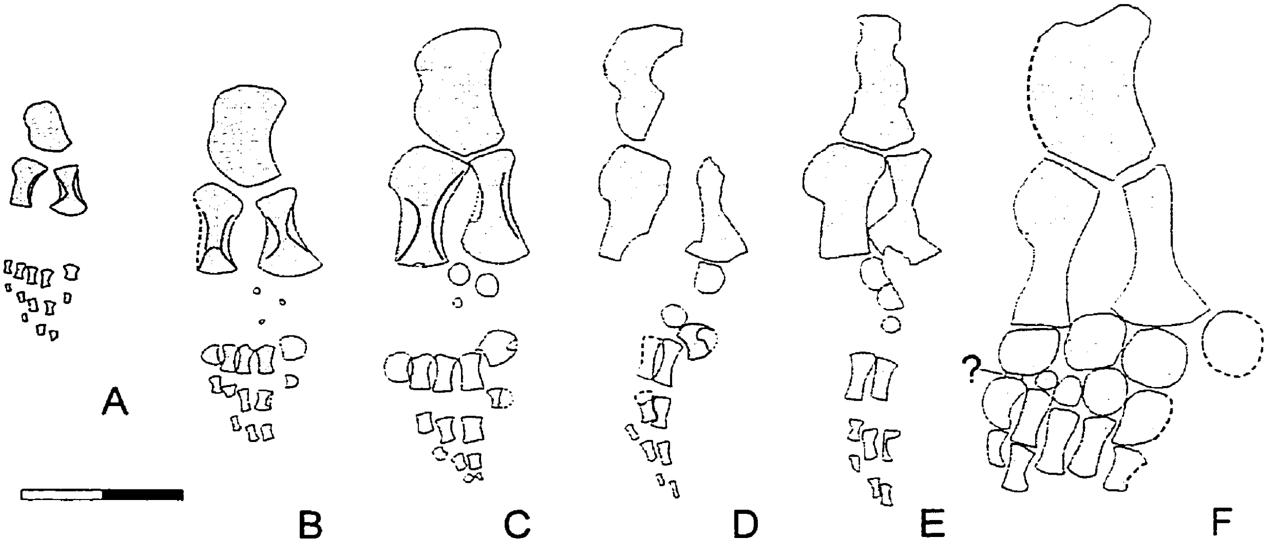
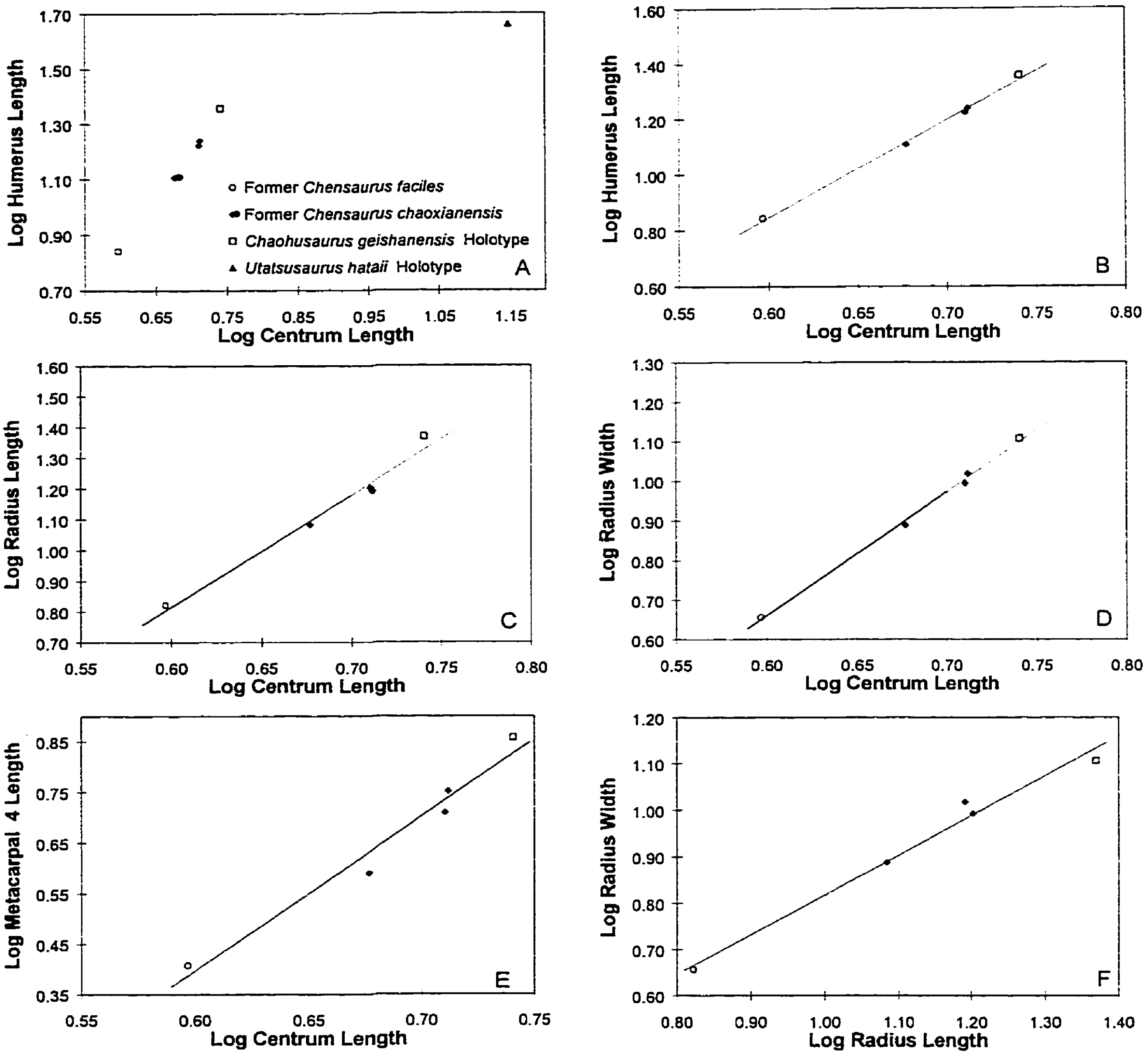

A
B
C
D
E
?
F

Figure 5-2. Logarithmic graphs showing allometric growth of the forefin elements in Chaohusaurus geishanensis.

The legend for the symbols is given in Fig. 5-2A.


Log Humerus Length
1.70
1.50
1.30
1.10
0.90
0.70
0.55
0.65
0.75
0.85
0.95
1.05
1.15
Log Centrum Length
○ Former *Chensaurus faciles*
● Former *Chensaurus chaoxianensis*
□ *Chaohusaurus geishanensis* Holotype
▲ *Utatsusaurus hataii* Holotype
A
Log Humerus Length
1.60
1.40
1.20
1.00
0.80
0.60
0.55
0.60
0.65
0.70
0.75
0.80
Log Centrum Length
B
Log Radius Length
1.60
1.50
1.40
1.30
1.20
1.10
1.00
0.90
0.80
0.70
0.55
0.60
0.65
0.70
0.75
0.80
Log Centrum Length
C
Log Radius Width
1.30
1.20
1.10
1.00
0.90
0.80
0.70
0.60
0.55
0.60
0.65
0.70
0.75
0.80
Log Centrum Length
D
Log Metacarpal 4 Length
0.85
0.75
0.65
0.55
0.45
0.35
0.55
0.60
0.65
0.70
0.75
Log Centrum Length
E
Log Radius Width
1.20
1.10
1.00
0.90
0.80
0.70
0.60
0.80
0.90
1.00
1.10
1.20
1.30
1.40
Log Radius Length
F

to be within the range of 0.97 to 1.0, at 95 percent probability level (Table 5-1). The absence of correlation is rejected with more than 99 percent significance level by a t-test. Although the sample size is admittedly small, these statistics strongly support the hypothesis that the five specimens represent a growth series, and I therefore conclude that they belong to one species. Chaohusaurus geishanensis Young and Dong 1972 has priority as the name of this species.

SYSTEMATIC PALEONTOLOGY

Order Ichthyosauria Blainville, 1835

Genus Chaohusaurus Young and Dong, 1972

Type species—Chaohusaurus geishanensis Young and Dong, 1972

Emended Diagnosis—Small ichthyosaur with a short and narrow snout; posterior teeth labio-lingually wide, and swollen in lateral view; radius with a very well-developed anteroproximal prominence; anterior flange of humerus notched, at least in juveniles; large forefin in adults.

Chaohusaurus geishanensis Young and Dong, 1972

Holotype—IVPP V4001, presently in the Anhui Provincial Museum.

Referred Specimens—AGM P45-H85-25 (holotype of Chensaurus chaoxianensis), P45-H85-20 (holotype of Chensaurus faciles), P45-H85-24, P45-H85-23, IVPP V11361, V11362, and WCRAI 313.

Emended Diagnosis—As for the genus.

Synonymy—

Chaohusaurus geishanensis 1972 Young and Dong p.11

Anhuisaurus chaoxianensis 1985 Chen p.140

Table 5-1. Allometric and correlation parameters.

k,b: allometric parameters in the formula $Y=bX^k$, where X and Y are the measurements used (C, centrum length; H, humerus length; R, radius length; Rw, radius width; M4, metacarpal 4 length; u, ulnare maximum diameter). 95% confidence limit is given in brackets for k. r, correlation coefficient, with 95% confidence limit in brackets; p, significance level of the correlation; N, sample size; c, assumed value of X when Y starts its ossification (see equation 2 in text). The value of c was assumed to be approximately zero (i.e., equation 1 in text) for most combinations, except for the ones involving the ulnare, where the value of c was estimated by two different methods: average of the measurements from AGM P45-H85-20 and IVPP V11361 (marked "Average" in the table), and statistical estimation using Minerr function of Mathcad (noted "Minerr").

X-Y	k	b	r	p	N	c
C - H	3.5 (3.5 — 3.5)	5.5E-02	1.0 (0.97 — 1.0)	<0.01	5	0
C - R	3.6 (3.5 — 3.7)	4.6E-02	0.99 (0.84 — 1.0)	<0.01	5	0
C - Rw	3.1 (3.1 — 3.1)	6.2E-02	1.0 (0.97 — 1.0)	<0.01	5	0
C - M4	3.1 (3.0 — 3.2)	3.4E-02	0.98 (0.76 — 1.0)	<0.01	5	0
H - R	1.0 (1.0 — 1.1)	8.8E-01	0.99 (0.92 — 1.0)	<0.01	5	0
H - Rw	0.88 (0.87 — 0.89)	8.2E-01	1.0 (0.99 — 1.0)	<0.01	5	0
H - M4	0.88 (0.85 — 0.91)	4.4E-01	0.99 (0.87 — 1.0)	<0.01	5	0
R - Rw	0.85 (0.82 — 0.89)	8.5E-01	0.99 (0.87 — 1.0)	<0.01	5	0
C - u	14 (13 — 14)	7.8E-10	0.99 (0.50 — 1.0)	0.013	4	0
C - u (Average)	1.9 (1.3 — 2.4)	6.4E+00	1.0 (0.65 — 1.0)	<0.01	4	4.4
C - u (Minerr)	3.8 (3.4 — 4.3)	8.8E-01	1.0 (0.81 — 1.0)	<0.01	4	3.7
H - u	3.5 (3.4 — 3.5)	2.0E-04	0.99 (0.66 — 1.0)	<0.01	4	0
H - u (Average)	1.3 (1.3 — 1.4)	2.9E-01	1.0 (0.91 — 1.0)	<0.01	4	9.9
H - u (Minerr)	1.5 (1.4 — 1.5)	1.8E-01	1.0 (0.94 — 1.0)	<0.01	4	9.3

Anhuisaurus faciles 1985 Chen p.142

Chensaurus chaoxianensis 1991 Mazin et al. p.1208

Chensaurus faciles 1991 Mazin et al. p.1208

Chensaurus chaoxianensis 1996 Motani et al. p.347

Distribution--Lower Triassic (Spathian) of Anhui Province, P. R. China.

Taxonomic Discussion--In the following two paragraphs, I discuss the validity of the characters used by Chen (1985) to distinguish the two genera and three species. As will be shown, most of the characters cannot be confirmed in the specimens examined, and the rest are growth related, so there is no definitive character to distinguish the three species from each other.

Chen (1985) originally distinguished the two genera, Chensaurus and Chaohusaurus, on five features, but all of these are taxonomically insignificant, as shown below.

1) "Carpals are small and round in Chensaurus but large in Chaohusaurus". This is growth related. See Allometry section.
2) "Retroarticular process is long in Chensaurus but not so in Chaohusaurus". The retroarticular process is poorly known in both Chaohusaurus and Chensaurus, therefore this feature is unreliable.
3) "Mandible is flat and shallow in Chensaurus while not so in Chaohusaurus". The mandible of Chaohusaurus is only known from dorsoventral aspect, therefore this feature cannot be confirmed.
4) "Snout is slender in Chensaurus but not so in Chaohusaurus". The snout of Chaohusaurus is incomplete, therefore it is impossible to know its slenderness in the lateral view.

5) "Posterior teeth are mound-shaped in Chaohusaurus but not so robust in Chensaurus". The two most posterior maxillary teeth of the holotype of Chensaurus chaoxianensis (AGM P45-H85-25) are actually round and robust. The maxilla is detached from the original position and overlies the mandible, therefore it is possible that Chen (1985) overlooked these teeth. It is true, however, that there are more spherical crowns in the holotype of Chaohusaurus geishanensis than in that of Chensaurus chaoxianensis, and the absolute size of the teeth is also larger in the former. The holotype of Chensaurus faciles, the smallest of the three species, also has a spherical crown in the most posterior mandibular tooth. The size of this crown is identical to that of the largest maxillary crown of the holotype of Chensaurus chaoxianensis, which seems contradictory to my contention of a growth series: even Iguana iguana, which is commonly known for increasing the number of teeth as it grows, shows a increase in tooth size with growth (Kline and Cullum, 1985). However, Early Triassic ichthyosaurs tend to have larger mandibular than maxillary teeth (Nicholls and Brinkman, 1993;Motani, 1997), therefore the maxillary teeth of the holotype of Chensaurus faciles are expected to be smaller than those of Chensaurus chaoxianensis. The crown size and the number of robust crowns seem to increase with the size of the animals, and are taxonomically insignificant. Such increase in the robustness of posterior teeth during the ontogeny is known for Tupinambis teguixin and Varanus niloticus (Edmund, 1969).

6) Chen (1985) mentioned that Chensaurus chaoxianensis is about the same size as Chaohusaurus geishanensis, but my measurements of the humeral length show that the latter is larger than the former.

Chen (1985) recognized two species within Chensaurus, viz., C. chaoxianensis and C. faciles, for the following four reasons, none of which can be substantiated.

1) "shape of the humerus is different". I showed in Chapter 4 that the humerus of C. chaoxianensis was misinterpreted by Chen (1985), and its true shape is similar to that of Utatsusaurus except for a distinctive emargination in the anterior flange. The forefin of C. faciles was poorly documented by Chen (1985), who described the humerus as being squarish. The humerus, however, is actually of a common Early Triassic type, with an anterior flange (Fig. 5-1A), and there is an emargination on the anterior margin as in the type of C. chaoxianensis. Therefore, the general shape of the humerus does not differ between the two holotypes.
2) "posterior tooth crowns are conical in the latter while swollen in the former". See number five of the previous paragraph.
3) "snout is more elongated in the latter". The holotype of C. faciles is actually short snouted, judging from the skull impression preserved beside the mandible.
4) "latter species is smaller than the former". Again, growth related.

ALLOMETRY

Problem of Allometric Equation in Osteological Studies

The simple allometric equation

$$Y=bX^k \qquad (1)$$

postulates that the two structures being compared start their developments simultaneously. This assumption is not always true because many structures, including bones, are absent during early embryonic stages, at the time when the rest of the body is already growing. However, in postembryonic growth, initial size differences due to such different timings of growth initiation are usually much smaller than the measurements taken from specimens, and therefore equation (1) reasonably approximates the true relative growth between two structures. In the present study, equation (1) is used only when such an approximation is reasonable.

Problems arise when the initial size difference is sufficiently large, compared to the size of the specimens measured, to invalidate the justification of equation (1) as a close approximation of the true relative growth. One obvious example is in embryonic allometry. Huxley (1932) was aware of this problem, and pointed out that equation (1), when applied to embryonic allometry, leads to an overestimation of the growth coefficient k, because of the initial size difference. He proposed to use an alternative equation to avoid such overestimation, based upon the studies of Schmalhausen (cited in Huxley [1932]):

$$k = \frac{\log Y_1 - \log Y}{3[\log(X_1 - X_x) - \log(X - X_x)]} \qquad (2)$$

where Y_1 and Y are the weight of the structure Y at the time t_1 and t; X_1, X_x, and X are the linear sizes of the embryo at the time t_1, t_x, and t; t_1 and t are the points of time between which the growths are compared; and t_x is the time when the structure Y first appears (modified from Huxley [1932]). Huxley's (1932) idea was to compare the growths of two structures for the corresponding duration of time since each structure first appeared, not for a certain period of absolute time. He introduced an assumption that the linear growth of the embryo is proportional to the time elapsed, so that his equation does not contain a time factor. This assumption, however, has not been supported by the embryological studies since Huxley's (1932) time (e.g., Wasilait et al., 1992). Although Huxley's (1932) intention to consider the initial size difference is plausible, it has been forgotten, together with equation (2).

Huxley's (1932) approach to the embryonic allometry proved unsuccessful because of the assumption involved. Difficulties lie in the identification of equivalent duration times for two different structures whose appearances are asynchronous. I propose a different approach to solve this problem: compare the growths of two structures after the second structure has appeared, instead of considering equivalent duration times for each structure. With this approach, the allometric equation can be expressed as:

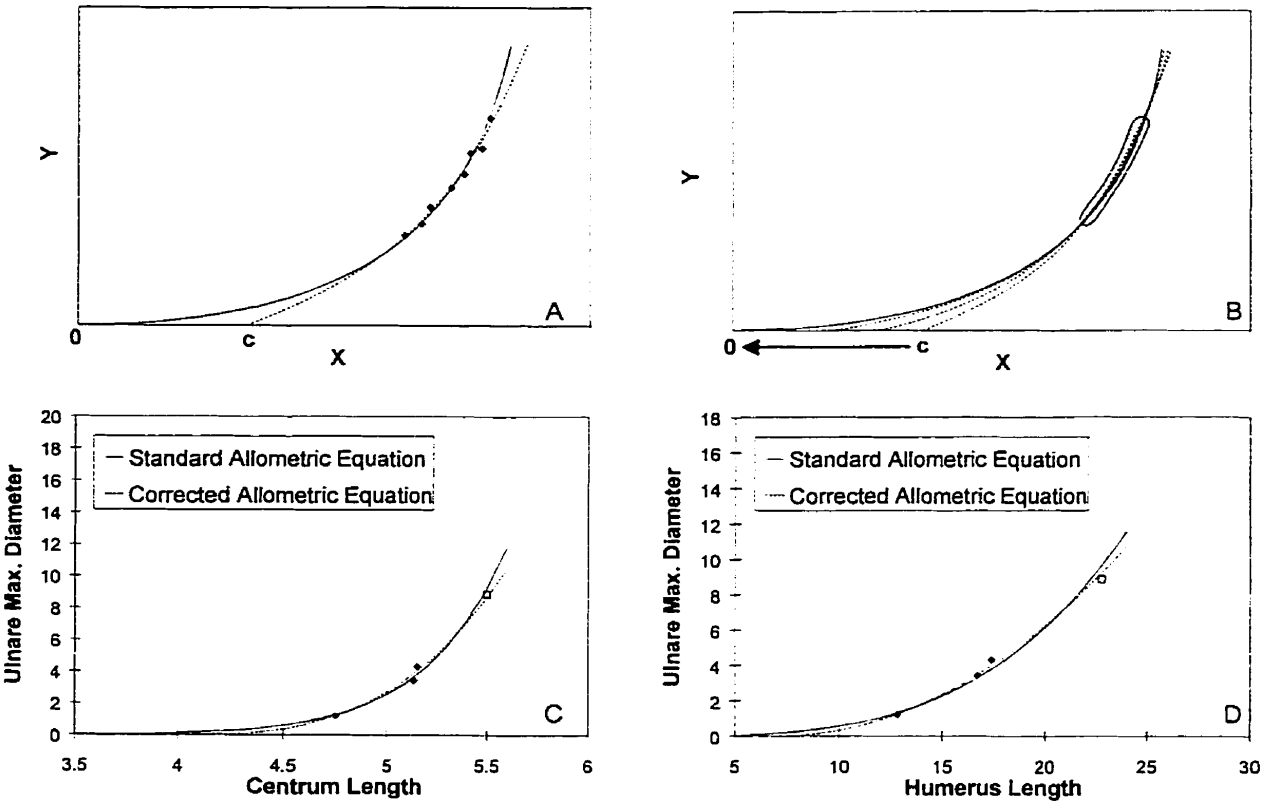
$$\begin{aligned} &Y=0 && (0 < X < c) \\ &Y=b(X-c)^a && (c \leq X) \qquad (3) \end{aligned}$$

where c is the initial size of structure X when structure Y starts its development (Fig. 5-3A, dotted line). Equation (3) approaches equation (1) as the value of c approaches zero (i.e., when the initial size difference is minor), therefore equation (1) can be considered as a special case of equation (3) (Fig. 5-3B). Equation (3) is not only logically superior to equation (1), but also increases the statistical fit, as will be shown in the next section. It is ironic that equations (2) and (3) are almost equivalent, although they are based on entirely different logical derivations.

Estimation of c is the main problem when using equation (3) for the studies of static allometry. If the growth series being examined is well represented by available specimens, the value of c can be estimated by finding the stage where the structure Y starts its development. Alternatively, the value of c that minimizes the discrepancy within a given data set can be found by calculation. Such calculations can be readily performed in mathematical software, such as Mathcad (by using Minerr function).

Figure 5-3. Two allometric equations.

A, a schematic graph showing equation (1) (solid line) and equation (3) (dotted line) for the same data; B, a schematic graphs showing how equation (3) approaches equation (1) as the c value approaches zero, for a given distribution of the data (shaded area); C, allometric growth of the ulnare to the centrum length; D, allometric growth of the ulnare to the humerus length.


Y
X
0
c
A
Y
X
0
c
B
20
18
16
14
12
10
8
6
4
2
0
Ulnare Max. Diameter
— Standard Allometric Equation
— Corrected Allometric Equation
C
3.5
4
4.5
5
5.5
6
Centrum Length
18
16
14
12
10
8
6
4
2
0
Ulnare Max. Diameter
— Standard Allometric Equation
— Corrected Allometric Equation
D
5
10
15
20
25
30
Humerus Length

Allometric Growth of the Ulnare

The carpal bones of amniotes are probably the most problematic structure for studying allometric growth because they do not ossify until after the other limb bones are ossified to some extent (Rieppel, 1992a,b,c,1993;Caldwell, 1994). Because the size of other bones is not negligible by the time the carpals starts their ossification, equation (3), instead of equation (1), should be used to describe the growth of the carpals relative to the rest of the body.

The growth of the ulnare relative to the anterior vertebral centrum was first analyzed. The ulnare is not ossified in the smallest individual of the series (Fig. 5-1A), but ossification is already started in the next smallest individual (Fig. 5-1B). I therefore used the average of the centrum lengths for these two individuals as the first estimation of c. With this estimation, a regression using equation (3) resulted in a higher value for the correlation coefficient, with a narrower confidence range, than when using equation (1) (Table 5-1, Fig. 5-3C). The allometric coefficient was 14 with equation (1), but was only 1.9 with equation (3), showing that equation (1) does overestimate the allometric coefficient (Table 5-1), as pointed out by Huxley (1932). The second estimation of c was obtained using the Minerr function of Mathcad (Table 5-1), and resulted in the slightly higher value of k (=3.8) using equation 3, which is still much smaller than the value derived from equation (1).

The growth of the ulnare relative to the humeral length was also analyzed (Table 5-1). In this case, two different estimates of c resulted in similar values for k, namely 1.3 (average of AGM and IVPP) and 1.5 (Minerr function of Mathcad). These values are smaller than that obtained using equation (1), which was 3.5, showing again that equation (1) overestimates k.

Allometric Growth of Other Forefin Elements

The humerus, radius, and the fourth metacarpal are largely ossified in the smallest individual of the growth series, therefore it is reasonable to use equation (1) for these bones. The relative growth of the humerus (length), radius (length and width), and of the fourth metacarpal (length) against the anterior dorsal centrum (length) are plotted on Fig. 5-2C-E, and allometric parameters and other statistics are summarized in Table 5-1. The allometric coefficient a is 3.5 for the humerus, showing a strong positive allometry relative to the vertebral centrum, and probably relative to the body length. Therefore, the unusually large forefin of the largest individual (the holotype) relative to its body can be attributed to allometric growth. All correlation coefficients are high and significant, but the sample size is admittedly small (Table 5-1).

The growths of the radius and the fourth metacarpal relative to the humerus (length) was also analyzed, but only the statistics are given (Table 5-1). The length of the radius grows isometrically to the humeral length, while the width of the radius shows a slightly negative allometry. Therefore, the radius becomes more elongated as it grows (Fig. 5-1). This is confirmed by the relative growth of the radial width against the radial length (Fig. 5-2F, Table 5-1). A similar trend of elongation is seen in the humerus, but the statistics are not given here because the sample size is too small (n=3). Motani (in press) reported that the humerus of the paratype of Utatsusaurus hataii is more elongated than that of the holotype (the paratype is larger than the holotype), which is consistent with this observation for Chaohusaurus geishanensis. The antero-proximal prominence of the radius becomes enlarged as the animal grows (Fig. 5-1). In fact, the youngest individual (Fig. 5-1A) has a small antero-proximal prominence with a short antero-proximal margin, much resembling that of Grippia longirostris (Chapter 3).

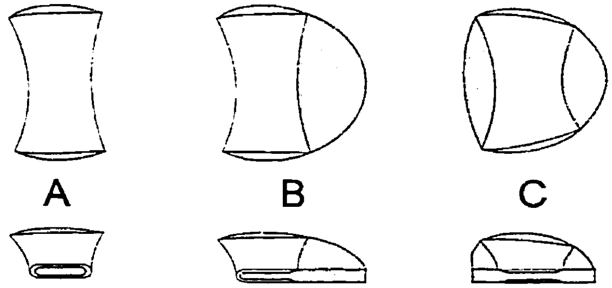
OSSIFICATION OF LUNATE ELEMENTS

The first and fifth metacarpals, and the first phalanx of the fifth digit, are antero-posteriorly biconcave in the smallest individual of the growth series (AGM P45-H85-20), while they are lunate in the other four specimens (Fig. 5-1). Because AGM P45-H85-20 preserves the forefin as a natural mold, it is unlikely that breakage caused the elements to appear biconcave, which is the case for IVPP V11362 (Chapter 4). This suggests that the lunate elements first became ossified as biconcave forms, as in normal metacarpals and phalanges—only at a later stage does the ossification of the anterior or posterior flange begin its development. This implies that the initial ossification of the shaft is perichondral, as in other tetrapods (Rieppel, 1992b;Caldwell, 1994), while the flange only becomes ossified endochondrally. Therefore, even when the bone appears biconcave in shape during its early ossification stages, perichondral ossification does not take place along one of its concave margins, because that margin is covered by cartilage (Fig. 5-4B). It is therefore inappropriate to infer the presence of perichondral ossification from concave shape alone. The loss of perichondral ossification in the lunate elements of ichthyosaurian fins was first suggested by Caldwell (in press a,b).

A similar flange structure is known in the first phalanx of the middle digit of birds (Gilbert et al., 1981). However, it differs from the lunate fin elements of ichthyosaurs in that its shaft is distinctively round, and the flange is thin (there is no difference in the thickness of the two areas in the ichthyosaurian elements). The flange may be associated with a ridge, which is

Figure 5-4. Ossification models for the limb elements of Triassic ichthyosaurs.

A, normal cylindrical type; B, lunate type; C, a type present in Grippia longirostris. White areas represent perichondral ossification, gray endochondral.


A
B
C

absent in ichthyosaurs. A preliminary observation of chick embryos, prepared and studied by McGowan (1984), suggests that this bone also first becomes ossified perichondrally in the shaft region. More detailed embryological study is necessary before describing the ossification process of this bone.

The lack of perichondral ossification along concave margins was also suggested for some biconcave forefin elements of Grippia longirostris (Chapter 3). These elements were preserved as dorsal and ventral plates, slightly shifted with respect to each other, and the concave margins are edged, rather than smooth as in the shaft of long bones. Based on this shifting, and the edged margins, I suggested in Chapter 4 that perichondral ossification may be absent along the concave margin of these elements, but the reasons remained unknown. Regarding the new information for Chaohusaurus, and the immaturity of the individual in question (Chapter 3), it is possible that these margins were also covered with cartilage, which was not ossified when the animal died (Fig. 5-4C).

SUMMARY

1. Specimens previously assigned to Chensaurus chaoxianensis and Chensaurus faciles represent young individuals of Chaohusaurus geishanensis Young and Dong 1972, so the first two names are junior synonym of the latter.
2. The forefin of Chaohusaurus geishanensis shows a strongly positive allometry relative to body length.
3. The standard allometric equation overestimates the allometric coefficient k, when the second structure (Y variable) starts its development later than the first one (X variable).

4. In such cases, an alternative equation (3) can be used as the substitute for the standard allometric equation.
5. Lunate elements in the first and fifth digits first become ossified as biconcave forms, and later become lunate.

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CHAPTER

6

EVOLUTION AND THE HOMOLOGY OF ICHTHYOSAURIAN FOREFINS

ABSTRACT

The evolution of the ichthyosaurian forefin is re-evaluated based on the largest set of data ever available, including recently reported Early Triassic forms. Three morphotypes of humeri are recognized. Re-identification of the forefin elements of various ichthyosaurs is made, based on the osteogenic sequence and, in its absence, topological similarity with those for which such data are available. The topology along the primary axis and digital arch is conservative among all ichthyosaurs analyzed. The analysis shows, contrary to previous studies, that Stenopterygius, and all other Jurassic ichthyosaurs, lack digit I of the forelimb. Digits I and II are absent in Shastasaurus. Perichondral ossification, which was previously reported to be absent from the notched forefin elements of Jurassic ichthyosaurs, seems to exist in these bones. The reduction of perichondral ossification of the long bones occurred in two or more separate phases, when viewed as a stratigraphic transformation series.

INTRODUCTION

Ichthyosaurs, which achieved the highest degree of aquatic adaptation among reptiles (Carroll, 1985), developed a unique limb structure adapted for swimming. Even in the earliest forms, the digital skeletons were integrated through close packing (Motani, in press, Chapters 3, 4, 5), and were probably enclosed in a single body of soft tissues, forming a fin-like structure. This special limb design, which was only paralleled by derived sauropterygians among nonmammalian amniotes, led to the unique modifications of the limb skeleton in the evolution of ichthyosaurs. By the Jurassic, ichthyosaurian limb skeletons were so modified that the homologies of the limb elements among these ichthyosaurs, and terrestrial amniotes, are difficult to recognize.

Kiprijanoff (1881) was the first to identify the proximal elements of Jurassic ichthyosaurs down to the metacarpal row, using the terminology for terrestrial amniotes. McGowan (1972) modified this identification suit by removing the centralia. This identification scheme was adopted by some workers (e.g., Johnson, 1977,1979), but others were cautious and did not give the identifications of forefin elements in their figures (e.g., Riess, 1986;Carroll, 1987). Recently, Caldwell (in press a) introduced the notion of developmental sequence to the identification of the forefin elements of Jurassic ichthyosaurs, and supported McGowan's (1972) interpretation. This identification will be discussed later in detail.

Although the forefins of Jurassic ichthyosaurs were figured in the literature as early as 1814 (Home, 1814), less derived Triassic forefins were not depicted until 1887, when Baur (1887) illustrated the proximal part of the forefin of Mixosaurus cornalianus (the first complete figure was given by Repossi [1902]). Extreme collection activity, at about the turn of the last century, resulted in the accumulation of more ichthyosaurian forefins from the Middle and Upper Triassic (Merriam, 1902,1903,1908;Wiman, 1910), but no complete Early Triassic forefins, which are the least derived in morphology, were known until very recently (Motani, in press, Chapters 3, 4).

The purpose of the present study is to conduct the first comprehensive comparisons among various ichthyosaurian forefins, including the recently discovered Early Triassic forms, by incorporating the developmental knowledge of chondrogenesis (e.g., Shubin and Alberch,

1986) and osteogenesis (e.g., Rieppel, 1992a,b,c,1993a,b,c,1994a,b) of tetrapod limbs. The hindfin is not included in this study, due to its poor fossil record (forefins are preserved far more frequently than hindfins).

MATERIALS

Abbreviations for the institutions are as following: BMNH-Natural History Museum, London; BRSMG-Bristol City Museum and Art Gallery, Bristol; IGPS-Institute of Geology and Paleontology, Tohoku University, Sendai; IVPP-Institute for Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing; PMU-Paleontologiska Museet, Uppsala Universitet, Uppsala; ROM-Royal Ontario Museum, Toronto; SMNS-Staatliches Museum für Naturkunde, Stuttgart; UCMP-Museum of Paleontology, University of California, Berkeley.

I examined most of the specimens myself, except for the holotype of Cymbospondylus buchseri, the lost holotype of Mixosaurus cornalianus, and some of the specimens figured by Caldwell (in press a). The taxonomic status of the humeri from the Middle Triassic of Spitsbergen, that were assigned to Pessopteryx by Wiman (1910), probably requires a revision, as Merriam [1911] suggested, therefore they are tentatively referred to as "Pessopteryx". Two isolated forefins from the Lower Liassic of England (ROM 954 from Lyme Regis and BMNH 33178 from Barrow-on-Soar) probably represent a new taxon, as will be explained later in the text. These specimens are referred to as a possible new Early Liassic taxon in the text.

HUMERUS

The humerus is the only element in ichthyosaurian forefins that never became flat and plate-like during its evolution, and it is also the one in which the shape is most variable. Ichthyosaurian humeri are uniquely shaped, and it was not until Johnson's (1979) study that a significant contribution was made to established the homology between the humeri of ichthyosaurs and terrestrial amniotes. Although Johnson (1979) made a significant contribution, her study mostly concerned Stenopterygius, a typical Toarcian (Early Jurassic) ichthyosaur, which only represents one morphotype among diverse ichthyosaurian humeri. Therefore it is necessary to expand her study to encompass a wider range of ichthyosaurs.

Only a few features are present among all ichthyosaurian humeri, including: curved and concave posterior margin; distal and proximal condyles nearly parallel with each other when seen in proximal view; presence of the anterior flange of the shaft, although it is sometimes reduced (Fig. 6-1:AF); weak ridge that runs from the deltopectoral crest to the middle of the shaft (termed deltopectoral ridge here), ending in a rugose area (Fig. 6-1:RS) that may not be well developed; and a tuberosity located just ventro-proximal to the articular facet for the ulna (Fig. 6-1:T, termed the postero-distal tuberosity here), which may not be remarkable. All humeri of pre-Middle Jurassic ichthyosaurs can be categorized into three basic morphotypes (Figs. 6-1, 6-2), with possible exceptions of those for Cymbospondylus petrinus and Merriamia zitteli. There are variations within each morphotype, but the basic features, as described below, are consistent.

Basic Types

Morphotype 1 (Fig. 6-1 A, D, G; Fig. 6-2 A-E)—The first type, which was common during the Early and Middle Triassic, is longer than wide, and has a large, thin bony flange projecting from the shaft anteriorly. This anterior flange may or may not have a notch in the middle of its anterior margin, or it may be concave as in Cymbospondylus petrinus (Fig. 6-2E). The head is directed proximally, and the deltopectoral ridge runs postero-distally (Fig. 6-1D). The articular facet for the radius is considerably larger than that for the ulna.

Figure 6-1. Features of the three morphotypes of humeri (right).

A, D, G- morphotype 1, Mixosaurus natans, ROM 30113 (cast of UCMP 9873); B, E, H- morphotype 2, Shastasaurus osmonti, ROM 30114 (cast of UCMP 9076); and C, F, I- morphotype 3, Ichthyosaurus communis, ROM 30148 (cast of OUM J29174). Directions of the views are: A-C, proximal; D-F, ventral; and G-I, dorsal. Abbreviations are: AF, anterior flange of the shaft; DPC, deltopectoral crest; DT, dorsal trochanter; RS, rugose surface; T, tuberosity proximal to the articular facet for the ulna (referred to as the postero-distal tuberosity here). The line connecting DPC and RS is called the deltopectoral ridge in the text. The images are laterally inverted in B, E, and H, to facilitate easier comparisons.

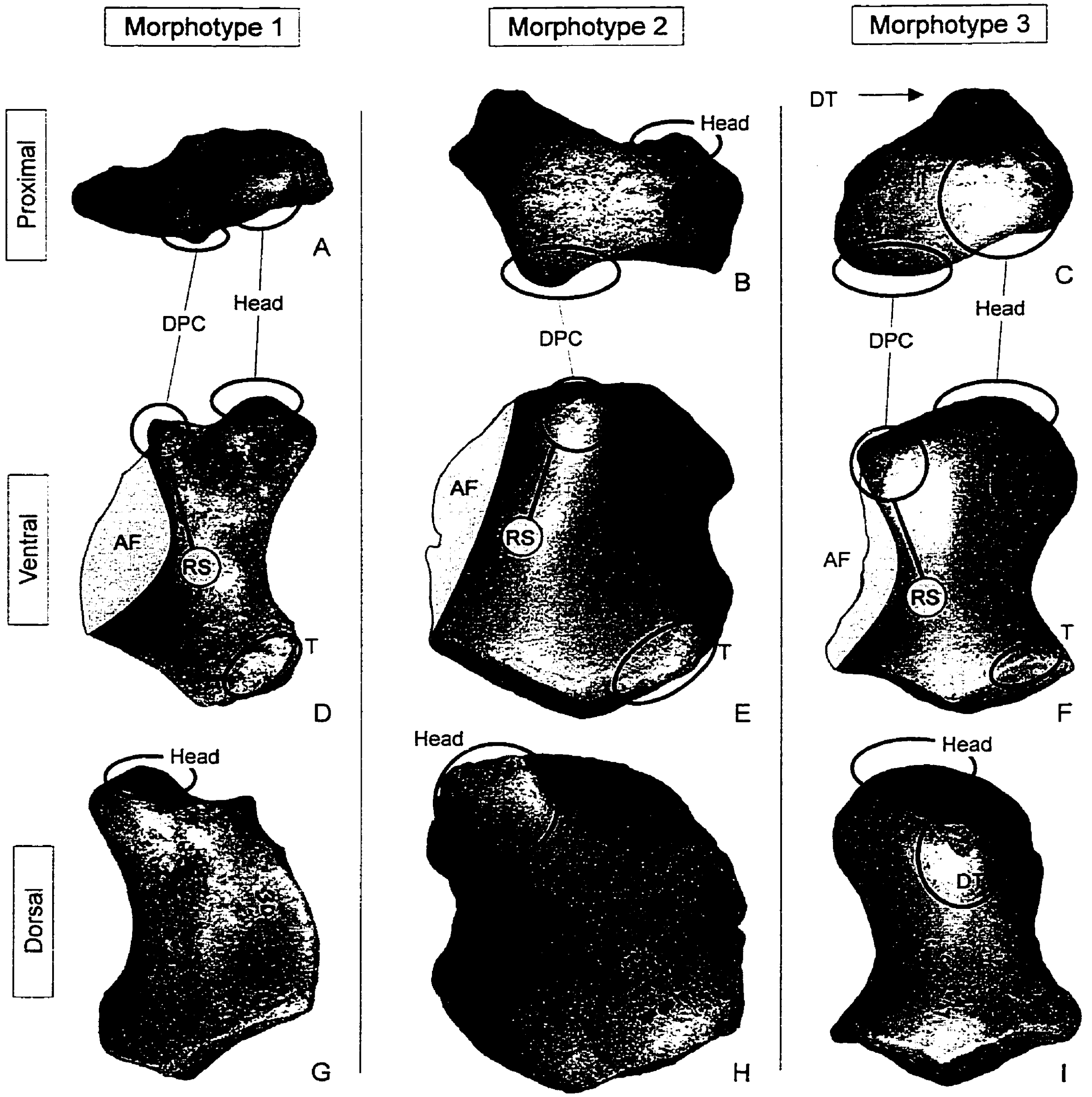
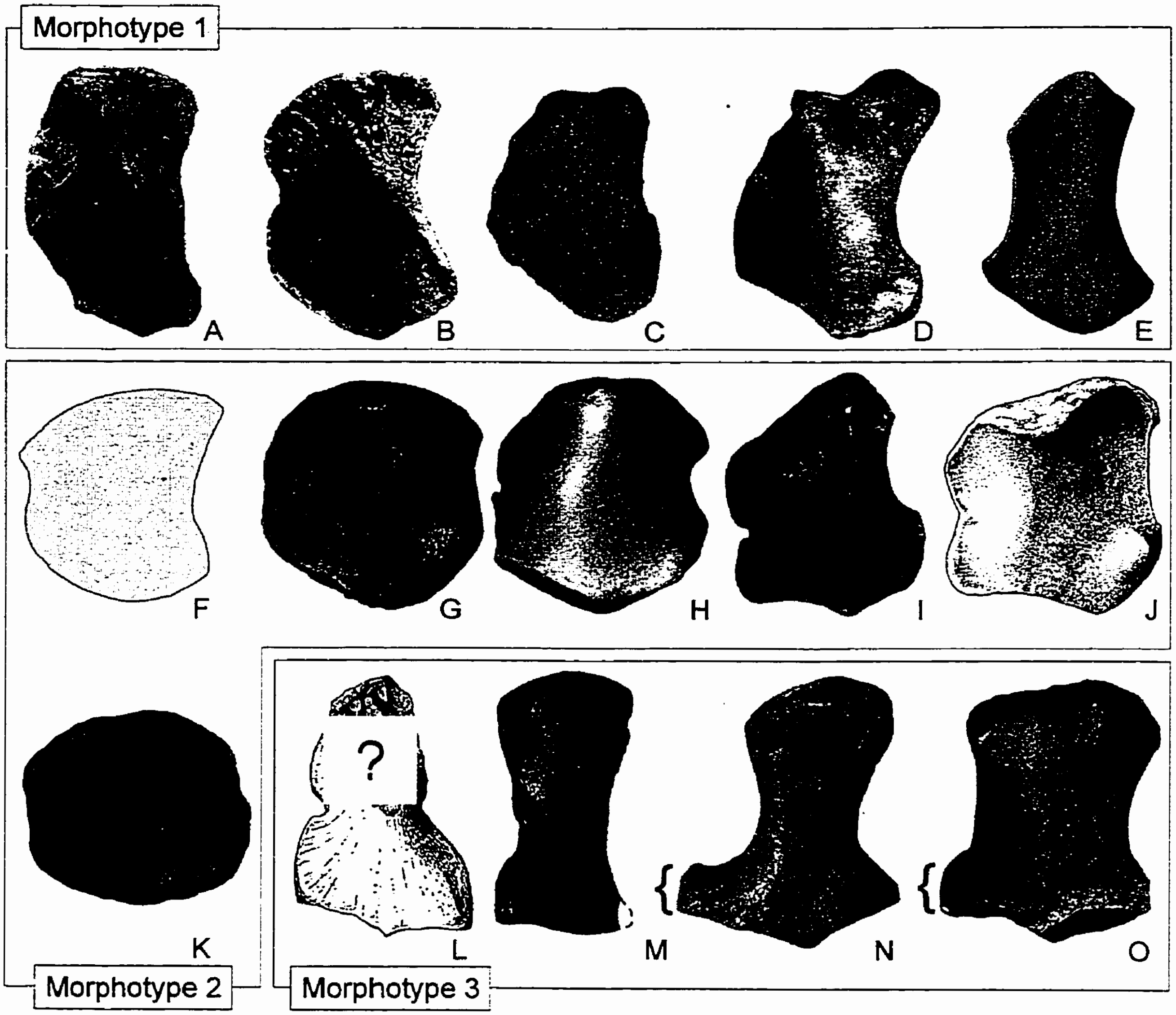

Morphotype 1
Morphotype 2
Morphotype 3
Proximal
Ventral
Dorsal
DT
Head
DPC
Head
Head
DPC
DPC
Head
A
B
C
AF
RS
T
D
AF
RS
T
E
AF
RS
T
F
Head
Head
Head
DT
G
H
I

Figure 6-2. Ventral views of various ichthyosaurian humeri belonging to the three morphotypes.

A, Utatsusaurus hataii (IGPS 95941); B, Chaohusaurus geishanensis (IVPP V11362); C, Grippia longirostris (PMU R474); D, Mixosaurus natans (ROM 30113, a cast of UCMP 9873); E, Cymbospondylus petrinus (modified from Merriam [1908]); F, Cymbospondylus buchseri (modified from Sander [1989]); G, "Pessopteryx" (modified from Wiman [1910]); H, Shastasaurus osmonti (ROM 30114, a cast of UCMP 9076); I, Shastasaurus neoscapularis (ROM 41993); J, Shonisaurus popularis (modified from Camp [1980]); K, Pessosaurus polaris (PMU R176); L, Merriamia zitteli (modified from Merriam [1903]); M, Hudsonelpidia brevirostris (ROM 44633); N, Leptonectes tenuirostris (BMNH R498); and O, Ichthyosaurus sp. (ROM). A-E, morphotype 1; F-K, morphotype 2, and L-O, morphotype 3. All humeri are depicted as the right one in ventral view (B, C, H, and I are laterally inverted). Not to scale.


Morphotype 1
A
B
C
D
E
F
G
H
I
J
K
?
L
M
N
O
Morphotype 2
Morphotype 3

Morphotype 2 (Fig. 6-1 B, E, H; Fig. 6-2 F-K)—The second type, which is known for some Middle and Late Triassic forms, is very robust, being as wide as long. A small but thick anterior flange is present, which may be emarginated in the middle. The articular facet for the radius is enlarged, being twice as wide as that for the ulna. The deltopectoral ridge runs antero-distally, or distally, from the deltopectoral crest, instead of postero-distally, as in the morphotypes 1 and 3. The postero-distal tuberosity is well pronounced. Most characteristically, the head is directed dorsally, not proximally as in the other two types (Fig. 6-1H).

Morphotype 3 (Fig. 6-1 C, F, I; Fig. 6-2 L-O)—The third type, which appeared in the Late Triassic, is longer than wide, as in the first type. The anterior flange exists but it is reduced, forming a ridge on the anterior margin of the shaft (Fig. 6-1F). In some individuals, however, the anterior flange may form a distinctive structure at the distal end (e.g., Fig. 6-2N, O). The head is directed proximally, and the deltopectoral ridge runs postero-distally (Fig. 6-1F). The articular facets for the radius and ulna are approximately equal in length.

Exceptions

Cymbospondylus petrinus—The anterior flange of this species is concave (Fig. 6-2E), instead of convex, but otherwise the humerus is of morphotype 1. The humerus clearly differs form that of C. buchseri, and other morphotype 2 humeri, in that it is not robust, and that the head is directed proximally. Therefore this humerus is tentatively assigned to group 1.

Merriamia zitteli—The humerus of this species was depicted by Merriam (1903), but I could not locate its proximal half in the only specimen known (UCMP 8099). This missing part is also lacking in the only published photograph of the specimen (McGowan 1972, fig. 4D). If Merriam's reconstruction is correct, the humerus differs from all other ichthyosaurian humeri in that the posterior margin is not smoothly convex (with the possible exception of Pessosaurus polaris [Fig. 6-2K], where the shaft is extremely reduced). Judging from what is preserved (Fig. 6-2L), the humerus resembles those of the morphotype 3 in that the articular facets for the radius and ulna are nearly equal in size.

FOREFIN MORPHOLOGY

The number of digits and carpals varies remarkably among ichthyosaurs, therefore it is necessary to establish the homologies of the fin elements. Oster et al. (1988:877) suggested that the homology of tetrapod limb elements should be established by comparing the morphogenetic process that create the limb, rather than by the resulting morphologies. Caldwell (in press a) was the first to introduce this notion of morphogenetic process to the identification of the fin elements of derived ichthyosaurs. His analysis supported the traditional identification scheme used by McGowan (1972). However, the present study disagrees with this identification of the forefin elements of Stenopterygius. To explain the logical consequences of this disagreement, it is first necessary to review the previous studies on the morphogenetic process of limb developments.

Studies of Limb Skeletal Development

The primary patterns of limb development is established by the time precartilage foci, formed by condensation of mesenchymal cells, are laid down (Oster et al., 1988). Shubin and Alberch (1986), by comparing the patterns of these precartilage condensations, established that chondrogenic development in many living tetrapods can be described as "a temporal and spatial iteration of branching and segmentation events" that follows a conservative pattern. The major features of this pattern for the forelimbs include (see also Caldwell [1994:fig.5]): 1) the humerus appears first as a de novo condensation; 2) the humerus bifurcates into the radius and ulna; 3) the radius becomes segmented to form the radiale, but usually no further segmentation occurs along this preaxial series; 4) the ulna bifurcates into the intermedium and ulnare; 5) the intermedium may give rise to the centralia; 6) the ulnare gives rise to dc4; 7) dc4 bifurcates into dc3 and mc4, and the rest of the distal carpals bifurcate into the metacarpal of the same digit and the more preaxially located distal carpal (except for the most preaxial distal carpal, which only gives rise to the metacarpal). This series of distal carpals, with digits emerging distally, is called a digital arch; 8) the base of the fifth digit appears as a de novo condensation. Because of the time lags among these processes, a proximo-distal axis of precartilage condensation, composed of the ulna, ulnare, dc4 and mc4, first appears in early chondrogenic stages, and this axis is called the primary axis (Burke and Alberch, 1985).

A series of studies by Rieppel (1992a,b,c,1993a,b,c,1994a,b), upon extant lizards, turtles, and alligators, showed that the osteogenic patterns do not necessarily mirror their chondrogenic precursors, due to ontogenetic repatternings. The major differences between the forelimb chondrogenesis and osteogenesis include: 1) the mesopodial region, which is the first to start chondrification in the autopodium (carpals, metacarpals, and phalanges), does not ossify until after the more distal part of the autopodium is ossified to some extent; 2) the chondrogenic sequence among the digits is IV>III>II>I>V, but the ossification sequence, so far as known, is III>IV>II>I>V (lizards) or III>II>IV>I>V (crocodilians and testudines); 3) the ossification of mc5 may be significantly delayed relative to the other four metacarpals, although it usually ossifies before hatching (except in some lizards). The reduction sequence of digits (viz., I>V>II>III>IV) is the reverse of the chondrogenic sequence, but the reduction of carpal elements (e.g., dc1>dc5>dc2,centrale>dc3 for six species of <u>Lerista</u>) seems to be the reverse of the ossification sequence in closely related taxa (e.g., Lacerta for Lerista) (Rieppel, 1992b). Rieppel (1994b) stressed the adaptive plasticity of the ossification process, as opposed to the conservatism of the chondrification pattern (Shubin and Alberch, 1986). He also pointed out that carpals differ from long bones in that they do not ossify perichondrally (i.e., from the surface of cartilage), but only endochondrally (i.e., from the ossification centre inside a cartilage): the shaft of long bones always ossify perichondrally first, then endochondrally.

Caldwell (1994) confirmed the delay of mesopodial ossification for three fossil diapsids from the Permian. He suggested that the lack of perichondral ossification in the mesopodials, which usually appears before endochondral ossification, may be the reason for this delay. Ontogenetic series for these three diapsids showed the early and progressive ossification of dc4, from which Caldwell (1994) concluded that the primary axis of limb development was running through the fourth digit in these diapsids, as in extant tetrapods.

Ontogenetic Data for Ichthyosaurs

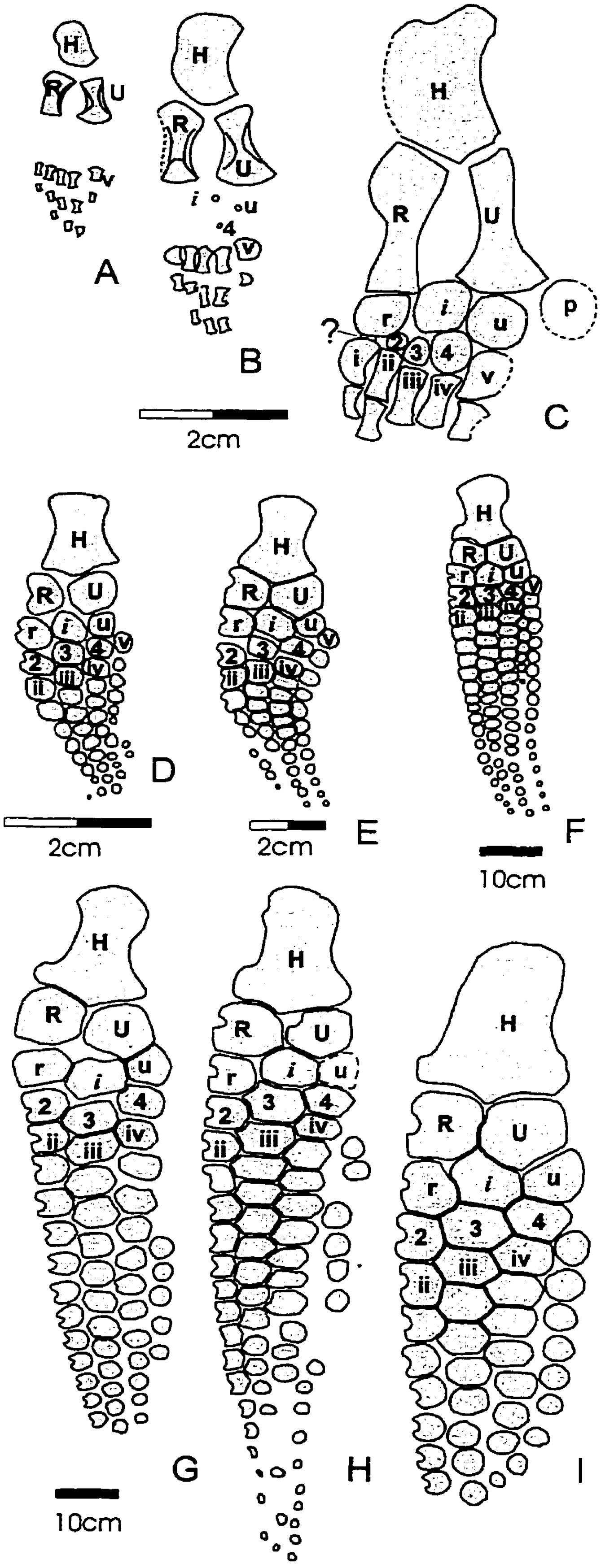
The results of the previous studies suggest that it is most logical to first identify the primary axis (viz., the fourth digit of basal amniotes) and the digital arch, which is what Caldwell (in press a) did. Because cartilage, or other soft tissues, is rarely preserved in fossils, the primary axis is best identified based on the ossification sequence of the forefin elements. However, growth series of the forefin have only been described for two ichthyosaurian genera, namely Chaohusaurus from the Lower Triassic (Chapters 4, 5) and Stenopterygius from the Lower Jurassic (Caldwell, in press a). Accordingly, the identification of the primary axes for these two genera is considered first.

Chaohusaurus—The forefin of Chaohusaurus is pentadactyl, with a topology resembling that of the forelimb of terrestrial diapsids (Fig 3A-C). The incompletely ossified mesopodial region in juvenile specimens show that the first three mesopodial elements to ossify are most likely the ulnare, intermedium, and dc4 (Fig. 6-3B, see also Chapter 4). This suggests that the primary axis was running through the fourth digit (Chapter 4). The first and fifth digits lag behind the other digits in the ossification process.

Stenopterygius—The forefin of Stenopterygius has up to six digits, the anterior three of which are much wider proximally than the rest (Figs. 6-3E, 6-4K). Despite the abundance of embryonic and juvenile specimens, information on the ossification sequence of digits is scarce for Stenopterygius. Among the series of five forefins of Stenopterygius figured by Caldwell (in press a:fig. 5A-E), ranging from embryonic to early postembryonic stages, only one is sufficiently well articulated to enable the identification of the digits down to the most distal elements (Caldwell, in press a:fig. 5D, depicted here as Fig. 6-3D), therefore this forefin is used here to establish the relative degree of ossification among the digits. Caldwell's [in press a] claim that the digits can be established with confidence for his fig. 5E seems implausible because of the extensive dislocation of postaxial elements. Caldwell (in press a:fig. 5D) identified the most posterior digit in this tetradactyl forefin as the fourth, but I disagree with this identification. The digit shows a delay in its ossification compared to the more anterior three digits. However, ossification of the fourth digit (primary axis) never lags behind that of digit I in extant lizards (Rieppel, 1992a-c,1993a), crocodilians (Rieppel, 1993b), testudines (Rieppel, 1993c), or in Early Triassic ichthyosaurs (Chapter 4), therefore it is very unlikely that this posteriormost digit is the fourth. Such delayed ossification is typical of the fifth digit (Rieppel, 1992a, b, c, 1993a, b, c, 1994a, b; Caldwell, in press a). The digit is accordingly identified as homologous with the fifth digit of basal diapsids and of Chaohusaurus. The more anterior three digits, which are wider proximally, as noted earlier, are identified as the second to fourth digits,

Figure 6-3. Growth series of three ichthyosaurs.

A-C, Chaohusaurus geishanensis (modified from Chapter 5); D-F, Stenopterygius (modified from Caldwell [in press a]); G, Temnodontosaurus burgundiae (SMNS 15950); H, T. burgundiae (SMNS N2A); and I, Temnodontosaurus sp. (SMNS 17980). The series for Temnodontosaurus (G-I) is only partial, and depicted only to show the ossification sequence within the most posterior digit. See Fig. 6-4 for abbreviations.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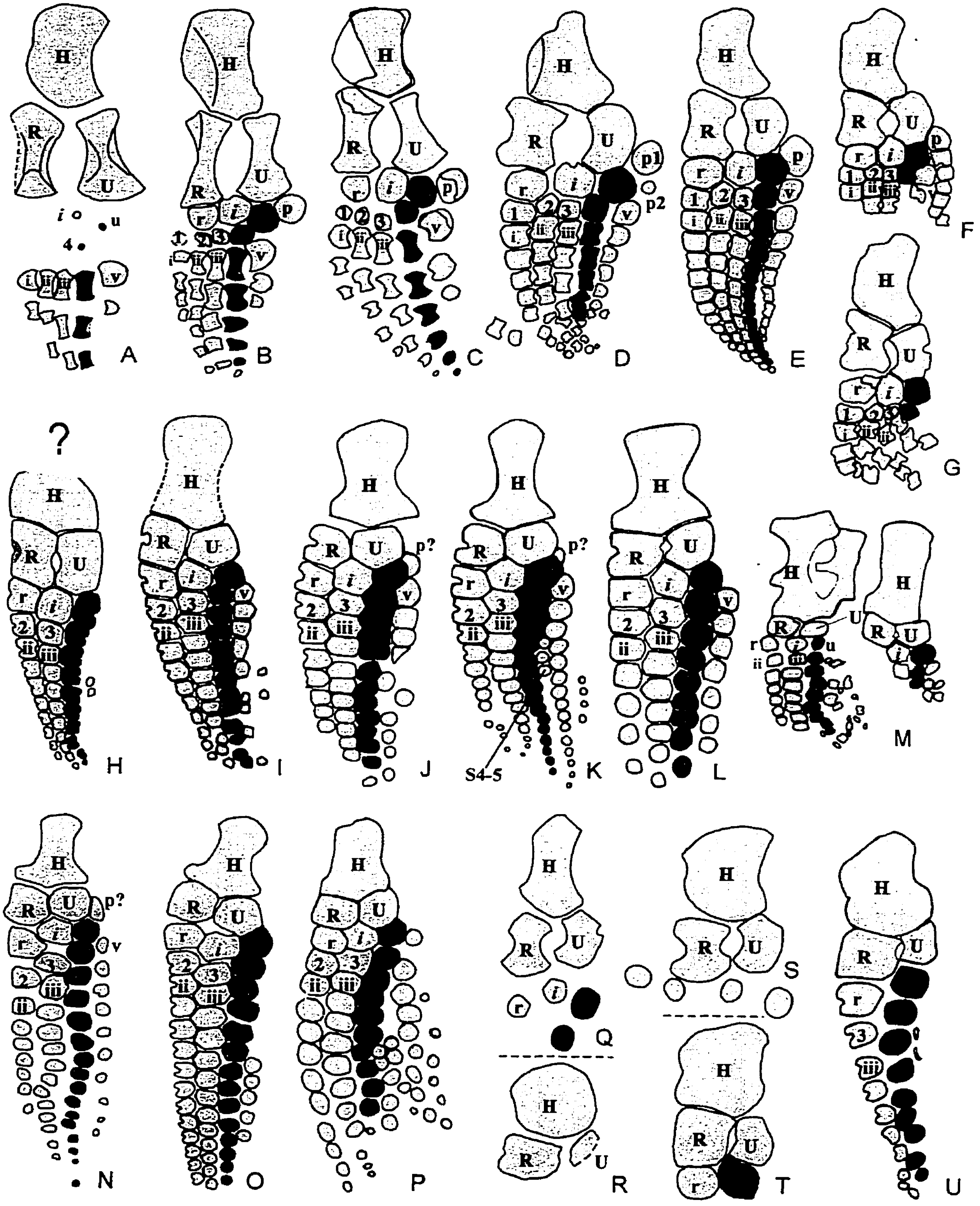
the first one having been lost. The loss of the first digit has been suggested for the hindfin of Stenopterygius (Caldwell, in press a), and this new identification for the forefin is also in accordance with the hindfin morphology. Note that the supernumerary digit S4-5 (S3-4 of Caldwell [in press a]), lying between the fourth and fifth digits, is now located posterior to the primary axis (Fig. 6-4K).

Caldwell (in press a) pointed out that, in later growth stages, the fifth digit shows an extended ossification (interpreted here as high count for phalangeal ossification), which led him to misidentify the digit as the fourth (there are some exceptions, to which I will return later). However, this increase in the number of phalanges is more likely due to the functional necessity of stiffening the postero-distal part of the forefin skeleton, as explained below. In Early Jurassic ichthyosaurs, such as Stenopterygius and Ichthyosaurus, where there is evidence of soft tissue, the forefin skeleton is located close the leading edge of the fin (Fig. 6-5A,B), contributing to the stiffness of this area, probably a hydrodynamic requirement. The forefin, as a whole, mainly grows postero-distally, as evident from SMNS 16811 (Fig. 6-4K) and BMNH R224 (Fig. 6-5C). These specimens also show that the distal part of the leading edge is supported by progressively more posterior digits. Thus, when the osteogenesis stops in digit II (Fig. 6-5C, first arrow), the next digit (digit III) takes over the role of supporting the leading edge. When the osteogenesis stops in this digit (Fig. 6-5C, second arrow), the leading edge is supported by digit IV (Fig. 6-5C, third arrow), and so on. As a result of this growth pattern, the antero-distal part of the functional forefin is supported by the postero-distal part of the forefin skeleton in mature individuals (Fig. 6-5C). A possible mechanism for this pattern of growth is that the leading edge may experience the highest hydrodynamic stresses, stimulating local ossification. Consequently, the more posterior digits develop higher counts for phalangeal

Figure 6-4. Forefins of selected ichthyosaurs.

A, *Chaohusaurus geishanensis* (modified from Chapter 4); B, *Utatsusaurus hataii* (modified from Motani [in press]); C, *Grippia longirostris* (modified from Chapter 3]); D, *Mixosaurus cornalianus* (BMNH R5702); E, *M. cornalianus* (modified from Repossi [1902]); F, *M. nordenskioeldii* (PMU R186); G, *M. nordenskioeldii* (PMU R191); H, *Merriamia zitteli* (modified from Merriam [1903]); I, possible *Ichthyosaurus*(?) *janiceps* (ROM 41991, modified from McGowan [1996a], see McGowan [1996a] for its identification); J, possible new taxon from English Lower Lias (BMNH 33178); K, *Stenopterygius macrophasma* (SMNS 16811); L, *Leptonectes tenuirostris* (modified from McGowan [1991]); M, *Hudsonelpidia brevirostris* (modified from McGowan [1995]); N, *Eurhinosaurus longirostris* (SMNS 14931); O, *Temnodontosaurus burgundiae* (SMNS 15950); P, *Leptopterygius disinteger* (SMNS 15390); Q, *Cymbospondylus petrinus* (modified from Merriam [1908]); R, *Pessosaurus polaris* (PMU R176); S, *Cymbospondylus buchseri* (modified from Sander [1989]); T, *Shonisaurus popularis* (modified from McGowan and Motani [in preparation]); and U, *Shastasaurus neoscapularis* (modified from McGowan [1992]). All forefins are depicted as the right forefin in ventral view (A, E, P, and U were laterally inverted). Abbreviations are: H, humerus; R, radius; U, ulna; i, intermedium; p, pisiform; r, radiale; u, ulnare; S4-5, an accessory digit between digits IV and V. Arabic numerals are distal carpals, roman numerals are metacarpals. Not to scale. Dark gray indicates the primary axis (fourth digit).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p?
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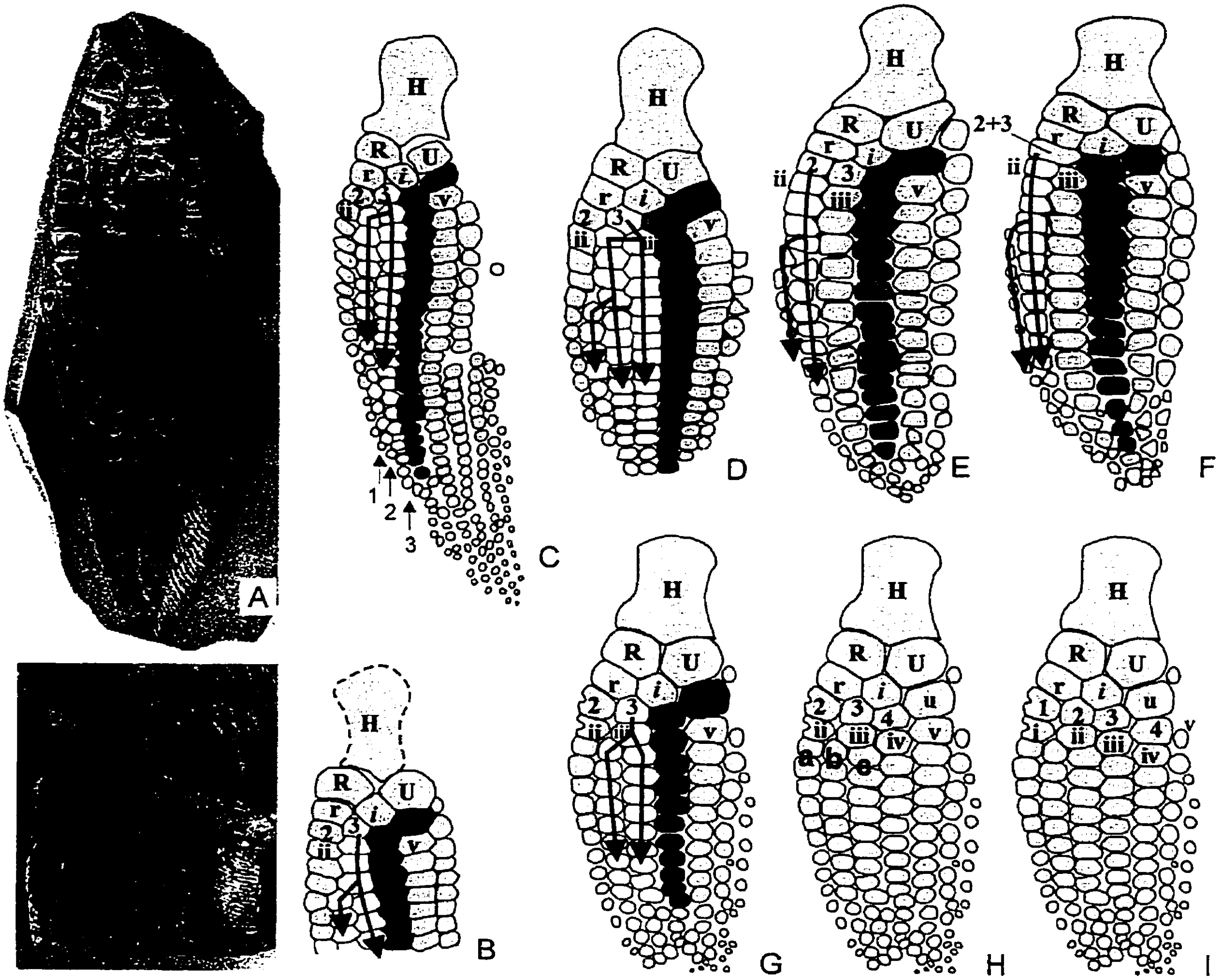
ii
iii
?
S4-5

Figure 6-5. The forefins of Ichthyosaurus.

A, BMNH 29672 (modified from Owen [1881]); B, BMNH R1664; C, BMNH R224; D, ROM 337; E and F, OUM J 13799 (modified from McGowan [1974]); and G-I, BRSMG Ce 16611. BMNH 29672 was originally described as the hindfin, but its shape and size are more suggestive of the forefin. All forefins are depicted as the right forefin in ventral view. Not to scale. Dark gray for the primary axis, and white for the digits with bifurcation. Arrows indicate a possible bifurcation scenario for a given forefin. A and B shows the anteriorly shifted position of the skeleton within the entire forefin. I is an alternative identification of the digits falsified in the text.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ossification than the more anterior ones. Therefore, the extended ossification is probably an unreliable guide for identifying the primary axis of an ichthyosaurian forefin, where hyperphalangy occurs.

The extended ossification of the more posterior digits, supporting the leading edge of the fin, is not unique to ichthyosaurs: some sauropterygians also have well developed posterior digits participating the leading edge of the fin (e.g., Pistosaurus figured by von Huene [1948]). This convergence suggests that the elongation of posterior digits may be correlated with the enclosure of the limb skeleton in a single epidermis envelope forming a fin. This feature is more evident in some species than in the others, both in ichthyosaurs and sauropterygians, due to differences in the adaptations of the forefin. For example, the feature is absent in Temnodontosaurus burgundiae (Figs. 6-3, 6-4O), and even some species of Stenopterygius (Fig. 6-3F, those with high phalangeal counts). In these forms, the forefins are long and narrow, and grows straight distally rather than posterodistally. Thus, the most anterior digit supports the entire leading edge, and has as many ossifications as the more posterior digits. These species of Stenopterygius (S. longipes and S. cuneiceps, see McGowan [1979]) have narrow fins compared with the ones with broad-based forefins, discussed earlier.

The postero-distal growth of the forefin also explains the appearance pattern of accessory digits. Accessory digits are poorly developed in narrow-finned species, where the fin does not grow postero-distally but distally, therefore the following argument only applies to broad-finned species with a postero-distal fin growth. As the growth continues, the limb skeleton starts to extend postero-distally by ossifying extra digits (as many as three in Ichthyosaurus, one in Stenopterygius), many of which are not ossified proximally (Figs. 6-4K, 6-5C). The addition of new digits posteriorly might appear to stiffen the trailing edge of the forefin as growth proceeds, but this is not the case. This is because accessory digits have a different ossification sequence from the more anterior digits. Ossification commences in the middle element, then extend both distally and proximally (Caldwell, in press a). As they only ossify in the vicinity of the leading edge (Fig. 6-5C), they stiffen the leading edge, rather than the trailing edge of the forefin. This ossification sequence, which reflects the mechanical demand, is in accordance with the adaptive plasticity of ossification pattern mentioned by Rieppel (1994b). Caldwell (in press a) also pointed out an interesting correlation between the growths of two types of accessory digit, S4-5 and digit VI (Fig. 6-4K), which he identified as S3-4 and digit V. Here, the growth of one deters that of the other. This is possibly because the growth of S4-5 leads to the more posterior location of digit V, which reduces the mechanical needs for the extended ossification of digit VI.

The developmental mechanism that makes posterior digits participate in the leading edge in the distal part of the fin of broad-finned ichthyosaurs is unknown. This is largely because the formation of hyperphalangy is poorly understood, due to the absence living analogues. Considering the fact that the pattern of limb skeleton is laid down by the segmentation and bifurcation of precartilaginous foci (Oster et al., 1988), the topology of hyperphalangy is most likely established during the embryonic stages (unless a very extraordinary delay of chondrogenic process occur distally in the digits, allowing the segmentation of precartilaginous foci, even after the proximal elements are ossified). Therefore, digits IV and V probably have more phalangeal cartilages than the more anterior digits, by the time a broad-finned ichthyosaur is born. What then, regulated the number of phalanges for each digit? One possible explanation is that the number of extra segmentations each digit underwent may have been regulated by the shape of embryonic forefins: recurring extra segmentation events in the growing digits may have been inhabited when the latest precartilage focus reached the ectodermal envelope distally, probably due to regulatory interactions with the ectoderm. If this had been the case, narrow-finned ichthyosaurs, with nearly straight leading edge, would have had extended digit II, because the digit would not reach the leading edge until late, while in broad-finned ichthyosaurs, posterior digits would have undergone more segmentation events than anterior ones, because segmentation events in anterior digits would cease earlier than those in posterior digits, due to the posteriorly curved leading edge. This hypothetical scenario effectively explains the shape of the forefins skeletons depicted in Figs. 6-3F, 6-4K, and 6-5C, but it is speculative.

Topological Conservatism of the Primary Axis

The forefin elements of those ichthyosaurs for which the growth series of the forefin are not known can only be identified based on the topological similarity with the forefins of the two genera described above (viz. Chaohusaurus and Stenopterygius). Fortunately, despite the variability of the fin skeleton shape, the topological interrelationships of the elements near the primary axis and digital arch are conservative between these two genera. This is to be expected because of the conservatism of chondrogenic pattern in this area (Shubin and Alberch, 1986) that determines the primary arrangement of the elements (Oster et al., 1988). The conservative features include: 1) the ulnare is located distal to the ulna; 2) the intermedium is anterior to the ulnare, in between the ulna and radius; and 3) dc4 is located distal to, and slightly anterior to, the ulnare, with a contact with the intermedium (Fig. 6-3C,E). The identifications of the primary axis and digital arch, based on these features, are given for other ichthyosaurian forefins in Fig. 6-5.

Shastasauridae—The only exception where the above features are absent is in Shastasaurus and Shonisaurus, where only two proximal carpals are present (Fig. 6-4T,U). This situation is interpreted here as the loss of the intermedium, or its fusion with the ulnare (McGowan and Motani, in preparation). Shastasaurus (and probably Shonisaurus) has only two primary digits, which are identified as the third and fourth (Fig. 6-4U). The rudimentary digit located posterior to these two may be digit V, but it may also be a neomorph (i.e., equivalent of digit VI of Stenopterygius). There are two reasons to support the latter identification. First, the sixth digit of Stenopterygius shows a similar ossification pattern to this digit. Secondly, if this were digit V, the digital reduction sequence of I>II, with the retention of digit V, would contradict the known digital reduction sequence (viz., I>V>II>III), which is the reverse of the chondrogenic sequence. If the digit is a neomorph, however, the digital reduction sequence would be I>V=II for shastasaurids, which is in accordance with the known sequence for extant lizards. However, these two reasons may not be sufficient to reject the possibility of the digit being the fifth. It is possible that the anterior limitation of physical space, again, lead to the loss of digit II. Also, because of the independence of digit V from the digital arch during chondrogenesis, there may be more flexibility in the timing of the loss of digit V, compared to those integrated by the digital arch.

Comparison of the Manus

Having identified the limb elements, it is now possible to compare the manal morphology among various ichthyosaurs. The positions of mc5 and the pisiform, if any, seem to be conservative: mc5 contacts the ulnare and dc4, while the pisiform touches the ulna and ulnare (compare Fig. 6-4C,E,J,K,N). The only exception is Utatsusaurus (Fig. 6-4B), where mc5 does not contact the ulnare, as it is located more distally. The more distal location of mc5 in Utatsusaurus, compared to the others, may be due to the retention of a cartilaginous dc5, which is lost in others. The space left between mc5 and the ulnare of Utatsusaurus may seem too small for this, but dc5 is usually much smaller than dc4. If this were the case, the failure of a carpal element to ossify again precedes its phylogenetic loss (Rieppel, 1994b).

Digit I is lost in all Late Triassic and later ichthyosaurs depicted in Fig. 6-4H-P, U. In the same ichthyosaurs, the fifth digit tend to have smaller proximal elements compared to those belonging to the digital arch (Fig. 6-4). These ichthyosaurs also lack any supernumerary digit anterior to the primary axis (digit IV), although accessory digits may occur posterior to the axis as in Stenopterygius and Leptopterygius disinteger (Fig. 6-4K,P). The latter two conditions are not true for Ichthyosaurus (Fig. 6-5) as will be discussed in the next section.

I hesitate to identify the digit posterior to digit IV of Merriamia (Fig. 6-4H) and Temnodontosaurus (Fig. 6-4O, see McGowan [1996c] for the latest revision of this genus) as homologous with digit V of other ichthyosaurs, because of their extremely decreased development. This digit may be better developed in other specimens of Temnodontosaurus (Fig. 6-3), but it seems to ossify from the middle elements towards the more proximal and distal ones. This ossification pattern is similar to that of digit VI of Stenopterygius (Caldwell, in press a), which is a neomorph that does not exist in Early Triassic ichthyosaurs. The pisiform, which usually exists in ichthyosaurs with digit V, also seems to be absent from Temnodontosaurus and Merriamia. These observations suggest the possibility that digit V of Temnodontosaurus, and possibly of Merriamia, is lost, and the most posterior digit is a neomorph (see also earlier section on shastasaurids). This hypothesis is in accordance with the common digital loss sequence, in which digit V is lost following the loss of digit I. However, it is premature to arrive at a conclusion at this point, because: 1) the ossification sequence within digit V of Stenopterygius is not well established (it may have ossified from the middle, as in digit VI), and 2) it is also possible that the ossification pattern of digit V merely changed in these two genera.

Ichthyosaurus

The forefin of Ichthyosaurus largely differ from those of the other Early Jurassic ichthyosaurs, therefore it is worth devoting a section to this genus.

Identification of Elements—Based on the conservative topological features in the area of the primary axis and digital arch, described earlier, the primary axis and the digital arch of Ichthyosaurus forefin can be identified as in Fig. 6-5B-G. Digit I is lost, as in all other Late Triassic and later ichthyosaurs. With this identification, mc5 contacts the ulnare and dc4, which is again in agreement with all other Late Triassic and later ichthyosaurs.

Merck (1996) gave a different identification for Ichthyosaurus forefin elements (Fig. 6-5I), based on a congruence test he devised, but his identification is problematic both topologically and methodologically. The topological problems include: 1) presence of the first digit, which is absent from all other late Triassic and later ichthyosaurs; 2) lack of contact between the intermedium and dc4; and 3) lack of contact between mc5 and the ulnare (Fig. 6-5I). There are two different levels of methodological problems. First, the method is supposed to utilize phylogenetic information to determine homologies, but the phylogeny, in a cladistic sense, is based on pre-established homologies, therefore the method is tautological. Secondly, the best phylogenetic hypothesis is selected as the simplest explanation of all available data, whereas the "phylogeny" his method uses is based on a partial data set (i.e., excluding the forefin features). In this way, the method is merely adjusting the data for forefins so as not to contradict the rest of the data, not the phylogeny. It is true that the inclusion of forefin data in the phylogenetic reconstruction would be also considered tautological. Homologies therefore should be established on developmental data.

McGowan (1974:fig. 5) pointed out an interesting example where the numbers of distal carpal ossification differ between the right and left forefins of one individual of Ichthyosaurus communis. These forefins are depicted here as Fig. 6-5E (right) and F (left). The right forefin has three distal carpal ossifications as in all other forefins of Ichthyosaurus, but the left forefin only has two. The anteriormost distal carpal ossification of the left forefin is almost as wide as the combined dc2 and 3 (Fig. 6-5). Therefore, it is likely that dc2 and 3 of the left forefin has been fused to form a single ossification.

Diagnostic Features of Ichthyosaurus Forefin—The forefin of Ichthyosaurus (Fig. 6-5A-I), from the Lower Liassic of England, differ from all other Lower Jurassic forefins (Fig. 6-4J-P) in that: 1) digital bifurcation occurs anterior to the primary axis; 2) the ulnare is larger than the intermedium, possessing a large articular facet for mc5; 3) the fifth digit, including mc5, is wide and robust. These features are absent from the forefin of I(?). janiceps from the Upper Triassic of Canada (McGowan, 1996a; nearly identical to Fig. 6-4I), suggesting a possible paraphyly or polyphyly of the genus as currently designated.

Supernumerary Digits— The supernumerary digits anterior to digit IV are most likely formed by digital bifurcation during the chondrogenesis, because: 1) digital trifurcation is a very unlikely event due to specific constraints involved (Oster et al., 1988); 2) iterated segmentation of a de novo condensation of precartilage mesenchymal cells is not known anterior to the primary axis; and 3) bifurcation is a basic phenomenon in the digital arch formation (Shubin and Alberch, 1986), and the gene controlling these bifurcation events may be expressed later, causing digital bifurcation.

Digital bifurcation seems to occur most commonly from digit III. In Fig. 6-5H, three digits exist anterior to digit IV, one of which is supernumerary. There are two possible bifurcation scenarios for this forefin: 1) the anterior two digits (a and b of Fig. 6-5H) emerged by the bifurcation of mc2, accordingly these digits represent digit II; and 2) bifurcation of mc3 formed the posterior two digits (b and c of Fig. 6-5H), therefore these digits represent digit III. It is not logical to identify one of the two digits resulting from digital bifurcation as the continuation of the original digit, because the two digits are developmentally equal (Oster et al., 1988). When considering the postaxial dominance in the limb development (Shubin and Alberch, 1986), the second scenario is more likely. The elements of digit c are shifted posteriorly relative to mc3, due to the presence of digit b that partially occupies the distal space of mc3. This is unlikely to happen if digit b emerged from mc2, because the space distal to mc3 would be occupied by the first phalanx of digit III by the time mc2 bifurcates. Mc4 is directly distal to dc4, suggesting that the bifurcation did not occur in digit IV.

While many other forefins can be interpreted as having a bifurcated digit III (e.g., Fig. 6-5B-D), some others appear to have a bifurcated digit II (Fig. 6-5E,F, see also fig. 4B, C of McGowan [1972]). In these forefins, the anterior branch of bifurcated digit II only ossifies in very small elements, unlike that of the bifurcated digit III of the other forefins. This seems to be related to the limited anterior space: by the time the bifurcation occur in digit II, most of the available space is already occupied by the more posterior digits that have the advantage of an earlier development. Another piece of evidence for this limited space hypothesis concerns the width of digits. In the forefins with digit II bifurcation, digits III, IV and V are of similar width (Fig. 6-5E, F), while in the fins with digit III bifurcation, the elements of digits II and III, distal to the bifurcation, are narrower than those of digits IV and V (Fig. 6-5B-D, G).

To summarize, two general tendencies seem to be present in the pattern of supernumerary digits anterior to the primary axis: 1) bifurcation is present at least in digit II or III, and sometimes in both; 2) on average, the anterior branch of the bifurcated digit has smaller elements compared to the posterior one. These observations can be explained by the combination of the postaxial dominance of limb development (Shubin and Alberch, 1986) and the limited available space in the area along the leading edge. The fact that many digital bifurcations in Ichthyosaurus occur from mc3, which in turn resulted from the bifurcation of dc3 (Shubin and Alberch, 1986), suggests it is possible that the gene controlling the bifurcation in the digital arch was expressed for an extra time.

The supernumerary digits posterior to the primary axis (viz., digits VI-VIII) seems to appear in the manner similar to digit VI of Stenopterygius (digit V of Caldwell [in press a]), that is, the ossification does not start from the most proximal element, but from that in the middle. This is another example of the modified ossification pattern in the posterior supernumerary digits suggesting that this feature was common among the various Late Triassic and later ichthyosaurs.

Possible New Taxon

Two isolated forefins from the Lower Lias of England (BMNH 33178 [Fig. 6-4J] and ROM 954) may represent a new taxon, because of their dissimilarities with the forefins of contemporary ichthyosaurs. They differ from Ichthyosaurus fins in that the digital bifurcation does not occur anterior to the primary axis; the ulnare is not enlarged; the fifth digit is narrower than the more anterior digits; and the notches are present in the majority of leading-edge elements (they may occasionally exist in two or three elements in Ichthyosaurus). Leptonectes (see McGowan [1996b] for this new generic name) has large numbers of rounded elements in all digits, especially in digit V (Fig. 6-4L), the feature that is absent from these forefins. Temnodontosaurus has a reduced digit V, and lacks the pisiform (Fig. 6-4O), which are inconsistent with these two forefins.

It should be noted that the forefins show a close resemblance to those of Stenopterygius (Toarcian, some 20 m.y. younger) and of Ichthyosaurus(?) janiceps (middle Norian, several m.y. older) in manal morphology. However, it is difficult to determine with which of these forefins they have more in common. BMNH 33178 seems to have the supernumerary digit S4-5, which typically occurs in many, but not all, Stenopterygius specimens, while it is clearly absent from ROM 954. The only specimen of I.(?) janiceps, and ROM 41991 (a forefin from the nearby locality that strongly resemble that of I.(?) janiceps (Fig. 6-4I), has no sign of S4-5, but the sample size is admittedly small. The humeri of both BMNH 33178 and ROM954 are proximally wide, while both forefins seem to be mature considering the packing of the elements (Johnson, 1977). This is in disagreement with Stenopterygius, which tend to have proximally narrow humerus in adults (Johnson, 1977), while in accordance with ROM 41991 (McGowan, 1991).

No new taxonomic name is given to these forefins at this point, considering the lack of associated skeletons and a well established phylogeny of the Ichthyosauria. However, the presence of an undescribed species in the Lower Liassic, possessing this type of forefin, seems reasonable, because the same type of forefin is known from both older (Norian) and younger (Toarcian) stages.

PERICHONDRAL OSSIFICATION

Caldwell (in press a,b) was the first to point out that the reduction of perichondral ossification played an important role in the evolution of ichthyosaurian forefin. He suggested that the degree of PCO (perichondral ossification) reduction progressed through the ichthyosaurian evolution, viewed as a stratigraphic time series. While this view approximates well the general tendency of PCO reduction through time, it lacks the resolution, partly because the taxa examined were too few (five genera, which are now recognized as four) and lacked Late Triassic forms. In the following sections, I will analyze the PCO reduction in ichthyosaurian forefins with a higher resolution, by including more taxa, and by examining selected forefin elements separately. It will be shown that PCO reduction occurred in two phases in ichthyosaurs, and several suits of elements showed different patterns.

Interpretation of Notches

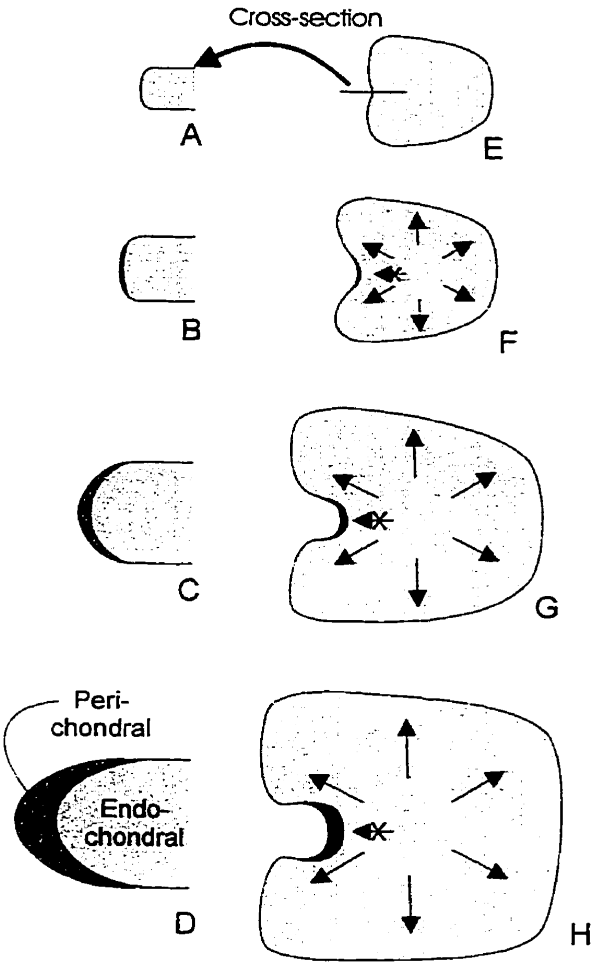
One of the largest differences between Caldwell (in press b) and the present study is the interpretation of the notched margins of forefin elements, which are commonly present in most Late Triassic and Early Jurassic ichthyosaurs. Since the interpretation of this structure is very important, it is discussed first.

There are three major reasons to conclude that perichondral ossification occurred along the notched margin of fin elements.

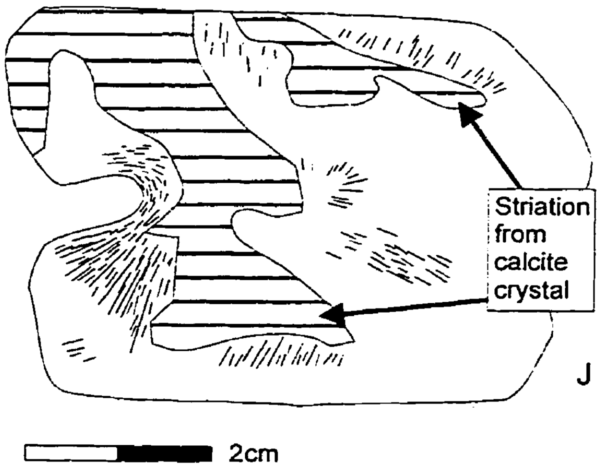
1) The morphology of notched elements.—The following observations were made for ROM 954 (a possible new taxon from the English Lower Lias) and ROM 44295 (an undescribed large ichthyosaur from the Upper Triassic of British Columbia). ROM 44295 is also supplied with an accession number from Royal British Columbia Museum (RBCM EH.91.2.6). ROM 954 has been entirely extracted from matrix while ROM 44295 is partly embedded in matrix, although the anterior aspect is free. The notched forefin elements of these specimens are sufficiently large to permit examination of small surface details (Fig. 6-6I, J).

Figure 6-6. Notched fin elements of Late Triassic and later ichthyosaurs.

A-H, Schematic diagrams showing hypothetical ossification pattern of notched elements, where perichondral ossification spread from the anterior aspect, both dorsally and ventrally. A-D depict the cross section of the element in the notched area, while E-H gives the dorsal (or ventral) view of the element corresponding to A-D. Dark gray indicates perichondral (and periosteal) ossification, light gray endochondral. I-J, The fourth phalanx of digit II of ROM 44295. Striations along the notch suggest a proximo-distal growth of the surface bone in this area. See text for details.


Cross-section
A
E
B
F
C
G
Peri-
chondral
Endo-
chondral
D
H


I


Striation from calcite crystal
J
2cm

There is a narrow band of bone along the notched margin that stretches in a proximo-distal direction. The surface striations of this area are generally in a proximo-distal direction, as in the shaft of the long bones of terrestrial amniotes, indicating the proximo-distal growth of the surface bone in this region (Fig. 6-6I, J). In the other areas of the notched elements, the striation radiates from the center of the dorsal (or ventral) surface, indicating the growth of the bone from the center to the circumference. The margin of the element is of unfinished bone, except along the notched margin, where the finished surface of the dorsal (or ventral) side smoothly curves and connects with that of the ventral (or dorsal) surface (Fig. 6-6D).

2) The absence of an alternative mechanism.—There is no alternative mechanism for forming notches in multiple elements along the leading edge, as admitted by Caldwell (in press b).

3) Presence of evolutionary intermediate.—As will be described later, PCO reduction proceeds from the proximal and distal corners of a long bone towards the middle (Fig. 6-4), and various degrees of this reduction process are represented in the fossil record. For example, the radius of Merriamia zitteli (Figs. 6-4H, 6-7F) has a shaft, but because it is reduced, the shape of the shaft region appear as the intermediate status between the proper shaft and a notch.

One possible falsification of this interpretation of notches is the presence of notches in carpal elements: perichondral ossification is usually absent from the carpals (Rieppel, 1992a;Caldwell, 1994,in press b). However, there are cases where carpal bones develop perichondral ossifications, such as in crocodilians (Caldwell, in press b), therefore its appearance in the carpals of derived ichthyosaurs is an acceptable assertion.

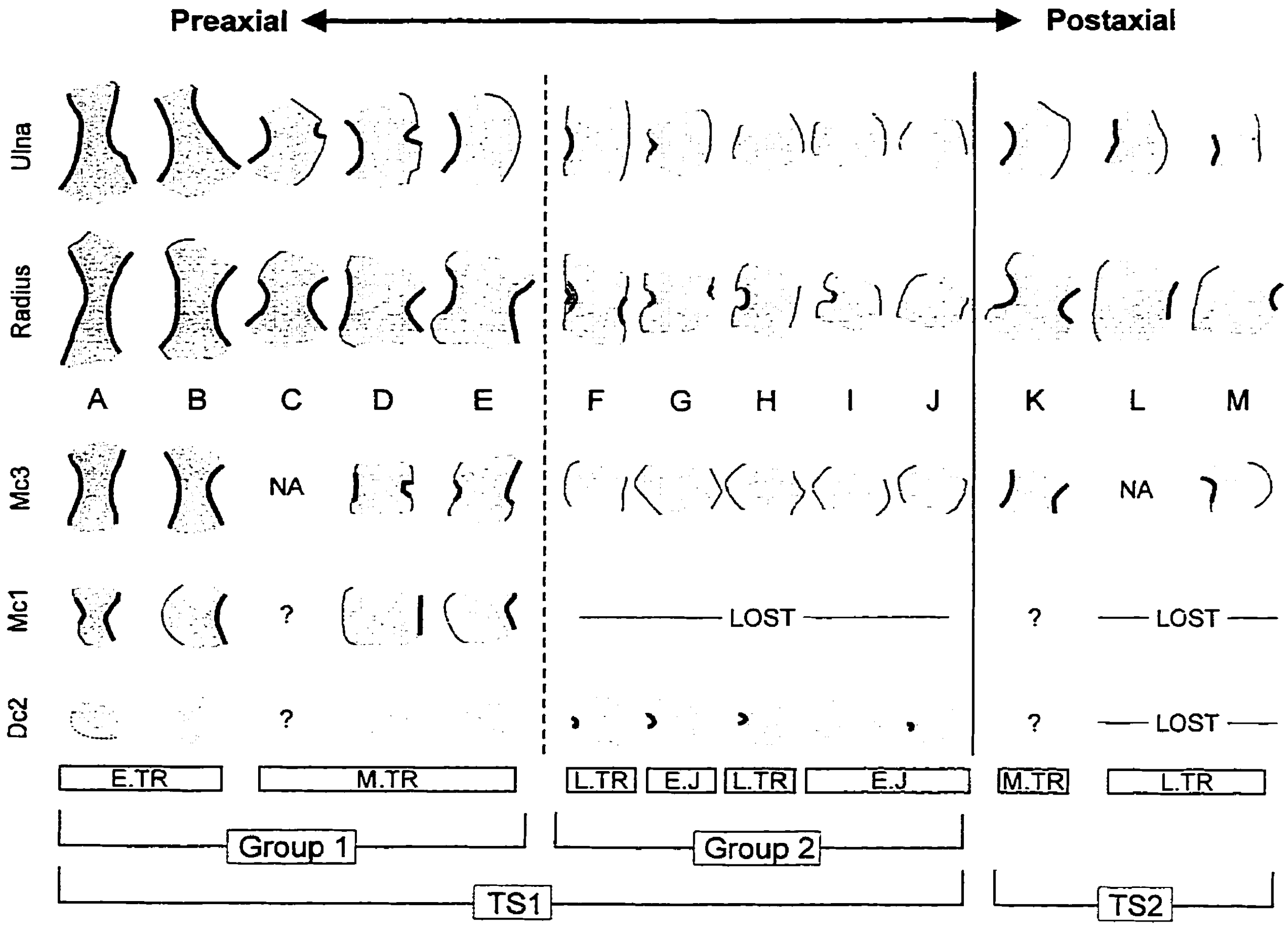
Caldwell (in press b), on the contrary, suggested that no perichondral ossification is present along the notched margins of the leading-edge elements of Stenopterygius. He gave two reasons for his conclusion: 1) no surface bone is observable in juvenile specimens along the notch; and 2) ontogenetic series indicates surface bone from one surface eventually grows to contact that from the other side. Both of these observations, however, can be explained by the growth of perichondral (and periosteal) bone (Fig. 6-6A-H). The perichondral ossification along the notch, which never occupies a large proportion of the bone surface, is most likely very small during the early growth stages. The ossification also starts from the anterior aspect of the bone, and it is only after a certain stage that it is observable from the dorso-ventral aspect (Fig. 6-6A-H). Therefore it is very difficult to confirm its existence in small individuals unless a micropreparation is conducted from the anterior angle, and observed under the microscope (such a process was not mentioned in Caldwell [in press a]). He did not specify what features indicate the ossification process that he mentioned as the second reason. If it was based on the fact that the smooth connection between the dorsal and ventral sides is more remarkable in larger individuals, it can also be explained by the growth of perichondral ossification from the anterior aspect towards dorsal and ventral aspects, as mentioned earlier (Fig. 6-6A-D). If the surface bone of the dorsal side were to grow to meet that of the ventral side, as suggested by Caldwell (in press b), the surface striation in the notched area would be perpendicular to the notched margin, reflecting this direction of growth. This, however, is not the case (Fig. 6-6I, J).

Reduction

The reduction of perichondral ossification for the radius, ulna, mc1, mc3, and dc2, are figured for 13 species of Triassic and Early Jurassic ichthyosaurs (Fig. 6-7). The reduction was judged relative to the respective bones of terrestrial amniotes, in which perichondral ossification is never reduced in the shaft region (Caldwell, in press b). Because the phylogenetic

Figure 6-7. Perichondral ossification reduction in various forefin elements.

Thick lines indicate the presence of perichondral bone, while thin lines indicate the part of the element that has lost perichondral ossification relative to terrestrial amniotes (representing ancestral states). A, Utatsusaurus hataii (IGPS 95941); B, Grippia longirostris (PMU R472); C, Cymbospondylus petrinus (modified from Merriam [1908]); D, Mixosaurus nordenskioeldii (PMU R191); E, M. cornalianus (BMNH R5702); F, Merriamia zitteli (modified from Merriam [1903]); G, Leptonectes tenuirostris (modified from McGowan [1991]); H, possible Ichthyosaurus(?) janiceps (ROM 41991, modified from McGowan [1996a]); I, possible new taxon from the English Lower Lias (BMNH 33178); J, Temnodontosaurus burgundiae (SMNS 15950); K, Cymbospondylus buchseri (modified from Sander [1989]); L, Shonisaurus popularis (modified from McGowan and Motani [in preparation]); and M, Shastasaurus neoscapularis (ROM 41993). See text for grouping.


Preaxial
Postaxial
Ulna
Radius
A
B
C
D
E
F
G
H
I
J
K
L
M
Mc3
NA
NA
Mc1
?
LOST
?
LOST
Dc2
?
?
LOST
E.TR
M.TR
L.TR
E.J
L.TR
E.J
M.TR
L.TR
Group 1
Group 2
TS1
TS2

relationships among these ichthyosaurs has yet to be established, the 13 species are arranged in Fig. 6-7 according to the relative perichondral bone reduction of the radius and ulna. This sequence is almost identical to the stratigraphic sequence of the same taxa, supporting Caldwell's (in press b) view of stratigraphic transformation series. Shastasaurid ichthyosaurs, which differ remarkably from the rest of the Ichthyosauria in their humeral morphology (Figs. 6-1, 6-2), are separated from the main transformation series, and depicted on the right hand side of Fig. 6-7 as the second series.

Terminology and grouping—PCO reduction seems to occur in two different directions that are defined relative to the element being examined. The first direction is inter-elemental, meaning the side(s) of an element facing (an)other element(s). Caldwell suggested that the consequence of such a reduction is the formation of a new joint between adjacent elements, resulting in a more robustly integrated fin skeleton. The second is peripheral, meaning the side of an element not facing any other elements, but directed toward the fin margins. This second direction does not exist for those elements that are entirely surrounded by other elements (such as mc3 of non-shastasaurids). For example, the preaxial direction is peripheral for the radius, but inter-elemental for the ulna.

The main transformation series (left hand side of Fig. 6-7) will be referred to as TS1, and the second series as TS2. In TS1, two groups can be recognized according to the similarity in PCO reduction, which are tentatively named group1 and 2, to keep the description brief and readable. The two groups comprise the following taxa, respectively: group1—basal ichthyosaurs, such as Utatsusaurus, Grippia, and Mixosaurus; group2—Late Triassic non-shastasaurid taxa, viz., Merriamia and Ichthyosaurus janiceps, and Early Jurassic ichthyosaurs. Note that this grouping corresponds with morphotypes 1 and 3 of the humerus. As mentioned earlier, TS2 comprises the ichthyosaurs with the morphotype 2 humeri, such as Cymbospondylus buchseri, Shonisaurus and Shastasaurus.

Radius and Ulna—The radius and ulna show a similar pattern. PCO reduction first appears in the proximal corner of the peripheral side (Fig. 6-7A), then on the distal corner of the same side (Fig. 6-7B, radius). PCO loss on these corners were judged based on the surface striations, which intersects with the corner margin, indicating the growth towards the margin, not parallel to (striations are parallel to the shaft margin, where PCO exists). From these two corners, the reduction proceeds towards the middle of the shaft (Fig. 6-7C-J). In the ulna, peripheral PCO was entirely lost in some Middle Triassic forms (Fig. 6-7E), and lacking in all later forms (both in TS1 and 2). In the radius of TS1, the reduction proceeded more slowly compared to in the ulna: peripheral PCO remained along the notched margin, and did not disappear until Early Jurassic (Fig. 6-7J). In TS2, the peripheral PCO of the radius is entirely lost in Late Triassic forms (Fig. 6-7L, M).

In TS1, inter-elemental PCO reduction did not occur until Late Triassic (i.e., not until group 2 appeared), and it never appeared in TS2, even in Late Triassic forms. In group 2, the reduction appeared on the distal and proximal corners of the inter-elemental side (Fig. 6-7F), and proceeded toward the middle of the shaft (Fig. 6-7G-J), which is the same manner as peripheral PCO reduction.

The shape variation of the radius and ulna seems to be correlated with the degree of PCO reduction. The most remarkable effect is the shortening of the elements: in both radius and ulna, the reduction of PCO is directly reflected in the decrease of the length/width ratio (Fig. 6-7). This is reasonable because PCO reduction involves the shortening of the shaft. PCO loss on one side alone does shorten the element, but not as much as when the loss occurs on both sides.

Mc3—The third metacarpal shows a different pattern of PCO reduction compared to the radius and ulna. In TS1, mc3 has no peripheral direction, being surrounded by other elements. Inter-elemental PCO reduction first occurred in Middle Triassic forms (Fig. 6-7D, E), earlier than in the epipodial elements. The reduction first appeared on the four corners of the element, and was completed rapidly because no Late Triassic forms has an indication of PCO in mc3. The situation is slightly different in TS2, because mc3 became a leading edge element in later forms (Fig. 6-7M), due to the loss of the digits I and II. Peripheral PCO reduction seems to be absent from the only example of these later forms (Fig. 6-7M).

Mc1—The first metacarpals are only known for group 1 ichthyosaurs (Fig. 6-7). Peripheral PCO loss was present even in the earliest known forms (Fig. 6-7A, B), some of which already lost peripheral PCO entirely (Fig. 6-7B).

Dc2—All early members of the group 2 ichthyosaurs have notches in their carpal elements, at least for the ones on the leading edge. These notches, bearing peripheral PCO, are absent in later members of the group. A reasonable phylogeny for these ichthyosaurs is required to assess whether the absence of PCO in later forms represents a secondary loss, or the retention of plesiomorphic feature (i.e., absence of PCO in group 1 ichthyosaurs).

Implication—Two different phases of PCO reduction are recognizable along the stratigraphic sequence: 1) peripheral PCO reduction that started in the earliest ichthyosaurs, but slowed down after the Middle Triassic and 2) inter-elemental PCO reduction that did not occur until Late Triassic, but progressed very rapidly once it appeared. The second phase only appeared in a group (probably a clade) of ichthyosaurs that survived into the Jurassic (viz., group 2). Merriamia zitteli, from the early Late Triassic, marks the transition from the phase 1 to 2, for having: 1) initiation of inter-elemental PCO reduction in epipodials, and nearly entire loss from the manus and 2) almost no increase in peripheral PCO reduction compared to Mixosaurus from the Middle Triassic. These specific appearance patterns of the two phases suggest that two different mechanisms controlled these two separate phases of PCO reduction.

It is also noticeable that elements close to the distal margin of the forefin do not fit into the two patterns pointed out in the previous paragraph, showing yet another pattern of PCO reduction. Even in the earliest forms, the most distal elements possess no PCO, peripherally or inter-elementally (Fig. 6-3).

Caldwell (in press b) pointed out the postaxial dominance of PCO reduction in ichthyosaurs, which coincides with the ossification sequence (not its reverse) in extant diapsids. This observation seems to be re-confirmed in the present study, but only for peripheral PCO reduction: the radius usually shows less reduction compared to the ulna, and mc1 compared to mc5 in the group1 ichthyosaurs (Fig. 6-3A-G). On the other hand, there seems to be no postaxial dominance in inter-elemental PCO reduction, which appeared suddenly in all inter-elemental margins of proximal elements in Late Triassic (see Merriamia zitteli). However, inter-elemental PCO reduction seems to be proximally dominant in M. zitteli (Fig. 6-4H), which is again in accordance with the ossification sequence. The entire absence of PCO in the most distal elements of the earliest ichthyosaurs, pointed out earlier, is in accordance with the reverse of the ossification sequence in extant diapsids. These discrepancies again suggest the multiple mechanisms causing different patterns of PCO reduction.

Appearance

As mentioned earlier, perichondral ossification appeared in the carpals of group 2 ichthyosaurs. Because this feature is lacking in earlier ichthyosaurs and most terrestrial amniotes, it is probably synapomorphic for group 2 ichthyosaurs. PCO is usually present only in the radiale and dc2 (Fig. 6-4F, G, I), but it is also present in the ulnare and dc4 in Merriamia zitteli, the earliest member of group2 (Fig. 6-4E). The appearance of the carpal PCO in ichthyosaurs is convergent with that in crocodilians, but no ichthyosaurs are known to have a complete shaft, as in the latter. This may be because the mechanism for inter-elemental PCO loss was already established in ichthyosaurs by the time the carpal PCO appeared (Figs. 6-3, 6-4).

The presence of the carpal PCO in group 2 suggests that the carpals developed the features of the long bones in these ichthyosaurs, before the long bones became carpal-like through the reduction (and ultimately the loss) of perichondral ossification. It is noteworthy that the proximal carpals of Merriamia zitteli are slightly longer than wide, which is unusual for ichthyosaurs (some ichthyosaurs have been described as having elongated proximal carpals, but these are due to tectonic deformation of the specimens [Chapter 2]).

SUMMARY

1. There are three types of humeri, defined according to the direction of the head, the relative proportion of the distal facets, and completeness of the anterior flange, which exists in all ichthyosaurian humeri, even if reduced. The extreme robustness of humerus is also characteristic of one of the three types.
2. The forefin elements of Chaohusaurus and Stenopterygius can be identified, based on osteogenic sequences, showing that the latter lacks digit I, contrary to the traditional view.

3. Chaohusaurus (Early Triassic) and Stenopterygius (late Liassic) have the identical arrangements of elements in the area of the primary axis and digital arch, suggesting the topology of this area is probably conservative among all ichthyosaurs, as predicted by conservatism of chondrogenic process among amniotes (Shubin and Alberch, 1986). This topological conservatism allows the identification of the forefin elements of other ichthyosaurs.
4. Shastasaurus lacks digit I and II, while having a vestigial digit posterior to digit IV, which is tentatively identified as digit V. If this were digit V, however, its retention after the loss of digit II would contradict the digital loss sequence in known for lizards, which is the reverse of chondrogenic sequence (Rieppel, 1994b).
5. Two factors seem to be important in the determination of forefin topology for Early Jurassic ichthyosaurs: postaxial dominance of limb development (constraint by an inherent developmental mechanism) as pointed out by Shubin and Alberch (1986), and the anterior limitation of the space availability (physical constraint posed upon by being enclosed in a fin).
6. A suit of evidence supports the existence of perichondral ossification in the notched fin elements of Jurassic and Late Triassic ichthyosaurs. Two negative pieces of evidence against its existence, pointed out by Caldwell (in press b), can be explained by the growth of perichondral (and subsequent periosteal) bone.
7. Reduction of perichondral ossification (PCO) in the long bones of ichthyosaurian forefins occurred in two major phases, when viewed as a stratigraphic transformation series. The first one, which was the reduction of peripherally located PCO, started in the Early Triassic and slowed down after the Middle Triassic. The second one, which only concerns the inter-

elemental PCO, started in the metacarpals and phalanges of Mixosaurus, and was completed in some Late Triassic forms.

8. Reduction of perichondral ossification (PCO) is not necessarily postaxially dominant, different phases showing different gradients. The relationships between the sequences of ossification and PCO reduction cannot be explained simply.

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CHAPTER 7

REDESCRIPTION OF A DEFORMED SKULL OF UTATSUSAURUS HATAII

ABSTRACT

The tectonically deformed skull of Utatsusaurus hataii, an Early Triassic ichthyosaur, is redescribed, based on a retrodeformed image. Compared to the skull of Ichthyosaurus, from the Lower Jurassic, the present skull seems less derived from a typical terrestrial diapsid condition. For example: 1) the supratemporal, squamosal and quadratojugal are all present; 2) a clear transverse flange is present on the pterygoid; 3) the postorbital-squamosal contact is present along the upper temporal fenestra; and 4) the frontal forms the dorsal margin of the orbit. The skull also has typically ichthyosaurian features, such as: 1) the postfrontal has a posterior process that overlies the postorbital; 2) the orbit is very large; 3) a long, pointed snout, formed by the premaxilla is present. Other features include: 1) the upper temporal fenestra has a wide anterior terrace; and 2) the external naris faces dorsally.

INTRODUCTION

Our knowledge of the early evolution of the Ichthyosauria is limited, largely due to the lack of information regarding the earliest forms. The earliest ichthyosaurian species have been reported from the Lower Triassic (Spathian) of the Northern Hemisphere, although fragmentary specimens are known from the lower stage, the Smithian (Callaway and Massare, 1989). There are three major localities: Spitsbergen that yields Grippia longirostris (Wiman, 1929,1933; Mazin, 1981), Anhui Province, China, that yields Chaohusaurus geishanensis and similar forms

(Young and Dong, 1972; Chen, 1985, Chapter 5), and Miyagi Prefecture, Japan, that yields Utatsusaurus hataii (Shikama et al., 1978). Due to incomplete preservation, none of the above stated species are completely known, preventing a phylogenetic assessment of ichthyosaurian relationships with other amniotes. The most poorly documented part is the skull: it has been described in some detail for G. longirostris (Wiman, 1929;1933; Mazin, 1981), but these descriptions are not without errors, resulting in disagreements in the interpretation of the cheek and temporal regions (Callaway, 1989; Chapter 9). An adequate description of an Early Triassic ichthyosaurian skull is long overdue.

Since the description of Utatsusaurus hataii by Shikama et al. (1978), many additional ichthyosaurian specimens have been collected from the Lower Triassic of Miyagi Prefecture, Northeast Japan. Amongst the most remarkable findings are two scattered skeletons with skulls (Minoura et al., 1993). Unfortunately, however, the specimens have undergone much tectonic deformation, obscuring the original shapes. The specimens are from the Spathian, roughly the same horizon as the type locality of Utatsusaurus hataii. Minoura (1994) gave a reconstruction based on the skulls by retrodeforming the images using Sdzuy's (1966) method. However, since his retrodeformation did not remove distortion completely (Minoura, 1994:64), this reconstruction has errors.

The purpose of the present study is to redescribe the better preserved one of the two skulls, based on undeformed images generated by my own technique (Chapter 2).

MATERIAL

The abbreviations for the institutions are: HUG-Hokkaido University, Department of Geology, Sapporo; and IGPS-Institute of Geology and Paleontology, Tohoku University, Sendai.

The material for the present study is specimen 1 of Minoura et al. (1993), now registered as HUG 9372. The skull of this specimen is better preserved than the other (specimen 2 of Minoura et al. [1993]). The specimen was preserved in slaty shale, and is therefore deformed. Distortion is so extensive that the original symmetry of the skull has been completely lost (Fig. 7-1A).

RETRODEFORMATION TECHNIQUE

Theoretical Background

It is not the purpose of the present paper to retrodeform the specimen in all three dimensions, because such would require a three-dimensionally digitized image of the specimen, which cannot be obtained easily. Instead, retrodeformation of the two dimensional images of the specimen is performed, using the retrodeformation method described in Chapter 2. This method only restores the original proportions, not the size or direction, of the image, which is a common limitation of all available retrodeformation technique (Chapter 2).

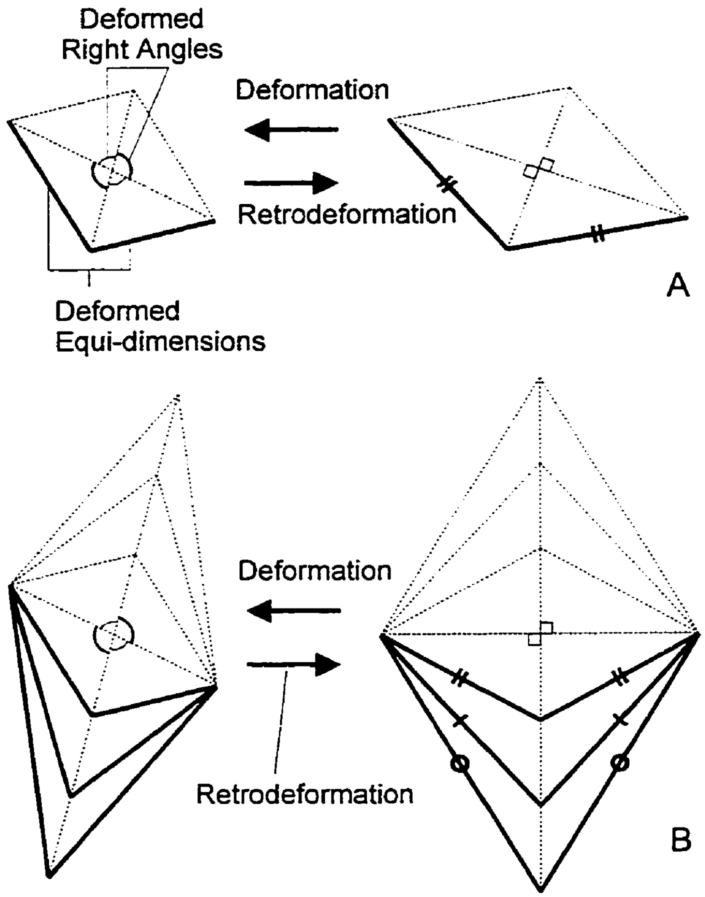
Tectonic deformation may occur in several different ways, but only the simplest type is discussed here. In this type, the strain in the deformed rock, and in the fossils it contains, is simple (Ramsay and Huber, 1983), which means it can be expressed in terms of an ellipsoid (called strain ellipsoid). When there is no strain, the ellipsoid is spherical. The strain can be considered simple when the following conditions are met.

1) deformation is homogeneous within the area being analyzed.

2) deformation is passive, that is, there is no extension but only compression within the area being analyzed.

Figure 7-1. Schematic diagrams depicting the relationship between deformed right angle and deformed equi-dimensions.

A: there is one deformed right angle for a given pair of deformed equi-dimensions. B: there are many pairs of deformed equi-dimensions for a given deformed right angle.


Deformed
Right Angles
Deformation
Retrodeformation
Deformed
Equi-dimensions
A
Deformation
Retrodeformation
B

To remove a simple strain, it is first necessary to find the strain ellipsoid in the area being analyzed. Once the strain ellipsoid if found, retrodeformation can be achieved by extending the image of a fossil along the two minor axes of the strain ellipsoid, so that the ellipsoid becomes a sphere (i.e., no strain). When dealing with two-dimensional images, it is not necessary to consider the whole strain ellipsoid, but only its cross-section, which is an ellipse, in the plane of view. Then, two-dimensional retrodeformation can be achieved by extending the image in the direction of the minor axis of this ellipse, so that the ellipse becomes a circle (Chapter 2). Such a simple extension is a linear transformation, which can be expressed by a two by two matrix (matrix B of Chapter 2).

Most of the published studies of fossil retrodeformation try to find these ellipses either graphically or by calculation (e.g., Lake, 1943; Hills and Thomas, 1944; Sdzuy, 1966; Ramsay and Huber, 1983; Cooper, 1990; Hughes and Jell, 1992; and Rushton and Smith, 1993). On the contrary, I devised a method to calculate the matrix B first, instead of finding the strain ellipse directly (Chapter 2). The method utilizes matrix algebra, therefore simplifying the calculation process, as well as enabling the use of statistical method to calculate the best-fit matrix for the data available. This method is applicable to various kinds of fossil specimens, including those of isolated vertebrate skeleton, as long as the above stated two assumptions are reasonable.

Three different types of measurements can be used for finding the strain ellipse (Cooper, 1990; Chapter 2):

i) deformed right angle—an angle that was 90 degree before the tectonic deformation.

ii) deformed equi-dimensions—dimensions that were equal prior to tectonic deformation.

iii) deformed equi-angles—angles that were equal prior to tectonic deformation.

Traditionally, it was believed that at least two deformed right angles, three deformed equi-dimensions, or three deformed equi-angles were required to find the strain ellipse. I showed mathematically that two pairs of equi-dimensions were also sufficient for the purpose, using matrix algebra (Chapter 2). This finding expanded the applicability of retrodeformation technique because two pairs of equi-dimensions occur more often than three equi-dimensions. However, the statement made in Chapter 2 can be further elaborated, by mentioning some exceptional cases where two pairs of equi-dimensions are insufficient, as explained below.

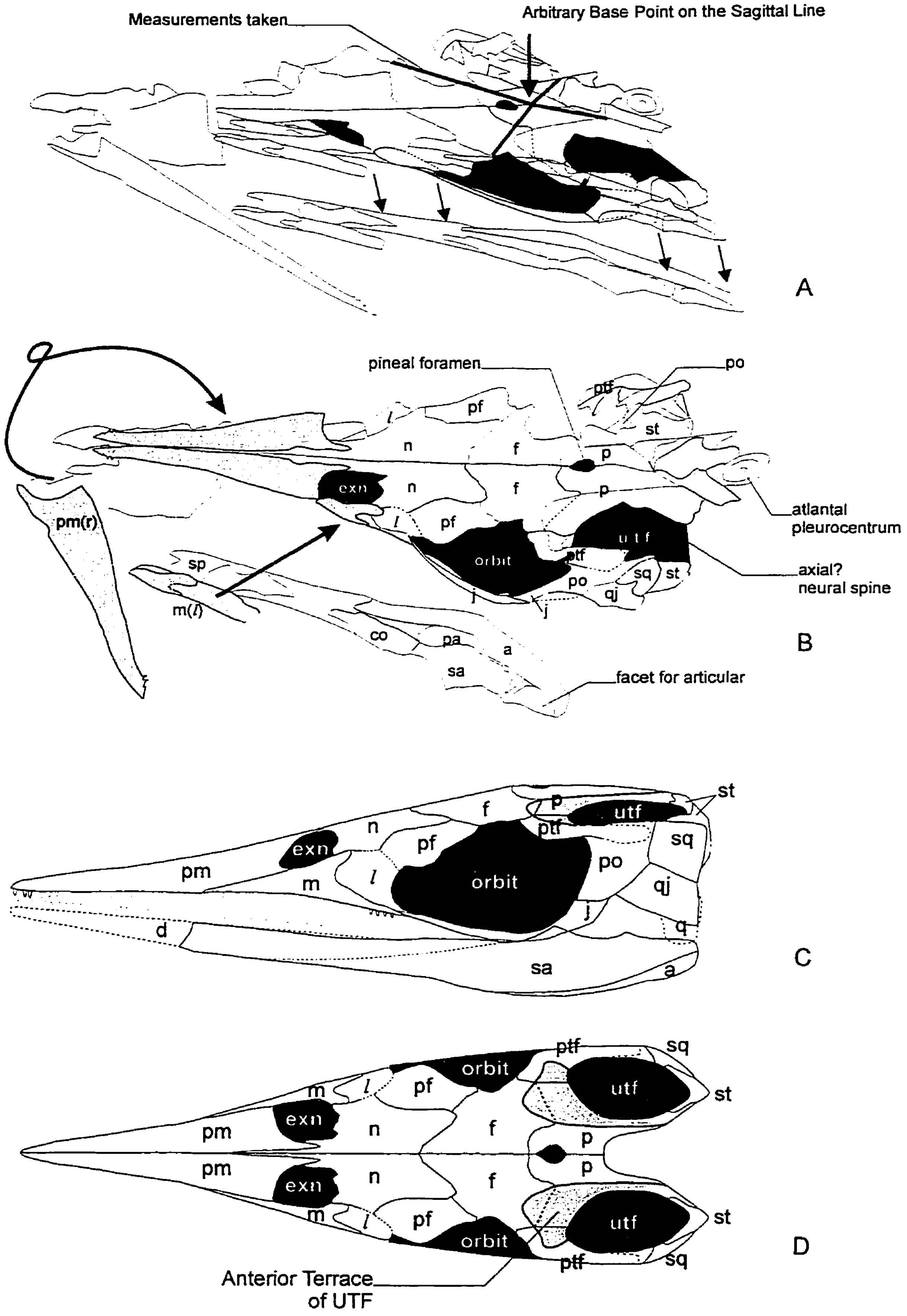
For a given pair of deformed equi-dimensions, there is one deformed right angle (Fig. 7-2A). This is because a pair of deformed equi-dimensions defines a deformed rhomboid, whose diagonals form a deformed right angle (Fig. 7-2A). Therefore, two pairs of deformed equi-dimensions are usually equivalent to two deformed right angles, and hence contain sufficient information to find the strain ellipse. However, the correspondence between deformed right angles and deformed equi-dimensions is not one to one: there are more than one pair of equi-dimensions for a given deformed right angle (Fig. 7-2B). Consequently, if two pairs of deformed equi-dimensions measured happen to represent the same deformed right angle, they contain insufficient information for finding the strain ellipse. Therefore, two pairs of deformed equi-dimensions are sufficient for finding the strain ellipse, as long as they do not represent the same deformed right angle.

Problem with an Isolated Skull

This modified statement indicates that it is impossible to retrodeform an isolated, well-articulated trilobite (or a vertebrate skull), preserved from the dorso-ventral aspect, because many pairs of deformed equi-dimensions on the specimen represent only one deformed right

Figure 7-2. Reconstruction of the skull of Utatsusaurus hataii.

A: HUG 9372 from the dorsal view. The left mandibular ramus, originally overlain by the skull, was moved graphically so that it is visible (small arrows). The measurements for retrodeformation were taken for thick straight lines, which intersect at the arbitrarily chosen base point (large arrow). B: retrodeformed image based on A. The left maxilla and right premaxilla (light gray) were moved so that they articulate with the skull. The width of the premaxilla was reduced to 70.7 percent, assuming that the inclination was close to 45 degree when articulated. C, D: reconstruction of the skull (C, left lateral; D, dorsal), based on B. Light gray indicates the anterior terrace of the upper temporal fenestra. Abbreviations: a, angular; co, coronoid; d, dentary; exn, external naris; f, frontal; j, jugal, l, lacrimal, m, maxilla; n, nasal; p, parietal; pa, prearticular; pf, prefrontal; po, postorbital; ptf, postfrontal; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal; st, supratemporal; utf, upper temporal fenestra.


Measurements taken
Arbitrary Base Point on the Sagittal Line
A
pineal foramen
po
ptf
pf
l
st
n
f
p
exn
n
f
p
atlantal pleurocentrum
pm(r)
l
pf
u t f
orbit
ptf
sp
po
sq
st
axial? neural spine
m(l)
j
j
qj
co
pa
a
sa
facet for articular
B
st
p
f
utf
n
ptf
sq
exn
pf
pm
m
l
orbit
po
qj
d
j
q
sa
a
C
ptf
sq
orbit
m
l
pf
utf
st
pm
exn
n
f
p
pm
exn
n
f
p
m
l
pf
orbit
utf
st
ptf
sq
Anterior Terrace of UTF
D

angle, being based on a single lateral symmetry (as in Fig. 7-2B). This is very inconvenient considering that it is rare to find two or more vertebrate skulls occurring together. If the postcranial skeleton occurred with the skull, it would be possible to obtain sufficient information for finding the strain ellipse. However, this is only possible when the dorsal direction of the skull is perpendicular to the bedding plane (provided that the dorsal aspect is being retrodeformed). This is because the postcranial skeleton usually lies on the bedding plane, and it is almost impossible to find deformed equi-dimensions by viewing the skeleton from other directions.

One way to retrodeform an isolated skull is to tackle the problem with a different assumption. In the previously mentioned model, it was assumed that the lateral symmetry of the skull is complete, therefore the distance between, say, the posterior end of the right prefrontal and an arbitrary base point on the sagittal line is equal to the distance between the posterior end of the left prefrontal and the same base point (as in Fig. 7-1A), once the image is retrodeformed. This assumption, however, is not exactly true: the symmetry of the skull is only present on average, considering all possible errors that may occur during the ontogenetic developmental processes. Therefore, it should be assumed that the lateral symmetry of the skull is only present on average in a retrodeformed image of a deformed skull. Accordingly, the matrix representing the retrodeformation process can be estimated by finding a matrix that minimizes the discrepancy regarding the symmetry of the skull in the retrodeformed image. This can be achieved by taking many measurements and analyzing them by the method described in Chapter 2 to find a solution that minimizes the discrepancy in the data.

Measurements and Calculation

The specimen was scanned from the dorsal aspect as a 256-color bitmap, using a flatbed image scanner (HP ScanJet IIcx), at the resolution of 300 dpi. The left mandibular ramus was preserved ventral to the skull, and was therefore hidden from the view. To facilitate the retrodeformation of the left mandibular ramus, it was detached from the original position and located beside the skull before the image scanning (Fig. 7-1A, small arrows), retaining the original direction. The horizontal and vertical directions of this bitmap image were set as the **x** and **y** axes, respectively, for the measurement.

Two sets of reference points were selected from the skull roof, each comprising symmetrical points on the right and left sides (viz., the posterior ends of the right and left prefrontals, and the postero-medial end of the anterior margin of the anterior terrace of the upper temporal fenestra, see Fig. 7-1A). An arbitrary base point was set on the sagittal line of the skull (Fig. 7-1A), and the line connecting this point with each of previously selected symmetrical points are measured as vectors with **x** and **y** components. It would be ideal to have more than two reference points, but it was not possible because of the way the skull has been preserved.

Measurements were taken using CorelDraw 5.0, and Mathcad 5.0 Plus was used to calculate the elements of the strain matrix (matrix B) from the vectors obtained, using the method described (Chapter 2).

Image Manipulation and Skull Reconstruction

The retrodeformation of tectonic deformation was achieved by linearly expanding the original image of the skull (Fig. 7-1A) according to the result of the calculation. The retrodeformed image is given in Fig. 7-1B, but the relative size to the original image (Fig. 7-

1A) is not to scale. In spite of the small sample size, the retrodeformed skull appears almost symmetrical, validating the retrodeformation performed. The detached premaxilla and maxilla were re-articulated with the skull by moving their images (Fig. 7-1B, arrows).

The reconstruction of the skull is given in Fig 1C (lateral) and D (dorsal), based on Fig. 7-1B. Because a reasonable height/length ratio of the skull cannot be estimated from the present specimen, relative height of the skull was determined by referring to the skull of a contemporaneous ichthyosaur, Grippia longirostris (Wiman, 1929, 1933; Mazin, 1981; Chapter 8).

All image manipulations were performed using the CorelDraw 5.0 suit. First, suture lines were scanned as a bitmap file, then the file was traced into a postscript file by using CorelTrace 5.0. This postscript file was imported to CorelDraw 5.0, where the manipulation of the vectored image was performed.

SYSTEMATIC PALAEONTOLOGY

Order ICHTHYOSAURIA Blainville 1935

Genus UTATSUSAURUS Shikama, Kamei, and Murata 1978

Type species—Utatsusaurus hataii Shikama, Kamei, and Murata 1978

Diagnosis—Because the present study reveals that most of the diagnostic characters of Grippia longirostris are also present in U. hataii, a large-scale revision involving phylogenetic analysis is required before emending the diagnosis for the genus.

UTATSUSAURUS HATAII Shikama, Kamei, and Murata 1978

Synonymy—

Utatsusaurus hataii Shikama et al., 1978: p. 83.

Grippia microdenta Minoura, 1994: p. 65.

Diagnosis—As for the genus

Type specimen—IGPS 95941

Paratypes—IGPS 95942, 95943, and 95944

Referred specimens—See Shikama et al. (1978).

Locality and horizon—The present specimen was from the Osawa Formation of Ogatsu Town, Miyagi Prefecture. The same formation is exposed in the type locality of Utatsusaurus hataii, located some 20 km north (Minoura et al., 1993). Details of their occurrence are well reported in Minoura et al. (1993), hence are not repeated here.

Reasons for the identification—The specimen is here identified as belonging to Utatsusaurus hataii because of its close osteological similarity to the holotype, and because of the geological settings described. For example, the tooth morphology and implantation are identical to those for U. hataii (Motani, 1996), so is the shape of the mandible. An unusual discoidal ossification, identified as atlantal pleurocentrum, exists both in the type of U. hataii and the present specimen. The present specimen is larger than the holotype, but the holotype is immature (Motani, in press). One of the paratypes is as large as this new specimen.

REDESCRIPTION

General Account

The skull has been compressed from the left dorso-lateral aspect, revealing the dorsal and left sides. All the preserved bones are paired, including the parietal and frontal (the occipital region is not preserved). The left half of the skull is articulated, except for the premaxilla, maxilla, and the jugal. The right half is partially disarticulated, especially in the temporal region, but the elements are still associated with each other. This unique preservation is very convenient for morphological studies because the right half clarifies the sutures between the bones, while the left half shows the way the bones are integrated (Fig. 7-1A, B).

The posterior part of the mandible is preserved almost in situ, but the anterior part is slightly shifted to the left side, dislocating the left maxilla on its way. The left mandibular ramus is better preserved than the right one. The tip of the snout has been disarticulated, and bent back toward the left postero-lateral direction (Fig. 7-1A), the two disarticulated dentaries, and the right premaxilla, being almost parallel with each other.

As in Ichthyosaurus from the Lower Jurassic (Sollas, 1916;McGowan, 1973), most of the bones overlap with one another in the present specimen. Therefore, the sutures were identified when overlapping of the bone is obvious, or the lines are symmetric with respect to the median line.

Snout (Fig. 7-1)

Premaxilla—Only the right premaxilla, disarticulated but complete, is preserved. The bone is short compared to that of a typical Jurassic ichthyosaur (McGowan, 1974a,b,1976,1979), but the premaxilla is long compared to that of the majority of amniotes. There is a dental groove along the tooth bearing margin, and three anterior teeth are preserved in situ. The implantation seems to be subthecodont. The posterior margin of the bone is concave, as in Grippia longirostris (Mazin, 1981:fig.3), therefore it is most likely that the bone forms the antero-dorsal margin of the external naris. However, when viewing this bone dorsally, it is likely that the posterior processes of the right and left premaxillae do not meet along the sagittal line, therefore revealing the underlying nasal in between them (Fig. 7-2). This condition is present in all later ichthyosaurs. The anterior tip of the bone is pointed, rather than rounded, forming a smooth tip of the snout.

Maxilla—Only the left maxilla is preserved, and was disarticulated by the lateral displacement of the mandible, as previously mentioned. The bone has a dorsal lamina in the middle, which extends postero-medially. This lamina overlies the lacrimal, forming the postero-ventral margin of the external naris in the superficial view. The bone has a dental groove along its tooth bearing margin, which is not sufficiently wide to accommodate two tooth rows as in Grippia longirostris.

Lacrimal—Both lacrimals are preserved. The sutures for the left lacrimal is not apparent, which could raise doubts regarding the presence of a separate lacrimal. However, the right one is slightly disarticulated, clarifying that it is a separate bone. Because of the way the right lacrimal is preserved, it is difficult to reconstruct the sutures in articulation. The lacrimal extends all the way from the orbit to the external naris, therefore forming the postero-ventral margin of the latter opening. However, it is covered by the dorsal lamina of the maxilla anteriorly, therefore it is not visible when articulated.

Nasal—Both nasals are almost completely preserved. The bone has a medial process anteriorly, forming the postero-dorsal margin of the external naris. The anterior part of this process seems to be overlain by the postero-medial process of the premaxilla. The bone is large, and is overlapped laterally by the prefrontal, while overlying the frontal posteriorly. The bone also contacts the lacrimal antero-laterally, but the suture is not clear. There is no internasal foramen as in Ichthyosaurus (McGowan, 1973).

Skull Roof (Fig. 7-1)

Frontal—The left frontal is complete while the right one is broken laterally. Unlike in Jurassic ichthyosaurs, the frontal is largely exposed. The bone is overlain by the nasal anteriorly, the prefrontal antero-laterally and by the parietal posteriorly. This topological arrangement is in agreement with that in Ichthyosaurus (McGowan, 1973). The frontal contacts the postfrontal postero-laterally, but it is not clear whether it is overlain by the latter. Between the prefrontal and postfrontal, the frontal is slightly constricted, forming the dorsal margin of the orbit. It seems that the posterior part of the bone joins the anterior terrace of the upper temporal fenestra, a bony depression excavated on the parietal, postfrontal and probably on the frontal (Fig. 7-1C, D: light gray). The margin between the anterior skull roof and this terrace is marked by a clear line excavated on the bones, forming a step. Two artificial excavations were accidentally chiseled, along the median line of the bone, during the preparation, therefore they should not be misidentified as the pineal foramen. Minoura (1994) interpreted a transverse line running in the middle of the frontal as the fronto-parietal suture, but this is unlikely. The line does not have its counterpart on the right side, nor do the surface striations of the bone changes their directions at the line. Besides, there is a clearer suture posterior to this line, at least medially.

Prefrontal—The left prefrontal is in situ while the right one is very slightly tilted along its antero-posterior axis, revealing the suture. This tilting, however, did not change the position of the bone, therefore it was reasonable to use the posterior end of this bone as one of the reference points for retrodeformation. The bone overlies the nasal and frontal medially, and contacts the lacrimal anteriorly. The bone forms the antero-dorsal margin of the orbit, and there is a prominent lateral process, as in Grippia longirostris (Mazin, 1981; Chapter 8).

Postfrontal—Both postfrontals are broken posteriorly. The bone contacts the frontal antero-medially, where it forms the lateral part of the anterior terrace of the upper temporal fenestra. Antero-laterally, the bone forms the postero-dorsal margin of the orbit, and posteriorly, there is a posterior process overlying the postorbital (Fig. 7-1C). This bar is incompletely preserved on both sides, but they left clear depressions on both postorbitals, showing the posterior extent of the process. Such a depression is also known in the holotype of Grippia longirostris (Chapter 8).

Parietal—The left parietal is complete, while the right one is broken. Antero-medially, the bone has a wide process that extends anteriorly to enclose the pineal foramen in the middle. However, this process of the parietal seems to overlie the frontal, therefore it is possible that the frontals enclose the pineal foramen beneath the superficial cover of the parietal, or at least form its anterior margin.

The parietal seems to form a large part of the anterior terrace of the upper temporal fenestra, but its suture with the frontal is not clear (dotted in Fig. 7-1). A postero-lateral process forms the postero-medial margin of the upper temporal fenestra. This process is a thin plate of bone that is directed nearly vertically, but becomes more horizontal anteriorly and continues to the anterior terrace of the upper temporal fenestra. The right and left postero-lateral processes are not in contact with one another medially, leaving a V-shaped gap between them. This same process forms a narrow plane that is directed almost vertically, but anteriorly it gradually becomes horizontal, continuing into the anterior terrace of the upper temporal fenestra.

Temporal and Cheek Regions (Fig. 7-1)

Supratemporal (Fig. 7-3)—The left supratemporal is preserved in articulation with the squamosal, while the right one is disarticulated and shifted anteriorly. The right supratemporal appears larger than the left one, but this is an artifact of tectonic deformation. The supratemporal is almost U-shaped from the dorsal view (Fig. 7-3C, F), forming the posterior margin of the upper temporal fenestra. It partially overlaps the squamosal laterally, and the parietal medially. The articular facets for these two bones, which are clearly sculpted on the supratemporal (Fig. 7-3D, E), only occupy the anterior three-fifths of each ramus of the U. Laterally, there is a prominence, dorsal to the articular facet for the squamosal (dorso-lateral prominence in Fig. 7-3D, E), but such a structure does not exist on the medial side. The posterior two-fifth of the bone, which is visible from the posterior view in articulation, is dorsally rounded to form a slope (posterior slope in Fig. 7-3D, E). This half-dome, however, is very small. There is a small ridge at the posterior end of the bone (posterior ridge in Fig. 7-3D, E).

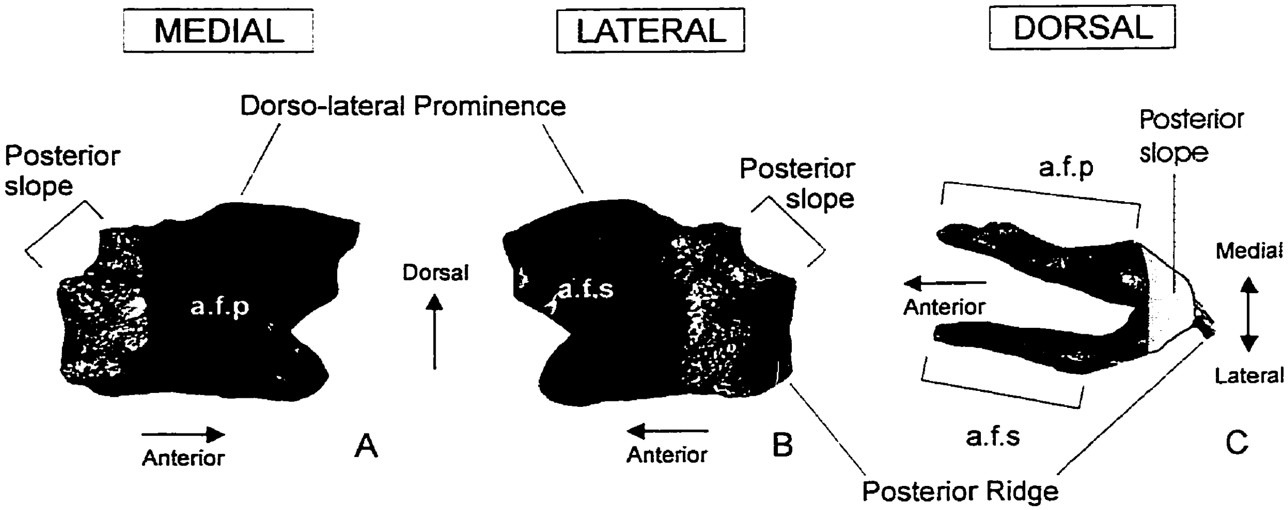
Squamosal—The right squamosal is missing, while the left one is broken posteriorly. The bone joins the lateral margin of the upper temporal fenestra for about one fourths of its extent. This is in contrast to the condition in Grippia longirostris, where the squamosal is entirely eliminated from the margin of the upper temporal fenestra by the supratemporal. The bone slightly overlies the postorbital anteriorly, thus forming a postorbito-squamosal contact along the margin of the upper temporal fenestra. Ventrally, the bone contacts the quadratojugal by slightly overlying it.

Quadratojugal—Only a partial left quadratojugal is preserved, which is as large as the squamosal. It occupies the postero-ventral corner of the cheek region, but, because the bone is incomplete, no articular facet for the quadrate is preserved.

Postorbital—The surface of the left postorbital is not well preserved, but the suture is clearly seen in the right one, which is incomplete ventrally. The bone forms the posterior

Figure 7-3. The left supratemporal (not retrodeformed).

A: medial view. B: lateral view. C: dorsal view. Abbreviations: a.f.p., articular facet for the parietal; a.f.s., articular facet for the squamosal. See text for details. Scales in centimetres.


MEDIAL
LATERAL
DORSAL
Dorso-lateral Prominence
Posterior slope
a.f.p
Dorsal
Anterior
A
Posterior slope
a.f.s
Anterior
B
a.f.p
Posterior slope
Anterior
Medial
Lateral
a.f.s
C
Posterior Ridge

margin of the orbit, as well as the lateral margin of the upper temporal fenestra, although it is largely overlapped by the posterior process of the postfrontal along the latter margin.

Jugal—The left jugal is preserved in two parts. The first segment is a narrow bar that forms the ventral margin of the orbit. The second forms the postero-ventral corner of the orbit, and is overlain by the postorbital dorsally. The suture between the postorbital and jugal is clearly seen in medial view.

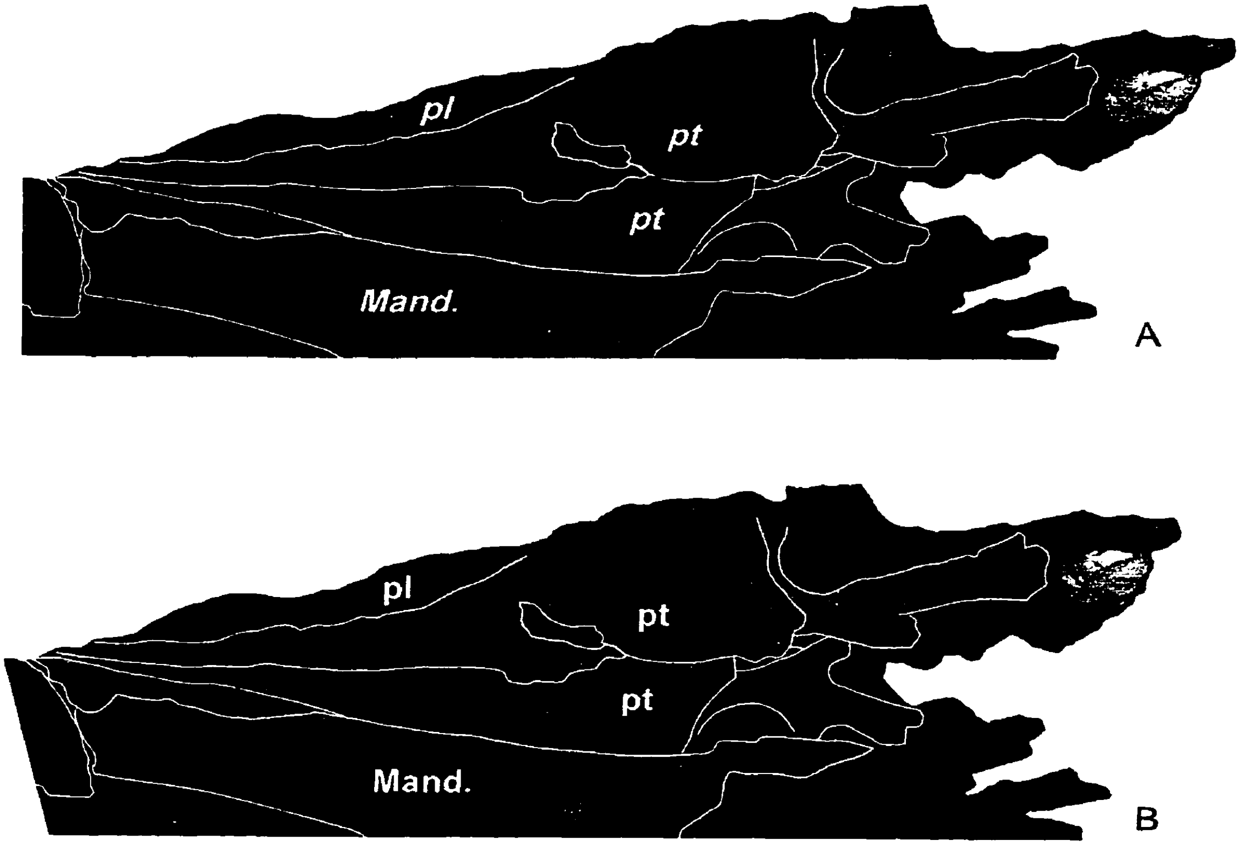
Palate (Fig. 7-4)

Pterygoid—The pterygoid has a well-marked transverse flange, which inclines antero-laterally rather than antero-posteriorly (Fig. 7-4B). The bone has two rami posteriorly: the quadrate ramus is a long plate of bone that continues postero-laterally to reach the quadrate, and the medial ramus is a small process that projects postero-medially from the base of the quadrate ramus. These two rami seem to be homologous with the more expanded quadrate and medial wings of Ichthyosaurus (McGowan, 1973). The interpterygoid vacuity is absent, or very narrow if it existed (Fig. 7-4B). Due to the extreme reduction of this vacuity, and to the anterior inclination of the transverse flange, the posterior part of the palate resembles that of Claudiosaurus germaini (Carroll, 1981).

Palatine and others—The palatine is only fragmentarily preserved, being articulated with the pterygoid (Fig. 7-4), in the same manner as in Ichthyosaurus (McGowan, 1973). There seems to be no ectopterygoid in the present specimen, but the palate is not well preserved laterally. The anterior part of the palate is concealed by the overlapping mandible, therefore little is known about the vomer.

Figure 7-4. Palatal view of HUG 9723.

A, original image. B, retrodeformed image. Retrodeformation in B was made so that the angle of the right and left transverse flange of the pterygoid become equal. Although this retrieved the symmetry, the original shape may have been wider or narrower.


pl
pt
pt
Mand.
A
pl
pt
pt
Mand.
B

Dentition

Most of the teeth are disarticulated from the jaw margins, except for some anterior teeth of the right premaxilla, and some of the maxillary teeth. The teeth preserved in situ are labio-lingually wider than they are disto-mesially, as in the holotype. Many detached teeth were found beside the skull in accumulations. Other features of the teeth are also identical to what were described for the holotype (Motani,1996), therefore no further description is given here.

Two teeth are visible on the transverse flange of the pterygoid, which are much smaller than the marginal teeth. Although they may be dislocated germ teeth of the marginal dentition, it is possible that Utatsusaurus retained the pterygoidal dentition, although vestigially.

DISCUSSION

The skull of Utatsusaurus appears typically ichthyosaurian for having: 1) an elongated premaxilla forming a pointed snout; 2) a large orbit; 3) a ventrally emarginated cheek region; and 4) the postfrontal extending posteriorly to join the upper temporal fenestra. However, it differs from the skull of Ichthyosaurus (McGowan, 1973) in that: 1) the frontal is largely exposed; 2) the frontal forms the dorsal margin of the orbit; 3) the supratemporal, squamosal, and quadratojugal are all present; 4) the dorsal lamina of the maxilla excludes the lacrimal from the external naris in superficial view; 5) the pineal foramen in enclosed solely by the parietal; 6) the anterior terrace of the upper temporal fenestra is present; and 7) the external naris is directed dorsally.

The supratemporal of Utatsusaurus resembles the bone identified as the squamosal by McGowan (1973) for Ichthyosaurus from the Lower Jurassic, in that: 1) it borders the posterior margin of the upper temporal fenestra; 2) there is a partial dome-like structure postero-dorsally (this feature is much more pronounce in Ichthyosaurus, where the dome partially covers the upper temporal fenestra); and 3) the posterior ridge is present, which receives the quadrate laterally, and the opisthotic medially. The presence of a separate squamosal and quadratojugal in the present specimen is compelling evidence that this bone is correctly identified as the supratemporal, therefore it is possible that the bone in Ichthyosaurus is actually the supratemporal, rather than the squamosal. However, the bone in Ichthyosaurus is much larger relative to the skull than it is in the present specimen. Further discussion is postponed until the skull of other Triassic ichthyosaurs are described (Chapters 8 and 9).

Minoura (1994) applied the same principle of retrodeformation as in the present study, although he used Sdzuy's (1966) graphical method. The reason his retrodeformation proved unsuccessful is because his measurements were taken from the postcranial skeleton (mainly vertebral centra) that are exposed on the bedding plane, which intersects the plane of view for the skull. Therefore, the present study does not indicate inaccuracy of Sdzuy's (1966) method: it should be possible to obtain the same results by analyzing the skull measurements as described by Sdzuy (1966).

SUMMARY

1. Utatsusaurus hataii has three bones in the posterior cheek region, identified as the supratemporal, squamosal, and quadratojugal.
2. The upper temporal fenestra has an anterior terrace that is formed by the parietal, frontal, and postfrontal.
3. The parietal has a long postero-lateral process.
4. The dorsal lamina of the maxilla covers the lacrimal when articulated, therefore it appear as if the lacrimal is not joining the external naris.

5. The posterior process of the postfrontal is present, but it only partially overlies the postorbital, therefore the latter participates in the margin of the upper temporal fenestra.
6. Rudimentary pterygoidal teeth seem to exist.
7. The interpterygoidal vacuity is absent, or very narrow.

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CHAPTER

8

SKULL OF GRIPPIA LONGIROSTRIS (ICHTHYOSAURIA) REEXAMINED

ABSTRACT

The skull of Grippia longirostris is redescribed, based on a newly prepared referred specimen and the examination of others. Previous reconstruction of the temporal region is proved incorrect, and the skull, instead, resembles that of Utatsusaurus hataii. The upper temporal fenestra is much smaller than the orbit. The postorbital, a large bone participating the upper temporal fenestra, is dorsally overlain by a postero-lateral process of the postfrontal, a common feature among early ichthyosaurs. The quadratojugal is not large, and does not enter the upper temporal fenestra. There is no contact between the prefrontal and postfrontal, so the frontal is not excluded from the orbital margin. The external naris faces dorsally, rather than laterally.

INTRODUCTION

Grippia longirostris from Spitsbergen was the first Early Triassic ichthyosaur to be described (Wiman, 1929). Since then, four more genera (now considered three, see Chapter 5) have been described from the Lower Triassic, but Grippia longirostris remained the most important to the study of ichthyosaurian evolution because it was the only species with reasonably well described skulls, although fragmentary.

The original description of Grippia longirostris was based on a single specimen, comprising a partial skull and dislocated limb elements. This skull, which was destroyed during the World War II (Motani, 1997), enabled Wiman (1929) to identify many of the sutures, except for the snout and the occipital region, which were not preserved. Four years later, Wiman (1933) described additional specimens, among which were four partial skulls. Based on these new specimens he changed his previous interpretation of sutures, and gave a reconstruction of the skull for the first time (Wiman, 1933:pl. 1, fig.). However, the snout and the occipital regions remained unknown. About half a century later, Mazin (1981) described two additional partial skulls, also from the Lower Triassic of Spitsbergen. These specimens, although fragmentary, preserved the posterior margin of the upper temporal fenestra for the first time, which enabled Mazin (1981:fig. 6) to give a revised reconstruction of the skull.

The recently discovered skull of Utatsusaurus hataii from Japan (Chapter 7), also from the Lower Triassic, resembles the reconstructed skull of Grippia longirostris (Wiman, 1933; Mazin, 1981). However, the arrangements of the bones do differ between the two species, as currently described, especially in the temporal and cheek regions. Such a large difference in the temporal region is unlikely considering their close forefin morphologies (Motani, in press; Chapter 3). This is especially true considering that the forefin appears to be more plastic than the skull in the better studied ichthyosaurs from the Lower Jurassic (McGowan, 1973,1974a,b,1976,1979). The purpose of the present study is to critically evaluate the published reconstructions of the skull of Grippia longirostris, through reexamination and new preparation of the available material.

MATERIALS AND METHODS

The abbreviations for the institutions are as follows: IGPS: Institute of Geology and Paleontology, Tohoku University, Sendai; NSM: National Science Museum, Tokyo; PMU: Paleontologiska Museet, Uppsala Universitet, Uppsala, Sweden. Specimens with the prefix SVT are stored in the Institut de Paléontologie du Muséum National d'Histoire Naturelle, Paris, France.

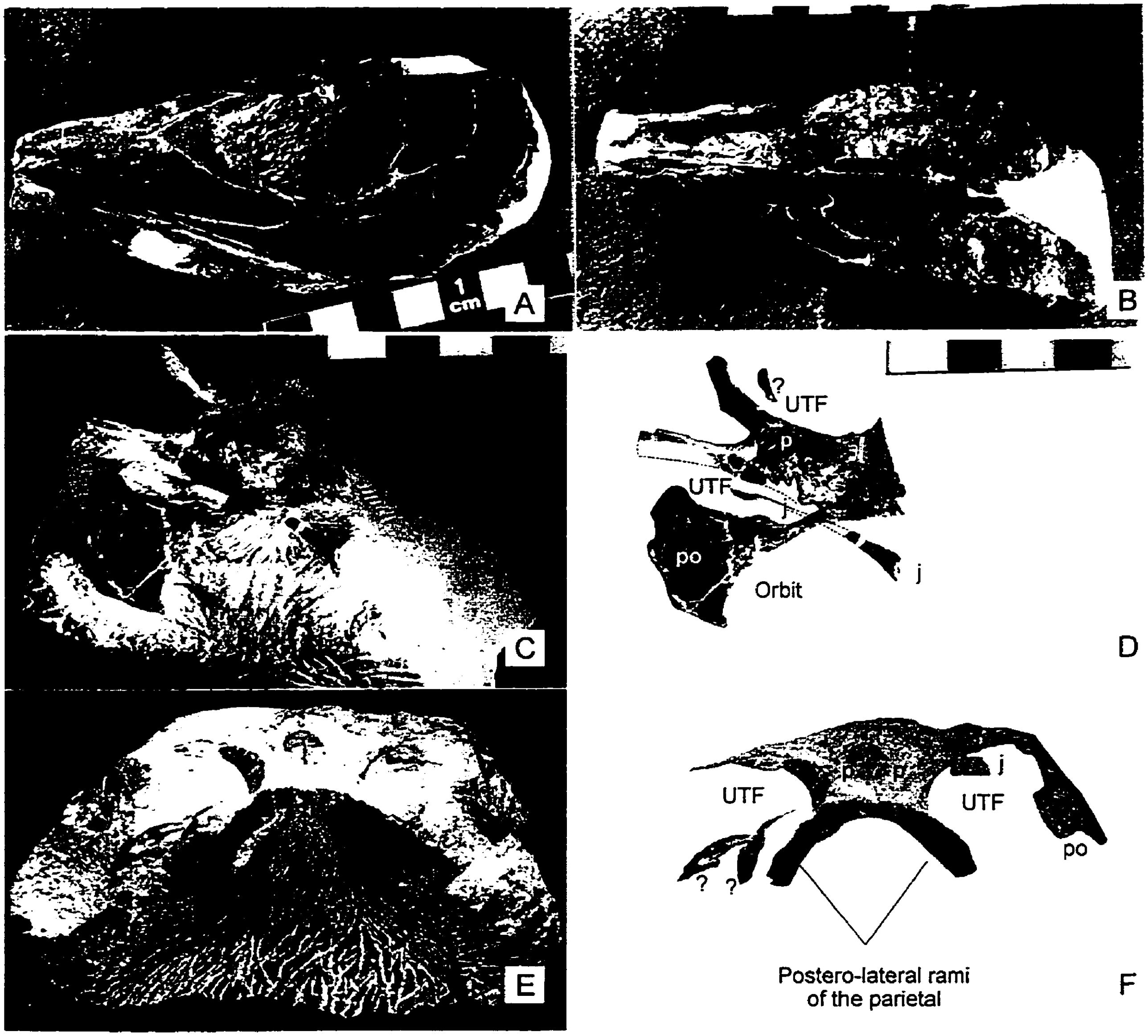
All of the known skull material for Grippia longirostris was examined. The descriptions that follow are based on seven specimens, namely PMU R445 (a cast of the lost holotype), R443, R444, R449, R452 (Wiman's [1933] nodules 2, 4, 5, and 3, respectively), SVT 201 and 202.

With permission from the Paleontologiska Museet, Uppsala Universitet, additional preparation was performed on PMU R443, to reveal the shapes of the parietal and postorbital. Because acid preparation proved unsuitable, airscribers and needles were used, under the binocular microscope.

The holotype was the best skull ever found for the species, therefore its cast (PMU R445) is important for the present study. The sutures were painted on the cast with white ink (Fig. 8-1A, B), probably by Carl Wiman, who described the original specimen (Wiman, 1929) and who was also at the Paleontological Institute of Uppsala. Although the authenticity of these sutures may be questionable, they follow the topological features of the cast surface for the most part. This was confirmed by making a cast of the cast, therefore eliminating the visual bias of the inked lines. Moreover, the pattern of the sutures painted on this cast shows a surprising resemblance to that of the skull of Utatsusaurus hataii, a contemporaneous ichthyosaur. Being a thickly painted plaster cast, PMU R445 does not replicate details of the

Figure 8-1. Two partial skulls of Grippia longirostris.

A, B: a cast of the holotype (PMU R445) in left lateral (A) and dorsal (B) views. See also Figure 2 for the dorsal direction of this compressed specimen. The quality of this cast is discussed in the text. C-F: a newly prepared specimen (PMU R443) in right antero-lateral (C, D) and postero-dorsal (E-F) views. A large postorbital forms the lateral margin of the upper temporal fenestra (C, D). The parietal has a long postero-lateral ramus that does not reach the very posterior margin of the upper temporal fenestra. Abbreviations: UTF, upper temporal fenestra; j, jugal; p, parietal; po, postorbital. "?" indicates unidentified bone fragments.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original, such as the surface striation of bones, and it is therefore difficult to confirm sutures based on the change of direction of surface striations.

REDESCRIPTION

General Account

The skull bones of Jurassic ichthyosaurs largely overlap with each other (Sollas, 1916; McGowan, 1973), and the same is also true for Early Triassic forms. When the surface bone layer is broken or weathered away, it merely exposes the deeper element beneath, shifting the apparent suture lines accordingly. It is therefore important to consider the breakage of the surface layer when studying ichthyosaurian skulls.

PMU R445 will be referred to often in the following descriptions, but it should be noted that, in spite of its importance, it is a cast (see Materials and Methods).

PMU R443 (Fig. 8-1C-F)—Before preparation, only the dorsal part of the skull roof was exposed. According to the cross-section through the middle of the slab, obtained by CT-scanning, the specimen comprises only the partial skull roof, right postorbital, scattered jugals, and the impression of the left postorbital. There were no palatal or occipital elements. The preparation revealed the right postorbital, both jugals, and the postero-lateral rami of both parietals (Fig. 8-1C-F), which are well preserved, having been buried in matrix. Newly exposed bones are black and preserve surface striations, while previously exposed ones are white, with extensive recrystallization of calcite that obliterated surface features.

Snout

The snout of Grippia longirostris is not completely preserved in any of the specimens, so there is insufficient evidence to warrant a short snout as reconstructed by Mazin (1981). The premaxilla has a concave posterior margin, which overlies the narrow antero-medial process of the nasal medially. This configuration is most clearly seen in SVT 201 (Mazin, 1981:fig. 3). Mazin (1981:fig. 6B) reconstructed the premaxillae as forming only the antero-medial part of the external naris, as if they underlie the nasals and maxillae, but this reconstruction is contrary to the evidence. Moreover, neither the nasals nor maxillae overly the premaxillae in any other ichthyosaurs. The posterior processes of the right and left premaxillae, however, do not meet along the sagittal line, thereby revealing the nasal in between them. This condition seems to be universal among ichthyosaurs, because it is also present in all other determinate ichthyosaur skulls, including that of Utatsusaurus hataii (Chapter 7)

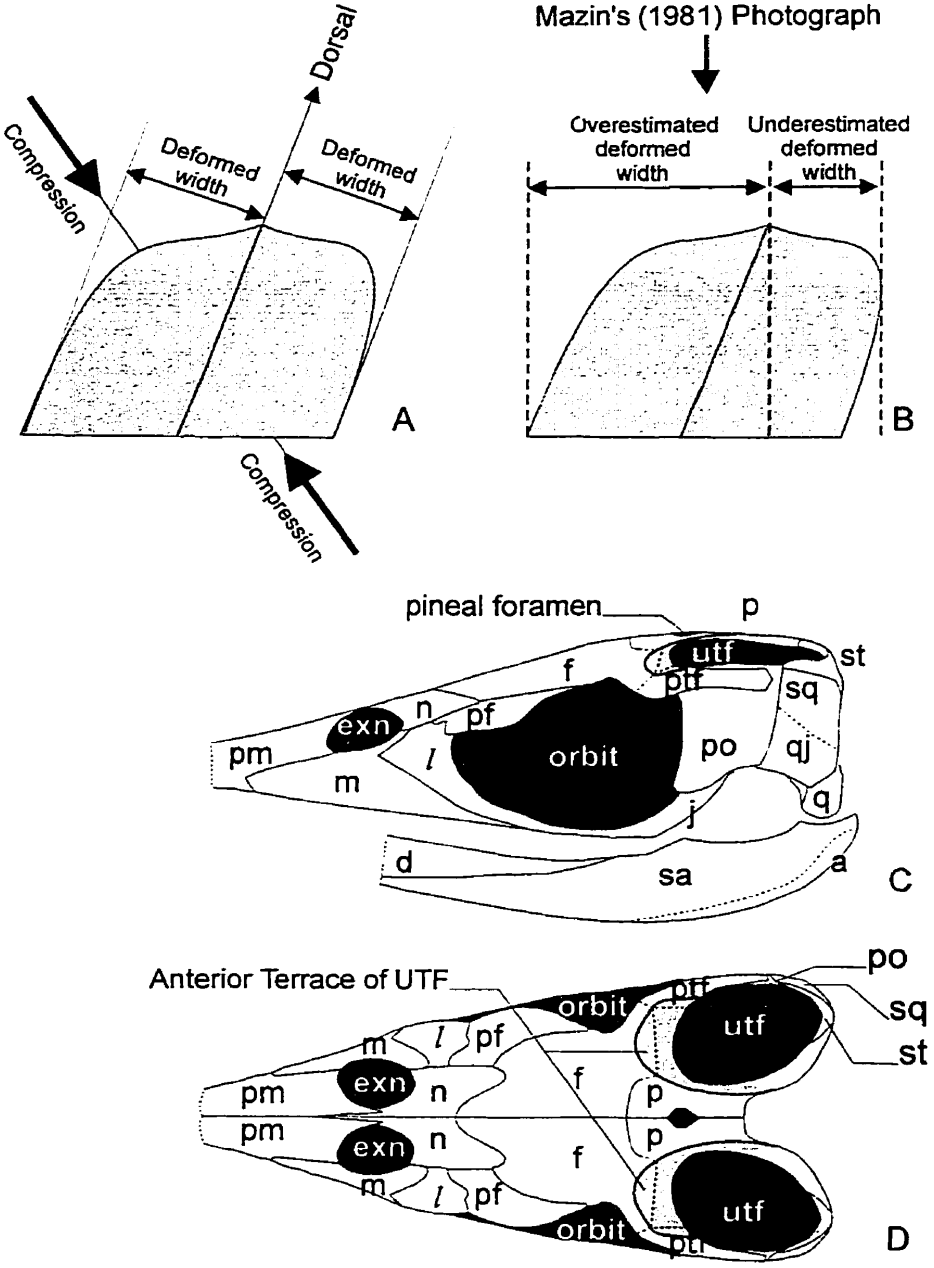
The external naris faces dorsally, rather than laterally as in later ichthyosaurs (Fig. 8-2D). It is bordered by the premaxilla anteriorly, the nasals postero-dorsally, and by the maxilla postero-ventrally, as seen in superficial view. However, it is likely that the lacrimal, whose anterior region is concealed by the dorsal process of the maxilla, forms the posterior margin of the external naris in the deeper layer, as in Utatsusaurus. The maxilla is deep, probably reflecting the possession of the second tooth row comprising the replacement teeth (Motani, 1997).

Skull Roof

The frontal is largely exposed. It is slightly constricted in the middle, where it forms the dorsal margin of the orbit (Fig. 8-2). This participation of the frontal to the orbital rim is difficult to establish, but it is the best interpretation of what is preserved in PMU R445 (Fig. 8-1B) and SVT201 (Mazin, 1981:fig. 3). This condition is also in accordance with that in Utatsusaurus. Wiman (1933:taf. 1, figs.2,4) figured a contact between the prefrontal and

Figure 8-2. A new reconstruction of the skull of Grippia longirostris.

A, B: schematic diagrams depicting the compression in PMU R445 (cast of the holotype) viewed posteriorly. The arrow in A indicates the true dorsal direction, while that in B indicates the false dorsal direction, from which Mazin's photograph (1981:pl. 1, fig. A2) was taken. C, D: a proposed reconstruction of the skull in left lateral (C) and dorsal (d) views. See text for detail. a, angular; d, dentary; exn, external naris; f, frontal; j, jugal, l, lacrimal, m, maxilla; n, nasal; p, parietal; pf, prefrontal; po, postorbital; ptf, postfrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal; utf, upper temporal fenestra.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postfrontal, forming the upper margin of the orbit, which excludes the frontal from the orbital margin. However, none of the specimens show any evidence of a prefrontal-postfrontal contact. Wiman's (1933) figures were based on PMU R443 (Fig. 8-1E) and R444, on which the suggested sutures corresponding to his reconstruction were ink-lined. However, the specimens are badly weathered and recrystallized, leaving no original structures on the bone surface. Any suture reconstruction based on the weathered parts of these specimens would be unreliable, therefore Wiman's (1933) interpretation should be disregarded. Mazin's (1981) specimens (SVT 201 and 202) do not show such a contact either, so it is likely that he simply followed Wiman's (1933) sutures.

The prefrontal forms the antero-dorsal margin of the orbit (Fig. 8-2). The bone has a well developed prominence projecting toward the orbit, forming a small shelf (broken in PMU R445, but well preserved in SVT 201). This well-developed prominence of the postfrontal seems to be a common feature for Early Triassic ichthyosaurs, because it is also present in Utatsusaurus.

The fronto-parietal suture is clearly seen only in PMU R445, close to the sagittal line (Fig. 8-1B). The suture starts perpendicular to the sagittal line, and gradually curves posteriorly till it suddenly disappears (Fig. 8-2). The pineal foramen seems to be located posterior to this suture, and is therefore enclosed between the parietals (Fig. 8-2). Wiman (1933:taf. 1, fig. 3) figured the fronto-parietal suture for PMU R443, but the specimen does not preserve any surface features of the bone, as previously mentioned, therefore his reconstruction is unreliable.

The outline of the parietal was poorly known until recent preparation of PMU R443 revealed the complete shape of the posterior region. The parietal has a long postero-lateral ramus that forms the postero-medial margin of the upper temporal fenestra (Figs. 8-1C-F, 8-2), but not the posterior margin, which is occupied by the supratemporal. The postero-lateral rami of the right and left parietals do not meet medially, instead they leave a V shaped gap between them. The presence of these separate rami is in accordance with Utatsusaurus, but contrasts the condition in Ichthyosaurus (McGowan, 1973), where the two parietals contact along the sagittal line towards the posterior end of the skull.

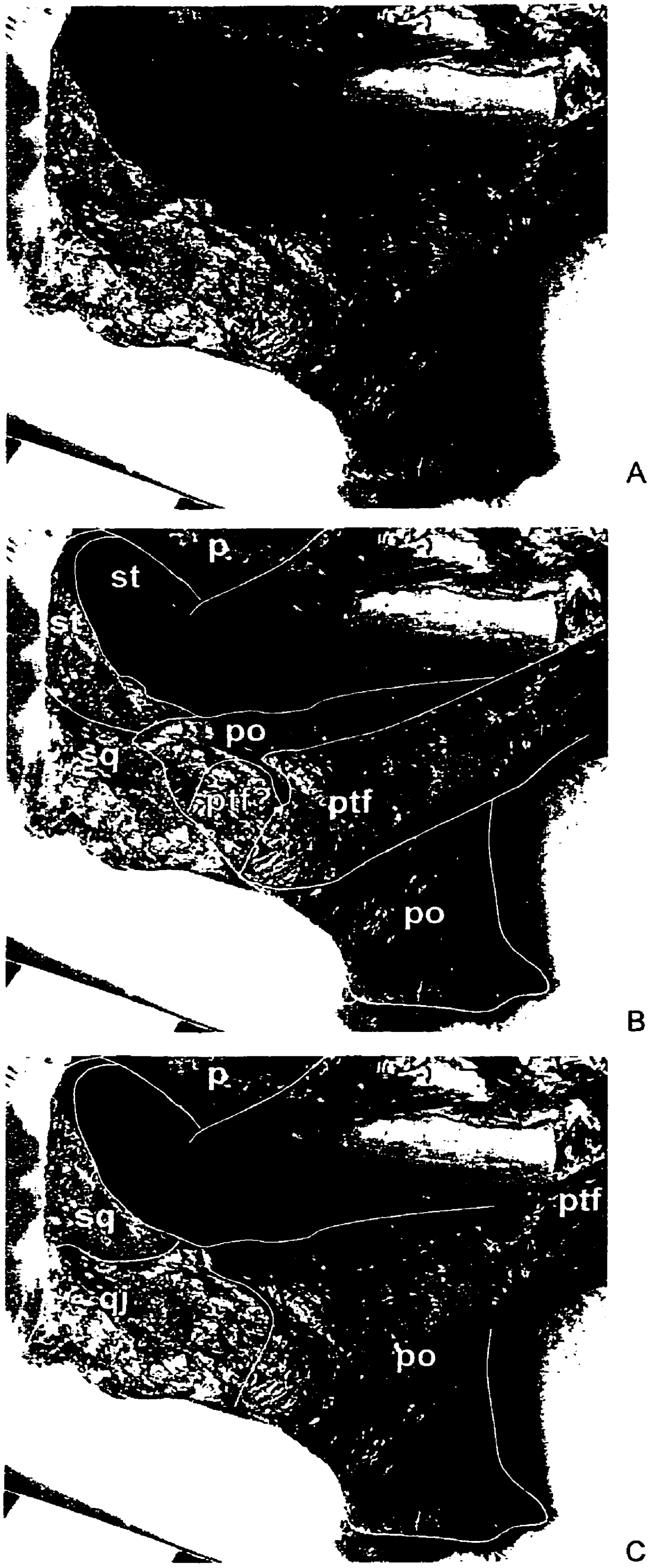
One remarkable feature of the skull roof is the development of a large terrace along the anterior margin of the upper temporal fenestra (Fig. 8-2), as in Utatsusaurus. This structure is most clearly seen in SVT 201 (Mazin, 1981:fig. 3), but is also present in PMU R445. The anterior margin of this terrace is parabola-shaped, and deeply curved on the skull roof (Fig. 8-2). The terrace seems to be formed by the parietal, frontal, and postfrontal (Fig. 8-2), and is postero-medially continuous with the ventro-medial flange of the parietal. Mazin (1981:fig. 6) figured only the anteriormost tip of the terrace, referring to it as the attachment point of the M. adductor mandibulae internus pseudotemporalis, but it is a much larger structure, involving the whole width of the skull.

Temporal and Cheek Regions

The temporal region is best preserved in SVT 202 (Fig. 8-3). The upper temporal fenestra is formed by the parietal, postorbital, postfrontal, and the supratemporal, which excludes the squamosal from the margin. The upper temporal fenestra is much smaller than the orbit, in contrast to the reconstruction by Mazin (1981:fig. 6, discussed later). The postfrontal has a long posterior process that overlies the postorbital near its dorsal margin (Fig. 8-2), but this does not exclude the postorbital from contributing to the upper temporal fenestra. This posterior process can be seen in two specimens, viz., SVT 202 (Fig. 8-3B) and PMU R445

Figure 8-3. Interpretation of the temporal region in SVT 202.

A, a photograph of the right temporal region from the postero-lateral aspect. B, the same image with the newly proposed suture patterns. C, the same image with Mazin's (1981) interpretation of sutures. The postero-lateral process of the postfrontal is clearly present (B), although it is lacking in Mazin's interpretation (C). The antero-dorsal corner of the quadratojugal, as reconstructed by Mazin (C), seems to be a crack, rather than a suture line. See text for detail. Abbreviations in Fig. 8-2.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(Fig. 8-1A, only as the impression). A similar posterior process of the postfrontal is known in Cymbospondylus petrinus (von Huene, 1916;Massare and Callaway, 1990) and in Utatsusaurus hataii (Chapter 7). The participation of the postorbital in the margin of the upper temporal fenestra is also seen in two specimens, viz., SVT 202 (Fig. 8-3B) and the newly prepared PMU R443 (Fig. 8-1C-F). The latter specimen does not have a complete postfrontal, but this is convenient because the entire shape of the postorbital is observable (Fig. 8-1C-F). The postorbital is a large, lunate plate of bone, with a slight depression postero-ventrally, and its dorsal margin forms the lateral border of the upper temporal fenestra.

The posteriormost part of the upper temporal fenestra is formed by the supratemporal, a medium-sized bone that can be best described as a thin, U-shaped bone when seen in dorsal view. The supratemporal is only preserved in SVT 202 (Fig. 8-3B). The medial side of this bone partially overlies the lateral side of the postero-lateral ramus of the parietal, forming an overlapping suture. The lateral side partially overlaps with a plate of bone, which is most likely the partial squamosal. Dorsal to this articular facet for the squamosal, the supratemporal is expanded to form a prominence, thus excluding the squamosal from the upper temporal fenestra.

The squamosal is poorly known. The bone is only present in SVT 202, where it is recognized as the area that is neither the postorbital nor the supratemporal. This squamosal is obviously incomplete ventrally. In this specimen, the squamosal does not enter the upper temporal fenestra (Fig. 8-3B), due to the dorsal expansion of the supratemporal, and possibly also to the dorsal reduction of the squamosal. In PMU R445, it seems as if there is only one plate of bone posterior to the postorbital (Fig. 8-1A), which was interpreted by Mazin (1981) as a large quadratojugal. However, the dorsal half of this area, where the squamosal should be, is depressed, being discontinuous with the ventral half (quadratojugal). This depression suggests the dislocation of the surface bone from the dorsal area. It is therefore likely that there are two bones posterior to the postorbital, as Callaway (1989) and Massare and Callaway (1990) predicted, and the quadratojugal is not as large as previously interpreted. The presence of two bones in this area, the squamosal dorsally and the quadratojugal ventrally, is in accordance with Utatsusaurus.

The jugal comprises a long and slender anterior tube-like structure that curves gently to form the ventral border of the orbit, and a plate-like posterior end that articulates with the postorbital (Fig. 8-2). In PMU R443, the posterior plate-like part of the left jugal, although being slightly disarticulated, clearly continues under the postorbital, therefore the articulation between these two bones seems to be formed by the overlapping of the two bones, as in Utatsusaurus. The right jugal of PMU R443 is half broken, showing a donut-shaped cross-section (Fig. 8-1C, D).

Mazin (1981) gave a different reconstruction of the temporal and cheek regions, based on the same specimens (Fig. 8-3C), but it seems likely that at least one of the sutures he identified is actually the crack formed during diagenesis (the antero-dorsal border of the quadratojugal, see Fig. 8-3). Other questionable features of his reconstruction include: 1) the posterior process of the postfrontal is lacking, although it is surrounded by well defined structures; 2) the shape of the postorbital largely differs from the newly prepared postorbital of PMU R443, which has the same shape as that of PMU R445; 3) the quadratojugal is large and enters the border of the upper temporal fenestra, which is unlikely. I conclude that his reconstruction is questionable.

Palate

Only the very posterior part of the palate is preserved in PMU R449, as a natural mold. A silicon cast of this mold shows little difference from Wiman's figure (1933:taf. 1, fig. 6). The pterygoid has a transverse flange that developed antero-laterally as in araeoscelids, rather than postero-laterally as in typical diapsids, without any trace of pterygoidal teeth. The medial ramus of the pterygoid is only present as a small projection while the quadrate ramus is a narrow plate that curves from horizontal to vertical as it approaches the quadrate, as in Utatsusaurus and many basal diapsids. The palatine is fragmentary, and no palatal teeth are observable.

RECONSTRUCTION

A revised reconstruction of the skull, based on the above observations, is given in Fig. 8-2. The major differences between this reconstruction and that by Mazin (1981:fig. 6) include: 1) the skull is narrower; 2) the upper temporal fenestra is much smaller than the orbit; 3) the premaxilla overlies the nasal; 4) the postfrontal has a posterior process that overlaps the postorbital; 5) the quadratojugal does not enter the upper temporal fenestra; 6) the bone forming the posterior margin of the upper temporal fenestra is identified as the supratemporal; 7) the anterior terrace of the upper temporal fenestra is present; 8) ambiguous sutures are drawn with dotted lines; and 9) the snout is figured as missing.

The difference in the skull widths between the two reconstructions seems to have resulted from the different interpretations of PMU R445. The original specimen of this cast was deformed due to the diagenetic compression that occurred along the axis that runs approximately from the left dorsal to right ventral direction (Fig. 8-2A). As a result, the dorsal aspect of the specimen is tilted toward the right hand side of the skull (Fig. 8-2A). Mazin

(1981:pl. 1, fig. A2) published an essentially dorsal photograph of PMU R445, which was not taken from the true dorsal aspect, but from the distorted one (Fig. 8-2B). Consequently, the left half of the skull in his photograph appears wider than it should be, and the lateral side of the skull, which may not be seen dorsally, is largely exposed. Mazin's (1981:fig. 6B) reconstruction of the dorsal view of the skull has an outline that is nearly identical to this distorted left half of the skull. The rostrum of his reconstruction appears as in the photograph, but the cheek region is concealed by the unnaturally expanded upper temporal fenestra. Such a large upper temporal fenestra is not known either in PMU R443, R445, or SVT 201.

It should be pointed out that Mazin's (1981:fig.6B) sutural pattern differ between the two halves of the skull in the temporal region. The right half of the skull agrees with his reconstruction of the lateral view (Mazin, 1981:fig. 6A), and with his text, while the left half shows some resemblance to the reconstruction given in the present study (the posterior process of the postfrontal is present). However, the postorbital is missing from view in the left half, raising the question of the validity of the reconstruction on this side. Accordingly, the argument presented in this study is based on my comprehension that Mazin's (1981) interpretation is better reflected in the right half of his figure than in the left half.

SUMMARY

1. Previous reconstructions of the skull of Grippia longirostris are not in accordance with the existing suture pattern in available specimens, including a newly prepared partial skull (PMU R443).
2. The upper temporal fenestra has an anterior terrace, as in Utatsusaurus, with deep excavations on the parietal, postfrontal, and frontal.

3. The upper temporal fenestra is much smaller than the orbit. The relatively large upper temporal fenestra reconstructed by Mazin (1981) seems to be due to his misinterpretation of the dorsal direction in PMU R445.
4. The postfrontal has a postero-lateral process that partially overlies the dorsal part of the postorbital, while not eliminating the latter from the margin of the upper temporal fenestra.
5. The squamosal is poorly known, and lies dorsal to the quadratojugal, partially overlying the supratemporal. It seems to be reduced dorsally, and does not enter the upper temporal fenestra.
6. The quadratojugal is only present ventrally in the cast of the holotype (PMU R445), and it is unlikely that it entered the upper temporal fenestra.
7. The medium-sized supratemporal forms the posterior margin of the upper temporal fenestra, partially overlapping with the squamosal laterally and with the parietal medially.
8. The external naris faces dorsally, rather than laterally as in later ichthyosaurs.

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CHAPTER 9

PARVINATATOR WAPITIENSIS REEXAMINED

ABSTRACT

The holotype of Parvinatator wapitiensis has not only been tectonically deformed, but also partially disarticulated and broken. A new reconstruction of the skull, based on this new knowledge, revealed many errors in the original description. Newly established features include: 1) the supratemporal, squamosal, and quadratojugal are all present; 2) the supratemporal is not large; 3) the quadratojugal, previously misidentified as the squamosal, is not styloidal; 4) the postfrontal and prefrontal do not contact each other; and 5) the jugal does not contact the quadratojugal. A ichthyosaurian specimen from the same locality as this holotype, previously described as belonging to Grippia, is reassigned to P. wapitiensis, based on its forefin morphology.

INTRODUCTION

Long-term tectonic activity deforms the strata, altering the shape of fossils contained in the rocks. Although tectonic deformation of fossil vertebrates can cause misinterpretations of their morphologies, little effort has been made to remove the distortion from their images. This is in contrast to the situation in invertebrate paleontology, where mathematical and graphical methods have been devised to remove tectonic deformation (e.g., Lake, 1943;Hills and Thomas, 1944;Wellman, 1962;Sdzudy, 1966;Hughes and Jell, 1992;Rushton and Smith, 1993). I have proposed an easier algorithm for such retrodeformation processes, and applied the method to tectonically deformed ichthyosaurian specimens from the Lower Triassic of British Columbia, demonstrating the effectiveness and value of the method in vertebrate paleontology (Chapter 2).

Parvinatator wapitiensis Nicholls and Brinkman 1995 is a small ichthyosaur with a forefin resembling that of *Utatsusaurus hataii*, one of the earliest ichthyosaurs, from the Lower Triassic (Motani, in press). Its description was based upon a single specimen, from an unknown horizon of the Lower or Middle Triassic of the Sulphur Mountain Formation, British Columbia (Nicholls and Brinkman, 1995). The specimen comprises a partial skull and two forefins that are preserved in 3D, but it is clearly distorted by tectonic deformation.

The Lower Triassic of the Sulphur Mountain Formation has yielded other specimens of small ichthyosaurs, which were described by Brinkman et al. (1992). These specimens were described as comparable to *Grippia longirostris*, an ichthyosaur from the Lower Triassic of Spitsbergen, based on features of the forefin (note: Brinkman, et al. [1992] named them *Grippia* cf. *G. longirostris*, but it seems more appropriate to use cf. *Grippia* because *Grippia* is monotypic). However, I pointed out that the tectonic deformation had extensively modified the shape of these specimens (Chapter 2), and the features used by Brinkman et al. (1992) cannot be validated in the retrodeformed images of the specimens. Later, when reporting the first new complete forefin of *G. longirostris* from Spitsbergen, I showed that these Canadian specimens cannot be referred to *G. longirostris* (Chapter 3).

The purpose of the present study is three-fold: 1) to establish the tectonic deformation in the holotype of *Parvinatator wapitiensis*; 2) to redescribe the specimen; and 3) to show the close similarity between *P. wapitiensis* and the specimens described by Brinkman et al. (1992).

MATERIALS AND METHODS

Two specimens examined, RTMP 89.127.3 and 89.127.8., are stored in the Royal Tyrrell Museum of Paleontology, Drumheller (RTMP). RTMP 89.127.3, described by Brinkman et al. (1992), and referred to Grippia, comprises the anterior part of the skeleton, which includes a semi-articulated right forefin. RTMP 89.127.8 is the holotype of Parvinatator wapitiensis, which, as mentioned earlier, comprises a partial skull and two forefins.

Images of tectonically deformed fossils can be retrodeformed provided that the strain is simple, which requires satisfying the following two conditions:

1) deformation is homogeneous within the area being analyzed.
2) deformation is passive (i.e., there is no extension but only compression, see Ramsay and Huber, 1983) within the area being analyzed.

If it is reasonable to assume these conditions for a given deformed fossil, retrodeformation can be achieved by stretching its image in a particular direction, by a particular factor. This direction and factor can be found either graphically (see Cooper, 1990 for summary) or by calculation (Chapter 2), using the following three types of measurements.

i) deformed right angle—an angle that was 90 degrees before the tectonic deformation.
ii) deformed equi-dimensions—dimensions that were equal prior to tectonic deformation.
iii) deformed equi-angles—angles that were equal prior to tectonic deformation.

At least two deformed right angle, three deformed equi-angles, three equi-dimensions, or two pairs of equi-dimensions are required, although additional measurements are desirable to increase the accuracy (Chapter 2).

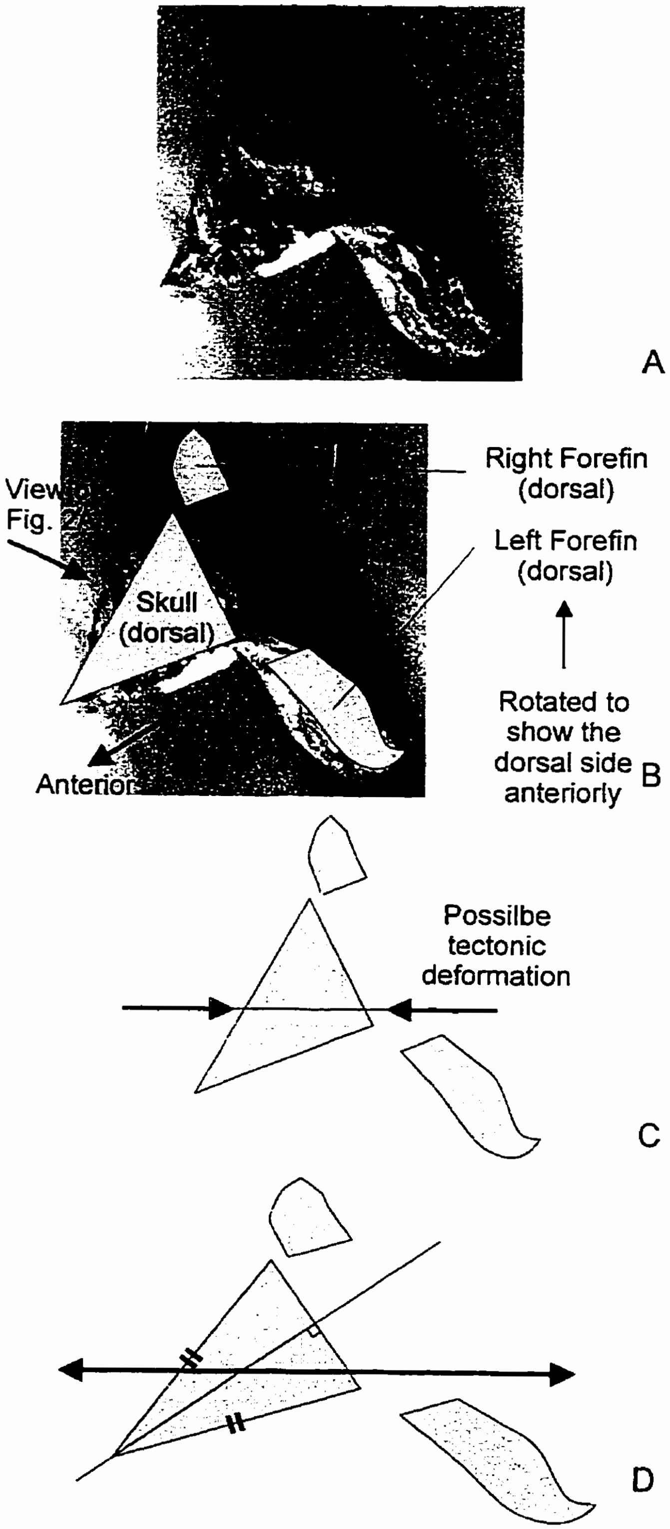
RTMP 89.127.3, being preserved on the bedding plane, contains many pairs of equi-dimensions, which enabled the retrodeformation of its image (Chapter 2). The holotype, however, has a unique three-dimensional preservation (Fig. 9-1A) that makes it impossible to find equi-dimensions from any viewing angle: the forefins are not on a single plane, and the dorsal side of the skull is very poorly preserved. Therefore it is not possible to calculate the retrodeformation direction and factor for any two-dimensional view of the specimen. Accordingly, it was only possible to roughly estimate a possible retrodeformation, through a rather unsophisticated method. First, various degrees of extension (every 10 percent between 120 to 150 percent) in various directions (every five degree) were performed on the image of the holotype. Then, from the resulting images, the one with the least distortion was selected, on the basis of its similarity with Utatsusaurus, Grippia, and Mixosaurus. Although this method lacks mathematical objectivity, it at least shows that a simple extension in one particular direction can make the holotype of Parvinatator wapitiensis appear similar to other early ichthyosaurs.

DEFORMATION IN THE HOLOTYPE

The holotype of Parvinatator wapitiensis has unequally sized right and left forefins, i.e., the size of each element in the left forefin is larger than the corresponding right element, resulting in the shorter total length of the right forefin (Nicholls and Brinkman, 1995:table 1). Nicholls and Brinkman (1995) interpreted this inequality between the forefins as a biological abnormality. They added that RTMP 89.127.3 (Grippia of Brinkman et al., 1992) also has

Figure 9-1. A antero-dorsal, and slightly lateral (left) view of the holotype of Parvinatator wapitiensis.

A, a photograph with gray overlays indicating general shapes of the skull and forefins. The forefins are rotated, showing their dorsal aspect anteriorly. The dorsal side of the skull is very poorly preserved, therefore it is only possible to draw its general outline. Upper arrow indicates the view angle of Fig. 9-2A. Lower arrow indicates the anterior direction. B, possible direction of the tectonic deformation, as judged from the shape of the skull. C, a diagram to show that a simple stretching can retrieve the symmetry of the skull.


A
View to
Fig. 2
Skull
(dorsal)
Anterior
Right Forefin
(dorsal)
Left Forefin
(dorsal)
Rotated to
show the
dorsal side
anteriorly
B
Possilbe
tectonic
deformation
C
D

unequally sized forefins, therefore this abnormality, due to limb injury, is not uncommon (Nicholls and Brinkman, 1995:525). However, I showed that the two radii of RTMP 89.127.3 became nearly equal after retrodeformation (Chapter 2), therefore their argument is unfound (the radius is the only identifiable complete element in the left forefin of this specimen).

Nicholls and Brinkman (1995) stated that the inequality of the right and left forefins in the holotype cannot be because of any "crushing", but did not give reasons why. The meaning of the word "crushing" is ambiguous, because it may mean any combination of breakage, disarticulation, and deformation. Among these three, deformation does cause such a modification of shape as seen in the forefins of the holotype of Parvinatator wapitiensis. Based on my own examination of the holotype, I conclude that it has undergone breakage, disarticulation, and deformation, as described in the following paragraphs.

Skull

When viewed dorsally, the general shape of the skull can be described approximately as a deformed isosceles triangle (Fig. 9-1A). Although poor preservation prevents the identification of any sutures, the lateral symmetry of the skull has clearly been lost. This general shape strongly suggests that the skull was compressed in a left posterior to right anterior direction (Fig. 9-1B). Unfortunately, lack of information on the dorsal side of the specimen prevents calculating the best retrodeformation process, as was done for RTMP 89.127.3 (Chapter 2) and Utatsusaurus (Chapter 7).

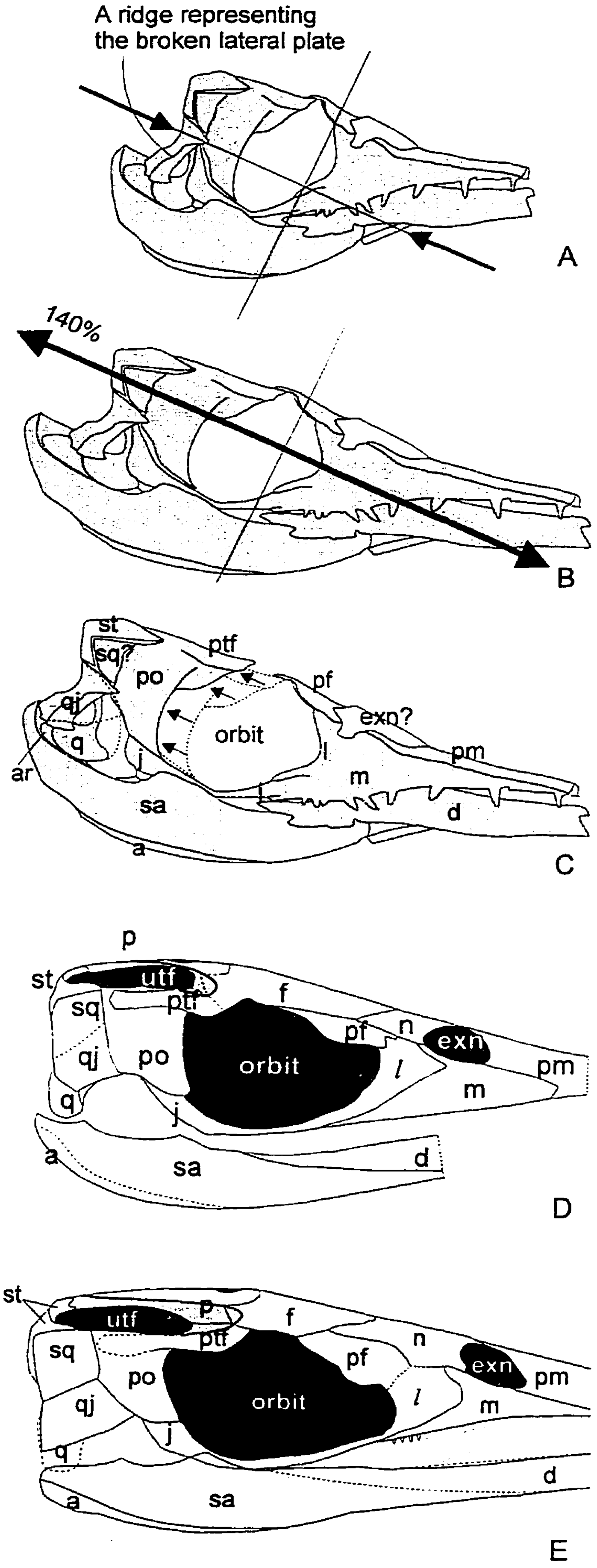
The right side of the skull is best preserved (Fig. 9-2A; see also Nicholls and Brinkman, 1995:figs. 1, 2), but it also suffers from deformation, disarticulation, and some breakage. The same tectonic deformation that distorted the dorsal view of the skull also affected this side. This is most evident in the shape of the mandible: the right mandibular ramus is appearing very deep, as if the animal were obligatory durophagous (Rieppel and Labhardt, 1979). This contrasts with its non-durophagous. Not even Grippia longirostris, which has a more durophagy oriented dentition, has such a deep mandible as in the present specimen (Motani, 1997). The orbit also shows some indication of deformation: ichthyosaurian orbits are never higher than long as in this specimen. The bones of the cheek region appear too slender, compared to the corresponding elements in Utatsusaurus hataii and Grippia longirostris; the jugal also seems too steeply curved.

A possible retrodeformation was estimated by the method outlined earlier. Recently acquired information of the cranial morphology of Utatsusaurus (Chapter 7), Grippia (Chapter 8) and Mixosaurus (Chapter 10) was used to select the best retrodeformation (see Materials and Methods). The resulting image (Fig. 9-2B) appears normally ichthyosaurian, in that the mandible is no longer deep, the bones of the cheek region appear wider, and the jugal is gently curved. Although the retrodeformation given in Fig. 9-2B is based on rather subjective measures, the fact that it eliminated several unusual features by a single stretching procedure suggests that the obtained result reasonably approximates the original shape of the animal.

Even after this retrodeformation was performed on the image of the skull, the orbit was still higher than long (Fig. 9-2B). This is because the posterior part of the skull is disarticulated from the rest, and has shifted anteriorly. In Utatsusaurus (Fig 2E, see also Chapter 7), Grippia (Fig. 9-2D, see also Chapter 8), Mixosaurus (Chapter 10), and Cymbospondylus (Massare and Callaway, 1990), the posterior plate of the jugal underlies the postorbital, forming an articulation. Because of the wide phylogenetic distribution of this feature among early

Figure 9-2. The skull of the holotype of Parvinatator wapitiensis (A-C) compared to those of Utatsusaurus hataii (D) and Grippia longirostris (E).

A, the right lateral view of the holotype skull. B, a possible retrodeformation of the image in A. C, reconstruction of the skull, by moving the disarticulated postorbital region to its original place. D, a reconstruction of the skull of Grippia longirostris (modified from Chapter 8). E, a reconstruction of the skull of Utatsusaurus hataii (modified from Chapter 7). Abbreviations: a, angular; d, dentary; exn, external naris; f, frontal; j, jugal, l, lacrimal, m, maxilla; n, nasal; p, parietal; pf, prefrontal; po, postorbital; ptf, postfrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal; utf, upper temporal fenestra.


A ridge representing
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ichthyosaurs, it is likely that Parvinatator also had a similar articulation. Therefore the entire postorbital region of the present image was moved posteriorly, so that the postorbital and jugal articulate correctly (Fig. 9-2C). Interestingly, the direction of this movement was almost parallel to the directions of the retrodeformation, and of the skull roof, but this may be coincidental. With this proper articulation between the jugal and postorbital, the orbit is very similar to that of Utatsusaurus and of Grippia: it is roughly oval, longer than high, and has two protrusions, antero-dorsally formed by the prefrontal and postero-dorsally formed by the postfrontal.

The posterior end of the skull is more problematic. The quadratojugal of ichthyosaurs usually comprises a lateral plate, which articulates with the postorbital anteriorly, and a postero-medial columnar region that articulates with the quadrate ventrally(McGowan, 1973). In the present specimen, the right quadratojugal is slightly rotated to show its anterior aspect, and the lateral plate is broken off ventrally, leaving its base as a ridge on the posterior styloidal region (Fig. 9-2A). The dorsal part of the lateral plate, still intact, partially overlies the postorbital, but this is probably due to the rotation and dislocation of the element, rather than a natural articulation. A possible extent of the lateral plate is dotted in Fig. 9-2C. The right quadrate is also rotated to show its anterior aspect, while the right supratemporal seems to be dislocated laterally, and is largely broken. The squamosal is largely covered by the dislocated supratemporal, but can be seen posterior to the middle part of the postorbital (Fig. 9-2C). It is distinguished from the postorbital by a difference in the direction of its surface striations.

My identifications of the sutures in the cheek region differ largely from that of Nicholls and Brinkman (1995). First, Nicholls and Brinkman (1995:figs 2, 5) interpreted the squamosal, as identified in the present study, as part of and extensive supratemporal. However, there is a layer of matrix between this piece of bone (squamosal) and the true supratemporal (appearing as a narrow, white gap between the squamosal and supratemporal in Fig. 9-2A-C here), clearly separating the two bones into two different levels, therefore their interpretation is very unlikely. Secondly, Nicholls and Brinkman (1995:fig. 2) divided the element that I identified as the quadratojugal into two segments. The dorsal segment was interpreted as part of the supratemporal, the ventral part as the squamosal, and the quadratojugal was believed lost. However, there is matrix between the true supratemporal and the dorsal part of the quadratojugal, clearly separating the two, while no matrix separates the dorsal and ventral parts of the quadratojugal. The dorsal and ventral parts of the quadratojugal may seem discontinuous, depending on the viewing angle, due to the broken lateral plate. However, it is clear from the anterior view that the ridge on the ventral part, which represents the rudiment of the broken lateral plate, is continuous with the dorsally preserved lateral plate. The ventral columnar part of the quadratojugal is depicted as being exceedingly thin in their diagrams (Nicholls and Brinkman, 1995:figs.2,5). The ridge structure representing the broken lateral plate was not depicted.

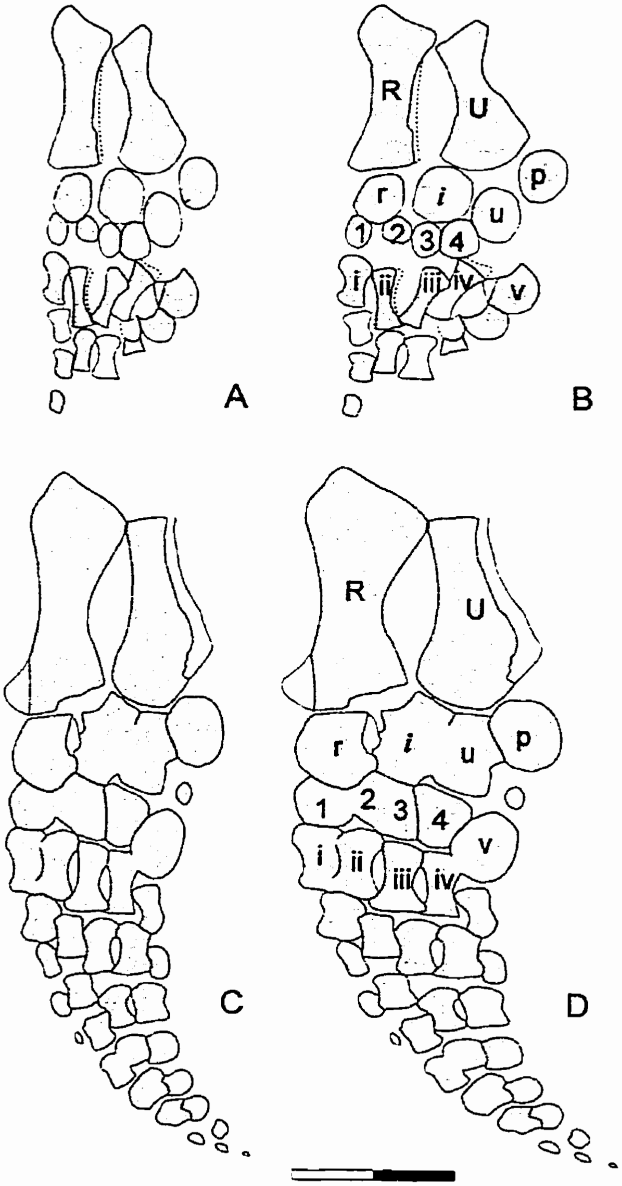
Forefins

Both forefins are preserved obliquely to the bedding plane. Some of the fin elements overlap others, sometimes leading to breakage of the elements involved. Nicholls and Brinkman (1995) claimed that there is no overlapping in the left forefin. However, Caldwell (in press:fig. 5B) recognized that at least several elements partially overlap one another, although not as extensively as in the right forefin, which agrees with my interpretation (Fig. 9-3C, D). Only the left forefin is treated in the following section, because it is better preserved than the right one (Nicholls and Brinkman, 1995). Due to overlapping and breakage of bones, the distinction between adjacent elements is not always clear, especially in the carpals. Therefore, I have not attempted to draw their contact margins in Fig. 9-3C, D. The outlines of the elements depicted by Nicholls and Brinkman (1995:fig. 3) sometimes reflect the breakage rather than the real shape. Also, Nicholls and Brinkman (1995:fig. 3) depicted the fifth metacarpal as a round element, but its preaxial margin is actually not well preserved in the specimen. Given that a rounded metacarpal V is not known in any Early or Middle Triassic ichthyosaurs (Chapter 6), it is unlikely that the animal had such a metacarpal. Instead, the metacarpal of the holotype was probably lunate.

There is little doubt that the forefins of the holotype have undergone tectonic deformation, based on the following evidence: 1) the holotype is from the Sulphur Mountain Formation, from which tectonically deformed specimens are known (Chapter 2); 2) the skull of the holotype seems to be tectonically deformed, and tectonic deformation cannot affect only the skull; 3) the holotype has elongated proximal carpals, which is very unusual for ichthyosaurs (the similarly elongated carpals of RTMP 89.127.3 was shown to be an artifact of deformation [Chapter 2]); 4) the right and left forefins differ in size, which can be more satisfactorily ascribed to tectonic deformation than to a biological abnormality. Unfortunately, there is not enough information on which to base the calculation of the best retrodeformation process, and therefore the same method used for the skull was used to estimate a possible retrodeformation process. The retrodeformation chosen is depicted here in Fig. 9-3D. This diagram may not represent the best possible retrodeformation, but it at least shows that the unusual features seen in the forefin can be explained as a result of a simple compression.

Figure 9-3. Forefins of Parvinatator wapitiensis.

A, the right forefin of RTMP 89.127.3. B, retrodeformed image of A (modified from Chapter 2). C, the left forefin of the holotype (RTMP 89.127.8). D, a possible retrodeformation based on C. Scale in centimetre.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TAXONOMY OF RTMP 89.127.3

Right Forefin of RTMP 89.127.3

The right forefin of RTMP 89.127.3 was well described by Brinkman et al. (1992). However, it is necessary to point out a new observation before discussing the taxonomy of the material. My examination of the specimen revealed that at least some elements are incompletely prepared. For example, metacarpal II and the radius are clearly covered by matrix postaxially (possible extents of the bones are dotted in Fig. 9-3A), and it is possible that several other elements are similarly covered (e.g., metacarpal III appears much narrower than the first phalanx of the same digit, which is very unlikely). This incomplete preparation tends to occur along the margin of the shaft of long bones, as reported by Motani (in press) for the holotype of Utatsusaurus hataii. The implication of these observations is that the elements may not be as narrow as they are depicted in Fig. 9-3A and B, and the relative widths of the long bones of this specimen should therefore not be used taxonomically.

Taxonomic Discussion

RTMP 89.127.3, previously described as belonging to Grippia, resembles the holotype of Parvinatator wapitiensis in its forefin morphology and also in its geological occurrence. Therefore it seems most appropriate to assign the specimen to this species. I will review various features in the following section to test the hypothesis that this specimen represent a young individual of P. wapitiensis.

Osteological maturity—One of the features used by Johnson (1977) for establishing immaturity in Stenopterygius (Lower Jurassic) was the occurrence of rounded carpal elements that do not lie in contact. I also used this feature for Early Triassic ichthyosaurs (Motani, in press; Chapter 3). Presence of similar carpals in RTMP 89.127.3 is therefore taken as evidence of its immaturity. The holotype, on the other hand, has angular carpal elements, indicating osteological maturity. Furthermore, the holotype is about 150 percent of RTMP 89.127.3 in radial length. All of these facts are in accordance with the hypothesis that RTMP 89.127.3 is a young individual of Parvinatator wapitiensis.

Forefin shape—When comparing the retrodeformed images (Fig. 9-3B, D), the left forefin of the holotype resembles the right one of RTMP 89.127.3. The forefins are typical of Early Triassic species in having: 1) a long ulna with a fan-shaped distal end; 2) a long radius with an antero-proximal prominence; 3) elongated metacarpals II to IV; and 4) elements on the posterior margin without postaxial perichondral ossification. These features are all common among Utatsusaurus hataii (Motani, in press), Grippia longirostris (Chapter 3), Chaohusaurus geishanensis (Chapter 5), and the present form (Figs. 9-3, 9-4). The most striking similarity between the two specimens is the biconcave shape of metacarpal I (Fig. 9-3B, D), which retains perichondral ossification along its preaxial margin. This element is lunate in G. longirostris (Fig. 9-4B) and in C. geishanensis (Fig. 9-4C), due to the loss of preaxial perichondral ossification (Chapters 3, 5). Metacarpal I of U. hataii is incompletely known (Fig. 9-4A), but it was probably biconcave, as in the present form (Motani, in press). The two forefins are about the same size as that of C. geishanensis, which is much smaller than those of U. hataii and G. longirostris (Figs. 9-3, 9-4). When considering all of the above features , the forefins are more similar to each other than to any other ichthyosaurian forefins, which is in accordance with the present hypothesis.

There are two possible differences between the two forefins: the shape of metacarpal V and the relative width of other metacarpals. Both of these features, however, were shown to be insignificant earlier in this paper: the fifth metacarpal of the holotype was probably lunate, as in RTMP 89.127.3, and the metacarpals of RTMP 89.127.3 are wider than they appear.

Geological and geographical settings—The holotype (Nicholls and Brinkman, 1995:522) and RTMP 89.127.3 (Brinkman et al., 1992:466) are from a single locality of the Wapiti Lake area (locality D of Callaway and Brinkman, 1989). RTMP 89.127.3 is from the Spathian (Lower Triassic) section of the Vega-Phroso Member of the Sulphur Mountain Formation (Brinkman et al., 1992), while the holotype is from an unknown horizon of the Lower or Middle Triassic (Nicholls and Brinkman, 1995). Although the horizons cannot be identified as the same, they cannot be positively shown to differ either. The close geographical occurrence is supportive of the present hypothesis.

Conclusion—Considering the all available evidence, there seems to be no critical feature that falsify the hypothesis that RTMP 89.127.3 represents a young individual of Parvinatator wapitiensis. Instead, several features, such as the shape of metacarpal I, osteological maturity of the specimens, and geographical setting, positively support the hypothesis. It is also clear that RTMP 89.127.3 cannot be assigned to any other species than P. wapitiensis, and I conclude that the specimen should so be assigned.

SYSTEMATIC PALEONTOLOGY

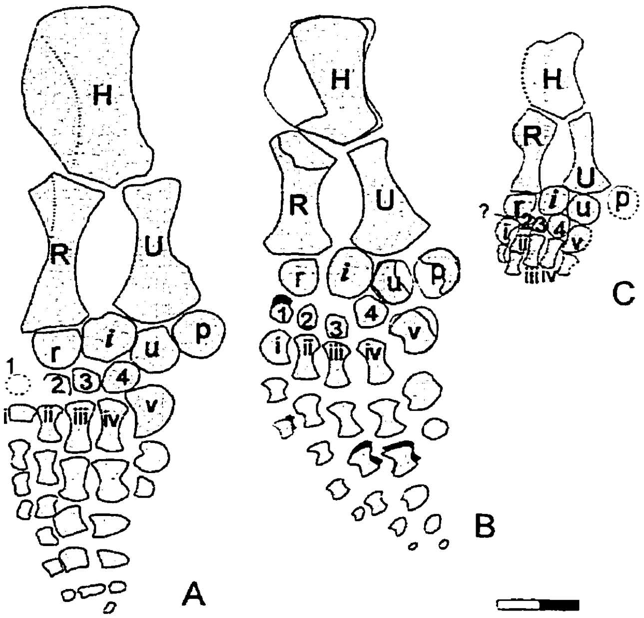
Order Ichthyosauria Blainville 1835

Genus Parvinatator Nicholls and Brinkman 1995

Type species—Parvinatator wapitiensis Nicholls and Brinkman 1995

Figure 9-4. Forefins of Early Triassic ichthyosaurs.

A, Utatsusaurus hataii (modified from Motani, in press). B, Grippia longirostris (modified from Chapter 3). C, Chaohusaurus geishanensis (modified from Chapter 5). Scale in centimetre.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Emended Diagnosis—Very small ichthyosaur with metacarpal I retaining perichondral ossification preaxially; seven phalanges in the longest digit; posterior teeth not rounded (crown height/width ratio higher than 1); teeth disto-mesially compressed, at least in maxilla; relative tooth size (Massare, 1987) approximately 0.1.

Comment—The original diagnosis for the genus contained several features that are now shown to be absent. The supratemporal, squamosal, and quadratojugal are all present, instead of the quadratojugal being lost. The contact between the jugal and the quadratojugal (misidentified as the squamosal by Nicholls and Brinkman [1995]) is an artifact of dislocation of the postorbital region in the holotype. The cheek region is emarginated ventrally, but not as diagnosed by Nicholls and Brinkman (1995).

Parvinatator wapitiensis Nicholls and Brinkman 1995

Holotype—RTMP 89.127.8.

Referred Specimen—RTMP 89.127.3

Emended Diagnosis—As for the genus.

Synonymy—

Parvinatator wapitiensis Nicholls and Brinkman, 1995: p.522

Grippia cf. G. longirostris Brinkman, Zhao, and Nicholls, 1992: p.466

Grippia sp. in press. Caldwell fig. 5A

Distribution—D locality (Callaway and Brinkman, 1989), Sulphur Mountain Formation of Wapiti Lake area, British Columbia. Probably from the Lower Triassic.

Comment—The description given by Nicholls and Brinkman (1995) contained some errors. Previously mentioned features, due to the misidentification of the elements in the cheek region, and to the oversight of the effect of disarticulation, deformation, and breakage, are not repeated here. Other new findings that contradict with the original description include: 1) the contact between the postfrontal and prefrontal seems to be absent; 2) the quadrate is not a long shaft of bone, rather, its medial side is concealed by the overlying jugal; and 3) the tooth implantation cannot be established, only the lateral side of the jaw having been prepared (Motani, 1996).

SUMMARY

1) The holotype of Parvinatator wapitiensis had been tectonically deformed.
2) A new reconstruction of the skull, based on a retrodeformed image and consideration of disarticulation and breakage of the bones, indicates various errors in the original description.
3) The supratemporal, squamosal, and quadratojugal are all present, and are similar to those of Utatsusaurus hataii and Grippia longirostris. The supratemporal is not greatly enlarged as was originally described.
4) The contact between the postfrontal and prefrontal seems to be absent.
5) RTMP 89.127.3 is osteologically immature. It resembles the holotype of Parvinatator wapitiensis in forefin morphology and geographical occurrence, and is therefore considered to be a young individual of this species.

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CHAPTER

10

NEW OBSERVATIONS ON THE SKULL OF MIXOSAURUS (ICHTHYOSAURIA)

ABSTRACT

Reexamination of the skulls of Mixosaurus atavus revealed previously unrecognized features of the skull roof, such as a long sagittal crest reaching the nasal, and a largely expanded anterior terrace of the upper temporal fenestra, also reaching the nasal. The anterior terrace of the upper temporal fenestra is much smaller in Utatsusaurus and Grippia. These features are also present in M. cornalianus, and in M. nordenskioeldii, therefore seem to be the shared derived characters defining Mixosaurus. The supratemporal, squamosal, and quadratojugal are all present in Mixosaurus atavus, and even in Ichthyosaurus(?) longifron from the Toarcian (Lower Jurassic), therefore the absence of the squamosal in Ichthyosaurus and Platypterygius is a derived condition which probably appeared in the Jurassic.

INTRODUCTION

Mixosaurus is the commonest genus of Triassic ichthyosaurs, which ranged from a small to middle size (i.e., less than one metre to over two metres). The genus Mixosaurus was named by Baur (1887) based on Ichthyosaurus cornalianus Bassani 1886, because its forefin was sufficiently different from that of Ichthyosaurus. M. cornalianus is well represented by many skeletons from the Middle Triassic of the Monte San Georgio and Tessin areas on the border of Switzerland and Italy, and it is the only Triassic ichthyosaur for which completely articulated skeletons are known. Ever since Repossi (1902) published the first adequate figures, M. cornalianus has been the architypical of primitive ichthyosaurs from the Triassic.

Although many additional specimens have been collected, Mixosaurus cornalianus is far from well studied. Since Repossi (1902), the only significant contribution was made by Besmer (1947), who conducted a detailed study of the dentition of the species. Various other authors gave short accounts of M. cornalianus (e.g., Merriam, 1908;Wiman, 1912; von Huene, 1925,1935), but the morphology of this species, especially of the cranium, is still not well understood. This is partly because of the preservation of material, where the specimens are all severely compressed by diagenetic effect.

The cranial morphology is better known in another species of this genus, Mixosaurus atavus, where two partial skulls, with three-dimensional preservations, are known. It was Fraas (1891) who reassigned Ichthyosaurus atavus Quenstedt 1852, from the Middle Triassic of Germany, to Mixosaurus. Apart from these skulls, this species is represented only by isolated elements, and therefore its postcranial morphology is very poorly known. The first skull, which was described by von Huene (1916), is not well preserved. The second skull, described by Edinger (1934), is much better preserved, but it only comprises less than half of the skull. Based on these two specimens, von Huene (1935) gave a reconstruction of the skull, but this has some major errors.

A third species of Mixosaurus, M. nordenskioeldii (Hulke 1873) from Spitsbergen, was assigned to this genus by Dames (1895). This species remained poorly known until Wiman (1910) described additional specimens. M. nordenskioeldii is characterized by its large, rounded posterior teeth, suggesting a durophagous diet, but little is known about its cranium. Recently, Nicholls et al. (in press) synonymized a North American form, Phalarodon fraasi

Merriam 1910 with M. nordenskioeldii. P. fraasi has traditionally been distinguished from M. nordenskioeldii for having more robust posterior teeth, but Nicholls et al. (in press) showed that this distinction is insignificant: their new specimens showed that the upper dentition comprises smaller teeth than its lower counterpart in M. nordenskioeldii, and the lower one resemble that described as P. fraasi. They also found that the unusually large teeth of this species, together with the sagittal crest present in their new skull specimens, is sufficient to recognize this species as a separate genus, Phalarodon.

In one of the figures in the monograph of the ichthyosaurs from the Muschelkalk, von Huene (1916:taf. 1, fig. 1) figured a sagittal crest for the skull of Mixosaurus atavus, although he did not included this structure in his reconstruction of the skull (Huene, 1916:fig. 75). M. cornalianus also has a ridge preserved along the sagittal line of the skull, as figured by von Huene (1935:fig. 1). It is therefore possible that the sagittal crest is a common feature among the three species of Mixosaurus. However, it is difficult to make comparisons among the skulls of these species because there is insufficient information in the literature. Proper descriptions of the skulls are long overdue. The purpose of the present study is to clarify the cranial morphology of M. atavus and M. cornalianus through the examination of historical specimens.

MATERIALS AND METHODS

Abbreviations for institutions are: BMNH-Natural History Museum, London; MNB-Museum für Naturkunde, Berlin; SMC-Sedgwick Museum, Cambridge University; SMNS-Staatliches Museum für Naturkunde, Stuttgart; UCMP-University of California, Museum of Paleontology, Berkeley.

Five specimens of Mixosaurus, each containing a skull or partial skull, were examined: SMNS 15378, a skull of M. atavus described by von Huene (1916); MNB 5180, a skull of M.

atavus described by Edinger (1934); SMNS 54068, a slab with two skeletons of M. cornalianus; BMNH R5702, a skeleton of M. cornalianus.

Comparisons were made with the skulls of: Ichthyosaurus longifron (BMNH 33157) from the Toarcian (Upper Liassic) of France; Temnodontosaurus burgundiae (SMNS 13128) from the Toarcian of Germany; Shastasaurus alexandrae (UCMP 9017) from the Upper Triassic of California; and Cymbospondylus petrinus (UCMP 9950) from the Middle Triassic of Nevada. BMNH 33157 was figured by Owen (1881:pls. 23-26) in his description of I. longifron Owen 1881, therefore it is considered as the holotype of the species. This species probably does not belong to the genus Ichthyosaurus, which is known only from the Lower Liassic and older strata (McGowan, 1974;Chapter 6). Although it may belong to Stenopterygius, the commonest genus from the Toarcian, there is insufficient morphological information to base such an assignment. Therefore it will be tentatively referred to as Ichthyosaurus(?) longifron in the following sections.

Measurements were taken using dial calipers, and recorded to the nearest 0.1 mm. Two indices, used by Massare (1987), were calculated for the dentition,: relative tooth size, the height of the largest tooth divided by the skull width; and tooth shape index, the height of the largest tooth crown divided by its width.

MIXOSAURUS ATAVUS

General Accounts

MNB 5180—This is the only skull of Mixosaurus that is sufficiently complete and that retains its three-dimensional shape. This specimen preserves the left half of the skull, but without the tip of the snout and the posterior cheek region, that is, the squamosal and quadratojugal (Fig. 10-1). The bones of the occipital region and mandible are not preserved, and the palate is not exposed.

SMNS 15378—This specimen preserves the three dimensional arrangements of the skull elements, but most of the bones are weathered away, leaving their impressions (Fig. 10-2). These impressions often preserve the surface striation of the original bone, and are therefore sometimes useful in confirming sutures. The skull is distorted from a diagenetic compression, which seems to have occurred in the left-dorsal to right-ventral direction.

Major Structures

Anterior terrace of the upper temporal fenestra—The most remarkable feature of the skull of Mixosaurus atavus is the presence of an enormously enlarged anterior terrace of the upper temporal fenestra that reaches the nasal anteriorly (Figs. 10-1A, 10-3B). This terrace appears as a deep pool-like excavation occupying most of the skull roof (Fig. 10-1A). The presence of the anterior terrace of the upper temporal fenestra is a common feature among many Triassic ichthyosaurs, such as Utatsusaurus hataii (Chapter 7), Grippia longirostris (Chapter 8), Cymbospondylus petrinus (UCMP 9950), and Shastasaurus alexandrae (UCMP 9017), but it only reaches the posterior end of the frontal in these forms, and is never this deep. In the present specimen, this terrace is laterally strengthened by a thick bony bar formed by the prefrontal and postfrontal, which forms the high lateral wall of the excavation (Fig. 10-1D). Medial to the terrace is a thin bony crest, which will be described later. The anterior end of the terrace is marked by a ridge on the nasal, which curves to form a U-shape in dorsal view (Fig. 10-3B).

Figure 10-1. Skull of Mixosaurus atavus (MNB 5180).

A, left dorso-lateral view. A large excavation on the skull roof is the expanded anterior terrace of the upper temporal fenestra, and is therefore not a diagenetic breakage. B, posterior view. Only the supratemporal and parietal are preserved. The supratemporal has a ventral process. C, D, left lateral view. Notice the well developed sagittal crest. The posterior teeth appear wider in C than they actually are, because of their shadows. See Fig. 10-3 for abbreviations.

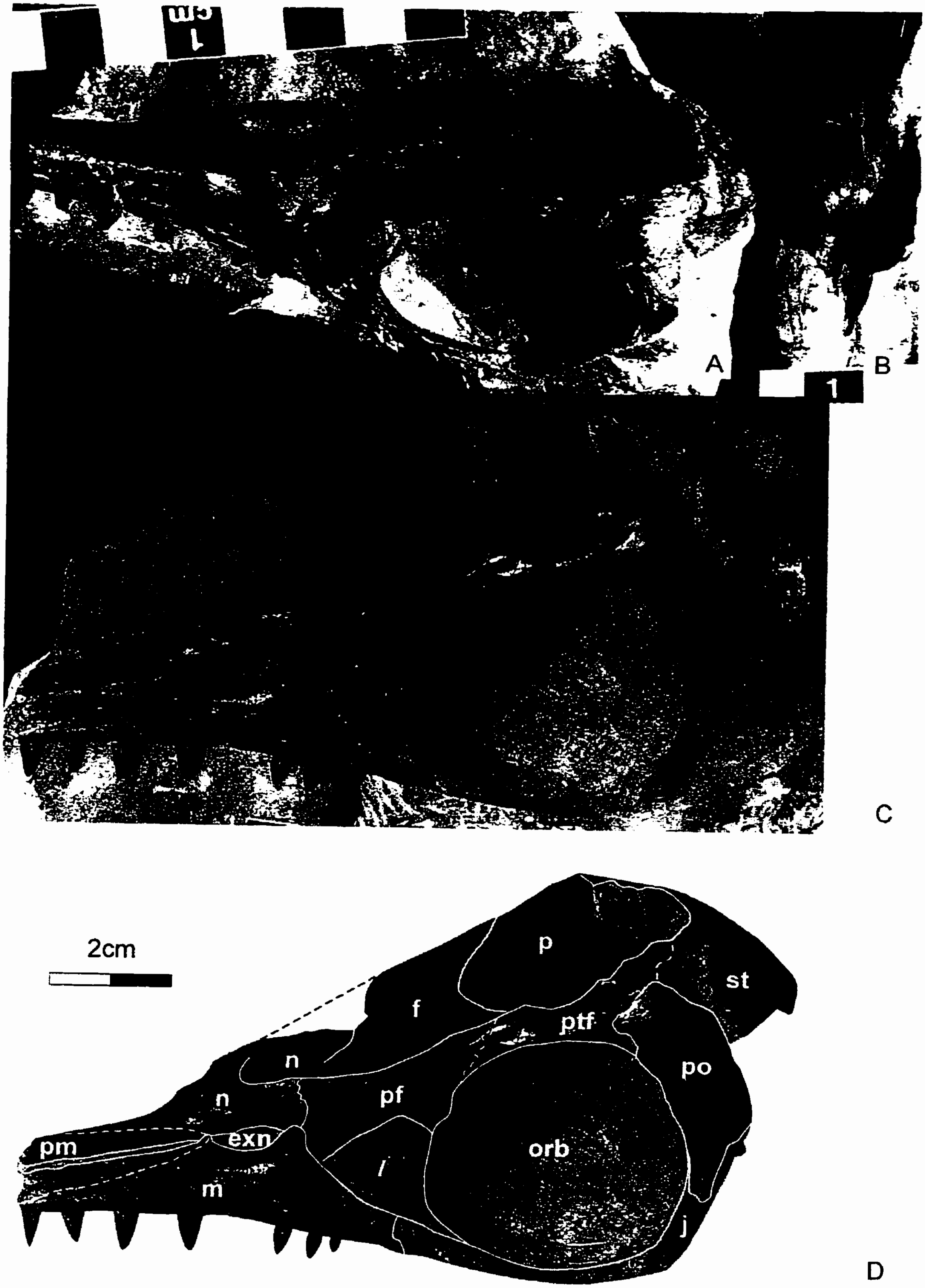
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Figure 10-2. Skull of Mixosaurus atavus (SMNS 15378).

A, B, left lateral view. A prominence of matrix on the skull roof is the endocast of the pineal foramen. See Fig. 10-3 for abbreviations.

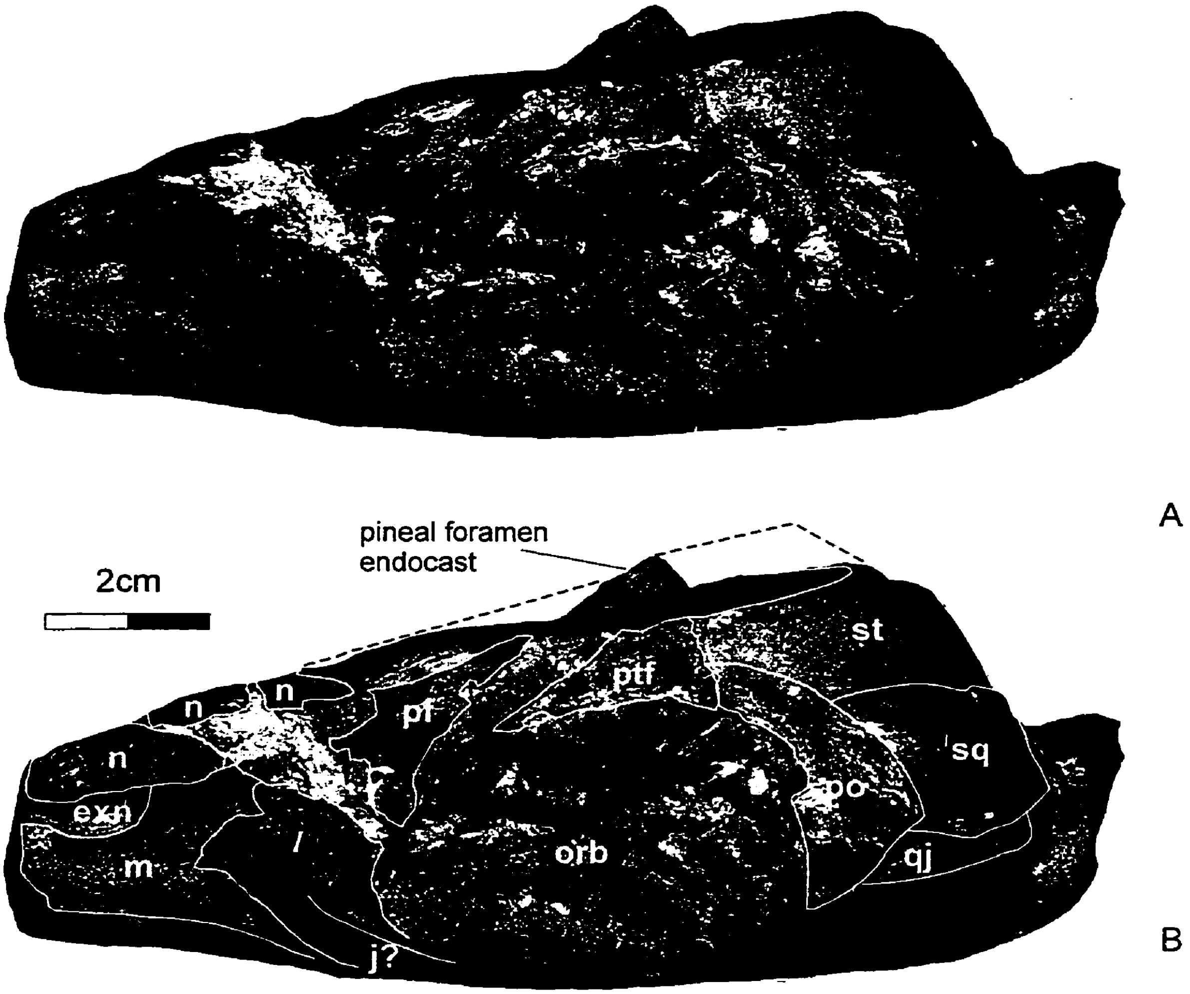
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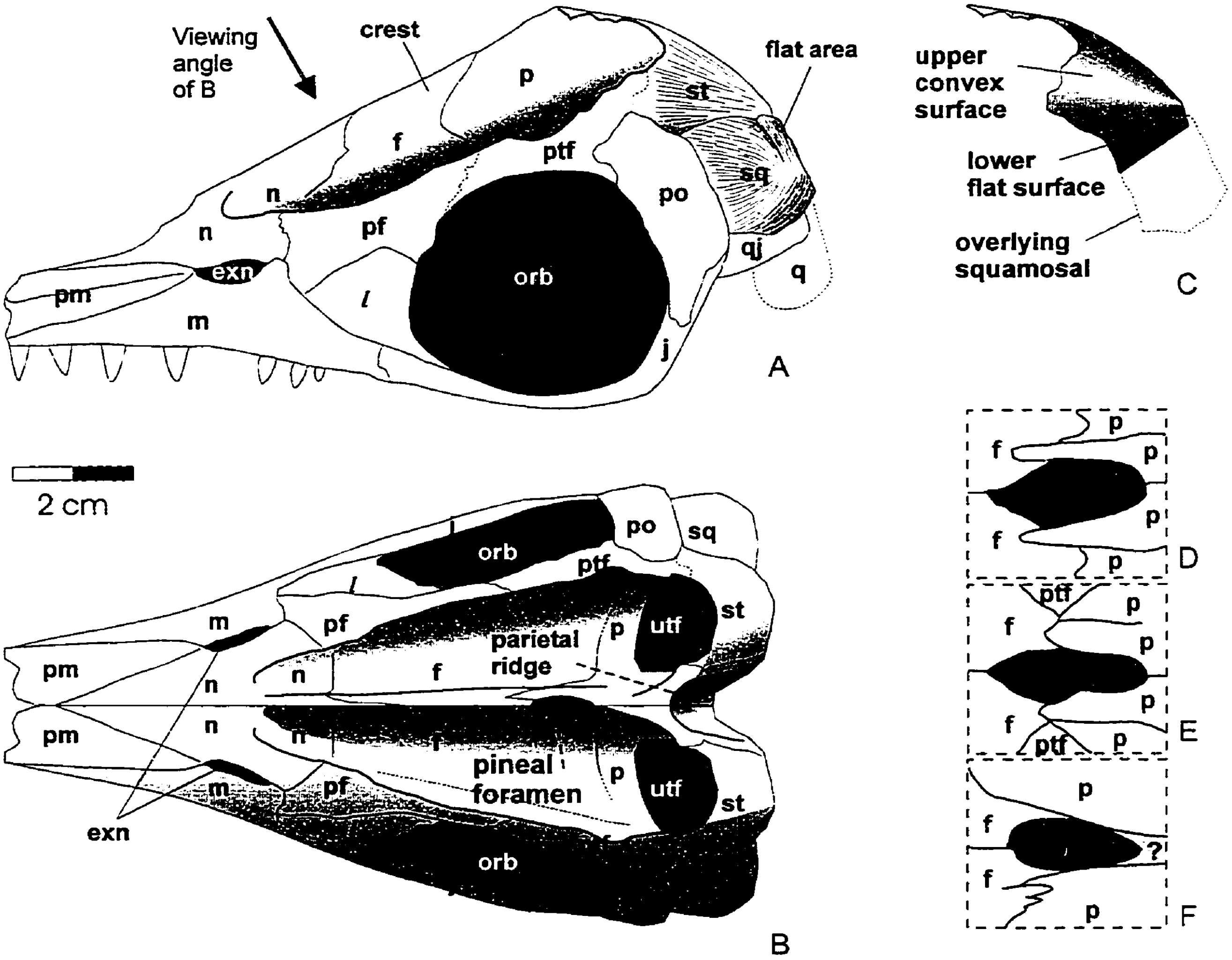
Figure 10-3. Reconstruction of the skull of Mixosaurus atavus, and comparisons with the pineal foramina of other ichthyosaurs.

A, left lateral view. B, dorsal and slightly anterior view, to show the upper temporal fenestrae that are not visible from the dorsal view. Mainly based on MNB 5180, but the squamosal and quadratojugal are based on SMNS 15378. The image of SMNS 15378 was linearly stretched so that its outline resembles that of MNB 5180, then the squamosal and quadratojugal were copied onto the image of MNB 5180. C, relationship between the supratemporal and squamosal. The squamosal overlies the lower flat surface of the supratemporal. See text for detail. D-F, pineal foramen of three ichthyosaurs. D, Cymbospondylus petrinus (UCMP 9950). E, Shastasaurus alexandrae (UCMP 9017); F, Ichthyosaurus(?) longifron (BMNH 33157). Abbreviations: exn, external naris; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; orb, orbit; p, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; ptf, postfrontal; sq, squamosal; st, supratemporal; and utf, upper temporal fenestra.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Edinger (1934) interpreted this excavation on the skull roof as a result of breakage during the preservation. She (1934:344) argued that a similar breakage was suggested by von Huene (1925:292) for the skull of Mixosaurus cornalianus. Such breakage, however, is unlikely, considering the completeness of the skull, which has a well preserved sagittal crest, anterior terrace, and prefrontal-postfrontal bar. Moreover, the structure of the upper temporal fenestra is complete as preserved (although broken antero-laterally). The surface of the anterior terrace tends to be rough compared to the lateral surface of the skull, but there are no cracks to indicate a large-scale collapse of the skull roof. Von Huene had a penchant for interpreting the depressions on ichthyosaurian skull roofs as diagenetic effects, because he always reconstructed ichthyosaurian skulls as having smooth dorsal surface. For example, he gave Cymbospondylus petrinus a smooth skull roof in his reconstruction (Huene, 1916:fig. 77), while depicting a clear depression in his sketch of the specimen (Huene, 1916:fig. 79), and the same is true for Shastasaurus alexandrae (Huene, 1916:fig. 83).

Sagittal Crest—Associated with the expansion of the anterior terrace of the upper temporal fenestra was the development of an enormous sagittal crest, formed by the nasal, frontal, and parietal (Fig. 10-1, 3). This crest is broken in SMNS 15378, leaving its base as a median ridge on the skull roof (von Huene, 1916:taf. 1, fig. 1). However, the height of the crest, prior to the breakage, can be estimated by the endocast of the pineal foramen (estimation dotted in Fig. 10-2B). The reconstructed crest appears lower than in MNB 5180, but it is probably because of the dorso-ventral compression of SMNS 15378, as mentioned before. The maximum height of the crest of MNB 5180 is 22.6 mm, which is greater than the width of the left anterior terrace of the upper fenestra at the same position (16.8mm).

Pineal Foramen—The pineal foramen is known only from the endocast in SMNS 15378. It appears as a narrow, oval structure when viewed dorsally (Fig. 10-3B), being accommodated in the sagittal crest, which is also narrow. The position of this endocast in SMNS 15378 corresponds to the frontal-parietal suture of MNB 5180. This is in accordance with the condition in many other Middle Triassic and later ichthyosaurs, such as Cymbospondylus petrinus (Fig. 10-3D), Shastasaurus alexandrae (Fig. 10-3E), and Temnodontosaurus burgundiae (SMNS 13128), but different from some others, such as Ichthyosaurus(?) longifron (Fig. 10-3F). In the former three taxa, the parietals has a process located antero-medially, which forms a fork when the right and left ones are articulated (Fig. 10-3D, E). This anterior fork of the parietals overlies the frontals, and the pineal foramen is enclosed between this parietal fork and the frontals (Fig. 10-3D-E). In I(?) longifron, however, the parietal does not have a distinctive process (Fig. 10-3F). Viewed dorsally, Mixosaurus atavus has the anterior fork of the parietal (Fig. 10-3B), although it appears different from other views because of the formation of the distinct sagittal crest. It is this forked area of MNB 5180 that corresponds to the position of the pineal foramen mold in SMNS 15378.

Upper temporal fenestra—The upper temporal fenestra, only preserved in MNB 5180, is very small, as pointed out by von Huene (1935). This opening is almost invisible from the dorsal aspect, being concealed by a dome-like overhang of the supratemporal. Therefore, Fig. 10-3B is given from a slightly anterior view, to show the upper temporal fenestra. This opening is posteriorly bordered by the supratemporal, and anteriorly by the parietal. Its anterior margin is broken laterally, but is seems likely that the postfrontal joins the margin antero-laterally. Neither the postorbital nor squamosal participates in its margin.

Orbit—The expansion of the anterior terrace of the upper temporal fenestra also affects the orbit: the dorsal margin of the orbit, formed by the frontal in Early Triassic ichthyosaurs (Chapter 7, 8), is bordered by a robust bar comprising the prefrontal and postfrontal in Mixosaurus atavus (Figs. 10-1, 10-2, 10-3). This bar, as previously mentioned, seems to mechanically strengthen the lateral margin of the anterior terrace of the upper temporal fenestra. The orbit is nearly circular, without any depression caused by the prominences of the prefrontal or postfrontal, which are present in Utatsusaurus hataii (Chapter 7) and in Grippia longirostris (Chapter 8).

External Naris—The external naris is directed laterally (Fig. 10-3), rather than dorsally as in Early Triassic ichthyosaurs (Chapter 7, 8). The boarder of the external naris is formed by the nasal and maxilla. The participation of the premaxilla in the its anterior border is minimal (Fig. 10-3), unlike in Utatsusaurus hataii (Chapter 7) and in Grippia longirostris (Chapter 8).

Cheek and Temporal Regions

Quadratojugal—The posterior cheek region is only preserved in SMNS 15378, where three elements seem to be present. The most ventral one is identified as the quadratojugal (Fig. 10-2). This poorly exposed bone clearly underlies the dorsally located element, identified as the squamosal, and is therefore not a part of the latter. Romer (1968) questioned von Huene's (1916) identification of this bone as the quadratojugal, because the bone appears so small, and is visible only on the left side of the skull. However, although the element is largely concealed by the overlying squamosal, it does not mean the element is small.

Squamosal—The squamosal is strongly convex, forming a dome-like protuberance in the cheek region (Fig. 10-3A, B). There is a flat area located postero-dorsally (Fig. 10-3A), showing a topological discontinuity with the main dome, but this wing belongs to the squamosal. The squamosal is known only from its impression, but abundant surface striations are preserved, as schematically reproduced here in Fig. 10-3A. Judging from these striations, the bone seems to have started its ossification from the middle part, near its posterior margin, spreading dorsally, ventrally and anteriorly (Fig. 10-3A). The dorsal margin of the squamosal is marked by a line representing the edge of the dome. The surface striations are differently oriented beyond this line (Fig. 10-3A), indicating the presence of another bone, the supratemporal.

Supratemporal—The bone dorsal to the squamosal is the supratemporal, which is the largest bone in the cheek and temporal region, and which forms the posterior margin of the upper temporal fenestra. The size of this bone relative to the skull is much greater than in Early Triassic ichthyosaurs (Chapter 7, 8). The posterior slope of the supratemporal (Chapter 7) is largely expanded, almost entirely covering the upper temporal fenestra in the true dorsal view (Fig. 10-3B is from a somewhat anterior direction).

The supratemporal is completely preserved in MNB 5180. The surface striations radiate from the most posterior end of the bone, where it forms a peak (Figs. 10-1B, 10-3A), therefore it is likely that the ossification centre was located at this peak. The lateral side of the supratemporal has two topologically distinct surfaces in MNB 5180. The upper one is strongly convex, while the lower one is almost flat, with a slight convexity (Figs. 10-1B, 10-3C). These two surfaces are smoothly connected with each other, and the surface striations also change continuously between the two, therefore there is little doubt that the lower surface is a part of the supratemporal. However, the lower surface is not visible in SMNS 15378, because the corresponding area is overlain by the squamosal. The surface striations of the squamosal in SMNS 15378 are distinctly different from those of the lower surface of the supratemporal in

MNB 5180. Furthermore, the former is much larger than the latter, therefore there is little possibility that the two structures are homologous. Accordingly, I conclude that the squamosal overlies the supratemporal in this area (Fig. 10-3A, C).

The supratemporal has a ventral process that is not visible from the lateral view, but which can be seen in the posterior view (Fig. 10-1B). This process is laterally compressed, and is located ventral to the posterior slope (Fig. 10-1B), therefore it is probably homologous with the posterior ridge of the supratemporal in Utatsusaurus hataii (Chapter 7). The lateral side of this ventral process is concave, forming an articular facet, probably for the quadrate. The shape of this supratemporal is strikingly similar to that of the bone identified as the squamosal in Jurassic and later ichthyosaurs (Romer, 1968;McGowan, 1973), suggesting that the latter bone may actually be the supratemporal, as discussed later.

Parietal—Apart from the median crest, the parietal resembles that of Jurassic ichthyosaurs. The postero-lateral process, which is long and flat in Utatsusaurus hataii (Chapter 7) and in Grippia longirostris (Chapter 8), is very short and robust as in Ichthyosaurus (McGowan, 1973). Also, there is a parietal ridge (McGowan, 1973:fig. 35), a structure that is absent in Early Triassic ichthyosaurs.

Other Features of Interest

Premaxilla—The premaxilla is known only as a partial impression of its posterior end, left behind on the nasal and maxilla in MNB 5180. The posterior end of the premaxilla is pointed, and barely participates in the anterior margin of the external naris. This is in contrast to the conditions in Utatsusaurus hataii (Chapter 7) and Grippia longirostris (Chapter 8), and Ichthyosaurus (Sollas, 1916), where the posterior end of the premaxilla is forked, forming the entire anterior margin of the external naris. Mazin (1981) depicted a pointed posterior end to the premaxilla of G. longirostris, in his reconstruction of the skull, but this has been shown to be incorrect (Chapter 8).

Pterygoid—This bone is known only in SMNS 15378. As figured by von Huene (1916:plate 1, fig. 2, without the overlay depicting sutures), the interpterygoid vacuity seems to be absent, or extremely reduced (he depicted this vacuity in the overlay of the same plate, and in his reconstruction [von Huene, 1916:fig. 75]). This absence, or extreme reduction, accords with the condition in Utatsusaurus hataii (Chapter 7). The quadrate ramus of the pterygoid is very wide proximally, forming a triangular wing medially, which meets the same wing of the other pterygoid along the median line. The suture between these wings is slightly elevated, forming a ridge, which von Huene (1916:fig. 75) figured as if it was a narrow process projecting posteriorly from the palatal ramus of the pterygoid. The quadrate ramus also has a small medial process distal to this proximal expansion, as in U. hataii (Chapter, 7), rather than a large medial wing as in Ichthyosaurus (McGowan, 1973).

Dentition—Seven maxillary teeth are preserved in MNB 5180 (Fig. 10-1D). The maxillary teeth are tightly implanted in bony sockets. The root is little exposed, unlike in Utatsusaurus hataii, where the bottom half of the exposed length of a typical tooth is occupied by the root (Motani, 1996). The crowns are conical (Fig. 10-1C,D), with vertical striations that are not as fine as those for Utatsusaurus hataii (Motani, 1996). No well-rounded tooth crowns, resembling those of Mixosaurus nordenskioeldii (Wiman, 1910:plate 5, figs. 9, 11), are present. The most posterior three crowns are slightly swollen, but these are also smaller than the more anterior four (note that the widths of the teeth appear exaggerated in Fig. 10-1C, because of shadows). The relative tooth size of MNB 5180 is 0.12, while the tooth shape index is 1.6, which suggest a crunching function for the teeth (Massare, 1987) .

In SMNS 15378, the cross-sections of several maxillary teeth are preserved in bony sockets. Other sockets are empty, the teeth having been lost. Empty sockets appear larger and more circular than the cross-sections of adjacent teeth. All cross-sections of teeth, where the dentine and pulp cavity are recognizable, are laterally compressed. For example, the penultimate tooth of the right maxilla has a disto-mesial width of 3.2 mm, compared with a labio-lingual width of 2.4 mm. Laterally compressed posterior teeth are also known in M. nordenskioeldii.

MIXOSAURUS CORNALIANUS

The skulls of SMNS 54068 and BMNH R5702 (Mixosaurus cornalianus) are similar in size to one another, and to those of MNB 5180 and SMNS 15378 (M. atavus). However, the teeth of BMNH R5702 (M. cornalianus) are much smaller than those of MNB 5180 (M. atavus). The relative tooth sizes for the anterior teeth vary between 0.03 to 0.04, and was probably less than 0.05 for the largest tooth, judging from Repossi's (1902:plate 8, figs. 2, 3) figures of the upper and lower dentitions. According to this figure, the posterior teeth are shorter than the anterior ones, although they are more robust. The only posterior tooth of BMNH R5702, a mandibular tooth exposed dorsally, is indeed more robust than the anterior teeth, confirming Repossi's (1902) description. A low relative tooth size of around 0.05 is typical of Early Triassic ichthyosaurs, such as Utatsusaurus hataii (Motani, 1996) and Grippia longirostris (Motani, 1997). These small teeth fall outside of Massare's (1987) tooth function categories.

All three skulls of Mixosaurus cornalianus examined show similar preservations: the skull roof, almost intact, is exposed dorsally, while the lateral side of the skull is partially disarticulated (Fig. 10-4). All three have a pair of large anterior terraces of the upper temporal fenestra that reach the nasal, as in M. atavus (Fig. 10-4). The prefrontal and postfrontal form a thick bar, lateral to the anterior terrace, again as in M. atavus, contributing to the mechanical strength of the skull roof (Fig. 10-4). This strengthening structure is possibly the reason why the skull roofs are well preserved in all three specimens, in spite of the extensive diagenetic compression observed. Medial to the anterior terrace is a ridge (Fig. 10-4), resembling the one preserved in the weathered skull of M. atavus (SMNS 15378) in which the sagittal crest is broken. It is not possible to establish the original height of this sagittal ridge, but, because there is little doubt that it is homologous to the sagittal crest of M. atavus, the ridge was probably higher in life, forming a crest.

The supratemporal is also similar to that of M. atavus in that it is large, with a well developed posterior slope. The upper temporal fenestra is not observable in any of the three specimens. Considering that this fenestra is concealed from the dorsal view in M. atavus by the well-developed posterior slope of the supratemporal, it is most likely that the same is also true for M. cornalianus. Other similarities to M. atavus include: 1) the postero-lateral process of the parietal is short and robust; 2) the parietal ridge is present; and 3) the posterior end of the premaxilla is pointed, rather than forked.

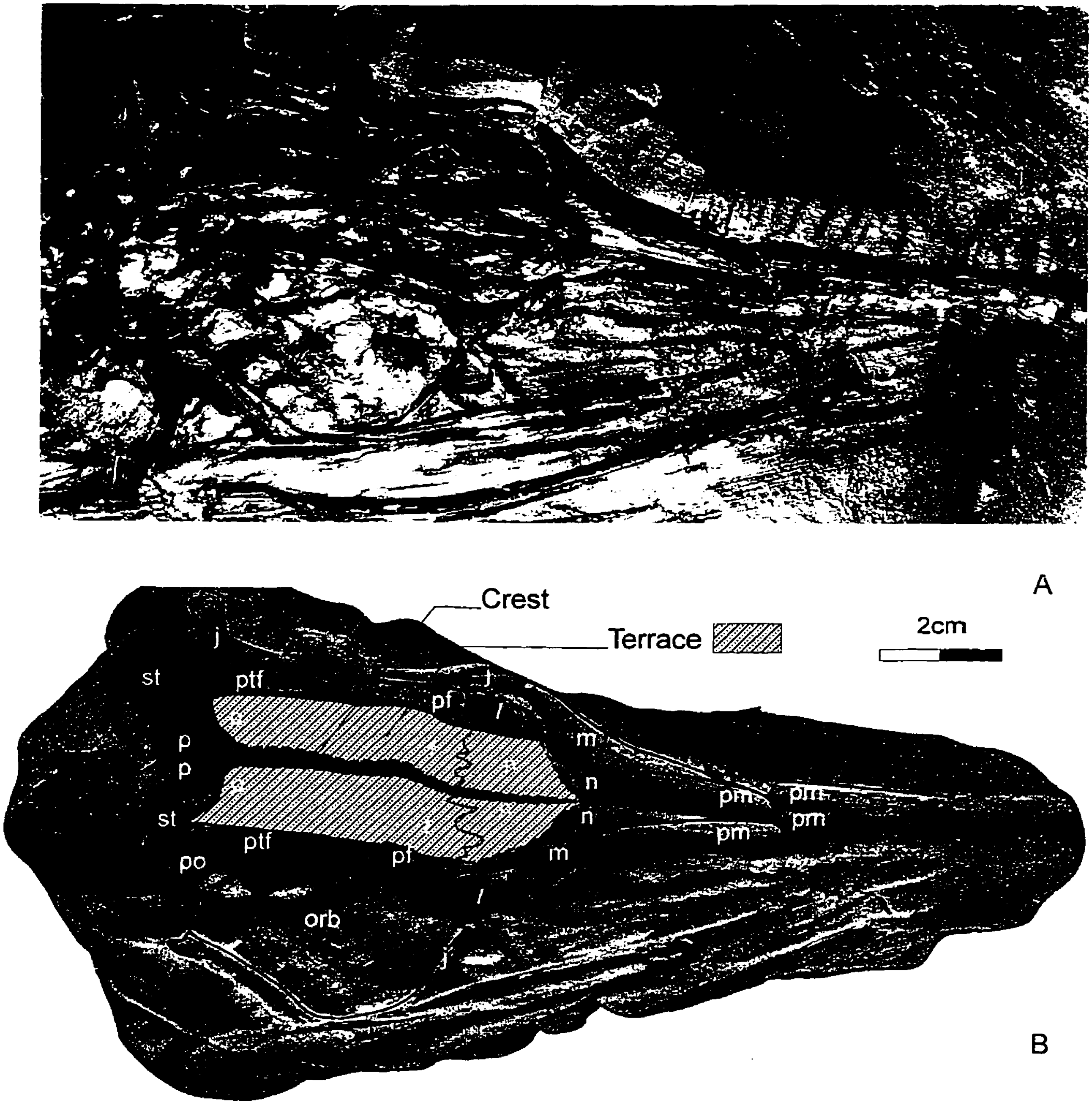
DISCUSSION

Taxonomic Status of Mixosaurus

The cranial morphologies of Mixosaurus cornalianus and M. atavus show a striking resemblance with each other, as described in the previous section. These two species are also of similar sizes. The only difference confirmed in the present study is in the dentition: the size of

Figure 10-4. Skull of Mixosaurus cornalianus (SMNS 54068, the individual on the right, with a scattered vertebral column).

The skull shares many features with that of M. atavus, such as a largely expanded anterior terrace of the upper temporal fenestra, the sagittal crest, and a thick prefrontal-postfrontal bar.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the teeth relative to the skull width is more than twice as large in M. atavus than in M. cornalianus. Because of this large difference in tooth size, it seems reasonable to recognize M. cornalianus and M. atavus as separate species.

Nicholls et al. (in press) referred Mixosaurus nordenskioeldii to Phalarodon, because they found it was sufficiently different from M. cornalianus in having a sagittal crest and rounded posterior teeth that are disto-mesially wide. However, the presence of the sagittal crest, or at least a sagittal ridge, was established for M. cornalianus in the present study, and a large sagittal crest is present in M. atavus. Therefore the presence of such an elevation along the median line of the skull is not characteristic of M. nordenskioeldii, but is a shared derived feature of the three species traditionally referred to the genus Mixosaurus. The shape of the posterior teeth is characteristic of M. nordenskioeldii, but this feature alone seems insufficient for assigning the species to a separate genus. Moreover, M. atavus has a dentition comprising large teeth, without rounded posterior crowns, which seems intermediate between that of M. cornalianus and of M. nordenskioeldii. Also, it seems difficult to recognize M. nordenskioeldii as a separate genus cladistically. The monophyly of the three species (M. cornalianus, M. atavus, and M. nordenskioeldii) seems robust, because of the presence of a large sagittal crest, and an expanded anterior terrace of the upper temporal fenestra. However, insufficient information is available for resolving the relationships among the three. Therefore the three species would most likely form a trichotomy in a cladogram, in which case it is not possible to distinguish one of them as a separate genus. A proper cladistic analysis is required for further discussion.

Cheek and Temporal Region

Because of its position and shape, the supratemporal of M. atavus is likely to be homologous with the bone identified as the squamosal in later ichthyosaurs, such as Ichthyoaurus (McGowan, 1973) and Platypterygius (Romer, 1968). Therefore it seems most appropriate to re-identify the latter bones as the supratemporal, as suggested by various authors before Romer (1968), and by Nicholls and Brinkman (1995).

One unusual feature of the supratemporal of Mixosaurus, and later ichthyosaurs, is that it is very large, unlike that in any other tetrapod except for Coelurosauravus, as reconstructed by Evans and Haubold (1987). However, this large bone shares three important features with the supratemporal of Utatsusaurus hataii, which is not as large, and which is undoubtedly the supratemporal (Chapter 7): 1) the posterior slope is present dorsally; 2) the posterior ridge is present ventral to the posterior slope; and 3) the bone is U-shaped in the dorsal view, forming the most posterior margin of the upper temporal fenestra. Because of these similarities, it seems most appropriate to interpret these bones as being homologous. The increased size of the supratemporal is a derived feature of Mixosaurus and later ichthyosaurs.

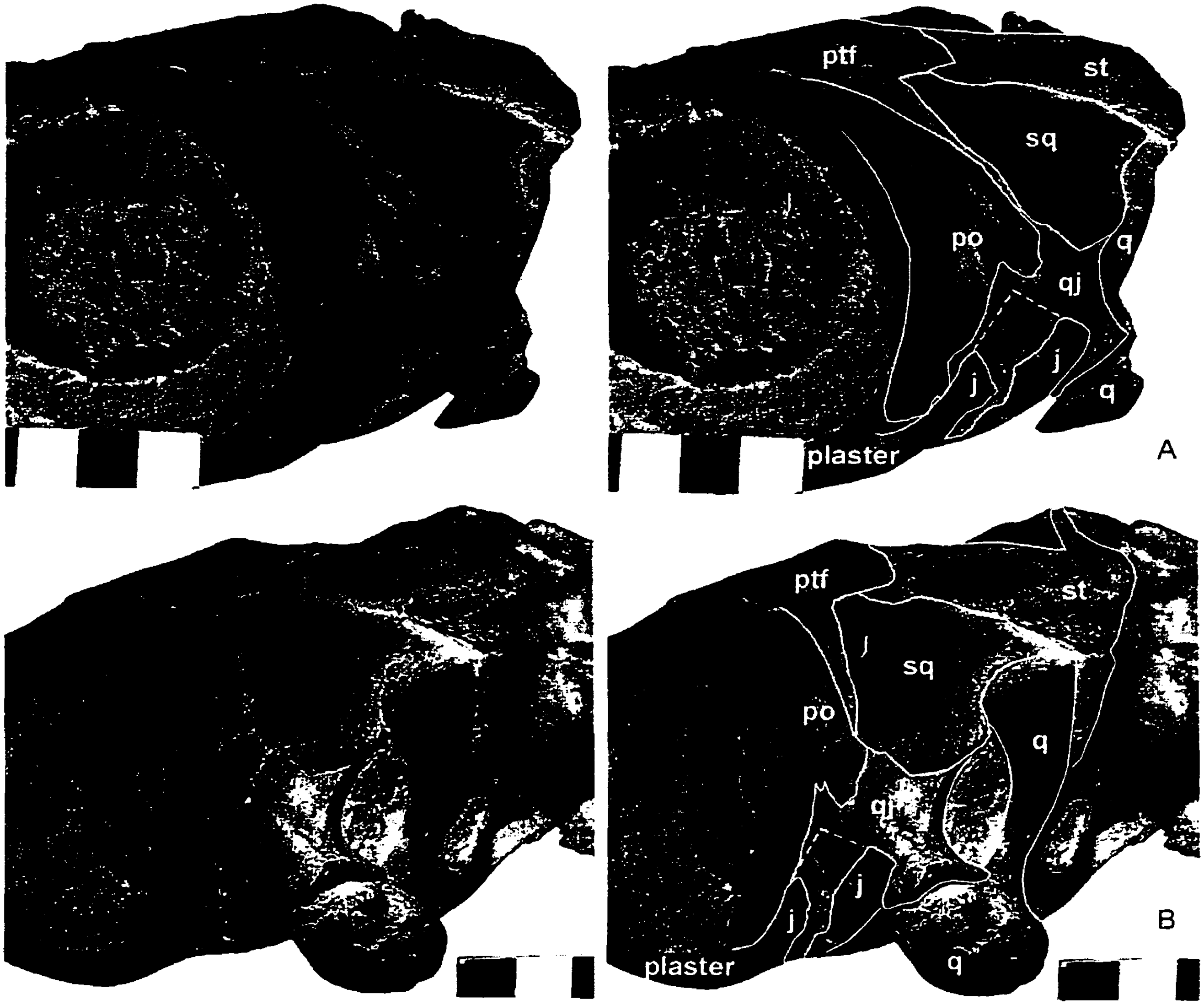
Before the studies of Romer (1968) and McGowan (1969), who independently reached the same conclusion that the supratemporal is absent in ichthyosaurs (Romer, 1968:35), various authors suggested the presence of two bones in the upper temporal region of ichthyosaurs. Romer (1968) referred to the dorsal one of these two elements as element A, the ventral one as element B, and argued that there was no sound evidence for the latter in any material. Since then, no objection has been made to this view that there is a single element in the upper temporal region, including Nicholls and Brinkman (1995), who properly identified the supratemporal. However, as my studies have shown, element B does exist in at least three

Triassic ichthyosaurs, namely, Utatsusaurus hataii (Chapter 7), Grippia longirostris (Chapter 8), and Mixosaurus atavus (present study). My preliminary examinations of Cymbospondylus petrinus (UCMP 9950) and Shastasaurus alexandrae (UCMP 9017) also revealed the presence of element B. Moreover, element B even exists in Ichthyosaurus(?) longifron from the Toarcian (Lower Jurassic), as depicted in Fig. 10-5. This bone, identified as the squamosal, shows a close resemblance to the squamosal of M. atavus, in that: 1) it overlies the quadratojugal ventrally; 2) it abuts the supratemporal dorsally; 3) it comprises a convex main body and somewhat flat postero-dorsal wing; and 4) its surface striations radiates from the middle part near its posterior margin (compare Fig. 10-5 with Fig. 10-3A).

There is only one bone ventral to the supratemporal in Ichthyosaurus (McGowan, 1973) and Platypterygius (Romer, 1968). Judging from Fig. 10-5, this bone corresponds to the quadratojugal of Ichthyosaurus(?) longifron and other ichthyosaurs, such as Mixosaurus atavus and Utatsusaurus hataii. Nicholls and Brinkman (1995) identified this element as the squamosal, but their identification is not plausible considering the new evidence presented above. Also, their argument was based on misinterpreted sutures of Parvinatator wapitiensis(Chapter 9). Therefore it is likely that the squamosal is absent from Ichthyosaurus and from Platypterygius. The loss of the squamosal before the supratemporal may seem unusual, considering the dominance of the squamosal in sphenodontians (e.g., Sues et al., 1994). However, the squamosal is lost before the supratemporal in some gekkonids such as Pachydactylus (de Beer, 1937:438), some pygopodids and anguids, Dibamus, and in snakes (Estes et al., 1988). Moreover, the supratemporal becomes ossified before the squamosal in Lacerta vivipara (Rieppel, 1992:5), therefore the dominance of the squamosal over the supratemporal is not universal among living diapsids.

Figure 10-5. Skull of Ichthyosaurus(?) longifron (BMNH 33157).

A, left lateral view of the cheek region. B, left postero-lateral view of the same region. This Late Liassic skull has three bones in the posterior cheek region, identified as the supratemporal, squamosal, and quadratojugal, as in Early and Middle Triassic ichthyosaurs. This contrasts with Ichthyosaurus (Early Liassic), where there are only two elements, the supratemporal and quadratojugal.


ptf
st
sq
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qj
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q
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A
ptf
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j
plaster
q
B

The holotype of *Ichthyosaurus zetlandicus* Owen 1881 (SMC J35176) preserves the squamosal on the left side of the skull, but it is absent from the right side. This suggests the possibility that the squamosal, which superficially overlies the quadratojugal and supratemporal, became disarticulated and lost after the animal died. If this were the case, it would be conceivable that the squamosal similarly became disarticulated and lost from the specimens of *Ichthyosaurus* and *Platypterygius* examined by McGowan (1973) and Romer (1968). However, it is also possible that the squamosal did not ossify on the right side of the skull of SMC J35176, nor in the specimens of *Ichthyosaurus* and of *Platypterygius*.

There are two other possible interpretations of the cheek region of *Mixosaurus* and later ichthyosaurs, but both are unlikely. The first interpretation is to identify the supratemporal of the present study as the squamosal, and the squamosal as a neomorph. This, however, seems implausible, because the morphological similarities between the supratemporal of *Utatsusaurus hataii* and of *Mixosaurus atavus* suggest their homology, as mentioned earlier. Furthermore, there is no necessity to assume the appearance of a neomorph when an alternative interpretation without a neomorph is plausible. The second interpretation is to consider the supratemporal and squamosal of the present study as two parts of one large bone, the squamosal. Such a large squamosal is known for some sauropterygians, such as *Placodus* (Rieppel, 1995), therefore it would suggest a close phylogenetic relationship between ichthyosaurs and sauropterygians if such a large squamosal existed in ichthyosaurs. However, as discussed earlier, this is unlikely for three reasons: 1) the squamosal of *M. atavus* seems to partially overlie the supratemporal, therefore it is most likely a separate bone; 2) each of the supratemporal and squamosal has its own ossification centre, also as mentioned earlier; 3) the arrangements of the supratemporal, squamosal, and quadratojugal in *Mixosaurus atavus* and *Ichthyosaurus*(?) *longifron* are very similar to those in *Utatsusaurus hataii* (Chapter 7) and *Grippia longirostris* (Chapter 8). The ventrally shifted location of the squamosal, obvious in the former two species, is already started in the latter two species. Therefore, I conclude that the interpretation of the cheek region as presented here is the most plausible.

SUMMARY

1. *Mixosaurus atavus* closely resembles the similarly sized *M. cornalianus* in its cranial morphology, but is distinguished from the latter by its teeth, which are more than twice as large. It also differs from a larger species, *M. nordenskioeldii*, in lacking rounded posterior teeth.
2. The presence of a long sagittal crest (or ridge), reaching the nasal, is a shared feature among three species of *Mixosaurus*, viz., *M. atavus*, *M. cornalianus*, and *M. nordenskioeldii*.
3. The dorsal depression preserved in mixosaurian skulls is not an artifact of the diagenesis, but is an enormously enlarged anterior terrace of the upper temporal fenestra. This enlarged anterior terrace is present in *M. atavus* and *M. cornalianus*, and probably also in *M. nordenskioeldii*. This anterior terrace is much smaller in Early Triassic ichthyosaurs.
4. The squamosal, supratemporal, and quadratojugal are all present in *Mixosaurus*, and in *Ichthyosaurus*(?) *longifron* from the Toarcian (Lower Jurassic).
5. *Ichthyosaurus* and *Platypterygius* lack the squamosal, but not the supratemporal or quadratojugal.

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CHAPTER

11

CENTRA SHAPE AND SWIMMING OF ICHTHYOSAURS

INTRODUCTION

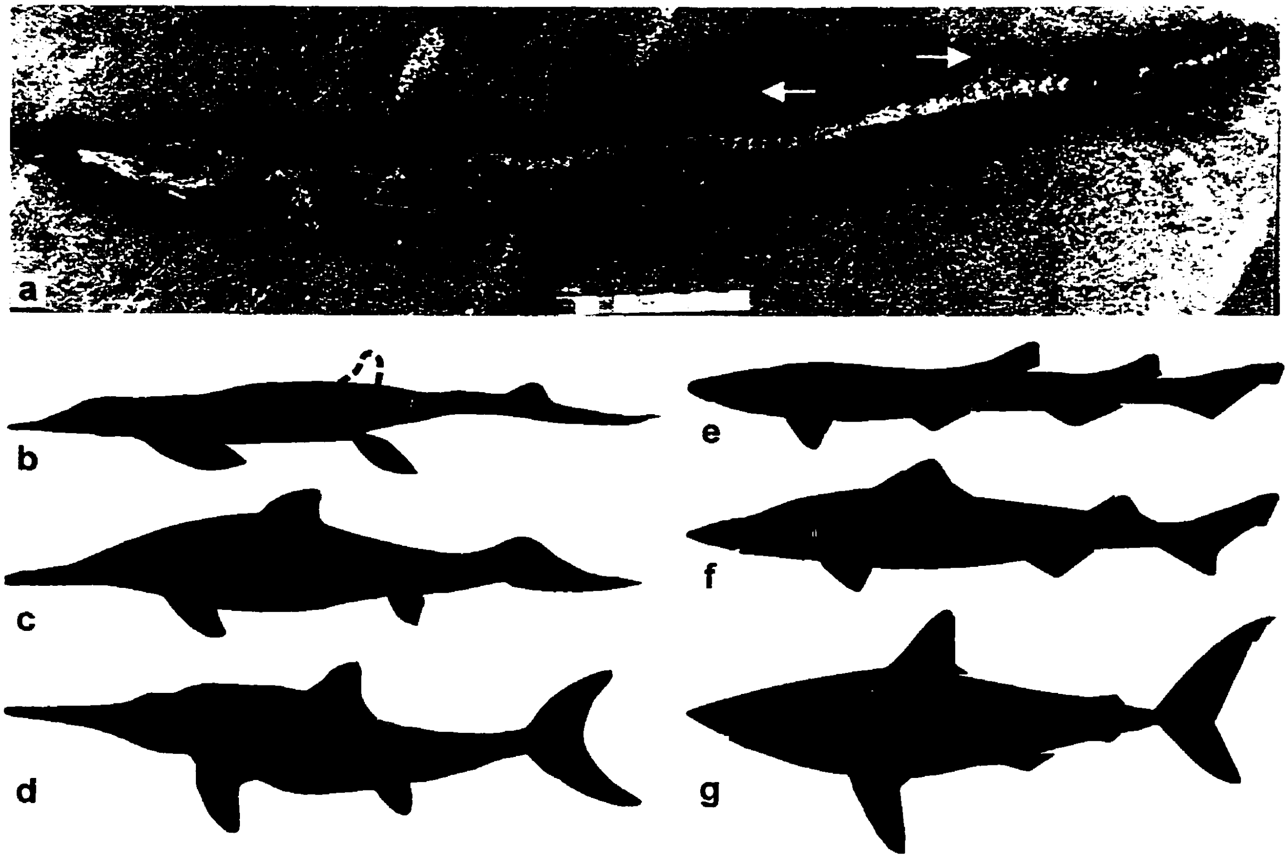
Ichthyosaurs are extinct marine reptiles, probably belonging to the Diapsida (Massare and Callaway, 1990), that ranged from the Early Triassic to Late Cretaceous (Baird, 1984; Callaway and Massare, 1989). Post-Triassic ichthyosaurs achieved the highest level of aquatic adaptation among reptiles (Carroll, 1985), with a streamlined body, lunate tail, and a dorsal fin, features exemplified today by thunniform (tuna-like) fishes (Fig. 11-1D). However, little is known of how such a body plan evolved from a terrestrial diapsid. Here I report the most complete specimen of the oldest known ichthyosaur, Chensaurus, representing a transition between the two body plans. The specimen, which has a partial skin impression, has a small caudal fin, a long and narrow body, and a high presacral vertebral count (Fig. 11-1A). These features all suggest an anguilliform swimming mode. Later ichthyosaurs retained the high vertebral count, but overcame the high swimming costs of this plesiomorphy, achieving a rigid thunniform bauplan by evolving discoidal vertebrae, and a deep fusiform body. Chensaurus therefore appears to be an evolutionary intermediate between the shorter-bodied terrestrial stock from which the group evolved, and advanced thunniform ichthyosaurs.

DESCRIPTION

The specimen was collected in 1989 from the Lower Triassic (Spathian) of Anhui Province, China, about 50 km southwest of the type locality of Chensaurus (Chen, 1985; Mazin

Figure. 11-1. Variation in body form among ichthyosaurs and sharks.

A, The new specimen of Chensaurus chaoxianensis, Wuwei Cultural Relic Administrative Institute, Anhui Province, China (WCRAI 313). The fossil has been cleaved along the sagittal plane, and is disposed on two slabs. The first arrow marks the position of a feature of uncertain identity (dorsal fin or hind fin), the second arrow marks the anterior end of the caudal fin. The body outline is the narrow black zone lying close to the dorsal edge of the vertebral column. It is easiest to see in the region between the arrows. The dark zone lying ventral to the vertebral column is a RECENT artifact (a separator, used during mold making). A fault in the cervical region displaced the skull and the first several vertebrae relative to the body. Scale bar 10 cm. B, reconstruction of WCRAI 313. Paired fins added from a smaller specimen, scaled to appropriate size. The questionable feature is depicted by the broken line. Note the narrow body and small caudal fin. C, Reconstruction of Mixosaurus cornalianus, modified from Kuhn-Schnyder (1974). The trunk is fusiform but the caudal fin is similar to that of Chensaurus. D, Stenopterygius quadriscissus, Paleontologiska Museet, Uppsala Universitet (PMU R158). Body outline preserved as a carbonaceous film, showing deep fusiform body, lunate tail and dorsal fin. E, Asymbolus vincenti, a scyliorhinid shark with a body outline resembling Chensaurus. F, Centrophorus harrisoni, a squalid shark similar in shape to Mixosaurus. G, Lamna nasus, a lamnid shark whose body plan is similar to Stenopterygius. E-G modified from Last and Stevens (1994).


a
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e
f
g

et al., 1991), which is also Spathian (You, 1992). Based on overall similarities, the specimen is tentatively identified as Chensaurus chaoxianensis (Chen) 1985. Its most remarkable feature is its slender trunk region (Fig. 11-1A), rare among ichthyosaurs. This slenderness is not a post-mortem artifact, because the gastralia are preserved in situ, the articulated series lying parallel to the vertebral column. Also noteworthy is that the body outline is partially preserved in the dorsal region. The outline of the caudal fin is the best preserved, located immediately dorsal to a change in orientation of the neural spines (Fig. 11-1A).

DISCUSSION

Sharks and ichthyosaurs are similar in that their vertebral columns continue into one of the caudal fin lobes: the upper and lower lobes respectively (McGowan, 1992). Also, they both have high precaudal vertebral counts (usually 60-110), in contrast to scombrid fishes (about 40), and cetaceans (usually 40-60). Sharks evolved several body forms, some of which are also found in ichthyosaurs (Fig. 11-1). Because of these similarities, sharks provide the best analogue for ichthyosaurs in overall body shape and locomotion, although differing in details.

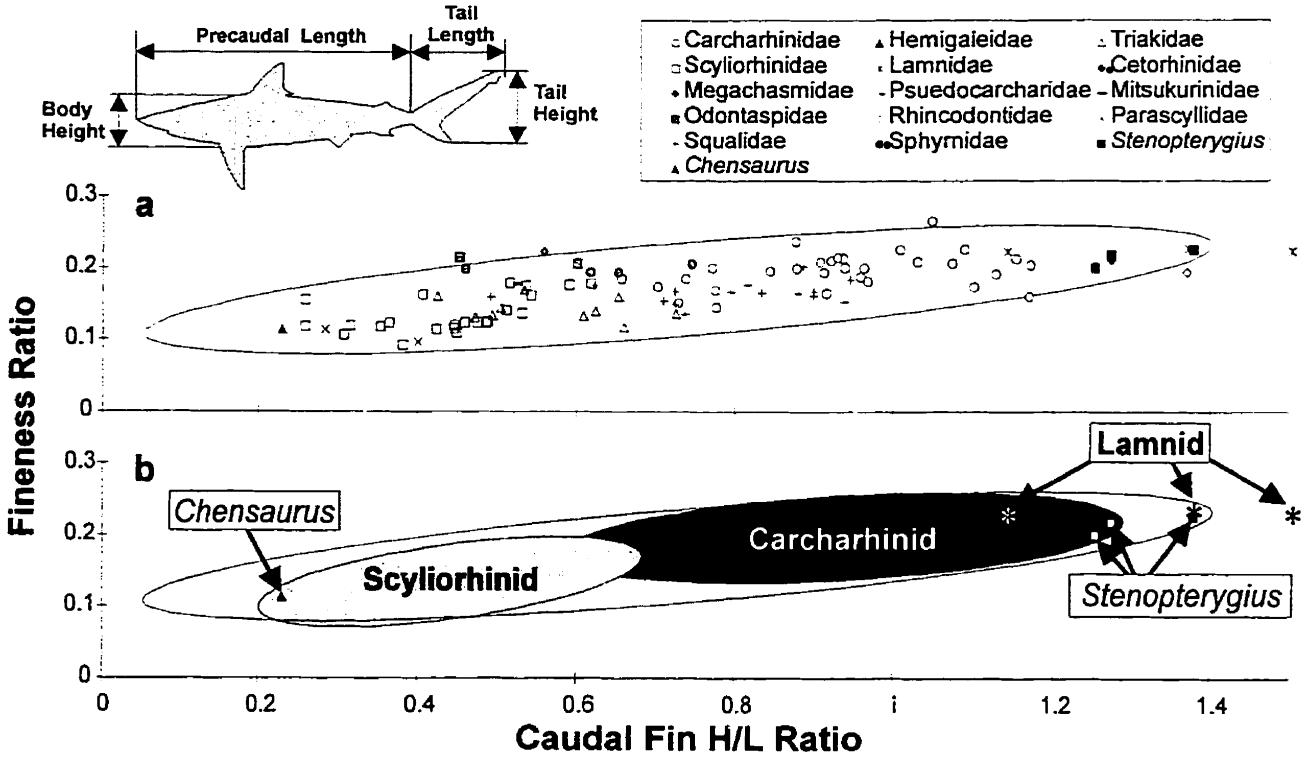
Vertebrates that swim by lateral undulations of the body may be described as anguilliform, sub-carangiform, carangiform, and thunniform, according to the proportion of the body utilized for the propulsion (highest in anguilliform and lowest in thunniform, see Webb and Blake [1985]). These modes are also associated with body shape, ranging from the elongate and flexible anguilliform swimmers to the deep and more rigid-bodied thunniform ones, as noted among teleosts and sharks (Webb and Keyes, 1982). Sharks range from being anguilliform to thunniform (McGowan, 1992), though some authorities avoid these categories, preferring to use informal groups defined on shape (Thomson and Simanek, 1977). The variation in body and tail shape among sharks is considerable, and I used two indices to quantify this: fineness ratio (precaudal length/body height) and tail H/L (tail height/length; Fig. 11-2A). These indices are positively correlated (r= 0.70; Fig. 11-2A) and show a trend from the more anguilliform sharks, as exemplified by scyliorhinids, to the more thunniform ones, like lamnids (Fig. 11-2B). Two ichthyosaur genera were added to the data: Stenopterygius (Fig. 11-1D), a typical post-Triassic form, interpreted as adapted for fast cruising (McGowan, 1992; Webb, 1988; Massare, 1988); and Chensaurus (Fig. 11-1B). Stenopterygius groups with the lamnid sharks, while Chensaurus lies at the extreme end of the scyliorhinid distribution, suggesting it was anguilliform, and a forerunner of the advanced thunniform ichthyosaurs.

Anguilliform swimming requires body flexibility, which is enhanced by high vertebral counts. The presacral count of C. chaoxianensis is about 40, some 50 percent higher than that of most limbed terrestrial amniotes, both living and extinct (Romer, 1956; Hoffestetter and Gasc, 1969). Most later ichthyosaurs have 40-50 presacrals (McGowan, 1974a, 1974b, 1979) except for long-bodied shastasaurids with approximately 65 (Merriam, 1908; Kosch, 1990). The presacral count of C. chaoxianensis is therefore already within the range of typical ichthyosaurs. This suggests that a high presacral count appeared early in ichthyosaurian evolution, as an adaptation for anguilliform swimming, and was retained in later forms.

The optimum efficiency of thunniform swimmers is achieved by a stiff body, limiting lateral propulsive movements to the caudal fin. Body stiffness is enhanced by restricting the degree of flexion between adjacent vertebrae. For ichthyosaurs, which have amphicoelous vertebrae, intervertebral flexion was probably largely a function of the thickness and compliance of the intervertebral discs. From simple geometry, the maximum angular displacement between adjacent vertebral centra decreases with increasing diameter, other

Figure. 11-2. The correlation between body shape and tail shape in sharks.

A, 95 % confidence ellipse fitted to data for 94 species, belonging to 14 families, ($r=0.70$, $^{**}P<0.01$; r for the population estimated at 0.58-0.80, $^{*}P<0.05$). Data were obtained by taking measurements from published figures (Hauff and Hauff, 1981; Last and Stevens, 1994). The boundary between precaudal and caudal regions was determined according to a published method (Springer and Garrick, 1964). B, Same as a, but for ease of comparison only three shark families are depicted. It was not plausible to fit a 95% confidence ellipse to the lamnid data because of the small sample size. Note that the ichthyosaurs, Chensaurus and Stenopterygius, lie at the two extremes of the shark distributions.

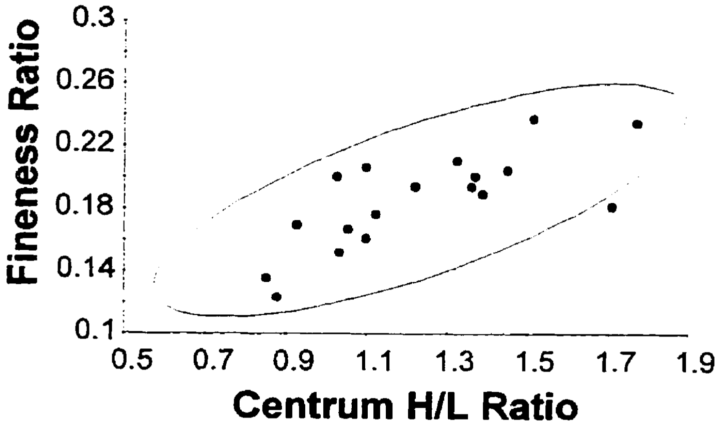

Precaudal Length
Tail Length
Body Height
Tail Height
Carcharhinidae
Scyliorhinidae
Megachasmidae
Odontaspidae
Squalidae
Chensaurus
Hemigaleidae
Lamnidae
Psuedocarcharidae
Rhincodontidae
Sphyrnidae
Triakidae
Cetorhinidae
Mitsukurinidae
Parascyllidae
Stenopterygius
a
b
Lamnid
Chensaurus
Carcharhinid
Scyliorhinid
Stenopterygius
Fineness Ratio
0
0.1
0.2
0.3
0
0.2
0.4
0.6
0.8
1
1.2
1.4
Caudal Fin H/L Ratio

dimensions remaining the same. C. chaoxianensis, and other Early Triassic ichthyosaurs, have cylindrical centra, but they became taller and wider in later forms, culminating in the discoidal centra typical of most ichthyosaurs. The depth of the centrum can be expressed by the ratio of centrum height to length (H/L). The ratio has values of 0.9 for C. chaoxianensis, 1.8 for M. cornalianus (Middle Triassic) and 2.5 for S. quadriscissus (Lower Jurassic). Ichthyosaurs therefore appear to have overcome the problem of retaining their high presacral counts—the antithesis of rigidity—by evolving deep discoidal centra. Associated with this change was a deepening of the body. Riess (1986) described Mixosaurus as an anguilliform swimmer, but his argument only establishes that they were axial swimmers, which accords with my hypothesis.

The only living animals with comparable centra are sharks, whose fossilized vertebrae are sometimes confused with those of ichthyosaurs. Sharks, as noted, usually have precaudal counts similar to ichthyosaurs. Significantly, the deeper bodied sharks tend to have the deepest centra (Fig. 11-3), with the exception of those with unusual precaudal counts. Thus the centrum H/L ratio for scyliorhinid sharks average about 0.8, compared with 2.0 for lamnids (Riess, 1986). This supports my contention that the evolution of a deep, fusiform body, typical of post-Triassic ichthyosaurs, was predicated upon the evolution of discoidal vertebrae. Anthracosaurs also have discoidal vertebrae, but their body plan is not comparable to that of ichthyosaurs: presence of both intercentra and pleurocentra resulted in about 80 joints in the presacral region, contributing flexibility to their presumed anguilliform locomotion.

Figure.11-3 The correlation between body shape and centrum shape in sharks.

Data for 18 species belonging to 6 families were obtained from the literature (Springer and Garrick, 1964; Last and Stevens, 1994), ($r=0.74$, $^{**}P<0.01$; r for the population estimated at 0.41-0.91, $^{*}P<0.05$). Two species, Prionace glauca (blue shark) and Eusphyrna blochii (winghead shark), are unusual in precaudal count, hence were not included: blue shark has about 146 precaudals, almost 52 percent more than average carcharhinid sharks, and winghead shark has about 50, nearly 47 percent less than average hammerhead sharks. Measurements for ichthyosaurs were taken for posterior dorsal vertebrae; those for sharks were for penultimate monospondylous vertebrae (Springer and Garrick, 1964).


Fineness Ratio
0.3
0.26
0.22
0.18
0.14
0.1
0.5
0.7
0.9
1.1
1.3
1.5
1.7
1.9
Centrum H/L Ratio

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CHAPTER 12

PHYLOGENY OF TRIASSIC ICHTHYOSAURS

ABSTRACT

A phylogenetic hypothesis for Triassic ichthyosaurs is proposed, for the first time based on cladistic analyses of discrete osteological characters. The order Ichthyosauria is explicitly shown to be monophyletic, again for the first time; at least nine characters support its basal node. Jurassic ichthyosaurs form a clade with Norian (Late Triassic) forms (Ichthyosauridae), which in turn forms a clade with *Toretocnemus* (Ichthyosauroidea). The sister group of the Ichthyosauroidea is the Mixosauroidea, comprising three species of *Mixosaurus*, and these two constitute the Ichthyosauriformes. The Shastasauriformes is the sister group of the Ichthyosauriformes, and these two form a clade encompassing all Middle Triassic and later ichthyosaurs, the Euichthyosauria. The relationships among Early Triassic ichthyosaurs, comprising the stem group of the Ichthyosauria, remains partially unresolved, but *Utatsusaurus hataii* and *Parvinatator wapitiensis* seems to be more basal than *Grippia longirostris* and *Chaohusaurus geishanensis*.

INTRODUCTION

The Order Ichthyosauria comprises aquatic reptiles with fish-like body shapes. Although they have been known to the scientific community for over 180 years, their internal phylogeny, and their phylogenetic position among amniotes, have yet to be established. They have been assumed to be monophyletic, but it has not been explicitly known what characters support the basal node of the Order.

The present study constitutes the first attempt to propose a phylogenetic hypothesis for Triassic ichthyosaurs, based on a cladistic analysis of a data matrix comprising discrete osteological characters. Also, this study establishes the monophyly of the Ichthyosauria, based on an explicit statement of the characters supporting its basal node. Such a study was previously impossible, because our knowledge on the earliest ichthyosaurs, from the Lower Triassic, was very limited. However, recent reexamination of these forms (Motani, 1996, 1997; Motani et al., 1996; Chapters 2-9) has clarified many of their characteristics, and, therefore, it is high time to conduct a phylogenetic analysis.

BRIEF HISTORICAL REVIEW

Prior to my study, there have been various attempts to resolve the interrelationships among ichthyosaurs. Early attempts include Baur (1887), Lydekker (1888), Merriam (1902, 1908), von Huene (1916, 1922, 1951, 1956), and Kuhn (1934), but the phylogenies they proposed were based on a few subjectively selected characters that they believed were phylogenetically important. The digital count of the forefin was considered especially important, and based on this character, it was generally accepted that the Ichthyosauria could be divided into a dichotomous grouping of narrow-finned (longipinnate) and wide-finned (latippinate) forms. More recently, McGowan (1972a) and Appleby (1979) presented versions of ichthyosaurian phylogeny, but they still followed the traditional dichotomy of latipinnates and longipinnates. It should be noted that the species level taxonomy of ichthyosaurs was not well established at that point, causing much difficulty.

The phylogenetic study of ichthyosaurs drastically changed after a series of studies by McGowan (1972b, 1974a,b, 1976, 1979), who made enormous contributions to the basic taxonomy of ichthyosaurs. He revised the species level taxonomy of all Jurassic and later ichthyosaurs, where many ambiguous species had been proposed over 150 years. He also gave phenograms for Jurassic and later ichthyosaurs (McGowan, 1974a,b, 1976, 1979), introducing the notion of objective taxonomy for the first time. He was also the first to show that the dichotomous division of ichthyosaurs into latipinnates and longipinnates is not well supported (McGowan, 1976).

Mazin (1982) was the first to introduce the notion of shared derived characters into ichthyosaurian phylogenetics. However, he did not use a falsifier based on parsimony, or probabilistic theories, to select among competing hypotheses. Instead, he depicted a tree of unknown derivation, to the nodes of which he assigned one or two shared derived characters to support them (Mazin, 1982:fig. 7). This tree was largely based on a belief that ichthyosaurs primitively possessed a durophagous dentition, a concept provocated by Peyer (1968) and followed by Mazin (1981). His phylogeny is therefore rather subjective in selection and polarization of characters, and largely disagrees with the result of the analyses described herein. He also did not establish the monophyly of ichthyosaurs.

Nicholls et al. (in press:fig. 14) also gave a phylogenetic tree for basal ichthyosaurs, recognizing the importance of shared derived characters in phylogenetic reconstruction. However, the derivation of this tree is also unknown. Nicholls et al. (in press) considered that durophagy is primitive for ichthyosaurs, and therefore their tree also reflects this subjective selection and polarization of characters.

The first and last truly cladistic study of ichthyosaurs was conducted by Callaway (1989), but only for the family Shastasauridae. Nevertheless, this was a large step in the study of ichthyosaurian phylogenetics. Using 33 osteological characters for seven ingroup and two outgroup taxa (Grippia and Petrolacosaurus), Callaway (1989) obtained a single tree. He did not include Mixosaurus or Jurassic ichthyosaurs in his data matrix, assuming that the Shastasauridae, sensu Callaway (1989), is monophyletic. It will be shown, however, that his Shastasauridae is actually polyphyletic, some of its members being more closely related to Mixosaurus and Jurassic ichthyosaurs than to Shastasaurus.

MATERIALS AND METHODS

Abbreviations for the institutions are: PMU, Paleontologiska Museet, Uppsala Universitet, Uppsala; UCMP, University of California, Museum of Paleontology, Berkeley.

The characters for all ichthyosaurian taxa were coded, based on personal examination of specimens, except for Cymbospondylus buchseri, which was coded based on the primary literature (Sander, 1989). Four outgroup taxa were coded, based on the primary literature, namely Petrolacosaurus kansensis (Reisz, 1981), Claudiosaurus germaini (Carroll, 1981), Hovasaurus boulei (Currie, 1981), and Hupehsuchus nanchangensis (Carroll and Dong, 1991).

MacClade 3.06 was used for constructing the character matrix, which contains 60 osteological characters for 15 ingroup and four outgroup taxa. The analyses were performed using PAUP 3.1.1 (Swofford, 1993), and also Hennig 86 1.5 (Farris, 1988) for confirmation. All characters were treated as unordered. The branch and bound (Hendy and Penny, 1982) option of PAUP, and the implicit enumeration option of Hennig 86 were used for searching for the most parsimonious tree(s). The latter option is guaranteed to find the most parsimonious tree(s) efficiently, therefore it is neither truly exhaustive, nor heuristic: it has been mathematically proven that there are no heuristic search methods that always find the most parsimonious tree(s) (Foulds et al., 1979). Therefore the “ie” command is likely to be Farris' own implementation of the branch and bound algorithm (Such is in conformity with Felsenstein's (1992) remark that Farris claimed that he introduced the notion of branch and bound to systematic biology earlier than Hendy and Penny [1982]). Polymorphic characters were coded as “?” for the analyses with Hennig 86, because the program does not allow multiple entries per character per taxon. The two Macintosh programs, PAUP and MacClade, were ran on Pentium PCs, using Executor 2.0, a Macintosh emulation program for PCs. This emulator was confirmed to work properly by reanalyzing published data matrices of Hillis et al. (1992), Rieppel (1993, 1994) and Caldwell (1996) using PAUP, and obtaining the same results as in the literature.

To test how well the obtained nodes represent the data, bootstrap frequency for the nodes (Felsenstein, 1985) were calculated using Heyjoe 3.0 (2/28/97 release) in Random Cladistics package (Siddal, 1994). The command line “outgroup= 0 1 2 3;cc -.;ie*;” was used to search for the most parsimonious tree(s) while ”outgroup= 0 1 2 3;cc -.;ie*;n;” was used for bootstrap searches, and 500 replicates were made for each analysis. This program was selected over the bootstrap option of PAUP 3.1 because it calculates the bootstrap frequency for each node in the most parsimonious tree(s), instead of constructing a bootstrap tree, which may contain a clade that does not exist in the most parsimonious topologies. Jacknife monophyly values were also calculated using Lanyon 2.0 in the Random Cladistics package. The command line used is “cc -.;ie;” in all searches performed.

The use of these statistical methods is based on the understanding that the character parsimony method is best justified as an approximation of a simple maximum likelihood method under the statistical framework, although the traditional philosophical justification for the parsimony method is almost equally plausible (see Appendix for details). Bootstrapping of phylogenetic data, first proposed by Felsenstein (1985), has been criticized as being statistically biased by various authors, but Efron et al. (1996) showed that these criticisms missed the point. Efron et al. (1996) also showed that bootstrap frequencies, sensu Felsenstein (1985), approximate the true confidence limit at the first order, although the accuracy can be improved with a more complicated algorithm. Decay analysis (Bremer, 1994) was not performed because it is not acceptable under the traditional justification of parsimony, and is inferior to jacknifing and bootstrapping under the statistical justification (see Appendix).

NEW TAXONOMIC DESIGNATION

The following two new taxonomic designations were made before conducting a phylogenetic analysis. This is because accurate taxonomy at the species level is prerequisite for a reasonable cladistic analysis.

Toretocnemus zitteli.—Merriamia zitteli and Toretocnemus californicus, from the Upper Triassic of California, are herein considered conspecific, because there are insufficient data to distinguish the two. These two genera were originally distinguished by Merriam (1903) based on two characters: 1) presence of two separate rib facets on a centrum in the pelvic region of T. californicus; and 2) the forefin is longer than the hindfin in M. zitteli while they are nearly equal in T. californicus. However, my examination of the type of M. zitteli (UCMP 8099) revealed that there were no pelvic centra, therefore the first character is invalid. Moreover, the presence of two rib facets on pelvic centra is not exceptional for ichthyosaurs: it is at least known for Mixosaurus cornalianus (Middle Triassic) and for Jurassic ichthyosaurs, although lacking in Cymbospondylus petrinus (Middle Triassic). The type of M. zitteli possesses two well-articulated fins side by side, but in different planes, which were identified as the forefin and hindfin of one individual by Merriam (1903). However, it is not possible to establish that these fins belong to one individual because of the unusual preservation, where partially articulated bones are three-dimensionally scattered. It is even possible that the two fins are the forefins of two different individuals. Accordingly, Merriam's (1903) second distinguishing character is also invalid. On the other hand, the two holotypes share many characteristics, such as the shape of the fins and the height/length ratio of the dorsal centra (of about 1.8, which is shared with Mixosaurus). The specimens were also collected from nearby localities within a single horizon. The generic name Toretocnemus Merriam 1903 has a priority over Merriamia Boulenger 1904, therefore the name for this species should be Toretocnemus zitteli.

Shonisaurus.—Callaway and Massare (1989a) assigned a group of specimens from a single Upper Triassic quarry in Mexico (UCMP 27141-6) to Shastasaurus altispinus. There were two reasons for this assignment: 1) the shape of the rib facets on UCMP 27142, an anterior dorsal centrum, is similar to that of Shastasaurus altispinus (UCMP 9083); 2) UCMP 27146, a fin element with a notch, resembles that of UCMP 9083. I have questioned this taxonomic treatment, pointing out that these two elements also resemble those of another Late Triassic ichthyosaur, Shonisaurus popularis (Chapter 1). I also pointed out that the following two features of UCMP 27141 are not known in Shastasaurus, but are known in Shonisaurus: 1) the absence of a dental groove; 2) a posteriorly elongated premaxilla separating the nasal from the external naris (Chapter 1).

A further examination of the specimens of Shastasaurus and Shonisaurus revealed an additional feature that is characteristic of Shonisaurus, namely the possession of very short vertebral centra, with height/length ratios of about 3.0, in the dorsal region. Such short dorsal centra are not found in any other ichthyosaurs except Ophthalmosaurus, from the Upper Jurassic. The specimens of Shastasaurus osmonti (UCMP 9076) and Shastasaurus altispinus (UCMP 9083) both have longer centra than Shonisaurus, with h/l ratios of about 1.9-2.2. UCMP 27142, an anterior dorsal centrum, is short as in Shonisaurus, with the h/l ratio of 3.2 (the maximum diameter was used instead of the height, because the specimen is distorted). Therefore, the UCMP 27142-6 complex probably represents a small Shonisaurus, rather than a Shastasaurus. It should be noted that the maximum diameter of UMCP 27142 is 111 mm, which is about half of the average of the same measurements for Shonisaurus popularis. It cannot be determined whether these specimens represent a small individual of Shonisaurus popularis, or a distinctive small species of the genus.

ANALYSIS

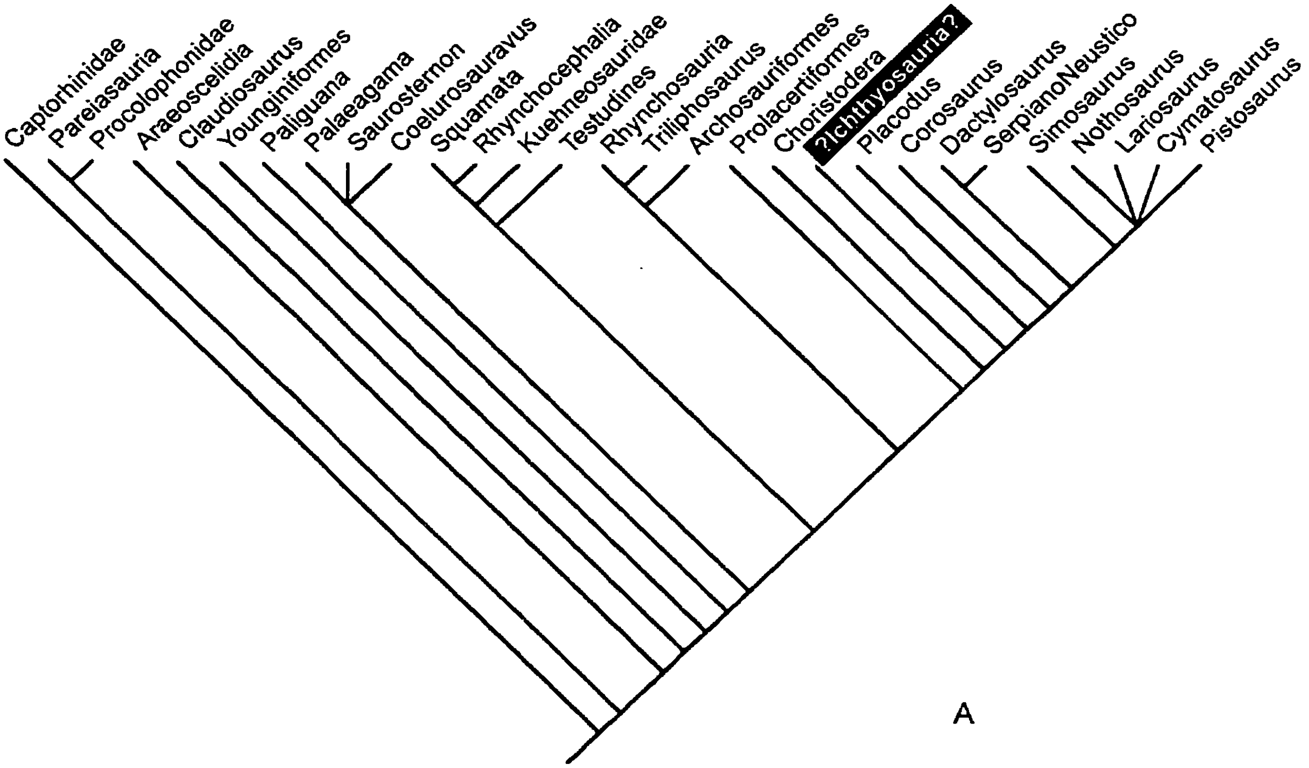
Ingroup selection—Fourteen better known taxa of Triassic ichthyosaurs, and one Jurassic ichthyosaur, are designated as the ingroup. These are: Utatsusaurus hataii, Grippia longirostris, Parvinatator wapitiensis, Chaohusaurus geishanensis (Early Triassic), Mixosaurus cornalianus, M. atavus, M. nordenskioeldii, Cymbospondylus petrinus, Cymbospondylus buchseri (Middle Triassic), Shastasaurus, Shonisaurus popularis, Hudsonelpidia brevirostris, Toretocnemus zitteli, Ichthyosaurus(?) janiceps (Late Triassic), and Ichthyosaurus communis (Early Jurassic). Shastasaurus from California comprises several very poorly known species that probably represent one species (McGowan, 1994), therefore they are treated as one unit, together with a Canadian species Shastasaurus neoscapularis.

Outgroup selection—The position of the Ichthyosauria within the Amniota is far from well established, causing difficulty in selecting the outgroup for the present analysis. Therefore, a preliminary phylogenetic analysis was conducted to find a suitable outgroup. The character matrix of Caldwell (1996), containing 93 characters for 29 taxa, was reanalyzed, with different character codings for the Ichthyosauria. PAUP 3.1.1 (Swofford, 1993) was used, with the same options as specified by Caldwell (1996), that is, heuristic searches using both TBR and SPR branch swappings, with twenty replicates of randomized additional sequences for each. Thirty equally parsimonious trees were obtained, the strict consensus of which is given in Fig. 12-1B. The tree is similar to the one obtained by Caldwell (1996), depicted here in Fig. 12-1A, except for the position of the Ichthyosauria.

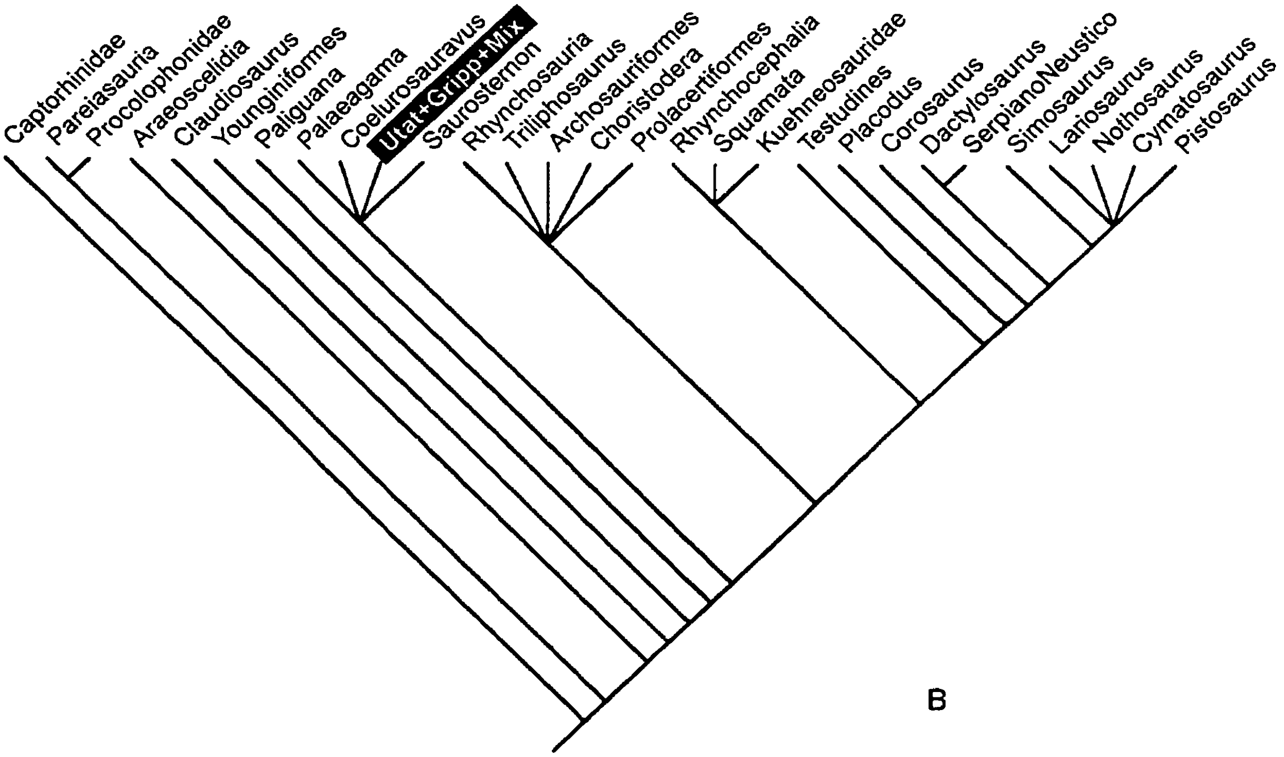
The new character coding used in the above analysis is mainly based upon two undescribed skeletons of Utatsusaurus hataii, and upon newly redescribed specimens of Grippia longirostris (Chapter 3, 8). These two species, both from the Lower Triassic, are not only the oldest known ichthyosaurs, but also seem least derived among ichthyosaurs in the morphology of the skull (Chapter 7, 8), forefin (Chapter 6), and vertebral centra (Chapter 11). The hindfin of Mixosaurus nordenskioeldii (PMU R187) from the Middle Triassic, was also used, because the hindfin is insufficiently known in any Early Triassic ichthyosaurs. The new character coding disagrees with that of Caldwell (1996) in about one third of the characters used. Caldwell's (1996) character coding was based mainly on the specimens of Parvinatator wapitiensis (see Chapter 9 for new taxonomic designation) and on the literature. The specimens of P. wapitiensis, however, were previously misinterpreted (Chapter 9). Therefore the present character coding more accurately represents the morphology of early ichthyosaurs.

Figure 12-1. Hypotheses regarding the phylogenetic position of the Ichthyosauria among diapsids.

A, a diapsid phylogeny proposed by Caldwell (1996), the strict consensus of 27 equally parsimonious trees (L 402,CI 0.567). B, a phylogenetic hypothesis obtained from a re-analysis of Caldwell's (1996) matrix, with different coding for ichthyosaurs (abbreviated as Utat+Gripp+Mix). The strict consensus of 30 equally parsimonious trees (L 391, CI 0.575). See text for interpretation.


Captorhinidae
Pareiasauria
Procolophonidae
Araeoscelidia
Claudiosaurus
Younginiformes
Paliguana
Palaeagama
Saurosternon
Coelurosauravus
Squamata
Rhynchocephalia
Kuehneosauridae
Testudines
Rhynchosauria
Triliphosaurus
Archosauriformes
Prolacertiformes
Choristodera
?Ichthyosauria?
Placodus
Corosaurus
Dactylosaurus
SerpianoNeustico
Simosaurus
Nothosaurus
Lariosaurus
Cymatosaurus
Pistosaurus

A


Captorhinidae
Pareiasauria
Procolophonidae
Araeoscelidia
Claudiosaurus
Younginiformes
Paliguana
Palaeagama
Coelurosauravus
Utat+Gripp+Mix
Saurosternon
Rhynchosauria
Triliphosaurus
Archosauriformes
Choristodera
Prolacertiformes
Rhynchocephalia
Squamata
Kuehneosauridae
Testudines
Placodus
Corosaurus
Dactylosaurus
SerpianoNeustico
Simosaurus
Lariosaurus
Nothosaurus
Cymatosaurus
Pistosaurus

B

Ichthyosaurs formed a clade with poorly known basal diapsids (Fig. 12-1B), namely *Palaeagama*, *Saurosternon*, and *Coelurosauravus*, but the monophyly of this clade is poorly supported. Moreover, the fossil records for these taxa are so incomplete that there are large numbers of missing entries for their character states. I therefore interpret Fig. 12-1B as indicating a non-neodiapsid affinity for the Ichthyosauria, rather than its close relationship with these three taxa. Considering inadequate data for these three taxa, I conclude that better known basal diapsids should be used as the outgroup in the analyses of the internal phylogeny of the Ichthyosauria. Three outgroup taxa were selected from basal diapsids in Fig. 12-1B: *Petrolacosaurus kansensis* (Araeoscelidia), *Claudiosaurus germaini*, and *Hovasaurus boulei* (Younginiformes). *Thadeosaurus calcanapi*, a more terrestrial younginiform than *H. boulei*, was also included in the outgroup initially, but it was subsequently removed because more than half of its characters were unknown. *Hupehsuchus nanchangensis*, an enigmatic aquatic reptile from the Middle Triassic of China, was also added to the outgroup, because of its similarities with ichthyosaurs (Carroll and Dong, 1991).

Character Description

Sixty osteological characters were used, many of which concern the skull and forefin. No hindfin characters were included in this main analysis because the hindfins are very poorly known for most ichthyosaurs. Only those characters that are cladistically informative (sensu Steel et al. [1993], who established that cladistically uninformative characters are phylogenetically informative) for establishing the internal phylogeny, or the monophyly, of the Ichthyosauria were used. The character matrix is given in Table 1.

1. Premaxilla, posterior end.—(0) concave, forming the anterior margin of the external naris; (1) pointed, scarcely entering the external naris; (2) straight, separating the nasal from the

external naris. Unlike in other ichthyosaurs and basal diapsids, the premaxilla of Mixosaurus has a pointed posterior end that hardly enters the anterior margin of the external naris. Mazin (1981) reconstructed a similar posterior end for the premaxilla of Grippia longirostris, but it is incorrect (Chapter 8). Cymbospondylus petrinus, and possibly Shonisaurus popularis (Camp, 1980), has a posteriorly elongated premaxilla that separates the nasal from the external naris. Callaway (1989) argued that Shastasaurus also has such a premaxilla, but the specimen upon which he based his argument cannot be assigned to Shastasaurus, as discussed earlier.

2. Maxilla, dorsal lamina.—(0) absent; (1) present. The dorsal lamina of the maxilla overlies the lacrimal along the posterior margin of the external naris in Early and Middle Triassic ichthyosaurs. The dorsal lamina of the maxilla also appeared in archosaurs, but in association with the antorbital fenestra, and therefore does not cover the lacrimal.
3. External naris, orientation.—(0) dorso-lateral; (1) lateral. In derived ichthyosaurs, the external naris appears very narrow from the dorsal view, due to its lateral orientation. In basal diapsids and Early Triassic ichthyosaurs, the external naris is equally visible from the dorsal and lateral aspects.
4. Prefrontal-postfrontal contact.—(0) absent, the dorsal margin of the orbit being formed by the frontal; (1) present, forming the dorsal margin of the orbit. The prefrontal and postfrontal do not meet in basal diapsids and Early Triassic ichthyosaurs. In Middle Triassic and later ichthyosaurs, the two bones meet dorsal to the orbit, eliminating the frontal from the orbital margin.

Table 12-1. Data matrix

```
                                      11111111112222222222333333
Taxon                        12345678901234567890123456789012345
----------------------------------------------------------------
Petrolacosaurus kansensis    00000000000000000000000000000000000
Claudiosaurus germaini       01000000000000001000000000000000001
Hovasaurus boulei            ???0000000001?0010????????00?00000?
Hupehsuchus nanchangensis    10?10?0000001???20????????1????010?
Utatsusaurus hataii          010011001000011001?1010000000110100
Grippia longirostris         0100110110000???0?111110001?0110101
Parvinatator wapitiensis     ?1?0?1?????????????1000???????????0
Chaohusaurus geishenensis    ???????????????????11?0????00?10101
Cymbospondylus petrinus      21111111111001??21100002201?1110101
Cymbospondylus buchseri      ???1111???0?????????00??????1?11110
Mixosaurus cornalianus       11111111212111?????0110100110110101
Mixosaurus atavus            11111111212111112112000??011???????
Mixosaurus nordenskioeldii   ????????2?2?????2?12201110?1??10101
Shastasaurus                 0?111110111001??2110000???1?1211110
Shonisaurus popularis        2?????????1???????100??220??1211110
Toretocnemus zitteli         ??????????????????100000?1???220?0?
Hudsonelpidia brevirostris   ??????????????????????????????20201
Ichthyosaurus(?) janiceps    0011111???????????1000000???2220201
Ichthyosaurus communis       00111112020111112010000001122220201


                             3333444444444455555555556  Coded
Taxon                        6789012345678901234567890  chars
-------------------------------------------------------------
Petrolacosaurus kansensis    0000000000000000000000000  60/60
Claudiosaurus germaini       0000000000000000000000000  60/60
Hovasaurus boulei            000000000?000?000000000?0  43/60
Hupehsuchus nanchangensis    ?000000001000001000010000  41/60
Utatsusaurus hataii          1100000010101000000010001  59/60
Grippia longirostris         010000001020100?00???00??  49/60
Parvinatator wapitiensis     11000000?010?01??????????  21/60
Chaohusaurus geishenensis    010000001?2010??????10001  28/60
Cymbospondylus petrinus      ?1001000???????1100021001  49/60
Cymbospondylus buchseri      ?1002000????1???????21???  23/60
Mixosaurus cornalianus       1100200010211011001011111  55/60
Mixosaurus atavus            ?????????????????????????  26/60
Mixosaurus nordenskioeldii   11001000102111110010?1111  41/60
                                       2
Shastasaurus                 12012001213230111000?1???  49/60
                                         1
Shonisaurus popularis        ?2012000??3?????100021?0?  30/60
Toretocnemus zitteli         ?1102101113230110000?????  30/60
Hudsonelpidia brevirostris   121021101?3221112101??1??  25/60
                                     2  2
Ichthyosaurus(?) janiceps    111021111032211??????????  36/60
                                     2  2
Ichthyosaurus communis       1220221000322111210111002  60/60
                                      1
```

5. Postfrontal, posterior process.—(0) absent; (1) present, overlying the postorbital. A distinctive posterior process of the postfrontal is one of the synapomorphies for all ichthyosaurs.
6. Postorbital shape.—(0) triradiate; (1) lunate. The postorbital of basal diapsids is triradiate, the posterior process forming the bar between the upper and lower temporal fenestrae. In ichthyosaurs, the postorbital is lunate, without having a distinct posterior process.
7. Postorbital, participation in the upper temporal fenestra.—(0) present; (1) absent. The postorbital forms the antero-lateral margin of the upper temporal fenestra in basal diapsids, which is also true for Early Triassic ichthyosaurs, although the postorbital is partially overlapped by the posterior process of the postfrontal. In derived ichthyosaurs, the postfrontal completely eliminates the postorbital from the upper temporal fenestra.
8. Squamosal, participation in the upper temporal fenestra.—(0) present; (1) absent; (2) squamosal lost. The squamosal enters the upper temporal fenestra in basal diapsids and Utatsusaurus (Chapter 7:fig. 7-2). In other ichthyosaurs, it is eliminated from the margin of the fenestra (Chapter 8:fig. 8-2; Chapter 10:fig. 10-3), or the bone itself is lost (Chapter 10).
9. Anterior terrace of upper temporal fenestra.—(0) absent; (1) present, but small, reaching the posterior part of the frontal anteriorly; (2) present, and large, reaching the nasal anteriorly.
10. Pineal foramen margin.—(0) formed by parietal; (1) formed by parietal and frontal; (2) formed only by frontal. The pineal foramen is enclosed between the parietals in basal diapsids and early ichthyosaurs. In most derived ichthyosaurs, it is on the border of the parietal and frontal (Chapter 10:fig. 10-3). In Ichthyosaurus, the foramen is entirely enclosed between the frontals (Sollas, 1916; McGowan, 1973).

11.Sagittal crest.—(0) absent; (1) present, but small, involving only the parietal; (2) present, and large, involving the parietal, frontal, and nasal. The parietals of some ichthyosaurs (e.g., Cymbospondylus petrinus) are nearly vertical along the median line, forming a small crest. A large sagittal crest, reaching the nasal, is a characteristic of Mixosaurus.

12.Parietal ridge.—(0) absent; (1) present. The parietal ridge (sensu McGowan, 1973) is a feature that is only present in derived ichthyosaurs.

13.Parietal supratemporal process.—(0) short; (1) long. The supratemporal process of the parietal, a postero-lateral process that forms the postero-medial margin of the upper temporal fenestra, is short in Petrolacosaurus and in derived ichthyosaurs (Chapter 10:fig. 10-3). It is long in Claudiosaurus and early ichthyosaurs (Chapter 7:fig. 7-2; Chapter 8:fig. 8-2).

14.Supratemporal posterior slope.—(0) absent; (1) present. In basal diapsids, the supratemporal is a small element without any distinct morphological feature. In ichthyosaurs, the bone is U-shaped in the dorsal view, with a slope on the postero-dorsal corner (Chapter 7, 10). This posterior slope is small in Utatsusaurus (Chapter 7:fig. 7-3), but well developed in Mixosaurus (Chapter 10:figs. 10-1, 3) and in Ichthyosaurus (McGowan, 1973), forming a partial roof over the upper temporal fenestra.

15.Supratemporal posterior ridge.—(0) absent; (1) present. The posterior ridge (Chapter 7: fig. 7-3) of the supratemporal is present in all ichthyosaurs with a known supratemporal (Chapter 10), but absent in basal diapsids.

16.Supratemporal ventral process.—(0) absent; (1) present. The ventral process of the supratemporal is known in some derived ichthyosaurs, such as Mixosaurus (Chapter 10: fig. 10-1) and Ichthyosaurus (McGowan, 1973).

17.Pterygoid, transverse flange.—(0) antero-lateral; (1) postero-lateral; (2) not well defined. The transverse flange of the pterygoid is antero-laterally oriented in Petrolacosaurus, Claudiosaurus, Utatsusaurus (Chapter 7: fig. 10-4), and in Grippia (Wiman, 1933:pl. 1, fig. 6). It is not well defined in later ichthyosaurs, and is postero-laterally oriented in other basal diapsids.

18.Interpterygoidal vacuity.—(0) present; (1) absent, or extremely reduced.

19.Plicidentine.—(0) absent; (1) present. The presence of folded dentine walls in the teeth, without secondary embayments, is characteristic of ichthyosaurs (Chapter 1). It is paralleled by varanid lizards.

20.Tooth horizontal section.—(0) circular; (1) disto-medially compressed; (2) laterally compressed. Early Triassic ichthyosaurs have disto-mesially compressed teeth (Motani, 1996:fig. 3). Laterally compressed teeth are only known in Mixosaurus (Chapter 10) among the ingroup taxa.

21.Posterior tooth crown.—(0) conical; (1) rounded; (2) flat. Ichthyosaurs usually have conical teeth in the posterior part of the jaws. Some Triassic ichthyosaurs (viz., Chaohusaurus geishanensis, Grippia longirostris, and Mixosaurus cornalianus) have rounded tooth crowns posteriorly, which are as high as they are wide. M. nordenskioeldii has flat tooth crowns that are much wider than high.

22.Tooth size relative to the skull width.—(0) normal (over 0.1); (1) small (below 0.05). This character is based on Massare's (1987) index to express the size of the teeth relative to the gullet width (substituted by skull width). There seems to be a clear dichotomy in the distribution of this feature among ichthyosaurs. The possession of small and numerous teeth is typical of some Early Triassic ichthyosaurs (Motani, 1996, 1997), and Mixosaurus cornalianus (Chapter 10).

23.Maxillary tooth row.—(0) single; (1) multiple. Grippia longirostris has two maxillary tooth rows, and the lingual row seems to comprise replacement teeth for the labial one (Motani, 1997). Mixosaurus nordenskioeldii has three tooth rows (Nicholls et al., in press). It is not known whether tooth replacement occurred, as in Dracaena guianensis (Dalrymple, 1979), or whether additional lingual rows were added throughout life, as in Captorhinus aguti (Ricqlès and Bolt, 1983).

24.Upper dental groove.—(0) present throughout jaw margin; (1) only present anteriorly; (2) absent. A dental groove, homologous to that of the subthecodont condition in primitive amniotes, exists in most ichthyosaurs (Chapter 1). Mixosaurus differs from others in having no dental groove in the maxilla (Chapter 1). Cymbospondylus petrinus and Shonisaurus popularis have no dental groove in the upper jaw (Chapter 1).

25.Lower dental groove.—(0) present throughout jaw margin; (1) only present anteriorly; (2) absent. The lower dental groove shows a different character-state distribution than its upper counterpart (Chapter 1), and is therefore treated as a separate character.

26.Bony fixation of teeth.—(0) present; (1) absent.

27.Pterygoidal teeth.—(0) present; (1) absent. Pterygoidal teeth are absent from ichthyosaurs, except in Utatsusaurus hataii, which has vestigial teeth on the pterygoid.

28.Interclavicle shape.—(0) cruciform; (1) triangular; (2) T-shaped. T-shaped interclavicles appeared in ichthyosaurs in the Jurassic (or Late Triassic). Triangular ones are typical of Mixosaurus.

29.Scapula, anterior margin.—(0) continuously fan-shaped; (1) fan-shaped distally and emarginated proximally; (2) straight, being covered with perichondral bone. In basal diapsids, and in early ichthyosaurs, the anterior margin of the scapula ossification (or the corresponding part of the scapulocoracoid) is smoothly curved, forming a complete fan without any emargination. In shastasaurids, the fan is emarginated proximally, but there seems to be no perichondral bone along the emargination. In Jurassic, and some Late Triassic ichthyosaurs, the scapula blade is straight, with perichondral ossification covering the anterior margin.

30.Scapula and coracoid ossifications.—(0) fused to form scapulocoracoid; (1) separate, being weakly articulated except near glenoid; (2) separate, being articulated with each other by a large articular facet.

31.Humerus, distal articular facets.—(0) not terminal; (1) terminal, radial facet being larger than ulnar facet; (2) terminal, two facets being nearly equal. The distal articular facets of the humerus are not terminal in basal diapsids, but they are terminal in all ichthyosaurs. The radial facet is larger than the ulnar one in most Triassic ichthyosaurs, but the two facets are nearly equal in some Triassic and in all Jurassic ichthyosaurs (Chapter 6:figs. 6-1, 2).

32.Humerus, head orientation.—(0) proximal; (1) dorsal. The head of the humerus is oriented roughly proximally in most basal diapsids and ichthyosaurs. Shastasaurids, however, have a humeral head that is directed completely dorsally (Chapter 6:fig. 6-1).

33.Humerus, anterior flange.—(0) absent; (1) present and complete; (2) present but reduced proximally. No basal diapsids have an anteriorly expanded bony flange on the humerus. All ichthyosaurs have the anterior flange of the humerus, although it may be reduced proximally in some forms (Chapter 6:fig. 6-1). Hupehsuchus nanchangensis was described as having the anterior flange of the humerus (Carroll and Dong, 1991), but the bone identified as the humerus is more likely a scapulo-coracoid (coded according to the literature).

34.Humerus, relative width exclusive of anterior flange.—(0) longer than wide; (1) wider than long. Shastasaurids have a short and robust humerus that is not known in other ichthyosaurs (Chapter 6:figs. 6-1, 2).

35.Humerus, distal and proximal ends, exclusive of anterior flange.—(0) nearly equal; (1) distal end wider than proximal end. Only Petrolacosaurus, Utatsusaurus (Motani, in press), Parvinatator (Chapter 9:fig. 3), and derived shastasaurids (Chapter 6:fig. 6-2), have equally sized proximal and distal ends of the humerus.

36.Propodial + epipodial versus manus length.—(0) propodial + epipodial longer; (1) manus longer. Utatsusaurus, Parvinatator, and most outgroup taxa have the primitive state.

37.Radius, peripheral perichondral bone loss.— (0) none; (1) partial; (2) complete. The peripheral and inter-elemental perichondral bones became reduced in two separate phases through ichthyosaurian evolution (Chapter 6). Also, these two phases started asynchronously in various elements (Chapter 6). Therefore, peripheral and inter-elemental perichondral bone reductions in various elements are treated as separate characters. Although the degree of reduction can best be described as a continuous transformation series, such a character is not suitable for cladistic analyses. Therefore each of these characters are given only three discrete states.

38.Radius, inter-elemental perichondral bone loss.—(0) none; (1) partial; (2) complete. See character 37 and Chapter 6 (fig. 6-7).

39.Radius/ulna relative size.—(0) nearly equal; (1) radius much larger than ulna. This feature is independent of character 37, because a large ulna may have small articulation with the humerus. Enlarged radius is one of the feature characteristic of Shastasaurus and Shonisaurus.

40.Ulna, peripheral perichondral bone loss.—(0) none; (1) partial; (2) complete. See character 37 and Chapter 6 (fig. 6-7).

41.Ulna, inter-elemental perichondral bone loss.—(0) none; (1) partial; (2) complete. See character 37 and Chapter 6 (fig. 6-7)..

42.Epipodial elements.—(0) longer than wide; (1) wider than long. Epipodial elements are generally shorter in later ichthyosaurs. However, because the length/width ratios of radius and ulna show a continuous distribution among various ichthyosaurs, it is difficult to delineate between different states. The ratio seems to be roughly correlated with the degree of perichondral bone loss, therefore it would be redundant to make a separate character describing the details of length/width ratio variation. Accordingly I only give two discrete states to the present character, which is independent of the degree of perichondral bone loss.

43.Radiale, perichondral bone.—(0) absent; (1) preaxially present. Some Late Triassic and later ichthyosaurs developed perichondral ossification along the anterior margin of the radiale and the carpal distal to it (Chapter 6:fig. 6-7). These perichondral ossifications appear as notches along the anterior margin.

44.Ulnare/intermedium relative size.—(0) ulnare larger than intermedium; (1) intermedium larger than ulnare; (2) intermedium lost.

45.Manual pisiform.—(0) present; (1) absent.

46.Metacarpal I peripheral perichondral bone loss.—(0) none; (1) partial; (2) complete; (3) digit I lost. See character 37 and Chapter 6 (fig. 6-7).

47.Metacarpal III inter-elemental perichondral bone loss.—(0) none; (1) partial; (2) complete. See character 37 and Chapter 6 (fig. 6-7).

48.Metacarpal V perichondral bone loss.—(0) none; (1) peripherally complete; (2) complete; (3) metacarpal V not ossified.

49.Manual accessory digit VI.—(0) absent; (1) present.

50.Maximum phalangeal count.—(0) five or less; (1) seven or more.

51.Iliac blade.—(0) present; (1) absent.

52.Pubis, obturator foramen.—(0) closed; (1) open; (2) part of obturator fossa. One possible problem of this character is the distinction between states (0) and (1), because the obturator foramen is incompletely closed in small juveniles of Hovasaurus boulei while fully closed in larger specimens (Currie, 1982). However, no fully closed obturator foramina are known for Shastasaurus, Shonisaurus, or Cymbospondylus, although known specimens are unlikely to be small juveniles.

53.Pubis, styloidal or plate-like.—(0) plate-like; (1) styloidal.

54.Pubis/ischium relative size.—(0) nearly equal or ischium slightly larger than pubis; (1) pubis twice as large as ischium. An enlarged pubis, which is twice as large as the ischium, is characteristic of Mixosaurus.

55.Ischium, styloidal or plate-like.—(0) plate-like; (1) styloidal. This character is independent of character 54.

56.Presacral count.—(0) 30 or less; (1) between 40 and 50; (2) 55 or more. The holotype of Cymbospondylus buchseri is posteriorly incomplete, preserving only 51 of the presacral vertebrae. The 51st rib, however, is as long as the more anterior ribs, indicating that the pelvic girdle lies well posterior to this vertebrae (ribs become gradually shorter anterior to the pelvic girdle in all known ichthyosaurs. Therefore, C. buchseri was coded "2".

57.Posterior dorsal centra shape.—(0) cylindrical; (1) discoidal. The posterior dorsal centra are cylindrical in most amniotes, except in derived ichthyosaurs which have thin, discoidal centra.

58.Anterior dorsal neural spine.—(0) normal; (1) narrow, high, and straight. Anterior dorsal neural spines of most ichthyosaurs are similarly shaped, although there are some variations. Mixosaurus differs from others in having narrow, high neural spine that are almost perpendicular to the vertebral column.

59.Mid-caudal centra height.—(0) no increase; (1) remarkable increase. Rapid increase of the centra height in the mid-caudal region is characteristic of Mixosaurus.

60.Caudal fin.—(0) absent; (1) upper lobe supported by well developed neural spines; (2) with tailbend and low neural spines, suggesting a lunate caudal fin.

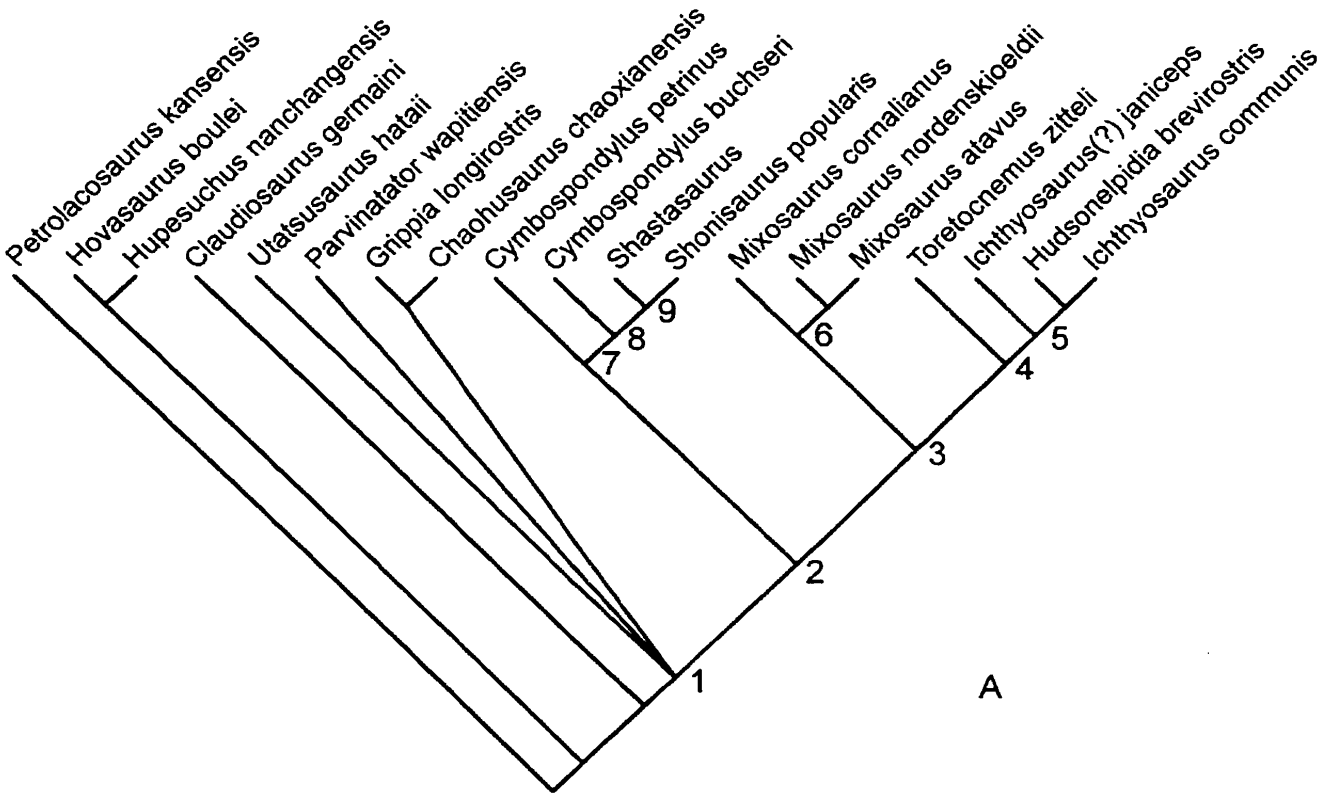
RESULTS

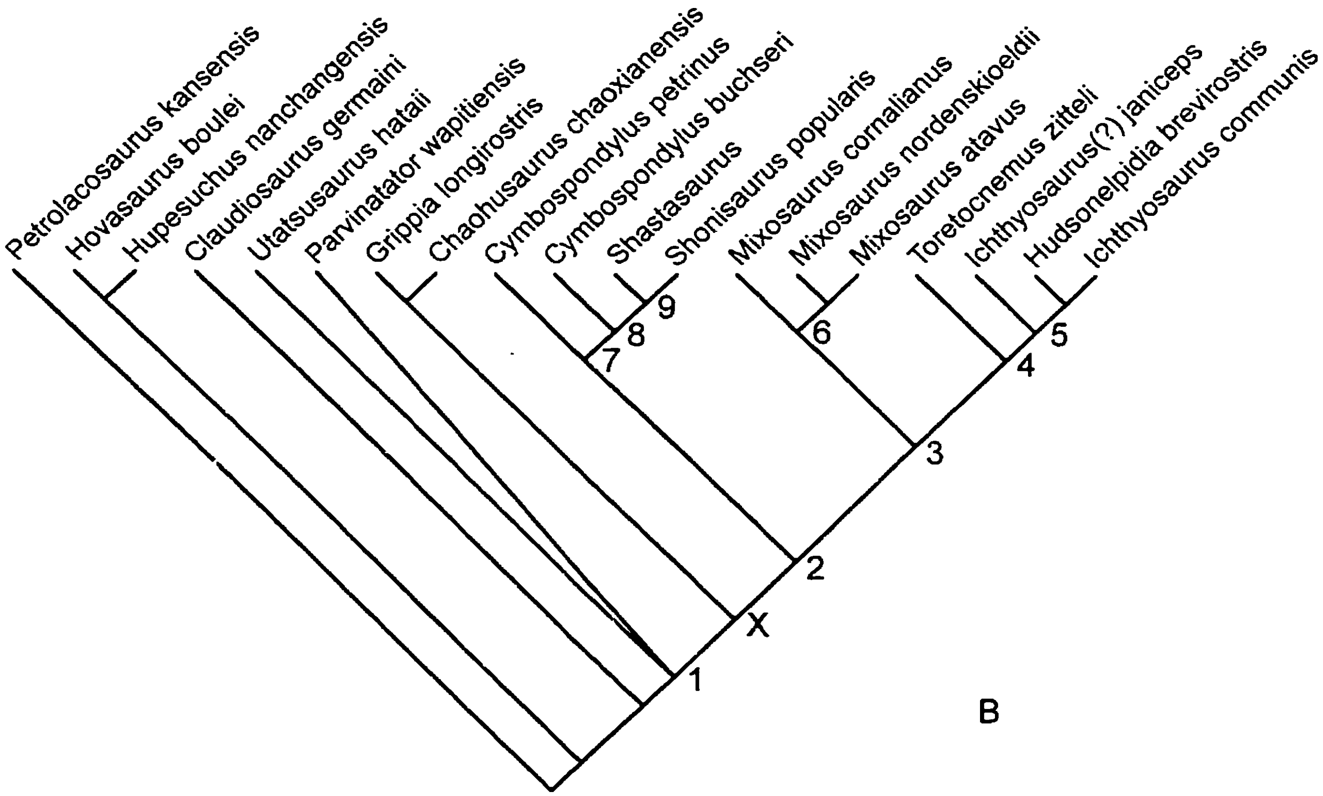
Initial Analysis

Both PAUP 3.1 and Hennig 86 found four equally parsimonious trees with the tree length of 129, when considering the polymorphic entries (122 without). The consistency index was 0.736, while the retention index was 0.813. The strict consensus of the four is given in Fig. 12-2A, which lacks resolution among Early Triassic ichthyosaurs, but which is fully resolved for Middle Triassic and later forms. The relationships among the outgroup taxa should not be inferred from Fig. 12-2A, because only those characters that are informative for the ingroup monophyly, and its internal phylogeny, were included in the analyses. It should be noted that

Figure 12-2. Phylogenetic hypotheses obtained from the current analyses.

A, the strict consensus of four equally parsimonious trees (L 129, CI 0.729) obtained from the initial analysis. B, the strict consensus of three equally parsimonious trees (L 129, CI 0.729) obtained from the second analysis. Numbered nodes define the following clades: 1, Ichthyosauria; 2, Euichthyosauria; 3, Ichthyosauriformes; 4, Ichthyosauroidea; 5, Ichthyosauridae; 6, Mixosauroidea; 7, Shastasauriformes; 8, Shastasauroidea; 9, Shastasauridae; 10, Grippidia. X represents the weakly supported node discussed in the text. Relationships among the outgroup taxa should not be inferred from these trees.


Petrolacosaurus kansensis
Hovasaurus boulei
Hupesuchus nanchangensis
Claudiosaurus germaini
Utatsusaurus hataii
Parvinatator wapitiensis
Grippia longirostris
Chaohusaurus chaoxianensis
Cymbospondylus petrinus
Cymbospondylus buchseri
Shastasaurus
Shonisaurus popularis
Mixosaurus cornalianus
Mixosaurus nordenskioeldii
Mixosaurus atavus
Toretocnemus zitteli
Ichthyosaurus(?) janiceps
Hudsonelpidia brevirostris
Ichthyosaurus communis
9
8
7
6
5
4
3
2
1
A


Petrolacosaurus kansensis
Hovasaurus boulei
Hupesuchus nanchangensis
Claudiosaurus germaini
Utatsusaurus hataii
Parvinatator wapitiensis
Grippia longirostris
Chaohusaurus chaoxianensis
Cymbospondylus petrinus
Cymbospondylus buchseri
Shastasaurus
Shonisaurus popularis
Mixosaurus cornalianus
Mixosaurus nordenskioeldii
Mixosaurus atavus
Toretocnemus zitteli
Ichthyosaurus(?) janiceps
Hudsonelpidia brevirostris
Ichthyosaurus communis
9
8
7
6
5
4
3
2
X
1
B

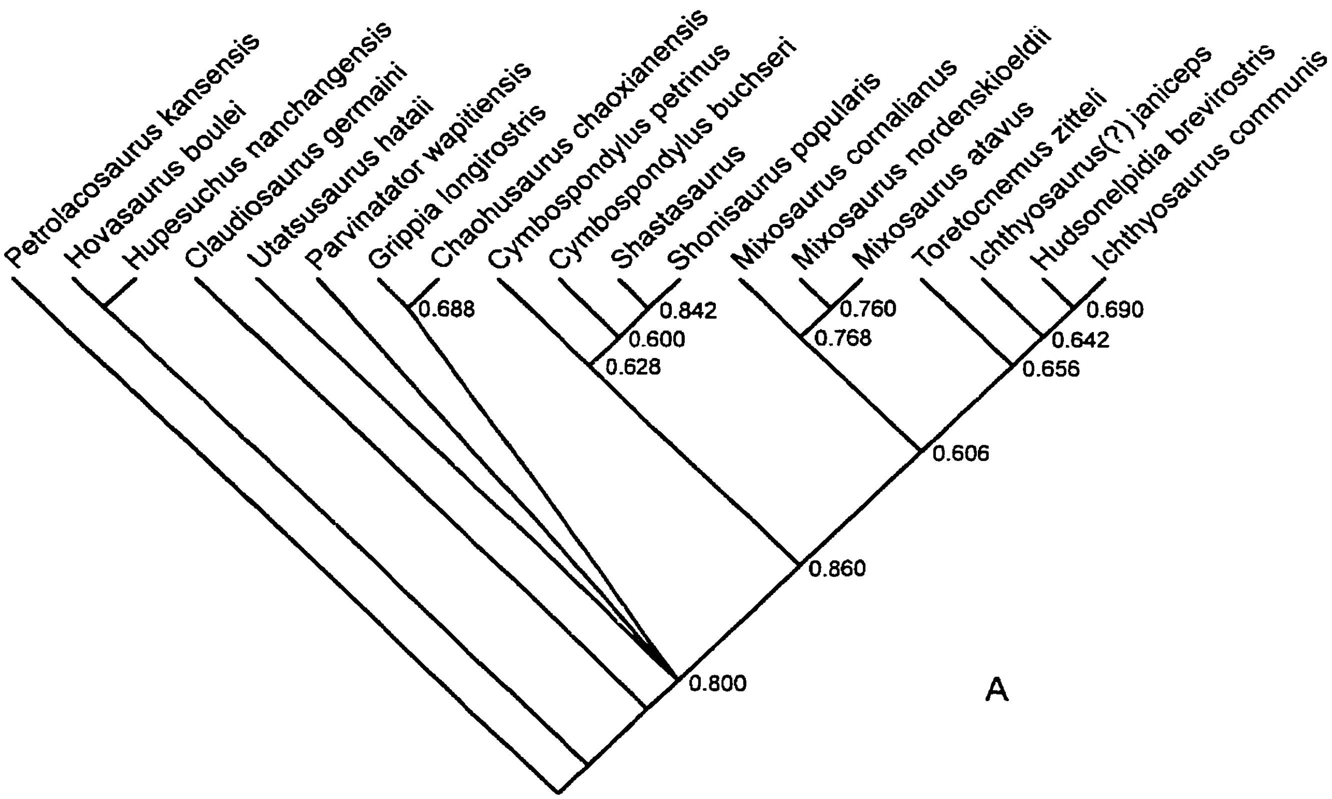
there is a limitation to the accuracy of this tree, because the character matrix contains a high number of missing entries, due to incompleteness of the fossil record. Bootstrap frequencies and jacknife monophyly values for each node of this tree are given in Fig. 12-3A and 4A, respectively.

Second Analysis

The missing entries caused one clear problem in the most parsimonious character optimization in the first analysis. In one of the most parsimonious trees, metacarpal I was reconstructed to be unambiguously lost for the clade defined by the node 2 (Fig. 12-2), and reappeared in Mixosaurus. However, this is because the character states for the two species of Cymbospondylus were coded as "?", although they most likely had the first digit: phalanges of C. buchseri are much narrower than proximal carpals, which is a common feature among pentadactyl ichthyosaurs, namely Mixosaurus and Early Triassic ichthyosaurs. When coding the two species of Cymbospondylus as having a lunate metacarpal I, as in Mixosaurus and Grippia, the inferred phylogeny slightly changed. Both PAUP and Hennig 86 now gave three equally parsimonious trees, with a length of 129, and the consistency and retention indices were 0.736 and 0.815, respectively. All three were among the most parsimonious topologies in the previous analysis, and the tree that disappeared is the one that was causing the problem in the character optimization. The strict consensus of the three trees (Fig. 12-2B) has a better resolution for Early Triassic ichthyosaurs than Fig. 12-2A, due to the absence of the fourth topology. Bootstrap frequencies and jacknife monophyly values for each node of this tree are given in Fig. 12-3B and 4B, respectively.

Figure 12-3. Bootstrap frequencies for the nodes in Fig. 12-2.

Based on 500 replicates of non-heuristic searches. Values were calculated using Heyjoe 3.0 in the Random Cladistics package.


Petrolacosaurus kansensis
Hovasaurus boulei
Hupesuchus nanchangensis
Claudiosaurus germaini
Utatsusaurus hataii
Parvinatator wapitiensis
Grippia longirostris
Chaohusaurus chaoxianensis
Cymbospondylus petrinus
Cymbospondylus buchseri
Shastasaurus
Shonisaurus popularis
Mixosaurus cornalianus
Mixosaurus nordenskioeldii
Mixosaurus atavus
Toretocnemus zitteli
Ichthyosaurus(?) janiceps
Hudsonelpidia brevirostris
Ichthyosaurus communis
0.688
0.842
0.600
0.628
0.760
0.768
0.690
0.642
0.656
0.606
0.860
0.800
A

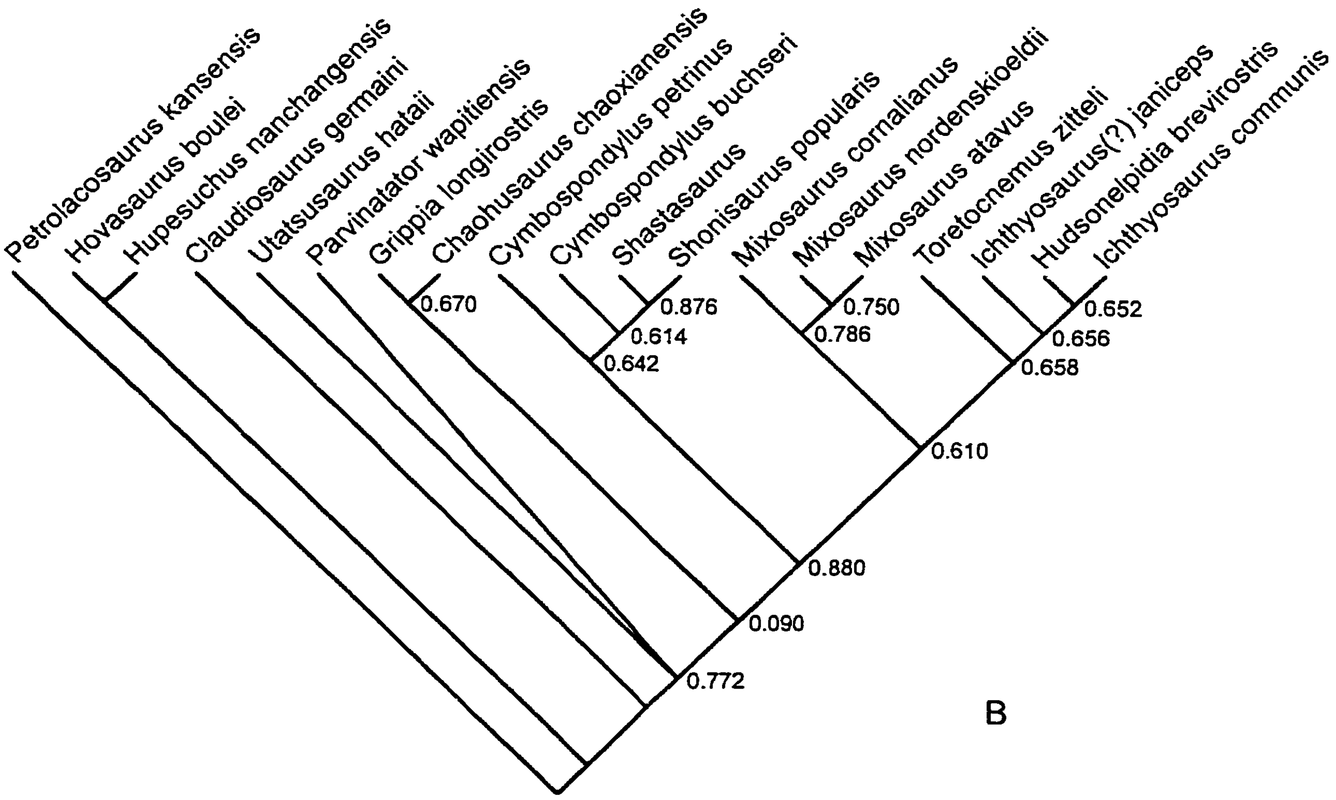
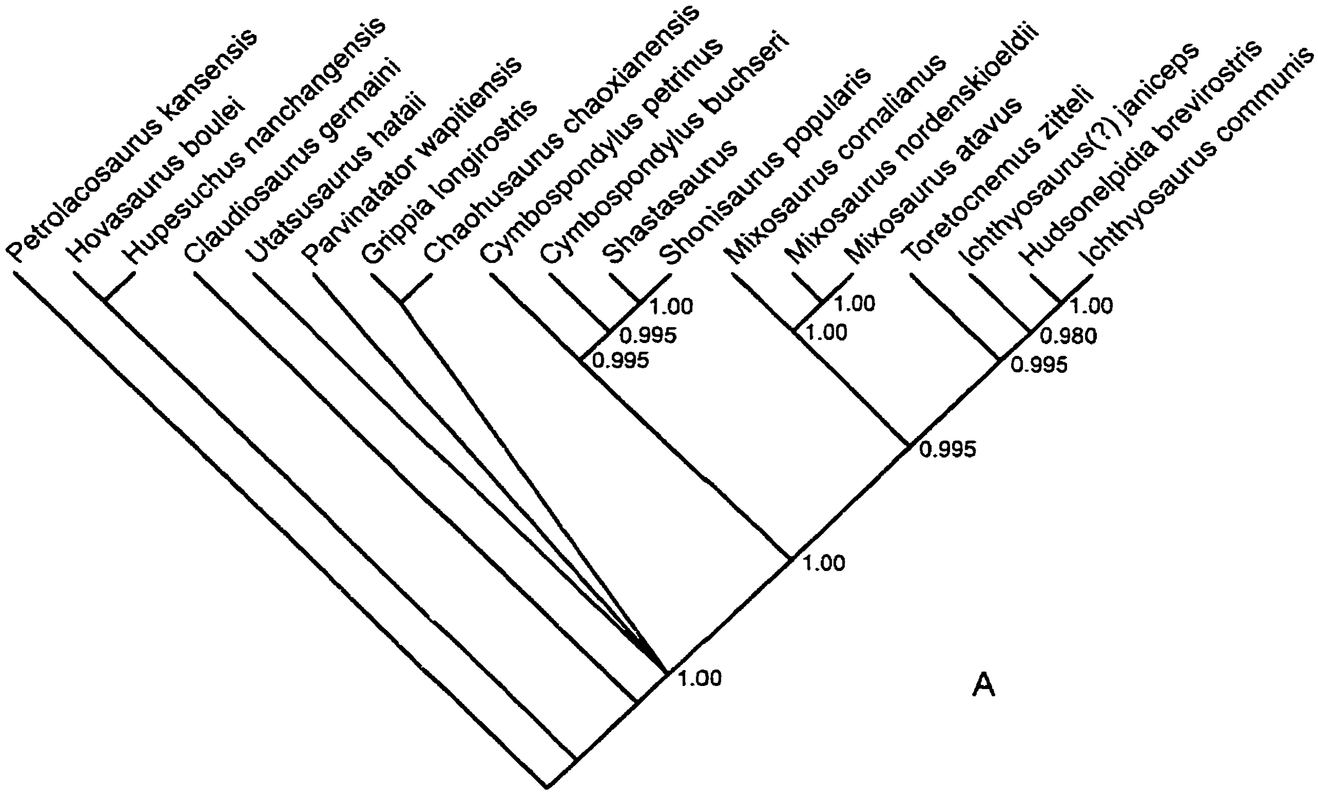
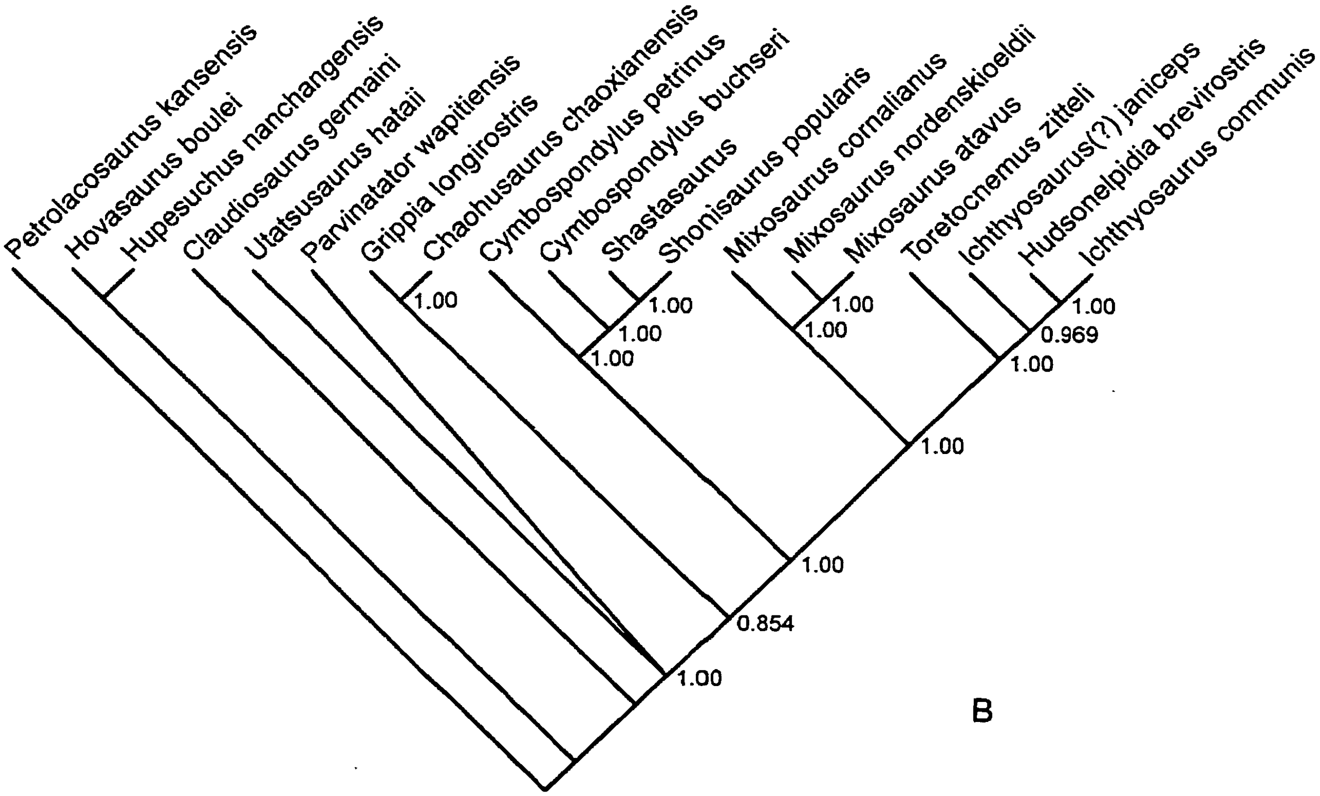

Petrolacosaurus kansensis
Hovasaurus boulei
Hupesuchus nanchangensis
Claudiosaurus germaini
Utatsusaurus hataii
Parvinatator wapitiensis
Grippia longirostris
Chaohusaurus chaoxianensis
Cymbospondylus petrinus
Cymbospondylus buchseri
Shastasaurus
Shonisaurus popularis
Mixosaurus cornalianus
Mixosaurus nordenskioeldii
Mixosaurus atavus
Toretocnemus zitteli
Ichthyosaurus(?) janiceps
Hudsonelpidia brevirostris
Ichthyosaurus communis
0.670
0.876
0.614
0.642
0.750
0.786
0.652
0.656
0.658
0.610
0.880
0.090
0.772
B

Figure 12-4. Jacknife monophyly indices for the nodes in Fig. 12-2.

Values were calculated using Lanyon 2.0 in the Random Cladistic package, with a non-heuristic search option.


Petrolacosaurus kansensis
Hovasaurus boulei
Hupesuchus nanchangensis
Claudiosaurus germaini
Utatsusaurus hataii
Parvinatator wapitiensis
Grippia longirostris
Chaohusaurus chaoxianensis
Cymbospondylus petrinus
Cymbospondylus buchseri
Shastasaurus
Shonisaurus popularis
Mixosaurus cornalianus
Mixosaurus nordenskioeldii
Mixosaurus atavus
Toretocnemus zitteli
Ichthyosaurus(?) janiceps
Hudsonelpidia brevirostris
Ichthyosaurus communis
1.00
0.995
0.995
1.00
1.00
1.00
0.980
0.995
0.995
1.00
1.00

A


Petrolacosaurus kansensis
Hovasaurus boulei
Hupesuchus nanchangensis
Claudiosaurus germaini
Utatsusaurus hataii
Parvinatator wapitiensis
Grippia longirostris
Chaohusaurus chaoxianensis
Cymbospondylus petrinus
Cymbospondylus buchseri
Shastasaurus
Shonisaurus popularis
Mixosaurus cornalianus
Mixosaurus nordenskioeldii
Mixosaurus atavus
Toretocnemus zitteli
Ichthyosaurus(?) janiceps
Hudsonelpidia brevirostris
Ichthyosaurus communis
1.00
1.00
1.00
1.00
1.00
1.00
1.00
0.969
1.00
1.00
1.00
0.854
1.00

B

Discussion

Jackknifing of the data matrix showed that the removal of Cymbospondylus petrinus or Mixosaurus cornalianus resulted in higher numbers of equally parsimonious trees, while removal of other taxa did not cause a profound effect on the number (Table 2). Chaohusaurus geishanensis, Cymbospondylus buchseri, Hudsonelpidia brevirostris, and Mixosaurus atavus have missing entries in more than half of their characters, but it is likely that these missing entries did not mislead the analysis because the obtained topology did not change when each of these taxa was removed. Parvinatator wapitiensis also has a large number of missing entries, and when this species was removed, the number of equally parsimonious trees increased by one. This is because the topology among the outgroup taxa became unstable. Therefore P. wapitiensis may be a key taxon in this particular data set.

Both bootstrap frequencies and jacknife monophyly values show that node X (Fig. 12-2B) is very weakly supported compared to any other nodes, suggesting the relationships among Early Triassic ichthyosaurs require further investigation. However, the monophyly of all Middle Triassic and later ichthyosaurs is strongly supported by both values, and Shastasaurus and Shonisaurus also form a robust clade. Bootstrap frequencies for the Shastasauriformes (Fig. 12-2:7), Mixosauroidea (Fig. 12-2:6), and Ichthyosauroidea (Fig. 12-2:4) are of similar levels (0.635-0.786) in Fig. 12-3B. Although these values are not as high as those for the previous two clades, jacknifing of any single taxon did not collapse these three clades (Fig. 12-4B), therefore they are considered here as moderately well-supported.

There are two discrepancies between the phylogeny suggested by the present analyses and the existing generic level taxonomy. First, the genus Cymbospondylus appeared paraphyletic, therefore a new genus should be designated to accept C. buchseri. Further

Table 12-2. Effect of removing a taxon from the data matrix.

The result was obtained by Lanyon 2.0 in the Random Cladistics package. See text for the distinction between the initial and second analyses. MEPT stands for multiple equally parsimonious trees. Cymbospondylus petrinus and Mixosaurus cornalianus had the largest effect in the number of MEPT (shaded), while other taxa did not have a profound effect. Note that the RI values in this table do not consider polymorphism.

	Initial Analysis			Second Analysis		
DELETED TAXON	Number of MEPT	Length	RI	Number of MEPT	Length	RI
(none)	4	122	80	3	122	80
Utatsusaurus hataii	3	118	81	3	118	81
Grippia longirostris	4	119	80	3	119	80
Parvinatator wapitiensis	5	121	80	5	121	80
Chaohusaurus geishanensis	4	122	80	3	122	80
Cymbospondylus petrinus	13	118	81	24	119	80
Cymbospondylus buchseri	4	121	80	3	121	80
Mixosaurus cornalianus	13	120	79	6	120	79
Mixosaurus atavus	4	122	79	3	122	79
Mixosaurus nordenskioeldii	4	118	80	3	118	80
Shastasaurus	4	116	81	3	116	81
Shonisaurus popularis	4	121	79	3	121	79
Toretocnemus zitteli	4	117	81	3	117	81
Hudsonelpidia brevirostris	4	120	80	3	120	80
Ichthyosaurus(?) janiceps	4	121	80	3	121	80

discussion will be given in the next section. Secondly, *Ichthyosaurus*(?) *janiceps* appeared as the sister group of the clade formed by *Hudsonelpidia brevirostris* and *Ichthyosaurus communis*, therefore it cannot be referred to the genus *Ichthyosaurus*. The forefin of this species has been shown to differ from those of *Ichthyosaurus*, which have 1) digital bifurcation anterior to the primary axis; 2) enlarged ulnare, fifth metacarpal, and fifth digit (Chapter 6). A new genus should be erected for this species.

Toretocnemus zitteli (or its junior synonym, *T. californicus*) has long been recognized as a member of the Shastasauridae, largely because it is from the Carnian (Upper Triassic) of Western North America, where other shastasaurids occur. However, *T. zitteli* is more closely related to Jurassic ichthyosaurs and to *Mixosaurus*, than to *Shastasaurus*. It forms a clade with Jurassic and Norian (Late Triassic) ichthyosaurs, recognized here as the Suprafamily Ichthyosauroidea. One of the synapomorphies for the Ichthyosauroidea is that the distal facets of the humerus are equally sized (character 31), which is not convergent with any other ichthyosaurs.

Hudsonelpidia brevirostris forms a clade with *Ichthyosaurus communis*, but it should be noted that various Jurassic ichthyosaurs were not included in the present analysis. Also, hindfin characters were not included in the analysis, and *H. brevirostris* is characterized by a mosaic of highly derived forefin and rather primitive hindfin characters (McGowan, 1995). It is therefore necessary to conduct another phylogenetic analysis that considers all Jurassic ichthyosaurs before discussing the phylogeny within the Ichthyosauridae.

A summary of the classification is given in Table 12-3.

Table 12-3. Summary of the Classification of the Ichthyosauria.

Numbers in brackets correspond to the node number in Fig. 12-2.

ICHTHYOSAURIA (1)	
Utatsusaurus	U. hataii
Parvinatator	P. wapitiensis
incertae sedis Thaisaurus	T. chonglakmanii
GRIPPIDIA (10)	
Grippia	G. longirostris
Chaohusaurus	C. chaoxianensis
EUICHTHYOSAURIA (2)	
SHASTASAURIFORMES (7)	
Cymbospondylus	C. petrinus
SHASTASAURIOIDEA (8)	
"Cymbospondylus" buchseri	
incertae sedis Pessosaurus	P. polaris
SHASTASAURIDAE (9)	
Shonisaurus	S. popularis
Shastasaurus	S. pacificus
	S. neoscapularis
ICHTHYOSAURIFORMES (3)	
MIXOSAUROIDEA (6)	
Mixosaurus	M. cornalianus
	M. atavus
	M. nordenskioeldii
ICHTHYOSAUROIDEA (4)	
Toretocnemus	T. zitteli
incertae sedis Californosaurus	C. perrini
ICHTHYOSAURIDAE (5)	
Macgowania	M. janiceps
Hudsonelpidia	H. brevirostris
Ichthyosaurus	I. communis
	I. brevirostris
	I. conybeari

(Other post-Triassic forms)

SYSTEMATIC PALEONTOLOGY

ICHTHYOSAURIA Blainville, 1835

Definition.— The last common ancestor of Utatsusaurus, Parvinatator, Grippidia, and Euichthyosauria, and all its descendants.

Diagnosis.—Posterior process of postfrontal present; postorbital lunate, without posterior process; anterior terrace of upper temporal fenestra present(lost in Jurassic forms); supratemporal U-shaped in dorsal view, with posterior slope and ridge; tooth cross-sections wider than long; scapula and coracoid separate in adults; humerus distal facets terminal, radial facet is larger than ulnar one; humerus with anterior flange; radial perichondral bone lost, at least antero-proximally; intermedium larger than ulnare; metacarpal I perichondral bone partially absent; metacarpal V without postaxial perichondral ossification; presacral count 40 or higher; caudal fin with at least dorsal lobe.

Discussion.—Although plicidentine may also be primitive for ichthyosaurs, it did not appear to be unambiguously present for the basal node of the Ichthyosauria, because its presence or absence has not been established for either Utatsusaurus hataii or Parvinatator wapitiensis.

UTATSUSAURUS Shikama, Kamei, and Murata, 1978

Type species: Utatsusaurus hataii Shikama, Kamei, and Murata, 1978

Referred species.—Type species only.

Diagnosis.—Tooth size relative to skull width small (less than 0.05); squamosal participates in upper temporal fenestra; medium-sized ichthyosaur, reaching 3m in total length.

UTATSUSAURUS HATAII Shikama, Kamei, and Murata, 1978

Utatsusaurus hataii Shikama, Kamei, and Murata, 1978: p. 83.

Locality and Horizon.— Lower Triassic (Spathian) of Miyagi, Japan.

PARVINATATOR Nicholls and Brinkman, 1995

Type species.—Parvinatator wapitiensis Nicholls and Brinkman, 1995.

Referred species.—Type species only.

Diagnosis.—Tooth size relative to skull width not typically small (more than 0.1); small ichthyosaur with total length about 1m or less.

PARVINATATOR WAPITIENSIS Nicholls and Brinkman, 1995

Grippia cf. G. longirostris Brinkman, Zhao, and Nicholls, 1992: p. 465.

Parvinatator wapitiensis Nicholls and Brinkman, 1995: p. 522.

Locality and Horizon.—Lower and possibly Middle Triassic (Spathian to Ladinian) of British Columbia.

Incertae sedis THAISAURUS Mazin, Suteethorn, Buffetaut, Jaeger, and Helmcke-Ingavat, 1991

Type species.—Thaisaurus chonglakmanii Mazin, Suteethorn, Buffetaut, Jaeger, and Helmcke-Ingavat, 1991.

Referred species.—Type species only.

THAISAURUS CHONGLAKMANII Mazin, Suteethorn, Buffetaut, Jaeger, and Helmcke-Ingavat, 1991

Thaisaurus chonglakmanii Mazin, Suteethorn, Buffetaut, Jaeger, and Helmcke-Ingavat, 1991:p. 1211.

Locality and Horizon.—Unknown horizon of the Triassic of Thailand (southern peninsula).

Discussion.—Thaisaurus chonglakmanii (Mazin et al., 1991) is too poorly known to be included in the cladistic analysis. Judging from preliminary descriptions (Mazin et al., 1991), this species is very similar to Chaohusaurus geishanensis from the south part of China, especially for having a radius with enlarged antero-proximal prominence, a very narrow snout, and for being small. While it is possibly congeneric or conspecific with C. geishanensis, the conclusion will be postponed until the material is examined.

GRIPPIDIA Wiman, 1933

Definition.— The last common ancestor of Grippia and Chaohusaurus, and all its descendants.

Diagnosis.—Posterior tooth crowns rounded.

GRIPPIA Wiman, 1929

Type species: Grippia longirostris Wiman, 1929

Referred species.—Type species only.

Diagnosis.—Two maxillary tooth rows present; medium sized ichthyosaur comparable to Utatsusaurus in size.

GRIPPIA LONGIROSTRIS Wiman, 1929

Grippia longirostris Wiman, 1929: p. 184.

Locality and Horizon.— Lower Triassic (Spathian) of Spitsbergen.

CHAOHUSAURUS Young and Dong, 1972

Type species: Chaohusaurus geishanensis Young and Dong, 1972

Referred species.—Type species only.

Diagnosis.—Antero-proximal prominence of radius extensively developed; small ichthyosaur, with total length of about 1m.

CHAOHUSAURUS GEISHANENSIS Young and Dong, 1972

Chaohusaurus geishanensis Young and Dong, 1972: p. 11.

Anhuisaurus chaoxianensis Chen, 1985: p. 140.

Anhuisaurus faciles Chen, 1985: p. 142.

Chensaurus chaoxianensis Mazin, Suteethorn, Buffetaut, Jaeger, and Helmcke-Ingavat, 1991: p. 1208.

Chensaurus faciles Mazin, Suteethorn, Buffetaut, Jaeger, and Helmcke-Ingavat, 1991: p. 1208.

Locality and Horizon.— Lower Triassic (Spathian) of Anhui Province, China.

EUICHTHYOSAURIA

Definition.— The last common ancestor of the Shastasauriformes and Ichthyosauriformes, and all its descendants.

Diagnosis.—External naris laterally oriented, with little exposure in dorsal view; prefrontal-postfrontal bar forming the dorsal orbital margin; postorbital eliminated from upper temporal fenestra; pineal foramen on parietal-frontal border; transverse flange of pterygoid not well defined; tooth cross-sections circular; ulna without post-axial perichondral ossification; iliac blade lost; posterior dorsal centra discoidal.

Discussion.—This group shows some resemblance to the order Euichthyopterygia Mazin 1982. However, there are distinct differences between the two. First, the Euichthyopterygia contained the Suborder Ichthyosauria Blainville 1835, while the Euichthyosauria is within the Ichthyosauria Blainville 1835. Secondly, the Euichthyopterygia, unlike the Euichthyosauria, contained Utatsusaurus hataii, while lacking Phalarodon fraasi, a junior synonym of Mixosaurus nordenskioeldii. The only diagnostic character for the Euichthyopterygia is among those for the Euichthyosauria (viz., the pineal foramen on the parietal-frontal border), but because of the above two differences, I conclude that a new name should be erected to avoid confusion.

SHASTASAURIFORMES Merriam, 1902

Definition.— The last common ancestor of the Shastasauroidea and Cymbospondylus, and all its descendants.

Emended diagnosis.—Both upper and lower dental grooves lost; scapula anterior margin emarginated, without being covered by perichondral sheath; pubis obturator foramen incomplete; presacral count over 55.

CYMBOSPONDYLUS Leidy, 1868

Type species.—*Cymbospondylus petrinus* Leidy, 1868.

Referred species.—Type species only.

Diagnosis.—Sagittal crest of parietal; jugal posteriorly expanded, well beyond the posterior margin of postorbital.

CYMBOSPONDYLUS PETRINUS Leidy, 1868

Cymbospondylus petrinus Leidy, 1868: p. 178.

Locality and Horizon.— Middle Triassic (Anisian) of Nevada.

SHASTASAUROIDEA Merriam, 1902

Definition.— The last common ancestor of "*Cymbospondylus*" *buchseri* and *Shastasaurus*, and all its descendants.

Emended diagnosis.—Humeral head dorsally directed; humerus as long as wide, exclusive of anterior flange; humerus proximal end as wide as distal one.

"*CYMBOSPONDYLUS*" *BUCHSERI* Sander, 1989

Cymbospondylus buchseri Sander, 1989: p. 164.

Locality and Horizon.—Middle Triassic (Anisian/Ladinian boundary) of Monte San Georgio, Switzerland.

Discussion.— "*Cymbospndylus*" *buchseri* forms a clade with *Shastasaurus* and *Shonisaurus*, with *Cymbospondylus petrinus* as the sister group. The humerus of "*C.*" *buchseri* is typically shastasauroid for being short relative to its width, and having a dorsally directed head and large proximal end. C. petrinus, on the other hand, has a primitive humerus resembling that of Early Triassic ichthyosaurs: it is relatively long, the head is directed proximally, and the proximal end is smaller than the distal one. As pointed out by Sander (1989), the scapula of this species resembles that of C. petrinus, in that it is triradiate due to the emargination on the anterior margin. The emargination on the anterior margin of the scapula, however, is present in all other Shastasauriformes. In fact, one of the better preserved scapulae of Shonisaurus resembles that of "C." buchseri in general shape. It is therefore likely that the resemblance between the scapulae of C. petrinus and "C." buchseri reflects the plesiomorphies for the Shastasauriformes, rather than a synapomorphy between the two species. Another feature shared between the two species, namely the diapophyses intersecting the anterior margins of the centra, is also known in Utatsusaurus and Mixosaurus, and therefore seems to be plesiomorphic for the Ichthyosauria. All other features used by Sander (1989) to diagnose Cymbospondylus are either plesiomorphic for the Shastasauriformes, Euichthyosauria, or for the Ichthyosauria. Considering all above evidence, I conclude that "C." buchseri cannot be assigned to Cymbospondylus. However, because this "C." buchseri is a metataxon, a new generic name is not given at this point.

Diagnosis.—This genus is currently a meta-taxon, although a discovery of a complete skeleton may change this.

Incertae sedis PESSOSAURUS Wiman 1910

Type species.—Pessosaurus polaris (Hulke, 1873).

Referred species.—Type species only.

PESSOSAURUS POLARIS (Hulke, 1873)

Ichthyosaurus polaris Hulke, 1873: p. 3

Shastasaurus polaris Yakowlew, 1903: p. 194.

Cymbospondylus (?) polaris Merriam, 1908: p. 149.

Pessosaurus polaris Wiman, 1910: p. 136.

Locality and Horizon.— Middle Triassic (Ladinian) of Spitsbergen.

Discussion.—Pessosaurus polaris, known only from a fragmentary vertebral series, jaw fragments, and a partial forefin, was not included in the cladistic analysis, due to lack of data. The humerus of one of the referred specimens (PMU R176), described by Wiman (1910, 1916), shows one important shastasauroid feature: it is wider than long (exclusive of the anterior flange). Because this feature is not convergent with any other ichthyosaurs, P. polaris is assigned here to the Shastasauroidea. The radius is possibly much larger than the ulna, which would support the above assignment, but this cannot be confirmed because the ulna of PMU R176 is broken. Wiman (1916:fig. 4) reconstructed the outline of the ulna before breakage as being as large as the radius. It is not known whether all of the referred specimens represent a single species or not, but they possibly do considering that 1) they occur from the Middle Triassic of Spitsbergen (except for some Canadian specimens that were recently assigned to this genus by Callaway and Brinkman [1989]); 2) they represent similarly sized individuals of ichthyosaurs; and 3) they show no features that contradicts their assignment to the Shastasauroidea.

SHASTASAURIDAE Merriam, 1902

Definition.— The last common ancestor of Shastasaurus and Shonisaurus, and all its descendants.

Diagnosis.—Scapula and coracoid articulate together by large facets; radius twice as large as ulna; radius postaxial perichondral bone lost; metacarpal I, and hence digit I, lost.

SHONISAURUS Camp, 1976

Type species.—Shonisaurus popularis Camp, 1976.

Referred species.—Type species only.

Diagnosis.—Dorsal centra three times as high as long; very large ichthyosaur, reaching 15m in total length.

SHONISAURUS POPULARIS Camp, 1976

Shonisaurus popularis Camp, 1976: p. 132.

Shonisaurus mulleri Camp, 1976: p. 132.

Shonisaurus silberlingi Camp, 1976: p. 132.

Locality and Horizon.— Upper Triassic (Carnian) of Nevada.

SHASTASAURUS Merriam, 1895

Type species.—Shastasaurus pacificus Merriam, 1895.

Referred species.—Shastasaurus neoscapularis McGowan, 1994.

Diagnosis.—Radiale with preaxial perichondral bone (notch).

SHASTASAURUS PACIFICUS Merriam, 1895

Shastasaurus pacificus Merriam, 1985: p. 57.

Shastasaurus alexandrae Merriam, 1902: p. 96.

Shastasaurus altispinus Merriam, 1902: p. 99.

Shastasaurus osmonti Merriam, 1902: p. 93.

Locality and Horizon.— Upper Triassic (Carnian) of California.

SHASTASAURUS NEOSCAPULARIS McGowan, 1994

Shastasaurus neoscapularis McGowan, 1994: p. 170.

Locality and Horizon.— Upper Triassic (Norian) of British Columbia.

ICHTHYOSAURIFORMES

Definition.— The last common ancestor of Mixosaurus and Ichthyosaurus, and all its descendants.

Diagnosis—Parietal ridge present; supratemporal process of parietal short and robust; supratemporal enlarged, with large posterior slope partially covering upper temporal fenestra.

MIXOSAUROIDEA Baur, 1887

Definition.— The last common ancestor of Mixosaurus cornalianus and M. nordenskioeldii, and all its descendants.

Emended diagnosis.—Premaxilla posteriorly pointed, scarcely entering external naris; long sagittal crest reaching nasal; large anterior terrace of upper temporal fenestra, reaching nasal; interclavicle triangular; metacarpal III perichondral bone partially lost; pubis more than twice larger than ischium; high, narrow neural spines; mid-caudal centra at least three times higher than long.

MIXOSAURUS Baur, 1887

Type species.—Mixosaurus cornalianus (Bassani, 1886).

Referred species.—Mixosaurus atavus (Quenstedt, 1852); Mixosaurus nordenskioeldii (Hulke, 1887).

MIXOSAURUS CORNALIANUS (Bassani, 1886)

Ichthyosaurus cornalianus Bassani, 1886: p. 20.

Mixosaurus Baur, 1887: p. 840.

Mixosaurus cornalianus Repossi, 1902: p. 365.

Locality and Horizon.—Middle Triassic of Italy/Switzerland border.

Diagnosis.—Tooth size relative to skull width small (less than 0.05).

MIXOSAURUS ATAVUS (Quenstedt, 1852)

Ichthyosaurus atavus Quenstedt, 1952: p. 129.

Mixosaurus atavus Fraas, 1891: p. 37.

Locality and Horizon.— Middle Triassic (Anisian) of Germany.

Diagnosis.—Tooth size relative to skull width not small (more than 0.1).

MIXOSAURUS NORDENSKIOELDII (Hulke, 1887)

Ichthyosaurus nordenskioeldii Hulke, 1887: p. 4.

Mixosaurus nordenskioeldii Dames, 1895: p. 1047.

Cymbospondylus(?) nordenskioeldii Merriam, 1908: p. 148.

Cymbospondylus (?) natans Merriam, 1908: p. 150.

Phalarodon fraasi Merriam, 1910: p. 381.

Phalarodon nordenskioeldii Nicholls, Brinkman, and Callaway in press.

Locality and Horizon.—Middle Triassic of Spitsbergen and North America.

Diagnosis.—Posterior mandibular tooth crowns nearly flat; medium sized ichthyosaur over 2m in total length.

ICHTHYOSAUROIDEA

Definition.—The last common ancestor of Toretocnemus and Ichthyosaurus, and all its descendants.

Diagnosis.—Humeral facets for radius and ulna equal in length; metacarpal I, and hence digit I, lost.

Discussion.—All Jurassic and later genera, not included in the cladistic analyses, are assigned here to Ichthyosauroidea, because they all have the above two diagnostic features.

TORETOCNEMUS Merriam, 1903

Type species.—Toretocnemus zitteli (Merriam, 1903).

Referred species.—Type species only.

Diagnosis.—Ulnare with postaxial perichondral bone (notch).

TORETOCNEMUS ZITTELI (Merriam, 1903)

Leptocheirus zitteli Merriam, 1903: p. 253.

Toretocnemus californicus Merriam, 1903: p. 260.

Merriamia zitteli Boulenger, 1904: p. 425.

Locality and Horizon.— Upper Triassic (Carnian) of California.

Incertae sedis CALIFORNOSAURUS Kuhn, 1934

Type species.—Californosaurus perrini (Merriam, 1902).

Referred species.—Type species only.

Diagnosis.—Dorsal centra height/length ratio about 1.6 or 1.7.

CALIFORNOSAURUS PERRINI (Merriam, 1902)

Shastasaurus perrini Merriam, 1902: p. 89.

Delphinosaurus perrini Merriam, 1905: p. 24.

Californosaurus perrini Kuhn, 1934: p. 27.

Perrinosaurus perrini Merriam, 1938: p. 143.

Locality and Horizon.— Upper Triassic (Carnian) of California.

Discussion.—Californosaurus perrini was not included in the cladistic analysis, because less than one third of the characters could be coded, but it is known to have equally sized distal facets of the humerus. Considering the uniqueness of this character to the Ichthyosauroidea, I conclude that C. perrini should be assigned to this taxon.

ICHTHYOSAURIDAE Bonaparte, 1841

Definition.—The last common ancestor of Macgowania, Hudsonelpidia, and Ichthyosaurus, and all its descendants.

Emended diagnosis.—Epipodial elements wider than long; manual accessory digit VI.

Discussion.—All Jurassic and later genera are referred to this family, because they all possess the above two diagnostic features. When adding Stenopterygius quadriscissus and Temnodontosaurus burgundiae to the data matrix in Table 1, PAUP found multiple equally parsimonious topologies among the Ichthyosauridae, but its monophyly was always supported. Only those genera that were included in the analysis are listed in the following section.

HUDSONELPIDIA McGowan, 1995

Type species.—Hudsonelpidia brevirostris McGowan, 1995.

Referred species.—Type species only.

Diagnosis.—Manual epipodials much shorter than wide while pes epipodials much longer than wide.

HUDSONELPIDIA BREVIROSTRIS McGowan, 1995

Hudsonelpidia brevirostris McGowan, 1995: p.295.

Locality and Horizon.— Upper Triassic (Norian) of British Columbia.

MACGOWANIA gen. n.

Type species.—Macgowania janiceps (McGowan, 1995).

Referred species.—Type species only.

Diagnosis.—As given for the type species by McGowan (1995).

Etymology.—In honor of Christopher McGowan, who described the type species, recognizing his enormous contribution to the ichthyosaurian biology.

MACGOWANIA JANICEPS (McGowan, 1995)

Ichthyosaurus janiceps McGowan, 1995: p. 25.

Locality and Horizon.— Upper Triassic (Norian) of British Columbia.

Genus ICHTHYOSAURUS de la Beche and Conybeare, 1821

Type species.—Ichthyosaurus communis Conybeare, 1822.

Referred species.—Ichthyosaurus breviceps Owen, 1881; Ichthyosaurus conybeari Lydekker, 1888.

Locality and Horizon.—Uppermost Triassic (uppermost Rhaetian) to the Lower Jurassic (Sinemurian) of England (McGowan, 1974b).

Diagnosis.—Digital bifurcation anterior to primary axis of forefin; ulnare larger than intermedium; digit V more robust than digit IV.

Note.—See McGowan (1974b) for taxonomy of this genus.

EXCLUDED TAXA

For Triassic ichthyosaurs described before 1989, only those that were found to be valid by Callaway and Massare (1989b) were included in the above classification. The validity of some of the taxa listed by Callaway and Massare (1989) have been subsequently questioned by others: Cymbospondylus piscous and C. nevadanus (Sander, 1989), and Himalayasaurus tibetensis (Lucas and Gonzalez-Leon, in press). I agree with these authors, and did not included these two species in the classification.

Taxa dubia

Svalbardosaurus crassidens.—This species was erected on three fragments of teeth from the Lower Triassic of Spitsbergen (Mazin, 1981a). However, it is inappropriate to base a species on fragments of teeth. Moreover, it is not possible to establish that these teeth are ichthyosaurian.

Mixosaurus maotaiensis.—The holotype of this species (Young, 1965) is too fragmentarily preserved, and it is difficult to distinguish this species from other species of Mixosaurus.

Shastasaurus careyi.—This species was based on two partial vertebral centra from the anterior dorsal or posterior cervical region (Merriam, 1902). These vertebrae differ from those of Shastasaurus in that they are very thin (diameter / length ratio of about 3.0 versus about 2.0 for Shastasaurus) and very large (about 180 mm in the maximum diameter, versus less than 100 mm in Shastasaurus). Both of these features are comparable with Shonisaurus from the same age (Carnian), which was not known when Merriam (1902) described this species. There is insufficient information to judge if these specimens belong to Shonisaurus popularis, but these specimens are clearly too incomplete for diagnosing a separate species.

Shastasaurus carinthiacus.—This species was based on vertebrae and ribs. While these bones seem to belong to Shastasaurus, they are too fragmentary to erect a separate species.

Problem of Omphalosaurus

Omphalosaurus has been referred to the Ichthyosauria by various authors (e.g., Kuhn, 1934; Cox and Smith, 1973; Mazin, 1983; Callaway and Massare, 1989b), but it is considered to be non-ichthyosaurian in the present study, as suggested by others (Merriam, 1911; Wiman, 1916; McGowan, 1972a). The reasons for this assignment are given below, and this requires an historical review of this genus.

Omphalosaurus was erected by Merriam (1906), who gave a preliminary description of the type species, O. nevadanus, based on a fragmentary skull, with two associated vertebrae, from the Middle Triassic of Nevada. Merriam (1906) did not assign this species to the Ichthyosauria, considering it as representing a distinct group of reptiles. The situation became complicated when a group of isolated fossils, containing Omphalosaurus-like teeth, were described from the Lower/Middle Triassic boundary of Spitsbergen (lower saurian level) by Wiman (1910). The postcranial bones in this group of fossils contained typically ichthyosaurian elements, such as the humeri resembling those of Shastasaurus, and discoidal vertebral centra with a deep amphicoely. Wiman (1910), assuming that all of these bones represent one species, erected a new genus and species Pessopteryx nisseri. Later, Merriam (1911) noticed the resemblance between the teeth assigned to P. nisseri and those of O. nevadanus, and suggested that the teeth of P. nisseri belonged to Omphalosaurus, which he did not consider was ichthyosaurian, while its postcranial bones belong to an ichthyosaur resembling Shastasaurus. Wiman (1916), having seen the description of additional dental material of Omphalosaurus by Merriam and Bryant (1911), accepted this argument. He concluded that it was likely that the specimens originally referred to P. nisseri comprised the jaw fragments of a non-ichthyosaurian reptile, Omphalosaurus, and the postcranials of an ichthyosaur, P. nisseri (Wiman, 1916). He also noted the co-occurrence of unidentified phalanx-like bones with these specimens, and suggested that these bones may belong to Omphalosaurus (Wiman, 1916).

For unknown reasons, Kuhn (1934) referred both Omphalosaurus and Pessopteryx to the Family Omphalosauridae, which was in turn referred to the order Ichthyosauria. This assignment appears to have been the origin of the inclusion of Omphalosaurus with the Ichthyosauria.

About 40 years later, Cox and Smith (1973) published yet another classification, in their review of the vertebrate fauna from the Triassic of Spitsbergen. They were not aware of Kuhn's (1934) classification, because it was not cited or mentioned. They obviously misinterpreted Wiman's (1916) intention regarding the division of the original Pessopteryx nisseri specimens, and stated "... Wiman's genus Pessopteryx is merely a junior synonym of Omphalosaurus, a genus which was first described from the Middle Triassic of California (Merriam, 1906; Wiman, 1916c)" (Cox and Smith, 1973:412). In their listing of the fauna, they assigned Omphalosaurus and Grippia to the family Omphalosauridae. The reasons for the addition of Grippia to the Omphalosauridae was not explained, but it was followed by other authors, further complicating the issue.

Mazin (1983) was the first, and the last, to state the reasons why Omphalosaurus should be placed in the Ichthyosauria. Being strongly influenced by Peyer's (1968) misconception that ichthyosaurs were primitively durophagous, he gave six reasons to support his view (Mazin, 1983), but none are significant as shown below:

1) Association.—Mazin (1983) questioned Wiman's (1916) suggestion that bones from two different species were mixed in Wiman's (1910) Pessopteryx. His argument was that it is

too much of a coincidence that one species should only be represented by teeth and the other only by postcranials. He considered it more likely that the teeth and postcranials belonged to a single species. This, however, is not true. Wiman (1910) described several typically ichthyosaurian teeth, with clear plicidentine, from the same level as P. nisseri (lower saurian level), which are sufficient large for ichthyosaurs with P. nisseri humeri.

2) Vertebrae.—Mazin (1983) argued that the two anterior cervical vertebrae associated with the type of Omphalosaurus nevadanus are ichthyosaurian-like for having amphicoelous centra lacking fused neural arches. These two are presumably the atlas and axis, judging from the association with the skull. While Mazin's (1983) argument may be true, the following should also be considered: i) unfused neural arch and centrum are commonly known for aquatic reptiles (Carroll, 1985), and it is also possible that the two may be unfused in young individuals; ii) atlantal and axial neural arches may be unfused to their corresponding centra in many amniotes; iii) the amphicoely seen in ichthyosaurian centra is much deeper than those seen in O. nevadanus; iv) anterior cervical centra tend to be shorter than the more posterior ones in aquatic reptiles. I conclude that the centra cannot reasonably establish that Omphalosaurus is ichthyosaurian.

3) Rounded tooth crown.—Mazin (1983) argued that the teeth of Omphalosaurus are similar to the posterior teeth of Grippia longirostris and of Mixosaurus cornalianus, although root plication is weak in O. nisseri and lacking in O. nevadanus. However, Motani (1997) showed that the posterior teeth of G. longirostris, although rounded, are far from typical durophagous teeth, being very small and having large pulp cavities surrounded by a thin dentine wall. Omphalosaurus, on the other hand, has large teeth with small or no obvious pulp cavities, and there is no similarity with G. longirostris except the crown is rounded.

Also, a rounded tooth crown is not primitive for ichthyosaurs, as shown by the cladistic analysis given earlier. I therefore conclude that this feature is insignificant. The dental plication will be discussed later.

4) Multiple tooth rows.—Mazin's (1983) argument was that although the teeth are distributed in several rows in Omphalosaurus, similar conditions are known in Grippia longirostris and Phalarodon fraasi (now referred to Mixosaurus nordenskioeldii), whose maxillary teeth are in two rows. However, neither of these two ichthyosaurs have multiple tooth rows in the mandible, as in O. nevadanus. Moreover, multiple tooth rows are not primitive for ichthyosaurs, but autapomorphic for each of these two species, as is clear from the results of the cladistic analysis given earlier.

5) Humerus.—Mazin (1983), assuming that the humeri of Pessopteryx belongs to Omphalosaurus, argued that they have some characteristics of Mixosaurus. This argument is invalid because of the assumption. Another aspect of the humerus will be discussed later.

There are several reasons why Omphalosaurus is unlikely to be ichthyosaurian.

1) Jaw symphysis.—except for some Jurassic ichthyosaurs, the jaw symphysis of ichthyosaurs is short. The posterior margin of the jaw symphysis of Omphalosaurus nevadanus is U-shaped as seen in the ventral view, which is a feature common among sauropterygians. Ichthyosaurs, on the other hand, have a V-shaped posterior margin.

2) Absence of plicidentine.—Mazin's (1983) claim that Omphalosaurus nisseri had weakly folded root dentine is incorrect. Among numerous teeth referred to this species, only two show an indication of plication in the dentine (Wiman, 1910:pl. 9, fig. 30). However, this plication, which is present for only less than half of the perimeter for each of the two teeth, is clearly not formed by the folding of the dentine. These teeth, and most of the referred teeth,

show no sign of the pulp cavity, which is always associated with the folded dentine of ichthyosaurs (otherwise the dentine cannot be folded). Moreover, the plication is too irregular compared to the more regular folding seen in ichthyosaurs.

3) Humerus.—The only humerus found in association with the teeth of Omphalosaurus is those of O. wolfi from Austria (Tichy 1995). This humerus, unlike those referred to Pessopteryx nisseri, is boomerang shaped, as in many sauropterygians.
4) Ichthyosaurian synapomorphy.—None of the synapomorphies for the Ichthyosauria, given earlier, have been positively identified for Omphalosaurus.

Based on the above reasons, I conclude that Omphalosaurus cannot be assigned to the Ichthyosauria; it may be related to sauropterygians, such as placodonts. The humeri referred to Pessopteryx by Wiman (1910) are clearly of shastasauroid origin, as suggested by Merriam (1911) and Wiman (1916). A formal taxonomic revision is beyond the scope of the present study.

SUMMARY

The monophyly of the Ichthyosauria was explicitly established for the first time, based on nine characters. The summary of the proposed classification for the Ichthyosauria is given in Table 12-3.

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Appendix A

APPENDIX: PROBABILISTIC JUSTIFICATION OF CHARACTER-STEP PARSIMONY

INTRODUCTION

Whether or not a character-step based parsimony method of phylogenetic analysis is the best methodology available has been a controversial issue. Some systematists argue that the method requires only one (or a few) assumption(s) (e.g., Brooks and McLennan, 1991), therefore it is superior to the other methods which involve more assumptions (Mickevitch, 1983). Other systematists, however, maintain that there are implicit assumptions underlying the method (Swofford and Olsen, 1990), hence it is not possible to argue the superiority of the methodology by merely comparing the number of explicit assumptions (Felsenstein, 1979, 1981b). Some of the former systematists employ probabilistic argument in support for parsimony (e.g., Sober, 1983), while others deny any probabilistic discussion (e.g., Mickevitch, 1983). Some other systematists dispute against probabilistic approach when criticizing other methodologies, while employing it to support Wagner parsimony (e.g., Farris, 1983).

In this appendix, I will try to clarify the elements involved in these arguments, and show that only two views are logically defensible: 1) deny any probabilistic argument for the sake of the inference of uncertainty, and use parsimony in the character-step count as the only falsifier or 2) justify Wagner parsimony in a probabilistic framework, as an approximation of the maximum likelihood method under certain conditions, and use statistical tests to infer the error level of the estimates. I will review the advantages and disadvantages of these two views, and argue that the latter is more plausible.

CRITICAL REVIEW

Four Categories of Tree Reconstruction Methods

Commonly used phylogeny reconstruction methods can be divided into four categories based on two criteria: 1) whether it uses a raw data matrix or a distance matrix; 2) whether it considers uncertainty of its inference or not (Table A1). Most tree reconstruction algorithms based on a distance matrix can be either probabilistic or non-probabilistic, depending on the kind of distance used with them. In contrast, methods that utilize raw data are clearly divided into probabilistic and non-probabilistic categories. Maximum-likelihood method (Felsenstein, 1973, 1981a) and closest tree method (Hendy, 1989), are the only probabilistic methods in this raw-data category, while various parsimony based methods are non-probabilistic. I will concentrate on these two kinds of raw-data based methodologies in the following sections.

Parsimony Principle and its Application

Some systematists do not distinguish between the parsimony principle itself and the way it is incorporated in the phylogenetic context, causing a confusion in the literature. Parsimony is a well established concept, but what actually matters in science is the way we apply general notions to specific problems. Therefore, it is pointless to try to establish the superiority of Wagner parsimony by justifying the notion of parsimony. For example, Brooks and McLennan (1991: 65) effectively explained that the concept of the parsimony principle itself does not require any assumption, but this does not mean the application of the parsimony principle in phylogenetic analysis requires only one assumption that evolution occurred. In fact, the method involves several more assumptions in the way it incorporates the principle. The principle of

Table A1. Four categories of phylogeny reconstruction methods, divided by two criteria: whether it is probabilistic or not, and whether it utilizes a raw data matrix or distance matrix.

Only raw data based methods are discussed in the text.

	Probabilistic	Non-probabilistic
Raw data matrix based	Maximum Likelihood Closest Tree	Wagner Parsimony Other Parsimony
Distance matrix based	NJ, UPGMA (corrected distance)	NJ, UPGMA (uncorrected distance)

parsimony can be applied in several different ways in systematic biology, and therefore there are more than one method in the literature that bear the name "parsimony", each involving different sets of assumptions (Table A2): e.g., Dollo parsimony (Farris, 1977; Felsenstein, 1979), Camin-Sokal parsimony (Camin and Sokal, 1965), polymorphism parsimony (Farris, 1978; Felsenstein, 1979), threshold parsimony (Felsenstein, 1981b), and Wagner parsimony (Kluge and Farris, 1969), which is generally used. Apart from these methods that consider the parsimony in the character-step count, compatibility methods also incorporate the principle of parsimony in that it minimizes the number of incompatible characters (Felsenstein, 1981b). Even in probabilistic methodologies, which favor the minimum unlikelihood and error level, the principle of parsimony is used. Therefore, to establish the superiority of Wagner parsimony, it is clearly not sufficient to justify the parsimony principle itself.

Explicit and Implicit Assumptions

One may argue that Wagner parsimony involves the least number of explicit assumptions of all the above listed parsimony methods, and is therefore superior to the others. For example, Dollo parsimony explicitly assumes that 1) any character state change is improbable; 2) development of a new character state is far less probable than its loss; whereas Wagner parsimony assumes only the former explicitly. However, Wagner parsimony, by not considering the difference between the forward and reversal changes, actually assumes implicitly that 2') development of a new character state and its loss are equally probable. Felsenstein (1992) listed such implicit assumptions of Wagner parsimony as following:

1) Ancestral states are unknown [when reconstructing unrooted trees]

Table A2. Assumptions of various parsimony methods.

Assumptions regarding four events (i.e., forward change of the character state, character-state reversal, retention of polymorphism in ancestral vertices, and multiple state change within one edge) are listed for five different parsimony methods. By not considering an event, a method implicitly assumes that the event is absent. The last column contains the amount that each method tries to minimize. **F**: forward change, **R**: reversal, and **P**: polymorphism in ancestors.

	Forward Change	Reversal	Polymorphism in Ancestors	Multiple State Change within an edge	Amount to be minimized
Wagner	Yes	Yes	No	No	F+R
Dollo	Yes but once	Yes	No	No	R
Camin-Sokal	Yes	No	No	No	F
Polymorphism	Yes	Yes	Yes	No	P

2) Different characters evolve independently

3) Different lineages evolve independently

4) Changes 0 → 1 and 1 → 0 are equally probable

5) Both of these kinds of changes are a priori improbable over the evolutionary time spans involved in the differentiation of the group in question

6) Other kinds of evolutionary event such as retention of polymorphism are far less probable than 0 → 1 changes

7) Rates of evolution in different lineages are sufficiently low that two changes in a long segment of the tree are far less probable than one change in a short segment.

It is clear that the number of explicit assumptions is not a proper criterion to compare the ability of different parsimony methods, because by not considering a given factor, a method implicitly assumes that the factor has no effect. The fact that Wagner parsimony has generally proved more useful than the other parsimony methods in actual studies is not because it assumes less, but because its assumptions are reasonable on average, that is, it does not assume extreme situations hence departures from the assumptions are compensated for in total.

Parsimony Framework versus Probabilistic Framework

As mentioned earlier, there are two different lines of philosophical thoughts underlying the phylogeny reconstruction methods based on discrete character states. One of them considers the phylogeny reconstruction problem under the framework of character-step parsimony, and the other under the probabilistic theories. Both lines are logically defensible within their own frameworks, although both have been criticized by proponents of the other. For example, some systematists argue that parsimony methods cannot be justified for assuming that evolution happened parsimoniously (mentioned by Brooks and McLennan, 1991), while others similarly criticize probabilistic methodologies for assuming that evolution occurred randomly (e.g., Carpenter, 1992). However, both of these criticisms are pointless, because the use of character-step parsimony or probabilistic theories does not postulate such assumptions. Instead, these two are used because they are considered to be the best falsifiers of competing phylogenetic hypotheses, or the severe test sensu Popper (1968), by systematists (Cavender, 1980; Mickevitch, 1983; Brooks and McLennan, 1991; Carpenter, 1992).

The more accurate way of comparing these two different approaches is to find out whether or not parsimony in the raw character-step count is a better falsifier than probabilistic values calculated from data. This, however, is difficult, because each of them is based on its own framework, and it is therefore necessary to view the two from a single perspective to make a comparison. There are three possible perspectives: 1) view probabilistic methods from the framework of character-step parsimony; 2) view character-step parsimony methods from a probabilistic framework; and 3) view both methods from outside of their own frameworks. The first option is not available because character-step parsimony cannot encompass probabilistic theories. The second option has been discussed extensively in the literature, as will be summarized later. The third option will be dealt with here, by comparing how each framework is justified, and what it provides.

A generally given justification for using Wagner parsimony in phylogenetic analyses is that parsimony is the principle that scientists use (Brooks and McLennan, 1991), but, as mentioned previously, such a justification of parsimony principle itself does not justify the way the principle is incorporated in phylogenetic contexts. Carpenter (1992), who emphasized that parsimony (i.e., Wagner parsimony, not parsimony principle) is the severe test for competing phylogenetic hypotheses, did not explain the reason. This is all because there is no scientific justification to use the principle of parsimony in the context of Wagner parsimony (and other character-step-count parsimony methods), except it gives the simplest explanation of existing evidence. Note that this simplicity is not because the method assumes less, but because it makes simple assumptions that hold well on average, as explained earlier. Because this framework portrays character-step parsimony as the only test, it is judgmental for not considering the errors associated with its inferences, and is deprived of expandability, as will be discussed later. This lack of test for errors is one of the two major disadvantage of character-step parsimony. The other disadvantage is that the method can be inconsistent (Felsenstein, 1978; Hendy and Penny, 1989; Zharkikh and Li, 1993), that is, it may positively mislead the conclusion as the data size increases. Steel et al. (1993) proved that cladistically uninformative characters (autapomorphies and symplesiomorphies) are phylogenetically informative, and their elimination leads to inconsistency of the method. Steel et al. (1993) also showed that a non-linear correction of raw data may compensate for such loss of information, making parsimony consistent, but such a treatment cannot be justified under the framework of character-step parsimony.

Probabilistic theories are considered the best falsifier because evolution is so complicated that probabilistic framework give the best interpretation, as it does for many other natural and social phenomena that do not necessarily have random mechanisms (Cavender, 1980). This framework is not judgmental, unlike the previous one, because it gives the measures of errors and uncertainty associated with the best hypotheses. Various statistical tests, made available over the years, can be used to assess these errors. Therefore, as Kishino and Hasegawa (1989: 175) argued, the probabilistic framework, which considers uncertainty of its inference, is superior to character-step parsimony that has an aura of certainty but which is without scientific justification. It should be also noted that maximum-likelihood analysis can be performed under a set of simple assumptions similar to that in Wagner parsimony, while being consistent.

When using a falsifier based on probabilistic theories, it is justifiable to use many statistical methodologies. However, probabilistic calculations involve a much greater computational burden than in the Wagner parsimony method, for a given data set, which prohibits the use of the former in many cases. Therefore, it would be convenient if the Wagner parsimony method can be justified by probabilistic theories, and the same analytical procedure that we are using in cladistic analysis can be applied to the data within a probabilistic framework.

PROBABILISTIC JUSTIFICATION FOR WAGNER PARSIMONY

Felsenstein (1973, 1978, 1979, and 1981b) and Farris (1973) were amongst the first to explore the probabilistic justification for Wagner parsimony. They both employed the maximum likelihood estimator to approach the problem, but in different ways. Farris concluded that the most parsimonious tree is the maximum likelihood tree, whereas Felsenstein's approach led to the conclusion that the most parsimonious tree approximates the maximum likelihood tree under certain conditions. Farris's (1973: 254) conclusion has shortcomings because, without explicitly assuming that multiple state changes within one edge (a branch of a phylogenetic tree is mathematically called an edge) is unlikely, he incorporated this assumption in his equation when he related the maximum likelihood solution to the most parsimonious one (otherwise, his equation (8) suggests that when replacing a set of forward and reverse changes that occurred within one edge with one forward change, both the likelihood and character-step count increase, i.e., the likelihood behaves against character-step parsimony).

Therefore, even though Farris (1973) claims his model is general, his conclusion is only valid in special cases (i.e., when characters change their states at most once within a given edge). Felsenstein's conclusion is more general, and most of the recent work on maximum likelihood estimation of phylogeny employ his approach. Another trial to justify Wagner parsimony as the maximum likelihood estimator was attempted by Sober, but proved unsuccessful (Felsenstein and Sober, 1986).

The necessary and sufficient condition for the Wagner parsimony solution to be the maximum likelihood estimate has not been explicitly identified. Felsenstein (1978) predicted the sufficient conditions to be 1) low rate of character state change per time and 2) approximately equal rate of character state change per time. Hendy and Penny (1989) mathematically proved that these two conjectures are sufficient in four-taxon cases, but there are counter examples for more than five-taxon cases: Wagner parsimony is inconsistent in reconstructing phylogenies with a long outgroup edge. As mentioned previously, Farris' (1973) study indicates another sufficient condition that none of the characters changes its state more than once within a given edge. It has been reported that there is a good agreement between the maximum likelihood estimation and Wagner parsimony solution when analyzing actual DNA sequence data (Debry and Abele, 1995). My own re-analysis of published morphological data matrices (Carroll and Dong, 1991 and Rieppel, 1993) showed that the maximum likelihood tree is identical to the 50% majority consensus tree of the most parsimonious trees.

Expandability

When Wagner parsimony is used as the falsifier, it is logically indefensible to incorporate statistical methods in the argument, because use of probabilistic theory cannot be accepted within the framework of character-step parsimony. Therefore, commonly used indices, namely CI, RI, and RCI, become effective only within the same data set (i.e., the same matrix with the same setting), and should not be used to compare among different data sets. Consequently, there is no need for CI, RI, or RCI, because within the same data set, they behave proportional to the reciprocal of the tree length. Moreover, neither majority rule consensus tree, bootstrap, jackknife, PTP, or g_1 statistics can be used along with Wagner parsimony. Decay analysis for testing the support for nodes (Bremer, 1994) is also unjustifiable under this parsimony framework, because the most parsimonious tree cannot be questioned or tested further. When Wagner parsimony gives multiple equally parsimonious solutions, which is more usual than rare in actual analyses, it is not possible to compare among them within the framework of parsimony. Therefore, although it is logically justifiable to use character-step parsimony as the falsifier, such a view prohibits the use of the above stated methods that are based on probabilistic theories.

With the probabilistic justification of character-step parsimony, however, it is possible to use many statistical methods along with parsimony analyses. Computer programs, such as PAUP and PHYLIP, are based on this very notion of probabilistic parsimony. Inversely, by using such statistical methods along with Wagner parsimony, through the above programs, a systematist automatically assumes that Wagner parsimony is probabilistically justifiable. This means that the systematist considers the most parsimonious tree as the most corroborated hypothesis, not because it is most parsimonious in step count, but because it is most likely in probabilistic theories. This is a point missed by many systematist who use statistical tests with Wagner parsimony, erroneously believing character-step parsimony is still the falsifier.

Bremer's (1994) decay analysis is not statistically profound, therefore it is inferior to other testing methods, such as jacknifing and bootstrapping. It is also not justifiable under the framework of character-step parsimony, as mentioned earlier, therefore its value in phylogenetics is questionable.

SUMMARY

Although it is logically defensible to use Wagner-parsimony to select most corroborated phylogenetic hypotheses, this logical framework omits the subsequent use of any statistical methodologies, leaving no option for further testing. The statistical framework is superior to that for Wagner parsimony because it considers uncertainty of its inference in a scientific manner, which Wagner parsimony cannot supply. It also allows usage of various statistical methods for testing, which, again, cannot be used within the framework of character-step parsimony. Therefore, a falsifier based on statistical theories better serves as the severe test of competing phylogenetic hypotheses sensu Popper (1968) than Wagner parsimony.

However, purely probabilistic methods require a great computational burden, which sometimes prohibit the use of these methods in practice. It is therefore useful to adopt probabilistic justification of character-step parsimony, developed by Felsenstein (1973, 1978, 1979, 1981b) and others, and incorporate the Wagner parsimony algorithm into probabilistic framework, and reduce the computational burden. When Wagner parsimony is probabilistically justified, however, the most parsimonious tree is regarded as the most corroborated hypothesis, not because it is most parsimonious in character-step count, but because it is most likely in statistical theory. Only within this alternative framework is it possible to use statistical tests along with character-step parsimony. The sufficient conditions for justifying Wagner parsimony as an approximation of maximum likelihood estimation are roughly known, and when using statistical methods along with Wagner parsimony, it is required that a systematist assumes that these conditions are fulfilled.

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Appendix B

BIOGRAPHY AND PUBLICATION LIST

BIOGRAPHY

1967	Born, Tokuyama, Yamaguchi, Japan	
1991	B. Sc., University of Tokyo (Geology/Paleontology)	
1994	M. Sc., University of Toronto (Vertebrate Paleontology)	
1994-1997	Ph.D. Program, University of Toronto	
	Major Subject	Vertebrate Paleontology
	Minor Subject	Systematic Biology

PUBLICATION

Peer Reviewed Publications and Book Chapters

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