



Ontogeny and sexual dimorphism in Champsosaurs (Diapsida, Choristodera)  
by Yoshihiro Katsura

A thesis submitted in partial fulfillment of the requirements for the degree Of Doctor of Philosophy in  
Biological Sciences  
Montana State University  
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Abstract:

Two species of Champsosaurus (Diapsida, Choristodera), possessing distinctive humeral and femoral morphologies, occurred sympatrically in the Early Paleocene of Montana. The humeral ecto- and entotuberosities of *C. ambulator* are situated more distally than those of *C. laramiensis*. The femoral internal trochanter is separated from the proximal articular surface in *C. ambulator*, but not in *C. laramiensis*. The phylogenetic significance of these limb morphologies is questioned because similar dimorphic variations occur in champsosaurs from other geological ages and locations.

Female champsosaurs may have been better adapted to a terrestrial life than males due to nesting behavior, resulting in variable limb morphologies between sexes. The observed morphologic variations are hypothesized to reflect sexual dimorphism. Pronounced muscular attachments and articular ends of *C. ambulator*-shape humeri, demonstrating an adaptation for walking, is suggested to belong to females. Similar morphological variations of humeri in extinct aquatic reptiles are also considered to represent sexual dimorphism, supporting the hypothesis in champsosaurs. Extinct and extant terrestrial reptiles with *C. ambulator*-like femora suggest that *C. ambulator*-shape femora demonstrate an adaptation to a terrestrial environment, indicating that they belong to females. An extinct aquatic reptile with *C. laramiensis*-like femora suggests that *C. laramiensis*-shape femora demonstrate an adaptation to an aquatic environment, indicating that they belong to males. No significant variations of humeral and femoral morphologies and cortical hyperplasia occurred in femora in juveniles suggests an aquatic niche for them.

No microstructural variations were found between *C. laramiensis*-shape and *C. ambulator*-shape femora, thereby between hypothesized sexes, in spite of their morphological differences. Thick periosteal cortices observed in juvenile femoral diaphyses were replaced by dense spongy bone, forming medullar limb bones in late ontogenetic stages in both hypothesized sexes.

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APPROVAL

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## ABSTRACT

Two species of *Champsosaurus* (Diapsida, Choristodera), possessing distinctive humeral and femoral morphologies, occurred sympatrically in the Early Paleocene of Montana. The humeral ecto- and entotuberosities of *C. ambulator* are situated more distally than those of *C. laramieinsis*. The femoral internal trochanter is separated from the proximal articular surface in *C. ambulator*, but not in *C. laramiensis*. The phylogenetic significance of these limb morphologies is questioned because similar dimorphic variations occur in champsosaurs from other geological ages and locations.

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No microstructural variations were found between *C. laramiensis*-shape and *C. ambulator*-shape femora, thereby between hypothesized sexes, in spite of their morphological differences. Thick periosteal cortices observed in juvenile femoral diaphyses were replaced by dense spongy bone, forming amedullar limb bones in late ontogenetic stages in both hypothesized sexes.

## INTRODUCTION

*Champsosaurus* (Diapsida, Choristodera) was a semi-aquatic, fresh-water reptile found in rocks of the Late Cretaceous through Early Eocene of North America and the Paleocene of Europe. The dorsoventrally flattened body of *Champsosaurus* is hydrodynamically suited to an aquatic life, which is comparable to modern crocodiles (Figure 1). An elongated snout with many sharp teeth is observed commonly in fish-eating animals, such as gharial (*Gavialis gangeticus*), the fresh-water, long-snouted crocodile of India. Therefore, a piscivorous diet is suggested for champsosaurs. Gigantism occurred in champsosaurs (Langston, 1958), and therefore, the size of body varied within species. Adult champsosaurs in the Early Paleocene are estimated to have been two to three meters in length.

In 1876, Cope described an unknown fossil vertebrate specimen from the Judith River Formation of north-central Montana, assigning it to the order Choristodera, family Champsosauridae, *Champsosaurus annectens*. The presence of two sets of temporal fenestrae clearly indicates that the order Choristodera belongs to Diapsida, a subclass within the class Reptilia. However, its relationship among Diapsida remains debatable. Romer (1956, 1966) placed Choristodera in the order Eosuchia (Reptilia; Lepidosauria). Erickson (1972) included it within the infraclass Lepidosauromorpha.

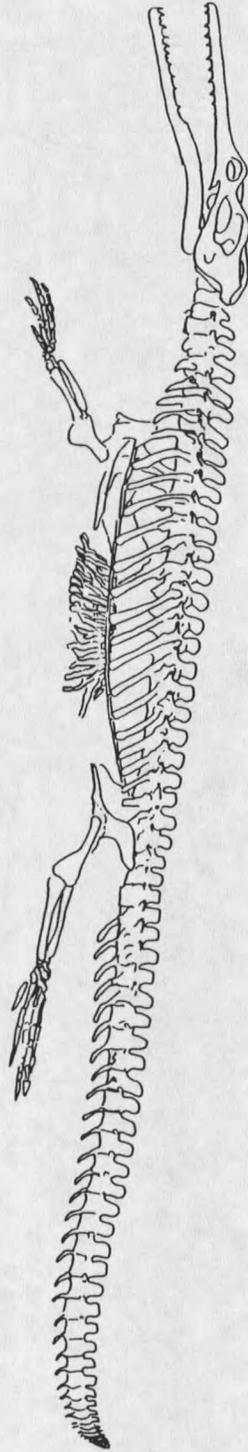
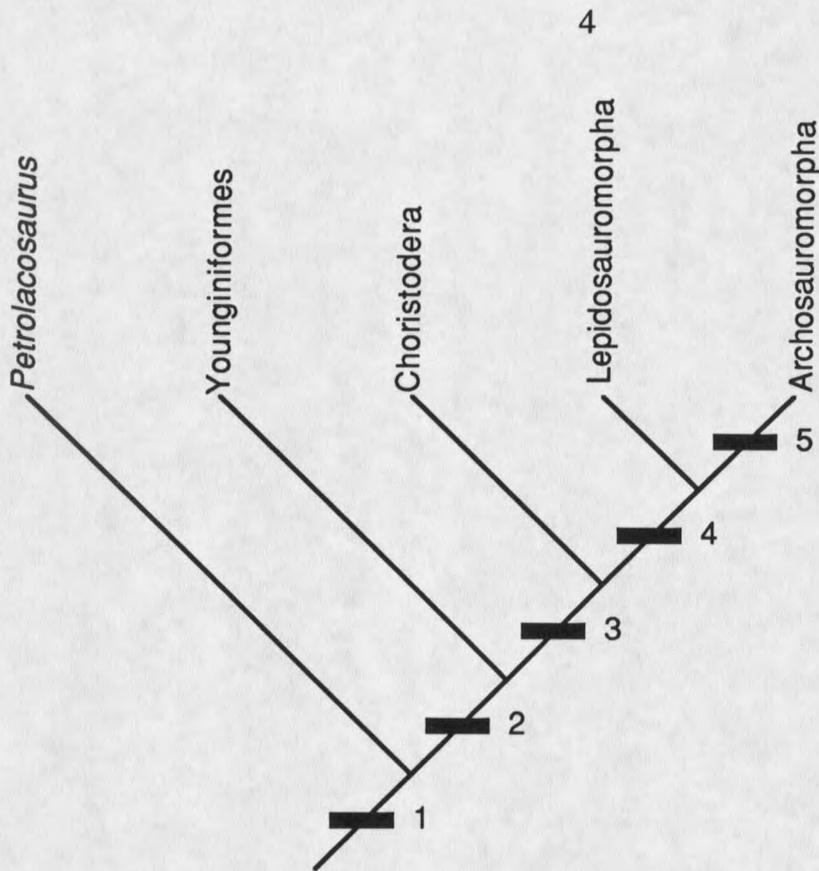


Figure 1. Reconstruction of the skeleton of *Champsosaurus*.  
It is based on Brown (1905) and Erickson (1985).

Using cladistic analysis, Benton (1985) placed the family Champsosauridae incertae sedis within the infraserie Diapsida. Erickson (1987) recategorized the order in the Archosauromorpha. Carroll (1988) stated that choristoderes were derived from eosuchians, but his non-cladistic classification placed the order incertae sedis within the subclass Diapsida. Evans (1988) included Choristodera within the superorder Archosauromorpha using cladistic analysis. However, Evans and Hecht (1993) excluded Choristodera from both Archosauromorpha and Lepidosauromorpha and considered it an early off-shoot within Diapsida with studies of the new genus, *Lazarussuchus*, described by Hecht (1992) (Figure 2).

Carroll (1988) included five genera in the family Champsosauridae, *Champsosaurus* (Cope, 1876), *Simoedosaurus* (Gervais, 1877), *Eotomistoma* (Young, 1964), *Tchoiria* (Efimov, 1975), and, *Khurendukhosaurus* (Sigogneau-Russell and Efimov, 1984). *Champsosaurus* occurred from the Late Cretaceous to Early Eocene in North America and Europe. *Simoedosaurus* is found in the Upper Paleocene of North America and Europe. *Tchoiria* and *Khurendukhosaurus* are found in the Lower Cretaceous rocks of Mongolia. The Upper Cretaceous of China produced *Eotomistoma* which Young (1964) originally described as a crocodylid. Sigogneau-Russell (1981) recognized that the type specimen of *Eotomistoma*, represented by the right half of a snout, belonged to a champsosaurid and therefore, described it as a new genus, *Ikechosaurus*. Carroll (1988) persisted in the use of the original genus name, *Eotomistoma*, but Evans (1989, 1990, 1991) and Hecht



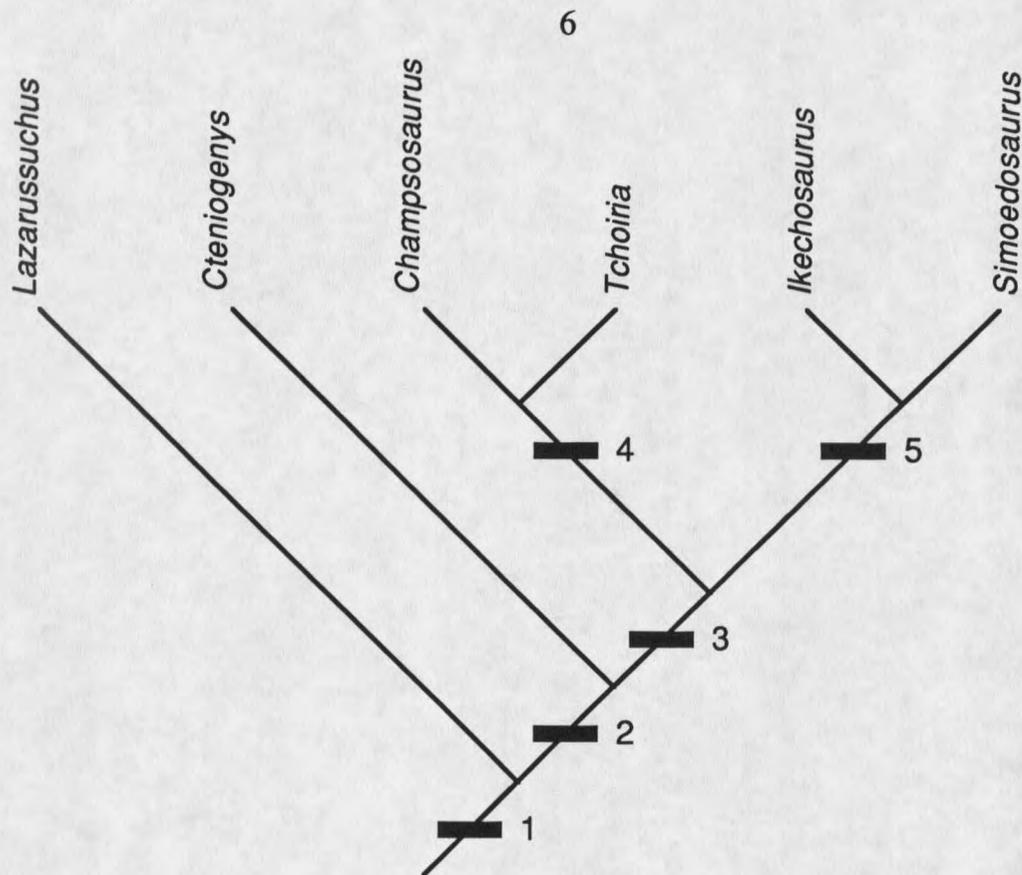
- Node 1: Lower and upper temporal fenestrae present; suborbital fenestra present; paroccipital process reaches suspensorium.
- Node 2: Ventral flanges on parietal; anteroventral process of squamosal narrow; trunk ribs mostly holocephalous; humeral ends robust.
- Node 3: Postparietal small or absent; tabulars absent; paroccipital process/cheek contact strong and broad; stapes slender and imperforate; no cleithrum; lateral centrale of manus small or absent; loss or fusion of fifth distal tarsal; hooked fifth metatarsal.
- Node 4: Prefrontal/nasal suture anterolaterally oriented; squamosal largely confined to dorsal half of skull; no tooth row on pterygoid flange; quadrate emargination present; well-developed retroarticular process.
- Node 5: Premaxilla with enlarged dorsolateral flange; external nares close to midline; pineal foramen reduced or absent; vertebrae not notochordal; dorsal transverse processes relatively long; cervical ribs dichococephalous; loss of entepicondylar foramen; no foramen between ulnare and intermedium; loss of medial centrale; presence of lateral calcaneal tuber; concave/convex joint between astragalus and calcaneum; metatarsal 4 elongated.

Figure 2. Cladogram of Diapsida suggested by Evans and Hecht (1993).

(1992) used the new genus name. Efimov (1983) described a new genus, *Irenosaurus*, recovered from the Lower Cretaceous of Mongolia.

Although choristoderes were once represented by these five moderate-sized genera living from the Cretaceous to Early Eocene, their phylogeny was recently reversed based on cladistic analyses. *Cteniogenys*, from the Middle Jurassic of the United States, England and Portugal, was originally identified as a lizard by Gilmore (1928). Using new material, the cladistic analysis suggested by Evans (1989) indicates that the genus belongs to the order Choristodera. Evans (1990) classified the choristoderes cladistically with 53 characters based primarily on the skull morphologies and recategorized these choristoderes into two groups, Champsosauridae (*Champsosaurus* and *Tchoiria*) and Simoedosauridae (*Simoedosaurus* and *Ikechosaurus*). Hecht (1992) described a new choristodere, *Lazarussuchus inexpectatus*, from the Oligocene of France, placing it within Choristodera using the phylogeny of Evans (1990) with five additional characters (Figure 3). The phylogenetic analysis indicates that the genus is most primitive among choristoderes although it occurred geologically later than the other genera.

Huene (1935) described *Pachystropheus rhaeticus*, from the Upper Triassic of Germany, as a choristodere. Romer (1966) tentatively placed this genus in the family Champsosauridae or Sphenodontidae (Lepidosauria; Rhynchocephalia). Carroll (1988) assigned it with some uncertainty to the family Sphenodontidae (Lepidosauromorpha; Sphenodonta), and Storrs and Gower (1993)



- Node 1: Elongation of preorbital skull; prefrontals meet in midline; pineal foramen lost; skull dorsoventrally compressed; loss or reduction of interpterygoid vacuity; reduced nasals; long, slender jaws with extended symphysis; first caudal incorporated into sacrum; caudal zygapophyses nearly or fully vertical.
- Node 2: Nares confluent; posterior displacement of choana; loss of metakinesis; palatal tooth batteries; hemispherical occipital condyle; notochordal canal closed; neurocentral sutures open; sacral and caudal ribs free; large free atlas pleurocentrum; unguis phalanges broad and low with reduced flexor tubercles.
- Node 3: Nasals fused; premaxilla without trace of dorsal process; small dorsally directed orbits; large posteriorly extended supratemporal fenestra; presacral vertebrae short and spool-like.
- Node 4: Narrow tapering preorbital skull; dentary symphysis extensive; postorbital free but excluded from orbit; reduced interpterygoid vacuity enclosed by pterygoids.
- Node 5: Tooth sockets transversely widened; relatively short, powerful preorbital skull; postorbital and postfrontal fused.

Figure 3. Cladogram of Choristodera suggested by Evans and Hecht (1993).

later placed it back within the Choristodera after studying new *Pachystropheus rhaeticus* material from the Upper Triassic of England. The modified humerus of *Pachystropheus* indicates that the geologically oldest choristodere was more adapted to an aquatic life than the others (Storrs and Gower, 1993). The cladogram of Choristodera excluded *Pachystropheus* because of the incompleteness of the specimens, especially the lack of the skull.

*Khurendukhosaurus* and *Irenosaurus* remain in an unknown position within Choristodera because of the lack of adequate materials. After examination of a new specimen, Brinkman and Dong (1993) suggested that *Ikechosaurus* is more closely related to *Champsosaurus* than *Simoedosaurus* because of the five derived cranial characters which *Ikechosaurus* and *Champsosaurus* share. However, their phylogenetic relationship remains debatable.

During most of the Cretaceous, the Western Interior Seaway extended north-south from the Gulf of Mexico to the Arctic, dividing the North American continent into two main land masses (Kauffman, 1977). As this seaway gradually withdrew during the Late Cretaceous and Early Paleocene, extensive basins opened on the eastern side of the highlands now represented by the Rocky Mountains. Alluvial systems were well developed there. The biogeographic distribution of champsosaurs ranged from present-day Alberta, Canada to New Mexico. No champsosaurs have been reported from the east side of the Western Interior Seaway.

Johnson and Hickey (1990) suggested, based on studies of the fossil flora, that this area changed to a sub-tropical or warm climate

in the Early Paleocene. Wolfe and Upchurch (1986) considered that the paleoclimate, initially represented by sub-humid, notophyllous, broad-leaved evergreen forests during the Late Cretaceous changed to successional mesothermal deciduous forests in the Early Paleocene. These climates provided an ideal habitat for aquatic and riparian vertebrates. Champsosaurs represented one of the main components of the riparian fauna from the Late Cretaceous throughout the Paleocene (Estes et al., 1969; Estes and Berberian, 1970; Russell, 1975; Estes, 1976; Lupton et al., 1980; Erickson, 1982; Hutchison, 1982; Bartels, 1983; Fiorillo, 1989; Katsura, 1992). Figure 4 shows the correlation and stratigraphic relationships of Upper Cretaceous and Paleocene rocks in eastern Montana and western North Dakota. All known champsosaur specimens have been recovered from terrestrial rocks except for some isolated elements found in the marine Bearpaw Shale (Figure 4). Erickson (1972) stated that these bones were carried to the sea by fluvial systems.

The Two Medicine Formation (Late Cretaceous) produces champsosaur material but not as abundantly as the Judith River Formation (Late Cretaceous) although deposition of the two formations are geologically equivalent. The Two Medicine Formation represents an upland deposition and is characterized by shallow stream channels with shallow floodbasin ponds and lakes. The climate was semi-arid and seasonal (Rogers, 1993 a; Varricchio, 1993). In contrast, the Judith River Formation was characterized by wider and deeper stream channels with swamps and floodplain ponds on the coastal plain, and its climate was humid (Rogers,















































































































































































