

REDESCRIPTION AND PHYLOGENETIC POSITION OF *CAYPULLISAURUS* (ICHTHYOSAURIA: OPHTHALMOSAURIDAE)

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ABSTRACT—The ophthalmosaurid *Caypullisaurus* from the Late Jurassic–Early Cretaceous of the Neuquén Basin, Argentina, is redescribed based on new information from recent discoveries. Cladistic analysis of *Caypullisaurus*, based on previous ichthyopterygian data sets and using NONA, yielded two most parsimonious trees. Two clades are recognized within the Ophthalmosauridae. *Caypullisaurus* is found to be nested with *Brachypterygius* and *Platypterygius*. Simultaneous, unconstrained analysis, using unambiguous character optimization, is suggested as the best way to analyze data sets with large amounts of missing data.

INTRODUCTION

TITHONIAN-AGE EXPOSURES of the Vaca Muerta Formation in the Neuquén Basin, Argentina, have yielded a rich marine reptile fauna (Gasparini, 1985; Gasparini and Fernández, 1997). Among this fauna, ichthyosaurs are the most common reptiles. Most of the ichthyosaur material is referred to *Caypullisaurus bonapartei* Fernández, 1997. This species was named based on the holotype, an adult ichthyosaur from Cerro Lotena (early Tithonian, Vaca Muerta Formation) which is the most complete skeleton of a mature ichthyosaur from the Jurassic of South America, as well as on other specimens from the Museo de La Plata collection. *Caypullisaurus* Fernández, 1997 has been included in cladistic analyses of the Ichthyosauria carried out by Motani (1999) and Maisch and Matzke (2000). Both analyses found *Caypullisaurus* to be an ophthalmosaurid; but its position within the clade differs between the two. One of the main problems in the analysis of the relationships of *Caypullisaurus* is that most of the skull sutures cannot be seen in the holotype. Thus, in Motani's (1999) and Maisch and Matzke (2000) data set, a high percentage of characters are scored as missing in *Caypullisaurus*.

Recently, and as a result of extensive field work carried out in Tithonian and Berriasian exposures of the Vaca Muerta Formation in the Neuquén Basin (32°–41°S, 68°–72°W), Argentina, new material referable to this species has been collected. In addition, our knowledge of the group has significantly increased since the original description of *Caypullisaurus*. This information about *Caypullisaurus* allows more extensive description of its morphology and reevaluation of its phylogenetic affinities.

MATERIALS AND METHODS

The following taxa for cladistic analysis were used as terminals: *Cymbospondylus piscosus* Leidy, 1868; *Stenopterygius* Jaekel, 1904; *Ichthyosaurus* de la Beche and Conybeare, 1821; *Mollisaurus* Fernández, 1999; *Brachypterygius* Huene, 1922; *Aegirosaurus* Bardet and Fernández, 2000; *Ophthalmosaurus* Seeley, 1874; *Caypullisaurus*, and *Platypterygius* Huene, 1922. Twenty-five characters (Appendix) were scored. Some of the characters have been taken from Motani (1999) and new information has been included. The character codings for taxa in this data matrix (Appendix) is based on personal examination of the material, except for *Cymbospondylus piscosus*, which was scored based on the descriptions and reconstructions of Sander (1989, 2000), Motani (1999), and McGowan and Motani (2003). Multistate characters were treated as non-additive (=unordered). *Cymbospondylus piscosus* sensu McGowan and Motani (2003) was chosen as root. Character polarity was determined a posteriori using simultaneous, unconstrained analysis. This method was selected because it often gives more parsimonious results than two-step, constrained analysis which includes a priori determination

of character polarity (Kitching et al., 1998). The data matrix was analyzed with Goloboff's (1998) parsimony program NONA. The exact method (Multiple Swapper option of NONA: MS+) was used. This option produces exact solutions for a data matrix of 18 taxa or less. Suboptimal trees, two steps longer, were retained in memory to calculate individual clade support using Relative Support (Goloboff and Farris, 2001).

For comparative purposes, and in order to compare clade definitions, the data sets of Motani (1999) and Maisch and Matzke (2000) were reanalyzed with NONA. As these data sets included more than 18 taxa, NONA was run using heuristic searches with random addition sequences and swapping by tree-bisection reconnection (mult*20; max*). Character optimization was carried out using WINCLADA (Nixon, 2002).

Abbreviations.—The following abbreviations are used to refer to repositories of specimens: MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires, Argentina); MLP, Museo de La Plata (La Plata, Argentina); MOZ, Museo Prof. P. Olsacher (Zapala, Neuquén Province, Argentina); QM, Queensland Museum, Australia.

Key to abbreviations used in figures: a, astragalus; an, angular; bo, basioccipital; c, calcaneum; d, dentary; exn, external nares; j, jugal; l, lacrimal; m, maxilla; n, nasal; pm, premaxilla; po, post-orbital; prf, prefrontal; ptf, postfrontal; q, quadrate; qj, quadrato-jugal; sa, surangular; sq, squamosal; st, supratemporal. Arabic numerals are distal tarsals, roman numerals are metatarsals.

SYSTEMATIC PALEONTOLOGY

Family OPHTHALMOSAURIDAE Baur, 1887
Genus CAYPULLISAURUS Fernández, 1997
CAYPULLISAURUS BONAPARTEI Fernández, 1997
Figures 1, 2

?*Platypterygius* sp. indet. GASPARINI AND GOÑI, 1990, p. 303, pl. 2, figs. 4, 5.

Ophthalmosaurus sp. indet. GASPARINI AND FERNÁNDEZ, 1997, fig. 3e.

Emended diagnosis.—Premaxilla-lachrymal contact below nares broad; postorbital region of skull not reduced; maxilla laterally exposed extending further anteriorly; humerus with three distal facets, anterior one being the smallest, articulating with preaxial accessory element and bearing two digits distally; large intermedium placed between radiale and ulnare, not between radius and ulna; distal border of radius straight and almost parallel to anterior border of intermedium and to distal facets of humerus for radius; phalanges polygonal and tightly packed.

Description.—New material from north of Neuquén Province permits better knowledge of *Caypullisaurus bonapartei*, principally related to the delimitation of bones of postorbital region. Both MOZ 6139 (Fig. 1.1, 1.2) and MOZ 6097 (Fig. 1.3, 1.4),

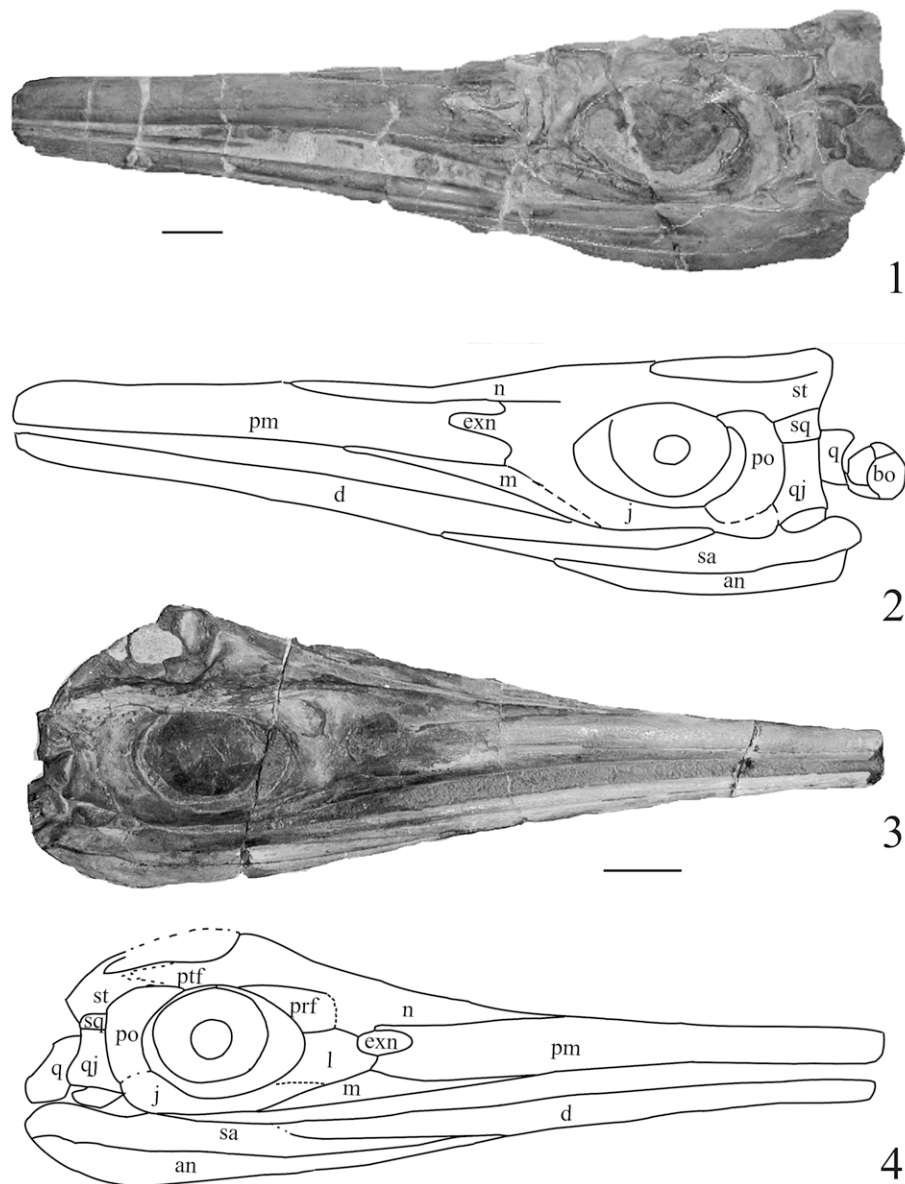


FIGURE 1—*Caypullisaurus bonapartei* Fernández, 1997, skulls. 1, 2, MOZ 6139 from Yesera del Tromen, Berriasian, Vaca Muerta Formation; 3, 4, MOZ 6067 from Trincajuera Creek, late Tithonian, Vaca Muerta Formation. Scale bars equal 10 cm.

have almost complete skulls and mandibles and have been preserved laterally compressed. In both, ventral edges of rostrum not prepared, so no details of dentition can be observed.

Based on skull length, *C. bonapartei* can be considered as a moderately large ichthyosaur. Skull of largest specimen (MOZ 6139) 1,515 mm long. Skull of *C. bonapartei* has robust and deep rostrum, with moderately large orbit and broad postorbital segment.

Premaxilla robust and deep, especially compared with that of other members of clade, such as *Ophthalmosaurus* and *Aegirosaurus*. Posteriorly, supranarial process makes a large contribution to dorsal edge of external nares while infranarial process has broad contact with lachrymal, excluding maxilla from ventral edge of external nares. Maxilla well exposed laterally, and its anterior portion forms a thin process extending well forward of external nares. Condition similar to one described in *Brachypterygius* (McGowan, 1976; Kirton, 1983). Since all specimens

known are laterally compressed, arrangement of skull roof bones difficult to distinguish. Nasal has no conspicuous features resembling nasals of *Ophthalmosaurus* as described by Kirton (1983). In MOZ 6139, nasal has small descending process on dorsal edge of external nares. Of all bones surrounding the orbit anterodorsally and dorsally, only prefrontal of MOZ 6097 can be traced with confidence. Extension of this bone in lateral view in *C. bonapartei* similar to that of *Brachypterygius* (Kirton, 1983, p. 113) and *Platypterygius australis* (M'Coy, 1867) (QM 2453). Thus, the prefrontal of these taxa forms less than half of anterior orbit margin, while in *Ophthalmosaurus* and *Aegirosaurus* it is more than half of margin. Sutures of prefrontal have been tentatively traced in the holotype of *Platypterygius sachicarum* Páramo, 1997) but the reconstruction of Páramo (1997, figs. 2, 3) suggests that this bone has a similar extension to that of *C. bonapartei*.

Postorbital area can be better detailed in MOZ 6097 (Fig. 1.3, 1.4). Postorbital region broad and most formed by postorbital.

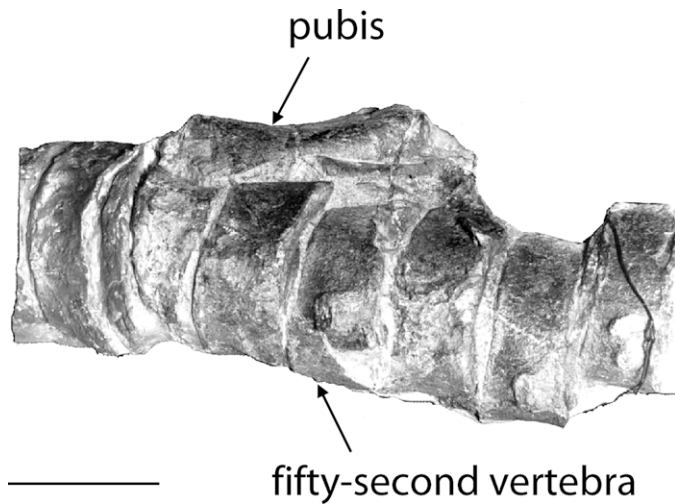


FIGURE 2—*C. bonapartei* holotype, MACN-N-32. Part of the vertebral column and pubis. Scale bar equals 10 cm.

Outline of this bone well defined along most of its extension in MOZ 6097 and MOZ 6139, although ventral union with jugal cannot be distinguished. Postorbital contacts postfrontal anterodorsally, supratemporal posterodorsally, squamosal and quadratojugal posteriorly, and jugal ventrally. As in *Platypterygius*, quadratojugal well exposed posterior to postorbital. Height approximately half height of postorbital region. Squamosal limited dorsally by supratemporal, anteriorly the posterior orbital, and ventrally the quadratojugal. This bone is roughly quadrangular both in MOZ 6097 and MOZ 6139. Within the clade Ophthalmosauria, squamosal has been described in *Ophthalmosaurus* and *Aegirosaurus*. Presence of this bone cannot be confirmed in *Brachypterygius* due to poor preservation of postorbital region. In *Platypterygius*, this bone seems to be absent, or at least not exposed in lateral view. In *Ophthalmosaurus* and *Aegirosaurus*, squamosal has an anterodorsally directed process, which contacts postfrontal. By contrast, in *Caypullisaurus*, squamosal more reduced and has no contact with postfrontal. Quadrate partly exposed in MLP 85-I-15-1 (Fernández, 1998, fig. 1) in MOZ 6097 and MOZ 6139. It has no different features from the one described in *Ophthalmosaurus* (Kirton, 1983). Basioccipital has been preserved in MOZ 6139 (Fig. 1.1, 1.2). It is displaced from its anatomical position and rotated in such a way that the condyle is pointing laterally. Broad area of condyle damaged. Condyle surrounded by relatively reduced extracondylar area. Reduction of area observed in *Caypullisaurus* similar to that of *Ophthalmosaurus*. Presence of laterally, well-exposed angular reaching as far anteriorly as surangular the most conspicuous character of mandible. This feature diagnostic of Ophthalmosauria (Motani, 1999).

New material of *Caypullisaurus* added no new information on postcranium from that given in previous papers (Fernández, 1997, 1998, 2001). However, our knowledge of ichthyosaur anatomy and its phylogenetic significance has increased since the original description of *Caypullisaurus* (Fernández, 1997) (Motani, 1999; McGowan and Motani, 2003). In this new context, two parts of *Caypullisaurus*'s postcranium are worthy of redescription: a pelvic girdle element and hindfin. In the holotype, a bone has been preserved attached to the fifty-first, fifty-second, and fifty-third trunk vertebrae (Fig. 2). Bone, 168 mm long, has a columnar aspect for most of its length and not curved. One of its ends slightly more expanded and lateromedially more compressed than the other, and therefore here identified as the distal end. From the three elements of pelvic girdle, bone identified as a pubis, as it is

TABLE 1.—Character matrix used for cladistic analysis.

Taxa	Characters																								
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
<i>Cymbospondylus piscosus</i>	0	0	0	0	0	1	0	0	1	?	?	1	1	0	0	0	0	0	?	0	0	0	?	0	0
<i>Stenopterygius</i>	0&1	2	0	1	1	1	0	0	0	?	0	1	0	1	0	0	0	0	1	0	0	0	1	2	1
<i>Ichthyosaurus</i>	1	2	0	0	1	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	0&1	2	2
<i>Mollesaurus</i>	2	2	0	?	?	?	?	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Brachypterygius</i>	?	1	?	?	?	?	0	0	0	1	2	0	0	1	1	0	1	2	1	0	1	0	?	?	?
<i>Aegirosaurus</i>	2	2	1	0	1	1	1	?	?	?	1	0	0	1	1	0	1	2	1	0	1	0	0	2	?
<i>Ophthalmosaurus</i>	1	2	1	0	1	0	1	0	0	1	1	0	0	1	1	1	1	2	1	0	1	0	0	2	2
<i>Caypullisaurus</i>	2	1	0&1	?	?	?	1	0	0	?	1	0	0	1	1	1	0	2	1	1	1	1	0	0	?
<i>Platypterygius</i>	2	1	0&1	1	2	1	0	?	?	?	2	0	0	1	1	0	0	2	1	0	1	1	?	?	?

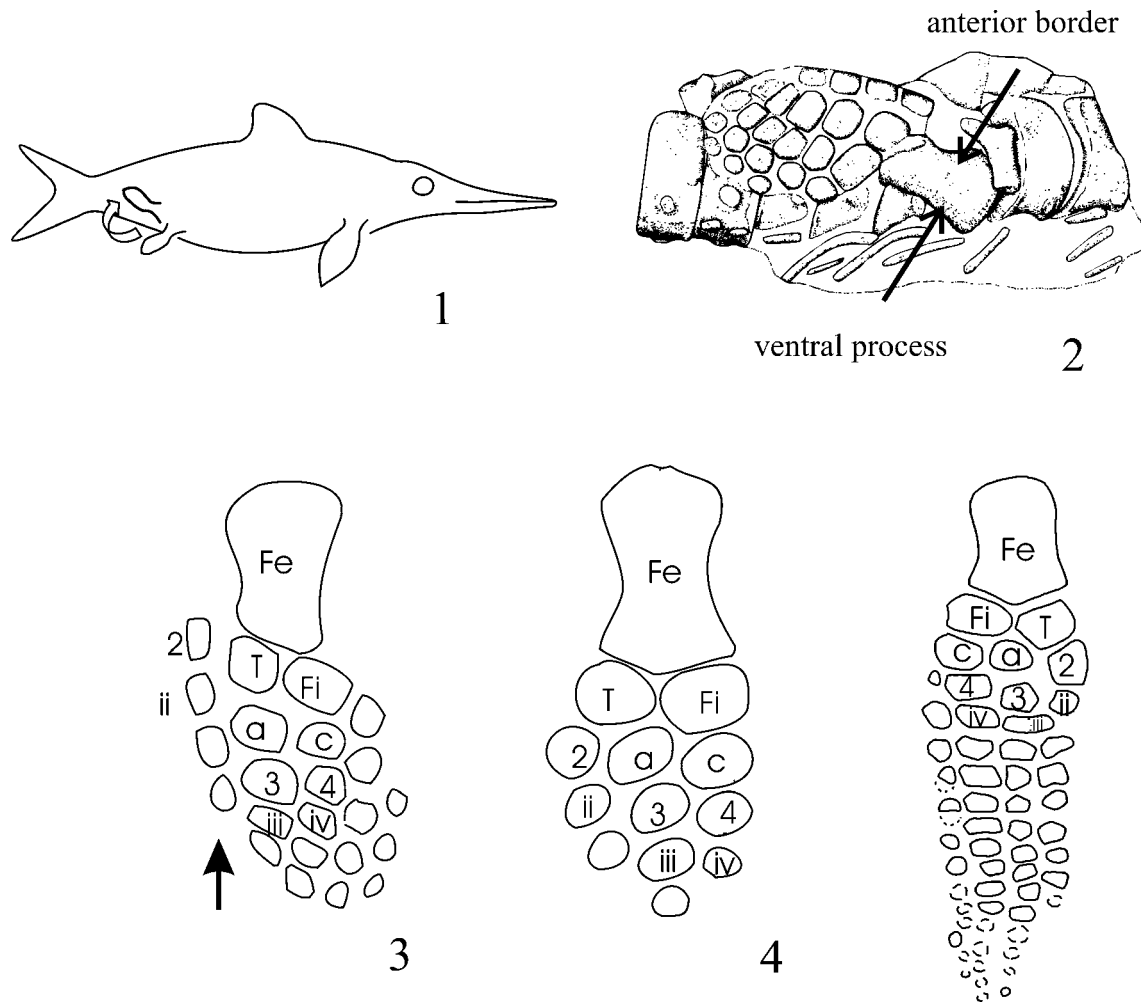


FIGURE 3—1, Diagram showing postmortem displacement of the MLP 86-XI-16-1 hindfin (arrow); 2, part of the vertebral column and right hindfin exposed in ventral view of MLP 86-XI-16-1; 3, right hindfin of MLP 86-XI-16-1 in ventral view; 4, left hindfin in dorsal view of *Ophthalmosaurus* (modified from McGowan and Motani, 2003); 5, right hindfin in dorsal view of *Aegirosaurus* (modified from Bardet and Fernández, 2000). 3–5, not to scale.

not curved as the ilium, and proximal and distal ends approximately the same width. By contrast, the ischium of Jurassic ichthyosaurs known (McGowan and Motani, 2003) is remarkably broader distally than proximally. In the holotype, proximal end of pubis partially broken, while anterior, posterior, and distal borders well preserved. No evidence of fusion with ischium. If fusion between pubis and ischium were present it must have been compressed only in its more proximal part of both elements.

Hindfin preserved articulated in MLP 83-XI-16-1. Fin particularly significant as its femur is three-dimensionally preserved, and its original orientation to remaining part of fin, as well as its relative position to the vertebral column, do not show great post-mortem displacement. As shown in Figure 3.1, hindfin rotated after death in such a way that it is preserved with its ventral surface exposed laterodorsally and overlying vertebral column (Fig. 3.2). Such preservation of hindfin of MLP 83-XI-16-1 is unusual and helps to resolve the problem of the correct orientation of femur, and therefore to evaluate whether provisional identification of femur features proposed on basis of isolated femora of *Ophthalmosaurus* (Kirton, 1983; McGowan and Motani, 2003) is correct. *Ophthalmosaurian* hindfins are poorly known. Most material described or figured (e.g., Andrews, 1910; Kirton, 1983) corresponds to disarticulated *Ophthalmosaurus* (Fig. 3.4). From

other members of clade only hindfin of *Aegirosaurus* known (Bardet and Fernández, 2000).

Preserved hindfin of MLP 83-XI-16-1 is the right one, and is included in a single block with a string of six vertebral centra. A fragment of a probable neural arch that was overlying the proximal part of the femur (Fernández, 1997, fig. 6) removed, as well as matrix surrounding femur. Femur has on its ventral surface a strong crestlike process very similar to one described in *Ophthalmosaurus* (McGowan and Motani, 2003) and, as in this genus, this process is located approximately equidistant from the anterior and posterior borders. Its extension is half the length of the femur and continues distally as a subtle ridge. In ventral view anterior border almost straight while proximal half curves distally. Small hollowed area between anterior border of femur and ventral process. Posterior border in this view curved along most of its length. Distally, facet for tibia slightly smaller than facet for the fibula, anteroproximally directed. Based on above description, provisional orientation of femur given by Kirton (1983) and McGowan and Motani (2003) is correct.

Tibia smaller than fibula. Two elements, distal to tibia and fibula, here tentatively identified as astragalus and calcaneum. Distal tarsals 3 and 4, metatarsals 3 and 4; and digits 3 and 4 identified distal to these elements. Anterior to digit 3 there is a digit that

here is interpreted as being slightly displaced anteriorly postmortem (Fig. 3.3). As in *Aegirosaurus* (Fig. 3.5), there is a digit posterior to digit 4, but in *Caypullisaurus* another accessory digit is added. Such a broad paddle has not been described for the other ophthalmosaurids.

Type.—Holotype, MACN-N-32. Skull and mandible, pectoral girdle, both forefins, and 53 articulated vertebrae and associated ribs from Cerro Lotena (39°11'S, 69°40'W).

Other material examined.—The redescription is based on the examination of the holotype and four other specimens also excavated from the Vaca Muerta Formation in the Neuquén Basin: MLP 83-XI-16-1, approximately 48 semiarticulated associated ribs, proximal part of right forefin with humerus, partial pectoral girdle, complete hindfin from Cerro Lotena (early Tithonian); MLP 85-I-15-1, skull and part of the forefin from Chacay Melehue (late Tithonian); MOZ-P6097, complete skull and mandible (Trincajuer Creek, late Tithonian); MOZ-P6139, skull and vertebrae (Yesera del Tromen, Berriasian).

Occurrence.—Vaca Muerta Formation (Tithonian–Berriasian), Neuquén and Mendoza provinces, Argentina (Spalletti et al., 1999).

PHYLOGENETIC RELATIONSHIPS OF *CAYPULLISAURUS*

The cladistic analysis produced two most parsimonious trees with a tree length of 39, consistency index (for informative characters only) of 0.70, and a retention index of 0.66 (Fig. 4). The topology of the strict consensus of these trees is congruent with the previous relationships proposed by Motani (1999) for *Stenopterygius*, *Ichthyosaurus*, and Ophthalmosauridae. *Stenopterygius* is in a basal position with *Ichthyosaurus* as the sister taxon of the Ophthalmosauridae.

The monophyly of the Ophthalmosauridae is confirmed. There are three unequivocal synapomorphies for this group: the angular largely exposed laterally (character 11), the platelike ridge on the humerus (character 14), and the presence of an extrazeugopodial element anterior to the radius (character 20).

Under unambiguous optimization (Fig. 4.1), clade definitions are as follows. Within the Ophthalmosauridae, the position of *Mollesaurus* is not resolved. The remaining genera are grouped in two clades. One includes *Ophthalmosaurus* and *Aegirosaurus*, and the other clade includes *Brachypterygius*, *Caypullisaurus*, and *Platypterygius*. The relationship of *Aegirosaurus* and *Ophthalmosaurus* is justified by three synapomorphies: the presence of a descending process of the nasal on the dorsal border of the nares (character 2), the triangular outline of the squamosal (character 4 state 1), and the postorbital is narrow (character 7 state 1). The monophyly of *Brachypterygius*, *Caypullisaurus*, and *Platypterygius* is supported by the long and narrow anterior process of the maxilla (character 1 state 1).

Under fast (ACCTRAN) optimization (Fig. 4.2), better resolution and clade support are obtained. *Mollesaurus* is placed as the sister taxon of *Aegirosaurus* and *Ophthalmosaurus*. The clade formed by these three taxa is supported by the medial and lateral ischium-pubis fusion in adults (character 23 state 2). The clade formed by *Brachypterygius*, *Caypullisaurus*, and *Platypterygius* is supported by the long and narrow anterior process of the maxilla (character 1 state 1), by the nasal and parietal contact (character 3), by the extreme reduction of the extracondylar area of the basioccipital (character 10 state 2), and by the presence of more than one anterior accessory digit in the forefin (character 21 state 1).

Under slow (DELTRAN) optimization (Fig. 4.3), the same topology is obtained, but the monophyly of the [*Mollesaurus* (*Aegirosaurus*, *Ophthalmosaurus*)] clade is supported by the moderate reduction of the extracondylar area of the basioccipital (character 10 state 1). Although clade definition and resolution of

ophthalmosaurid interrelationships are slightly improved under fast or slow optimizations, the unambiguous optimization is preferred here, as it is more conservative, especially due to the large amount of missing data. Thus, under fast optimization the clade formed by *Mollesaurus*, *Aegirosaurus*, and *Ophthalmosaurus* is supported by a missing value in *Mollesaurus* (23 state 2). Under slow optimization it assumes that the transformation of character 10 state 1 is unordered.

Mollesaurus is only known by part of its skull (Fernández, 1999). Consequently, 68% of the characters scored in the analysis are missing. As missing values can produce spurious cladograms, *Mollesaurus* was removed in a second analysis. Elimination of *Mollesaurus* proved to be safe (Wilkinson and Benton, 1995) as it does not alter topological relationships or increase the resolution. This second analysis found two trees of 39 steps (CI = 0.70; RI = 0.65).

Reanalysis of Motani's (1999) and Maisch and Matzke's (2000) data sets.—Simultaneous, unconstrained analysis of Motani (1999) was carried out using NONA. Heuristic searches found four trees (234 steps, CI = 0.59, RI = 0.84). Although this result is better than the one found by Motani (1999), the strict consensus tree shows the same topological relationships of the ichthyopterygian genera to the one published by Motani (1999, fig. 1). When *Aegirosaurus* is scored and included in this data set, using the same methodology, eight trees were found (244 steps, CI = 0.57; RI = 0.85). The strict consensus tree topology of the Ophthalmosauridae genera, as well as the location of *Ichthyosaurus* as its sister taxon, does not change: [*Ichthyosaurus* (*Brachypterygius*, *Aegirosaurus* (*Ophthalmosaurus* (*Caypullisaurus* *Platypterygius*)))].

To reanalyze the Maisch and Matzke (2000) data set, the all-zero ancestral outgroup was removed, and trees were rooted using *Thaisaurus* Mazin et al., 1991 as root. The methodology was the same as the one used to analyze Motani's (1999) data set. The heuristic searches found four trees (187 steps, CI = 0.65, RI = 0.89). *Stenopterygius* was found to be the sister taxon to Ophthalmosauridae. Within this last clade, only the relationship between *Ophthalmosaurus* and *Caypullisaurus* is resolved.

DISCUSSION

The hypothesis of the ingroup relationships of the Ophthalmosauridae as presented here agrees with the previous proposals of Motani (1999) and Maisch and Matzke (2000) in considering Callovian and post-Callovian ichthyosaurs as a monophyletic group, but the internal topology of this clade is different. According to Motani (1999), the phylogenetic sequence within the Ophthalmosauridae is: *Brachypterygius*, *Ophthalmosaurus*, *Caypullisaurus*, and *Platypterygius*. *Aegirosaurus* was not included as it was described a year later by Bardet and Fernández (2000).

Maisch and Matzke (2000) included *Aegirosaurus* in their data set. Although Callovian and post-Callovian ichthyosaurs form a single clade in their phylogenetic analysis, they did not consider *Aegirosaurus* as a member of the Family Ophthalmosauridae (Maisch and Matzke, 2000, p. 100).

There are two different clades within Ophthalmosauridae, one including the most stout ichthyosaurs (*Platypterygius*, *Caypullisaurus*, and *Brachypterygius*) and the other including *Aegirosaurus* and *Ophthalmosaurus*. The analysis also suggests that *Mollesaurus* is the sister taxon of *Aegirosaurus* and *Ophthalmosaurus*. However, as this proposal depends on assumptions about character transformations and, consequently, is not unambiguously supported, the location of *Mollesaurus* is unresolved at this stage.

The results produced by the reanalysis of Motani's (1999) and

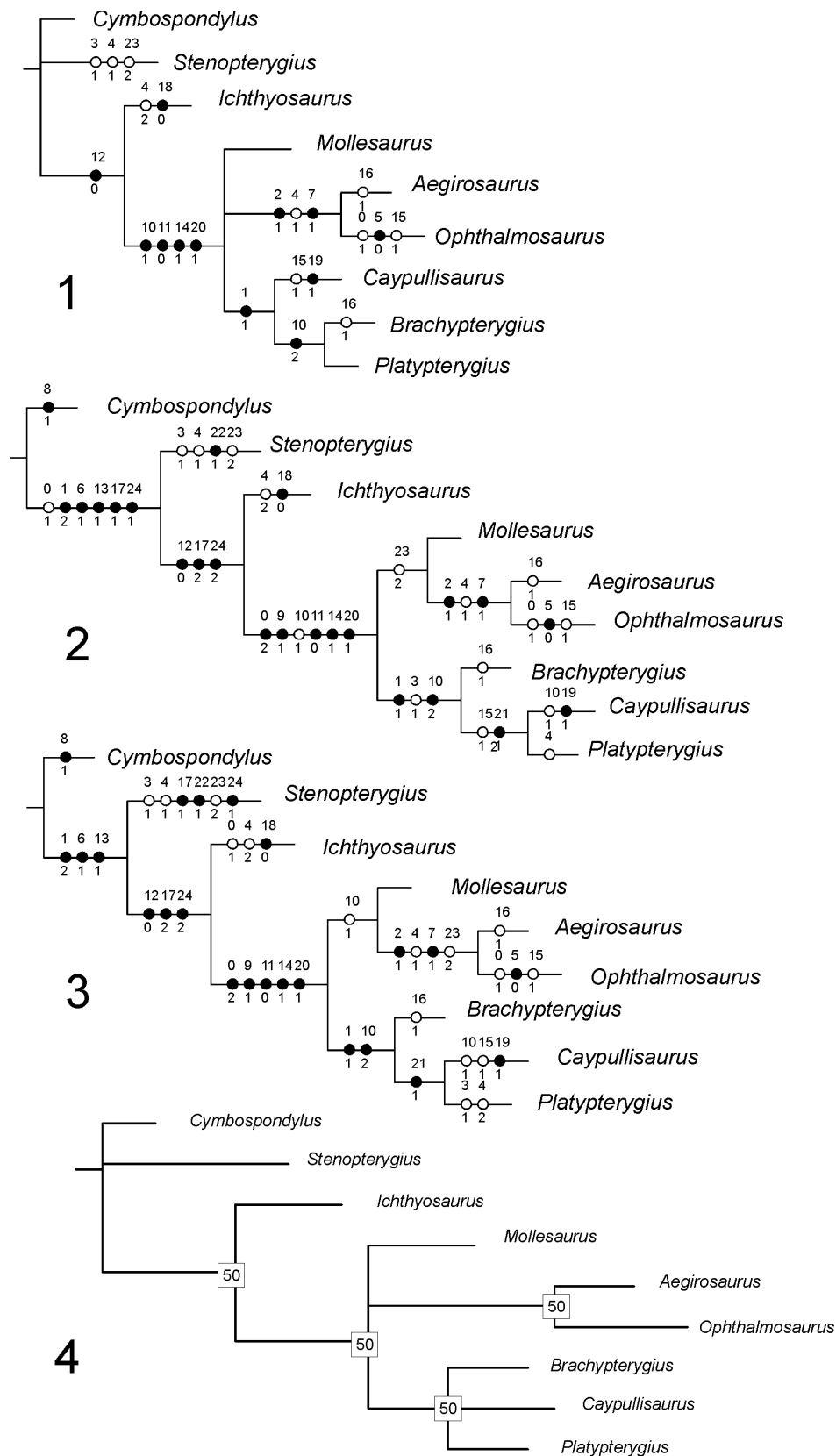


FIGURE 4—Phylogenetic position of *Caypullisaurus* Fernández, 1997 within the Ophthalmosauridae and different character optimizations. 1–3, One of the shortest trees; 4, strict consensus of two shortest trees obtained by NONA. Solid circles represent nonhomoplastic characters, open circles represent homoplastic characters, numbers above and below circles represent number of character and character states respectively, and numbers in squares indicate relative branch support (Goloboff and Farris, 2001); 1, unambiguous optimization; 2, fast (ACCTRAN) optimization; 3, slow (DELTRAN) optimization. See text for details on optimization discussion.

Maisch and Matzke's (2000) data set suggest an interesting methodological point. Commonly, criteria for choosing a character optimization method are not discussed in cladistic analysis, and ACCTRAN optimization is used in most analysis based on the proposal of De Pinna (1991). Nevertheless, the selection of a criterion to optimize character transformations acquires significance in the presence of missing data, as these can decrease the resolution (increasing the number of equally most parsimonious trees) and even produce spurious trees not supported by any possible combination of real values (Kitching et al., 1998).

An example of this emerges from the reanalysis of Motani's (1999) and Maisch and Matzke's (2000) data sets. The differences between the results obtained when such matrices are analyzed with NONA may be explained in terms of the criterion selected to collapse branches. Motani (1999) found 12 trees (254 steps) using the heuristic searches option of PAUP* 4D64 for DOS, while here four trees of 234 steps were found using NONA. PAUP* 4D64 for DOS forces us to choose between accelerated or delayed transformations, while NONA has a switch to disallow ambiguous optimization leading to strictly supported cladograms. When Motani's (1999) data set was analyzed allowing ambiguous optimizations (ambiguous = in NONA), twelve trees of 234 steps are found.

In the case of Maisch and Matzke's (2000) data set, the differences cannot be so clearly interpreted. According to Maisch and Matzke (2000, fig. 37) six most parsimonious trees of 192 steps were found. In all of these trees, *Aegirosaurus* is the sister taxon of the remaining Ophthalmosauridae. When this data set (including the all-zero ancestor) is re-analyzed with NONA to allow unambiguous optimizations, 24 trees of 196 steps are found. In the strict consensus, however, the position of *Aegirosaurus* is not resolved, although it is included within the remaining Ophthalmosauridae. Removing the all-zero ancestor and allowing ambiguous optimization resulted in 27 trees (187 steps). The strict consensus tree also found the position of *Aegirosaurus* to be unresolved.

When Kitching et al. (1998) analyzed optimization alternatives and the effects of missing values, they concluded that the preferred cladogram is the one of minimum length and with all its nodes unambiguously supported by data (strictly supported cladogram), and this is the criterion followed here. Based on the results from the reexamination of Motani's (1999) and Maisch and Matzke's (2000) data sets, it seems acceptable to analyze data sets with large numbers of missing character states to use programs that allow unambiguous optimizations to explore whether some of the cladograms are spurious or are supported by assumptions regarding character transformations.

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APPENDIX

Characters and data matrix used to analyze the phylogenetic position of *Caypullisaurus*. ? indicates missing data.

Cranial characters.—

0. Premaxilla/lacrimal contact below the external nares: (0) absent; (1) narrow; (2) broad. Maisch and Matzke (1997: character 1) and Motani (1999: character 3) defined this character as maxilla/external nares contact. Nevertheless, the maxilla could be excluded from the narial border to different degrees. In some forms such as *Caypullisaurus*, there is a broad contact between the premaxilla and lacrimal excluding the maxilla from the nares. In other forms, this contact is very narrow as in *Ophthalmosaurus*.
1. Anterior process of the maxilla in lateral view: (0) long and broad; (1) long and narrow; (2) short.
2. Descending process of the nasal on the posterior dorsal border of the nares: (0) absent; (1) present.
3. Nasal/parietal contact lateral to frontal: (0) absent; (1) present (Motani, 1999: character 7).
4. Squamosal: (0) without posterior descending process; (1) squamosal with a posterior descending process; (2) squamosal absent.
5. Sagittal eminence: (0) absent; (1) present but small (modified from Motani, 1999: character 16). Maisch and Matzke (2000: character 15) expressed this character as: continuous high sagittal crest on nasal, frontal and parietal absent (0) or present (1) and scored (0) for *Caypullisaurus*. Nevertheless, the *Caypullisaurus* specimens that I

examined have poorly preserved skull roofs so this character could not be recorded.

6. Right and left parietals' anterior process: (0) narrowly separated anteriorly, forming parietal fork, and frontal dorsally visible along the pineal foramen; (1) widely open, resulting in absence of clear fork (modified from Motani, 1999: character 19).
7. Postorbital: (0) broad; (1) narrow. This character is probably correlated with proportional enlargement of the orbit. In this paper it is preferred to use the postorbital narrowing as the orbit size cannot be used in incomplete skulls.
8. Interpterygoid vacuity: (0) present; (1) absent or extremely reduced (modified from Motani, 1999: character 27).
9. Basioccipital peg: clearly present (0); absent or extremely reduced (1) (Motani, 1999: character 29). This character could not be scored for *Caypullisaurus* as the only basioccipital known (MOZ 6139) has not been completely removed and its anterior face is still included in the matrix.
10. Extracondylar area of the basioccipital: (0) wide; (1) reduced; (2) extremely reduced (modified from Motani, 1999: character 30).
11. Angular lateral exposure: (0) extensive; (1) much smaller than surangular exposure (Motani, 1999: character 32).

Postcranial characters.—

12. Humerus distal and proximal ends: (0) nearly equal; (1) distal end wider than proximal end (Motani, 1999: character 55).
13. Humerus anterior flange: (0) present and complete; (1) present but reduced proximally (modified from Motani, 1999: character 53).
14. Ridge on the humerus platelike. (0) present; (1) absent (modified from Motani, 1999: character 56).
15. Humerus anterodistal facet for sesamoid: (0) absent; (1) present (modified from Godefroit, 1993: character 10 and Motani, 1999: character 57).
16. Humerus/intermedium contact: (0) absent; (1) present.
17. Radius peripheral "shaft": (0) complete; (1) notch or nearly complete; (2) absent (Motani, 1999: character 59).
18. Ulnare/intermedium relative size: (0) ulnare larger than the intermedium; (1) intermedium larger than the ulnare (Motani, 1999: character 66).
19. Location of the intermedium: (0) between radius and ulna; (1) distal to the ulna.
20. Extrazugopodial element anterior to the radius: (0) absent; (1) present (Motani, 1999: character 75).
21. More than one anterior accessory digit: (0) absent; (1) present.
22. Manual accessory digit between digits IV and V: (0) absent; (1) present (Motani, 1999: character 73).
23. Ischium-pubis fusion in adults: (0) absent; (1) present only medially; (2) present medially and laterally (modified from Motani, 1999: character 83).
24. Tibia peripheral shaft: (0) complete or nearly complete; (1) notched or largely reduced; (2) absent (Motani, 1999: character 92).