ABSTRACT—We present the description and taxonomic reassignment of a new genus and species, *Atacamaia solitaria*, gen. et sp. nov., from Lower Jurassic strata of northern Chile, South America. The fish is characterized by a combination of numerous intriguing characters, such as the presence of a broad parietal bone partially covered laterally by a series of a few large superciliary bones, a series of sclerotic bones, a lachrymojugal expanded anteriorly and markedly angled, and a metapterygoid with a well-developed ventral process that is ventral to the dorsal margin of the pterygoid plate. Addition of *Atacamaia* to previously published matrices produces unexpected collapses of certain nodes in the currently accepted phylogenetic hypothesis of Actinistia, creating many polytomies in the consensus tree. Our cladistic analysis suggests that *Atacamaia*, gen. et sp. nov., *Axelia*, and *Wimania* are closely related and together with *Piveteauchthys*, *Guizhoucoelacanthus*, and *Whiteia* are members of the order Coelacanthiformes. Based on previous analyses and our results, we recognize this grouping as the family Whiteidae. Members of Whiteidae are Triassic forms, except *Atacamaia solitaria*, gen. et sp. nov., from the Early Jurassic. The new fossil actinistian represents the youngest member of the family and the first discovered on the Paleopacific side of Gondwana; all other members are from China, Madagascar, and Spitsbergen. After comparison of previous hypotheses, we review the higher level taxonomy of Actinistia concerning the monophyly of Coelacanthiformes, Latimerioidei, Mawsoniidae, and Latimeriidae and propose a family diagnosis for Whiteidae.

http://zoobank.org/urn:lsid:zoobank.org:pub:1CE8B66D-30D2-44EB-87EF-882628478C3B

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Coelacanthiformes, a group of sarcopterygian fishes only known today by two species—*Latimeria chalumnae* and *L. menadoensis*—is represented by fossils from the Early Devonian (e.g., Cloutier, 1990; Schultze, 1993; Forey, 1998; Johanson et al., 2006) to the Late Cretaceous (e.g., Dutel et al., 2013). During the last few years, several new Mesozoic actinistians have been discovered and others have been revisited, increasing the knowledge of a group that is largely based on incompletely preserved specimens. A few examples are *Guizhoucoelacanthus* from the Middle–Upper Triassic of China (Geng et al., 2009) and *Luoipingoelacanthus eurylacrimalis* and *Yunnancoelacanthus acrotuberculatus* from the Lower Triassic of China (Wen et al., 2013). *Parnaibaia maranhaoensis* from the Lower Cretaceous of Brazil (Yabumoto, 2008), *Axelrodichthys araripensis* (e.g., Brito et al., 2010; Yabumoto and Brito, 2013), *Mawsonia* sp. from the Upper Jurassic–Lower Cretaceous of Uruguay (Soto et al., 2013), *Megalocoelacanthus* from the Upper Cretaceous of North America (Dutel et al., 2012), *Rebellatrix divaricera* from the Lower Triassic of British Columbia, Canada (Wendruff and Wilson, 2012), *Ticinopomis peyeri* from the Middle Triassic of Switzerland (Cavin et al., 2013), and *Dobrogeria aegyssensis* from the Lower Triassic of Romania (Cavin and Grădinaru, 2014).

The oldest South American sarcopterygian, *Coelacanthus* cf. *C. granulatus*, was reported from the upper Permian, Vitacua Formation, Bolivia (Janvier, 1992). Four coelacanthiform species are currently recognized in the Upper Jurassic and Lower Cretaceous of South America. Those fossils have been recovered on the Atlantic side of the continent, in Brazil and Uruguay, and have been assigned to the family Mawsoniidae, with three unquestionable genera represented in the continent: *Axelrodichthys* (Maisey, 1986), *Mawsonia* (Woodward, 1907 in Mawson and Woodward, 1907; Maisey, 1991), and *Parnaibaia* (Yabumoto, 2008). Currently, only two species are considered valid within *Mawsonia* (*M. gigas* and *M. tegumenstis*; Carvalho and Maisey, 2008). Recently, the southernmost occurrence of *Mawsonia* was reported from the Upper Jurassic–lowest Cretaceous of Uruguay (Soto et al., 2013).

A head of a coelacanth was recovered in the lower-to-middle Sinemurian (Lower Jurassic) of Quebrada Vaquillas Altas, Atacama Desert, northern Chile, during an expedition supported by National Geographic Society in 1994. The material was reported (but not described) as Actinistia, gen. nov., within the family Mawsoniidae by Arratia and Schultze (1999; following Cloutier, 1991), based on a few features, such as the shape of the palatoquadrate and an ‘L’-shaped postparietal. Although numerous fossil fishes (e.g., four genera of crossopterygiforms: *Arratia* and Schultze, 1985; and undescribed remnants of ganoid neopterygians: *Arratia*, 1987; *Arratia* and Schultze, 1999), have been reported from the Oxfordian (Upper Jurassic) of Domeyko Range in the Atacama Desert, only fragments of small leptolepid-like teleosts (*Arratia*, 1987; *Arratia* and Schultze, 1999; *Arratia* and Hikuroa, 2010) and the actinistian here described have been recovered in the lower-to-middle Sinemurian of Quebrada Vaquillas Altas.
Here we present a detailed description of the first fossil actinistian recovered in northern Chile, on the Pacific side of South America. A phylogenetic analysis of 35 taxa is performed to clarify the phylogenetic position of the Chilean fossil fish. The fish, only known from its head, exhibits a combination of characters that impacts the accepted phylogenetic hypothesis of Actinistia.

**Geologic Context and Age**

The studied specimen was recovered in the lower-to-middle Sinemurian (Lower Jurassic) of Quebrada Vaquillas Altas, Domeyko Range in the Atacama Desert, northern Chile. The age of the locality is based on numerous ammonites such as *Arnicoeras* sp., *Eparietites* sp., *Euasteroceras* sp., *Asteroxeras* sp., and the bivalve *Otapiria pacifica* (Covacevich and Escobar, 1979; Naranjo and Covacevich, 1979; Arratia, 1987; Arratia and Schultze, 1999). Previously, the locality was placed in the middle Sinemurian (Hillebrandt, 1971; Chong, 1977).

**Materials and Methods**

The material studied, a head of an actinistian (Fig. 1) represented by the lateral and medial views of the right side, was prepared mechanically by professional preparators under a binocular microscope. Neither abrasive machines nor chemicals were used because of the fragile nature of the specimen. Computer tomographic (CT) scanning was done at the Shared Materials Instrumentation Facility (SMIF) at Duke University. However, no optimal results were obtained due to the scarcity of bone preservation and the lateral compression of the head.

Illustrations of the specimen were prepared by the first author using a Wild FM 8 and a Leica MZ9 stereomicroscope equipped with a camera lucida. Thus, illustrations are based directly on specimens rather than on photographs. Photographs are not retouched or edited with Photoshop. The latter was only used to label figures.

**Phylogenetic Methodology**

The phylogenetic analyses were conducted using PAUP* (Phylogenetic Analysis Using Parsimony) software (version 4.0b10) for 32-bit Microsoft Windows (Swofford, 2002). The character matrix was constructed using MacClade for the analysis to run in PAUP*. All characters are unweighted, unordered, and considered to be independent of one another. The phylogenetic analysis used the list of characters of Forey (1998) and Dutel et al. (2012), with modifications noted (see Supplementary Data, Appendix S1). The data matrix with scoring of characters is presented in Supplementary Data, Appendix S2.

**Institutional Abbreviation—MNHN SGO.PV, Museo Nacional de Historia Natural, Santiago, Chile.**

**Systematic Paleontology**

**Actinistia** Cope, 1871

**Actinistia** Cope, 1871

**Ectantocephaliformes** Cope, 1871

**COELACANTHIFORMES** Huxley, 1861

**COELOPITUS** Huxley, 1861

**WHYTEIIDAE** Schultze, 1993

**Diagnosis**—Actinistia of moderate size, about 40–50 cm total length, characterized by the following unique combination of features: premaxilla with a dorsal lamina; anterior opening of the rostral organ contained within the premaxilla; supraorbital sensory canal opens as single pores through the supraorbital bones; jugal sensory canal with prominent branches; jugal sensory canal positioned in the center of the squamosal bone; pit-lines on postparietals; process on braincase for articulation of infrabranchial 1 present; and number of fin rays in first dorsal fin less than 8.

**Content**—The following genera are recognized within the family: *Atacamaia*, gen. nov., *Axelia*, *Guizhoucoelacanthus*, *Piveteauia*, *Whiteia*, and *Wimania*. See Supplementary Data, Table S1, for details in number of species, geographical distribution, and age of the species (see also, Broom, 1905; Moy-Thomas, 1935; Nielsen, 1936; Beltan, 1966; Gardiner, 1966; Elliott, 1987; and Liu et al., 2006).

**Comment**—The family name Whiteiidae was erected by Schultze (1993), without a diagnosis. Thus, this is the first diagnosis proposed for the family and it is based on a unique combination of characters.

**Atacamaia**, gen. nov. (Mawsoniidae); Arratia and Schultze, 1999:575, fig. 11.

**Diagnosis**—Based on a unique combination of characters: actinistian with postparietal shield shorter than the parietonasal shield, but broader; parietonasal and postparietal shields with raised areas; posterior margin of the postparietal shield deeply embayed and sunken in the median region; slightly ‘L’-shaped postparietal; supratemporal posterolaterally expanded; one pair of parietal bones present; parietal bones broad and partially overlapped by supraorbital bones laterally; dorsal half of orbit surrounded by sclerotic bones; lachrymojugal expanded anteriorly, and markedly angled; narrow, rectangular postorbital, metapterygoid with a well-developed ventral process that is ventral to dorsal margin of pterygoid plate; surface of skull roof bones covered by tiny tubercles and ridges; and angular covered by dense, coarse rugosities and tubercles.

**Etymology**—The generic name *Atacamaia* refers to the Atacama Desert in northern Chile, where the fossil was recovered.

**Atacamaia solitaria**, sp. nov. (Figs. 1–6)

**Diagnosis**—Same as genus.

**Etymology**—The specific name *solitaria* refers to the fact that this is the only Mesozoic coelacanthiform recovered on the Pacific side of the Gondwanan continents.

**Holotype**—MNHN SGO.PV 288. The specimen was collected by Kate Shaw during the 1994 expedition to the Atacama Desert under the leadership of the authors.

**Type Locality and Geologic Age**—Quebrada Vaquillas Altas, Domeyko Range, Atacama Desert, northern Chile (25°20′70″S/69°22′00″W longitude). The age of the rocks has been assigned to the Lower Jurassic, middle-to-upper Sinemurian (about 195–191 Ma; Covacevich and Escobar, 1979; Naranjo and Covacevich, 1979).

**Description**

The fish is only known by its head (Fig. 1), which is about 80 mm long and 60 mm deep (measuring the exposed lateral side). The head is partially three-dimensionally preserved, with lateral compression, so that part of the skull roof and the right lateral side of the head are observed in the same view. Palatoquadrate and branchial arches are preserved in medial view on the left side of the specimen. The head is damaged by the presence of a deep fracture that divides it, and numerous small fractures. The main fractures are represented in the illustrations as hatched areas. Remains of some identified bones of the braincase are observed close to the posterior border of the head in postero medial view.

Considering the approximate size of the head, the fish probably reached 40 cm in total length by comparison with other actinistians. The orbit is relatively large, with a diameter of about 25% of the preserved head length—the anterior tip of the snout is missing.

**Skull Roofing Bones**—The skull bones (Figs. 2, 4) covering the dorsal region of the neurocranium anterior to the level of
FIGURE 1. *Atacamaia solitaria*, gen. et sp. nov. Holotype MNHN SGO.PV 288 from the Lower Jurassic of Vaquillas Altas, Atacama Desert, Chile. Photograph of the dorsolateral view of the head. Scale bar equals 1 cm.

FIGURE 2. *Atacamaia solitaria*, gen. et sp. nov. Holotype MNHN SGO.PV 288 from the Lower Jurassic of Vaquillas Altas, Atacama Desert, Chile. Photograph of the skull roof. The focus of the photograph is centered in the medial region of the skull. Scale bar equals 1 cm.
the intracranial joint comprise an unknown number of nasal bones, the parietals, and supraorbitals. Posterior to the intracranial joint are the postparietals and supratemporals. All these bones are strongly sutured together. The surfaces of the parietal and postparietal are not flat. They present irregular raised areas, especially at both sides of the midline of the cranial roof so that the regions of the interparietal and interpostparietal sutures are deeper than the surrounding lateral sides. In contrast, the incompletely preserved nasal region shows a markedly anteroventral inclination that suggests the skull roof was not much longer anteriorly. The surface of the skull roofing bones is partially weathered, but it is still possible to observe regions that are covered by minuscule teeth. The few ridges radiate from posterior to anterior direction, diverging slightly from each other on the parieto-nasal shield, whereas they are numerous on the supratemporal.

The intracranial joint can be described as transversely undulated or with a posterior curvature at its mid-region. The position of the intracranial joint is not easily observed because the bones are partially broken, and in front of the fissure is a transverse breakage of the posterior region of the parietonasal shield that could be confused with the joint. The intracranial joint separates both the parietonasal and the postparietal shields. The parieto-nasal shield is longer than the postparietal shield. Thick, heavily ossified bones form both shields.

Only one pair of parietal bones (Figs. 3, 4) is present in Ata-camaia, gen. nov. They are broad in comparison with parietals of other members of the family. The dorsal aspect of the cranial roof shows that the left parietal broadens anteriorly to the position of the orbit, an unusual condition in coelacanthiforms. The interparietal suture is straight in its anterior part and slightly wavy in its posterior part, and it should not be confused

FIGURE 3. Atacamaia solitaria, gen. et sp. nov. Holotype MNHN SGO PV 288 from the Lower Jurassic of Vaquillas Altas, Atacama Desert, Chile. Camera lucida drawing of the dorsolateral view of the right side of the cranium. White square represents the area where a displaced piece of the parasphenoid covered with minuscule teeth is observed. The black arrow points to the intracranial joint. Hatched areas represent major fractures. Abbreviations: Ang, angular; Gu?, gular plate?; Lj, lachrymojugal; LR, lateral rostral; Mtg, metapterygoid; Na, nasal bone; Op, operculum; Pa, parietal bone; Ppa, postparietal bone; Preo, preorbital bone; Ptg, pterygoid plate; Qu, quadrate; Po, postorbital bone; S.o, sclerotic ossicles; Sob, supraorbital bone; Stt, supratemporal. Scale bar equals 1 cm.
with an incomplete longitudinal fracture that is parallel to the interparietal suture. The lateral surface of the right parietal is partially covered by remnants of supraorbital bones, which gives the skull roof a protruding lateral margin. The parietals suture anteriorly with the nasal bones, which are partially broken. The surface of each parietal is ornamented with small tubercles, which are still preserved in the posterolateral portion of the bones, and has radiating ridges close to the medial margin.

The number of nasal and rostral bones cannot be assessed because the most anterior region of the skull roof is missing. Sutures between supraorbital bones (Figs. 3, 4) are difficult to observe, but the supraorbitals seem to be moderately broad and large, and few in number, probably five. In dorsal view, the most anterior supraorbital is square and is the smallest of the series. The bones increase in size posteriorly, the fourth supraorbital being the largest. It is unclear if such a large bone is really one, because an incomplete division (suture) is seen under different light conditions. The supraorbitals are heavily ossified and ornamented by rugosities and tubercles that obscure the trajectory of the small pores of the supraorbital canal. The sensory pores open to the surface in an irregular fashion (Figs. 3, 4), and their number is difficult to see depending on the angle of observation. Based on the position of the sensory pores, we think that the trajectory of the canal was through the center of ossification of the supraorbitals, rather than closer to the suture with the parietal. Lateroventral to the second and third preserved supraorbitals is a big space that probably represents part of the ethmoidal region, and it was laterally covered by supraorbitals that were ventrolaterally expanded, as seen in some actinistians, such as *Whiteia woodwardi* (Forey, 1998; Lehman, 1952) and *Diplurus newarki* (Schaefter, 1952).

A preorbital bone (Fig. 3) is positioned lateroventral to the first and second preserved supraorbitals. The bone is moderately small and is sutured with the anterior region of the lacrymojugal and a lateral rostral, which is broken anteriorly.

The postparietal shield (Fig. 4) is formed by two halves that seem to be asymmetrical due to the position of the suture joining both postparietals medially. In general, the shape of the bones resembles that of an ‘L’ visible on the right side, whereas the left postparietal is not completely preserved. The postparietals occupy most of the surface of the postparietal shield. The surface of the postparietals is not flattened, but formed by prominent areas laterally and a markedly sunken median region, especially close to the posterior margin of the shield. Such surface morphology gives the postparietal shield a characteristic aspect of a ‘valley surrounded by hills.’ The posterior margin of the postparietal shield is markedly embayed, especially at its median region. In its most anterior portion, the postparietal shield is broader than the parietonasal shield, and it becomes progressively expanded posteriorly. The suture joining both postparietals is difficult to observe, but it seems to be interdigitated anteriorly and becomes straighter near the posterior margin of the postparietal shield. The lateral portion of the postparietal shield is covered by tubercles and rugosities, but the middle region is ornamented with slightly radiating ridges.

Pit-lines are difficult to observe due to the coarse ornamentation, but a short, narrow groove on the right postparietal is interpreted as a middle pit-line (Fig. 4); a series of small pits on the left postparietal probably represents the posterior pit-line.
A somewhat oval-shaped area near to the anterior margin of the postparietal is interpreted here as the medial branch of the otic canal. There are some irregularly positioned sensory pores opening in the postparietals that probably belong to the otic canal.

The course of the suture between the postparietal and supratemporal is slightly irregular and is obscured by the presence of numerous small tubercles and grooves. The supratemporal (Figs. 3, 4) is a large, slightly rectangular bone that is slightly shorter than the length of the postparietal. Its posteroverentral region is markedly bent. There are numerous small pores of slightly different sizes that make it difficult to follow the course of the canals, but based on the available information, we think that the otic, supratemporal, and postotic canals meet in the supratemporal. There are a few pieces of bones posteroverentral to the supratemporal and postparietal that are interpreted here as remnants of extrascapulars.

Cheek Bones—Only the sclerotic ossicles, lachrymojugal, and postorbital are preserved; in other words, only the elements surrounding the orbit are preserved. From the opercular series, only the operculum is preserved, and it will be described in this section.

The orbit is incompletely surrounded by 10 sclerotic ossicles (Figs. 3, 4) placed dorsally. Ossicles are lacking in the ventral part of the orbit, an arrangement only observed in this species. The anterior-most three sclerotic ossicles are small; they are followed by five elements that are slightly larger and deeper, with the ninth sclerotic ossicle being the largest of the series. It is possible that all ossicles placed dorsal to the orbit were as deep as the ninth ossicle, because of the large gap between the sclerotic ossicles and the lateral border of the supraorbitals.

An elongate lachrymojugal (Fig. 3) lies beneath the orbit. It is slightly sigmoidal-shaped, but curves anteriorly, producing an angle between the anterior tip of the bone and its main part. The anterior tip of the lachrymojugal is slightly expanded. The infraorbital canal is positioned almost at the mid-region of the lachrymojugal and is partially exposed due to damage on the external surface of the lachrymojugal. Numerous short sensory tubules branch in the lower part of the main canal; however, they are only seen under high magnification. A better description of sensory tubules and/or pores of the infraorbital canal is not possible due to incomplete preservation.

Behind the orbit, forming its posterior margin, lies the postorbital (Fig. 3), which is an elongate, rectangular bone. The postorbital is positioned mainly in front of the intracranial joint. The trajectory of the infraorbital canal is observed along the middle region of the bone, but no sensory pores open to the surface. The surface of the postorbital is covered by coarse rugosities and tubercle-like ornaments.

The operculum (Fig. 3) is a large bone that is posterior to the postorbital region of an enormous palatoquadrate, which is laterally exposed. The exact shape of the operculum is unknown, because its dorsal margin is hidden below the supratemporal and the posteroverentral margin is apparently not completely preserved. When the bone is reconstructed, it seems to be so large that there is no space for a suboperculum. The surface of the operculum is eroded, but a few remnants of ornamentation are preserved.

Jaws and Gular Plates—The lower jaw is represented only by a large and massive angular bone (Fig. 3), preserved in lateral view. Considering that apparently the lower jaw is missing a small, anterior portion, this would mean that the angular was very large and the dentary very small. The angular in other actinistians is elongate, but in Atacamaia, gen. nov., it is very deep anteriorly and narrower posteriorly, making interpretation difficult. The surface of the lower jaw is covered by a coarse ornamentation formed by rugosities and tubercles. No mandibular teeth or sockets for teeth have been observed. However, in a section of the angular, where the external surface of the bone is damaged, a small piece of bone covered with minute dentition is preserved. We interpret this piece as part of a displaced...
parasphenoid because of dentition being present and its setting in the bone. Below the lower jaw a narrow piece of bone is preserved. Because of its position, it could represent the lateral margin of the right gular plate (Fig. 3).

**Palatoquadrate**—The strongly ossified palatoquadrate (Figs. 5, 6) has a characteristic shape that is usually described as triangular in actinistians, and it is also short and very deep. The palatoquadrate consists of the pterygoid plate anteriorly, the metapterygoid posterodorsally, and the quadrate posteroven-trally. Its anterior pars autopalatine or autopalatine is not preserved. Its general shape is somewhat similar to that of *Latimeria*, but unlike *Latimeria*, the metapterygoid and quadrate are linked by bone in *Atacamaia*, gen. nov.

The metapterygoid (Figs. 5, 6) is a massive bone, apparently as large as that of *Megalocoelacanthus* (Dutel et al., 2012: fig. 11A) in relative size. The metapterygoid has a complex articulatory dorsal surface that is saddle-shaped, as has been described for other actinistians (e.g., Cloutier, 1990, 1991; Forey, 1998). The metapterygoid displays a well-developed ventral process that is ventral to the dorsal margin of the pterygoid plate (Fig. 6). In general, it is extremely difficult to describe and illustrate the bone because of its lateral protuberant areas and deep regions.

The quadrate (Figs. 1, 3) is a robust bone oriented vertically and with a double condyle for articulation with the lower jaw ventrally. Although both condyles are incompletely preserved, their asymmetric orientation can be observed on the right side of the head. The medial view of the head (Fig. 6) preserves a piece of the left quadrate in lateral view. Our interpretation is based on the fact that the external surface of the bone is ornamented. Due to the special features of the metapterygoid and quadrate, it was suggested to distinguish them from those of acanthodian and actinopterygians and to identify them as actinistian metapterygoid and quadrate (Arratia and Schultze, 1991).

The pterygoid plate (Figs. 3, 6) is somewhat triangular, very broad posteriorly, but markedly narrower anteriorly, with a sharp curvature at the anterior half of the preserved portion.

**FIGURE 6.** *Atacamaia solitaria*, gen. et sp. nov. Holotype MNHN SGO PV 288 from the Lower Jurassic of Vaquillas Altas, Atacama Desert, Chile. Camera lucida drawing of the medial view of the cranium. Abbreviations: Cbb, ceratobranchial bones; Mtg, metapterygoid; Ptg, pterygoid plate; Qu, quadrate Scale bar equals 1 cm.
The internal surface of the pterygoid plate is smooth. Below the pterygoid plate, fragments of other bones are preserved. It could be possible that these fragments could be part of the hyoid arch or the ‘urohyal’—the special actinistian urohyal (Arratia and Schultze, 1990).

**Branchial Arches**—Pieces of very long bones that here are interpreted as ceratobranchials (Fig. 6) are preserved in medial view. No dentition associated with the ceratobranchials has been observed.

**PHYLOGENETIC ANALYSIS**

To assess the phylogenetic relationships of actinistians, we conducted a cladistic analysis of 35 genera scored for 109 characters. The list of characters (Appendix S1) is mainly based on Forey (1998) like all recent analyses (Geng et al., 2009; Wendruff and Wilson, 2012; Cavin et al., 2013; Wen et al., 2013; Cavin and Grădinaru, 2014), with a few modifications from Dutel et al. (2013) and the addition of a few character states to accommodate the new fossil taxon, Atacamaia, which are explained in Appendix S1. The character-taxon matrix (Appendix S2) excludes three actinistian genera (Garnbergia, Indocoeoelacanthus, and Lualabea) that were included in the phylogenetic analysis of Forey (1998), due to their large amount of ambiguous or missing characters (‘?’). The total matrix has 37.1% of character states coded with question marks (nonapplicable characters are not included in this count). Polarization of characters is based on comparison with two outgroups, actinopterygians and porolepiforms (Forey, 1998). A second cladistic analysis was performed with characters from the head only.

**Cladistic Analysis 1**

The parsimony analysis with 35 genera recovered 2811 equally parsimonious trees of 289 steps (retention index = 0.6876; consistency index = 0.4152). Character-state optimization: ACCTRAN.

**Phylogenetic Results**—The topology of the consensus tree (Fig. 7) shows that the phylogenetic relationships within Actinistia (node A) are mostly unresolved at the basal nodes B and C; in contrast, node D (Coelacanthiformes) is mostly resolved. The topology of the consensus tree places Atacamaia, gen. nov., within the order Coelacanthiformes.

The monophyly of Actinistia (Fig. 7, node A) is supported by five synapomorphies: preorbital bone present (char. 10[1]); quadrate jugal absent (char. 33[0]); processus connectens failing to meet the parasphenoid (char. 71[1]); temporal excavation not lined with bone (char. 74[1]); and extracleithrum present (char. 88[1]). The last character is interpreted as uniquely derived among actinistians.

The monophyly of Coelacanthiformes (Fig. 7, node D) is supported by the following synapomorphies: intracranial joint with straight margin (char. 1[0]); processus connectens meeting parasphenoid (char. 71[0]); supraocciptal bone present (char. 76[1]); closed buccophyph生理 canal (char. 78[0]); prootic with complex suture with basioccipital (char. 82[1]); and a separate basioccipital present (char. 86[1]). The parsimony analysis interprets characters 82(1) and 86(1) as uniquely derived.

Among coelacanthiforms, Atacamaia, gen. nov., stands in a trichotomy with Axelilia and Wimania. This trichotomy is the sister to the polytomy formed by Piveteauia, Guizhoucoelacanthus, and Whiteia. We identify this clade as the family Whiteidae (Fig. 7, node E); its diagnosis is presented in the Systematic Paleontology section of this paper. The following characters support this node: jugal sensory canal with prominent branches (char. 46[1]); jugal canal running through center of bone (char. 47[0]); a process on braincase for articulation of infrabranchial 1 present (char. 84[1]); and number of fin rays in dorsal fin 1–8 (char. 96[2]). Although the four character states are unknown in

**FIGURE 7.** Result of the first phylogenetic analysis based on 35 actinistian taxa and 109 characters. Consensus tree of 2811 equally parsimonious at 289 evolutionary steps; consistency index: 0.4146; retention index: 0.6929. Numbers in italics represent bootstrap values over 50. See text and Appendix S1 for explanation of characters. Unique derived characters represented with an asterisk (*). Node A (Actinistia): 10[1], 33[0], 71[1], 74[1], and 88[1]. Node D (Coelacanthiformes): 1[0], 71[0], 76[1], 78[0], 82[1], and 86[1]. Node E (Whiteidae): 46[1], 47[0], 84[1], and 96[2]. Node E1: 1[2], 2[1], 7[0], 17[2], and 31[0]. Node F: 10[0], 27[1], and 42[1]. Node G: 13[1], 17[2], 35[1], 51[1], 52[0], 53[1], 91[1], 96[1], and 98[1]. Node G1 (Mawsoniidae): 14[0] and 56[0]. Node G2 (Latimeriidae): 3[1], 22[1]*, 30[0], 60[1], 79[1], and 109[1]*. Atacamaia, the parsimony analysis predicts that they were present in this taxon.

The trichotomy (Fig. 7, node E1) is supported by the following synapomorphies: intracranial joint margin undulated or excavated (char. 1[2]) as the condition present in Atacamaia and Axelilia, in contrast to Wimania with a straight intracranial joint; snout bones consolidated or tightly joined (char. 2[1]); one pair of
parietal bones (char. 7[0]); seven or more extrascapular bones (char. 17[2]); and preoperculum absent (char. 31[0]). The last two characters were coded with a question mark for Atacamaia. The last may be a correct prediction because no remnant of a preoperculum is found in the studied specimen of Atacamaia.

Axelia, Whiteia, and Wimania were included in the phylogenetic analysis of Forey (1998) and were interpreted as Coelacanthiformes incertae sedis. More recently, the Chinese coelacanthiform Guizhoucoelacanthus was added to the matrix of Forey (1998), and the topology of the consensus tree placed Guizhoucoelacanthus as the sister group of [Piveteauia + Whiteia] in a clade identified as the family Whiteiidae (Geng et al., 2009). Dutel et al. (2012:fig. 21; Fig. 8 herein) included two additional genera in their cladistic analysis, Axelia and Wimania, and the topology of their consensus tree shows the following arrangement: [Piveteauia + Whiteia + [Guizhoucoelacanthus + Axelia + Wimania]]. The inclusion of the new coelacanthiform Atacamaia produces significant changes to previous interpretations of this clade, leaving unresolved the phylogenetic position of Piveteauia, Whiteia, Guizhoucoelacanthus, and the trichotomy formed by Axelia + Wimania + Atacamaia.

Node F stands at the branching of Coelacanthus + the suborder Latimerioidei (node G). Three synapomorphies support this node: preorbital bone absent (char. 10[0]); parietal and postparietal bones unornamented (char. 27[1]); and postorbital bone reduced to a narrow tube surrounding the sensory canal only (char. 42[1]). Node F: 10[0], 27[1], and 42[1].

A trichotomy including Ticinepomis, the family Mawsoniidae, and the family Latimeriidae stands at the branching of the suborder Latimerioidei (Fig. 7, node G), which is supported by the following synapomorphies: postparietal descending process present (char. 13[1]); seven or more extrascapulars (char. 17[2]); lachrymojugal expanded anteriorly (char. 35[1]); lachrymojugal lying in a sutural contact with the supraorbital series (char. 51[1]).
sclerotic ossicles absent (char. 52[0]); retroarticular and articular separated (char. 53[1]); occipital neural arches expanded (char. 91 [1]); eight or nine fin rays in the first dorsal fin or D1 (char. 96[1]); and first dorsal fin or D1 with denticles (char. 98[1]). Although the topology of node G appears resolved in our analysis, it is partially resolved in Figure 8 (Dutel et al., 2012).

The family Mawsoniidae (Fig. 7, node G1) containing the genera Diplurus, Paranaibaia, Chinlea, Mawsonia, and Axelrodichthys is completely resolved in the parsimony analysis, and its monophyly is supported by two reversals: supratemporal descending process absent (char. 14[0]) and unmodified coronoid opposite to the posterior end of dentary (char. 56[0]). In addition, characters 92[1] (ossified ribs present) and 104[1] (scale ornament differentiated) are interpreted as possible characters supporting the monophyly of the family in some of the trees. Similar results were obtained by Dutel et al. (2012; compare Figs. 7 and 8).

The family Latimeriidae (Fig. 7, node G2) is strongly supported by numerous characters, four of which are interpreted as uniquely derived among actinistians. The seven genera included in the family, Holopogus, [Latimeria + Swenzia], [Libys + Megalocoelacanthus], Macropoma, and Undina, stand in a polytomy. This polytomy is supported by the presence of several median rostra (char. 3[1]); anterior branches of supratemporal commissure present (char. 22[1]); spiracular (postspiracular) absent (char. 30[0]); subopercular branch of the mandibular sensory canal present (char. 60[1]); parasphenoid with ascending laminae (char. 79[1]); and ventral swelling of the palatoquadrate present (char. 109[1]). The parsimony analysis interprets characters 22 [1], 60[1], and 109[1] as uniquely derived. Such results mostly agree with Dutel et al. (2012), with the exception of the position of Macropoma, which is the sister of [Latimeria + Swenzia] in Dutel et al. (2012), but it is placed in an unresolved position in our study (compare Figs. 7 and 8).

The content of the Mawsoniidae and Latimeriidae is the same in Cavin et al. (2013) and Cavin and Grädinaru (2014), and few Triassic genera are included above Latimeria in both analyses. Those are different results from the ones presented here. The only Triassic genus, Ticinopomis, appears in a trichotomy with the two families in our analysis. However, it appears at the base of the family Latimeriidae in Dutel et al. (2012). The difference between Wendruff and Wilson (2012) and other analyses cited herein is the placement of Diplurus within the Latimeriidae instead of Mawsoniidae.

**Cladistic Analysis 2**

The parsimony analysis with 35 genera and only characters from the head (chars. 1–87 and 109; see Appendix S1) recovered 3787 equally parsimonious trees of 236 steps (retention index = 0.6980; consistency index = 0.4153). Character-state optimization: ACCTRAN. This analysis was performed to test a previous interpretation about the taxonomic and phylogenetic position of the Chilean coelacanthiform that was based on the lateral view of the unprepared specimen MNHN SGO.PV 288: (1) as a new genus of Mawsoniidae (Arratia and Schultz, 1999); or (2) as a basal actinian taxon (Gallo and Miguel, 2014).

The strict consensus tree does not support Atacamaia, gen. nov., as a mawsoniid or as a basal actinian, but places it in a trichotomy with Axelia and Wimania (Fig. 9) as in that recovered in Cladistic Analysis 1 (Fig. 7, node E1). This branching is supported by five characters (1[2], 2[1], 7[0], 17[0], and 31[0]), which are the same supporting characters of node E1 in Cladistic Analysis 1. This trichotomy stands in an unresolved position with Piveteauias, Guizhoucoelacanthus, Whiteia, and the Latimeriodei. The inclusion of only cranial characters is devastating for Latimeriodei, because the family Mawsoniidae becomes a non-monophyletic group.

The results of this second cladistic analysis are of interest because they demonstrate that the selection of certain structures may mislead phylogenetic interpretations. Therefore, as many characters as possible should be included in a parsimony analysis. In addition, it demonstrates that the postcranial skeleton carries characters of significance in the evolutionary history of Actinistia, especially in relation to the family Mawsoniidae.

**CONCLUSIONS**

**Whiteiidae and the Phylogenetic Position of Atacamaia, gen. et sp. nov.**

According to this study, the family Whiteiidae includes the genera Atacamaia, Axelia, Guizhoucoelacanthus, Piveteauias, Wimania, and Whiteia. Schultz (1993) erected the suborder Latimeriodei including the families Latimeriidae Berg, Mawsoniidae Schultze (with the genera Alcoveria and Mawsonia), and Whiteiidae Schultz (including the genus Whiteia). Later, Axelia, Wimania, and Whiteia were classified as Coelacanthiformes incertae sedis by Forey (1998). Wendruff and Wilson (2012) included only one representative of the Whiteiidae, Whiteia, in their analysis. Cavin et al. (2013) and Cavin and Grädinaru (2014) included five whiteiid genera (plus the new studied fossil form), whereas Wen et al. (2013) considered only three whiteiid genera (plus the two new studied fossil taxa). The whiteiids were placed either in a polytomy with other genera (Cavin et al., 2013) or in successive sequence (Wen et al., 2013; Cavin and
Grădinaru, 2014). In contrast, the phylogenetic study of Geng et al. (2009), based on the list of characters and coding of Forey (1998), placed Whiteia, Piveteauia, and Guizhoucoelacanthus in the family Whiteidae Schultz, 1993, with Guizhoucoelacanthus as the sister of [Piveteauia + Whiteia]. In the recent phylogenetic study of Coelacanthiformes (Dutel et al., 2012; see Fig. 8 herein), the genera [Piveteauia + Whiteia + [Guizhoucoelacanthus + Axelia + Wimania]] form a well-resolved clade, which was not identified by a name. The addition of the new fossil actinistian to the phylogenetic analysis results in an unresolved topology of these genera, with Atacamaia standing in a trichotomy with Axelia and Wimania. Thus, the present study, based on a detailed morphological description of Atacamaia solitaria, gen. et sp. nov., gives a very different taxonomic interpretation to previous ones based on the unprepared specimen that was previously interpreted as a mawsonid (Arratia and Schulz, 1999) or a basal actinistian (Gallo and Miguel, 2014).

Atacamaia, gen. et sp. nov., Its Geographic Distribution and Age

Members of the family Whiteidae are known from Africa (Piveteauia and Whiteia), Asia (Guizhoucoelacanthus), Europe (Axelia and Wimania), Greenland (Whiteia), North America (Whiteia), and South America (Atacamaia, gen. nov.) (see Table S1 for details). Four genera occurred in the Panthalassic Ocean (Paleopacific), but not in the same regions. For instance, Axelia, Whiteia, and Wimania have been recovered in the northern Panthalassic Ocean, in Canada, Spitsbergen, and Greenland (Stensiö, 1921; Schaeffer and Magnus, 1976; Cloutier, 1990), whereas Atacamaia has been recovered in the southern Panthalassic Ocean, in northern Chile (Arratia and Schultz, 1999).

Independent of the enormous distance between the two regions, we remark that the fishes lived in different times. Whereas the northern Panthalassic species were recovered in Triassic strata, the southern Panthalassic species was recovered in the Lower Jurassic strata. Atacamaia solitaria, gen. et sp. nov., is the youngest known member of Whiteidae.

The genus Whiteia occurs from the northern Panthalassic Ocean, Spitsbergen, and Greenland to the south in Madagascar and South Africa. This occurrence of Early Triassic fishes around Pangaea has been known for a long time (Schaeffer and Magnus, 1976).

Among South American coelacanthiforms, Atacamaia solitaria, gen. et sp. nov., is the only one that has been recovered on the Pacific side during the Mesozoic, whereas all other coelacanthiform species have been recovered on the Atlantic side of the continent, making this a unique find. The only other possible Paleopacific species is Coelacanthus cf. C. granulatus from the Pernian of Bolivia (Janvier, 1992); even though Semperé et al. (1992) compared the marine deposits with similar deposits in Paraná and the Karoo Basin, the increasing thickness of the formation towards the west and paleogeographic maps indicate a possible connection with the Panthalassic Ocean. The Mawsoniidae, to which the Chilean coelacanth was assigned originally, are Gondwana forms from the eastern part of South America.

Acknowledgments

We thank Monumentos Nacionales of Chile and the National Museum of Natural History, Santiago, Chile, for permission to collect fossil fishes in the Atacama Desert and for permission to study the specimen described herein; the late I. Kong, University of Chile, Antofagasta, for his assistance during the field work; our volunteers, Drs. K. Shaw and J. Chorn, for helping collect specimens, and K. Shaw for recovering the specimen herein described; the late V. Covacevich (Servicio Nacional de Geologia y Minas, Chile, SERGEOMIN) for checking the age of the locality based on the newly collected invertebrates, which are deposited in the SERGEOMIN; C. Quezada-R. (University of Chile, Faculty of Sciences) for his assistance with the bootstrap analyses; T. J. Meehan (Lawrence, Kansas) for preparing the illustrations for electronic submission; and K. Sturm (Lawrence, Kansas) for her help double checking references and the matrix.

We thank the National Geographic Society for financial support of the expedition in the Atacama Desert, northern Chile, in 1994 (Award No. 5118-93).

Our thanks go to the reviewer L. Cavin and an anonymous reviewer for their suggestions and comments.

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Submitted July 26, 2014; revisions received October 9, 2014; accepted October 22, 2014.

Handling editor: Martin Brazeau.

Citation for this article: Arratia, G., and H.-P. Schultze. 2015. A new fossil actinistian from the Early Jurassic of Chile and its bearing on the phylogeny of Actinistia. Journal of Vertebrate Paleontology. DOI: 10.1080/02724634.2015.983524.