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THE TRIASSIC FISH FAUNAS OF THE CUYANA BASIN, WESTERN ARGENTINA

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Abstract: The continental deposits of the Cuyana Basin, western Argentina, have yielded the most diverse, but so far almost unstudied, Triassic ichthyofaunas of South America. Here, we review these faunas and show that only eight of the 29 named taxa can be considered valid, including the chondrostean *Neochallaia*, the acrolepid *Challaia*, *Guaymayenia*, a taxon of uncertain affinities, and five species of the perleidiform family Pseudobeaconiidae. The first three taxa most probably come from Middle Triassic sediments, while the pseudobeaconiids are of Late Triassic age. Other material, although not diagnostic, probably represents other species, and thus, the diversity of actinopterygians in the Cuyana basin is certainly higher than currently recognized. For the Late Triassic fish fauna, the absence of crown-group neopterygians and a single record of a sarcopterygian is noteworthy and probably indicates some degree of endemism in this fauna, also supported by the high abundance of pseudobeaconiids, which are unknown from other areas. Furthermore, on the basis of the age indicated by the fishes and the available geological information, we discuss the age of the local fauna of the Cerro Bayo, close to the city of Mendoza, and the Agua de la Zorra Formation, Uspallata.

Key words: Actinopterygii, Chondrostei, Acrolepidae, Perleidiformes, Pseudobeaconiidae, Triassic, Argentina.

THE oldest articulated actinopterygian remains are known from the Middle Devonian, but actinopterygians are still rare during that time (Friedman and Blom 2006). They evolved rapidly during the Carboniferous and Permian, and several actinopterygian lineages went to extinction at the Permo/Triassic boundary. However, the actinopterygian faunas recovered very rapidly during the Triassic, especially diversifying in shallow marine and brackish environments, giving rise to the very rich and diverse actinopterygian faunas of the Middle and Late Triassic. The Triassic is, therefore, a very important period in actinopterygian evolution (Benton 2004).

Several major evolutionary events happened during the Triassic actinopterygian radiation. A very important event in the evolution and history of these fishes is the origin of the Neopterygii, which is marked by the acquisition of a better control of the movements of both dorsal and anal fins, and consequently the improvement in their swimming capabilities. Although the Neopterygii appear in the fossil record already in the Permian, their first and rapid radiation occurred during the Triassic, producing a new variety of fishes with very distinct feeding specializations and habitat preferences. The oldest teleosts are also known from the Triassic, and the origin of this group, which includes most living actinopterygians, most probably took place during the Early or Middle Triassic (Hurley *et al.* 2007). In addition, and not less important, some actinopterygian groups are exclusively or almost exclusively known during the Triassic, i.e. luganoiids, redfieldiiforms, pholidopleuriforms, peltopleuriforms and perleidiforms. The interrelationships among these groups and between them and other actinopterygians are still unclear. However, as each of these species shows one or more of the neopterygian features (like the upper caudal fin rays elongate, the dorsal and anal fin rays equal in number to their endoskeletal supports, a premaxilla with nasal process, a coronoid process on the mandible or a vertical suspensorium), they certainly play a very important role for our understanding of the origin and first radiation of the Neopterygii and, consequently, the teleosts. The basal chondrosteans *Birgeria*, *Saurichthys* and other possible primitive Chondrostei (López-Arbarello *et al.* 2006) also lived during the Triassic, and they provide clues to the origin of the Acipenseriformes, which is probably the most successful group among Recent nonteleostean actinopterygians.

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Despite their importance, the history and phylogenetic relationships between the majority of the Triassic actinopterygian fishes are still unclear, and our knowledge of these fishes is mainly based on the fossil record of the Northern Hemisphere (Bürgin 1999; Chang and Miao 2004; López-Arbarello *et al.* 2006). Although important fish faunas have been reported, Triassic fishes of Gondwana are generally poorly known. The best-known Gondwanan Triassic fishes are those from the Karoo Supergroup in South Africa and the Sidney Basin in Australia (see López-Arbarello 2004 for an overview of the Triassic fish record in Gondwana). In South America, the Bermejo and Cuyana basins in north-western Argentina have yielded the best-preserved Triassic fishes of this continent (López-Arbarello 2004). Within the Bermejo basin, fishes are only known from the Los Rastros Formation, apart from isolated scales and bone fragments from the Ischigualasto and Ischichuca Formations. These fishes have been revised recently (López-Arbarello *et al.* 2006), and they include three genera (four species) of basal, non-neopterygian actinopterygians, one of them, *Challaia* Rusconi, 1946*a*, being referred to the Acrolepidae (*sensu* Aldinger 1937). The relationships of the other two genera within Actinopterygii are still uncertain, but, among them, *Gualolepis* López-Arbarello *et al.*, 2006, might represent a basal Chondrostei and the third genus, the subholostean *Rastrolepis* López-Arbarello *et al.*, 2006, might be related to the redfieldiiforms (López-Arbarello *et al.* 2006).

In contrast to this very sparse record from the Bermejo Basin, several diverse and well-preserved fish assemblages have been reported from the Cuyana Basin. However, little is known about the systematics and possible biogeographical significance of these fishes. Between 1876 and 1952, a total of 28 taxa were named from this basin, but these fishes are almost unknown, because most of them were exclusively published in local Argentinean journals of rather restricted circulation. Only three of these taxa have been studied in detail (Schaeffer 1955; Hutchinson 1973*a*; López-Arbarello and Zavattieri 2008), and the taxonomic status of the remaining species is doubtful. The present contribution includes a thorough taxonomic revision of these fishes, also including the recently described *Pseudobeaconia celestae* López-Arbarello and Zavattieri, 2008.

The taxa dealt with, here, basically represent three main faunas, the significance of which is discussed, including a discussion of the stratigraphic position and faunal contents of the Agua de la Zorra Formation in the region of Uspallata (Mendoza, Argentina), which is probably considerably older than currently assumed.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MCNAM, Museo de Ciencias Naturales y Antropológicas 'Juan Cornelio Moyano', Mendoza, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MLP, Museo de Ciencias Naturales de La Plata, La Plata, Argentina.

SYSTEMATIC PALAEONTOLOGY

OSTEICHTHYES Huxley, 1880
ACTINOPTERYGII Cope, 1887
ACTINOPTERYGII *incertae ordinis*

Genus GUAYMAYENIA Rusconi 1946*b*

Type and only known species. Guaymayenia paramillensis Rusconi, 1946*b*.

Diagnosis. As for the type and only species.

Guaymayenia paramillensis Rusconi, 1946*b*
Text-figure 1

v* 1946*b* *Guaymayenia paramillensis* Rusconi, pp. 186–188, figs 1–2.
1948*a* *Guaymayenia paramillensis* Rusconi; Rusconi, p. 169.
1957 *Guaymayenia paramillensis* Rusconi; Rusconi, p. 53.

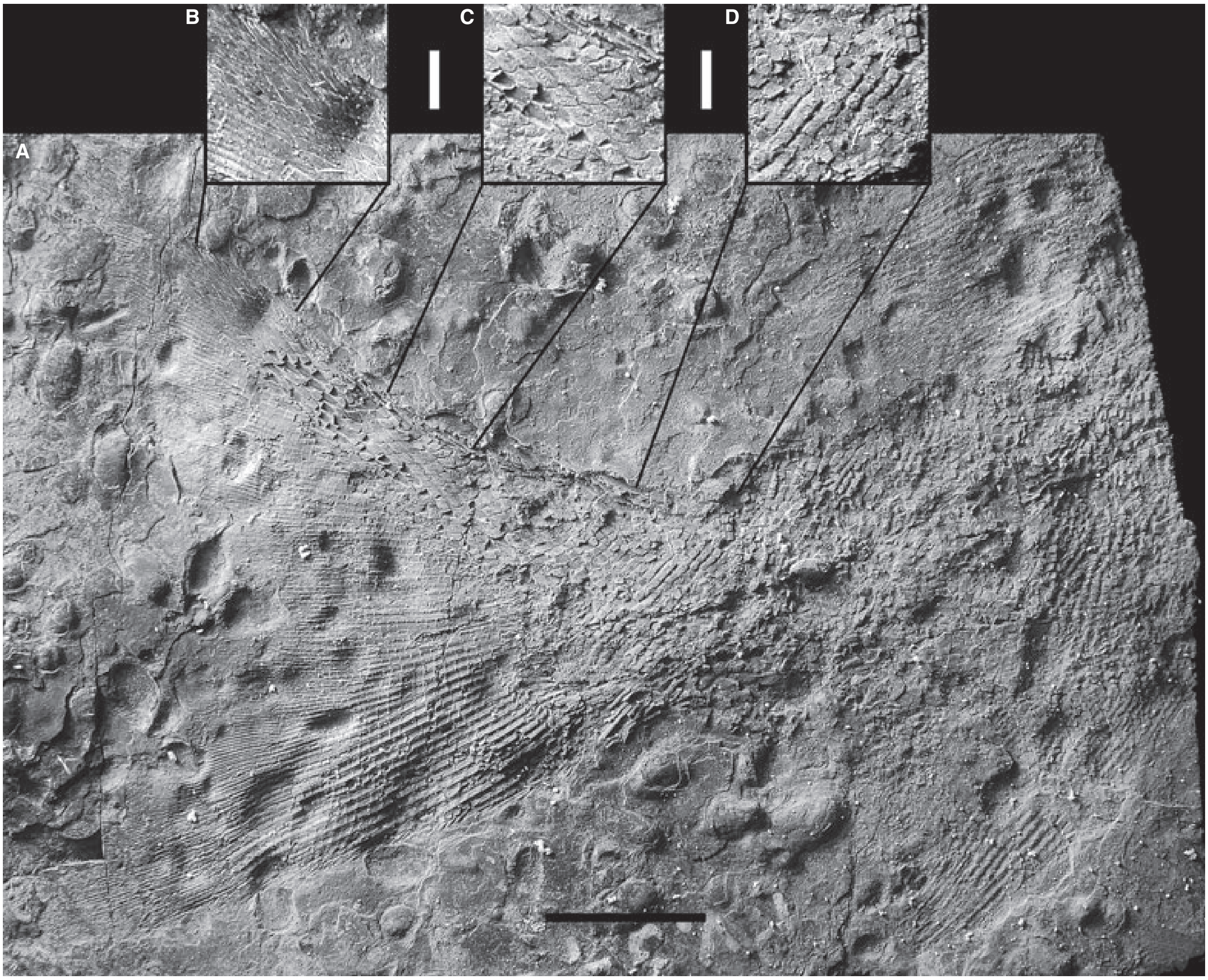
Holotype. MCNAM-PV 547.

Type locality. One kilometre South of Agua de la Zorra, Uspallata, Mendoza Province, Argentina.

Type horizon. Agua de la Zorra Formation, Cuyana Basin, probably Middle Triassic.

Diagnosis. Caudal fin heterocercal, equilobate and moderately cleft, with numerous ventral fringing fulcra and dorsal caudal fulcra, the ventral marginal rays increasing in length from the first to the eighth; dorsal, anal and caudal fin lepidotrichia ornamented with a median ridge; micromeric squamation; body covered with small, quadrangular rhombic scales, all the trunk scales being of equivalent size and shape; the scales on the body lobe of the tail are elongated in posterodorsal to anteroventral direction to diamond shape and slightly larger than those of the body.

Description. The specimen, consisting of the posterior portion of a fish only (Text-fig. 1), is 7.5 cm long, the total or standard length of the fish being unknown. The distance between the end of the dorsal fin and the hinge line is about 4 cm. The caudal peduncle is relatively shallow, and the caudal fin web is broad. The inclination of the dorsal and ventral borders of the pre-



TEXT-FIG. 1. *Guaymayenia paramillensis* Rusconi, 1946*b*. A, photograph of the holotype and only known specimen MCNAM-PV 547. B–D, detailed photograph of the same specimen showing diamond shape scales in the most posterior portion of the body lobe (B), scales in the central portion of the body lobe (C), and scales in the dorsal portion of the caudal peduncle (D). Scale bars represent 1 cm (black) and 2 mm (white).

served portion of the body suggests that the dorsal and anal fins are placed in the shallowing posterior half of the body. The dorsal fin is placed anterior to the anal fin, the origin of which is at about the same level as the end of the base of the dorsal fin. Both fins apparently have a triangular shape and are of comparable size. The dorsal and anal fin rays are very poorly preserved and cannot be counted. However, a few other features are preserved. The fin rays are segmented and distally branched, with all segments being short and of equivalent length. The lepidotrichia are ornamented with a median ridge, not a groove as described by Rusconi (1946*b*, p. 187).

The caudal fin is strongly heterocercal, equilobate and moderately cleft. There are about 64 lepidotrichia, not 52 as indicated by Rusconi (1946*b*, p. 187). They are segmented and bifurcate distally, the central rays bifurcating at least four times. Their basal segments, at least in the ventral lobe, are mostly covered with scales and are longer than the following segments, which are short and equivalent in length. The caudal fin rays also show a median ridge and not a groove as described by Rusconi (1946*b*, p. 187). The ventral marginal rays increase in length from the first to the eighth, and they are fringed with small fulcra. The fringing fulcra seem to become more slender posteriorly, but this might be an artefact of preservation.

The body is covered with quadrangular rhombic scales. Except for the ones in the body lobe of the tail, all the scales in the preserved portion of the body, including those close to the dorsal and ventral midlines, have a similar size and shape. The scales are very small, being between 0.5 and 0.7 mm height or length, making up a micromeric squamation, i.e. more than one row of scales per somite (Long 1988). Several of the preserved scales show the peg-and-socket articulation typical of the rhombic scales. The preservation is not good enough to be sure about the possible ornamentation of the scales, but they apparently have smooth surfaces and a straight posterior border.

The scales in the body lobe are slightly larger than the scales on the body (compare Text-fig. 1C–D). They further differ from the body scales in becoming more elongated (up to 1.5 times longer than high) in posterodorsal to anteroventral direction. The hinge line is imperfectly preserved, and it is not possible to count the exact number of scale rows in the body lobe. The scales in the body lobe articulate with each other through a sharp posterodorsal process, which is not visible superficially. The body lobe is dorsally framed with a series of dorsal caudal fulcra, which become more slender posteriorly.

Remarks. As described above, the holotype and only known specimen consist of the caudal peduncle and heterocercal tail of a fish. The dorsal and anal fins are only incompletely and poorly preserved. No cranial remains are preserved. Although the general preservation is rather poor, the combination of features included in the diagnosis has not been found in other basal actinopterygians, and thus, supports the validity of this taxon, although more material is needed to complete our knowledge of *Guaymayenia paramillensis*. According to the available information, among the Triassic actinopterygians, *G. paramillensis* resembles the cosmopolitan palaeonisciform *Pteroniscculus* White, 1933, which is known from Early Triassic sediments in East Greenland, Madagascar and North America, and the Middle Triassic of Australia. *Guaymayenia* and *Pteronisculus* share a broad and equilobate caudal fin web, a similar pattern of ventral marginal caudal fin rays and caudal ventral fringing fulcra, similar shape of the caudal peduncle, and similar position of the dorsal and anal fins. Both genera, as well as several Palaeozoic actinopterygians, have numerous and small scales covering the body, a feature that led Rusconi (1946*b*) to compare *Guaymayenia* with acanthodians. The exact number of rows of scales per somite is unknown in *Guaymayenia*. In *Pteronisculus*, there are about three rows of scales per somite (Nielsen 1942). Differing from *Guaymayenia*, the body scales in *Pteronisculus* are ornamented with fine striae, have serrated posterior margins, and their shape varies in different parts of the body, the scales being quadrangular only around the lateral line in the abdominal and caudal region (Nielsen 1942). Other actinopterygians with micromeric squamation differ from *Guaymayenia* in the general shape of the caudal fin, which is usually deeply cleft and with the dorsal lobe notably larger than the ventral lobe.

CHONDROSTEI *sensu* Patterson, 1982
CHONDROSTEI *incertae ordinis*

Genus NEOCHALLAIA Rusconi 1949*a*

Type and only valid species. Neochallaia tellecheai (Rusconi, 1948*b*) comb. nov.

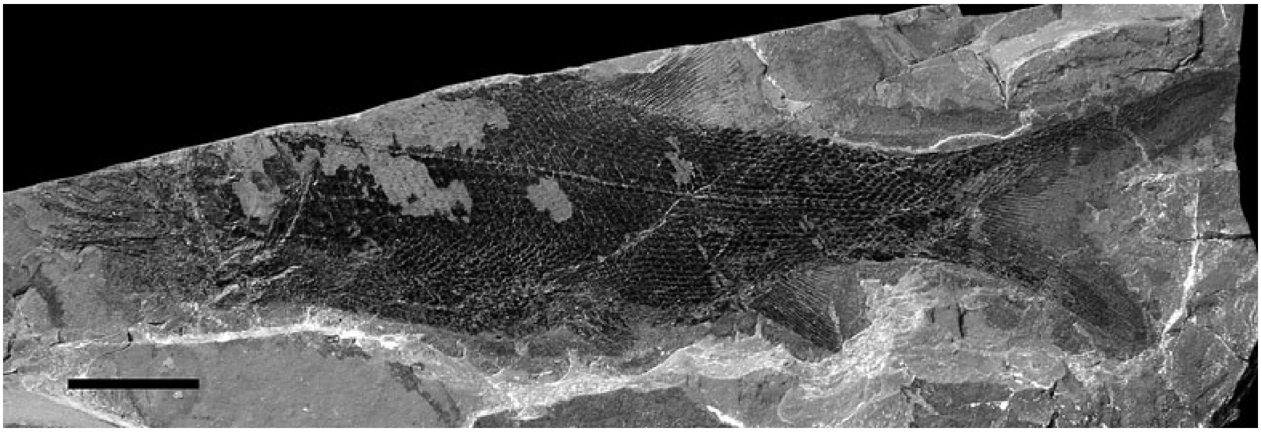
Diagnosis. As for the type and only valid species.

Neochallaia tellecheai (Rusconi, 1948*b*) comb. nov.
Text-figures 2–3

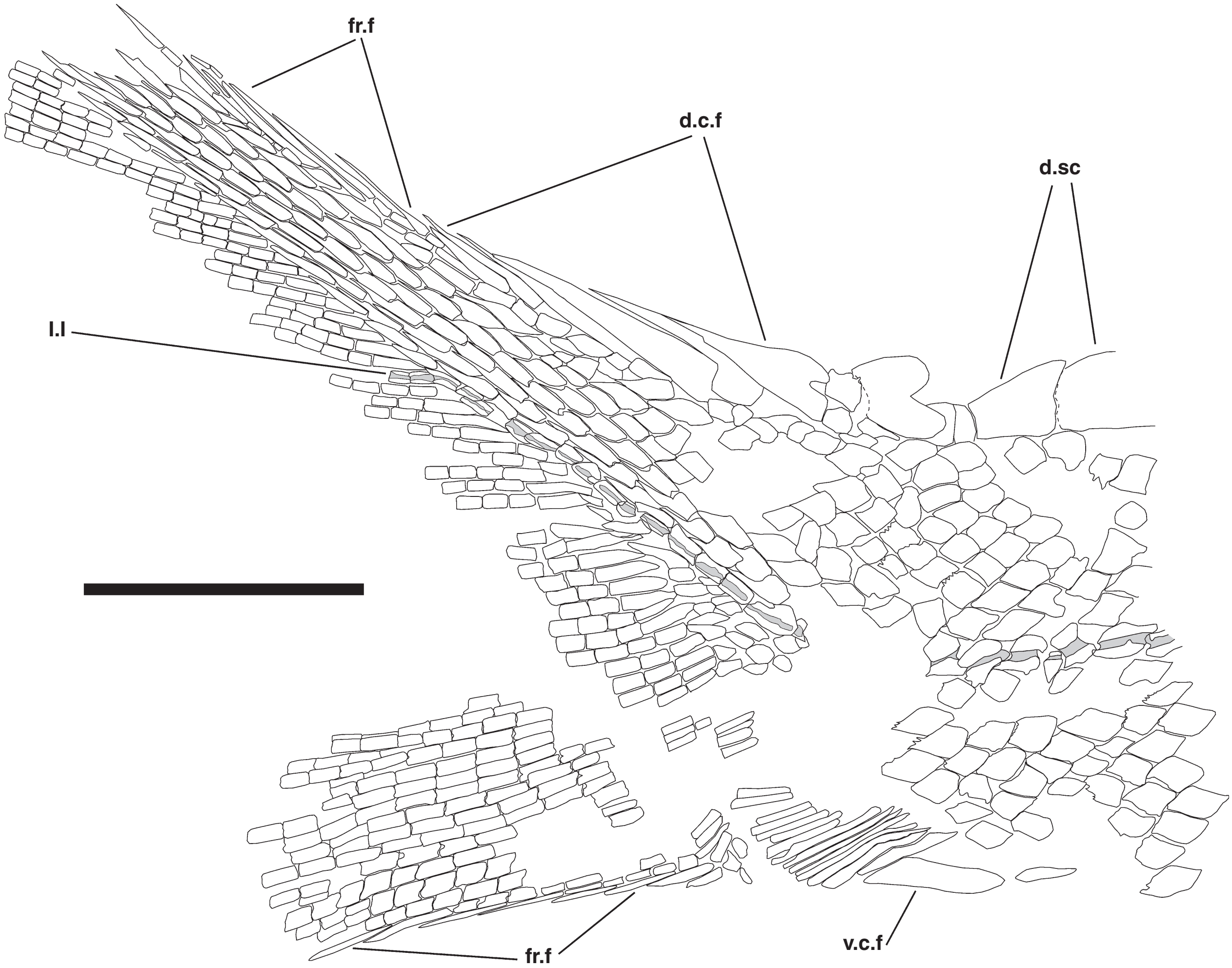
v* 1948*b* ?*Rhadinichthys tellecheai* Rusconi, 1948; Rusconi, pp. 241–242, figs 1–3.
v* 1948*b* ?*Challaia minor* Rusconi, 1948; Rusconi, pp. 242–244, figs 4–6.
* 1949*a* *Neochallaia minor* (Rusconi); Rusconi, pp. 231–234, fig. 1.
1957 ?*Rhadinichthys tellecheai* Rusconi; Rusconi, p. 55.
1957 *Neochallaia minor* (Rusconi); Rusconi, p. 55.

Holotype. MCNAM-PV 2702.

Referred material. MCNAM-PV 2720 (holotype of *N. minor*); MCNAM-PV 2722 (paratype of *N. minor*); MCNAM-PV 2703–2717, 2723–2730, 2801–2803, 2805, 2807–2809.



TEXT-FIG. 2. *Neochallaia tellecheai* (Rusconi, 1948*b*) comb. nov. MCNAM-PV 2702, holotype. Scale bar represents 1 cm.



TEXT-FIG. 3. *Neochallaia tellecheai* (Rusconi, 1948*b*) comb. nov. Line drawing of the partial tail of MCNAM-PV 2705. Abbreviations: d.c.f, dorsal caudal fulcra; d.sc, dorsal scutes; fr.f, fringing fulcra, l.l, lateral line; v.c.f, ventral caudal fulcra. Scale bar represents 0.5 cm.

Type locality. Area of the Cerro Bayo, 20 km west of the city of Mendoza, Mendoza Province, Argentina.

Type horizon. Most probably Cerro de Las Cabras Formation, Cuyana Basin, Middle Triassic (Stipanicic *et al.* 2002*a*).

Diagnosis. Small, fusiform actinopterygian with slender body; head length about 0.3 of SL (length from the tip of the snout to the base of the caudal fin at the hinge line); body depth about 0.3 of SL; skull roof bones ornamented with small tubercles; dorsal fin placed at the middle of the body; pelvic fin origin slightly anterior to dorsal fin origin; caudal fin strongly heterocercal, the dorsal lobe being longer than the ventral lobe; fin rays evenly segmented except for a slightly longer basal segment, and branched only very distally; the lateral line extends enclosed in tubular scales in the body lobe of the tail and, at least for a short span onto the fin web; body completely covered with small and numerous ganoid scales, with smooth surface and finely pectinate posterior border; scales on the body lobe with long and sharp posterodorsally directed posteroventral process; a series of large lanceolate dorsal median scutes preceding the caudal fin, which are ornamented with delicate ridges emerging latero-posteriorly from a main median ridge.

Pterygial formula.

$$\frac{\mathrm{D40}}{\mathrm{P20\ A40\ C63}}\mathrm{T68}$$

Remarks. Among the specimens here referred to *Neochallaia tellecheai*, Rusconi (1948*b*) recognized two different taxa tentatively referring one of them to the Permian genus *Rhadinichthys*, as ?*Rhadinichthys tellecheai*, and the other one to the local Triassic genus *Challaia*, as ?*Challaia minor*, which he had erected in 1946*a*. Rusconi did not make further studies on ?*Rhadinichthys tellecheai*, but in 1949*a*, he described new material of the other species and concluded that it represented a new genus *Neochallaia*, thus naming the species *Neochallaia minor*. After the thorough revision of the type and referred material of these two nominal taxa, it was found that they represent a single species. According to the rules of nomenclature (ICZN: Article 23), the species is named *Neochallaia tellecheai*, because it represents a distinct genus and, although in the same publication, *N. tellecheai* is described before *N. minor*.

Pending a detailed description of *Neochallaia tellecheai*, which is being prepared by one of us (ALA), only some systematically important features are here discussed. The tail of *Neochallaia tellecheai* strongly resembles that of acipenseriforms, not only because it is very heterocercal, but also for the presence of some special characters that indicate chondrostean affinities. As in the Acipenseriformes (Hilton 2004), the lateral line of *N. tellecheai* continues enclosed in a series of tubular scales following the posteroventral margin of the body lobe (Text-fig. 3). Peculiarly in *N. tellecheai*, at about half the length of the body lobe, this series of tubular scales flexes horizontally and continues on the fin web for at least a short span. In addition, the ganoid scales covering the body lobe are slender and articulate with each other in a very peculiar way, resembling the case in *Chondrosteus acipenseroides* (Hilton and Forey 2009). Each scale has a very long and sharp posteroventral process, which articulates between the main bodies of the two adjacent posterodorsal scales (Text-fig. 3). At the same time, the posterodorsal border of each scale, at the base of the posteroventral process, forms a step where the anteroventral border of the following scale articulates. Besides this general pattern, several scales in the body lobe of the tail of *Neochallaia* have capricious shapes and ways of linking, as it is also the case in *Acipenser* (e.g. Grande and Bemis 1996, fig. 10D; Hilton 2004, fig. 6A). Another interesting feature shared by *Neochallaia* and most acipenseriforms (Hilton 2004), including *Chondrosteus* (Hilton and Forey 2009), is the presence of a single ventral caudal fulcrum.

ACTINOPTERYGII *incertae ordinis*
Family ACROLEPIDAE Aldinger, 1937
(Restricted to the 'Acrolepidae Group A' of Aldinger 1937)

Genera included. Acrolepis Agassiz, 1833; *Acropholis* Aldinger, 1937; *Challaia* Rusconi, 1946*a*; *Plegmolepis* Aldinger, 1937; *Watsonichthys* Aldinger, 1937.

Diagnosis. Fusiform actinopterygians distinguished by the following combination of characters: suborbital bones present; postorbital plate of maxilla very large and trapezoid; more than 10 branchiostegal rays; operculum narrower than suboperculum; anteopercular bones present; height of anterior rays in median fins increasing rapidly posteriorly; small fringing fulcra, thick scales strongly ornamented with ganoin ridges, which are parallel or slightly anastomosing (characters based on own observations and partially Aldinger 1937, p. 254).

Remarks. Aldinger (1937) created the family Acrolepidae to include several basal actinopterygians, most of them from the Palaeozoic. The phylogenetic relationships of most of these genera are still unknown or controversial. However, Aldinger (1937) distinguished three groups (A, B and C) within the Acrolepidae. The fishes included in his Group A share a unique combination of characters that allows the diagnosis of a suprageneric taxon. The relationships between the fishes included in the other two groups remain controversial. Therefore, and considering that the family was named after the genus *Acrolepis*, which is included in Aldinger's Group A of the Acrolepidae, we here restrict the family to this group. We add to this family the genus *Challaia* Rusconi, 1946*a* (see below), and propose a familial diagnosis.

Genus CHALLAIA Rusconi, 1946*a*

Type species. Challaia magna Rusconi, 1949*b*.

Referred species. Challaia elongata (Cabrera, 1944) from the Los Rastros Formation in the Bermejo Basin (see López-Arbarello *et al.* 2006).

Diagnosis. Acrolepid fishes characterized by the following unique combination of characters: large maxilla with slender suborbital portion and large trapezoidal postorbital plate with large posteroventral expansion overlapping the lower jaw; preoperculum very inclined and narrow; at least one suborbital bone; numerous anteopercular bones, among them a very slender element laying on the dorsal border of the preoperculum; operculum narrowing upwards and much deeper, but narrower than suboperculum; two types of conical teeth on jaws, one type being much larger than the other one; scales ornamented with longitudinal ganoine ridges irregularly anastomosing posteriorly and not reaching the posterior margin of the scale.

Remarks. Among the acrolepids, *Challaia* resembles *Acropholis* and *Plegmolepis* in the presence of several anteopercular bones. On the other hand, *Challaia* shares with *Watsonichthys* the very long postorbital plate of the maxilla and very strong dentition. The slender anteopercular bone articulating on the dorsal border of the preoperculum, which is sometimes interpreted as a dermohyal, is common to all acrolepid genera.

Challaia magna Rusconi, 1949*b*
Text-figures 4–5

v* 1949*b* *Challaia magna* Rusconi, pp. 222–229, figs 1–4.
1957 *Challaia magna* Rusconi; Rusconi, p. 55.

Holotype. MCNAM-PV 2790.

Type locality. North of the Cerro Bayo, Departamento de Las Heras, Mendoza Province, Argentina.

Type horizon. Most probably Cerro de Las Cabras Formation, Cuyana Basin, Middle Triassic (Stipanicic *et al.* 2002*a*).

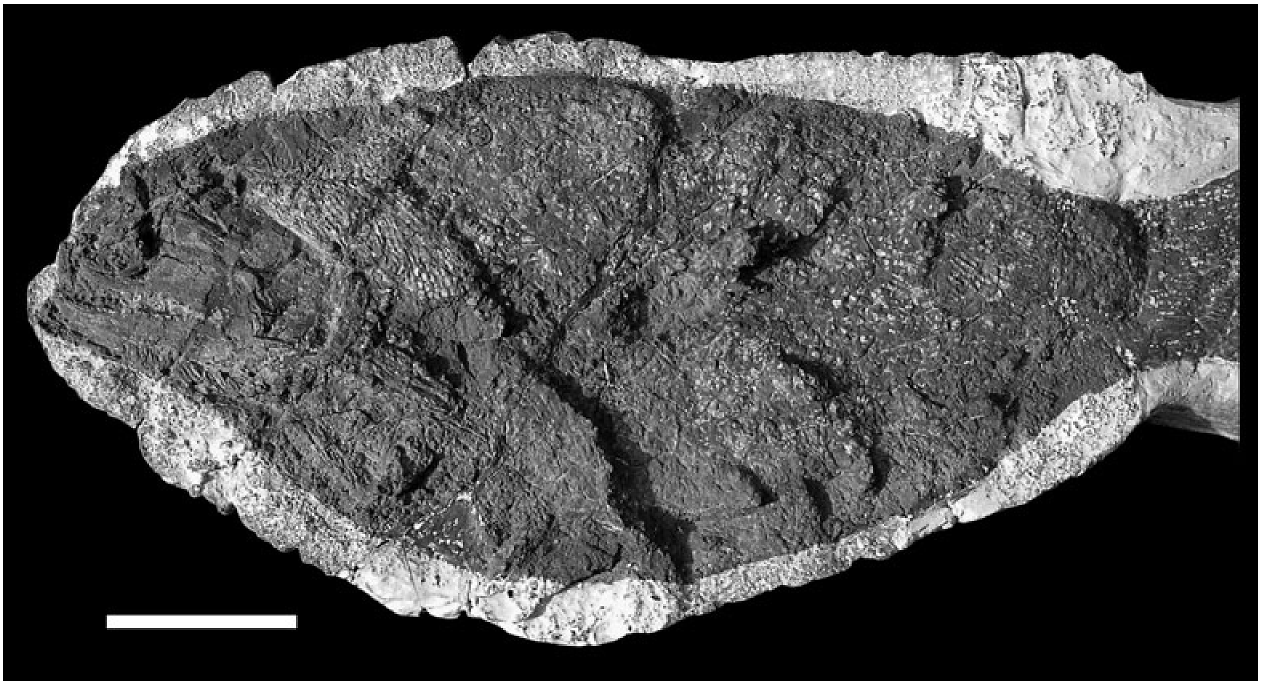
Diagnosis. Species of *Challaia* distinguished by the following combination of characters: large marginal teeth with a striated surface; five anteopercular bones; anterior border of preoperculum as deep as anterior portion of postorbital plate of maxilla; more than 20 branchiostegal bones.

Remarks. The species of *Challaia* are still relatively poorly known, represented by a few, incomplete specimens only. *Challaia magna* is currently under study. The diagnostic features of the genus can be recognized in the type and so far only known specimen, and several features distinguish this species from the only other known species of *Challaia*. The posteroventral expansion of the maxilla is rounded in *Ch. magna*, but subtriangular in *Ch. elongata*. The lower jaw of *Ch. magna* is proportionally more robust than in *Ch. elongata*. *Challaia elongata* further differs from *Ch. magna* in having only three anteopercular bones and a shallower anterior border of the preoperculum, which is only 0.5 of the depth of the anterior portion of postorbital plate of the maxilla. The scales in *Ch. magna* are further shallower than in *Ch. elongata* and with less number of ridges, the ridges being thicker in *Ch. magna*.

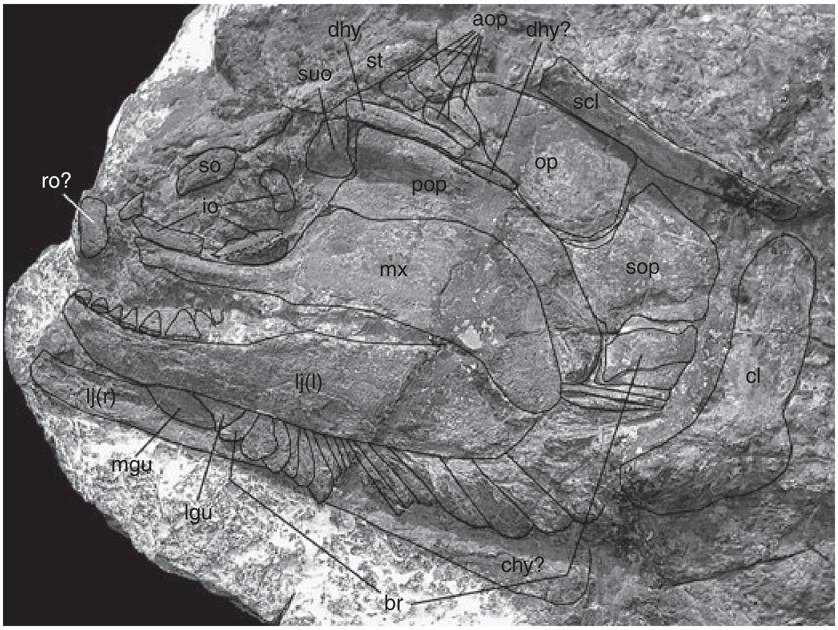
Rusconi named three other species of *Challaia*: *Ch. striata* Rusconi, 1946*a*, *Ch. multidentata* Rusconi, 1949*a* and *Ch. cacheutensis* Rusconi, 1950*a*. The three nominal species, however, are based on very incomplete and undiagnostic material, and two of the holotypes are lost (see below). Therefore, *Ch. magna* and *Ch. elongata* are the only valid species of this genus known so far.

Order PERLEIDIFORMES Berg, 1937
Family PSEUDOBEACONIIDAE López-Arbarello and Zavattieri, 2008

Diagnosis. Among the following combination of characters, an asterisk (*) indicates synapomorphies: small perleidiform fishes up to 120 mm in total length (TL); body depth 2–3.5 × in standard length (SL; the length of a fish measured from the tip of the snout to the base of the caudal fin); pelvic fins closer to anal than to pectoral fins; dorsal and anal fins of similar size; incomplete dorsal ridge of spine-like scales between skull and dorsal fin*; a series of median scutes on dorsal and ventral midlines



TEXT-FIG. 4. *Challaia magna* Rusconi, 1949*b*. MCNAM-PV 2790 (holotype). Scale bar represents 10 cm.



TEXT-FIG. 5. *Challaia magna* Rusconi, 1949*b*. Interpretation of several skull bones in MCNAM-PV 2790, holotype. Abbreviations: aop, anteopercular bones; br, branchiostegal bones; chy?, ceratohyal?; cl, cleithrum; dhy, dermohyal; io, infraorbital bones; lgu, lateral gular plate; lj(l), left lower jaw; lj(r), right lower jaw; mgu, median gular plate; mx, maxilla; op, operculum; pop, preoperculum; scl, supracleithrum; so, supraorbital bone; sop, suboperculum; st, supratemporal bone; suo, suborbital bone; ro?, rostral bone? Scale bar represents 1 cm.

from end of dorsal to caudal fin and from end of anal to caudal fin, respectively; flank scales approximately three times deeper than long; scales with straight posterior border, elevated central region and marginal concentric ridges of ganoine* (from López-Arbarello and Zavattieri 2008).

Genus PSEUDOBEACONIA Bordas, 1944

Type species. Pseudobeaconia bracaccinii Bordas, 1944.

Referred species. Pseudobeaconia elegans Bordas, 1944; *P. celestae* López-Arbarello and Zavattieri, 2008; *P. cuyana* (Bordas, 1944) comb. nov.

Diagnosis. Among the following combination of characters, an asterisk (*) indicates synapomorphies: fusiform pseudobeaconiids up to 50 mm SL; body depth 2.5–3.5 × in SL; head length 0.3 SL; skull with relatively thin, unornamented bones*; wide skull roof bones; parietals about half the length of frontals*; supraorbital sensory canal does not enter parietals; small postrostral; nasals wider dorsally than ventrally, do not articulate with antorbital*; suborbitals absent*; small antorbital and very slender infraorbital bones; maxilla not expanded posteroventrally*; slender lower jaw*; sharp conical teeth on maxillae, premaxillae, and lower jaws; suboperculum only slightly larger than operculum, both roughly oblong in shape, approximately as deep as long; three or four branchiostegal rays; cleithrum small with approximately equally large dorsal and anteroventral portions; dorsal fin slightly larger than anal fin; anal fin with 14 rays; caudal fin with 20 rays, four of which are in epaxial position; slender basal and fringing fulcra on unpaired fins; two preanal scutes (from López-Arbarello and Zavattieri 2008).

Pseudobeaconia bracaccinii Bordas, 1944
Text-figure 6A

*1944 *Pseudobeaconia bracaccinii* Bordas, pp. 454–455, pl. 1.
1973*a* *Pseudobeaconia bracaccinii* Bordas; Hutchinson, pp. 5–13, figs 1–5.
1973*b* *Pseudobeaconia bracaccinii* Bordas; Hutchinson, p. 292.
2008 *Pseudobeaconia bracaccinii* Bordas; López-Arbarello and Zavattieri, p. 1033, figs 6A, 7.

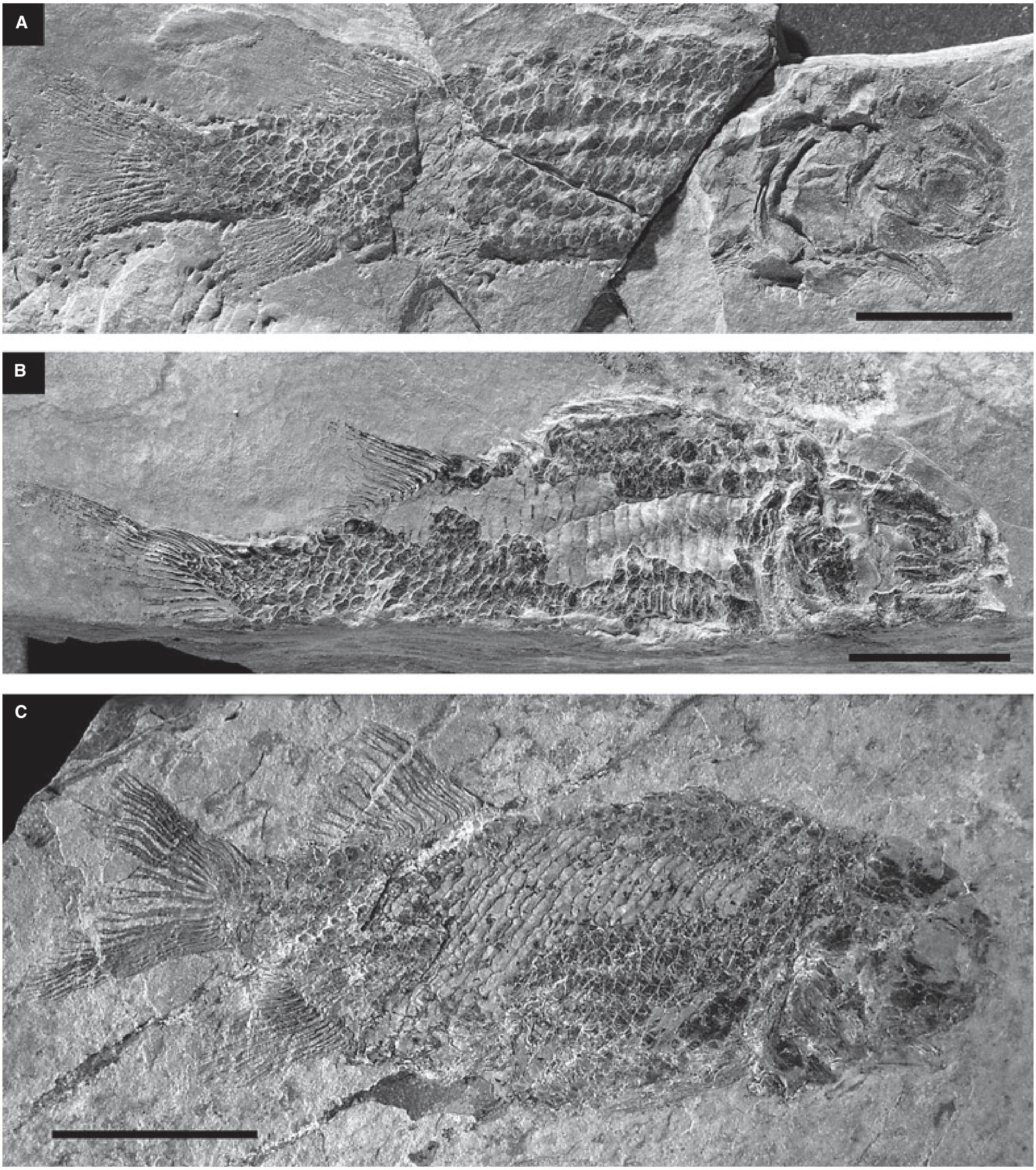
Holotype. MACN 14868 (specimen is lost).

Referred material. MCZ 12883–12891 and 12894–12915; CPBA-V 9799 and 9803.

Type locality. Quebrada de Santa Clara, Mendoza Province, Argentina, close to the border with the San Juan Province, about 800 m West of the Puesto de Santa Clara.

Type horizon. Santa Clara Abajo Formation, Cuyana Basin, lower Upper Triassic (Zavattieri *et al.* 2002*c*).

Diagnosis. A species of *Pseudobeaconia* distinguished by the following combination of primitive and advanced



TEXT-FIG. 6. Species of *Pseudobeaconia* Bordas, 1944. A, *Pseudobeaconia bracaccinii* Bordas, 1944, MCZ 12912 (photograph by G. Janßen). B, *P. elegans* Bordas, 1944, MCZ 12892 (photograph by G. Janßen). C, *P. celestae* López-Arbarello and Zavattieri, 2008, MCNA-PV 944b. Photographs in A and B are ©President and Fellows of Harvard College. Modified from López-Arbarello and Zavattieri (2008). Scale bars represent 1 cm.

characters: body depth three times in SL; anterior and posterior dermopterotics present; anterior supraorbital does not extend beyond the anterior border of the frontal; short infraorbital process of preoperculum; pectoral fin with one stout basal fulcrum and nine rays; posterior half of dorsal fin opposite to anterior half of anal fin; dorsal fin with three basal fulcra and 16 rays; anal fin with two basal fulcra; caudal fin with nine dorsal and three ventral basal fulcra; seven dorsal and four ventral precaudal median scutes; dorsal ridge with more than ten spine-like scales, starting almost immediately behind the skull (from López-Arbarello and Zavattieri 2008).

Pseudobeaconia elegans Bordas, 1944
Text-figure 6B

v* 1944 *Pseudobeaconia elegans*; Bordas, p. 456, pl. 1.
1973*a* *Pseudobeaconia elegans* Bordas; Hutchinson, pp. 13–17, figs 6–8.
1973*b* *Pseudobeaconia elegans* Bordas; Hutchinson, p. 292.
2008 *Pseudobeaconia elegans* Bordas; López-Arbarello and Zavattieri, pp. 1034–1035, figs 6B, 8.

Holotype. MACN 14869.

Referred material. MCZ 12892 and 12893.

Type locality. Quebrada de Santa Clara, Mendoza Province, Argentina, close to the border with the San Juan Province, about 800 m west of the Puesto de Santa Clara.

Type horizon. Santa Clara Abajo Formation, Cuyana Basin, lower Upper Triassic (Zavattieri *et al.* 2002*c*).

Diagnosis. A species of *Pseudobeaconia* distinguished by the following combination of primitive and advanced characters: body depth is 3.5 × in SL; anterior and posterior dermopterotics present; anterior supraorbital bone extends beyond the anterior border of the frontal; origin of anal fin opposite to end of dorsal fin; anal fin with two basal fulcra; caudal fin with six dorsal and one ventral basal fulcra; nine dorsal and five ventral precaudal median scutes (from López-Arbarello and Zavattieri 2008).

Pseudobeaconia celestae López-Arbarello and Zavattieri, 2008
Text-figure 6C

v* 1955 *Mendocinia brevis*; Schaeffer, pp. 4–15, figs 1–6, 8d.
1960 *Mendocinia brevis*; Romer, p. 128.
1973*a* *Mendocinia brevis*; Hutchinson, pp. 1–3, 18–19, fig. 9b.
1973*b* *Mendocinia brevis*; Hutchinson, pp. 296–301, 333–335, 347.
1988 *Mendocinia*; Gardiner, p. 261.
1989 *Mendocinichthys*; Gardiner and Schaeffer, p. 179, fig. 23d.
v* 2008 *Pseudobeaconia celestae* López-Arbarello and Zavattieri, pp. 1035–1041, figs 6C, 9–14.

Holotype. MCNAM-PV 944a/b.

Paratype. AMNH 8282.

Referred material. AMNH 8279 and 8287; MCNAM-PV 1238 and 3810–13.

Type locality. Yacimiento 2, south-western side of the Cerro El Mástil, on the eastern side of the Quebrada de los Leones, El Challao, in the vicinity of the city of Mendoza, Mendoza Province, Argentina.

Type horizon. Potrerillos Formation, Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Diagnosis. A species of *Pseudobeaconia* distinguished by the following combination of primitive and advanced characters: body depth is 2.5 × in SL; ventrolateral process of the parietal indenting in the dorsal border of the dermopterotic; anterior supraorbital does not extend beyond the anterior border of the frontal; preoperculum with high posterodorsal process; infraorbital process of preoperculum long and sharp; anterior margin of anal fin opposite the posterior end of dorsal fin; dorsal fin with two basal fulcra and 12 rays; anal fin with one slender basal fulcrum; caudal fin with three dorsal and two ventral basal fulcra; six dorsal and four ventral precaudal scutes (from López-Arbarello and Zavattieri 2008).

Pseudobeaconia cuyana (Bordas, 1944) comb. nov.
Text-figure 7

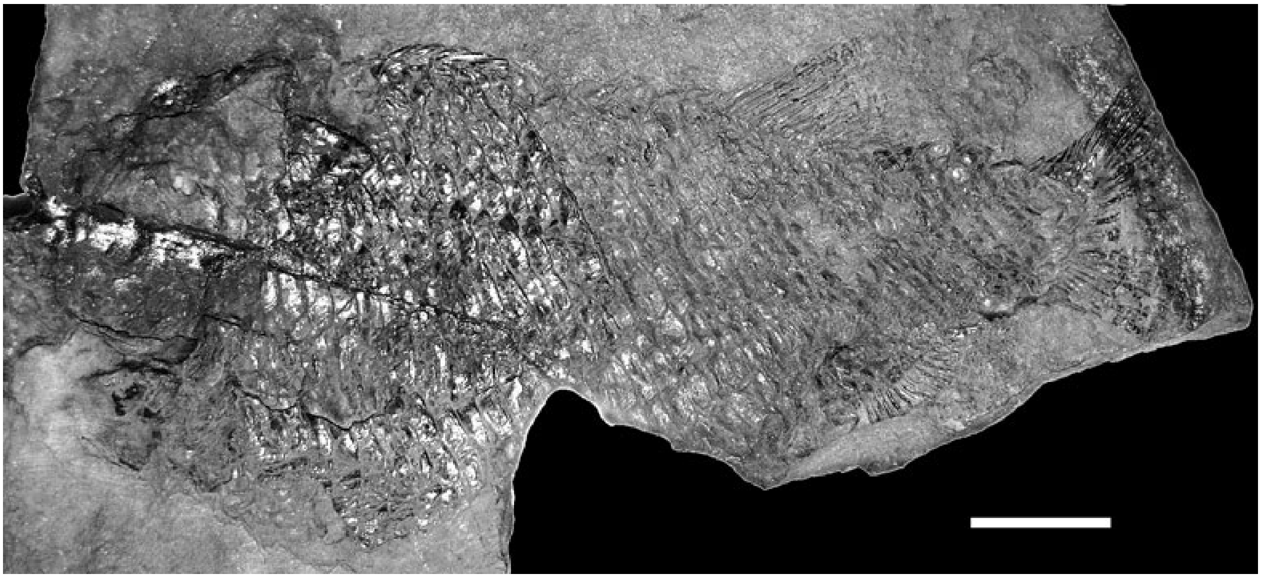
v* 1944 ?*Cleithrolepis cuyana* Bordas,
1988 ?*Cleithrolepis cuyana* (Bordas); Gardiner, p. 262.

Holotype. MACN 14879 (Text-fig. 7).

Type locality. Quebrada de Santa Clara, Mendoza Province, Argentina, close to the border with the San Juan Province, about 800 m west of the Puesto de Santa Clara.

Type horizon. Santa Clara Abajo Formation, Cuyana Basin, lower Upper Triassic (Zavattieri *et al.* 2002*c*).

Diagnosis. A species of *Pseudobeaconia* differing from all the other species of this genus in the following combination of characters: three dorsal and four ventral caudal



TEXT-FIG. 7. *Pseudobeaconia cuyana* (Bordas, 1944) comb. nov. MACN 14879, lectotype (photograph by J. B. Desojo). Scale bar represents 1 cm.

basal fulcra; four dorsal and three ventral dorsal precaudal scutes.

Remarks. Pseudobeaconia cuyana comb. nov. is based on a rather poorly preserved and incomplete postcranium. However, there is enough information to identify the fish in Pseudobeaconiidae (an incomplete dorsal ridge of spine-like scales between skull and dorsal fin, the morphology and ornamentation of the scales), and within this family, in the genus *Pseudobeaconia* (caudal fin with 20 rays, four of which are in epaxial position). *Pseudobeaconia cuyana* comb. nov. clearly differs from *Cleithrolepis* and other cleithrolepids or closely related taxa, in which the scales are much deeper, more than four times deeper than long (López-Arbarello and Zavattieri 2008), and there is a much higher number of caudal fin rays (27 in *Cleithrolepis major*; Gardiner 1988; 37 in *Cleithrolepis granulata*, at least 26 in *Cleithrolepidina extoni*, and 30 in *Hydropessum*; Hutchinson 1973*b*) with at least ten of them in epaxial position (10 in *Cleithrolepis major*; Gardiner 1988; 12 in *Cleithrolepis granulata*, and 10 in *Hydropessum*; Hutchinson 1973*b*).

Genus MENDOCINICHTHYS Whitley, 1953

Type species. Mendocinichthys brevis (Bordas, 1944).

Diagnosis. As for the type and only species.

Remarks. Mendocinichthys has recently been reviewed by López-Arbarello and Zavattieri (2008).

Mendocinichthys brevis (Bordas, 1944)

Text-figure 8

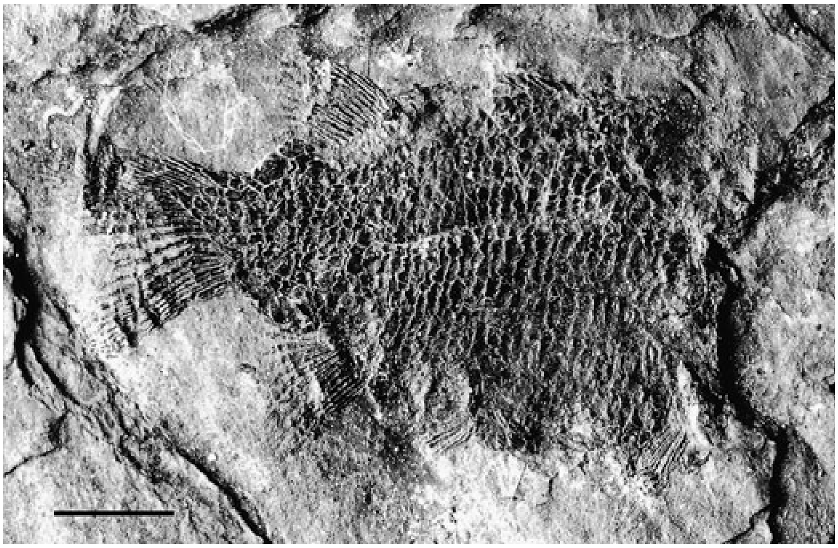
vp*	1944	*Mendocinia brevis* Bordas, pp. 458–459, pl. 2, photograph of the specimen MACN 15350 at the bottom right (erroneously labelled as MACN 15351 in the figure caption).
	1948*a*	*Mendocinia brevis* Bordas; Rusconi, p. 169.
	1953	*Mendocinichthys brevis* (Bordas); Whitley, p. 134.
	1957	*Mendocinia brevis* (Bordas); Rusconi, p. 54.
	2008	*Mendocinichthys brevis* (Bordas); López-Arbarello and Zavattieri, pp. 1041–1044, figs 15–17.

Lectotype. MACN 15350, incomplete specimen. Although no cranial elements are preserved, the postcranium is almost complete and well preserved.

Type locality. Village of El Challao near the city of Mendoza, Mendoza Province, Argentina.

Type horizon. Potrerillos Formation, Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Diagnosis. Small pseudobeaconiids of about 30 mm SL and maximum body depth about 0.5 SL; dorsal and anal fins of similar size; dorsal fin with five basal fulcra and 12 lepidotrichia, the basal segments of which are very high, about six times higher than the distal segments; caudal fin with 25 lepidotrichia, eight epaxial fin rays, three dorsal and three ventral basal fulcra; basal segments of epaxial caudal fin rays relatively and absolutely longer than the equivalent elements in the hypaxial rays; dorsal



TEXT-FIG. 8. *Mendocinichthys brevis* (Bordas, 1944), MACN 15350, lectotype. Modified from López-Arbarello and Zavattieri (2008). Scale bar represents 0.5 cm.

ridge with six spiniform scales; four large median scutes on dorsal midline from end of dorsal to caudal fin (from López-Arbarello and Zavattieri 2008).

NOMINAL TAXA HERE CONSIDERED NOMINA DUBIA

ACTINOPTERYGII *incertae ordinis*

Gyrolepidoides cuyanus Cabrera, 1944

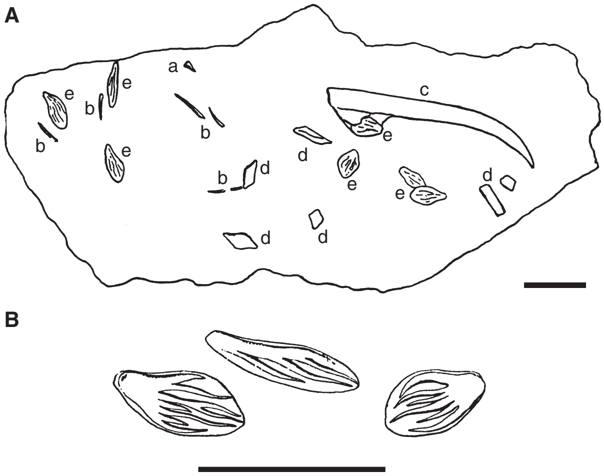
Text-figure 9

Holotype. MLP 44-VII-16-2.

Type locality. Left (northern) margin of the Mendoza River between Cacheuta and Potrerillos, Mendoza Province, Argentina. The locality is nowadays flooded by the Potrerillos Dam.

Type horizon. Probably Cacheuta Formation, Cuyana Basin (Rusconi 1957; Zavattieri *et al.* 2002*a*), upper Upper Triassic (Morel *et al.* 2002*a*).

Remarks. *Gyrolepidoides cuyanus* is based on a very incomplete and unidentifiable specimen, in which only impressions, a fragment of bone, and a tooth are preserved (Text-fig. 9). The impression identified by Cabrera (1944) as a preoperculum is not really identifiable. Most of the scales, which are all preserved as impressions only, do not show any articular process and are elongated and rounded, with one extreme narrower than the other. Therefore, they probably belong to, or close to, the dorsal or ventral midlines, where similarly striated scales are relatively common among basal actinopterygians, the species of *Challaia* (see below) among them. Other impressions of scales are rhomboidal and do not show any process or ornamentation. Also, conical dentition as the tooth preserved in this specimen is common among Triassic actinopterygians. Therefore, the material of *Gyrolepidoides cuyanus* is not diagnostic, and the name is regarded as a *nomen dubium*.



TEXT-FIG. 9. *Gyrolepidoides cuyanus* Cabrera, 1944. A, MLP 44-VII-16-2, drawing of the holotype and only known specimen. B, reconstructions of three isolated scales based on casts made from the holotype. Modified from Cabrera (1944). Labels: a, tooth; b, fragments of fin rays; c, imprint of a bone interpreted by Cabrera (1944) as a fragment of a preoperculum; d, imprints of rhomboid scales interpreted by Cabrera (1944) as some kind of branchiostegal elements; e, imprints of ornamented scales. Scale bars represent 1 cm.

ACTINOPTERYGII *incertae ordinis*

Gyrolepidoides multistriatus Rusconi, 1948*a*

Text-figure 10

Holotype. MCNAM-PV 587.

Type locality. Paramillos de Uspallata, Mendoza Province, Argentina.

Type horizon. Agua de la Zorra Formation, Cuyana Basin, probably Middle Triassic.

Remarks. As is the case with *Gyrolepidoides cuyanus*, the type and only specimen of *G. multistriatus* consists of some isolated scales only (Text-fig. 10). These scales are very similar to those of *G. cuyanus*, differing only in the total number of ridges. As mentioned above, the scales of the two *Gyrolepidoides* species closely resemble the scales in *Challaia*, in particular those of *Challaia striata* (see below). Even Rusconi (1948*a*, pp. 166–167, 183) found the same kind of scales, referable either to *G. multistriatus* or *Ch. striata* at the same locality in the Quebrada de Los Leones in El Challao. However, the fossils identified in different species of *Challaia* come from different localities and different stratigraphic units within the Uspallata Group, and most of them are also based on undiagnostic material. Therefore, a referral of the isolated scales of *G. multistriatus* to any particular taxon is not possible.

ACTINOPTERYGII *incertae ordinis*

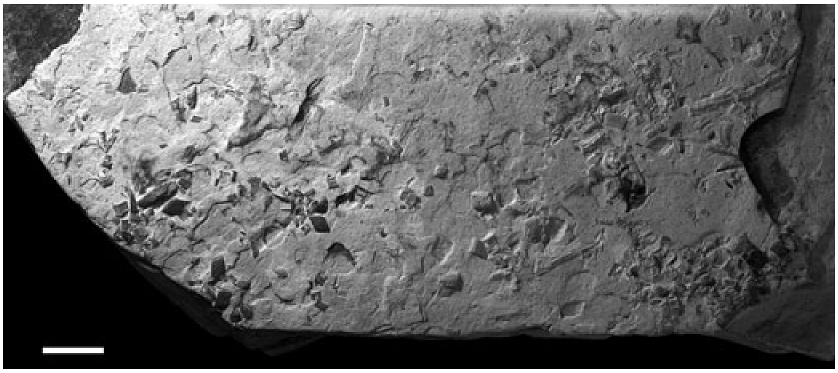
Cenechoia paramillensis Rusconi, 1946*a*

Text-fig. 11A

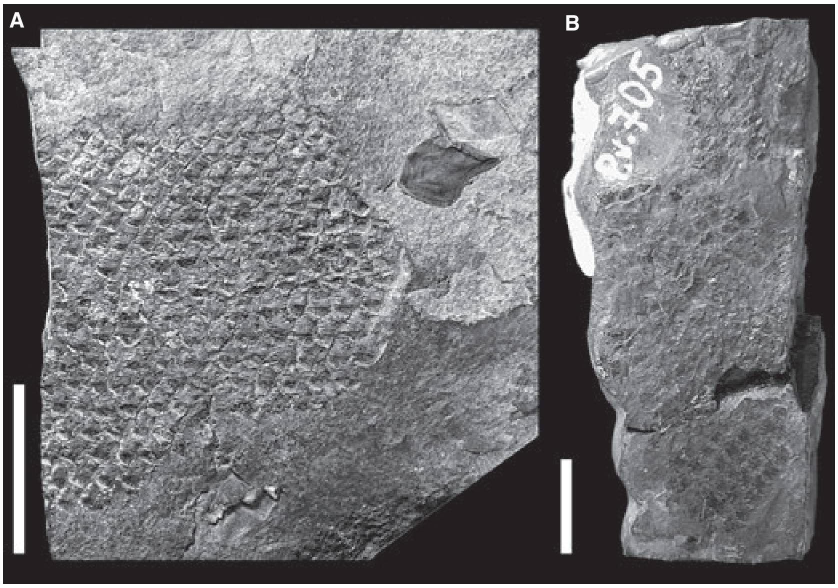
Holotype. MCNAM-PV 505.

Type locality. One kilometre South of Agua de la Zorra, Uspallata, Mendoza Province, Argentina.

Type horizon. Agua de la Zorra Formation, Cuyana Basin, probably Middle Triassic.



TEXT-FIG. 10. *Gyrolepidoides multistriatus* Rusconi, 1948*a*. MCNAM-PV 587, holotype. Scale bar represents 1 cm.



TEXT-FIG. 11. Genus *Cenechoia* Rusconi, 1946*a*. A, MLP 44-VII-16-2, holotype of *C. paramillensis* Rusconi, 1946*a*. B, MCNAM-PV 705, holotype of *C. sulcata* Rusconi, 1947. Scale bars represent 1 cm.

Remarks. Rusconi (1946*a*, 1947) named two species in the genus *Cenechoia* (see below). Both names are based on body fragments preserving only some rows of articulated scales (Text-fig. 12). In both cases, the scales are numerous and relatively small, with strongly dentated posterior borders. An ornamentation of longitudinal ridges is apparent in some scales. The scales are not rounded with crenulate posterior border as illustrated by Rusconi (1946*a*, fig. 4, 1947, fig. 1). This very incomplete and poorly preserved material is not enough to identify a taxon. The few known specimens most probably correspond to the same kind of fish, which might represent a distinct taxon, but the available material is too poorly preserved and not diagnostic. In the same rock containing the type of *Cenechoia paramillensis*, a broken fragment of a bone and two large and disarticulated scales are also preserved (Text-fig. 11A). These isolated elements most probably belong to a different fish, which cannot be identified.

ACTINOPTERYGII *incertae ordinis*

Cenechoia sulcata Rusconi, 1947
Text-figure 11B

Holotype. MCNAM-PV 705.

Paratype. MCNAM-PV 706.

Referred material. MCNAM-PV 707, PV 708.

Type locality. One kilometre South of Agua de la Zorra, Uspallata, Mendoza Province, Argentina.

Type horizon. Agua de la Zorra Formation, Cuyana Basin, probably Middle Triassic.

Remarks. See above comments for *Cenechoia paramillensis*.

ACTINOPTERYGII *incertae ordinis*

'*Eurynotus*' *uspallatensis* Rusconi, 1946*b*
Text-figure 12

Holotype. MCNAM-PV 546.

Referred material. MCNAM-PV 548, PV 551.

Type locality. One kilometre South of Agua de la Zorra, Uspallata, Mendoza Province, Argentina.

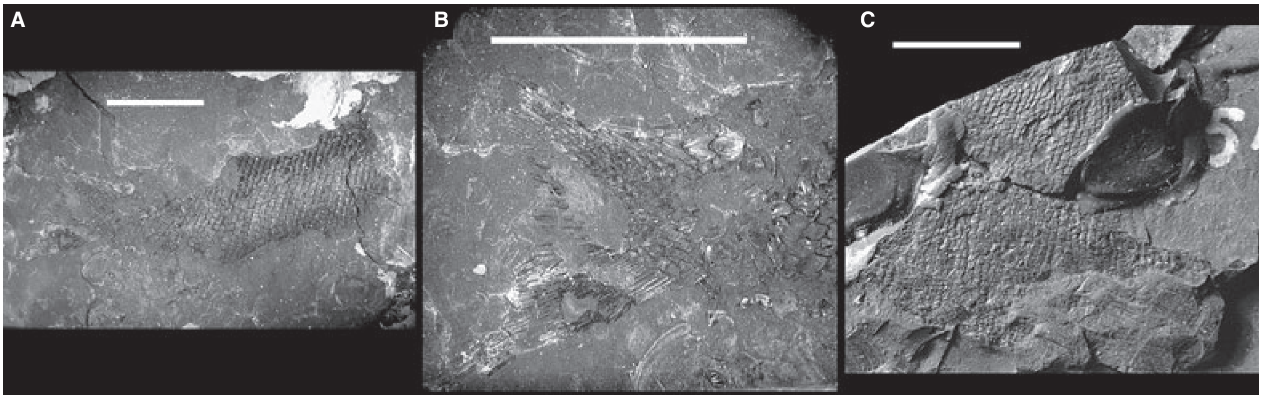
Type horizon. Agua de la Zorra Formation, Cuyana Basin, probably Middle Triassic.

Description. The holotype of '*Eurynotus*' *uspallatensis* consists of the partially preserved posterior portion of a fish, including several rows of articulated scales around the lateral line and the caudal peduncle and fin (Text-fig. 12A–B). Contrary to the reconstructions provided by Rusconi (1946*b*, figs 3–4), neither the dorsal and ventral midlines, nor the pelvic and anal fins are preserved. MCNAM-PV 548 (Text-fig. 12C) includes two partially preserved specimens, consisting of the middle portion of the bodies without fins or the dorsal and ventral midlines, showing similar scales to those in the holotype. A group of similar scales constitutes the specimen MCNAM-PV 551.

The tail in the holotype is hemiheterocercal with six epaxial fin rays (Text-fig. 12B). There are at least five dorsal precaudal scutes and two dorsal basal caudal fulcra, the latter fulcra being paired elements. There are at least ten rows of scales in the body lobe of the tail. The caudal fin rays are very incompletely preserved, and their number and branching pattern are unknown, but they are segmented, the segments being very long.

The rhombic scales on the caudal peduncle are rhomboidal, but they are rectangular, up to two times deeper than long, in the more anterior region.

Remarks. '*Eurynotus*' *uspallatensis* represents a basal, non-neopterygian actinopterygian, but the incomplete material does not allow the identification of a species or its referral to any particular group of actinopterygians.



TEXT-FIG. 12. '*Eurynotus*' *uspallatensis* Rusconi, 1946*b*. A, MCNAM-PV 546, holotype. B, detail of the tail in MCNAM-PV 546. C, two of the referred specimens (MCNAM-PV 548). Scale bars represent 1 cm.

ACTINOPTERYGII *incertae ordinis*

'*Semionotus*' *mendozaensis* Geinitz, 1885

Holotype. Unknown.

Type locality. Agua de la Zorra, Uspallata, Mendoza Province, Argentina.

Type horizon. Agua de la Zorra Formation, Cuyana Basin, probably Middle Triassic.

Remarks. It should be noticed that Geinitz named '*Semionotus*' *mendozaensis* in 1876, but the work was published in 1885. Although brief, Geinitz (1885) gave a description of the scales of '*S.*' *mendozaensis*, which he compared with *S. nilsoni* Agassiz, 1837, and thus, according to the International Code of Zoological Nomenclature (ICZN 1999: Art. 12.1), the name is available. However, Gainitz did not provide collection numbers of the specimens he described, which could not be identified. Moreover, nothing can be said from the description, but only that he was dealing with the rhomboid scales of some actinopterygian.

ACTINOPTERYGII *incertae ordinis*

'*Semionotus*' *unicristatus* Rusconi, 1946*c*

Holotype. Unknown.

Type locality. Cacheuta, Mendoza Province, Argentina.

Type horizon. Probably Cacheuta Formation, Cuyana Basin (Rusconi 1957; Zavattieri *et al.* 2002*a*), upper Upper Triassic (Morel *et al.* 2002*a*).

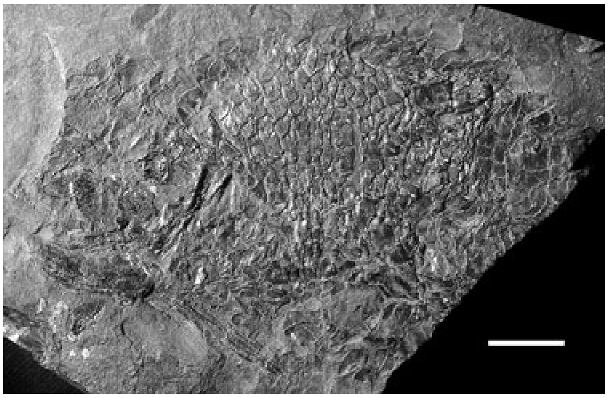
Remarks. The nominal taxon '*Semionotus*' *unicristatus* was named and briefly described and distinguished from '*S.*' *mendozaensis* by Rusconi (1946*c*, p. 15) in the last paragraph of a publication dealing with several newly proposed Triassic fish taxa. There is no indication of a particular specimen, no collection number and no illustration. The description does not allow identification further than the rhomboid scale of an actinopterygian fish.

ACTINOPTERYGII *incertae ordinis*

'*Semionotus*' *vallejensis* Rusconi, 1950*b*

Text-figure 13

Holotype. MCNAM-PV 552.



TEXT-FIG. 13. '*Semionotus*' *vallejensis* Rusconi, 1950*b*. MCNAM-PV 552, holotype. Scale bar represents 1 cm.

Type locality. One kilometre south of Agua de la Zorra (Quebrada Vallejos), Uspallata, Mendoza Province, Argentina.

Type horizon. Agua de la Zorra Formation, Cuyana Basin, (probably) Middle Triassic.

Remarks. '*Semionotus*' *vallejensis* is based on a partially preserved articulated fish specimen, including the incompletely preserved anterior part of the body and posterior part of the skull (Text-fig. 13). The skull bones are very poorly preserved and, thus, difficult to interpret. The skull bones are ornamented with ridges and shelves. The scales are mostly broken and also poorly preserved, but an ornamentation of tubercles and short ridges in the anterior half of the exposed area is evident. In the posterior half of the exposed area, several layers of ganoin form marginal concentric ridges. There are no characters preserved that would allow a referral to Semionotiformes, let alone the genus *Semionotus*. Furthermore, the material does not exhibit any diagnostic characters, so that the taxon must be considered a *nomen dubium*.

ACTINOPTERYGII *incertae ordinis*

?*Pholidophorus dentatus* Rusconi, 1946*c*

Holotype. MCNAM-PV 259. Lost.

Paratype. MCNAM-PV 260. Lost.

Type locality. Quebrada de los Leones, 2 km West of El Challao, Mendoza Province, Argentina.

Type horizon. Potrerillos Formation, Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Remarks. The only known specimens of ?*Pholidophorus dentatus*, two isolated single scales, each identified as holotype and paratype are presently lost (Cerdeño 2005, p. 13), and the specimens were never illustrated. According to Rusconi's (1946*c*) description, the scales were of the generalized type of romboid scales of any basal actinopterygian. Rusconi described them as rectangular, about three times deeper than long, with peg-and-socket articulation, smooth surface and dentated posterior border. Therefore, as it is not possible to examine the material and the description by Rusconi is too poor to allow any identification of the fish, the name is regarded as *nomen dubium*.

ACTINOPTERYGII *incertae ordinis*

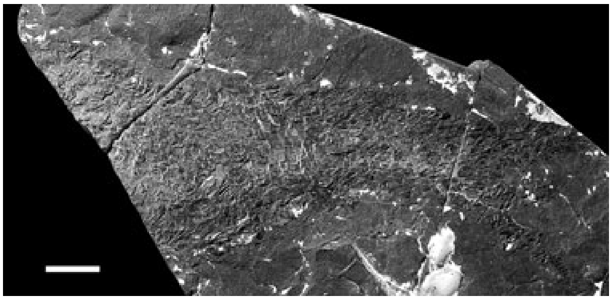
'*Pholidophorus*' *vallejensis* Rusconi, 1947
Text-figure 14

Holotype. MCNAM-PV 703.

Type locality. One kilometre South of Agua de la Zorra, Uspallata, Mendoza Province, Argentina.

Type horizon. Agua de la Zorra Formation, Cuyana Basin, probably Middle Triassic.

Remarks. MCNAM-PV 703 (Text-fig. 14) is a very incomplete and poorly preserved specimen consisting of the abdominal portion of an actinopterygian fish with articulated rhomboid scales, the most anterior rows showing strong peg-and-socket articulation, some remnants of the dorsal, anal and caudal fins including remains of segmented lepidotrichia and some dorsal fringing fulcra. The caudal fin was probably heterocercal, but it is too poorly preserved to be certain about this condition. Rusconi (1947, p. 24) referred this fish to the genus *Pholidophorus*, because he found it similar to '*Ph.*' *micronyx* Agassiz, 1834, a fish from the Late Jurassic of Solnhofen, Germany, which does not represent the genus *Pholidophorus* and has an uncertain systematic position (Arratia 2000). Nevertheless, apart from the general resemblance of these fossils at first glance, there is not meaningful anatomical similarity between the specimen MCNAM-PV 703 and the material of '*Ph.*' *micronyx*.



TEXT-FIG. 14. '*Pholidophorus*' *vallejensis* Rusconi, 1947. MCNAM-PV 703 holotype. Scale bar represents 1 cm.

ACTINOPTERYGII *incertae ordinis*

Neochallaia leonensis Rusconi, 1952
Text-figure 15

Holotype. MCNAM-PV 2147.

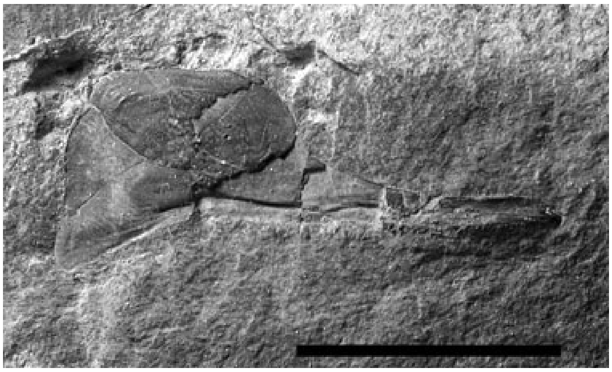
Paratype. MCNAM-PV 2160. Lost.

Referred material. MCNAM-PV 2145.

Type locality. About 300 m West of the Piletas de El Challao, Mendoza Province, Argentina.

Type horizon. Potrerillos Formation (Rusconi 1957; Marsicano *et al.* 2002; Zavattieri *et al.* 2002*b*), Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Remarks. Neochallaia leonensis is based on an isolated maxilla of a primitive actinopterygian fish, which looks very similar to the maxilla of *N. tellecheai* comb. nov. (Text-fig. 15). Rusconi (1952) distinguished the two species on the basis of some details of the dentition and superficial morphology of the bone. However, the maxilla of *N. tellecheai* comb. nov. is not well enough preserved to compare the details of possible ornamentation, and the series of teeth in *N. leonensis* is too incompletely preserved, so that the total number as well as the relative size and morphology of the teeth is unknown. The specimens MCNAM-PV 2160 (which included a portion of lower jaw) and MCNAM-PV 2145 could not be found and are probably lost (Cerdeño 2005, p. 13). Therefore, further comparisons are not possible, and the type and only available specimen, MCNAM-PV 2147, can only be tentatively identified as an undeterminate species of *Neochallaia*.



TEXT-FIG. 15. *Neochallaia leonensis* Rusconi, 1952. MCNAM-PV 2147, holotype. Scale bar represents 1 cm.

ACTINOPTERYGII *incertae ordinis*
ACROLEPIDAE

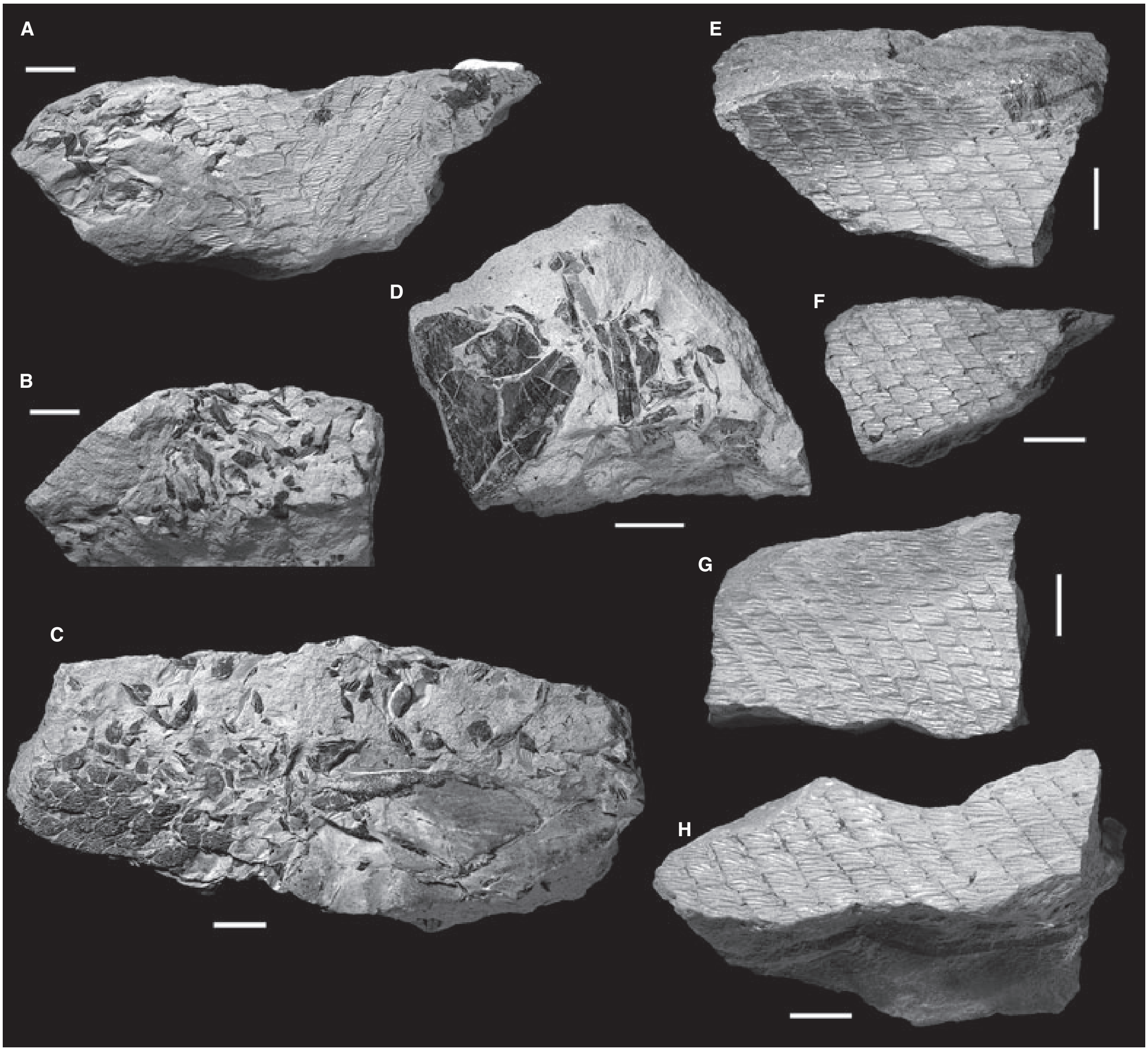
Challaia striata Rusconi 1946*a*
Text-figure 16

Holotype. MCNAM-PV 49.

Type locality. El Challao, Mendoza Province, Argentina.

Type horizon. Potrerillos Formation (Rusconi 1957; Marsicano *et al.* 2002; Zavattieri *et al.* 2002*b*), Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Remarks. MCNAM-PV 49 includes several fragments of a fish with impressions and fragments of articulated scales, some isolated scales and fragmentary preserved bones (Text-fig. 16). As explained by López-Arbarello *et al.* (2006, p. 255), the ornamentation of the scales of acrolepid fishes is similar to that of other basal actinopterygians, such as colobodontids and ptycholepids, among others. However, the scale features indicated in the diagnoses of the family Acrolepidae and the genus *Challaia* (see above), which are present in the scales in MCNAM-PV 49, strongly suggest that this specimen is most probably co-generic with the other fossils identified in *Challaia*, but it is undiagnostic at the species level. Yet, as other



TEXT-FIG. 16. *Challaia striata* Rusconi 1946*a*. MCNAM-PV 49, holotype. A–C, imprints of articulated and disarticulated scales and partially or completely preserved scales and skull bones. D, partially preserved skull bones. E–H, imprints of articulated scales. Scale bars represent 1 cm.

diagnostic features of the genus *Challaia* are not preserved in MCNAM-PV 49, we refrain from referring it to this particular genus, but rather regard it as an undeterminate acrolepid at this time.

MCNAM-PV 49 most closely resembles *Ch. magna*, but in the holotype and only known specimen of this species, the scales are not well enough preserved to be certain about the possible synonymy of these two nominal species. In *Ch. elongata*, the only other valid species in this genus, the anterior flank scales are deeper and with a higher number of ridges than in *Ch. magna* (López-Arbarello *et al.* 2006), suggesting that the relatively shallow scales in MCNAM-PV 49 would rather represent the latter taxon. However, the specimen MCNAM-PV 49 is too fragmentary, and the preserved scales might correspond to the more posterior or ventral regions of the body, where the scales are shallow and with less number of ridges in both species (López-Arbarello *et al.* 2006).

ACTINOPTERYGII *incertae ordinis*
ACROLEPIDAE

Challaia multidentata Rusconi, 1949*a*

Holotype. MCNAM-PV 2792, specimen lost.

Type locality. North of the Cerro Bayo, Departamento de Las Heras, Mendoza Province, Argentina.

Type horizon. Most probably Cerro de Las Cabras Formation, Cuyana Basin, Middle Triassic (Stipanicic *et al.* 2002*a*; see below).

Remarks. The holotype and only known specimen of *Challaia multidentata* Rusconi, 1949*b* is lost, and thus, a thorough revision is not possible. However, according to the original description by Rusconi (1949*b*, p. 234), the specimen most probably represented the previously described *Challaia magna*. Although there is no illustration of the specimen, according to Rusconi (1949*b*), MCNAM-PV 2792 consisted of a poorly preserved portion of a skull. Rusconi himself noticed the strong similarity with *Ch. magna*, although he still proposed a new binomien for this specimen based on its supposedly peculiar maxillar dentition. According to this author, the dentition in MCNAM-PV 2792 consisted of two rows of teeth: a marginal row of small conical teeth that he noted were later destroyed during the acid preparation (Rusconi 1949*b*. p. 234) and a medial row of large conical teeth with striated surface. *Ch. magna* was originally described with a single row of maxillar teeth, which are large, conical and with striated surface (Rusconi 1949*a*, p. 222). However, Rusconi (1949*b*, p. 234) later noticed the presence of an additional marginal row of small conical teeth in this species. Therefore, although the author concluded 'Sin embargo, las dos series de dientes de esta especie, muestran diferencias apreciables con relación a las de *Ch. Multidentata*' ('However, the two series of teeth in this species show notable differences with those of *Ch. Multidentata*'; translated by ALA), these differences have never been explained in detail. Therefore, although MCNAM-PV 2792 most probably represented *Ch. magna*, the name *Ch. multidentata* is regarded as a *nomen dubium* given that the specimen is lost.

ACTINOPTERYGII *incertae ordinis*
ACROLEPIDAE

?*Challaia cacheutensis* Rusconi, 1950*a*

Holotype. MCNAM-PV 768, specimen is lost.

Type locality. Area of the Mina Elcha, Cacheuta, Mendoza Province, Argentina.

Type horizon. Probably Cacheuta Formation (Rusconi 1957; Zavattieri *et al.* 2002*a*), Cuyana Basin, upper Upper Triassic (Morel *et al.* 2002*a*).

Remarks. ?*Challaia cacheutensis* is based on some isolated rhomboid scales ornamented with 12–14 longitudinal ridges, which, according to Rusconi (1950*a*) only covered the posterior half of the exposed area. The number of ridges in these scales is, thus, higher than in the undeterminate *Ch. striata*, but similar to the scales in *Ch. elongata* (14–16 ridges in the anterior portion of the flank to 6–8 ridges in the abdominal region; López-Arbarello *et al.* 2006). The ridges cover the whole exposed area of the scale in *Ch. elongata*, but they anastomose anteriorly. Similarly, ornamented scales, with longitudinal ridges covering the anterior portion of the exposed area only, are characteristic of *Ameghinichthys* Arratia *et al.*, 2004, from the Lower Tithonian Longing Member of the Ameghino Formation at Longing Gap, Antarctica. There are only 2–6 ridges in the known scales of *Ameghinichthys*, although the type and only specimen is very incomplete, and it is not possible to know the variation in the number of ridges in the scales at different parts of the body. Despite these similarities with other species of *Challaia* and *Ameghinichthys*, it is not possible to refer the scales described by Rusconi (1950*a*) to a particular taxon. Also, there is very little information available on ?*Ch. cacheutensis*, and the type and only known specimen is lost, and therefore, we prefer to regard this taxon name as a *nomen dubium*.

ACTINOPTERYGII
PERLEIDIFORMES
PSEUDOBEACONIIDAE

Anatoia semiovata Rusconi, 1946*c*

Text-figure 17

Holotype. MCNAM-PV 276.

Paratype. MCNAM-PV 239; specimen is lost.

Referred material. MCNAM-PV 155, 201, 214, 223.

Type locality. Yacimiento 1 of Rusconi (1948*a*), south-western side of the Cerro El Mástil, on the eastern side of the Quebrada de los Leones, El Challao, in the vicinity of the city of Mendoza, province of Mendoza, Argentina.

Type horizon. Potrerillos Formation, Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Remarks. The type material (Text-fig. 17), consisting of a small, ventral portion of a fish including some articulated scales, one poorly preserved pelvic fin, the proximal portion of the anal fin and a preanal scute, is not diagnostic. According to Rusconi (1946*c*, figs 2, 7), the paratype MCNAM-PV 239 was an almost complete specimen only missing the anterior portion of the skull. Unfortunately, however, the specimen is lost, and the information provided by Rusconi (1946*c*) is not detailed enough to diagnose a taxon. As it is the case in the holotype, the remaining referred specimens are also incomplete and very poorly preserved. The only distinctive features in the holotype are the characteristics of some well-preserved scales, about three times deeper than long, with straight posterior border, elevated central region and marginal concentric ridges of ganoine, which allow us to identify the fish as a member of the family Pseudobeaconiidae, but it cannot be referred to a particular genus or species within this family.

ACTINOPTERYGII
PERLEIDIFORMES
PSEUDOBEACONIIDAE

Anatoia debilis Rusconi, 1946*c*

Holotype. MCNAM-PV 238; specimen is lost.

Type locality. Yacimiento 1 of Rusconi (1948*a*), south-western side of the Cerro El Mástil, on the eastern side of the Quebrada de los Leones, El Challao, in the vicinity of the city of Mendoza, province of Mendoza, Argentina.

Type horizon. Potrerillos Formation, Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Remarks. The holotype of *Anatoia debilis* is unfortunately lost, and although the specimen was almost complete (Rusconi 1946*c*, fig. 8), there is very little information in the original description. Therefore, it is not possible to diagnose a taxon, and the name should be regarded as a *nomen dubium*. However, as is the case with *A. sulcata*, the morphology of the scales indicates that the fish was a Pseudobeaconiidae, based on Rusconi's description, but there is no distinct feature that allows its referral to a particular taxon within this family.

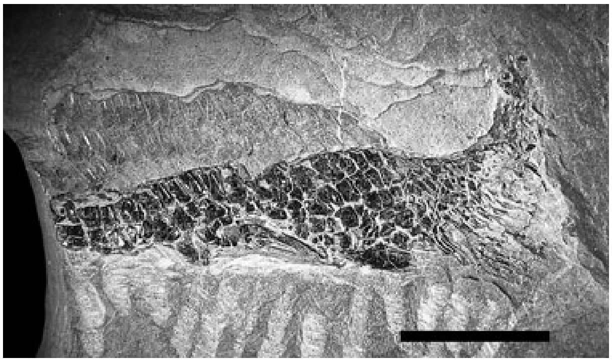
ACTINOPTERYGII
PERLEIDIFORMES
PSEUDOBEACONIIDAE

Pasambaya tellecheai Rusconi 1946*c*

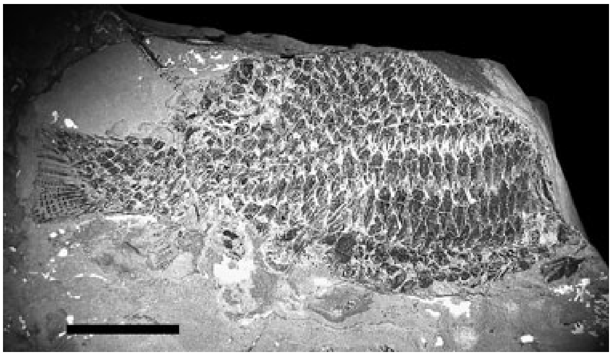
Text-figure 18

Holotype. MCNAM-PV 305.

Type locality. Yacimiento 2 of Rusconi (1948*a*), south-western side of the Cerro El Mástil, on the eastern side of the Quebrada



TEXT-FIG. 17. *Anatoia semiovata* Rusconi, 1946*c*. MCNAM-PV 276, holotype. Scale bar represents 1 cm.



TEXT-FIG. 18. *Pasambaya tellecheai* Rusconi 1946*c*. MCNAM-PV 305, holotype. Scale bar represents 1 cm.

de los Leones, El Challao, in the vicinity of the city of Mendoza, Mendoza Province, Argentina.

Type horizon. Potrerillos Formation, Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Remarks. The holotype and only known specimen of *Pasambaya tellecheai* (Text-fig. 18) probably represents a species of *Pseudobeaconia*. However, the specimen, a post-cranial portion of a fish with remnants of the anal fin, the proximal portion of the caudal fin and flank scales preserved in medial view, is too incomplete to allow further identification. So far, only one species of *Pseudobeaconia*, *P. celestae* López-Arbarello and Zavattieri, 2008, has been described from the area of El Challao; more species of this genus are known to be present in this area but have not been described yet (ALA pers. obs.).

ACTINOPTERYGII
PERLEIDIFORMES
PSEUDOBEACONIIDAE

Caminchaia draghii Rusconi 1946*c*
Text-figure 19

Holotype. MCNAM-PV 159.

Type locality. Yacimiento 1 of Rusconi (1948*a*), south-western side of the Cerro El Mástil, on the eastern side of the Quebrada de los Leones, El Challao, in the vicinity of the city of Mendoza, Mendoza Province, Argentina.

Type horizon. Potrerillos Formation, Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Remarks. Caminchaia draghii is only represented by a very incomplete specimen including the proximal portion of the dorsal fin, distal portion of the pelvic fin and a portion of the flank with several articulated scales (Text-fig. 19). Although poorly preserved, a few scales show the concentric ridges of ganoine and elevated central region distinct of the Pseudobeaconiidae. The relative size of the scales is smaller than in *Pseudobeaconia* or *Mendocinichthys*, and thus, the fish might represent a different genus. However, the holotype is not diagnostic, and the name is here regarded as a *nomen dubium*, until more material becomes available to test the possible validity of this taxon.

ACTINOPTERYGII
PERLEIDIFORMES
PSEUDOBEACONIIDAE

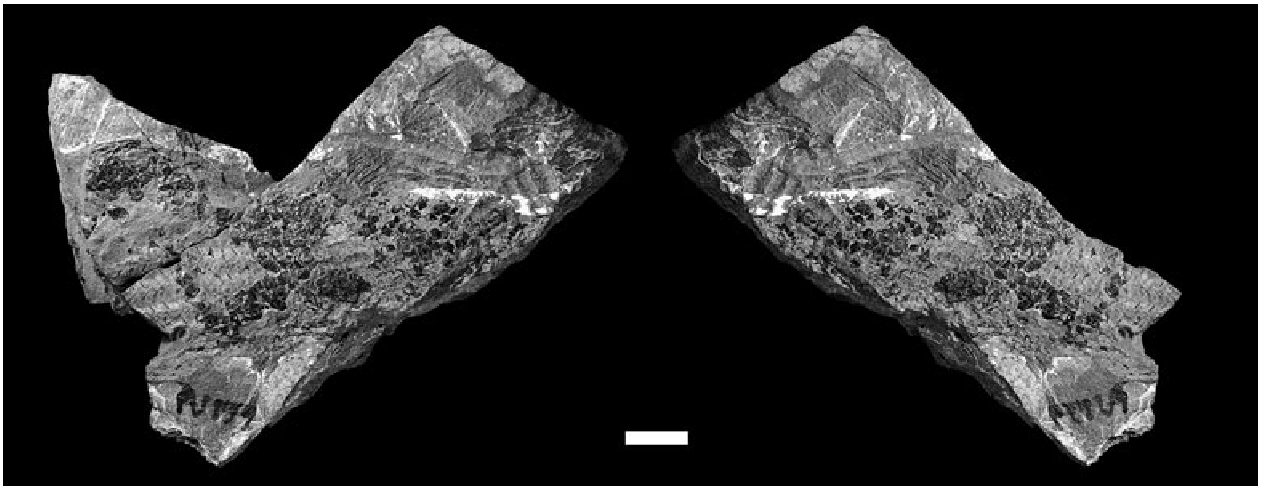
Echentaia obesa Rusconi 1946*c*
Text-figure 20

Holotype. MCNAM-PV 215.

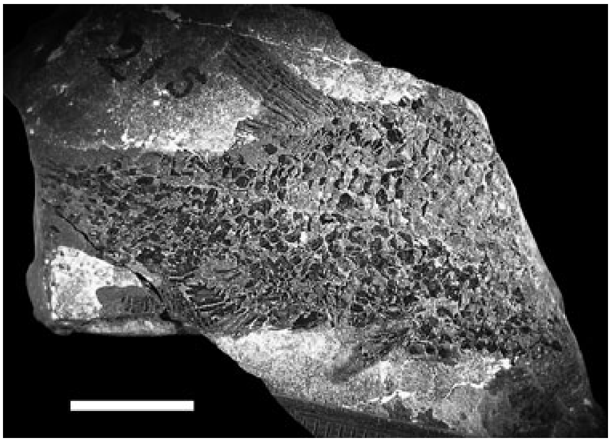
Type locality. Yacimiento 1 of Rusconi (1948*a*), south-western side of the Cerro El Mástil, on the eastern side of the Quebrada de los Leones, El Challao, in the vicinity of the city of Mendoza, province of Mendoza, Argentina.

Type horizon. Potrerillos Formation, Cuyana Basin, lower Upper Triassic (Morel *et al.* 2002*b*).

Remarks. The holotype and only known specimen of *Echentaia obesa* (Text-fig. 20) is an incomplete fish, including a portion of the postcranium, with partially



TEXT-FIG. 19. *Caminchaia draghii* Rusconi 1946*c*. MCNAM-PV 159, holotype – in part and counterpart. Scale bar represents 1 cm.



TEXT-FIG. 20. *Echentaia obesa* Rusconi 1946*c*. MCNAM-PV 215, holotype. Scale bar represents 1 cm.

preserved pectoral, pelvic, dorsal and anal fins. The skull and caudal fin are not preserved. Only the poorly preserved, distal, segmented portion of five rays is preserved of the pectoral fin. The pelvic fin includes five or six distally segmented rays and a series of fringing fulcra. In the anal fin, the proximal portions of 13 distally segmented rays are preserved together with one basal fulcrum and two fringing fulcra. The origin of the dorsal fin is closer to the pelvic than to the anal fin. There are 14 partially preserved dorsal fin rays, but the total number was certainly higher. The dorsal fin rays are also distally segmented, and there are remains of at least two basal fulcra and several fringing fulcra. The specimen is, however, not diagnostic, but it is very similar to the holotype of *Caminchaia draghii* and probably represents the same taxon, which, as explained above, might be a distinct genus of the Pseudobeaconiidae.

ACTINOPTERYGII
PERLEIDIFORMES
PSEUDOBEACONIIDAE

?*Amblypterus lujanensis* Rusconi, 1949*a*

Holotype. MCNAM-PV 2767; specimen is lost.

Type locality. Area of the Mina Elcha, Cacheuta, Mendoza Province, Argentina.

Type horizon. Probably Cacheuta Formation (Rusconi 1957; Zavattieri *et al.* 2002*a*), Cuyana Basin, upper Upper Triassic (Morel *et al.* 2002*a*).

Remarks. ?*Amblypterus lujanensis* is based on isolated scales only. According to the description provided by Rusconi (1949*a*, p. 235), the scales had marginal concentric ridges and elevated central region, and thus, they might have represented a species of the perleidiform family Pseudobeaconiidae (see López-Arbarello and Zavattieri 2008). However, the type and only known specimen is lost, and thus, the name is here regarded as a *nomen dubium*.

DISCUSSION

Based on the taxonomic discussions presented in the previous section, only eight of the 29 named species from the Cuyana Basin can currently be regarded as valid. This is mainly attributed to the poor quality of the available material, which, in many cases, is neither identifiable nor diagnosable. However, the real diversity of actinopterygians in this basin is very probably considerably higher than indicated by the only eight valid species that can be formally recognized.

Four among the valid species belong to a single genus, *Pseudobeaconia*, which together with *Mendocinichthys brevis* represents the same family, Pseudobeaconiidae, the monophyly of which has recently been demonstrated (López-Arbarello and Zavattieri 2008). Several of the nominal species here regarded as *nomina dubia* (*Anatoia semiovata*, *A. debilis*, *Pasambaya tellecheai*, *Caminchaia draghii* and *Echentaia obesa*) also represent the family Pseudobeaconiidae. The specimens referred to these nominal taxa might represent one of the recognized species of *Pseudobeaconia* or *Mendocinichthys*. Indeed, all of them come from the Potrerillos Formation and were found in the same area and probably the same stratigraphic level as *Pseudobeaconia celestae* or *Mendocinichthys brevis*.

The other three valid species recognized in the Cuyana Basin represent more primitive actinopterygians. One of them, *Challaia magna*, is a member of the Acrolepidae, which otherwise includes the Palaeozoic genera *Watsonichthys*, *Acrolepis*, *Acropholis* and *Plegmolepis* (Aldinger 1937). *Neochallaia tellecheai* comb. nov. probably represents a basal Chondrostei, and *Guaymayenia paramillensis* closely resembles the Early–Middle Triassic *Pteronisculus*, which, as many other primitive actinopterygians, is currently classified in the poorly defined Palaeoniscidae (Carroll 1988).

The actinopterygian assemblages and their possible stratigraphic value

The actinopterygians of the Cuyana Basin represent two main faunal associations: the one of Potrerillos and Santa Clara, dominated by perleidiforms, and the one of Cerro Bayo/Agua de la Zorra, dominated by more primitive actinopterygians. The first association is rather typical of the

Late Triassic, which is in agreement with the age proposed for the sediments that have yielded the material (Morel *et al.* 2002*a*, *b*). The second fauna, however, suggests a somewhat older age than currently accepted for the strata they came from.

An overview of the current state of knowledge of the geology of the Cuyana Basin was given by Zavattieri *in* López-Arbarello and Zavattieri (2008). A brief summary is provided here to put the following comments into context. The Cuyana Basin, located in western Argentina, is the largest continental Triassic rift basin in southern South America. Its exposures extend for more than 500 km in NNW–SSE direction, mainly in Mendoza and San Juan provinces. It includes several sub-basins with variations in the sedimentary infill, depending on their positions within the basin, different locations of the hinterland and uplift pulses as a result of tectonic processes. The most complete and best-known succession of the Cuyana Basin is represented by the Uspallata Group. The following phases have been identified in this succession (Kokogian *et al.* 1993; López Gamundí *et al.* 1994; Jones *et al.* 1999):

- Synrift I Sequence Set (Río Mendoza and Cerro de Las Cabras Formations),
- Synrift II Sequence Set (Potrerillos and Cacheuta Formations),
- Sag Set (Río Blanco Formation).

These sedimentary cycles and a correlative geological evolution are found in different palaeogeographical positions of the Cuyana Basin on both flanks of the Precordillera. Two good examples of these sequences, which can be correlated, occur in the sub-basin of Santa Clara (represented by the Peñasco Group) in the north-eastern margin of the basin, and that of the Potrerillos-Cacheuta sub-basin (represented by the classical Uspallata Group sequence) situated near its western margin, although differences in the source of sediments and their facies occur.

The chronology of the Argentinean Triassic sequences cannot be compared directly to the marine and continental sequences in the Northern Hemisphere and, thus, a local stratigraphic chart has been proposed (Stipanicic and Marsicano 2002). While revising the fish faunas of the Cuyana Basin and their stratigraphic implications, we found several conflicts concerning the chronology of the sedimentary successions in this basin. The Léxico Estratigráfico de la Argentina published by the Argentinean Geological Society under the supervision of the Argentinean Stratigraphic Committee is aimed at providing a standardized stratigraphic nomenclature and, thus, includes all the stratigraphic units accepted as valid by the Committee and their accepted correlations. The Léxico Estratigráfico de la Argentina is not complete yet, and only two volumes have been published so far, the second of which, Volume VIII, corresponds to the Triassic and was edited by Stipanicic and Marsicano (2002). According to this volume on the Triassic, the chronostratigraphic position of the Uspallata Group, and its accepted correlation with the marine sequences adopted in the International Stratigraphic Chart, is indicated in Table 1.

TABLE 1. Chronostratigraphy of the Uspallata Group.

Formation	Age
Río Blanco	uppermost Upper Triassic (latest Late Triassic–Rhaetian)
Cacheuta	upper Upper Triassic (late Late Triassic–Norian)
Potrerillos	lower Upper Triassic (early Late Triassic–Carnian)
Cerro de Las Cabras	uppermost Middle to lowermost Upper Triassic (latest Middle to earliest Late Triassic–Ladinian–early Carnian)
Río Mendoza	upper Middle Triassic (Middle Triassic–Ladinian)

Based on Stipanicic and Marsicano (2002).

Although a complete review and revision of the chronostratigraphy of the Triassic sequences of the Cuyana Basin is certainly beyond both the scope of this study and the expertise of the authors, we hope to contribute with new observations and evidence that might help to clarify these conflicts. With this aim, we discuss the possible correlation and age of the studied fish associations.

Potrerillos and Santa Clara. The two fish associations, dominated by pseudobeaconiid perleidiforms, are very similar, supporting the correlation and probably also the Late Triassic age of the Potrerillos and Santa Clara Abajo Formations previously proposed in Stipanicic and Marsicano (2002). However, perleidiforms are known all throughout the Triassic, and the Pseudobeaconiidae, so far endemic to Western Gondwana, cannot be correlated outside Argentina. The potential sister group of the Pseudobeaconiidae is the Early Triassic *Meidiichthys* from South Africa, but this fish is very poorly known, and a thorough revision of this taxon is necessary to establish its relationships with certainty (López-Arbarello and Zavattieri 2008). In the cladistic analysis of López-Arbarello and Zavattieri (2008), the deep-bodied 'perleidiforms' appear together as the sister group of the clade containing *Meidiichthys* and Pseudobeaconiidae. Within this group, the taxa range from the Early Triassic of South Africa and Australia (*Hydropessum*, *Cleithrolepis*, *Cleithrolepidina*) to the Late Triassic of Europe (*Dipteronotus* and *Felberia*). As endemic lineages apparently evolved among the more derived perleidiforms (López-Arbarello and Zavattieri 2008), these fishes are of little help in global chronostratigraphic correlation, although they might be useful for local stratigraphic correlations.

Cerro Bayo North. Two of the eight species we recognize as valid were found in the area of the Cerro Bayo, but exact locality information is, unfortunately, not available. According to Rusconi (1957), these fishes and the material that he named *Challaia multidentata* (which most probably represents *Ch. magna*) come from levels that he identified as the 'Horizonte Bayense'. The 'Horizonte Bayense' is not a valid geological unit and has been interpreted as part of the late Late Triassic (Norian) Cacheuta Formation (Stipanicic *et al.* 2002*b*). However, *Challaia* is otherwise known from the late Middle Triassic (Ladinian) Los Rastros Formation of the Bermejo Basin (López-Arbarello *et al.* 2006), suggesting an older age for the fishes of the Cerro Bayo. It should be noted that the age of the Los Rastros Formation is accepted as Ladinian on the basis of a radiometric dating (40AR/39Ar of 228 Ma; Rogers *et al.* 1993) of the lower part of the unconformably overlying Ischigualasto Formation (López-Arbarello *et al.* 2006). Also, as explained above, *Challaia* is a member of the Acrolepidae, which otherwise includes Palaeozoic taxa and probably also some Australian Early Triassic taxa (*Myriolepis*, *Leptogenichthys*, and *Mesembroniscus*).

In addition, the geological map of the area of the Cerro Bayo (Folgera *et al.* 2004) indicates that the only Triassic sediments cropping out at the Cerro Bayo can be referred to the Las Cabras, Potrerillos and Río Blanco formations; the Cacheuta Formation has not been mapped in this area. Of the formations present, the Potrerillos and Río Blanco formations are of Late Triassic age, but both of these units have only very limited exposures at the Cerro Bayo. In contrast, the Las Cabras Formation has extended outcrops in the area of and around the Cerro Bayo, and this unit is of Middle Triassic age, which is in good accordance with the age indicated by the fishes. Thus, we suggest that this fish fauna comes from the Las Cabras Formation.

Agua de la Zorra. The lacustrine sequence of Agua de la Zorra was originally described as Agua de la Zorra Formation by Harrington (1971), who correlated this and the other Triassic units of this area with the Upper Triassic Potrerillos and Cacheuta Formations, although without discussing his reasons for doing so further. This correlation was generally accepted by subsequent authors (e.g. Stipanicic and Marsicano 2002), and thus, the age of these units is generally accepted as Upper Triassic. The Agua de la Zorra Formation was thus correlated with the Cacheuta Formation (Stipanicic and Marsicano 2002). However, own observations of the geology in the area of Agua de la Zorra and a review of the relevant literature raised some doubts about this assignment. Kokogian *et al.* (1993; see also Kokogian *et al.* 2001) presented an interpretation of the geology of the Cuyana Basin on the basis of sequence stratigraphy, in which they recognized two third order sequences within the basin. Both sequences include a synrift and a postrift sequence, with the former being represented by mainly coarse clastic sediments and often volcanics (mainly tuffs) and the second by finer, often lacustrine or overbank deposits. According to Kokogian *et al.* (1993), the first sequence encompasses the Río Mendoza and Cerro de las Cabras formations of Middle Triassic age, and the second sequence includes the Potrerillos and Cacheuta formations, of Upper Triassic age. Zerfass *et al.* (2004) noted that these two sequences can be correlated with two synrift–postrift sequences in the Bermejo Basin, comprising the Ischichuca, Los Chañares and Los Rastros formations (Middle Triassic) and the Ischigualasto and Los Colorados formations (Upper Triassic), respectively. Given the geology of the Agua de la Zorra Formation, which is composed of at least four cycles of lacustrine sediments, this unit clearly corresponds to a postrift phase of the sequences proposed, and thus might be correlated with the upper part of the Cerro de las Cabras or the Cacheuta Formation. However, several lines of evidence suggest that this formation rather represents a correlative of the Cerro de las Cabras than of the Cacheuta Formation.

First, the geological relations of this unit are more consistent with a correlation with the Cerro de las Cabras Formation. According to Kokogian *et al.* (2001), the first sequence in the Cuyana Basin usually unconformably overlies the basement, which might be formed by several units, including the marine Devonian sediments of the Villavicencio Formation and the volcano-sedimentary sequence of the Choiyoi Group. On the other hand, the top of the first sequence is overlain unconformably by the base of the second sequence. Indeed, the underlying unit of the Agua de la Zorra Formation, the Paramillos Formation, unconformably overlies the Villavicencio Formation and the Choiyoi Group. Although Harrington (1971) stated that the Portezuelo Bayo Formation at Agua de la Zorra conformably overlies the Agua de la Zorra Formation, it should be noted that Kokogian *et al.* (2001, p. 39) note that '…this contact [between sediments of the first and second sequence] might sometimes seem pseudo-concordant, but is always related to important changes in the lithology…' Indeed, there is a notable change in sedimentation between the Agua de la Zorra and Portezuelo Bayo Formations, the latter being dominated by sandstones with occasional conglomerates, whereas the former is mainly composed of silt- and mudstones, with a few intercalations of fine-grained sandstones (Harrington 1971; OWMR pers. obs.).

Second, the sedimentology of the Portezuelo Bayo Formation corresponds well to that of the Carnian Ischigualasto Formation of the Bermejo Basin, with a high content of silciclastic sediments and frequent tuffs (Harrington 1971; Zerfass *et al.* 2004). As the Ischigualasto Formation represents the basis of the second sequence in the Bermejo Basin (Milana and Alcober 1994), this similarity is in accordance with a stratigraphic correlation of these units, especially given the general correlation of the evolution of the two basins (Zerfass *et al.* 2004).

Third, and most importantly, Ramos and Kay (1991) reported on two radiometric dates of basalts in the area of Agua de la Zorra. These datings resulted in ages of 235 ± 5 and 240 ± 10 Ma for these magmatic rocks, which would place them in the Middle Triassic. The basalts represent sills in the Agua de la Zorra Formation, and thus, these ages give a minimum estimate of the age of this unit, although Ramos and Kay (1991) noted that the intrusion of these sills was probably shortly after the deposition of the sediments. Thus, a Middle Triassic age is most likely for the sediments of the Agua de la Zorra Formation, in accordance with a correlation of these deposits with the Cerro de las Cabras Formation.

As only one valid taxon is recognized, the fish association of Agua de la Zorra is basically unknown. Fishes are not abundant and very poorly preserved, being mostly disarticulated or semiarticulated remains that cannot be identified. However, the single valid taxon identified so far, *Guaymayenia paramillensis*, is a very primitive actinopterygian probably related to the Early Triassic *Pteronisculus*.

Comparison with other Triassic fish assemblages

As is the case for most time periods, the fossil record of continental fishes from the Middle to Late Triassic is considerably poorer than that of marine forms. Especially for the Middle Triassic, continental fish faunas are extremely poorly known, so if the fishes of the Agua de la Zorra Formation and the Cerro Bayo can be confirmed to come from this time, they are, together with the fishes from the Los Rastros Formation of the Bermejo Basin (López-Arbarello *et al.* 2006), certainly of great potential importance for our understanding of the evolution of freshwater actinopterygians in the Middle Triassic.

For the Late Triassic, important continental fish assemblages are known from the Chinle Formation (or Chinle Group) of western North America (see Schaeffer 1967, Johnson *et al.* 2002, Milner *et al.* 2006) and the Keuper of southern Germany (Berger 1832; Strüver 1864; Deecke 1889; Schoch and Wild 1999; López-Arbarello 2008). Further Late Triassic continental fish faunas have been reported from northern Asia (Chang and Miao 2004). All of these faunas include sarcopterygians, with both lungfishes and coelacanths being represented (Schoch and Wild 1999; Schultze and Kriwet 1999; Chang and Miao 2004; Milner *et al.* 2006). Both of these groups are conspicuously absent from both the Cuyana and Bermejo basins (Marsicano *et al.* 2001). Another group that is widespread in the Northern Hemisphere, being well represented in the European Keuper (López-Arbarello 2008), the Chinle Formation (Milner *et al.* 2006), and in China (Chang and Miao 2004), are the semionotiforms. Although some specimens from the Cuyana Basin had been referred to this group, our revision of the available fish material from this basin did not yield any evidence for the presence of semionotiforms.

The absence of these groups, which are all well represented in Late Triassic continental fish faunas from the Northern Hemisphere, was already commented on by Marsicano *et al.* (2001, p. 135), who noted that '… it cannot be established with certainty if this absence really represents a high degree of endemism of the local ichthyofaunas, a taphonomic problem, or just the lack of detailed studies of the available materials' (translated by OWMR). However, with the study presented here, the third possible reason (lack of detailed studies of available material) can be discarded. Given the abundance of fish remains in the Cuyana Basin, and the intensive collection efforts in the Upper Triassic formations of the Bermejo Basin (Ischigualasto and Los Colorados formations), which have yielded all kinds of both large- and small-sized vertebrate remains, a taphonomic bias also seems rather unlikely. Especially, lungfish tooth plates would be expected to be preserved in sedimentary environments such as that of the Ischigualasto Formation (Currie *et al.* 2009), and there is no reason to assume a bias against semionotiforms in the sediments that contained the fish fauna of the Cuyana Basin revised here, because many of the remains preserved represent fishes of a similar size and state of ossification.

This leaves us with the first possibility, the actual absence of these forms in the Late Triassic of western Argentina. The reason for this absence is probably different for the sarcopterygians on one hand and the semionotids on the other. Both coelacanths and dipnoans are also common in the Late Permian of Brazil (Toledo and Bertini 2005). A coelacanth is furthermore known from the Early Triassic of Bekkerskraal in South Africa, and dipnoans are present in the Early Triassic fauna of the Cassanga series in Angola and in the locality of Gosford, Australia (López-Arbarello 2004). All these occurrences indicate that sarcopterygians were present in southern Pangea at the beginning of the Mesozoic. Thus, their absence in western Argentina in the Late Triassic might be attributed to a local or regional extinction event because of climatic or other palaeoecological factors. Indeed, a single dipnoan tooth plate has been found in the Carnian Santa Maria Formation of Brazil (Richter and Toledo 2007), indicating that the absence of this group in the Middle and Late Triassic of Argentina might have been a local pattern. Alternatively, dipnoans might simply have been extremely rare, as it is the case in the Santa Maria Formation, and have therefore not been reported so far.

In the case of the semionotiforms, the first continental forms of this group appear in the late Early Triassic (Bundsandstein) of eastern France (Deecke 1889). In the Late Triassic, these fishes were widespread in the Northern Hemisphere in both continental and marine environments, but they are absent from both environments in the Southern Hemisphere. Thus, their absence in western Argentina is most probably a primary absence: these fishes probably originated in the Tethyan realm of the Northern Hemisphere and did not reach southern Pangea until the Early Jurassic. In the Early Jurassic, a taxon closely related to *Semionotus bergeri* (the type species of *Semionotus*) and currently kept in the same genus, *S. capensis*, is present in continental environments of the Clarens Formation of southern Africa. Semionotiforms are later represented in the Middle and Late Jurassic of Africa and the Late Jurassic of Australia and probably also South America, and they are well represented in the Early Cretaceous of South America and Africa (see detailed information in López-Arbarello 2004 and López-Arbarello *et al.* 2008).

This indication of a rather high degree of endemism of the fish fauna of the Cuyana and Bermejo basins is in accordance with the finding that the most abundant fishes from the Late Triassic of the Bermejo Basin can be referred to the single family Pseudobeaconiidae, which is unknown outside South America (López-Arbarello and Zavattieri 2008). Whether this endemism was local and restricted to southern South America, or whether it might have been more regional and extended to other regions of southern Pangea cannot be evaluated in the lack of Late Triassic fish faunas from most of the southern Pangea. However, it might be noted that dipnoans seem to be rather common in the Late Triassic Maleri Formation of India (Kutty *et al.* 1987), indicating that at least this group was present in other southern Pangean continental faunas.

CONCLUSIONS

The palaeontological studies of Triassic actinopterygians of the Cuyana Basin in Western Argentina led to important conclusions concerning the systematics of these fishes and the stratigraphic position and age of the bearing sediments. To date, a total 29 actinopterygian taxa were named from this basin, but these fishes are almost unknown, because most of them were exclusively published in local Argentinean journals of rather restricted circulation. Only four of these taxa have been studied in detail, and the taxonomic status of the remaining species is doubtful. After a thorough taxonomic revision of these fishes, only eight among the 29 named species are accepted as valid.

Guaymayenia paramillensis Rusconi, 1946*b*, from the probably Middle Triassic Agua de la Zorra Formation, is a basal actinopterygian probably related to the Early Triassic *Pteronisculus*. *Neochallaia tellecheai* (Rusconi, 1948*b*) comb. nov., from the probably Middle Triassic of the Cerro Bayo, is another primitive actinopterygian, which might be a member of the Chondrostei. This taxon shows some very interesting features also present in acipenseriforms, but further study is necessary to be certain about its systematic relationships. *Challaia magna* Rusconi, 1949*b*, also from the Middle or Late Triassic of the Cerro Bayo, is a member of the Acrolepidae, which otherwise includes Palaeozoic taxa and probably also some Australian Early Triassic taxa. The genus *Challaia* is otherwise known from the late Middle Triassic (Ladinian) Los Rastros Formation of the Bermejo Basin where it is represented by a different species, *Challaia elongata*.

The other five valid taxa represent a single family of perleidiform fishes, the Pseudobeaconiidae, which is endemic of Western Gondwana. Within this family, they represent two genera, *Pseudobeaconia* (with *P. bracaccinii*, *P. elegans*, *P. celestae* and *P. cuyana* comb. nov.) and *Mendocinichthys brevis*.

Although only a few species were found to be valid, clarifying their systematic relationships, as well as the possible relationships of the other, undiagnosable material, led us to the recognition of two faunal associations: the one of Potrerillos and Santa Clara, dominated by perleidiforms, and the one of Cerro Bayo / Agua de la Zorra, dominated by more primitive actinopterygians. The first association is rather typical of the Late Triassic, which is in agreement with the age proposed for the bearing sediments. The second, however, suggests an older age that currently accepted for the bearing strata. Studying the literature we found geological information supporting this last hypothesis, in particular, the radiometric dating of 235 ± 5 and 240 ± 10 Ma (Late Middle Triassic) of the basalts sills in the Agua de la Zorra Formation.

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NOTE ADDED AFTER ONLINE EARLY VIEW PUBLICATION: Text-figure 16 was published with incorrect labelling in the online Early View version in February 2010. It has been corrected in this version.