

GEORGE GAYLORD SIMPSON

ASSOCIATE CURATOR OF VERTEBRATE PALAEOLOGY IN THE AMERICAN MUSEUM
OF NATURAL HISTORY NEW YORK

A SPECIMEN OF

PSEUDOSTYLOPS SUBQUADRATUS AMEGHINO



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BY

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SOMMARIO

Il genere e la specie *Pseudostylops subquadratus* AMEGHINO, 1901, erano finora conosciuti soltanto per via di un singolo dente difettoso, e i caratteri e i rapporti di parentela di questo animale furono interpretati in modo incompleto e del tutto erroneo. Un esemplare, scoperto dal Dr. Egidio Feruglio e attualmente conservato nel Museo dell'Istituto di Geologia della R. Università di Padova, rivela quasi tutta la dentatura superiore e viene indicato in questo lavoro come *neotipo*, descritto ed illustrato. Esso conferma l'appartenenza del *Pseudostylops* alla fauna ad *Astraponotus* della Musters Formation della Patagonia. Il *Pseudostylops* rappresenta un valido genere della famiglia *Notohippidae*, del sottordine *Toxodonta*, dell'ordine *Notoungulata*. Esso è parente, ma non diretto ancestrale, del *Rhynchippus* della formazione di Deseado, ed è molto più primitivo del susseguente e più tipico *Notohippidae*.

Pseudostylops with its single species *P. subquadratus* Ameghino, 1901, was described from Patagonian strata on the basis of a single tooth. The type specimen barely sufficed to show that a peculiar animal existed. It gave little or no information regarding the real characters of that animal, and none regarding true relationships. The name, consequently, has remained merely a name, with little or no contained meaning or recognized significance. Such cases are unfortunately common in paleontology. At the worst, they represent a sort of caveat, the author being unaware of what he has but wishing nevertheless to ensure credit for discovering it.

At the best, as in this case, the author recognizes that he has something new which really requires a name, for the purposes of his enquiry, and he does the best he can to interpret it, even though that best cannot be very good.

In any case a genus like *Pseudostylops* necessarily remains obscure and nearly valueless until some fortunate later discovery brings to light a more complete, truly explanatory specimen which can confidently be referred to the genus. In this case, such a specimen has now been discovered by Dr. Egidio Feruglio. This is a left upper jaw with most of the teeth. It includes the homologue of the type of *Pseudostylops subquadratus*, and so can be identified as of that species, and it gives so much additional information that it fully defines the genus and certainly places it in the classification. Previous classifications prove to be very erroneous, placing *Pseudostylops* not only in the wrong family but also in the wrong order of mammals.

Dr. Feruglio has very kindly forwarded to me for study his entire collection of fossil mammals made during several years of geological work in Patagonia. Some of these, particularly those from the Río Chico Formation, basal Tertiary, have been included with his permission in description of the material found by the Scarritt Expeditions, under my leadership. The fine specimen of *Pseudostylops* does not compare with any in our collections and is here described separately. I am very much indebted to Dr. Feruglio for this privilege, as well as for much valuable assistance and cooperation in the field and in connection with other studies. I wish also to express my thanks to Professor G. Dal Piaz for translating the accompanying summary and other assistance with publication. The accompanying drawings are by Mrs. Mildred Clemans of the staff of the American Museum of Natural History in New York.

The specimen described, together with the rest of the Feruglio Collection, is now in the Istituto di Geologia della R. Università di Padova.

OCCURRENCE

The specimen bears the number 31 of Dr. Feruglio's field notes, designating a lot of fossils collected by him on May 29, 1927, in the great barranca south of Lake Colhué-Huapí, Southern Chubut, Argentina. The following geological section is summarized from records supplied by Dr. Feruglio:

From the bottom of the barranca upward:

Base of barranca

1	Somber varicolored days	14 m.
2	« Argiles fissilaires » of Ameghino	44 m.
3	a Pale-colored ash beds with some gypsum	10 m.
	b Pale greenish ash bed	} 42 m.
	c Pale ashes with two or three levels with manganese	
	d Pale greenish-yellow ash bed	} 39 m.
	e Pale ashes	
	f Hard, concretionary, cornice-forming tuff, so-called « tosquilla »	14 m.
	g Pale ashes	27 m.

Top of barranca

No fossils were found in 1 or 2, but on other evidence I believe 1 to belong to the Rio Chico beds and 2 to a lithologic facies of the Casamayor. The Feruglio Collection contains only an unidentifiable fragment from 3c), but the American Museum Collection includes fossils from levels corresponding to 3b) to 3e) of Dr. Feruglio's section, which indicates that all these beds, with the possible exception of the very top, belong to the Casamayor.

The specimen here described came from the upper part of 3f, and with it were found the following:

Eohyrax sp. Isolated upper and lower teeth.

?*Archaeohyrax* sp. Isolated lower teeth.

?*Periphragnis* sp. Broken teeth.

Propyrotherium cf. saxium Half a molar.

These are Musters genera, and *Pseudostylops* is also given by Ameghino as from the Musters (his « Astraponotense »). The American Museum collection also includes some specimens from the same horizon, and all are of Musters genera and species. The formation then is definitely Musters, and the fauna that of *Astraponotus*. The Casamayor-Musters contact is probably at the contact of 3e) and 3f), but possibly in the upper part of 3e). No fossils were found in 3g) near this section, so it is uncertain whether these highest beds are of Musters or later age.

IDENTIFICATION

Pseudostylops subquadratus was named by Ameghino in 1901¹. Although the designation might give the impression that several specimens had been studied, in fact the whole description could have been, and evidently was, based on one tooth, then identified as a permanent upper molar. Genus and species were referred to the Trigonostylopidae and compared distantly with *Edvardocopeia*. In 1904² Ameghino figured the tooth from the crown, internal, and anterior aspects and correctly indicated it as a left upper premolar. He retained it in the Trigonostylopidae.

The specimen is now preserved in the Museo Argentino de Ciencias Naturales, under the number 10904, where I have examined it. With it is a note, by Ameghino, which is abbreviated but which apparently says, « parecido a *Notopithecus* y también *Trimerostephanos* ».

The tooth is somewhat worn, and the internal base is broken. The comparable tooth of the Feruglio specimen, P³, has the posterior edge broken and is less worn. In spite of these difficulties the correspondence in structure and in size is so exact, and is so impossible to duplicate in any other animal of these faunas, that it seems highly probable that the two specimens are of the same species.

Ameghino's genus and species were, in fact, based on a specimen barely determinable in itself and giving no real indication of affinities. In order to validate the name and to establish it in a real and useful sense, I hereby propose that the present specimen be accepted as conspecific with Ameghino's type and that this specimen of the Feruglio collection be the neotype of *Pseudostylops subquadratus* Ameghino, 1901.

DESCRIPTION

The dental formula is 3.1.4.3. Despite the somewhat incomplete nature of the specimen, little or no doubt attaches to the identification of the teeth. The median premaxillary suture and

¹ Bol. Acad. Nac. Ci Cordoba, XVI, p. 395.

² An. Mus. Nac. Buenos Aires, IX, p. 282, fig. 381.

the premaxillo-maxillary suture are shown, so that the anterior three teeth are shown to be in one premaxillary, and to be a complete set of left incisors. From its form, its closeness to the premaxillo-maxillary suture, and the presence of a short diastema posterior to it, the next tooth must be a canine. There follow an alveolus and then three premolariform teeth, the only question regarding which is whether the most posterior, being more worn than the others, may not be a deciduous tooth. This is, however, disproven by the fact that it is distinctly premolariform, whereas last milk teeth of notoungulates are decidedly molariform, and by the fact that no replacing tooth lies beneath it, as revealed by a break across the specimen from which an excavation could be made without this being visible externally after the break was repaired. The following molariform tooth must be M^1 and the next M^2 . M^3 is missing, but fragments of bone show that a dental crypt was present posterior to M^2 , and this clearly was for the last molar.

Except for a very small diastema between the canine and P^1 , considerably shorter than either of these teeth, the teeth are all closely crowded together.

I^3 and the canine are unworn. P^{2-3} are slightly worn. P^4 and M^1 are worn just deeply enough to have the apical pattern obliterated. M^2 is imperfect preserved. The apical pattern was truncated on the anterior half, but probably was still preserved on the posterior half. From the remnant of its crypt, M^3 may not have been fully erupted. The animal is thus a young adult or late adolescent.

The incisors and canines are disposed in a semicircle, the incisors more transverse than anteroposterior. I^{1-3} are all large and increase slightly in size from I^1 to I^3 .

The tips of I^{1-2} are broken off. The preserved bases are quadrate in section and have heavy enamel on the labial surface which also covers the adjacent corners but is absent on the rest of the mesial and distal faces and on the lingual face. These teeth were very high-crowned but not of persistent growth. The long axis is strongly curved. I^3 has the crown preserved. The labial face is evenly convex. There is a single apex, mesial in position,

with a strong sharp crest running posteroexternally from it. The lingual surface is excavated, the crown as a whole being spatulate, with an ill defined vertical swelling near the middle. The basal region is imperfect, but apparently a small basal lingual cingulum was present. The deeper part of the tooth, not well exposed, was apparently quadrate, as in I¹⁻². There is heavy enamel on the labial surface and very light enamel on the end of the lingual surface but not above this.

The canine is much smaller than I³ but of rather similar form. The crown proper is much lower and the apex is recurved inward. There is a strong, continuous lingual cingulum.

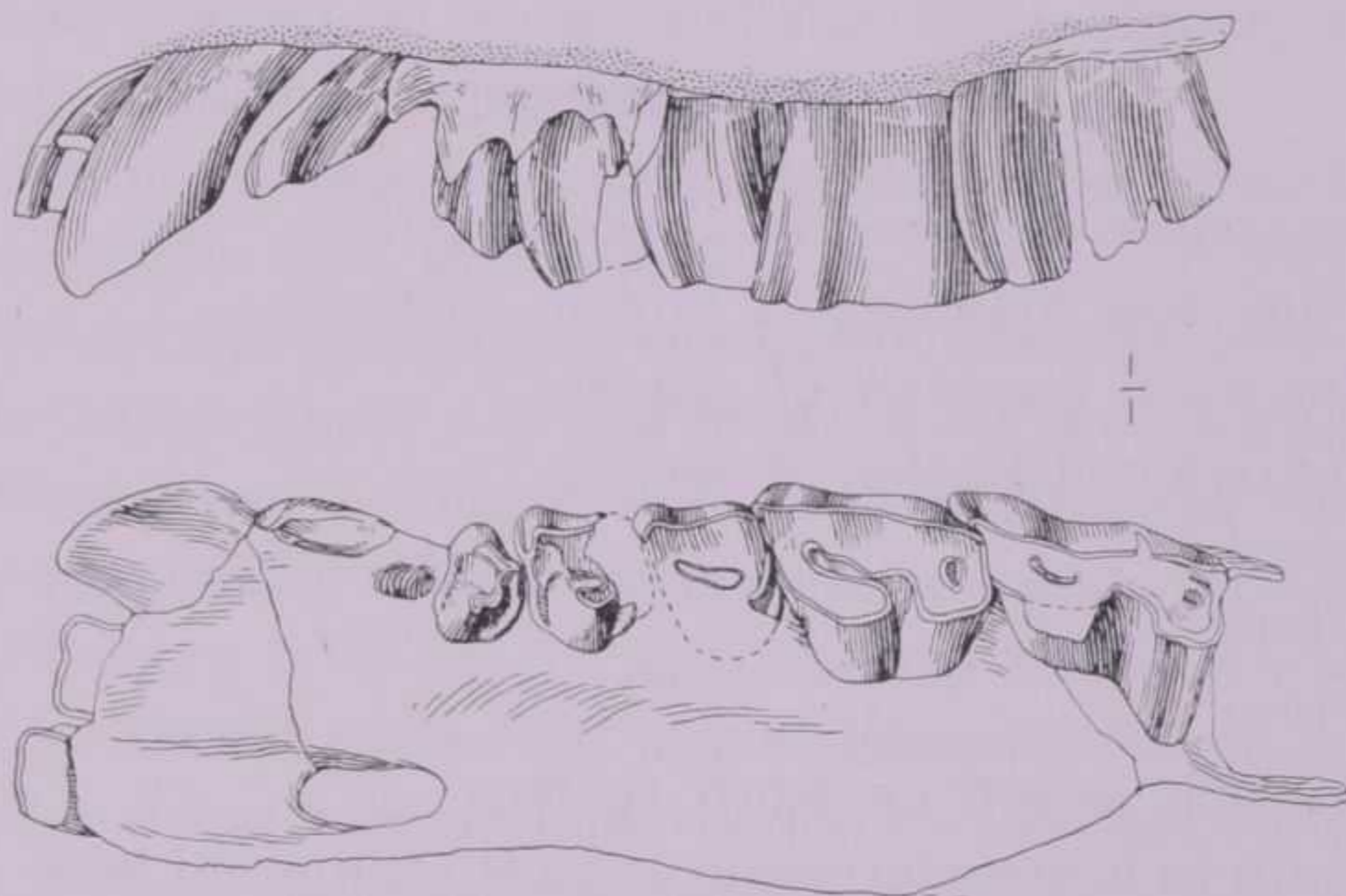
P¹ is represented only by an alveolus, which shows it to have been a very small tooth. Anterior to this there are uncertain indications of another, much smaller, possible alveolus which, if original, might also be for P¹ or for a deciduous tooth.

P² has an oval or subtriangular crown. The high outer wall has a prominent fold ending in the paracone and a smaller metacone is less definitely indicated on the sharp ectoloph posterior to this, but without a corresponding second external fold. There is a very small parastylar fold but no metastyle.

The protocone, although well developed, is lower than the ectoloph. From its apex a sharp, prominent, winding loph curves first posteroexternally then anteroexternally and is confluent with the ectoloph at the metacone. It is slightly swollen in the middle, suggesting an included conule. Below this is a strong posterior cingulum which runs into a vertical crest on the posterior face of the protocone. There is a large shallow fossa anterior to the transverse loph bounded anteriorly by a sharp cingulum from the parastyle, which ends abruptly on the anterior base of the protocone. The enamel which encircles the crown is thick, but that on the grinding surface is very thin, and may even be lacking in the floor of the main fossa.

P³ is better displayed in the type than in this specimen, on which the posterior margin is broken away. It is basically like P², but aside from details sufficiently clear from the figures differs in that the transverse loph is more angulate with the conule dis-

placed internally to occupy the position of a hypocone, the posterior cingulum is not connected with the protocone apex, and the central fossa is deeper and narrower, opening anteriorly except in an advanced stage of wear. Only the external part of P⁴ is preserved, and it is well worn. As far as observable, it differs from P³ only in being larger and higher crowned. The fossa is closed in this stage of wear and apparently closes earlier than on P³ and forms a narrow, slightly oblique, anteroposterior lake.



Pseudostylops subquadratus Ameghino, 1901. Left upper jaw with I¹⁻³, C, and P² - M². External and crown views. Natural Size.

M¹ is bowed as in the toxodonts but to a less degree. The outer face is very high and is convex vertically. The inner face is considerably less high and is concave vertically. Proportions and size would differ greatly in different stages of wear. In this stage, the grinding surface is much longer than wide. Farther up the crown, the length decreases and the width increases so that the deeply worn tooth would be square, or even transverse. The outer face is flatter than on the premolars. There are small parastyle and paracone folds, separate at this level but confluent farther up the crown, and a vague convexity in the metacone region. The internal face is divided by a deep fissure into slightly larger protocone and slightly smaller hypocone columns. The fissure communicates, at this level, with a long, narrow, deep fossa extending anteroexternally into the crown. There is also a small oval fossa, here closed, in the posterior part of the crown.

The apex of M² had decayed and cracked considerably before burial, and so is not clear. The general outline and structure of the tooth are like M¹, but it is larger. The main, or anterior, fossa seems to have been cut off from the internal fissure in an earlier stage of wear than on M¹. Of M³ it can only be said that it was large, apparently at least as large as M². There appears in places to be a very light deposit of cement on the less exposed parts of the crowns, but if present this is so slight that it can hardly be distinguished from mere enamel discoloration.

MEASUREMENTS

I ¹	Transverse diameter of broken surface	8.0 mm.
I ²	Transverse diameter of broken surface	8.9 »
I ³	Maximum diameter of crown	11.3 »
C	Maximum diameter of crown	6.2 »
P ²	Length	6.9 »
P ²	Width	9.0 »
P ³	Width	11.0 »
M ¹	Ectoloph length on worn surface	8.1 »
M ¹	Width in horizontal plane at level of internal base	14.7 »

AFFINITIES

It is at once apparent that *Pseudostylops* has no relationship to the Trigonostylopidae, where Ameghino placed it on the evidence of his single tooth. It is obviously a true notoungulate, a toxodont, and a member of the family Notohippidae (in a broad sense, including the Rhynchippidae). It differs from the majority of the Notohippidae, or Notohippinae, in their more advanced and characteristic form typified by the Colhué-Huapí *Argyrohippus* in the very slight development or absence of cement, the much simpler molar pattern,¹ and the less reduced anterior teeth. These are all points of resemblance to the earlier and simpler forms, the « Rhynchippidae » of Loomis.

¹ It is quite probable (as insisted by Patterson) that completely unworn molars of this type would show homologues of most or all of the complex folds seen in *Argyrohippus* but in the latter they are preserved even in advanced stages of wear, while in *Rhynchippus*, *Pseudostylops*, etc., if ever present, they disappear almost immediately. This is a real distinction.

Resemblance to the Deseado genera *Rhynchippus*, *Morphippus*, and *Eurygenium* is close and undoubtedly indicative of true affinity, but the genera are distinct and *Pseudostylops* apparently could not be directly ancestral to any of these. The distinction is shown among other characters, by the increase in size from I¹ to I³ in *Pseudostylops*, the greatly reduced canine, the transverse premolars and their somewhat simpler and distinctly different pattern (note especially P²) and perhaps by the fact that the median external molar pit, if present, was extremely shallow, being already obliterated on M¹ while in *Rhynchippus*, at least, it persists to a later stage of wear.

In the Musters Formation previously recognized Notohippids are *Eomorphippus* and *Interhippus*.¹ *Interhippus deflexus*, the sole Musters species and the only one surely referable to the genus, is founded on one upper and one lower molar, of doubtful association. Comparison is difficult and necessarily limited but *Interhippus* is apparently distinct from *Pseudostylops* because the upper molar type is of nearly equal length and width but has four external fossas, while that of *Pseudostylops* is much longer than broad and has only two, and perhaps would have still fewer were it worn to a point (relatively deeper on the crown than in *Interhippus*) where it has length and breadth equal.

Eomorphippus, with the two species *obscurus* and *rutilatus*, was based on a number of isolated upper and lower teeth, not all of which are really congeneric. It is quite possible that some teeth belonging to the same genus as *Pseudostylops subquadratus* are included among these specimens, but the material does not happen to include any closely comparable teeth so that such identity cannot at present be established, if it does exist. Some of the *Eomorphippus* material is surely distinct, notably the premolar figured by Ameghino.² The genus *Eomorphippus* is in any event of extremely dubious standing. It was published at the same time as *Pseudostylops*,³ and the latter name, having been based on ma-

¹ *Nesohippus* has been listed as of this fauna, but apparently by a *lapsus*, as no species or specimens from this horizon have been described or are known to me in collections. *Interhippus* is also reported from the Deseado, but the genotype is from the Musters.

² An. Mus. Nac. Buenos Aires, IX, p. 310, fig. 413.

³ On a previous page, but there is no legal requirement to follow page priority, and it seems to me ridiculous to do so when this would result in a loss of clarity and stability.

terial really of one genus (however inadequate) and now being clearly and well established as to characters and affinities, should surely be retained even in the very unlikely case that the genera should prove to be synonymous.

Edvardocopeia, with which Ameghino compared *Pseudostylops* in the original description, is another very doubtful genus detailed comparison with which would serve little purpose. It was based essentially on an upper premolar, which has since been lost or mislaid. Judging from Ameghino's figure, this tooth slightly resembles P² of *Pseudostylops*, but not to the point of suggesting generic identity and it equally resembles premolars of several distantly related groups. It is much larger than P² of *P. subquadratus*.

Pseudostylops is thus established as a valid genus of the Notohippidae, the earliest known in that family. In comparison with other notohippids it is distinctly primitive in most respects, but has minor aberrant characters perhaps excluding it from the direct ancestry of known later genera.