A NEW LEPIDOSAUVROMORPH REPTILE FROM THE MIDDLE TRIASSIC OF THE DOLOMITES (NORTHERN ITALY)

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Abstract. A new genus and species of diapsid reptile is described. The specimen was collected from the Anisian (Middle Triassic) succession of Monte Prà della Vacca (Kühlschotenkopf) in the Dolomites of Braies (Bolzano/Bozen, Northern Italy). Despite being incomplete, the specimen shows enough characters to allow its placement within Lepidosauromorpha, close to the Middle Jurassic genus Marmoreta. The importance of this find lies in the great rarity of lepidosauriforms of Anisian age, an epoch approximating the appearance of the first members of the true Lepidosauria (rhynchocephalians and squamates). The new genus may thus add knowledge to the diversity of early lepidosaurs. Some characters of the skeleton, mainly of the forelimbs, suggest a terrestrial, perhaps arboreal life style.

Introduction

According to most recent definitions (Evans 1984, 1988; Gauthier 1984; Gauthier et al. 1988) the Lepidosauria are considered as the group comprising Rhynchocephalia (Sphenodon and its fossil relatives) and Squamata, (lizards, snakes and amphibiaenians) along with their immediate common ancestor. The fossil history of Rhynchocephalia can be followed back until early Late Triassic (Fraser & Benton 1989), suggesting that the primary dichotomy between rhynchocephalians and squamates occurred earlier, possibly in the Early Triassic (Evans 1991) but our understanding of the early evolution of the Lepidosauria is vague, particularly for the Squamata, that have a fossil record dating only to the Jurassic (Evans 1984, 1988, 1991; Waldman & Evans 1994). Most authors (e.g. Evans 1984, 1988; Gauthier et al. 1988), regard Permian and Triassic taxa like Paliguana and kueheneosauroids, previously considered as primitive members of the Squamata (e.g. Carroll 1975, 1977), neither as primitive lizards nor lepidosaurians, representing instead independent radiations of squamate-like diapsids on the stem of the Lepidosauromorpha.

Evans (1991) and Waldman & Evans (1994), considered Marmoreta from the Middle Jurassic of England as a probable sister taxon of Lepidosauria and suggested that it must represent a late survivor of a lineage dating back to the Early Triassic.

In recent years an Anisian (Middle Triassic) horizon, rich in fossil plants and vertebrates has been discovered by Mr. Michael Wachtler in the Braies (Prags) Dolomites (Northern Italy). For this reason a research project, supported by the Museo Archeologico e Natura of Bolzano (Alto Adige) under the leadership of Prof. C. Broglio Loriga from the Ferrara University has been started, with the aim to study the taxa collected in the deposit and the palaeoecology and paleoenvironmental evolution of the succession. In this fossiliferous horizon, Mr. Michael Wachtler also recovered a partial skeleton of a diapsid reptile. Its description and taxonomic assessment is the aim of the present paper.

Stratigraphical setting and age

The reptile was collected from a rich plant horizon, that outcrops on the western slope of Monte Prà della Vacca (Kühlschotenkopf in German) in the Braies/Prags...
Dolomites (northern Dolomites) (Fig. 1). This area has been famous in the palaeontological literature since the 19th century, mainly for the Anisian (Pelsonian) brachiopods and ammonoids of the "alpiner Muschelkalk" (Loretz 1875; Mojsisovics 1879, 1882; Bittner 1890). In addition, the Braies/Prags Dolomites have made fundamental contributions concerning the Dolomites stratigraphy (e.g. Pia 1937; Bechstädt & Brandner 1970; De Zanche et al. 1992; Senowbari-Daryan et al. 1993).

The deposit is located in the lower part of the Anisian basal succession, which has variously named: Pragser Schichten (Pia 1937), siltitische Mergel und Knollenkalke (= Pragser Schichten p.p.) (Bechstädt & Brandner 1970), Dorn Formation of the Braies Group (Pisa et al. 1978; Fois & Gaetani 1984; De Zanche et al. 1993; Senowbari-Daryan et al. 1993; De Fafili et al. 2000). Senowbari-Daryan et al. (1993) considered the Dorn Formation in the Braies area as an hemipelagic carbonate-terrigenous sequence of mar-
original basin environment, about a hundred metres deep. In
the Monte Prà della Vacca / Kühwiesenkopf section, the
Dont Formation is more than 200 m thick, and the fossilifer-
erous horizon is placed at about 75 m from its base (Bro-
glio Loriga et al. 2002 b), which is represented by a massive
carbonate platform (bed K3, enclosure 2 of Bechstädt &
Brandner 1970; Fig. 1) belonging to the Algenwelenkalk
unit of Bechstädt & Brandner (1970), now attributed to
the Gracillis Formation (De Zanche et al. 1992; Senowbari-
Daryan et al. 1995) (Fig. 1).

The plant horizon, placed just above bed K 11 of
Bechstädt & Brandner (1970, enclosure 2), is about one
tablerick; plants are concentrated in silstone, marly
silstone and carbonitic silstone layers some centime-
tres-thick (Fig. 1). The fossiliferous layers have a lens
shape, therefore their number and thickness may change
laterally. They are alternated with silty and marly lime-
stone layers, containing sparse terrestrial plant remains.
Marine organisms (fishes, bivalves, brachiopods, amino-
noids and gastropods) are present, but not abundant,
throughout the horizon. Occurrence and preservation of
terrestrial and marine fossils together must be related to
very rapid burial events caused by gravity flows within
a marine basin, connected with heavy storms in the
terrestrial domain (Tintori et al. 2001; Broglio Loriga et
al. 2002 a, b).

At the base of the deposit, a layer of carbonatic silt-
stone, about 30 cm thick, represents a marker bed, easily
recognizable because its upper surface is rich in trunks,
roughly N-S oriented (Fig. 1). Large but rare plant re-
mains (trunks) are also present at the top of a limestone
bank situated about two metres below (Fig. 1). This unit
of nodular, massive wackestone and packstone contains
a rich marine assemblage with foraminifers, byssate bi-
valves (Mysidioptera) and brachiopods (Punctospiriferella
and Angustobrytis).

The deposit is characterized by a rich assemblage
of plants representing by at least 17 genera (Kustatscher
et al. 2002; Broglio Loriga et al. 2002 b). In addition, rare
specimens of marine and freshwater fishes (Tintori et
al. 2001), ammonoids (Storia sp.), bivalves (“Prospondylus
comptus” Goldfuss), and gastropods have been dis-
covered.

The Dont Formation of the Dolomites is tradition-
ally considered Pelsonian – Illyrian in age (Delfrati et al.
2000, with ref.). The section of Monte Prà della Vacca /
Kühwiesenkopf has been dated mostly on the basis of
brachiopod assemblages by Bechstädt & Brandner (1970,
tab. A). The deposit is situated just above the brachi-
opod horizon 2 and below the brachiopod horizon 3 (Fig.
1), both referred to Pelsonian (Bechstädt & Brandner
1970). The same age is also supported by the benthic fo-
raminifera (Broglio Loriga et al. 2002 b). Therefore, the
stratigraphic segment bearing the deposit belongs to the
Pelsonian (Anisian, Middle Triassic) (Broglio Loriga et
al. 2002 b).

Plate 1 - Megachirella wachteri gen. et sp. n.; KUH 1501 holotype.
Scale bar equals 1 cm.

Plate 2 - Megachirella wachteri gen. et sp. n.; KUH 1501 holotype.
A) right anterior limb; B) skull; C) detail of left quadrate,
D) right carpus. Scale bar equals 0.5 cm.
Tab. 1 - Measurements taken on the specimen.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Length of the axis</td>
<td>6 mm</td>
</tr>
<tr>
<td>Length of the fourth cervical vertebra</td>
<td>4 mm</td>
</tr>
<tr>
<td>Length of the fourth dorsoventral vertebra</td>
<td>3.2 mm</td>
</tr>
<tr>
<td>Length of the right humerus</td>
<td>12.8 mm</td>
</tr>
<tr>
<td>Maximum width at the distal head of the right humerus</td>
<td>6 mm</td>
</tr>
<tr>
<td>Length of the right ulna</td>
<td>10 mm</td>
</tr>
</tbody>
</table>

* the length of the vertebrae quoted here is referred to the distance between the anterior and posterior ends of the neural arches (zygapophyses excluded) since the centra are obscured by matrix or other bones.

Description

The specimen (Pl. 1, 2) is exposed in dorsal view, apart for the right anterior limb which is exposed on ventral view. The skeleton is incomplete but articulated. The entire snout region is missing, along with the posterior half of the body, the pelvic girdle and the posterior limbs. The right anterior limb is complete, but its distal portion was originally overlapped by ribs. The left humerus is the only preserved element of the left anterior limb. Unfortunately a layer of pyrite crystal encrusts many bones, especially in the carpal region and at the articulation between vertebrae and ribs. The pyrite has been carefully removed only in those areas where the detachment of the crust did not damage the underlying bone.

The skull

As noted above, the snout region and the anterior half of the orbital region are missing. Only the posterior region of the frontals is preserved (Pl. 2B; Fig. 2). The frontals form a rather wide and flat table ornamented by small tubercles, the left portion of the table is incomplete. However, the preserved portion is wide enough to detect that no suture between frontals is present. The posterior margins of the frontals form a zigzag suture with the parietals. The parietals are narrow but deep, anteroposteriorly elongate and approximately two times longer than wide; a faint line runs between the two bones, but it is more probably a fracture and it is feasible that the two bones where they are fused together. The parietals border medially an upper temporal fenestra which is longer than wide. The general outline is superficially similar to that of *Marmorella* (Evans 1991; Waldman & Evans 1994), but the peculiar high parietal crest of this latter genus is absent in our specimen. No pineal foramen can be detected between the parietals; if present it could have been placed close to the frontoparietal suture. The postorbital is “Y” shaped with a narrow, very elongate squamosal process. The postfrontal enters the upper temporal fenestra, but it cannot be described in detail since it is largely covered by the displaced frontal plate. The jugal is a narrow sub-triangular bone, with a curved orbital border. The posterior margin of this bone is deeply concave and bears a pointed, free-ending quadratojugal process, indicating that the lower temporal fenestra was ventrally open. The quadratojugal is absent. The left squamosal is almost completely crushed and partially encrusted by pyrite crystals, the right one is detectable (even if disarticulated). It is stout and widens in its lateral portion where it houses ventrally the concavity which forms the articular area for the quadrate; a narrow quadrate descending process points anteriorly to

Fig. 2 - *Megachirella uuchi* gen. et sp. n.; KUH 1501 holotype. A) drawing of the preserved portion of the skull; scale bar equals 1 cm. B) tentative reconstruction of the preserved portion of the skull in lateral (left) view. Abbreviations are: a) angular; ar) articular; ch) ceratohyal; d) dentary; f) frontal; j) jugal; mx) maxilla; pa) parietal; pf) postfrontal; po) postorbital; pop) process of the opisthotic; pr) prearticular; q) quadrate; sq) squamosal.
meet the postorbital and a more robust one extends medially to reach the parietal, forming the posterior border of upper temporal fenestra. In its general shape (Pl. 2 C; Fig. 2) it recalls the elements figured by Robinson (1962) and Colbert (1970) for Kuehneosaurus and, at a lesser extent, Icarosaurus.

The quadrates (Pl. 2 C; Fig. 2) are deformed being somewhat flattened dorsoventrally due to compression, but their morphology is clearly visible: they show a convex, rounded dorsal articulation for the squamosal and a large double ventral condyle for the articulation with the lower jaw. Posteriorly the bone is deeply embayed, forming part of the middle ear cavity. Its anterior margin is prominent giving to the bone a general outline that recalls that of kuehnesaurids, particularly Kuehneosaurus (Robinson 1962; Colbert 1970) and some lepidosaurs. It can be suggested that the quadrate was mobile, but it is not possible to ascertain which was its degree of mobility with respect to the pterygoids and, as a consequence, it cannot be stated if there was a true streptostylic pattern or the mobility of the bone was limited as in kuehnesaurids (Evans 1984).

The occipital region is partially exposed, the opisthotic bears strong paroccipital processes; the sutures between exoccipital and paroccipital cannot be detected.

On the left half of the skull some smooth bones are visible, they are probably the palatine and the pterygoid exposed on their dorsal side, their preservation, however, is too poor to allow any description.

**Lower jaw**

Only few fragments of both dentaries are detectable, however it can be noticed that they were rather deep, giving a robust appearance to the lower jaw. Few, stout teeth are preserved, placed on a shelf in the lingual side of the dentaries, suggesting a subpleurodont implantation. The surangular and the angular are very elongate, prearticular is long and stout, the articular bears a wide condyle for the quadrate and continues posteriorly with a prominent retroarticular process.

**Vertebrae and ribs**

The first twelve vertebrae are preserved articulated in the specimen, followed by a gap in the stone slab, which is followed by three other vertebrae, these latter belonging to the mid region of the trunk. The cervical series consists of six vertebrae which are longer than the dorsal ones (Tab.1). The atlas can hardly be

![Fig. 3](https://example.com/fig3.png)

Fig. 3 - *Megachirella vachieri* gen. et sp. n.; KUH 1501 holotype. Anterior dorsal region as preserved. The black area represents a crack in the slab; the grey one the area covered by pyrite layer. Abbreviations are: cl) clavicle; d1) first dorsal vertebra, d2) second dorsal vertebra; icl) posterior tip of the stem of the interclavicle; sc) tip of the dorsal blade of the scapula; st) sternal plate. Scale bar equals 1 cm.
seen because it is covered by skull bones and partially overlapped by the following axis. This latter is very elongate and stout, as in *Marmoretta* (Evans 1994). The neck is a little telescoped so that the posterior end of each centrum overlaps for a little extent the anterior end of the following vertebra, obscuring details of the zygapophyses, but permitting to detect part of the posterior articular surface of the centrum. This latter is slightly concave. The neural arch is wide and bears a low neural spine. Zygaphyses, where visible, seem to bear horizontally directed articular surfaces, thus allowing a good lateral mobility to the neck, while reducing probably vertical movements. The dorsal vertebrae (Fig. 3) bear low neural spines and well developed neural arches, the zygaphyses are flat and with horizontally directed articular facets. There are no traces of a zygosphene-zygantrum system, but this may be due to poor preservation. In some dorsal vertebrae a short but stout transverse process spring out laterally in the middle of the vertebral body. The cervical ribs are slender and rather elongate, they run parallel to the axis of the vertebral column until the fourth/fifth cervical vertebra. Unfortunately the rib head is always covered by matrix or overlapping vertebrae.

The anterior dorsal ribs are long and robust, deeply arched and hollow, as shown by the by the collapse of the proximal portion and by the filling of the original cavity by white crystals of calcium carbonate in the distal part of some ribs. Careful removal of the layer of pyrite crystals that encrusted the proximal portion of most vertebrae and of the centra revealed that the dorsal ribs are holocephalous. When removing the distal portion of some ribs to clear the carpus, the ribs revealed to be hollow, thin walled, with the cavity filled with calcite crystals. Several thin gastralia are exposed on the right side of the specimen where the overlying ribs have not been preserved.

**Shoulder girdle**

The shoulder girdle is almost completely obscured by vertebrae and ribs thus very little can be seen. The right clavicle almost entirely exposed in its anterior view: it is a rather stout, crescent shaped bone tapering at each end. Two stout vertically oriented structures represent the dorsal portion of the scapular blades, their robustness suggest that these bone were well developed; the exposed portion shows a gently concave anterior outline. Posterior and ventral to the last the dorsal ribs, two paired plate-like structures are partially visible, separated from each other by a rod-like structure which ends with a rounded tip. On a topological basis the paired structures may be interpreted either as the posterior portion of paired sternal plates or less probably, of wide coracoids. The narrow and pointed structure represents the posterior tip of the stem of the interclavicle.

![Fig. 4 - Megachirella walcotti gen. et sp. n.; RUH 1501 holotype. Right humerus in dorsal view. Abbreviations are: dpc deltoid crest, ecf entepicondylar foramen, enf entepicondylar foramen; up ulnar patella. Scale bar equals 0.5 cm.](image-url)
tal surfaces of both radius and ulna are encrusted by the layer of pyrite crystal that could not be removed. It cannot therefore be ascertained whether distinct epiphyses were present or not. The distal margin of the ulna shows a slight embayment of its medial margin, where it contacts the intermedium.

The carpus and part of the manus (Fig. 5) are visible. The carpus is made up by several elements and its pattern is not easily interpreted, owing to the presence of the layer of pyrite crystals which make it rather difficult to see the boundaries between elements. In addition, some displacement has occurred among carpal bones and thus the identification of some elements must be considered tentative. Distal to the radius a laterally expanded bone is interpreted as the radiale. Proximal to this latter an elongate intermedium contacts the ulna and distally the medial centrale, a tiny rounded bone almost identical in shape and size to the lateral centrale. Lateral to the intermedium there is a large rounded bone, here interpreted as the ulnare. However, since this area is covered by the pyrite layer, it is not possible to determine whether this layer conceals a small pisiform. The medial centrale does not reach the fourth distal carpal as in younginoids (Carroll 1988). At least four distal carpals are present, the fourth being by far the largest one. The fifth distal carpal is apparently very small. The first and fifth metacarpals are much shorter and stouter than the others. The distal head of the first metacarpal bears a well developed trochlea allowing greater mobility of the proximal phalanges, and suggesting a strong grip. Metacarpals I-IV are only partially visible, but they appear as elongate rod-like bones. The fifth metacarpal articulates with the fourth distal carpal along the medial margin of its proximal end. The manus has been preserved with digits contracted, i.e. the phalanges do not lie flat but, are vertically oriented in the matrix, except for the unguals which are horizontally placed above the basis of the digits as if they were grasping something. For this reason no phalanges are visible apart the unguals, with the exception of the first digit which was cleaned laterally; it consists of two phalanges, the last one being a long, pointed and stout claw. The unguals of the following three digits are also very stout, elongated and sharply pointed, suggesting that the manus was proportionally very wide and with good grasping abilities.

**Taxonomic assessment**

As can be inferred from the description above, all preserved characters of *Megachirella* gen. n. fit the diagno-
sis for advanced diapsids as defined for instance by Benton (1985) and Evans (1988). According to most authors (e.g. Gauthier 1984; Benton 1985; Evans 1988; Carroll 1988) most diapsids fall within one of two major clades, Archosauria (prolacertiforms, rauisuchians, and archosaurs) and Lepidosauria which comprises squamates, rauisuchians and other basal taxa like younginids, Sauropterygia Kuehneosauridae, Paleguana and Marmoretta (Evans 1988, 1991, 1994).

With reference to the characters sets proposed by Evans (1984, 1988, 1991) and Gauthier et al. (1988) for diapsid phylogeny, Megachirella gen. n. does not show any significant synapomorphy of the Archosauria, while it shares some of the derived characters diagnosing the Lepidosauria, namely: a postfrontal which enters the upper temporal fenestra with loss of postorbital-parietal contact, the presence of paired sphenoidal plates, and an interclavicle with an elongate posterior stem.

Within Lepidosauria, Megachirella gen. n. may be nested within a more restricted assemblage, the Lepidosauriformes (sensu Gauthier et al. 1988) which comprises (Paliguanina, Kuehneosauridae + Marmoretta + Lepidosauria, Evans 1991) on the basis of the presence of the following derived characters: prominent conch formed largely from quadrat, quadrat bowed in lateral view, long paroccipital process which reaches the quadrat, large retroarticular process, quadratojugal extending below occipital condyle, ectepicondylar foramen complete, first and fifth metacarpals shorter than second and fourth.

Megachirella gen. n. shows some superficial resemblance to members of the Kuehneosauridae, like the loss of quadratojugal, an incomplete lower temporal bar and the possible presence of a mobile quadrate. However, other key characters that could nest Megachirella gen. n. within Kuehneosauridae are either unknown (confluent nares) or absent, like the shortening of cervical vertebrae, the elongation of the transverse processes of the dorsal vertebrae, the height of the neural arches and the presence of platycoelous vertebrae. Megachirella gen. n., with its moderately elongate neck and stubby but short transverse processes seems to be more similar to Marmoretta (the sister group of the Lepidosauria according to Evans 1991, 1994). The pattern of the carpus of Megachirella gen. n., if the proposed identification is correct, reveals some similarity with that of Sphenodon. In fact it shows a proximodistally compressed radial and the exclusion of the mental centrale from the inner margin of the carpus (Romer 1956; Carroll 1988). Rauisuchians are known from the Middle Triassic (Fraser & Benton 1989) but the pattern of their carpus is mostly unknown since most Triassic genera are found as isolated bones, thus the tiny, grain-sized carpal bones may escape sieving or are difficult to identify and interpret (Evans, pers. comm.). The similarities between the carpus of Megachirella gen. n. and that of Sphenodon may either be considered as phylogenetically informative or, more probably, as a primitive condition, as for the moderately elongate neck, as it is found in Marmoretta (Evans 1991). Other characters speak against close relationships with rhyonocephalians. Namely: the few preserved teeth are stout but not acrodont and there are no remains of a palatine tooth row. At present knowledge, Megachirella gen. n. can be considered with some confidence as belonging to Lepidosauriformes, but any attempt to clarify better its taxonomic position is tentative due to the incompleteness of the skull and poor preservation of postcranial elements. Some resemblances with Marmoretta (Evans 1991) are present, namely: large upper temporal fenestra, lower temporal bar incomplete, frontals and possibly also parietals fused, separated postfrontals and postorbitals, weakly pleurodont teeth. Unfortunately, the incompleteness of the skull in Megachirella gen. n. and the scarcity of postcranial elements in Marmoretta do not allow a further clarification of the relationships between these two taxa.

Mode of life

Evans (1991) and Waldman & Evans (1994) suggested an aquatic lifestyle for Marmoretta, based on the abundance of bones in a predominantly aquatic assemblage quoting also the peculiar structure of the temporal regions of the skull, with large fenestrae and a high parietal crest as consistent with this interpretation. Megachirella gen. n. does not show any skeletal correlate which can be considered unequivocally as an adaptation to aquatic life. Many characters speak instead for terrestrial habits, like the robustness of the fore-limbs, the height of the scapular blade, the high level of ossification of the carpus and the size and shape of the claws. In addition, the presence of hollow ribs also speaks against aquatic habits since aquatic reptiles usually show pachyostotic, or at least robust, ribs and massive gastralia which act as a ballast, helping sinking into water. It is thus our opinion that the collected specimen represents an allochthonous terrestrial element transported, together with plants, within a marine marginal basin environment. During the Pelsonian, emerged lands with fluvial areas and low relief are recorded few kilometres south- and westward from the Kühlwiesenkopf / Monte Prà della Vacca area (Bosellini 1968; Senowbari-Daryan et al. 1993).

Further inference about lifestyle of Megachirella gen. n. may be obtained by analysis of the pattern of the manus: the phalanges are stout and with well developed articular surfaces at least for the unguals; these latter, when covered by horny sheats, surely formed very long curved and sharp claws, more useful in a terrestrial environment rather than in an aquatic one. The wide base of the claws housed the insertion of powerful flexor muscles, a pattern which allows both a strong grip and using the claws as clinging devices, especially if these latter are
latterly compressed (Hildebrand 1974; Cartmill 1985) as occurs in *Megachirella* gen. n. However, the rest of the skeleton of *Megachirella* gen. n. is not highly modified for scansional adaptation, as for instance in chameleons (Peterson 1984) or in drepanosaurs (Renesto 1994a, b, 2000), thus it is feasible that *Megachirella* gen. n. was not specialized for arboreal life, but lived like some extant semi-arboreal forms, like anolid lizards (Peterson 1971), feeding on insects and other invertebrates both on the ground and on trees and branches.

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