

A Huge Caseid Pelycosaur from North-Western Sardinia and Its Bearing on European Permian Stratigraphy and Palaeobiogeography

Authors: Ronchi, Ausonio, Sacchi, Eva, Romano, Marco, and Nicosia, Umberto

Source: Acta Palaeontologica Polonica, 56(4) : 723-738

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2010.0087>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A huge caseid pelycosaur from north-western Sardinia and its bearing on European Permian stratigraphy and palaeobiogeography

AUSONIO RONCHI, EVA SACCHI, MARCO ROMANO, and UMBERTO NICOSIA



Ronchi, A., Sacchi, E., Romano, M., and Nicosia, U. 2011. A huge caseid pelycosaur from north-western Sardinia and its bearing on European Permian stratigraphy and palaeobiogeography. *Acta Palaeontologica Polonica* 56 (4): 723–738.

Skeletal remains, some loose on the surface and others still embedded, have been recovered from the uppermost part of an outcrop of the Permian Cala del Vino Formation located near Torre del Porticciolo (Alghero, Nurra, NW Sardinia). Taphonomic analysis suggests that all the elements pertain to a single individual; ongoing studies indicate the fossil represents a large caseid close (or referable) to *Cotylorhynchus*; otherwise restricted to a narrow geographic and stratigraphic zone of the central USA. The new finding, the first of a caseid in Italy and one of few in Europe, enlarges the known distribution of the family and provides a significant and key chronostratigraphic constraint for the continental succession of this area and, in turn, helps establish a stratigraphic framework for the Permian units cropping out in Italy and southern France.

Key words: Synapsida, Pelycosauria, Caseidae, taphonomy, stratigraphy, Permian, Italy.

Ausonio Ronchi [ausonio.ronchi@dst.unipv.it], Dipartimento di Scienze della Terra, Università di Pavia, v. Ferrata 1, 27100 Pavia, Italy;

Eva Sacchi [eva.sacchi@uniroma1.it], Marco Romano [marco.romano@uniroma1.it], and Umberto Nicosia [umberto.nicosia@uniroma1.it], Dipartimento di Scienze della Terra, “Sapienza” Università di Roma, P. le A. Moro 5, 00185 Roma, Italy.

Received 3 September 2010, accepted 2 February 2011, available online 7 February 2011.

Introduction

Skeletal remains of a large tetrapod have been recovered from a level of the Permian Cala del Vino Formation cropping out near Torre del Porticciolo (Alghero, Nurra, NW Sardinia) (Ronchi et al. 2008a). The bone-bearing bed lies nearly 30 m below the lower boundary of the Conglomerato del Porticciolo, an easily recognizable lithostratigraphic unit that, locally, marks the beginning of the Triassic sequence (Cassinis et al. 2003). No large vertebrate has yet been reported from the Late Palaeozoic of Italy. In Sardinia, the only relevant discovery of fossil vertebrates is that of some small branchiosaurid amphibians from the Autunian Perdasdefogu Basin (Ronchi and Tintori 1997; Werneburg et al. 2007).

The discovery reported herein provides an important new age constraint on the fossil bearing unit, and forms the basis for improvement in knowledge of stratigraphy and palaeobiogeography of Permian deposits in the central Mediterranean area.

Institutional abbreviations.—FMNH, Field Museum of Natural History of Chicago; MPUR (NS), Museum of Paleontology, University of Rome (New Series).

Geological setting

In Sardinia, post-“Autunian” continental deposits (fluvial and volcanoclastic) crop out extensively only in its north-western region of Nurra (Fig. 1). “Autunian” is a traditional European term, previously considered an age, which now indicates a characteristic flora. In any case, as stated by Broutin et al. (1999) and by Ronchi et al. (2008b), referring to the International Stratigraphic Chart by IUGS, it spans from the latest Ghzelian to the early Sakmarian. Significant Autunian successions characterize small basins (Perdasdefogu, Escalaplano-Mulargia, Seui-Seulo, and Montarbu) in the central to south-eastern part of Sardinia (see Ronchi et al. 2008b for a review).

In contrast, scattered Early Permian outcrops occur in the south-western portion of the island (see Cassinis and Ronchi 2000; Cassinis et al. 2000; Ronchi et al. 2008b). Concerning Nurra, the Late Palaeozoic–Early Mesozoic continental succession ranges discontinuously from Early Permian to the Anisian (Neri et al. in Cassinis et al. 2000; Fontana et al. 2001; Cassinis et al. 2002b; Cassinis et al. 2003). From the base to the top, it includes six named units, most with unconformable relationships: Punta Lu Caparoni Formation, Pedru Siligu Formation, Porto Ferro Formation, Cala del Vino Formation,

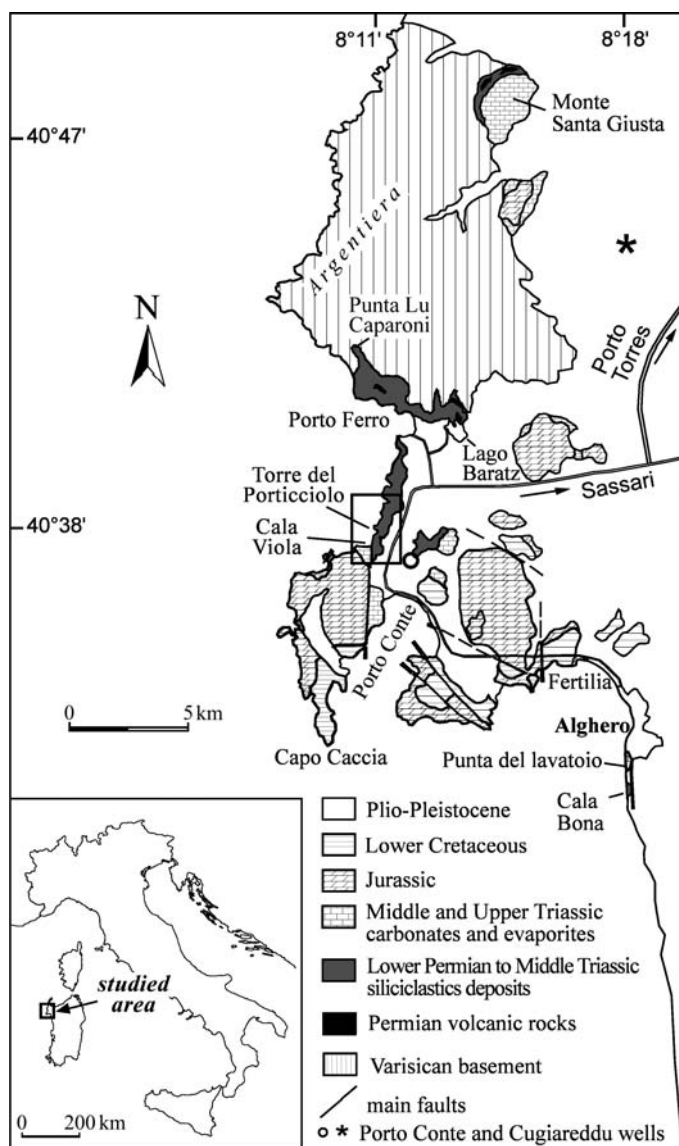


Fig. 1. Location of Permian and Triassic outcrops in the Nurra area (north-western Sardinia).

Conglomerato del Porticciolo, and Arenarie di Cala Viola. These units, some of which contain interbedded volcanic products, are ascribed to three major sequences (Cassinis et al. 2002b, 2003; Ronchi et al. 2008b), as summarized in Fig. 2.

Up to the present, only two biochronological constraints are available for this entire Permian and Triassic continental succession:

(1) At its base, in the Punta Lu Caparoni Formation (first sequence), Pecorini (1962) recorded a rich “late Autunian” macroflora assemblage. This age-attribution was confirmed by other findings by Gasperi and Gelmini (1980), Broutin et al. (1996), and Broutin et al. (2000). The sporomorph association found by the same authors also confirms the late “Autunian” attribution of the formation (Broutin et al. 2000).

(2) At the uppermost levels, the presence of *Equisetum mougeotii* in the Arenarie di Cala Viola (third sequence), led Pecorini (1962) to assign these siliciclastic deposits to the

Lower Triassic. Two different sporomorph assemblages from similar units in the subsurface (Cugiarreddu well: Pomesano Cherchi 1968) led Pittau (in Cassinis et al. 2000) and Pittau and Del Rio (2002) to tentatively ascribe the Arenarie di Cala Viola respectively to the late Induan?–early Olenekian and late Anisian.

The second sequence, here informally named the “Nurra Group”, and where the osteological material was recovered, attains a thickness of about 600 m and has hitherto yielded almost no stratigraphically meaningful fossils.

In the fluvial deposits, only the abundance of rhizolites and various kinds of bioturbations testify to paleoenvironments rich in life and subjected to alternately wet and dry to sub-arid climatic conditions. Therefore, as said above, the age attribution of this alluvial megacycle, which represents the bulk of the Permian and Triassic clastic deposition, is constrained only by the presence of “Autunian” floras at the base of the first sequence (i.e., Punta Lu Caparoni Formation) and of Anisian microfloral remains in its uppermost unit (i.e., Arenarie di Cala Viola, third sequence).

Radiometric datings and previous age attribution of the second Permian sequence.—In northern Nurra, at the base of the Permian and Triassic clastics (previously “Buntsandstein” after Pecorini 1962) of Mt. Santa Giusta (Fontana et al. 2001), a volcanic unit crops out. These volcanic rocks, which have already been tentatively correlated to those lying at the top of the Pedru Siligu Formation (cropping out at Casa Satta and named as V2 in Fig. 2), were first isotopically dated by Lombardi et al. (1974) and Edel et al. (1981). Only the latter author gave reliable ages, these being 296 ± 8 Ma and 297 ± 9 Ma. More recently the same volcanic unit was investigated by Buzzi et al. (2008), who gave an isotopic age of 291.5 ± 1.5 Ma (^{40}Ar – ^{39}Ar step heating technique on biotite), corresponding to the early–middle Sakmarian. To-date, the pertinence of Casa Satta volcanics to a second magmatic episode and also its correlation with the Santa Giusta ignimbrites appears debatable.

Previously, different ages have been ascribed to the bone-bearing unit (Cala del Vino Formation). In particular, on the basis of regional stratigraphic correlations, the top of the Permian portion was referred to the Late? Permian by Pecorini (1962). Vardabasso (1966) agreed with this interpretation and distinguished in the whole clastic succession a Permian and a Triassic (“Buntsandstein”) parts, in the former envisaging, below, “Saxonian” facies and, upper, non-evaporitic Zechstein facies of ?Late Permian age. Gasperi and Gelmini (1980) subdivided the “Permotriassic” continental deposits of Nurra into four informal units, also hypothesizing a large gap (ranging from Autunian to the Permo-Triassic boundary?) between the second and the third one. Subsequently a generic Early Triassic age was suggested for the third and fourth units (sensu Gasperi and Gelmini 1980) by Sciunnach (2001, 2002), on the base of data that seem to us weak and debatable. Before, Cassinis et al. (1996) had also ascribed the third unit of Gasperi and Gelmini (1980) to a generic Buntsandstein but with not a precise age-at-

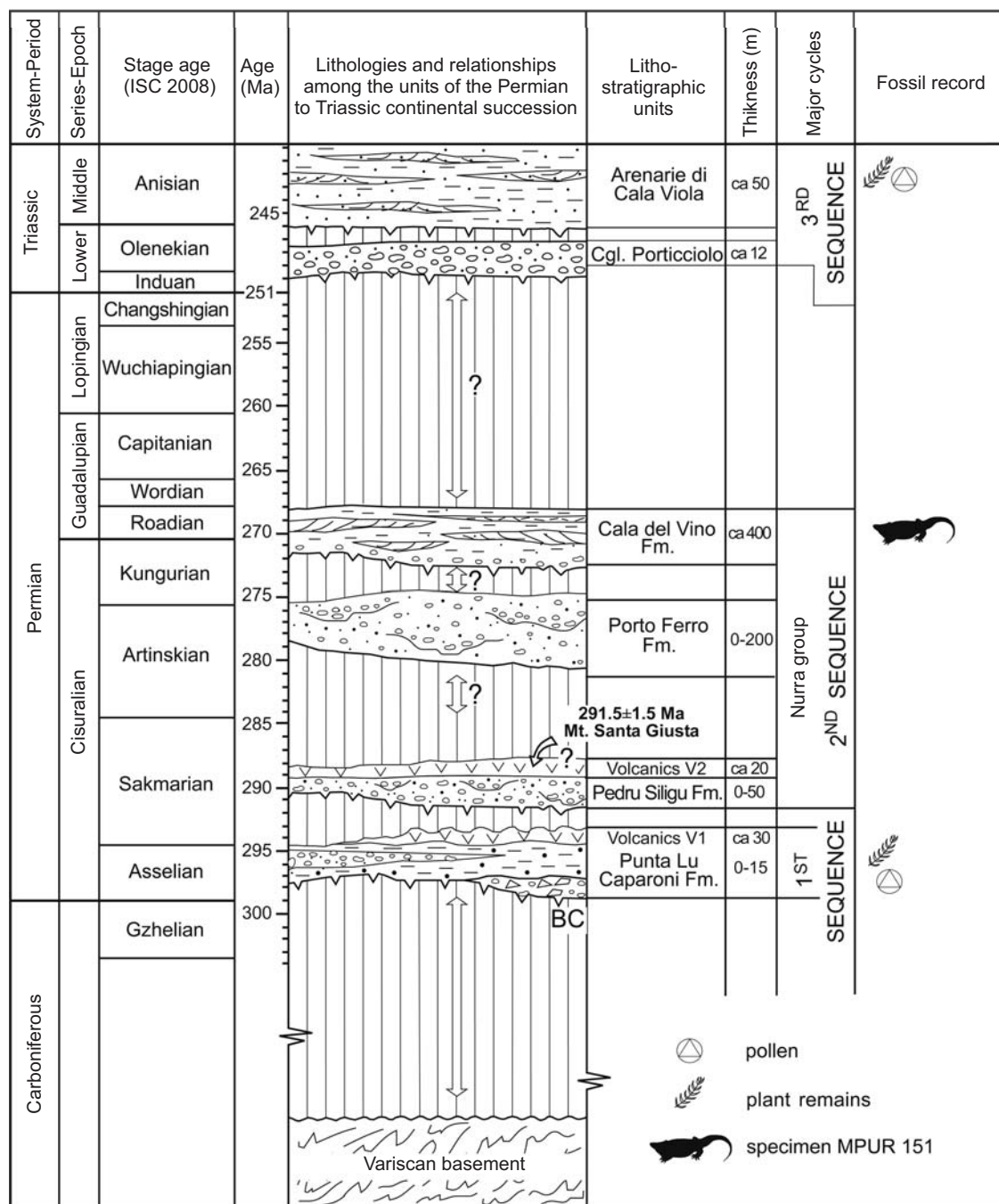


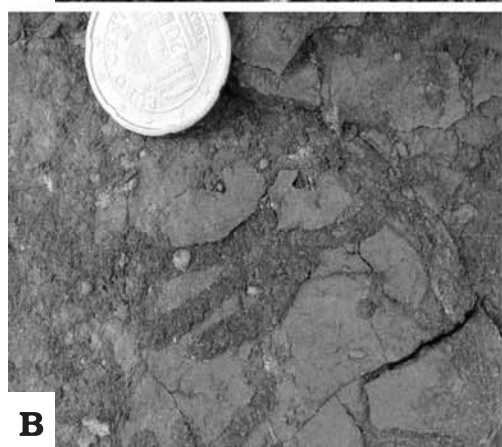
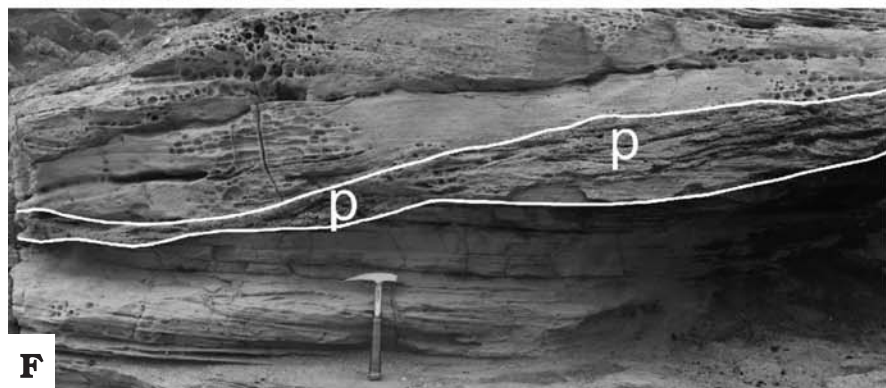
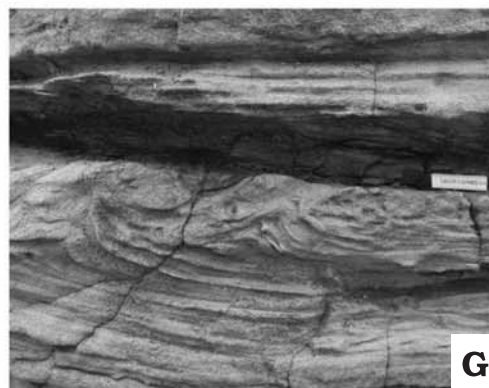
Fig. 2. Stratigraphy of the three major Permian and Triassic sequences of Nurra. BC, basal conglomerate.

tribution. Costamagna and Barca (2002: 82), stating that “...it was not possible to establish a boundary between ‘Buntsandstein’ Triassic facies and ‘Rotliegendes’ facies”, even ascribed to the Triassic all the clastic deposits overlying the Autunian Punta Lu Caparoni Formation.

Recently, a detailed lithostratigraphic correlation between Permian and Triassic successions of Nurra and southern Provence, France (Cassinis et al. 2002b, 2003) has confirmed the contiguity of the two regions during that time-interval and fixed unambiguously the paleoposition of, at least this part, of the Sardinia-Corsica block before its Cenozoic counter-clock-

wise drift to the southeast. Consistently, on the base of the same lithostratigraphic correlation with the St.-Mandrier Formation of the Toulon-Cuers Basin in Provence, unit 3 (corresponding to the Cala del Vino Formation of this paper) has been ascribed to “undefined Late Permian (Tatarian?) times”, according to the bipartite subdivision of the Permian system (Cassinis et al. 2003: 119).

The Torre del Porticciolo section.—The Cala del Vino Formation consists of an alternating dark red, poorly cemented, mudstone-siltstone deposit and grey-greenish sandstone

**A****B****P****C****D****E****F****G**

bodies characterized by different geometries and sizes. The former alluvial plain fine sediments appear homogeneous and deeply bioturbated, while the latter bodies often have lenticular shape and erosive bases and, where not amalgamated, with internal trough cross- to plane parallel-stratification. Laminations also occur in the medium to fine ripple cross-laminated sandstone. Many of these sandstone bodies show lateral accretion and are thought to represent pointbars. The lenticular sandstone at the top of these bars could represent the infill of small chute-channels cut at the bar top during the main floods. Such lithologies and fluvial architecture are typical of a meandering-channel alluvial system (Fontana et al. 2001; Ghinassi et al. 2009). These deposits were laid down by medium-scale, bed-load streams, under a relatively mild semi-arid climate. This is confirmed also by carbonate palaeosols which repeatedly drape the top of bars (Fig. 3F). Nodular caliches and tubular rhizolites are very frequent inside both the coarse-grained sand bodies (Fig. 3E) and the alluvial plain muds. Water-escape structures can be also observed in some sandstone horizons (Fig. 3G).

The vertebrate remains were found in an alluvial plain mudstone-siltstone layer on top of the promontory which separates the Porticciolo Gulf from the northern coast (Fig. 3A), characterized by other small gulfs (e.g., Cala del Vino, Cala del Turco, etc.). They were recovered in the Cala del Vino Formation, in a level about 30 m below the unconformable contact with the Conglomerato del Porticciolo, which represents the basal unit of the Triassic (third) sequence (Fig. 3C).

The entire Permian–Triassic succession of Nurra is strongly affected by brittle to ductile compressive tectonics referable to different Pyrenean orogenic phases: in particular, in the Porticciolo area a double fold occurs with further refolding of the axis. A subsequent extensional tectonic phase led to the development of a number of normal faults with limited offset. These complex tectonics phases, which affected the whole succession, are the principal reasons why we can not yet give a definitive and exact stratigraphic position of the vertebrate-bearing level within the Cala del Vino Formation. It is nevertheless clear that in this sector of the coast it is a lower part of the formation that is covered by the basal conglomerate of the Triassic (Marc Durand, personal communication 2009). To the NNE up Porto Ferro, cliffs offer a long section through the Cala del Vino Formation with good exposure, practically continuous for more than 300 m, and without significant tectonic disturbance; its monoclinical structure (dipping to the north) allows to show a marked coarsening-upward trend from sandstone (as at Porticciolo) to conglomerate; the corresponding angular unconformity below the subhorizontal Triassic, can

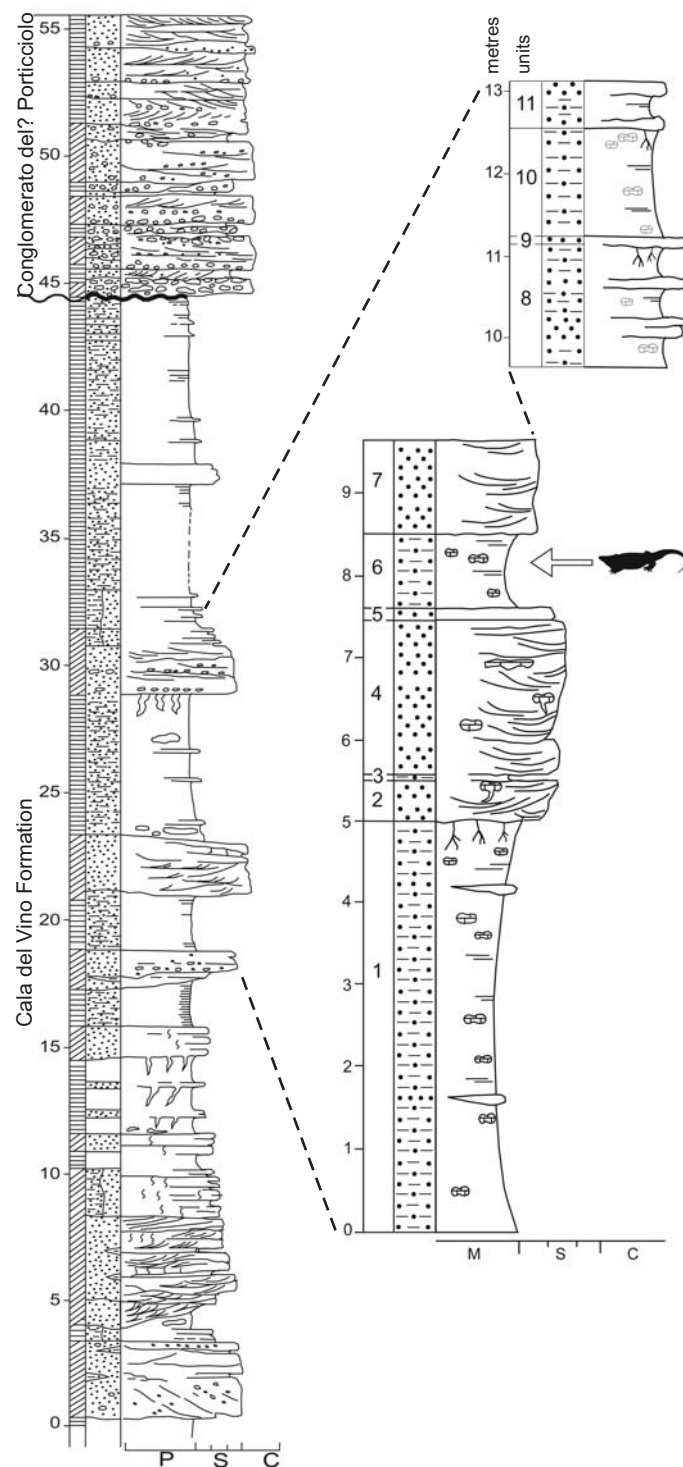


Fig. 4. Columnar section of the Torre del Porticciolo outcrop.

be seen 500 m south of the Tower. Nevertheless, a detailed stratigraphic section, which includes the bones bearing deposit, was measured and is hereafter described (Fig. 4). The log starts approximately at sea-level, at the base of the small cliff of the promontory on which lies the Porticciolo Aragonese tower and consists of the following units:

Unit 1: 5 m thick body of wine-red micaceous siltstone and mudstone beds with scattered, very fine sandstone lenses (Fig.

← Fig. 3. **A.** The Torre del Porticciolo promontory. **B.** Meniscate burrows within silty shale/mudstone (coin diameter 22 mm). **C.** The Conglomerato del Porticciolo, the basal unit of the Triassic (T), unconformably resting on the Permian Cala del Vino Formation (P) (in the circle a hammer for scale). **D.** Wine-red micaceous siltstone and mudstone beds with sandstone lenses (in the circle a booklet for scale 20 cm wide; asterisk marks the exact location of the find). **E.** Rhizolites (r) (hammer for scale). **F.** Palaeosol (p) draping a bar (hammer for scale). **G.** Water escape structures (white scale bar 6 cm).

3D); these fine sediments appear deeply amalgamated by bioturbation, and ripple-laminations rarely occur. Rhizolites and small caliche nodules frequently occur throughout the unit. Root traces are developed at the topmost part of this unit and mottling structures frequently occur.

Unit 2: a fine-to-medium sandstone body with scattered quartz pebbles, about 0.45 m thick, with through cross-bedding; yellow-orange rhizolite concretions occur in its middle-upper portion.

Unit 3: 0.15 m thick red siltstone interval.

Unit 4: a large medium-grained fairly cemented quartz sandstone bar, 1.90 m thick, characterized by large through cross-stratification and coarsening upward; yellowish small to large-sized rhizolitic concretions with elongated to nodular shape are frequently developed all throughout the unit. A parallel lamination is poorly preserved at its top. As for unit 2, lateral persistence of such sandstone bars is very variable.

Unit 5: a homogeneous, poorly cemented, grey fine sandstone horizon 0.20 m thick.

Unit 6: 1.10 m thick micaceous siltstone layer with no

sedimentary structures; these fine sediments appear very poorly cemented. This is the horizon which hosted the vertebrate remains.

Unit 7: 1.15 m thick gray-greenish and poorly cemented but well sorted sandstone body with very subtle cross-laminae. The section continues about 30 m to the west, in the direction of the tower.

Unit 8: 1.50 m thick interval showing an alternation of reddish fine sandstone lenticular bodies with shaley siltstone-mudstone beds; those last are pervasively affected by meniscate burrows (*Scoyenia* type; Fig. 3B).

Unit 9: 0.20 m thin medium-grained greyish, well cemented, sandstone body.

Unit 10: 1.30 m thick homogeneous mudstone interval with mm-to-cm sized carbonate nodules and rhizolites. Thin oversize clast horizons are not rare inside these overbank fine sediments.

Unit 11: 0.60 m thick body of micaceous mudstone inter-layered with fine-grained sandstone. Upwards the section is offset and complicated by small faults and folding.

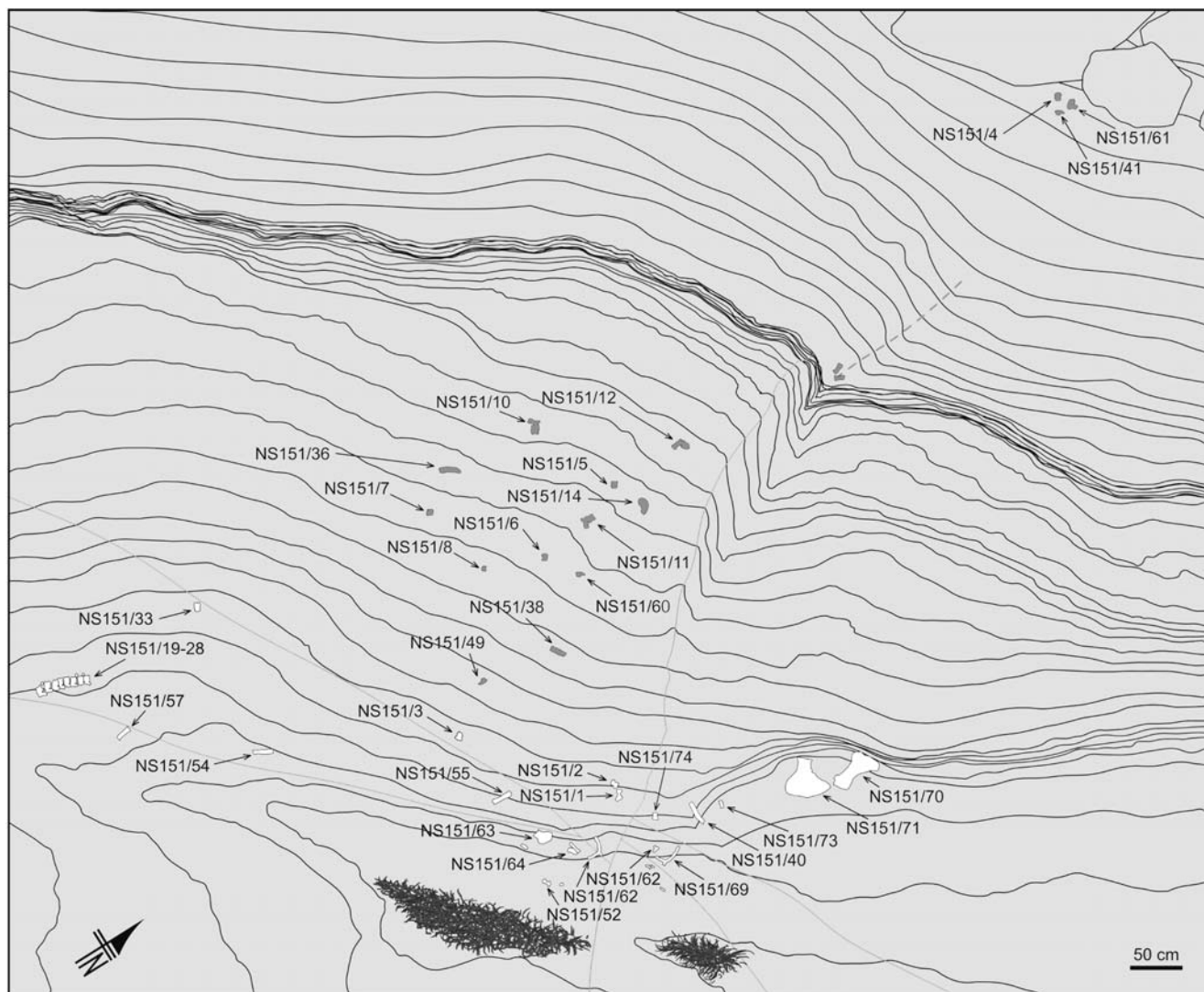


Fig. 5. Map of recovered bones. White: embedded bones; grey: bones displaced on the ground surface.



Fig. 6. Caseid pelycosaur cf. *Cotylorhynchus* sp. from Cala del Vino Formation, Permian: Late Kungurian–Roadian; NW Sardinia, Italy. Articulated portion of the axial skeleton (MPUR 151/19–28).

Taphonomy

Even taking into account the rarity of Paleozoic vertebrates (Reisz and Laurin 2001) and the consistent high probability that all the bones pertained to the same individual, most of the bones were found disarticulated. For this reason, an initial phase of study was to determine whether the remains represent one or more individuals. In order to address this question, the location of each bone was mapped (Fig. 5), data on the state of preservation were carefully collected, and the material was analyzed, mostly in the framework of the taphonomic schemes of Behrensmeyer (1978) and Voorhies (1969).

All the bones were found in a confined area, a belt measuring nearly 2 m in width and 8.50 m in length. Some bones were recovered loose on the ground surface, and others still embedded. Those found still in place did not lie on the same bedding plane but were embedded, flat lying, at different depths, in a thickness of around 40 cm of homogeneous red siltstone lacking sedimentary structures. The final position of bones could have resulted at least in part from sediment compaction.

Some of the embedded bones were still articulated (two pedal elements and eight caudal vertebrae reclined on the right side and grossly parallel to the bedding plane with three proximal portions of haemal arch) (Fig. 6), whereas others were displaced in the sedimentary matrix, i.e. the distal portion of the left ulna (MPUR 151/63) and two large fragments of the badly crushed right scapulocoracoid (MPUR 151/70–71). Among these displaced bones, some were fragmentary. Analysis of fracture surfaces indicates that these bones were broken before being buried. In this case, the fractures are angular and mostly perpendicular to the bone shaft (Fig. 7). Frequently, rib fragments show fractures (Fig. 8) that are perpendicular to their long axes, parallel to each other, straight and clean. We interpret such breaks as occurring after permineralization. This

fracturing phase must be related to tectonic activity that took place much later than burial (Gonzalez Riga and Astini 2007). Thus, both compression and fracturing have been considered meaningless as biostratigraphic characters (Lee Lyman 2010).

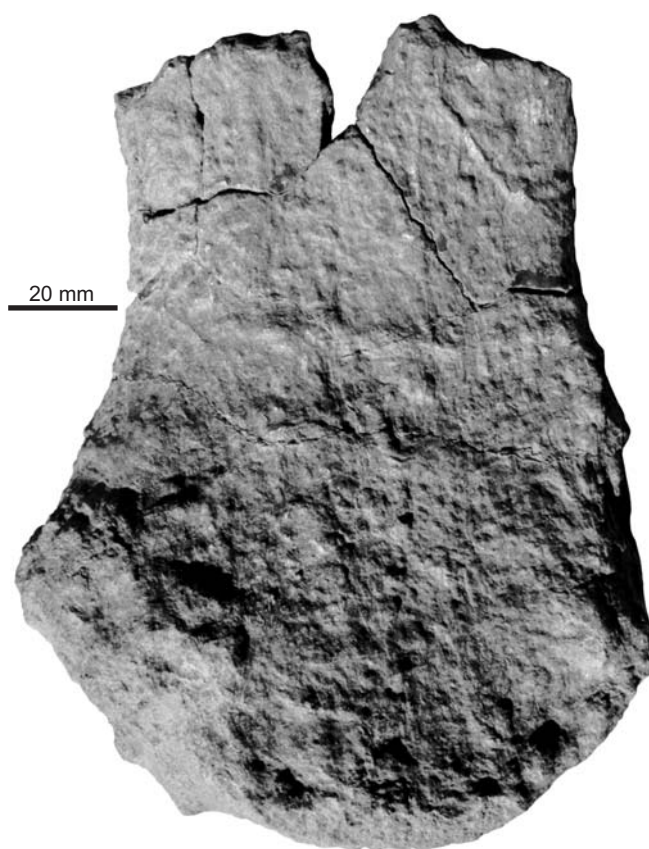


Fig. 7. Caseid pelycosaur cf. *Cotylorhynchus* sp. from Cala del Vino Formation, Permian: Late Kungurian–Roadian; NW Sardinia, Italy. Distal portion of the left ulna crushed before burial (MPUR 151/63). The fractures are angular and mostly perpendicular to the bone shaft.

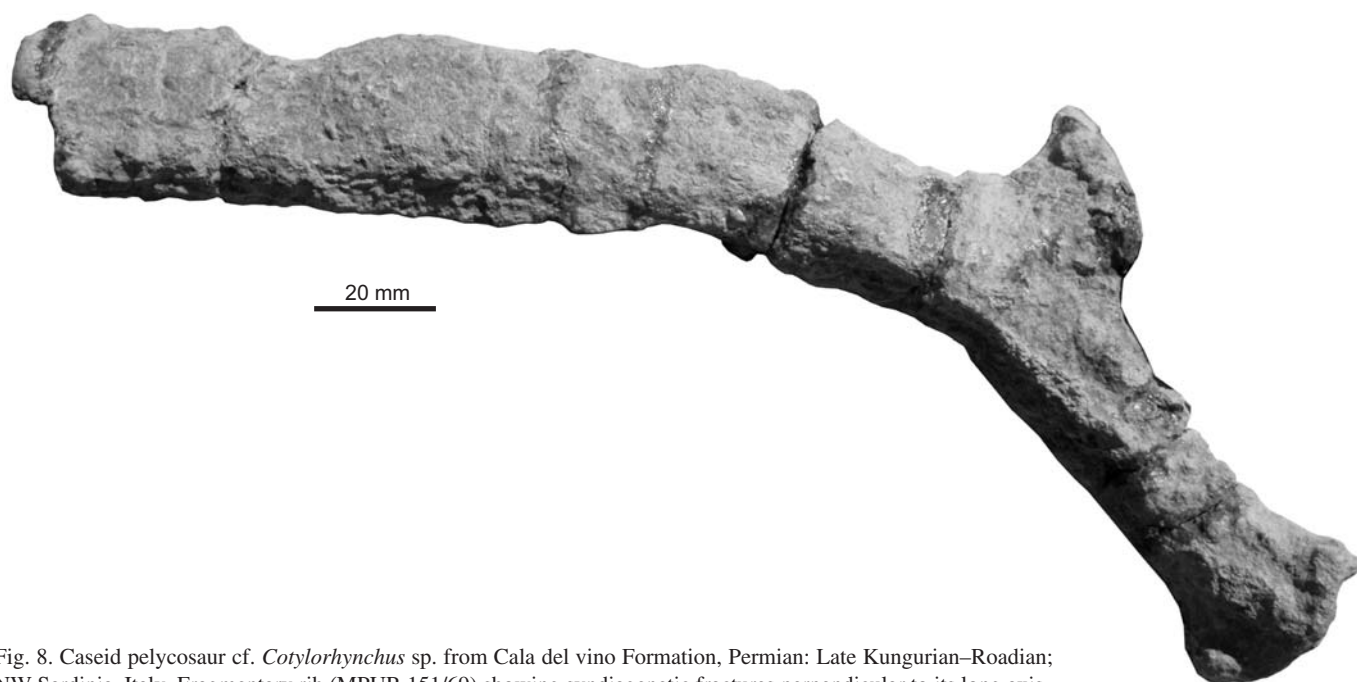


Fig. 8. Caseid pelycosaur cf. *Cotylorhynchus* sp. from Cala del vino Formation, Permian: Late Kungurian–Roadian; NW Sardinia, Italy. Fragmentary rib (MPUR 151/69) showing syndiagenetic fractures perpendicular to its long axis.

The non-embedded elements, including some caudal vertebrae, a few pedal elements and rib fragments, resulted from recent erosion of the same sedimentary body which embeds the other fossil bones. Study of the isolated vertebrae shows that they are caudals and that they are comparable, in shape and preservation, to those that were found in articulation. Moreover, some of them fit each other and with the most proximal articulated vertebra (both in size and deformation pattern), indicating they were also articulated before the recent erosion.

Because surrounding rock matrix is poorly cemented and only lightly indurated, we were able to completely free skeletal elements from the rock, allowing three-dimensional observation of the material. Some bones show a slight degree of compression (for the caudal centra around 20%), probably by the overlying sediment weight.

Taking into account the ablation order suggested by Voorhies (1969), the preservation in the same place of long bones, vertebrae, ribs and foot elements suggest short transportation of the body and relatively speedy burial. Nevertheless, the presence of the distal portions of the foot, among the first that are usually displaced far from the body during the decay processes, may be related to the presence of particularly robust tendons connecting the pedal elements, suggested as peculiar adaptations of the huge caseids (Olson 1968).

The presence of bones that were buried after having been broken (i.e., ulna, ribs, haemal arches, etc.) suggests that the transportation phase was energetic and violent.

The bone material is, in general, quite well preserved, so that most of the recovered bones show an almost complete cover of periosteal tissue. Also present and irregularly distributed on the surface of many bones are the “rugosity and the strong tubercles”, considered by Romer (1956: 226) as evi-

dence of the “... firm union with the fibrous tissue of the dermis”. In the recently fragmented bones, where the observation of internal structure is allowed, the cavities of the cancellous tissue are free both from sediments and recrystallized minerals. Neither flaking nor mosaic surface fractures or cracking are apparent, and no scavenging traces have been observed, though the good surface preservation could have allowed perfect observation of such features (Holz and Barberena 1994). Thus, weathering evidences fall in Behrensmeyer’s (1978) stage “0”, suggesting a very short interval of pre-burial exposition. Accordingly, the biostratinomic processes were concluded when the collagen was still abundantly present within the bones, and a relatively early entombment is indicated (Holz and Barberena 1994; Pérez et al. 2009).

The most parsimonious explanation of this set of phenomena seems a complex and multiphase biostratinomic process. In order to explain all the evidence, and excluding from consideration diagenetic deformation, we must hypothesize that, soon after death, the body was subjected first to a transport phase, from the place of death to a second deposition place, as for instance ending stranded on a river bank. This first phase of transport was probably due to a short and high energy flow, strong enough to break some bones. Thereafter, the body, still on sediment surface and partially crushed, was subject to a further short phase of decay, a phase to which we ascribe the ablation of some portions of the fragile haemal arches broken down during the phase of violent transport. Subsequently, all the remains could have been loaded with a large amount of fine grained sediment (probably in a flash-flood), transported, packed within sediments, and ultimately deposited all together, in a third place, not too far from the previous one. This would explain why the bones lie at different depths within the sedimentary body.

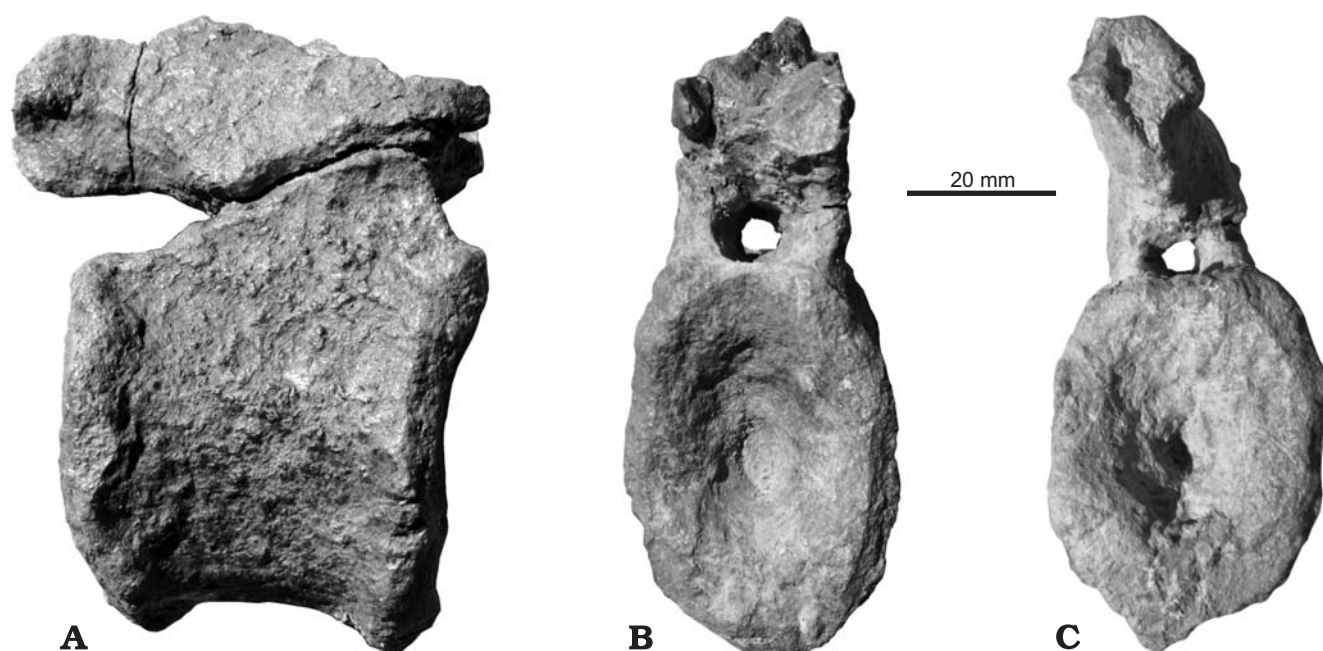


Fig. 9. Caseid pelycosaur cf. *Cotylorhynchus* sp. from Cala del vino Formation, Permian: Late Kungurian–Roadian; NW Sardinia, Italy. Caudal vertebra (MPUR 151/27), in lateral (A), anterior (B), and posterior (C) views.

In conclusion, although most of remains were found isolated, if we accept the foregoing sequence of taphonomic processes and take into consideration the non-repetitive nature of the skeletal elements, the fact that dimensions of the elements are congruent with each other, the identical kind of preservation, the confined area of discovery, and the non-random distribution of body parts, we must refer all the recovered bones and fragments to the same individual. The occurrence of such isolated individuals indicates, according to Bandyopadhyay et al. (2002), a normal attritional death; moreover, in agreement with the studies of Behrensmeyer (1978), Holz and Barberena (1994), and Pérez et al. (2009), the time of subaerial exposure of the Sardinian specimen could have been limited to a short interval spanning between several days and a few tens of days.

Systematic palaeontology

Synapsida Osborn, 1903

Caseosauria Williston, 1912

Caseidae Williston, 1912

?*Cotylorhynchus* sp. Stovall, 1937

Taxonomic background of Caseidae.—The Caseidae, monophyletic according to Maddin et al. (2008), includes a compact, small group of genera of pelycosaur-grade synapsids. Members of this group were first described by Williston (1910, 1913) and Stovall (1937), and subsequently studied by Olson (1954, 1955, 1962, 1968), Olson and Beerbower (1953), Olson and Barghusen (1962), Stovall et al. (1966) and Reisz (1986, 2005). As many as nine genera (and 16 spe-

cies) have been placed in the family, namely: *Casea* (the family name-bearing genus), *Cotylorhynchus*, *Angelosaurus*, *Ennatosaurus*, *Oromycter*, *Caseoides*, *Phreatophasma*, *Trichasaurus*, and *Caseopsis*.

Caseoides was later considered as a caseid of uncertain position, because “nothing is known of the skull and the few postcranial elements are poorly preserved” (Reisz 1986: 62).

Phreatophasma was considered a therapsid “incertae sedis” in Romer (1956) and ascribed to Caseidae by Olson (1962, 1968); based on a single femur, it was assigned only tentatively to the family by Reisz (1986) as well as by Carroll (1988). Subsequently it was excluded from caseids and moved to an indeterminate family by Ivakhnenko et al. (1997). Maddin et al. (2008) retained the classification of Ivakhnenko et al. (1997).

Trichasaurus has been considered “probably a caseid” by Romer and Price (1940) and a caseid by Romer (1956). Subsequently it was transferred to Labidosauridae by Stovall et al. (1966) and finally was considered among the “pelycosaurs incertae sedis” by Reisz (1986), Carroll (1988), and Maddin et al. (2008).

Maddin et al. (2008) considered *Caseopsis* a doubtful taxon, and for this reason excluded it from their phylogenetic analysis, even though it was not formally excluded from the family.

At present the family groups six genera (and one uncertain taxon) including 13 formalized species; moreover three as-yet undescribed taxa are known (see below).

Material.—At present the material includes more than 180 complete bones or fragments, ranging in size from more than 40 cm to a few mm-long minute fragments. Some bones, still articulated, were moulded in place before removing to pre-

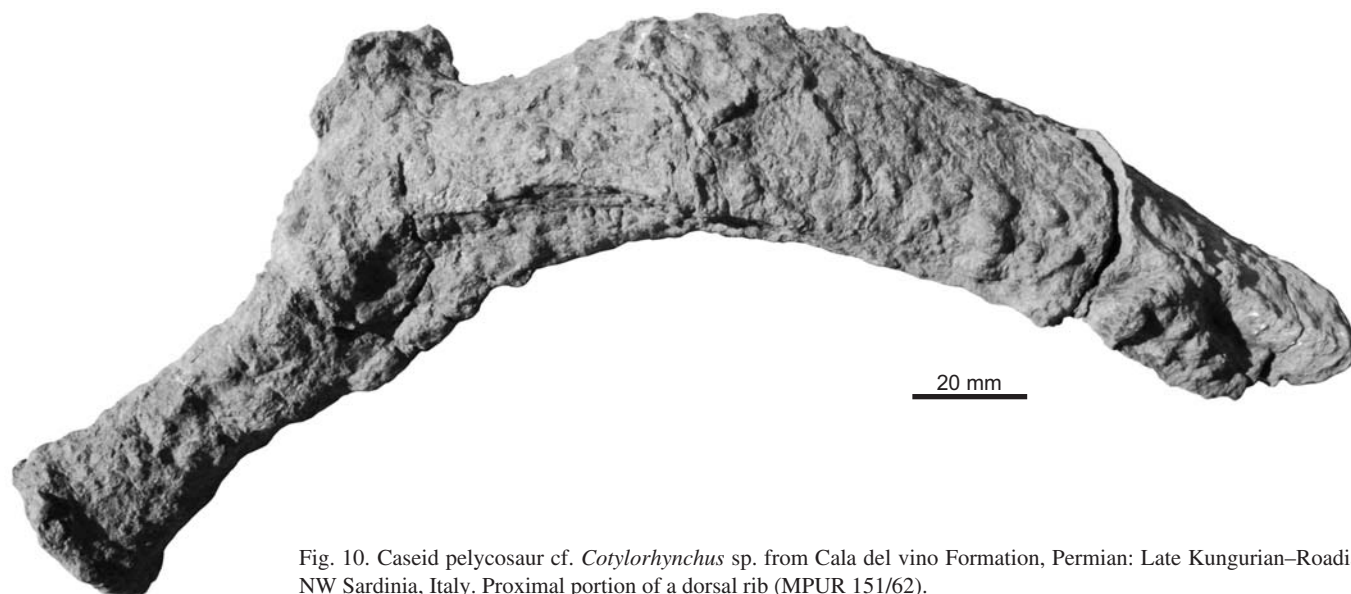


Fig. 10. Caseid pelycosaur cf. *Cotylorhynchus* sp. from Cala del vino Formation, Permian: Late Kungurian–Roadian; NW Sardinia, Italy. Proximal portion of a dorsal rib (MPUR 151/62).

serve their original relative positions, and some fragmented and/or incomplete bones have been restored. Every complete or fragmentary bone has been labelled with the acronym MPUR NS followed by 151 (specimen number) and by a slash and a serial number starting at 1 (for simplicity below will be reported only MPUR 151/ and the serial number).

Among the recovered material, a number of elements have been identified as follows: 15 well preserved caudal vertebrae, and numerous large fragments clearly referable to at least eight other vertebrae; seven proximal portions of haemal arches; three proximal segments of dorsal ribs and ten undetermined fragmentary ribs; distal portion of a left ulna; right scapula and badly crushed right coracoid plate; 12 pedal elements. Comparisons were made with material housed at the FMNH.

Description.—The available, taxonomically meaningful elements are few: the skull of the Sardinian specimen was not found, so the most diagnostic elements are lacking. This made difficult the attribution of the specimen mostly taking into consideration the absolutely prevailing “craniocentric” taxonomy, widespread in the concerned literature. So we were obliged to base our study on the few available elements that, nevertheless, early steered our attention to particular members of the Caseidae.

The vertebrae are amphicoelous, with the centrum as long as wide (Fig. 9). Their maximum length ranges from 25 to 50 mm. The centra are half as high as the complete vertebrae and show the typical pelycosaurian sub-cylindrical shape (“spool-shaped” according to Romer and Price 1940). Preservation does not allow us to observe if the notochord was really interrupted (discontinuous). In the ventral part the bevellings for the insertion of the proximal portion of the haemal arches (intercentra) are apparent. Bevellings are small and more apparent on the posterior margin of the centra. On some centra, a narrow groove is present ventrally. The neural arch width never exceeds the centrum width and thus the vertebrae can

be considered “narrow” (sensu Sumida and Modesto 2001). Zygapophyseals facets are gently sloping (ca. 30°). The neural spines are posteriorly inclined and gradually decrease in height posteriorly. The neural canals show a circular section, with a diameter of around 7–9 mm (Fig. 9B, C). The shape and proportions of the vertebrae of the Sardinian specimen are typical of caseid pelycosaur. Vertebra MPUR 151/28 is very similar to the caudal FMNH UR 894, labeled as *Cotylorhynchus hancocki*, particularly in having a well preserved longitudinal groove on the ventral surface of the centrum. The Sardinian vertebrae are comparable in size and morphology to those described by Olson (1962) for *Cotylorhynchus hancocki*, and can be tentatively referred to the postsacral vertebrae starting at the 12th.

The ribs are massive and elliptical to concavo-convex in cross-section. Some of them show a shallow, longitudinal groove. Among the recovered material, three well-preserved proximal portions (MPUR 151/13, MPUR 151/62, MPUR 151/69), show a well-developed capitulum and a tuberculum reduced to an oval area, facing upward and inward typical of the “rounded bodied, barrel shaped edaphosaurs” (Romer 1956: 292) (Fig. 10). Specimen MPUR 151/13 is closely comparable to ribs of *Cotylorhynchus romeri* and is particularly similar to one illustrated as rib 13–14 by Stovall et al. (1966) in their fig. 5; specimen MPUR 151/62 corresponds to their rib illustrated as no. 17 while MPUR 151/69 is closely similar to rib 19 of the same published illustration. Specimen MPUR 151/62 is comparable in known details to FMNH UR 266, ascribed to *C. hancocki*. These ribs also permit us to estimate the dimensions of the corresponding presacral vertebrae at around 10 cm in length, well corresponding to or slightly longer than pre-sacral vertebrae 9–12 of *C. hancocki* (Olson 1962: 42, table 19), or dimensionally comparable to the vertebra FMNH UR 566 labeled as *C. hancocki*.

Two scapulocoracoid portions were found close each other lying flat in the same bedding plane. One of the two portions is a right scapular blade, a sheet of bone thin and

high. The bone is characterized by the typical narrowing just above the supraglenoid buttress while the dorsal termination is antero-posteriorly expanded, with an unfinished edge. It probably continued with a cartilaginous suprascapula, as generally found in early amniotes (early reptile sensu Romer 1956). The expanded upper portion of the scapular blade has a gently hollow surface on the lateral side and the bone axis shows, dorsally, the typical gently inward bending. Below the maximum narrowing of the scapular blade, the bone shows a thickened posterior edge that probably represents the dorsal portion of the supraglenoid buttress. There is no supraglenoid foramen, as in all known caseid scapulocoracoid in which this portion is preserved (Olson 1968). The second portion of the scapulocoracoid is a badly crushed partial coracoid plate. In the upper part of the bone there is a long and low depression which could be the glenoid fossa. The preserved portion of the coracoid plate is somewhat deformed, showing a concave surface instead of the typical convex structure. The ventral portion of coracoid plate, below the glenoid cavity, is badly crushed and hard to prepare so at the moment is not possible to determine the presence of a supracoracoid foramen. This foramen, carrying nerve and vessels in living forms (Romer 1956), is present in all known scapulocoracoids of caseids (Olson 1968) and probably is a familial plesiomorphy. Because of poor preservation the suture between the scapula and the coracoid plate can not be observed. Moreover it is impossible to check for the presence of one or two coracoids. Nevertheless, well-preserved caseid specimens lack sutures between the elements of the scapulocoracoid. The presence of two coracoids is only hypothetical, as already recognized by Olson (1968: 258) who stated “the existence of the two coracoids, thus, is merely conjectural, based on the condition of other pelycosaurs”.

Concerning the partial left ulna, only its distal head and the distal portion of the axis are preserved. The head, with a sub-crescentic distal outline, is somewhat flattened and wide in a typical pelycosaurian fashion (Reisz 1986). The dorsal surface is better preserved, compared to the ventral one, and shows rugosity and strong tubercles that probably indicate the origins of ligamentous connections to the forefoot elements (Olson 1968). The articular surface for the pisisform, ulnare and intermedium is wide and deep, with only the intermedium's portion of the surface visible in dorsal view. The preserved bone shows the greatest thickness at the level of the articular surface and thins proximally. The lateral margin of the preserved axis is nearly straight while the medial margin is gently concave in outline to face inwardly the left radius.

The preserved foot bones are: one mesopodial fragment, three metapodials, five non-ungual and three unguis phalanges. Taken as a whole, the foot was very large and formed by bulky elements. The mesopodial is flat sub-discoid in shape and shows a particularly cancellous internal structure. Metapodials, distally and proximally expanded, show large and sloping articular surfaces. One phalanx (the one found articulated with the metapodial) is wider proximally than distally, where it is characterized by a crescentic termination. The other

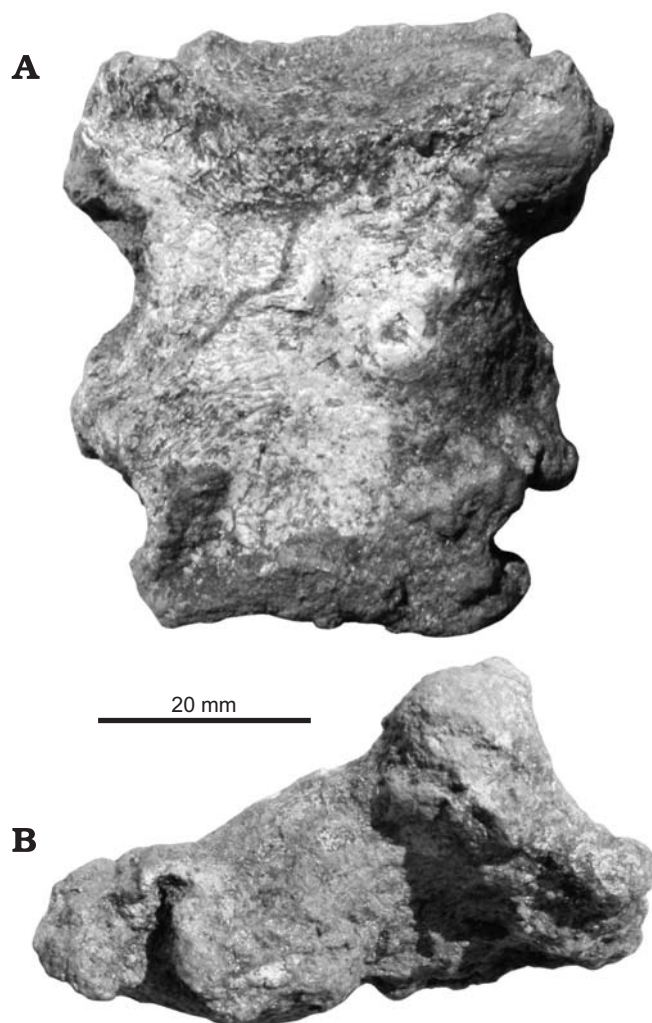


Fig. 11. Caseid pelycosaur cf. *Cotylorhynchus* sp. from Cala del vino Formation, Permian: Late Kungurian–Roadian; NW Sardinia, Italy. Non-ungual phalanx (MPUR 151/4), in dorsal (A) and left lateral (B) views.

non-ungual phalanges are as long as wide and bear, proximally and distally, strongly developed accessory scars for the tendon insertion (Fig. 11). All the non-ungual phalanges are characterized by sloping articular surfaces. The best preserved unguis (MPUR 151/41) is triangular in outline and claw-shaped (Fig. 12), gently curved downward, with a strong flexor tubercle and a longitudinal groove for blood vessel on each side. The massive construction, the sloping articular surfaces and the strong tubercle on the unguis phalanges are typical of caseids (Reisz 2005). The protruding and massive flexor tubercle on the ventral surface of the unguis phalanx permits good morphological comparison with *Cotylorhynchus* (Maddin and Reisz 2007), *Casea* and, to a lesser extent, with *Oromycter*. In particular, unguis MPUR 151/41 is strikingly similar in shape to FMNH PR 272 (catalogued as *Cotylorhynchus romeri*), even though their dimensions are quite different, and the non-ungual MPUR 151/2 is comparable to IV 1 and III 1 of FMNH UR 836 (catalogued as *Cotylorhynchus bransoni*), although the latter are a little more slender.

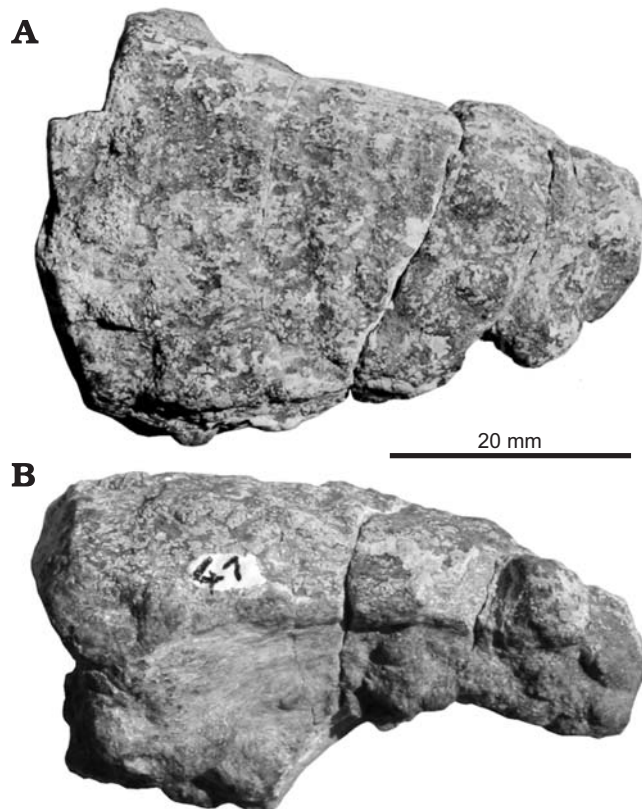


Fig. 12. Caseid pelycosaur cf. *Cotylorhynchus* sp. from Cala del vino Formation, Permian: Late Kungurian–Roadian; NW Sardinia, Italy. Claw-shaped phalanx (MPUR 151/41), in dorsal (A) and right lateral (B) views.

Metapodial MPUR 151/1 resembles Mt IV of FMNH UR 988, UR 836 and UR 905 catalogued as *Cotylorhynchus bransoni*, and also resembles that of FMNH PR 272 (catalogued as *C. romeri*) even if more medially compressed, while is completely unlike that of the other bones of the carpus and tarsus. If MPUR 151/1 actually is a Mt IV, the observed differences suggest unexpectedly high variability of the genus or a still unknown new taxon.

In conclusion, preserved characteristics of specimen MPUR 151, in particular the unique morphology of the pedal bones, are completely sufficient for its identification as a caseid. Caseids phalangeal elements are highly apomorphic, differing radically from those observed in other pelycosaurs (Romer and Price 1940). The massive and short phalanges in MPUR 151, their proximal and distal expansion, the presence of distal accessories scars for tendon insertion and the strongly tilted articular surfaces, not perpendicular to the bone axis, represent certain exclusive synapomorphies of Caseidae (see Reisz 2005: 909). The very large and bulky skeletal elements of the Sardinian specimen preclude reference to the small and lightly built caseids *Casea*, *Caseoides*, *Oromycter*, and *Ennatosaurus*, which are less than half as large in linear dimensions. Among Caseidae, only *Cotylorhynchus* and *Angelosaurus* are morphologically and dimensionally comparable to the specimen under study. However, the short, wide and smooth unguals of

Angelosaurus, which are hoof-like rather than claw-shaped, suggest that *Angelosaurus* can be excluded as well.

Based on foregoing consideration, the Sardinian specimen, a gigantic pelycosaur with a total estimated length of nearly 6 m, could be ascribed either to one of the known species of *Cotylorhynchus* or to a closely related new taxon.

Stratigraphic and palaeobiogeographic inferences

Age attribution.—It is worth noting, as a prefatory comment, that both Sigogneau-Russell and Russell (1974) and Reisz (1986) commented on the need to re-evaluate the species of caseids. Indeed, Sigogneau-Russell and Russell (1974), in establishing *Casea rutena*, reviewed literature and cast grave doubt on the validity of some caseid taxa (particularly the ones established only on the basis of dimensional differences), indirectly suggesting that significant lumping or synonymization is called for. More or less the same opinion was shared by Reisz (1986: 60), who stated “These species [of *Cotylorhynchus*] should be restudied thoroughly ...” and that “It is likely that further studies of this important taxon will result in the synonymy of the three species”. Re-examination of all fossils ascribed to Caseidae is thus strongly in need, though there is general agreement as to composition of the family and the validity of most genera.

Regardless of the validity of individual species, specimens referred to Caseidae have been reported from a small number of horizons in North America, in Western and Central Europe, and in Russia. Among caseids, the taxa that can be compared to the Sardinian one are, presently, limited to the known North American large caseids (*Cotylorhynchus*), which are important constituents of the Redbankian LVF and of the Littlecrotonian LVF, in the North American Land Vertebrate faunochrons (Lucas 2006). The occurrence of large caseids can be either ascribed to the Sakmarian to Wordian interval (in agreement with Reisz and Laurin 2001) or to the Kungurian (pro parte) and Roadian (Lucas 2006), or restricted to the interval Sakmarian to Kungurian, according to Lucas (2002), Kemp (2006) and Maddin et al. (2008). These different interpretations seem to depend, at least partially, on the questioned age of the Chickasha Formation, considered late Kazanian (Roadian, Wordian pro parte) in Reisz and Laurin (2001, 2002) but “base Guadalupian” (?Roadian) in Lucas (2002) and uppermost Lower Permian in Modesto et al. (2001).

Only four caseids are currently known from the Western Europe:

(1) A still undescribed caseid (Maddin et al. 2008) is present at the Early Permian site of Bromacker (Tambach Formation, central Germany).

(2) The small *Casea rutena* comes from the “Saxonian” beds of the Rodez Basin (southern France; Sigogneau-Russell and Russell 1974), and a second larger taxon from the

same basin is presently under study (Sébastien J. Steyer, personal communication 2009); their stratigraphic position is still unclear.

(3) A taxon described only as a “3-m-long caseid pelycosaur, similar to *Cotylorhynchus*” (Lucas et al. 2006: 4), thus definitely smaller than the Sardinian specimen, was recently found at the classic site of Lodève (Hérault, southern France), “higher in that section (in respect to the La Lieude tracksite)” (Lucas et al. 2006: 4). The deposits in question are definitely post-Cisuralian but still below the Illawarra reversal (Marc Durand, personal communication 2009).

All that considered, a late Kungurian–Roadian age is suggested as the most probable for the Sardinian specimen, which thus assumes great relevance in constraining the age of the fossil bearing level at the Torre del Porticciolo section, to a time interval not younger than Roadian.

Regional correlation.—Assuming a late Kungurian–Roadian time interval for the Cala del Vino Formation and considering the late Induan?–Olenekian age attributed to the basal conglomerate of the succeeding Triassic cycle (Cassinis et al. 2003), a very long gap is thus evidenced between the sediments of the Permian cycle and the overlying Triassic deposits.

At this juncture it is worth briefly reviewing the chronostratigraphic framework of the terrigenous Permian rocks of Italy and southern France, which comprise the entire Alpine and Central Mediterranean area.

As a whole, few reliable calibration points are available from the Late Paleozoic continental deposits cropping out in the Alpine and Central Mediterranean areas. In the Alpine region, stratigraphically meaningful data consist of scattered sporomorph associations and a few invertebrate and vertebrate fossils. In particular, land vertebrates are quite rare (Nicosia et al. 2005) and we can only list: a beautiful but biochronologically useless specimen of which only the outline of the soft tissues is well preserved (*Tridentinosaurus antiquus* Dal Piaz in Leonardi 1959) from a tuffaceous bed inside the Athesian Porphyric Complex (Nicosia et al. 2005); some tetrapod footprint-bearing levels within the Collio Formation, from different basins in the Central and Southern Alps (Ceoloni et al. 1987; Nicosia et al. 2000; Avanzini et al. 2008), and the well known tetrapod footprint association from the Arenaria di Val Gardena (Conti et al. 1977; Nicosia et al. 2005).

The Early Permian footprint-bearing levels, well calibrated by isotopic dating of the interdigitating and overlying volcanic units, were formed in a time interval between about 283 Ma and 277 Ma (Avanzini et al. 2008) and up to 274 Ma (Marocchi et al. 2008). These levels thus range from Sakmarian (pro parte) to Kungurian.

The Late Permian tetrapod ichnoassociation of the Arenaria di Val Gardena comes from sedimentary units laid down after the Illawarra Reversal Event (≈ 265 Ma), and referred, by sporomorphs, by the overlying fusulinid bearing beds and by sequence stratigraphy, to the Wuchiapingian

(Massari et al. 1988; Nicosia et al. 2005; Valentini et al. 2009). Thus, a gap of variable but significant extent (approximately between 274 and 258 Ma) is present in the fossil record of the Alpine region as a whole (Cassinis et al. 2000; Cassinis and Perotti 2007).

In Sardinia Late Paleozoic calibration elements are also few: tetrapod footprints were found from the Upper Carboniferous (Stephanian) sediments of the San Giorgio basin (Conti et al. 2004); and Early Permian “branchiosaurs” are known from the Rio su Luda Formation in the Perdasefogu basin (Ronchi and Tintori 1997; Ronchi et al. 1998; Werneburg et al. 2007). The latter fossils formed the basis for significant biostratigraphic and paleobiogeographic correlations with the Thuringian Forest Basin (Germany). The already cited “Autunian” plant remains were reported from the Nurra deposits and from many other continental basins in the central, SE and SW part of the island (see the review of Broutin and Ronchi in Cassinis et al. 2000 and Ronchi et al. 2008b).

From the basins of Southern France, palaeogeographically and lithostratigraphically correlated to northern Sardinia, two occurrences are critical to chronostratigraphical assessment, both concerning ages estimated on the basis of ichnological data.

According to Durand (2006, 2008), an ichnoassemblage from the Les Pradineaux Formation (in literature tentatively correlated to the Saint-Mandrier Formation, which is correlated, in turn, to the Cala del Vino Formation), from a site near the town of Saint-Raphaël, reveals a stage of evolution more advanced than the Early Permian (Cisuralian) ones (Gand and Durand 2006) of the Lodève Basin, which have been studied in detail (Gand et al. 2000). Through the occurrence of some tracks ascribed to therapsids (i.e., *Lunaepes* and *Planipes*), the ichnoassociation could be referred to the “tapinocephalid stage”, corresponding to the North American Roadian and Wordian (Cassinis et al. 2002a). From the revision of all the previous age determinations, Durand (2006; 2008), taking into account also palaeobotanical and palynological data, as well as an ostracod association, concluded that the Pradineaux Formation as a whole could be of Wordian age. A Middle Permian age was also ascribed to that ichnoassociation by Valentini et al. (2009), by correlation with similar tracks from the South African *Tapinocephalus* Assemblage Zone.

A second ichnoassemblage was uncovered from the Gonfaron site, within the La Motte Formation, the uppermost unit in the Bas-Argens basin (also called the Fabregas Formation, Gonfaron Formation or Pelitic Formation in the other Provence basins). This track assemblage has been considered Middle Permian in age by Gand and Durand (2006) and by (Durand 2006). A Roadian age was ascribed to the tentatively correlated Saint-Mandrier Formation by Durand (2008).

As stated above, on the base of the specimen reported herein a late Kungurian to Roadian age could be ascribed to the Cala del Vino Formation. Thus, accepting the lithostratigraphic correlation between the fossil bearing unit and the Saint-Mandrier Formation (correlated in turn to the Pradineaux Formation from the Bas-Argens and Estérel Permian

basins), a Wordian age has to be considered as doubtful for the deposits cropping out in basins of southern France.

Durand (2006, 2008) stated that the sub-Triassic unconformity represents, in Provence, a hiatus probably as long as 10–15 Ma, encompassing at least the entire Lopingian and the majority of the Induan. In the light of the new discovery, this gap must be increased (at least in NW Sardinia) to include the most of the Middle Permian.

Taking into consideration all the data, the same large gap below the Triassic cycle sediments, signaled by Cassinis et al. (2000) in the Alps and by Durand (2006) in Provence, now seems to be also present in Sardinia and in most of the successions in the western Mediterranean area. It includes, at least, a large part of the Middle Permian and the entire Late Permian, ranging from around 270 Ma to nearly 248 Ma. At present, the only known exception is represented by the Wuchiapingian Arenaria di Val Gardena of the Southern Alps (Valentini et al. 2009).

Palaeobiogeography.—The new discovery is important palaeobiogeographically because it expands known range of caseids to the Mediterranean area. Thus, a land connection between North America and southern Europe during the late Kungurian–Roadian is suggested. The existence of such a route for faunal interchange has already been proposed by Sumida et al. (1996) for the Sakmarian and by Reisz and Laurin (2001) for the Wordian. Consistently, the structural and environmental continuity between these land areas, already suggested on the base of shared ichnoassociations (Avanzini et al. 2001), is substantiated for the whole Early Permian and for most of the Middle Permian.

Conclusions

The presence of a huge caseid in the Nurra Permian deposits, the first uncovered in Italy and the fifth in all of the Western Europe (considering also the much smaller forms), represents an important source of information and allows some inferences with respect to the generally poor fossil vertebrate record in Palaeozoic continental sediments (Reisz and Laurin 2001). The new finding represents in fact a decisive biostratigraphic constraint to fix the age of Cala Del Vino Formation, previously referred to “undefined Late Permian (Tatarian) times” (Cassinis et al. 2003) and even to an Early Triassic “Buntsandstein” (Sciunnach 2001, Costamagna and Barca 2002), as being late Kungurian–Roadian. This age is consistent with biostratigraphic results gathered in the Permian rocks of the Provence basins, and confirms the validity of the correlations proposed by Cassinis et al. (2003) on purely sedimentological criteria.

The new discovery allows also to better define the time of occurrence of caseids in Western Europe and to confirm continuity in the terrestrial environment between North America and Europe for the whole Early Permian and for the most of the Middle Permian: a continuity necessary for migration of land dwelling animals.

Acknowledgements

We are grateful to Marco Morandotti and Enrico Bortoluzzi (students of Pavia University, Pavia, Italy) for bringing the vertebrate remains to our attention. We are deeply indebted to Luciano A. Trebini (Soprintendenza Archeologica per la Sardegna, Sassari, Italy) for its assistance both in the field and in the sea of bureaucracy. The Soprintendenza Archeologica di Sassari kindly gave us the authorization to the study. Francesco Battista, Paolo Citton, Teresa Coppola, Giovanni Gaglianone, Claudia Leoncini, Riccardo Manni, and Massimo Santantonio of “Sapienza” (University of Rome, Rome, Italy) are acknowledged for their help during field work. Kenneth D. Angielczyk, Olivier C. Rieppel, and William F. Simpson are warmly acknowledged for the kind reception of some of us (ES, MR) at the Field Museum (Chicago, USA). ES and MR are grateful to Richard L. Cifelli and Kyle L. Davies for the help during their visit to the Sam Noble Oklahoma Museum. Sébastien J. Steyer actively supported our visit to the specimens at the Museum national d’Histoire naturelle, Paris. Sean Modesto (Cape Breton University, Sydney, Nova Scotia) and Stuart S. Sumida (California State University, S. Bernardino, USA) gave us their invaluable help with suggestions, literature and showing more than a normal interest. Simone Maganuco (Museo di Storia Naturale, Milano, Italy) is also acknowledged for his suggestions and Giacomo Oggiano (Università degli Studi di Sassari, Sassari, Italy) for sharing his fundamental knowledge of the geology of the area. This manuscript was greatly improved by the constructive reviews of Giuseppe Cassinis (University of Pavia, Pavia, Italy) and Marc Durand (Université Henri Poincaré, Nancy, France). ES was partially supported by a scholarship of the Field Museum of Natural History of Chicago. The research was partially supported by MIUR funds (PRIN 2008, resp. Giacomo Oggiano).

References

- Avanzini, M., Ceoloni, P., Conti, M.A., Leonardi, G., Manni, R., Mariotti, N., Mietto, P., Muraro, C., Nicosia, U., Sacchi, E., Santi, G., and Spezzamonte, M. 2001. Permian and Triassic tetrapod ichnofaunal units of northern Italy, their potential contribution to continental biochronology. *Natura Bresciana, Monografia* 25: 89–107.
- Avanzini, M., Neri, C., Nicosia, U., and Conti, M.A. 2008. A new Early Permian ichnocoenosis from the “Gruppo Vulcanico Atesino” (Mt. Luco, southern Alps, Italy). *Studi Trentini Scienze Naturali Acta Geologica* 83: 213–236.
- Bandyopadhyay, S., Roy Chowdhury, T.K., and Sengupta, D.P. 2002. Taphonomy of some Gondwana vertebrate assemblages of India. *Sedimentary Geology* 147: 219–245.
- Behrensmeyer, A.K. 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4: 150–162.
- Broutin, J., Calsia, P., and Ronchi, A. 2000. Paleontological data. In: G. Cassinis, L. Cortesogno, L. Gaggero, P. Pittau, A. Ronchi, and E. Sarria (eds.), *Late Paleozoic Continental Basin of Sardinia. Field Trip Guidebook. 15–25 Sept. 1999*, 90. Pavia University, Brescia.
- Broutin, J., Cassinis, G., Cortesogno, L., Gaggero, L., Ronchi, A., and Sarria, E. 1996. Research in progress on the Permian deposits of Sardinia (Italy). *Permophiles* 28: 45–48.
- Broutin, J., Châteauneuf, J.J., Galtier, J., and Ronchi, A. 1999. L’Autunien d’Autun reste-t-il une référence pour les dépôts continentaux du Permien inférieur d’Europe? *Géologie de la France* 2: 17–31.
- Buzzi, L., Gaggero, L., and Oggiano, G. 2008. The Santa Giusta ignimbrite (NW Sardinia): a clue for the magmatic, structural and sedimentary evolution of a Variscan segment between Early Permian and Triassic. *Bollettino della Società Geologica Italiana* 127: 683–695.
- Carroll, R.L. 1988. *Vertebrate Paleontology and Evolution*. 698 pp. W.H. Freeman and Company, New York.
- Cassinis, G. and Perotti, C. R. 2007. A stratigraphic and tectonic review of

- the Italian Southern Alpine Permian. In: Q. Yang and D.H. Ervin (eds.), Contributions to Permian and Carboniferous Stratigraphy, Brachiopod Palaeontology and End-Permian Mass Extinction in Memory of Professor Yu-Gan Jin. *Paleoworld* (Special Issue) 16: 140–172.
- Cassinis, G. and Ronchi, A. 2000. General stratigraphy. In: G. Cassinis, L. Cortesogno, L. Gaggero, P. Pittau, A. Ronchi, and E. Sarria (eds.), *Late Paleozoic Continental Basin of Sardinia. Field Trip Guidebook 15–25 Sept. 1999*, 25–26. Pavia University, Brescia.
- Cassinis, G., Cortesogno, L., Gaggero, L., and Ronchi, A. 2000. Permian Sardinian Basin—An overview. In: G. Cassinis, L. Cortesogno, L. Gaggero, P. Pittau, A. Ronchi, and E. Sarria (eds.), *Late Paleozoic Continental Basin of Sardinia. Field Trip Guidebook. 15–25 Sept. 1999*, 19–20. Pavia University, Brescia.
- Cassinis, G., Cortesogno, L., Gaggero, L., Ronchi, A., and Valloni, R. 1996. Stratigraphic and petrographic investigations into the Permian–Triassic continental sequences of Nurra (NW Sardinia). *Cuadernos de Geología Ibérica* (Special Issue) 21: 149–169.
- Cassinis, G., Durand, M., and Ronchi, A. 2002b. The Permian and Triassic continental framework of Nurra (NW Sardinia). *Rendiconti della Società Paleontologica Italiana* 1: 297–305.
- Cassinis, G., Durand, M., and Ronchi, A. 2003. Permian–Triassic continental sequences of Northwest Sardinia and South Provence: stratigraphic correlations and palaeogeographical implications. *Bollettino della Società Geologica Italiana* (Volume speciale) 2: 119–129.
- Cassinis, G., Nicosia, U., Lozovsky, V.R., and Gubin, Y.M. 2002a. A view of the Permian continental stratigraphy of the Southern Alps, Italy, and general correlation with the Permian of Russia. *Permophiles* 40: 4–16.
- Costamagna, L.G. and Barca, S. 2002. The “Germanic” Triassic of Sardinia (Italy): a stratigraphical, depositional and palaeogeographic review. *Rivista Italiana di Paleontologia e Stratigrafia* 108: 67–100.
- Ceoloni, P., Conti, M.A., Mariotti, N., Mietto, P., and Nicosia, U. 1987. Tetrapod footprints from Collio Fm. (Lombardy, Northern Italy). *Memorie di Scienze Geologiche* 39: 213–233.
- Conti, M.A., Leonardi, G., Mariotti, N., and Nicosia, U. 1977. Tetrapod footprints from the “Arenarie di Val Gardena” (North Italy). Their paleontological, stratigraphic and palaeoenvironmental meaning. *Paleontographia Italica* 70: 1–91.
- Conti, M.A., Nicosia, U., Petti, F.M., Pillola, G.L., Piras, S., Sacchi, E., and Zoboli, D. 2004. Italy’s earliest tetrapod footprints: the Sardinian Upper Carboniferous ichnofaunas. *32nd International Geological Congress, Florence, Italy, 20–28 August 2004*, 599. Nuova Cesat, Florence.
- Durand, M. 2006. The problem of transition from the Permian to the Triassic series in southeastern France: comparison with other Peritethyan regions. In: S.G. Lucas, G. Cassinis, and J.W. Schneider (eds.), Non-marine Permian Biostratigraphy and Biochronology. *Geological Society Special Publication, London* 265: 281–296.
- Durand, M. 2008. Permian to Triassic continental successions in southern Provence (France): an overview. *Bollettino della Società Geologica Italiana* 127: 697–716.
- Edel, J.B., Montigny, R., and Thuizat, R. 1981. Late Palaeozoic rotations of Corsica and Sardinia: new evidence from paleomagnetic and K–Ar studies. *Tectonophysics* 79: 201–223.
- Fontana, D., Neri, C., Ronchi, A., and Stefani, C. 2001. Stratigraphic architecture and composition of the Permian and Triassic siliciclastic succession of Nurra (north-western Sardinia). In: G. Cassinis (ed.), Permian Continental Deposits of Europe and Other Areas. Regional Reports and Correlations. «Natura Bresciana», *Annali del Museo Civico di Scienze Naturali di Brescia, Monografia* 25: 149–161.
- Gand, G. and Durand, M. 2006. Tetrapod footprint ichno-associations from French Permian basins. Comparisons with other Euramerican ichnofaunas. In: S.G. Lucas, G. Cassinis, and J.W. Schneider (eds.), Non-Marine Permian Biostratigraphy and Biochronology. *Geological Society Special Publications, London* 265: 157–177.
- Gand, G., Garric, J., Demathieu, G., and Ellenberger, P. 2000. La palichnofaune de vertébrés tétrapodes du Permien supérieur du bassin de Lodève (Languedoc, France). *Paleovertebrata* 29: 1–82.
- Gasperi, G. and Gelmini, R. 1980. Ricerche sul Verrucano. 4. Il Verrucano della Nurra (Sardegna nord-occidentale). *Memorie della Società Geologica Italiana* 20 (for 1979): 215–231.
- Ghinassi, M., Durand, M., Ronchi, A., and Stefani, C. 2009. Permian–Middle Triassic continental succession of NW Sardinia. In: V. Pascucci and S. Andreucci (eds.), *Field-trip Guidebook, 27th IAS Meeting of Sedimentology, Alghero, Italy 20–23 Sept. 2009*, 37–50. Edes, Sassari.
- Gonzalez-Riga, B.J. and Astini, R.A. 2007. Preservation of large titanosaur sauropods in overbank fluvial facies: A case study in the Cretaceous of Argentina. *Journal of South American Earth Sciences* 23: 290–303.
- Holz, M. and Barberena, M.C. 1994. Taphonomy of the south Brazilian Triassic paleoherpetafauna: pattern of death, transport and burial. *Palaeogeography, Palaeoclimatology, Palaeoecology* 107: 179–197.
- Ivakhnenko, M.F., Golubev, V.K., Gubin, Y.M., Kalandadze, N.N., Novikov, I.V., Sennikov, A.G., and Rautian, A.S. 1997. *Permian and Triassic Tetrapods of Eastern Europe*. 216 pp. GEOS, Moscow.
- Kemp, T.S. 2006. The origin and early radiation of the therapsid mammal-like reptiles: a palaeobiological hypothesis. *Journal of Evolutionary Biology* 19: 1231–1247.
- Lee Lyman, R. 2010. What taphonomy is, what it isn’t, and why taphonomists should care about the difference. *Journal of Taphonomy* 8 (1): 1–16.
- Leonardi, P. 1959. *Tridentinosaurus antiquus* Gb. Dal Piaz, rettile protosauro permiano del Trentino orientale. *Memorie di Scienze Geologiche* 21: 3–15.
- Lombardi, G., Cozzupoli, D., and Nicoletti, M. 1974. Notizie geopetrografiche e dati sulla cronologia K–Ar del vulcanismo tardopaleozoico sardo. *Periodico di Mineralogia* 43: 221–312.
- Lucas, S.G. 2002. The reptile *Macroleter*. First vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia: Discussion. *Geological Society of American Bulletin* 114: 1174–1175.
- Lucas, S.G. 2006. Global Permian tetrapod biostratigraphy and biochronology. In: S.G. Lucas, G. Cassinis, and J.W. Schneider (eds.), Non-Marine Permian Biostratigraphy and Biochronology. *Geological Society Special Publications, London* 265: 65–93.
- Lucas, S.G., Cassinis, G., and Schneider, J.W. 2006. Non-marine Permian biostratigraphy and biochronology: an introduction. In: S.G. Lucas, G. Cassinis, and J.W. Schneider (eds.), Non-Marine Permian Biostratigraphy and Biochronology. *Geological Society Special Publications, London* 265: 1–14.
- Maddin, H. and Reisz, R.R. 2007. The morphology of the terminal phalanges in Permo–Carboniferous synapsids: an evolutionary perspective. *Canadian Journal of Earth Sciences* 44: 267–274.
- Maddin, H., Sidor, C.A., and Reisz, R.R. 2008. Cranial anatomy of *Ennatosaurus tecton* (Synapsida: Caseidae) from the Middle Permian of Russia and the evolutionary relationships of Caseidae. *Journal of Vertebrate Paleontology* 28: 160–180.
- Marocchi, M., Morelli, C., Mair, V., Klotzli, U., and Bargossi, G.M. 2008. Evolution of large silicic magma systems: New U–Pb zircon data on the NW Permian Athesian Volcanic Group (Southern Alps, Italy). *Journal of Geology* 116: 480–498.
- Massari, F., Conti, M.A., Fontana, D., Helmold, K., Mariotti, N., Neri, C., Nicosia, U., Ori, G.G., Pasini, M., and Pittau, P. 1988. The Val Gardena Sandstone and Bellerophon Formation in the Bletterbach Gorge (Alto Adige, Italy): biostratigraphy and sedimentology. *Memorie di Scienze Geologiche* 40: 229–273.
- Modesto, S., Sidor, C.A., Rubidge, B.S., and Welman, J. 2001. A second varanopseid skull from the Upper Permian of South Africa: implications for Late Permian “pelycosaur” evolution. *Lethaia* 34: 249–259.
- Nicosia, U., Avanzini, M., Barbera, C., Conti, M.A., Dalla Vecchia, F.M., Dal Sasso, C., Delfino, M., Gianolla, P., Leonardi, G., Loi, M., Mietto, P., Morsilli, M., Paganoni, A., Petti, F.M., Piubelli, D., Raia, P., Renesto, S., Ronchi, A., Sacchi, E., Santi, G., and Signore, M. 2005. I vertebrati continentali del Paleozoico e del Mesozoico. In: L. Bonfiglio (ed.), *Paleontologia dei Vertebrati in Italia*, 41–66. Museo Civico di Storia naturale di Verona, Verona.
- Nicosia, U., Ronchi, A., and Santi, G. 2000. Permian tetrapod footprints from W Orobic Basin (Northern Italy). Biochronological and evolutionary remarks. *Geobios* 33 (6): 753–768.

- Olson, E.C. 1954. Fauna of the Vale and Choza: 7. Pelycosauria, Family Caseidae. *Fieldiana: Geology* 10: 193–204.
- Olson, E.C. 1955. Parallelism in the evolution of the Permian reptilian fauna of the Old and New Worlds. *Fieldiana: Zoology* 37: 385–401.
- Olson, E.C. 1962. Late Permian terrestrial vertebrates, USA and USSR. *American Philosophical Society Transaction* (new series) 52: 1–224.
- Olson, E.C. 1968. The family Caseidae. *Fieldiana: Geology* 17: 225–349.
- Olson, E.C. and Barghusen, H. 1962. Permian vertebrates from Oklahoma and Texas. *Oklahoma Geological Survey Circular* 59: 5–48.
- Olson, E.C. and Beerbower, J.R. Jr. 1953. The San Angelo Formation, Permian of Texas, and its vertebrates. *Journal of Geology* 61: 381–423.
- Osborn, H.F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs of the American Museum of Natural History* 1: 449–507.
- Pecorini, G. 1962. Nuove osservazioni sul Permico della Nurra (Sardegna nord-occidentale). *Atti Accademia Nazionale dei Lincei, Rendiconti Classe di Scienze Fisiche, Matematiche e Naturali* 32: 377–380.
- Pérez, L.M., Otero, A., Apesteguía, S., and Gallina, P.A. 2009. Estratigrafía y análisis tafonómico de *Bonitasaura salgadoi* Apesteguía, en el sitio “La Bonita” (Cretácico superior, Río Negro, Argentina). *Revista Museo Argentino Ciencias Naturales* (new series) 11: 39–48.
- Pittau, P. and Del Rio, M. 2002. Palynofloral biostratigraphy of the Permian and Triassic sequences of Sardinia. *Rendiconti della Società Paleontologica Italiana* 1: 93–109.
- Pomesano Cherchi, A. 1968. Studio bio-stratigrafico del sondaggio Cugiarreddu nel Trias e Permico della Nurra (Sardegna nord-occidentale). *Pubblicazione dell'Istituto di Geologia e Paleontologia dell'Università di Cagliari* 61: 7–51.
- Reisz, R.R. 1986. Pelycosauria. In: P. Wellnhofer (ed.), *Handbuch der Paläohelvetologie* 17A. 102 pp. Gustav Fischer Verlag, Stuttgart.
- Reisz, R.R. 2005. *Oromycter*, a new caseid from the Lower Permian of Oklahoma. *Journal of Vertebrate Paleontology* 25: 905–910.
- Reisz, R.R. and Laurin, M. 2001. The reptile *Macroleter*: First vertebrate evidence for correlation of Upper Permian continental strata of North America and Russia. *Geological Society of America Bulletin* 113: 1229–1233.
- Reisz, R.R. and Laurin, M. 2002. Reply. *Geological Society of America Bulletin* 114: 1176–1177.
- Romer, A.S. 1956. *Osteology of the Reptiles*. 772 pp. The University of Chicago Press, Chicago.
- Romer, A.S. and Price, L.I. 1940. Review of the Pelycosauria. *Geological Society of America* (Special Paper) 28: 1–538.
- Ronchi, A. and Tintori, A. 1997. First amphibian find in Early Permian from Sardinia (Italy). *Rivista Italiana di Paleontologia e Stratigrafia* 103 (1): 29–38.
- Ronchi, A., Broutin, J., Diez J.-B., Freytet, P., Galtier, J., and Lethiers, F. 1998. New paleontological discoveries in some Early Permian sequences of Sardinia. Biostratigraphic and paleogeographic implications. *Comptes Rendus de l'Académie des Sciences, Paris* 327: 713–718.
- Ronchi, A., Manni, R., Sacchi, E., Nicosia, U., Citton, P., Coppola, T., Romano, M., Bortoluzzi, E., and Trebini, L.A. 2008a. First large vertebrate find in the Permian deposits of Nurra (NW Sardinia). 84° Congresso Società Geologica Italiana, Sassari, September 15–17, 2008. *Rendiconti Online Società Geologica Italiana* 3: 689.
- Ronchi, A., Sarria, E., and Broutin, J. 2008b. The “Autuniano Sardo”: basic features for a correlation through the Western Mediterranean and Paleoeurope. *Bollettino della Società Geologica Italiana* 127: 655–681.
- Sciunnach, D. 2001. Heavy mineral provinces as a tool for palaeogeographic reconstruction: A case study from the Buntsandstein of Nurra (NW Sardinia, Italy). *Eclogae Geologicae Helvetiae* 94: 197–211.
- Sciunnach, D. 2002. The Permo-Triassic clastics of Nurra: sedimentology, heavy mineral provinces and palaeogeography. *Rendiconti della Società Paleontologica Italiana* 1: 177–184.
- Sigogneau-Russell, D. and Russell, D.E. 1974. Étude du premier Caséidé (Reptilia, Pelycosauria) d'Europe occidentale. *Bulletin du Muséum National d'Histoire Naturelle* 230: 145–215.
- Stovall, J.W. 1937. *Cotylorhynchus romeri*, a new genus and species of pelycosaurian reptile from Oklahoma. *American Journal of Science* 34: 308–313.
- Stovall, J.W., Price, L.I., and Romer, A.S. 1966. The postcranial skeleton of the giant Permian pelycosaur *Cotylorhynchus romeri*. *Bulletin of the Museum of Comparative Zoology* 135: 1–30.
- Sumida, S. and Modesto, S. 2001. A phylogenetic perspective on locomotory strategies in early amniotes. *American Zoologist* 41: 568–597.
- Sumida, S., Berman, D., and Martens, T. 1996. Biostratigraphic correlations between the Lower Permian of North America and Central Europe using the first record of an assemblage of terrestrial tetrapods from Germany. *PaleoBios* 17 (2–4): 1–12.
- Valentini, M., Nicosia, U., and Conti, M.A. 2009. A re-evaluation of *Pachypes*, a pareiasaurian track from the Late Permian. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 251: 71–94.
- Vardabasso, S. 1966. Il Verrucano sardo. *Atti del Symposium sul Verrucano, Pisa, settembre 1965*, 293–310. Società Toscana di Scienze Naturali, Pisa.
- Voorhies, M. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. *Contributions to Geology* (Special Paper) 1: 1–69.
- Werneburg, R., Ronchi, A. and Schneider, J.W. 2007. The Early Permian branchiosaurids (Amphibia) of Sardinia: Systematic palaeontology, palaeoecology, biostratigraphy and palaeobiogeographic problems. *Palaeogeography, Palaeoclimatology, Palaeoecology* 252: 383–404.
- Williston, S.W. 1910. New Permian reptiles: rhachitinous vertebrae. *Journal of Geology* 18: 585–600.
- Williston, S.W. 1912. Primitive reptiles. *Journal of Morphology* 23: 637–666.
- Williston, S.W. 1913. The skulls of *Araucoscelis* and *Casea*, Permian reptiles. *Journal of Geology* 21: 743–747.