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FIRST AMPHIBIAN FIND IN EARLY PERMIAN FROM SARDINIA (ITALY)

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Riassunto. Viene segnalata per la prima volta in Italia una fauna a vertebrati d'acqua dolce di età Permo-Carbonifera. Il ritrovamento, effettuato nel bacino di Perdasdefogu (Sardegna), consiste essenzialmente di anfibi branchiosauri, forme dotate di branchie esterne, rinvenuti in grande quantità in un livello di pochi centimetri di spessore.

L'attribuzione di tali esemplari alla specie *Branchiosaurus* cf. *"B." petrolei* (Gaudry 1875), forma tipica dei bacini della Francia centrale, conferma l'appartenenza del blocco Sardo-Corso al medesimo bacino idrografico dell'attuale Europa continentale, senza alcun braccio marino interposto. Alcuni episodi di mortalità di massa sono stati individuati facendo ritenere che le condizioni ambientali del bacino potessero cambiare radicalmente secondo l'andamento stagionale. Pur non costituendo oggetto della presente nota, si segnala pure la presenza di resti di squali xenacantidi e di resti di acantodi: anche in questo caso si tratta dei primi ritrovamenti italiani.

Abstract. An amphibian fauna from Permo-Carboniferous boundary beds is recorded for the first time in Italy. A thin fossiliferous level has been found in the Perdasdefogu Basin in southeastern Sardinia; it yields several specimens of *Branchiosaurus* cf. *"B." petrolei* (Gaudry 1875), often in mass mortality assemblages. Repeated mass mortality events testify to sudden changes in the environment of the basin, possibly due to seasonal variations. The finding of specimens very close to *Branchiosaurus petrolei*, which is a common species in the Central France basins, confirms that Sardinia at the time belonged to the same hydrographic basin of continental Europe, with no seaway in between. Furthermore, though not the primary focus of this note, we report the first discovery of xenacanth teeth and acanthodian spines in Italy.

Introduction.

A rich amphibian fauna is recorded from the Perdasdefogu Permian basin in southeastern Sardinia. These specimens, not previously documented in Sardinia or elsewhere on the Italian peninsula, were recovered in summer 1995 during Ph.D. field studies (A. R.). Subsequently, more detailed paleontological field work was undertaken, resulting in the collection of many other amphibians and the discovery of silicified limestone yielding xenacanth teeth, acanthodian spines, actinopterygian remains and well preserved ostracods.

Permo-Carboniferous vertebrates in Italy are rare, being mainly limited to tetrapod footprints from several Permian localities in the Alps (Ceoloni et al., 1988). Only the ichnogenus *Salichnium (Saurichnites) heringi* (Geinitz, 1885), referrable to amphibian lepospondyles, has been found (Fondi, 1980) in Upper Carboniferous (Westphalian D?) sediments of the San Giorgio Basin (Iglesiente, SW Sardinia).

This note describes only the amphibians, while studies of the xenacanths and acanthodians are still in progress.

Geological setting.

The Perdasdefogu Basin crops out over an area of about 20 Km^2 in the Ogliastra region (SE Sardinia) (Fig. 1). It corresponds to one of the intramontane troughs that formed within the island during the extentional and transtentional tectonic phases that characterized the end of the Hercynian Orogenesis (Fontana et al., 1982). The largest and best known of those Basins are the Punta Lu Caparoni in the Nurra region, the Seui-Seulo in the Barbagia region, the Perdasdefogu in the Ogliastra region, the Escalaplano and Lago di Mulargia in the Gerrei region and the San Giorgio in the Iglesiente region. The Sardinian (late)-posthercynian deposits are represented by two main sedimentary sequences. The first is mostly Autunian and partly Stephanian (documented only in the San Giorgio Basin) and the second is Permo-Triassic. A Horst and Graben tectonic style controlled the thickness of fluvio-lacustrine depositional sequences within the continental basins, with significant differences from one locality to another. Important volcanic episodes occurred at the time, both within the late Paleozoic troughs and in their external areas.

Stratigraphy of the Perdasdefogu Basin. Permian deposits occur over a wide area in the Perdasdefogu ba-

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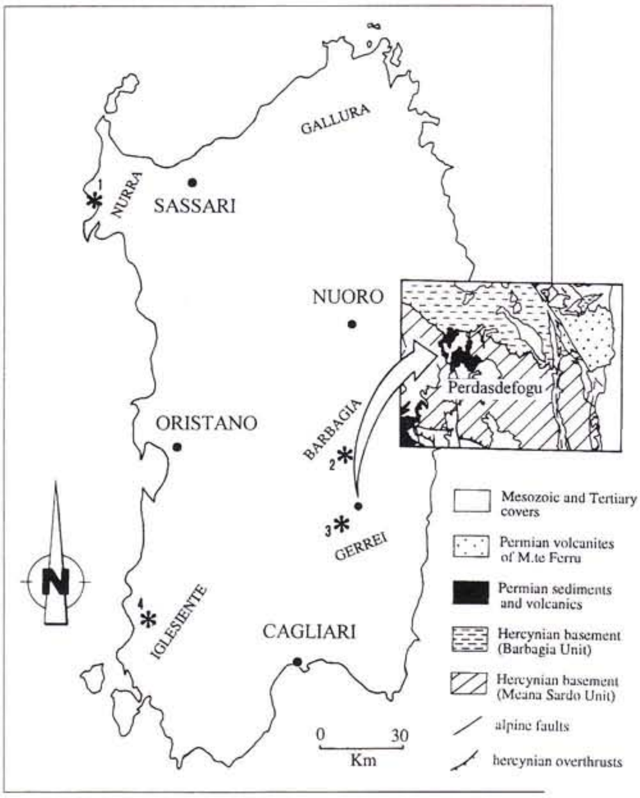


Fig. 1 - Geographical location and geological sketch map of Perdasdefogu Basin. Asteriscs showing the position of the main Permian or Permo-Carboniferous Basin in the isle: 1) Punta Lu Caparoni-Cala Viola (Nurra); 2) Seui-Seulo (Barbagia); 3) Escalaplano-Mulargia (Gerrei); 4) San Giorgio (Iglesiente).

sin, but lie mainly under Late Paleozoic volcanics or below the Jurassic dolomitic cover that protected them from erosion., as shown by recent drilling (Sarria, 1987).

The 250 to 300 m thick Permian volcanic-sedimentary sequence is subdivided, from base to top, as follows. The Hercynian metamorphic basement is unconformably covered by a clastic, fluvio-lacustrine succession beginning with a basal conglomerate and proceeding with a predominant finer clastic deposition. The basal conglomerate is mainly made up of metamorphic, scarcely elaborated clasts, eroded from the underlying crystalline units; it is always present at the base of the sequence, but it rarely exceeds a few tens of meters in thickness.

The overlying black clastic unit, typically lacustrine, is about one hundred meters thick and is made up of irregular alternating levels of black varved shales and laminated siltstone to sandstone, sometimes interrupted by thin conglomerate layers. The siltstones and shales predominate, frequently rich in organic matter and with sub-millimetrical laminae.

Volcanic breccias, sometimes with lava episodes; are frequent within this succession. Their thickness shows great vertical and lateral variations. The volcanism was contemporaneous with the sedimentation and its products probably caused the frequent silicification of the clastic sediments. Scarce fossil flora findings (Maxia, 1938) similar to those of Seui Basin (Barbagia) allow an assignment of these sediments to the Autunian. This age was confirmed by abundant fossil plant remains found by Broutin et al. (1996). The upper part of the sequence, 30 to 50 m thick, shows lacustrine gray limestones and dolostones, affected by a different degree of silicification (black "cherts" in decimetrical beds or irregular lenses are very frequent). Many centimetrical to decimetrical anthracite layers are intercalated within the siliceous-carbonatic unit. The coal-bearing intercalations have been the object of both economic exploitation for over a century as well as mining and geological studies (Binaghi e Brundo, 1928; Fois, 1939; Sarria, 1987).

A final volcanic episode, over 150 meters thick, tops the Permian sequence of the basin.

The fossiliferous level. The amphibian-bearing bed possibly belongs to the upper part of the lower lacustrine sequence; the outcrop conditions and a nearby fault make it difficult to give this thin sequence a more precise stratigraphic attribution.

The half meter succession has been subdivided into eight levels (Fig. 2) on the basis of lithology and paleontological content. From bottom to top:

A. Yellow-ochre and whitish medium-coarse sandstone. 6 cm;

B. Black, marly, varved shale and siltstone, with very thin laminae. 1 cm;

C. Yellow-gray clay. 2 cm;

D. Gray, cohesive, laminated shale and siltstone. This level yields few, scattered amphibians and some plants remains. 7.5 cm;

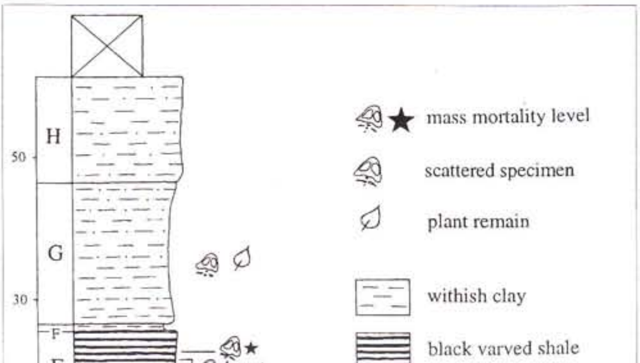


Fig. 2 - Detailed stratigraphy of the amphibian bearing beds.

E. Black coal-bearing varved shale and siltstone with very thin laminae. In this very fissile level there are at least two small layers with amphibian mass mortality multi-events. Scattered specimens have been found also throughout the bed toghether with plant remains. 9 cm;

F. Whitish clays, not laminated. 1 cm;

G. Light-gray laminated shale passing to siltstone toward the top, yielding very rare amphibians and more frequent floral remains (*Ernestiodendron filiciforme*). 20 cm;

H. Gray, laminated, well cemented shale and siltstone. 15 cm.

Paleoenvironment and taphonomy.

In the lower Permian, the European climate was tropical and characterized by the alternation of wet and dry seasons, with large temperature amplitudes (Barron & Fawcett, 1995). During the Early Permian, in the Perdasdefogu Basin there was a typical lacustrine low accumulation of fine detrital material, varved and rich in organic matter. This depositional low energy environment shows reducing (authigenic pyrite is frequently found inside diagenetic nodules, sometimes together with gypsum crystals) and probably bottom euxinic conditions. Perhaps the ancient lake was wide and with seasonally changing shorelines. The frequent variability of the unit thickness can be related to a highly uneven morphology of the bottom (Schneider 1994). Nevertheless, the plant remains and the rich ostracod fauna frequently occurring in different sequence levels, seem to indicate that the lake was mainly shallow. Fresh water ostracodes suggest that salinity did not exceed 2-3‰ (Lethiers, pers. comm.).

The lower shaly-silty part of the sequence is referrable to a swampy or shallow pond environment. The presence of *cone in cone* structures confirms a palustrine habitat rich in organic matter, a few centimeters deep, in which plants grew. Small scale slumpings have been often observed within the fine detrital deposits. In thin section they show millimetrical black volcanic glass levels alternating with white dolomitic ones. These *peperites* s.l. indicate very regular and frequent (months? years?) pyroclastic episodes deposited in a quiet subaqueous environment. Tectonic shocks like violent eruptions or earthquakes produced the mobilization of these layers, here generally associated with volcanic breccias.

The carbonate unit (composed of limestones and dolomites, often silicified) was probably linked to slightly deeper lacustrine conditions (10 to 20 m). The unit is characterized by 1) the presence of shallow water ostracods always with silicified articulated valves (rapid burying within a soft sediment) and sometimes with preserved eggs; 2) the presence of several decimetrical layers of anthracite which indicates a temporary lowering of water level and the onset of swampy conditions; 3) the presence of algal films and pisolites in some calcareous levels. Presence of the algae was probably more prevalent than it appears due to the heavy silicification that reduces their remains to white ghostly shapes.

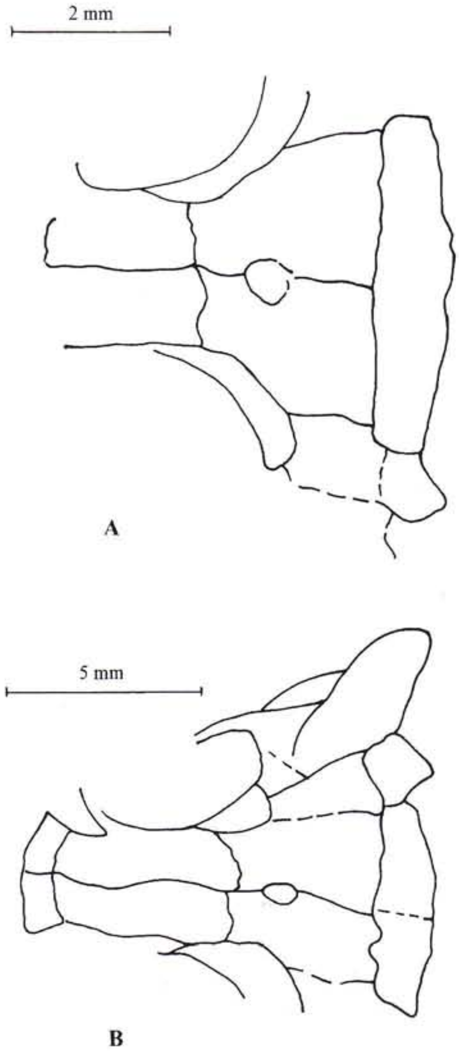


Fig. 3 - *Branchiosaurus* cf. *B. petrolei* from Perdasdefogu Basin, Lower Permian. Camera-lucida limestones drawings from A) specimen n. 1; B) specimen n. 42d.

It is likely that synsedimentary volcanic outflows from nearby sources were responsible for the increase in water temperature, thus promoting suitable conditions for limestone precipitation, as in the Bas-Argens and Estérel Basin (Toutin-Morin, 1985; 1992).

Preservation of most amphibians is rather poor (Pl. 1). Bone material is almost reduced to powder and sutures between bones are usually not detectable. However, in a few cases, the dermal skull pattern is visible as a natural mold on the shaly matrix (Fig. 3). Probably, complete removal of the bone material will provide more molds, but several attempts with acid or thin nee-

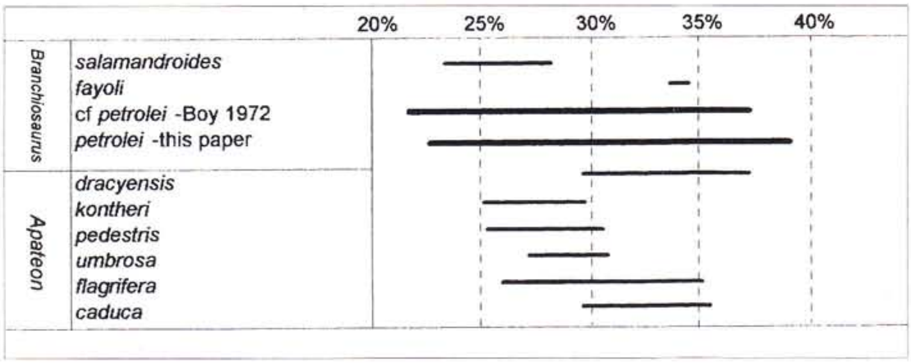


Fig. 4 - Variability of skull length (Sl) versus infraorbital width (Iow) in *Branchiosaurus* and *Apateon* species. After Werneburg (1989) with the addition of *Branchiosaurus* cf. *B. petrolei* from the Perdasdefogu Basin and the *Branchiosaurus (Protriton)* cf. *B. petrolei* specimens from Saar-Nahe-Gebiet (after Boy, 1972).

dles were not satisfactory, due to the softness of the matrix. The skull outline, usually visible, allows some measurements (Tab. 1; Fig. 4, 6A).

The main fossiliferous beds are D and E. The first yields rare specimens, usually of very small size. This layer is also very hard and splitting along the laminations is difficult since the rock tends to break into very small fragments. A few specimens found within level D show an almost uncrushed skeleton: however, the bone material is very brittle and somewhat powdered.

Bed E is by far the most interesting layer. Fossils are widespread throughout the thin laminated bed (12 to 15 laminae for mm), but concentrations are present in at least a few levels. The upper accumulation level, about five cm from the base, is the richest, being made of a few contiguous laminae composed almost exclusively of *Branchiosaurus* specimens. Repeated mass-mortality events affecting specimens of rather similar size imply that the events took place more or less in the same period of the year. This can also be considered a clue to annual deposition of the shaly laminae.

We can only suggest a few hypotheses regarding the causes of the mass-mortality events. The lack of sedimentary traces of desiccation, suggests that the basin bottom must have remained submerged. Indeed, fossils are preserved fully articulated and without the distortion usually related to desiccation. In a few specimens, the preservation of very fine structures, such as external gills (shown at least in specimens n. 14, 18, 39, 42b, 43), argues against desiccation as an underlying cause of mass-mortality.

Thus, a change in water chemistry must have provoked the rapid death of all the amphibians. This could be due to summer overheating of the basin, or to anoxia, induced by decomposition of organic matter after proliferation of aquatic vegetation. Phreato-magmatic eruptions or the presence of subaqueous fumaroles could also have poisoned the waters, causing extintions of the living communities. In any case, additional factors are likely responsible for the detailed preservation that characterizes the skeletons in this material. Since the depth of the basin was limited, possibly only few meters at maximum; the return to normal water conditions would have led to the reworking of skeletons lying on the bottom by other organisms or gentle currents. In our opinion, microbial films could have played an important role in preserving small organisms, sealing off extreme conditions on the bottom just after the mass

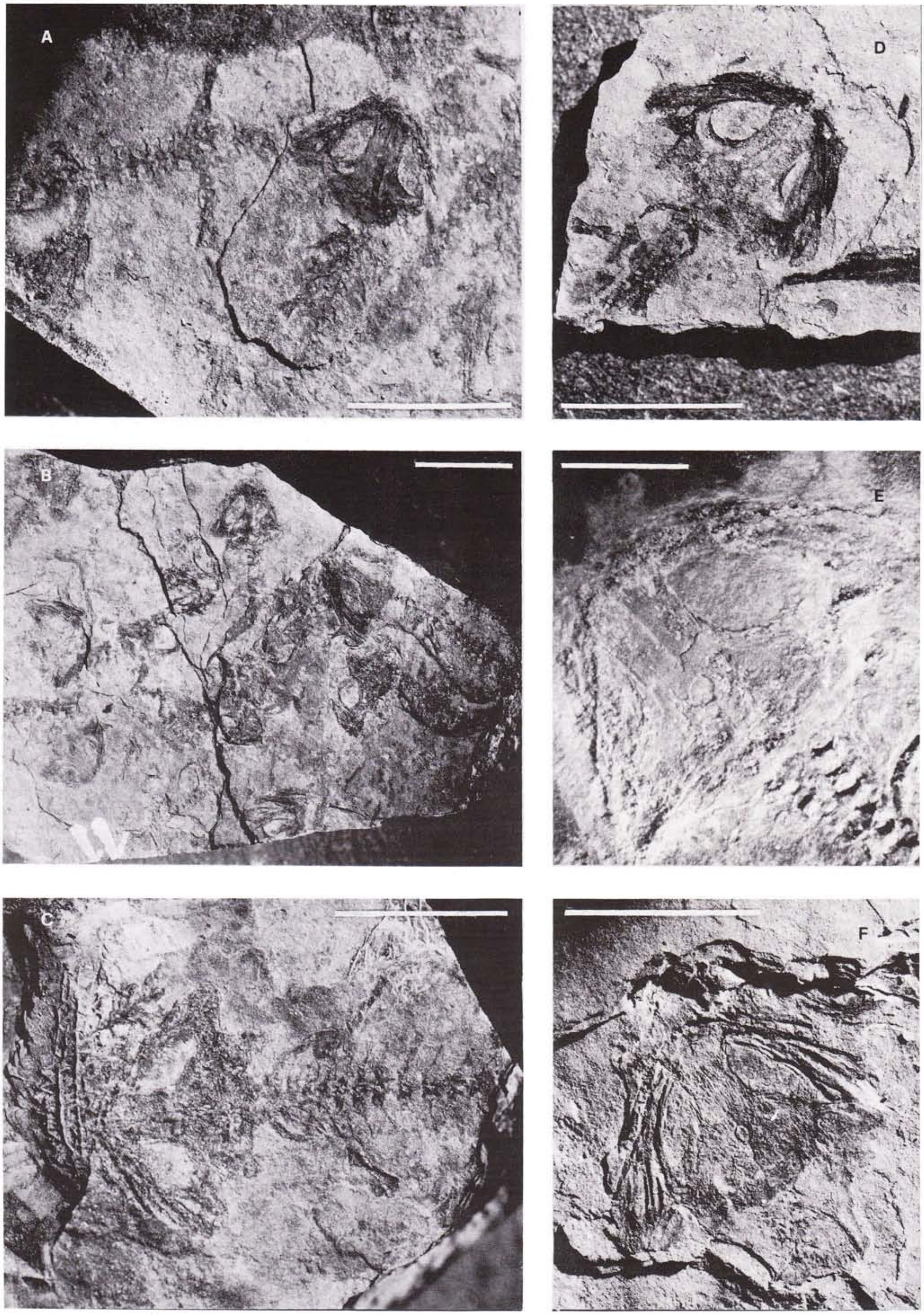
Specimen n.	**10a**	**10b**	**11a**	**11b**	**11c**	**11d**	**12a**	**12b**	**12c**	**12d**	**13**	**14a**	**14b**	**15**	**16**	**17**	**18b**	**18**	**19**	**20**	**21**	**22**	
IOw	23	25	25	20	26	20	16	22	21	27	23	27	26	20	25	25	27	17	27	28	27	26	
Sl	97	90	90	68	91	63	59	74	70	92	80	96	75	72	93	82	89	46	96	91	87	70	
IOw/Sl	0,24	0,28	0,28	0,29	0,29	0,32	0,27	0,3	0,3	0,29	0,29	0,28	0,35	0,28	0,27	0,3	0,3	0,37	0,28	0,31	0,31	0,37	

Specimen n.	**23**	**24a**	**25br**	**26d**	**27d**	**28d**	**28d**	**29d**	**30d**	**31d**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42a**	**42b**	**43**
IOw	18	33	37	13	22		20	26	22	23	28	25	23	22	32	26	35	25	23	24	30	37	23
Sl	68	96	150	44	78	49	66	80	81	83	89	91	79	57	92	94	154	86	65	85	107	128	69
IOw/Sl	0,26	0,34	0,25	0,3	0,28	0	0,3	0,33	0,27	0,28	0,31	0,27	0,29	0,39	0,35	0,28	0,23	0,29	0,35	0,28	0,28	0,29	0,33

Tab. 1. - *Branchiosaurus petrolei* from the Perdasdefogu Basin. Measurements of the infraorbital width (Iow) and skull length (Sl) and their ratio.

PLATE 1

Branchiosaurus cf. *B.* petrolei from the Perdasdefogu Basin. A) Slab n. 27, showing mass-mortality events on two subsequent laminae. B) Slab n. 11, showing mass-mortality events on four subsequent laminae. C) Specimen n. 32. D) Skull and pectoral girdle of specimen n. 19. E) Specimen n. 1. F) Specimen n. 42d. Scale-bars equal 10 mm except Fig. E (3 mm).


A
D
B
E
C
F

mortality event. Gall (1990) described a similar biosedimentary environment in the Grès a Voltzia (Triassic of the Vosges region) and in the Lithographic Limestone of Cerin (Late Jurassic, France).

Another factor that will need further evaluation is the paucity of plant remains in the amphibian bed, especially when compared to the overlying bed G, where plants are abundant while amphibians are almost absent. This also seems to be true in the other outcrops at this same stratigraphic level. Plant remains are usually found, but no traces of amphibians have been recorded so far. Terrestrial plants are always preserved as small fragments and only indeterminate minute debris is often found.

Taxonomic remarks.

The Sardinian specimens (Pl. 1) belong to the Branchiosauridae, an Amphibia group which is not well established at both generic and specific level. The group is very common in the coeval basins of France and Germany (Boy, 1972, 1978, 1986; Heyler, 1957, 1974, 1975, 1994; Werneburg, 1989). Though we include several specimens, our material shows a rather poor preservation. Subtle variations between different species (see for instance Werneburg 1989, but also Heyler 1994) require a larger sampling of specimens to understand possible intraspecific variability among different European populations. In fact, French and German faunas usually have been treated separately and comparisons between them were based mainly on bibliographical data (but see Heyler, 1974, 1975).

Anatomical characters are often difficult to observe and interpret due to poor preservation and high variability of skull patterns in these small amphibians (Heyler, 1975). Only very few specimens from our group provide a good view of the skull pattern (Fig. 3a,b) but, as previously noted, this does not help in their specific determination. We can only observe that the postfrontal bone has a rather long anterior tip, but probably it does not reach the prefrontal bone, and the contact between the supratemporal postparietal bones is usually very short, the parietal being very large in its posterior region.

Nevertheless, few remarks are possible on the basis of measurements which allow only a provisional comparison with specimens from the German basins. Unfortunately, the French material from Autun and Montceau-les-Mines (Heyler, 1957, 1994) has not been analysed biometrically in the same way, so that a similar comparison is impossible. Furthermore, the two sites are not contemporary, so that branchiosaurids from Montceau-les-Mines might not be conspecific with those from Autun.

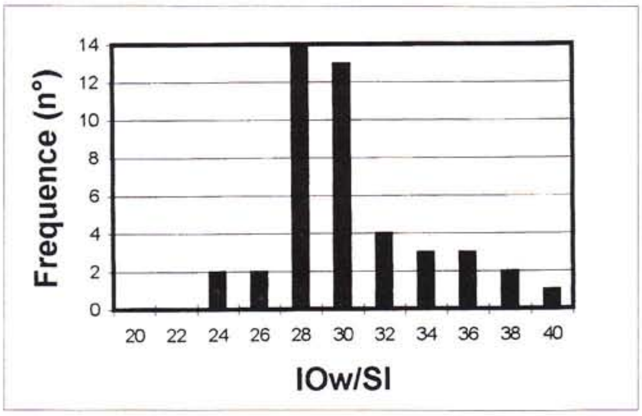


Fig. 5 - *Branchiosaurus cf. B. petrolei* from Perdasdefogu Basin: frequency histogram of the Iow/Sl ratio showing an almost typical unimodal distribution of the parameter.

Werneburg (1989) made clear that one of the most significant morphometric parameters of the skull is the ratio between skull length and infraorbital width. Though this parameter provides a striking feature to distinguish related genera (Werneburg, fig 5, 1989), it is less effective in identifying species. Furthermore, our specimens show a very wide variability that encompasses all *Branchiosaurus* and *Apateon* species considered by Werneburg (1989) (Fig. 4). A frequency histogram seems to exclude the presence of two species (Fig. 5). A similarly wide range is shown by the specimens of *Branchiosaurus (Protriton)* cf. *B. petrolei* using measurements provided by Boy (1972) (Fig. 4). After a comparison with recently published data (Werneburg, 1989) such variability seems to be unique among these amphibians.

Also, a comparison of earlier measurements on *Branchiosaurus (Protriton)* cf. *B. petrolei* (Boy 1972; cited as *Branchiosaurus petrolei* in Boy, 1977) and those from our specimens (Fig. 6a,b), shows very similar results. Thus, in these first stages of our research, we consider our specimens as very similar to *Branchiosaurus (Protriton)* cf. *B. petrolei* sensu Boy (1972) and, therefore, to *Branchiosaurus petrolei* (Gaudry 1875), the well known species from the French localities of Autun and Montceau-les-Mines (Heyler, 1957, 1994).

Both Boy and Heyler repeatedly pointed out the difficulties of separating these two groups of specimens, but they never compared them directly (Boy, 1976, 1977, 1978; Heyler 1974, 1975, 1994).

After studying additional material, Boy (1986) re-established the genus *Apateon* Meyer and reconsidered the position of the specimens he previously attributed to *Branchiosaurs* cf. *B. petrolei*, ascribing them to the species *Apateon pedestris* Meyer 1844 and designating a neotype for it. This decision was made on the basis of a close similarity between juvenile specimens of German *Branchiosaurus (Protriton)* cf. *B. petrolei* and the poor

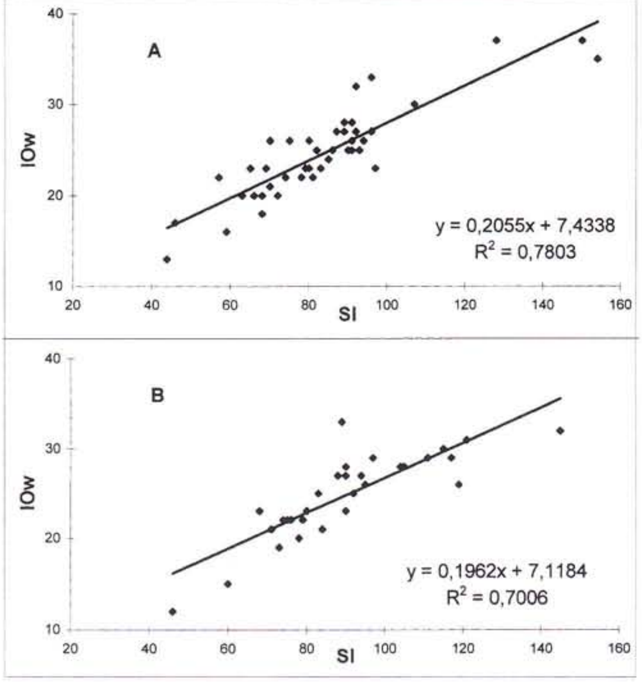


Fig. 6 - Scatter diagram of skull length (Sl) and infraorbital width (Iow), with regression line in A) *Branchiosaurus* cf. *B. petrolei* from the Perdasdefogu Basin; B) *Branchiosaurus (Protriton)* cf. *B. petrolei* from Saar-Nahe-Gebiet (data after Boy, 1972).

original picture of *Apateon pedestris* (the original specimen was lost during World War II). The original picture, until then was disregarded by Boy (1972, 1976, 1977, 1978) and also not considered by Carroll et. al. (1972). Boy's revision is questionable, both because juveniles do not always show the distinguishing characteristics of the species, and because it does not support nomenclatural stability. In fact, Heyler (1994) did not agree with that decision because the generic name *Branchiosaurus* was well established and used, while *Apateon* had become obsolete due to its doubtful meaning. Indeed, Heyler (1994) considered *Apateon pedestris* Meyer 1844 as *nomen nudum* (as both genus and species) (which can be used as *Apateon pedestris* Boy 1986). In this case, if the identity with the German material is proved, *Branchiosaurus petrolei* must be considered the valid name and have priority.

On the other hand, Boy (1986, 1987) and Werneburg (1989) noted a close similarity between the German material, then ascribed to *Apateon pedestris,* and the French *Branchiosaurus petrolei,* which they considered as *Apateon* cf. *petrolei* or as a subspecies of *Apateon pedestris* (Boy 1987). Unfortunately, no final comparison between the German and the French material was made by those authors. A revision of Autun specimens as well as studies of new material from Southern France and Spain are currently under way (Werneburg, pers. comm) and this will surely provide a deeper understanding of these faunas.

The paleogeographical setting of the Sardinian area at the time should also be considered. The area was closer to the French rather than the German basins, impliyng that the Sardinian fauna should be more similar to the French specimens. In light of the previous discussion and lacking sound anatomical characters for a positive classification as one of the known European species, we prefer to tentatively ascribe our specimens to *Branchiosaurus* cf. *B. petrolei* (Gaudry, 1875).

Conclusions.

Age. The plant remains discovered in the Perdasdefogu Basin suggest an Autunian age (Broutin et al., 1996). The two ostracods recovered in the sequence (*Candona* n.s. cf. *C. planidorsata* and *Whipplella* aff. *W. carbonaria*) also occur in the uppermost Stephanian/ basal Autunian of some French basins (Lethiers, pers. comm.). If we consider the vertebrates, *Branchiosaurus petrolei* is very common in the Stephanian B-C of Montceau-les-Mines (Heyler, 1994) as well as in the basal Autunian of Autun (Heyler, 1957, 1994). Given the close similarity between *Branchiosaurus petrolei* and the German species *Apateon pedestris,* we may also consider the distribution of the latter species, which characterizes the very basal Autunian (Asselian) (Werneburg, 1989; Schneider, 1995). Schneider et al. (1988) used xenacanth teeth as well as insect wings to complement stratigraphic data. In our case no insect remains were found, while the study of xenacanth teeth is in progress. We must therefore rely mainly on the branchiosaurid amphibians and tentatively ascribe our fossiliferous level to the very basal Permian, not excluding the possibility that the uppermost Carboniferous might also be present.

Paleogeography. Many geological and magnetostratigraphic data have confirmed that in Permo-Carboniferous times the Corsica-Sardinia Block was linked to stable Europe, located close to an area between Southern France (Provence area) and Spain (Catalonian Pirenees), and that only during Upper Oligocene-Lower Miocene times it rotated counterclockwise toward its present position in the Tyrrhenian sea (Alvarez, 1972; Westphal et al., 1973; 1976; Zjiderveld et al., 1970; Chabrier & Mascle, 1974; Bellon et al., 1977, Broutin et al., 1995). Nevertheless, there is some discussion concerning both the original position of this microplate with respect to stable Europe and the possible relative movements within the same block in late-paleozoic times (Arthaud & Matte, 1977; Edel et al., 1981).

So far, paleontological data supporting this paleogeographical interpretation were scarce and limited to some plant remains. The discovery of this vertebrate fauna, yielding amphibians as well as fresh water fishes such as xenacanths and acanthodians, gives further support to the Permo-Carboniferous geography of continental Europe. Similar amphibian discoveries have been recorded in many other Permo-Carboniferous basins such as Autun and Montceau-les-Mines in France and Saar-Nahe, Saale and Döhlen in Central Europe (Heyler, 1957, 1994; Boy, 1972, 1986; Werneburg, 1989). Thus, Sardinia-Corsica and stable Europe had to be connected throughout a unique drainage system that allowed the spreading of these strictly aquatic animals. Although recent paleogeographic maps (Scotese and Langford, 1995) show that high mountains occupied the entire region, the new data presented here seem to confirm that this morphology did not act as a physical barrier, such as a mountain range, to prevent these small acquatic organisms from migrating from southern Central Europe to the Sardinia-Corsica area, widening significantly their migration routes described by Werneburg (1988). Thus, this work adds important paleontological elements which further strengthen the paleogeographic similarities of Sardinia especially with the French Permo-Carboniferous troughs.

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