

Palaeoenvironment and palaeoecology of three Cretaceous snakes: *Pachyophis*, *Pachyrhachis*, and *Dinilysia*

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The palaeoecology of three Late Cretaceous snakes is evaluated. *Pachyophis woodwardi* Nopcsa, 1923 and *Pachyrhachis problematicus* Haas, 1979, are Cenomanian in age and are found in carbonate rocks deposited in marine inter-reef basin environments of the European and African Tethys Sea. *Dinilysia patagonica* Woodward, 1901, Coniacian in age, is considered closely allied to living anilioid snakes, and is found in clastic rocks deposited in a terrestrial inter-dune basin environment in northern Patagonia, Argentina. All three snakes are known from well preserved and articulated specimens found in sediments where detailed sedimentological and taphonomic analyses are possible. *Pachyophis* and *Pachyrhachis* were laterally compressed, have pachyostotic ribs and vertebrae, and small, narrow heads. These two snakes are interpreted as aquatic predators living in and around the margins of reef mounds on a shallow water carbonate platform. *Dinilysia* was a large bodied snake with a relatively large head, and is interpreted here as a terrestrial predator that lived in a dry, interdune basin environment dominated by aeolian sedimentation. Sedimentary units preserve ichnological evidence of burrowing insects and rooting plants.

Key words: *Dinilysia*, *Pachyrhachis*, *Pachyophis*. snakes, phylogeny, palaeoecology, palaeobiogeography, palaeoenvironment, Cretaceous.

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Introduction

The origin of snakes has been termed a major event in vertebrate evolution. The importance accorded to this event underscores not so much the event itself, but rather the difficulties associated with finding answers to the seemingly intractable questions of

snake origins and relationships. Historically, the fossil record of snakes has contributed little information to these phylogenetic studies as the only taxon for which a reasonable amount of anatomical data existed was *Dinilysia patagonica* Woodward, 1901 (Estes *et al.* 1970). The available data on *Dinilysia* were frustratingly sparse as only a single skull and a small number of articulated dorsal vertebrae were known (Hecht 1982; Rage & Albino 1989).

Recently however, several studies have re-described a number of 'snake-like' reptiles and identified them as Cretaceous marine snakes: *Pachyophis woodwardi* Nopcsa, 1923 (Lee *et al.* 1999) and *Pachyrhachis problematicus* Haas, 1979 (Caldwell & Lee 1997; Lee & Caldwell 1998). Interestingly as well, while many modern snakes retain vestiges of the pelvic girdle and femur, *Pachyrhachis* has a nearly complete hindlimb (Caldwell & Lee 1997; Lee & Caldwell 1998).

The result of these redescrptions is that the morphology of two Cretaceous snakes has been added to the diverse character sets employed in the analysis of snake, and overall squamate, phylogeny. Lee (1997, 1998), Rage (1997), Zaher (1998), and Caldwell (1999, 2000), have published independent studies detailing snake ingroup and outgroup relationships using these new data. In addition to the re-characterizations of *Pachyrhachis* and *Pachyophis* as snakes, even more recent studies have identified and named two new Cretaceous marine snakes that also possess hindlimbs: *Haasiophis terrasanctus* (Tchernov *et al.* 2000), from the same quarries as *Pachyrhachis*, and *Podophis descouensi* (Rage & Escuillé 2000), from Cenomanian rocks in Lebanon. The effect of these four new marine snakes, and their characters, on our understanding of snake phylogeny has yet to be fully realized. However, it is clear, and previously unrecognized as well, is that during the Late Cretaceous a large number of snakes, currently of uncertain interrelationships, were aquatically adapted and living in marine ecosystems (Caldwell & Lee 1997; Lee *et al.* 1999; Rage & Escuillé 2000; Tchernov *et al.* 2000). This new palaeoecological information is intriguing in its own right, but more importantly may ultimately bear on questions and problems of snake origins (Caldwell & Lee 1997; Tchernov *et al.* 2000).

In addition to our review of the palaeoecology of Cretaceous marine snakes, we present new information on *Dinilysia* that has resulted from fieldwork collections made by a team led by Dr. J.F. Bonaparte, and from preliminary geological fieldwork. Collections by Bonaparte's team have produced one articulated cranial and postcranial skeleton, three skulls and several articulated strings of vertebrae of *Dinilysia*. This new anatomical information, added to previous studies on *Dinilysia* (Estes *et al.* 1970; Hecht 1982; Rage & Albino 1989), provides a far more complete anatomical understanding of this Cretaceous snake. Preliminary study of the rocks adds sedimentological and palaeoenvironmental data to palaeoecological studies. In association with new information on *Pachyophis* (Lee *et al.* 1999) and *Pachyrhachis* (Caldwell & Lee 1997; Lee & Caldwell 1998), it is possible to characterize the two known ecotypes of Cretaceous snakes: (1) a laterally compressed marine snake; (2) a more cylindrical-shaped terrestrial snake.

We present here a review and interpretation of all available palaeoenvironmental data, with a particular emphasis on our interpretations of the lithological and sedimentological data from the new *Dinilysia* localities. We also compare the palaeoecology of Cretaceous marine and terrestrial snakes. Our focus is on *Pachyophis*, *Pachyrhachis*,

and *Dinilysia*, as we have not personally examined *Haasiophis* and *Podophis*. We also examine the palaeobiology of *Dinilysia* specifically, emphasizing our current interpretations of its feeding and mode of life.

Abbreviations. — NMC, Canadian Museum of Nature, Ottawa, Canada; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MUCPv, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; USNM, Smithsonian Institution, United States National Museum, Washington, D.C., U.S.A.

Palaeoenvironment

Pachyophis woodwardi Nopcsa, 1923

Locality and stratigraphy. — The holotype was collected from a quarry in Selista (= Selisca, Selisce), an eastern suburb of Bilek (Bileca), in East Herzegovina about 40 km inland (NE) from Dubrovnik (Nopcsa 1923). Langer (1961), based on fish assemblages, considered the localities at Komen and Lesina (Hvar Island, Croatia) to be Cenomanian–Turonian, with the aigialosaur localities placed in the lower part of the sections (Early Cenomanian). The *Pachyophis* locality at Selisca-Bilek is somewhat younger, ranging from Middle to probably Late Cenomanian (Sliskovic 1970).

Lithology and sedimentology. — The known specimens of *Pachyophis* are preserved in finely bedded, carbonate mudstones showing some dolomitization (derived by observation of degree of fizzing when applying several drops of dilute HCl on undisturbed surfaces *versus* scratched surfaces). There is no evidence of bioturbation in the slab preserving the type specimen (personal observation). Locality data and descriptions of the quarry and outcrop around Selista are not currently available.

Palaeogeography. — During the mid-Cretaceous (Albian through Turonian), the land masses of what are now modern Italy and the former Yugoslavia were largely submerged during a major marine transgressive phase (Fig. 1). The non-submerged portions formed an island in the European Tethys Seaway that was only a short distance offshore of the southern coast of the main bulk of the European land mass. The shallow, submerged continental margins formed large carbonate platforms that supported the development of extensive reef complexes (Follmi 1989). Longitudinally, during the mid-Cretaceous, this part of central Europe was slightly to the east of its modern geographic position, though latitudinally this area has only moved about 5 degrees north since that time. Ultimately, the major geographic and tectonic influence on the Tethys was the northern movement of Africa towards Europe.

Fauna and flora. — As with all European Tethyan localities of this age, the most common non-vertebrate fossils are the reef forming rudist bivalves and scleractinian corals. These animals dominate the environments of the northern and southern margins of the European Tethys and at the time would have produced rich and diverse micro- and macro habitats for other marine organisms.

At Selista there is a second described snake, *Mesophis nopcsai*, considered distinct from *Pachyophis* (Bolkay 1925), but the only known specimen is apparently now lost (Rage 1984). In addition, from a geographically proximal locality in Komen, Slovenia, there is a very diverse fauna of other marine lizards such as dolichosaurs, aigialosaurs, and adriosaur (Kornhuber 1873, 1893, 1901; Seeley 1881; Kramberger 1892; Nopcsa 1908, 1923). It seems probable that *Pachyophis* coexisted along the northern shore of the Cretaceous European Tethys within a diverse assemblage of other marine squamates. A diverse fish fauna is also present in many localities in the Yugoslavian and Italian Cretaceous Tethyan basins (Jurkovsek *et al.* 1996).

Interpretation. — The lithology and sedimentology is suggestive of a sheltered environment with limited wave action (Nopcsa 1923). The rocks at Selista were likely deposited in environments analogous to the patch-reef and inter-reef basin systems discussed for the 'Ein Yabrud locality (see below; see also

Scanlon *et al.* 1999; Lee *et al.* 1999), and for the Trieste-Komen Plateau (Jurkovsek *et al.* 1996). Rudist bivalves and scleractinian corals form reef mounds throughout the region. Lying between these reef mounds are inter-reef lagoons containing laminated mudstones and wackestones. As with 'Ein Yabrud and Komen-Trieste, the Selista locality appears to have been a similar environment.

***Pachyrhachis problematicus* Haas, 1979**

Locality and stratigraphy. — Both the holotype and paratype specimens of *Pachyrhachis problematicus* (Haas 1979, 1980a, b), and the single specimen of *Haasiophis terrasancus* (Tchernov *et al.* 2000), were found in limestone beds exposed in stone quarries near the town of 'Ein Yabrud, situated near the West Bank city of Ramallah, 20 km north of Jerusalem (Fig. 1). All fossils referred to as the 'Ein Yabrud Flora and Fauna', apparently come from a single horizon; there is uncertainty regarding the provenance of the fossil unit as the original collections including the snake fossils were purchased from quarry workers, not systematically collected by research teams. However, the fossil-bearing horizon is within the Amminidav Formation (middle portion of the Judea Group; Arkin *et al.* 1965), the type section of which is an 83 m thick unit of dolomites that are locally interbedded with thin limestones. Based on stratigraphic correlations given by Braun (1970), Chalifa (1985) indicated that the fossil-bearing horizon in the 'Ein Yabrud quarries is from the lower part of the section. Biostratigraphic correlations using fish faunas from other Tethys margin localities indicates the horizon to be uppermost Lower Cenomanian (Chalifa 1985, 1989a, b).

Lithology and sedimentology. — Lithologically, and as described in Scanlon *et al.* (1999), the fossil-bearing limestones of 'Ein Yabrud are thinly bedded carbonate mudstones that are pinkish-tan on fresh surfaces and pink to reddish-orange on weathered surfaces. Fine horizontal laminae are the only primary sedimentary structures observed. Biogenic structures and bioclastic inclusions were not observed (grain inclusions were less than 10%). There was no evidence of any terrigenous clastic component. However, thin-section analysis remains to be done.

As there remains some confusion on the matter, it is important to re-iterate here that carbonate muds are genetically very different than clastic muds (Chalifa & Tchernov 1982). Rather, carbonate muds are chemical precipitates. Their thickness is unrelated to the type and kind of events (e.g., storms) that produce clastically derived beds of muds, silts, and sands. Therefore, the lithology of rocks from 'Ein Yabrud bear only on palaeoenvironmental interpretations that describe marine environments with no obvious, nor required, proximity to a clastic source (Lee & Caldwell 1998; Scanlon *et al.* 1999).

Palaeogeography. — Beginning in the early part of the Late Cretaceous (Albian through Turonian), what is now the modern Middle East was submerged during a major marine transgressive phase and formed an extensive carbonate platform with numerous patch-reefs and intra-platform basins (Follmi 1989). The continental palaeoshoreline of Northeast Africa was near the southern end of the modern Sinai Peninsula, approximately 450 km to the southwest of the modern 'Ein Yabrud (Smith *et al.* 1994). To the west of the 'Ein Yabrud reef and basin system, along the shelf margin, there was an extensive barrier reef system. The 'Ein Yabrud locality lies within the marine carbonate sequence deposited on this platform (Fig. 1).

Fauna and flora. — Rocks at 'Ein Yabrud contain a rich vertebrate fauna of fishes and reptiles. The fishes include pycnodonts, skates, and rays, as well as a large number of actinopterygian fishes (Gayet 1980; Chalifa & Tchernov 1982; Chalifa 1985, 1989a, b; Nursall 1996). The reptiles include *Pachyrhachis*, *Haasiophis*, one pterodactyl, two pelomedusid turtles (Haas 1978a, b), and the fragmentary and undescribed remains of mosasauroids (Carroll & deBraga 1992), including the newly described 'aigialosaur', *Haasia gittelmani* Polcyn, Tchernov, & Jacobs, 1999. All plant fossils found at 'Ein Yabrud are isolated vegetative structures such as leaves and stalks or stems (Chalifa & Tchernov 1982; Chalifa 1985).

Interpretation. — We accept the palaeoenvironmental interpretation of 'Ein Yabrud as given by Scanlon *et al.* (1999). These authors consider the palaeoenvironment to be similar to that proposed for the palaeoenvironments of Hakel, Lebanon, and Solnhofen, Germany (Hüchel 1970, 1974;

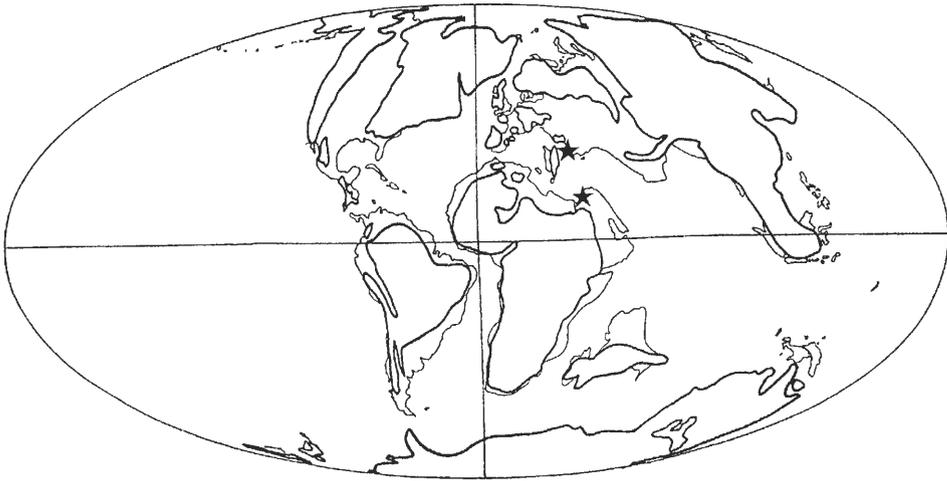


Fig. 1. Cenomanian palaeogeographic map. The palaeogeographic position of *Pachyrhachis problematicus*, and the locality of 'Ein Yabrud, (closed 'star', Northeast coast of Africa). The palaeogeographic position of *Pachyophis woodwardi*, and the locality of Selista, Bosnia-Herzegovina (closed 'star', Southern Europe). Heavy lines indicate palaeocoastlines, thin lines indicate coastal margins of modern continents (adapted from Smith *et al.* 1994).

Meyer & Schmidt-Kaler 1984): lagoonal environments located between patch reefs emplaced on an extensive, shallow, carbonate platform.

Dinilysia patagonica Woodward, 1901

Locality and stratigraphy. — Sometime before 1901, the holotype specimen of *Dinilysia* (MLP 26-410) and two additional specimens (MLP 79-II-27-1 and MLP 71-VII-29-1) were collected at Boca del Sapo, just north of Neuquén city, Neuquén Province, Argentina. Several other less complete specimens were found during the intervening years in exposures immediately to the north of the campus of the Universidad Nacional del Comahue in Neuquén city (MUCPv 38 and MACN-N 26). The most recent collections made by J.F. Bonaparte (1991 and 1994–95) come from a series of new localities (referred to as the Tripailao Farm Sites), near Paso Córdoba, southeast of Neuquén city, Río Negro Province, Argentina. In 1991 Bonaparte's fieldteam quarried and collected a relatively complete articulated specimen that included the skull (MACN-RN 976). In 1994–95, Bonaparte's team returned to the area and located three more skulls (MACN-RN 1013–1015) and a number of articulated strings of vertebrae (MACN-RN 1016–1021). The 1991 quarry was located by MWC in October of 1998, using a map from J.F. Bonaparte, and is approximately 2 meters square. The location of the other smaller quarries remains unknown.

Though exact quarry maps are not available, from the first quarry the preservation of the articulated individual indicates that it was somewhat coiled at the time of death or burial. The orientation of the specimen (right side up *versus* upside down) is not known. All of the skulls collected so far possess lower jaws and other delicate cranial elements. If post-mortem transport had occurred there is little chance these elements would have remained in either association or articulation. As a result, interpretations of a fluvial palaeoenvironment are not well supported by the taphonomic data.

The fossils at all the localities occur in rocks of the Late Cretaceous (Coniacian–Santonian) Bajo de la Carpa Member of the Río Colorado Formation (Neuquén Group). Sediments of the Neuquén Group range in age from the latest part of the Turonian to the Late Campanian. These sediments are part of the Argentine portion of the Andean Basin (Fig. 2), one of the Pacific basins of southern South America (Riccardi 1988). The Río Colorado Formation is the last continental formation and is over-

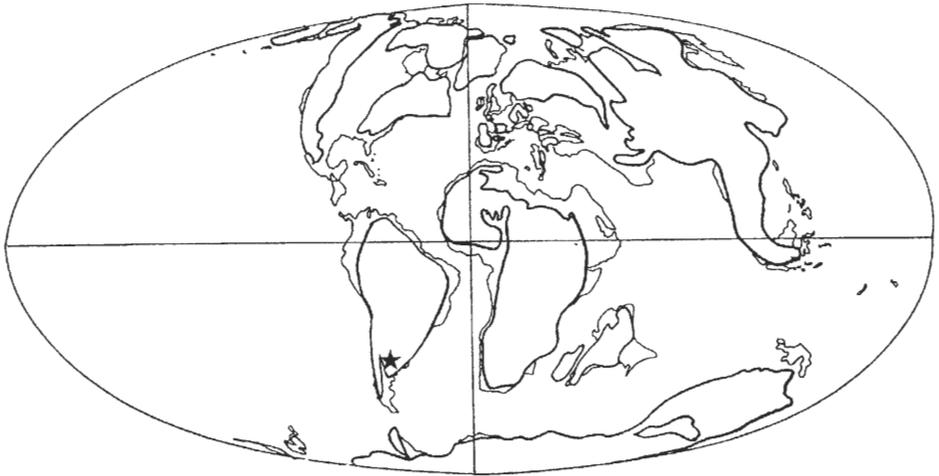


Fig. 2. Coniacian palaeogeographic map. The palaeogeographic position of *Dinilysia patagonica*, and the location of modern Neuquén, is indicated by a closed 'star'. Heavy lines indicate palaeocoastlines, thin lines indicate coastal margins of modern continents (adapted from Smith *et al.* 1994).

lain unconformably by the Allen Formation of the Malargüe Group (the Allen Formation was laid down during a major marine transgressive phase occurring in the Late Cretaceous) (Cazau & Uliana 1972). The Río Colorado Formation is attributed by Bonaparte (1991) to the Coniacian based on its vertebrate fauna.

Lithology and sedimentology. — There are two broad lithological groups represented in the studied sections of the Río Colorado Formation exposed at the Tripailao Farm site. The first is a poorly sorted, coarse-grained conglomeratic sandstone that weathers red to bright pink, and on fresh surfaces is light pink. The second lithology is a fine-grained sandy siltstone that on fresh and weathered surfaces is bright iron-red.

The finer-grained, non-conglomeratic units are at the base of all measured sections at the Tripailao Farm. To date, these lower beds at the Tripailao Farm have not produced any snake fossils and so will not be discussed further in this study. However, fragmentary snake fossils have been found in the sandy siltstone facies closer to Neuquén; this may represent some variation in snake habitat preferences. The beds characterized by the poorly sorted, coarse-grained conglomeratic lithologies are rich in very well-preserved vertebrate fossils. Two broad sedimentological-facies groups are recognized in these upper beds.

The first is a massive, structureless sandstone characterized by a distinct ichnofabric overprinting all primary sedimentological features (Figs. 3, 4). The ichnofabric represents intensive bioturbation of the sediments. It is also important to note that the trace fossils assemblages are particularly well preserved. The top of these beds represent palaeo-surfaces, and we treat these bioturbated beds as paleosols. The second sedimentological group is also a massive, structureless sandstone, but is characterized by the absence of any trace fossils. These non-burrowed units vary from 20 to 200 cm in thickness and display no visible primary sedimentary structures. These two facies alternate, i.e., burrowed unit/non-burrowed unit, throughout the sections exposed at the Tripailao Farm Site (Figs. 3, 4).

Observations of beds and lamina at the 1991 quarry show that the lower surface of the quarry is a planar caliche nodule conglomerate with extensive, radiating burrows moving downward into a structureless sandstone. Above the burrowed caliche conglomerate bed is a 40 cm thick bed of structureless sandstone with small, interspersed caliche nodules. The articulated specimen of *Dinilysia* was found at the contact of the thin bed of caliche conglomerate and the bottom of the non-burrowed bed of structureless sandstone (Figs. 3, 4B).

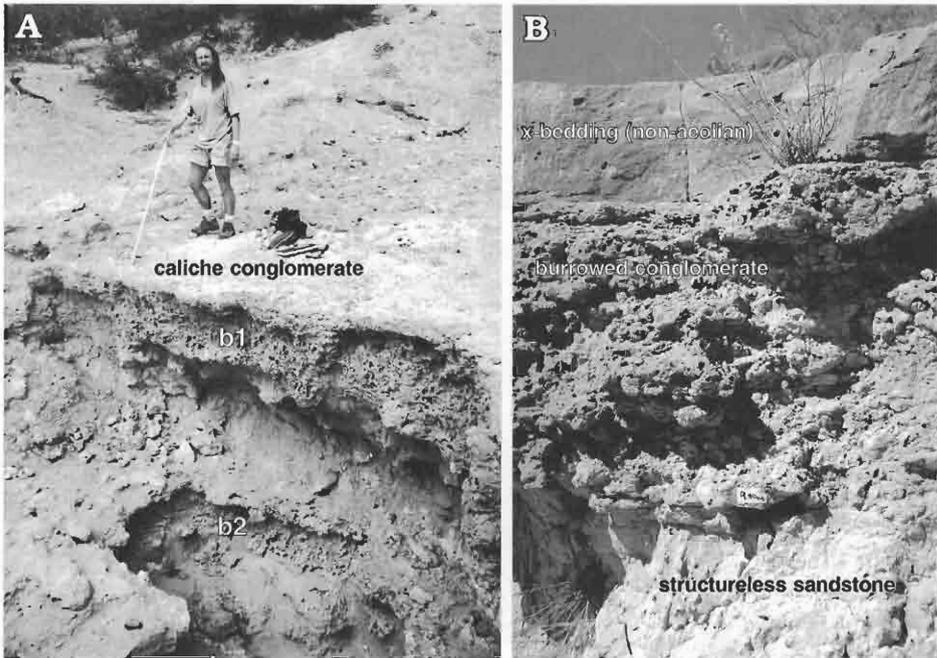


Fig. 3. Sedimentology at Tripailao Farm Section and University Section, Neuquén. **A.** Cliff face, Tripailao Farm Section. Two burrowed horizons (B1, B2) with structureless sandstone interbeds, capped by a planar sheet of caliche conglomerate (pogo stick is 1.5 m in length). **B.** Outcrop at University Section. Note the structureless sandstone, a burrowed, caliche conglomerate horizon, and a cross-bedded capstone (x-bedded).

The burrowed caliche conglomerates are interpreted as deflation lag deposits. Caliche nodules form in the structureless sandstones when the groundwater table is high. Subsequent deflation of surrounding sediments (wind and erosion) concentrates the nodules into deflation lag conglomerates. Stabilization of these deflation conglomerates on palaeosurfaces is evidenced by the burrowing and root casts systems running through them and into the lower structureless sandstone units.

Palaeogeography. — During the Coniacian (Fig. 2), South America was some distance north and east relative to its current geographic position (Smith *et al.* 1994). The localities at Neuquén are on the eastern edge of the Andean Basin and received their sediment load from the Andean High (Andesitic volcanic debris) and the Pampean Range to the Northeast (Riccardi 1988). Topography and geography taken together would have produced a dry continental climate strongly influenced by the highland climates of the Andes and Pampean Range (see Riccardi 1988).

Fauna and flora. — Including *Dinilysia*, the currently described vertebrate fauna includes four crocodiles (two terrestrial notosuchians, one sebecosuchian, and an indeterminate species), two small theropod dinosaurs (a digitigrade, running species and an adaptive type similar to the ornithomids of Laurasia), two birds (a flightless terrestrial species and a flying enantiornithine), and fragmentary, though plentiful, remains of titanosaurid sauropods (Bonaparte 1991; Chiappe & Calvo 1994; Chiappe 1996).

Our field observations note extensive burrow and root systems throughout the units we studied. We currently consider the burrow makers to be insects (Figs. 3A, 4A), and most probably hymenoptera (bees, ants, and wasps) and coleopterans (beetles). It also seems likely that many of the traces are root casts. The intensity of activity in the burrowed horizons would suggest a large and diverse insect and floral community in association with the diverse vertebrate assemblage. To the best of our knowledge, whole body fossils of insects and plants have not been found.

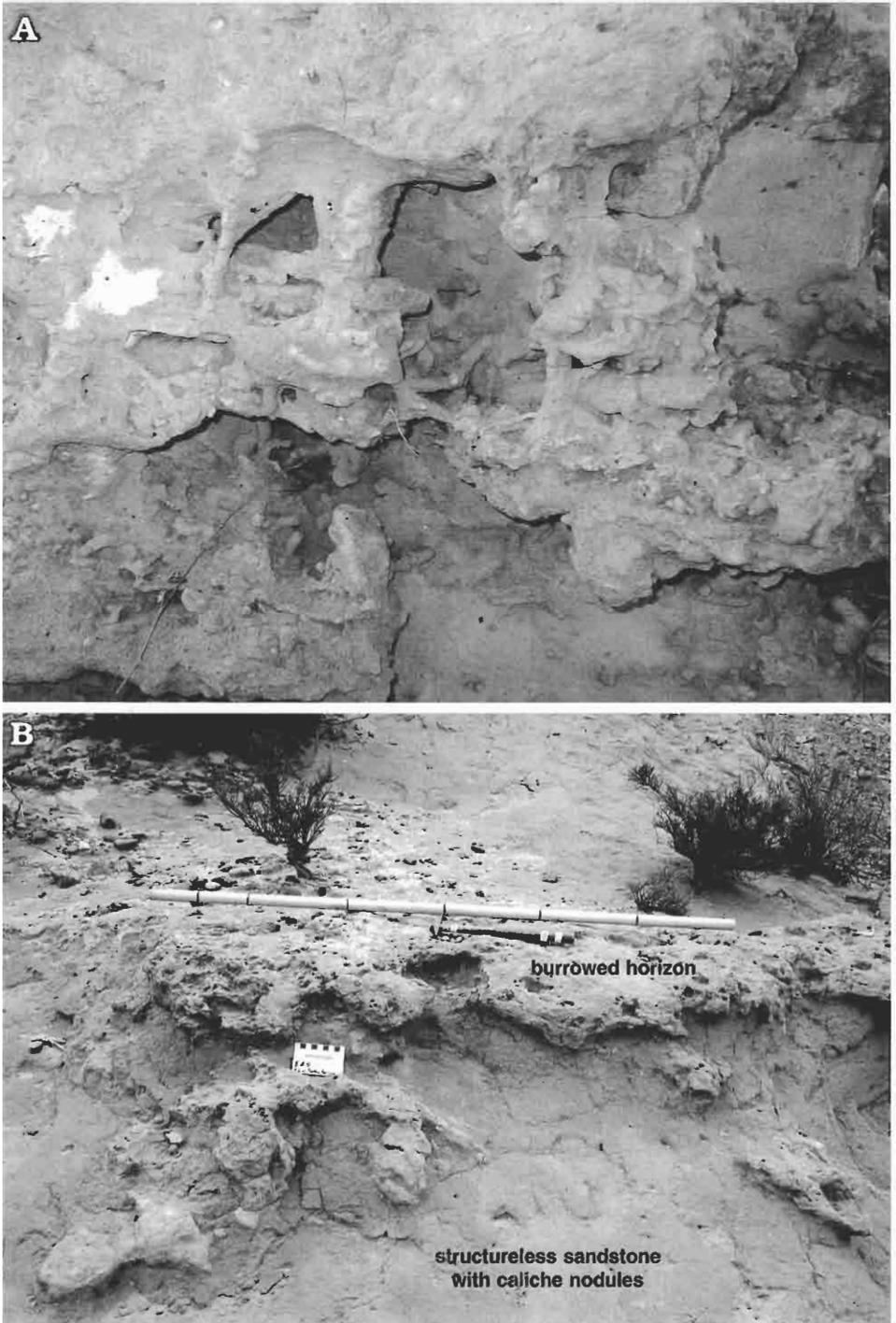


Fig. 4. Sedimentology at Tripailao Farm Section. **A.** Detail of burrows and root casts. **B.** Burrowed horizon overlaying structureless sandstone unit with some minor caliche nodules.

Interpretation. — Eberth (1993) described the palaeoenvironment of a dune-interdune basin from Campanian redbeds exposed near Bayan Mandahu, Inner Mongolia, Peoples' Republic of China. He interpreted the Bayan Mandahu sediments as preserving lateral facies variations consistent with an aeolian dominated dune-interdune basin that is flanked by fluvial and lacustrine systems. He subdivided the Bayan Mandahu deposits into three sedimentation zones, the third of which is pertinent to the rocks of the Río Colorado Formation examined in this study (Bajo de la Carpa Member). Zone 3 is the most distal zone in Eberth's basin reconstructions. He describes this Zone as dominated by aeolian dune and structureless aeolian deposits with rare lacustrine and interdune fluvial deposits, intrabasin streams and ponds, extremely common caliche nodules forming caliche conglomerates, and dense trace fossil accumulations radiating downward from the base of the caliche conglomerates.

The facies characteristics of Eberth's (1993) Bayan Mandahu Zone 3, are virtually identical to lateral and vertical facies successions so far observed for the Río Colorado Formation as exposed at the Tripailao Farm sections. Previous to this description, the depositional environment of the Río Colorado Formation, in particular the Bajo de la Carpa Member, had been described as high-energy channels, in a braided stream, fluvial-dominated environment (Cazau & Uliana 1972). Chiappe & Calvo (1994) had considered the beds within Neuquén city to be low energy channels; they noted the intense bioturbation and coarse sandstone lithology, but still interpreted the depositional environment as dominantly fluvial. However, we note that they are describing the locality of one of the birds and place it within what we interpret as a bed of structureless, massive sandstones. In contrast to previous interpretations, we give identity the thick, structureless, massive sandstone beds, as windstorm deposited. Genetically, the sediments for the burrowed units also appear to have been windstorm-deposited. The difference is that post-deposition, these burrowed beds were then stabilized for a period of time (possibly between storm seasons) during which they were burrowed by insects, and were penetrated by extensive rooting systems from plants (Figs. 3A, 4A). The bioturbated beds therefore represent paleosols and palaeo-surfaces. Collating all other information sources leads to our preliminary interpretation of the Río Colorado Formation as a dune-interdune environment, located on the eastern edge of the Andean Basin, and bordered by fluvial systems.

Cretaceous snake palaeoecology: A discussion

The adaptive origin of snakes has recently regained some its status as an intriguing and enigmatic event in the history of vertebrate evolution. This resurgence is due to the large number of recent descriptions of fossil snakes that still possessed identifiable limbs and without question inhabited marine environments (Caldwell & Lee 1997; Lee *et al.* 1999; Scanlon *et al.* 1999; Rage & Escuillé 2000; Tchernov *et al.* 2000). These studies have presented a number of surprising and unpredicted findings (a diverse assemblage of Cretaceous marine snakes), as well as proposing contradictory and controversial hypotheses of snake relationships and origins (snakes as the sister-group of aquatic lizards). Predictions based on the widely received hypothesis of snake origins and relationships (burrowing adaptations and a burrowing lizard ancestor) would have anticipated fossorially adapted fossil snakes to be found in terrestrially deposited rocks.

The new data on Cretaceous fossil snakes presents new morphologies, new environments, and when analyzed cladistically discovers new synapomorphies, that stand in contrast to the accepted view that snake ancestry is to be found unequivocally within an as yet poorly defined clade of burrowing squamates (Caldwell & Lee 1997; Lee 1998; Caldwell 1999; contra Tchernov *et al.* 2000; Rieppel & Zaher 2000). Such a marked contrast to predicted morphologies and phylogenetic hypotheses has re-invigorated the debate on the origins of snakes.

The temporal and spatial distribution of Cretaceous snakes habitats is informative on the timing of origin events, and on the radiation of early snakes. However, as a caveat to the following discussion, it is not our opinion that temporal and spatial habitat data are at all informative on the adaptive origin of snakes. Hypotheses regarding the adaptive origin of snakes, i.e., fossorial *versus* marine, must be made in the context of phylogenetic patterns that find a closest snake sistergroup relationship with either an aquatic, or alternatively, burrowing clade of squamates (see Caldwell 1999). Only then it is possible to create process hypotheses regarding snake origins.

Habitats in time and space. — As discussed above, the Cretaceous marine snakes, *Pachyophis*, *Pachyrhachis*, *Haasiophis*, and *Podophis*, and the terrestrial snake *Dinilyisia*, are ecological components of two very distinct habitats. Temporally, the palaeoenvironments of the Tethyan marine snakes and *Dinilyisia* are separated by only 10 million years at the most. Spatially, the Southern Tethyan margin, as formed by the northern coastline of Cretaceous Africa, was still very much a part of the Gondwanan faunal provinces that included Cretaceous South America. Therefore, despite the ecological separation, *Dinilyisia* and the marine snakes are relatively proximal to each other in time and space.

With respect to *Dinilyisia*, Scanlon & Lee (2000) reconstructed a potentially close sistergroup relationship with madtsoiid snakes, a group of poorly known Gondwanan snakes (Albino 1994, 1996). Madtsoiids and *Dinilyisia* share an unresolved node that is basal to all extant snakes; Scanlon & Lee's (2000) Pachyophiidae is basal to the unresolved madtsoiid – *Dinilyisia* node). Interestingly, the fossil record of both madtsoiids and *Dinilyisia* is restricted to the Gondwanan continents of South America, Africa, Madagascar and Australia from the Cretaceous through the Quaternary (Albino 1994). If both the known fossil record and reconstructed phylogenetic relationships are accurate, it is reasonable to hypothesize that these two terrestrial snake lineages originated on Gondwanan continents as was previously suggested by Albino (1994, 1996).

The possible Gondwanan center of origin and radiation for both madtsoiids and *Dinilyisia* is also pertinent to the conflicting phylogenetic hypotheses that find Cretaceous marine snakes to be basal snakes (Caldwell & Lee 1997; Scanlon & Lee 2000), *versus* the hypothesis that they are derived macrostomatan snakes (Tchernov *et al.* 2000). The known fossils of *Pachyophis*, *Pachyrhachis*, *Haasiophis*, and *Podophis*, are currently restricted to the northern and southern margins of Cretaceous Tethys Seaway. As mentioned, the coastline of North Africa, a Gondwana continent, formed part of the Tethyan margin.

Marine snake palaeoecology. — The palaeoecology of *Pachyophis* and *Pachyrhachis* have been considered in detail elsewhere (Lee *et al.* 1999; Scanlon *et al.* 1999), as have some aspects of the palaeoecology of *Podophis* (Rage & Escuillé 2000) and *Haasiophis* (Tchernov *et al.* 2000). For the purposes of this paper, these studies are sufficient as our intention was to characterize the palaeoenvironment of these marine snakes against our re-analysis of *Dinilyisia*. The fossil record of these four snakes shows they were important constituents of the marine ecosystems in which they lived. *Pachyophis* and *Pachyrhachis*, as well as *Podophis* and *Haasiophis*, were laterally compressed snakes with small, narrow heads, and elongate bodies. *Pachyrhachis* was the largest of the four, measuring approximately 1.2 m in length, while *Pachyophis*,

Podophis, and *Haasiophis* were all much smaller (less than 50 cm). All four snakes were probably very competent at plucking their prey from within cracks and crevices in the coral and bivalve reef-systems of the Tethyan seaway, and may in fact have eaten quite large prey. As described by Haas (1980a), the body cavity of the type specimen of *Pachyrhachis* contains a partial tooth plate from a pycnodont fish. If this prey item was ingested whole, then *Pachyrhachis* may have been able to eat fairly large prey items (Lee & Caldwell 1998; Tchernov *et al.* 2000) suggesting a large gape as in many modern snakes.

Collectively, this diverse assemblage of marine snakes represents a distinct predator guild living on a vast and diverse platform reef ecosystem extending along the north and south margins of the European and African Tethys Seaway (Fig. 1). Throughout the Albian and Cenomanian, the European and African epeiric carbonate platforms supported extensive reef complexes formed by rudist bivalves and scleractinian corals (Bein 1971; Saint-Marc 1981; Jurkovsek *et al.* 1996).

Habitat of *Dinilysia*. — In complete contrast, *Dinilysia* is a constituent of a diverse terrestrial tetrapod fauna living in a large, relatively dry (or at least seasonally dry) continental basin in the southern part of Cretaceous Argentina (Figs. 2, 3, 4). The palaeoenvironment, as interpreted above, is an interdune basin bounded by two large highlands to the west and northeast. Seasonal windstorms moved large amounts of sediment into the basin with some regions, such as that preserved at the Tripailao Farms Site, showing a dominant aeolian sedimentation regime. The margins of the interdune region are bounded by braided fluvial systems; e.g., the siltstone beds preserved at the base of the Tripailao Farm Site.

Lateral facies variations indicate a variety of micro-environments within the basin (dune-interdune, marginal dune, presence of fluvial systems, etc.). The stratified caliche conglomerates, characteristic of Eberth's Zone 3 (1993) and the outcrops at the Tripailao Farm Site, show that water was at least seasonally present in the interdune region. The presence of water is also confirmed by the root casts traces intermingled with the extensive insect burrow systems. The palaeoecosystem at the Tripailao Farm Site contained a variety of vertebrates, but also a fairly dense foliage and large insect fauna. As compared to modern environments, we visualize the palaeoenvironment of Cretaceous Río Colorado Formation at Tripailao Farm Site as similar to the Mojave desert with its migrating dunes, vegetation, and seasonal water supplies.

Feeding of *Dinilysia*. — *Dinilysia*, as compared to the marine Cretaceous snakes, was a large-bodied, cylinder-shaped snake (approx. 2 meters in length), with a relatively large, broad, head and large orbits. Living in a Mojave desert-like environment, populated by a relatively thick foliage, *Dinilysia* may have been an agile, and relatively large ambush predator.

The principle factor affecting the size-choice of prey items ingested by snakes is the gape size. Gape size is dependent on the flexibility and expandability of a number of skulls bones, with an important one being the range of extension between the mandibular tips. If the maximum gape is large, regardless of the size of the snake, the size of the prey item consumed can be enormous relative to the size of the head, and it can also be large relative to the mass of the snake. If the gape size is restricted, the mass of the prey item can be significant if it's circumference can still pass through the gape.

Among the basal modern snakes, though there are some exceptions, small snakes tend to prey on small prey animals and large snakes tend to feed on large prey animals (scolecophidians eat worms and termites, while pythons and boas eat birds and mammals). In part, and ignoring the cranial kinematics contributing to maximum gape size, this is because if a snake is large, its mouth is usually correspondingly large, and so an apparently large prey item can be consumed.

For example, pipesnakes eat elongate animals such as caecilians, other snakes, amphisbaenians or limbless lizards (Greene 1983). However, if we scale up the pipe snake, *Anilius scytale* (skull length, 2–3 cm) to 7 or 8 times its natural size to match the size of *Dinilysia* (skull length, 17–20 cm), we would find that its snake prey have become correspondingly large. Therefore, even if *Dinilysia* had a restricted gape comparable to anilioids rather than boas and pythons, it would still be able to eat fairly large prey items, as would a much larger *Anilius*.

Estes *et al.* (1970) and Frazzetta (1970) examined the osteology of *Dinilysia* and compared it to that of boiids, *Anilius* and *Cylindrophis*. In comparison to anilioids, boiids possess a substantially more mobile and less stoutly constructed jaw apparatus, permitting a greater gape (Frazzetta 1970). Also, the mechanical acquisitions in the skull of living boiids would have allowed consumption of heavy prey that were diverse in terms of shape such as rodents, pangolins, porcupines, lizards and birds (Greene 1983). If, as Frazzetta (1970) notes, *Dinilysia*'s skull was kinematically more similar to boiids, then it could well have consumed diverse and large prey. Among the vertebrate fauna preserved in the Río Colorado Formation at Neuquén and Río Negro sites, the notosuchian crocodiles, the theropod dinosaurs and the flightless birds were small and medium-sized terrestrial adaptive types. It is very likely that they were among the prey items selected by *Dinilysia*. It is also very likely that it preyed on the young of all of these different tetrapods.

Mode of life of *Dinilysia*. — Frazzetta (1970) presented an interpretation of the mode of life of *Dinilysia* based on his hypothesis that the eyeball was dorsally exposed. Without access to the palaeoenvironmental data we have presented here, Frazzetta (1970) hypothesized that *Dinilysia* might be an aquatic snake, and interpreted the flattened skull as indicating a more dorsal orientation of the eyeball in the ocular cavity. In the context of his interpretation of *Dinilysia* as an aquatic predator, this is a reasonable inference. He compared his hypothesized aquatic habitat for *Dinilysia*, and his conclusion that the eyeball was dorsally exposed, to the dorsally oriented eyeballs and semiaquatic or aquatic habits of modern snakes such as *Eunectes* (the anaconda).

We have already presented data indicating that *Dinilysia* was not living in an aquatic environment, but rather in a relatively dry interdune region. Seasonal precipitation may have produced flash floods and temporary bodies of standing water, as it does in modern desert environments, but there is no sedimentological evidence of their existence. Therefore, if standing water was a non-permanent aquatic habitat, we cannot look to the habitat, adaptations, and feeding behaviour of anacondas for insight on modes of life for *Dinilysia*.

To examine Frazzetta's (1970) suggestion that the eyeball might be dorsally exposed, we examined whole body specimens and dried skulls of the snakes *Eunectes murinus* (whole body: CMN 18695 and 34904; skull: CMN 3145), *Xenopeltis unicolor* (whole body: CMN 32435, 27442; skull: USNM 122782), *Loxocemus bicolor* (whole

body: CMN 27285; skull: USNM 348509), and *Cylindrophis rufus* (whole body: CMN 35067; skull: USNM 297456).

We note that dorsoventral compression of the skull is most pronounced in *Xenopeltis*, followed by *Cylindrophis*, *Loxocemus*, *Dinilyisia*, and finally *Eunectes*. However, from examination of the whole body specimens, only *Xenopeltis* and *Eunectes* have eyeballs showing some degree of dorsal exposure. The eyes are laterally directed in *Cylindrophis* and *Loxocemus*. A laterally directed eye is common for most snakes, including sea snakes. Surprisingly, even the vestigial eye spots of scolecophidians are directed laterally, not dorsally. Because dorsoventral compression of the skull does not seem to be obviously related to the morphologies producing a dorsally exposed eye, we must look to other anatomical features.

The margins of the ocular cavity/orbit are prescribed by the prefrontal, frontal, postorbital (and variably, a supraorbital), maxilla, and sometimes the ectopterygoid. If the ocular cavity is more open dorsally, the bones and their shapes, margins, and articulations create more of a circular or oval opening in dorsal view. For example, when viewed dorsally, the ocular cavity of *Cylindrophis* is shaped more like a semi-circle or quarter-moon. In *Xenopeltis*, the ocular cavity is very ovate in dorsal view; *Eunectes* has a more open ocular cavity because it lacks a supraorbital bone and the frontals are proportionally more narrow than in other boiids. The shape and relative size of the ocular cavity of *Dinilyisia* is more like *Eunectes*. Again, based on these comparisons, Frazzetta's (1970) suggestion that *Dinilyisia* might have a dorsally directed eyeball is not unreasonable.

However, the range of habitats exploited by *Xenopeltis* and *Eunectes*, as compared to the palaeoenvironment of *Dinilyisia*, suggests caution in presuming a specific habitat related to dorsal exposure of the eyeball. The two known species of *Xenopeltis* are cryptic snakes that burrow into loose substrates during the day, and emerge onto the surface at night to feed. Prey items include small mammals, amphibians and reptiles. *Xenopeltis* are certainly not aquatic, and, as daytime burrowers, and nighttime feeders, the adaptive significance for the more dorsal position of the eyeball is not clear and is of little assistance in interpreting the condition in *Dinilyisia*. In complete contrast, *Eunectes* is one of the largest living snakes and occupies a range of aquatic habitats in South America, mainly in the largest rivers such as the Amazonas and Orinoco, and feeds rather generally on very large prey. It lurks just below the water surface and employs an ambush technique in capturing its prey. It uses its more dorsally placed eyes to watch for prey at the waters surface while submerging its large and rather obvious body. While there are similarities in size and skull shape with *Dinilyisia*, the differences in the environment and habitats of these two snakes are large, and likely quite significant.

The results of this examination indicate that the osteology of the orbital region, and the degree of compression of the skull, are not distinct and reliable indicators of the direction of the eyeball. The skull of *Dinilyisia* is somewhat dorsoventrally flattened, and the ocular cavity is somewhat enlarged and opened dorsally. We also note that the degree to which both of these features are expressed is influenced by an unknown amount of taphonomic compression.

Hecht (1982) compared *Dinilyisia*'s vertebrae with vertebrae of other aquatic snakes as *Paleophis*, *Pterospheenus*, *Acrochordus*, Laticaudidae, and Hydrophiidae. He concluded that vertebral morphology indicates a terrestrial or semifossorial mode of life. We agree with this interpretation and suggest that *Dinilyisia* was a large bodied

snake with a relatively large head, that lived in a dry, desert-like environment. Desert environments, like all environments, contain a variety of substrates (loose wind blown sediments, rocky outcrops and other hard substrates), and a variety of floral ground covers. *Dinilysia* may well have taken advantage of loose, sandy substrates in which to hide during some part of the day. It may also have taken advantage of the ground cover afforded by plants. There is no evidence to suggest it was a burrowing snake, and it seems certain, based on the regional geology, that it was not an aquatic snake. The best comparison is likely with surface living, desert snakes such as rattlesnakes, asps, and vipers: large bodied snakes with large heads and active, predatory habits that often hide just below the surface of loose, sandy, substrates while they watch for prey, or wait out the daylight to end before coming to the surface to feed.

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