

NEW CRETACEOUS MARINE VERTEBRATE ASSEMBLAGES FROM NORTH-WESTERN VENEZUELA AND THEIR SIGNIFICANCE

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ABSTRACT—Two new assemblages of fossil fishes are reported from the Cretaceous of Venezuela. One occurs in the Apon Formation (Aptian–Albian) and includes ichthyodectids, pycnodontids, as yet unidentified elopocephalans, plus the aspidorhynchid *Vinctifer*. The other assemblage is from the La Luna Formation (Cenomanian–Santonian) and includes *Squalicorax*, *Enchodus*, *Belonostomus*, plethodids, and pachyrhizodontids. The occurrence of *Vinctifer* is of considerable biostratigraphic and biogeographical interest in view of previous claims about its temporal range and distribution. *Vinctifer* ranged throughout the Aptian and Albian, especially in Brazil, where its occurrence may be of ecological significance in marking a transition from enclosed basinal environments to more open marine conditions.

INTRODUCTION

Sedimentary sequences of Cretaceous age occur over large parts of Venezuela. These strata, mostly consisting of carbonates which were deposited in shallow to moderate depths on a submerged platform, are an obvious but little-prospected source of vertebrate fossils, especially fishes. Liddle (1928) mentioned scales of fishes from the La Luna Formation (Cenomanian–Santonian), but gave no descriptions. Kehrler (1938) and Rod and Maync (1954) also mention these occurrences. To date, however, the only described material comprises some enchodontid skull fragments and isolated scales of various taxa (Weiler, 1940; discussed below). No Lower Cretaceous material has been previously noted.

Outcrops of Cretaceous marine limestones occur within block-faulted terrain in the Perija foothills, along the western margin of the Maracaibo Platform, in quarries, cliffs and stream sections near Villa del Rosario, approximately 75 km SW of Maracaibo. Within these strata there are two important new assemblages of fossil vertebrates, especially fishes. Ammonites associated with these fossils indicate an Aptian–Albian age for one assemblage and a Cenomanian–Santonian age for the other (Renz, 1982; details are given below). This preliminary report is intended to document these occurrences and comment upon some aspects of their significance. Many of the fossils noted here are still awaiting study and description, and therefore specific identifications and descriptions are avoided.

The best exposures are seen at the Rosarito, La Luna, and Catatumbo quarries, all situated about 20 km WNW of Rosario (Fig. 1A). The Cretaceous succession of the Maracaibo Platform was described in consid-

erable detail by Gonzales de Juana et al. (1980), and their stratigraphic nomenclature is followed here (Fig. 1B). The sequence begins unconformably with the Rio Negro Formation (Barremian and Neocomian). The overlying Cogollo Group comprises the Apon, Lisure, and Maraca formations (Aptian and Albian). This group is overlain by the La Luna Formation (Cenomanian–Santonian), which is one of the chief oil reservoirs in Venezuela. Fossil fishes are reported here from the Apon and La Luna formations.

OCCURRENCES

Until now the only Cretaceous fishes reported from Venezuela were of Upper Cretaceous age, from various localities in the La Luna Formation (see references above). The Apon Formation (Aptian to early Albian) has produced an assemblage of fossil fishes, particularly from Rosarito Quarry. These fishes include an ichthyodectid close to *Ichthyodectes*, pachyrhizodontid-like elopocephalans, an aspidorhynchid identified as *Vinctifer* (Maisey, 1992), and pycnodonts. The specimens of *Ichthyodectes* and elopocephalans are articulated but incomplete. Pycnodontids are represented only by toothplates, and *Vinctifer* is known from a single well-preserved braincase (Fig. 2). The presence of *Vinctifer* here is of considerable biostratigraphic and biogeographical interest, and will be discussed further below. Other vertebrates are represented by a large ichthyosaurian vertebra; the only previous record of a marine reptile from the Cretaceous of Venezuela is a supposed mosasaur tooth from the younger La Luna Formation (Weiler, 1940:246).

Ammonites documented by Renz (1982) from Rosarito Quarry include *Deshayesites columbianus*, *D?*

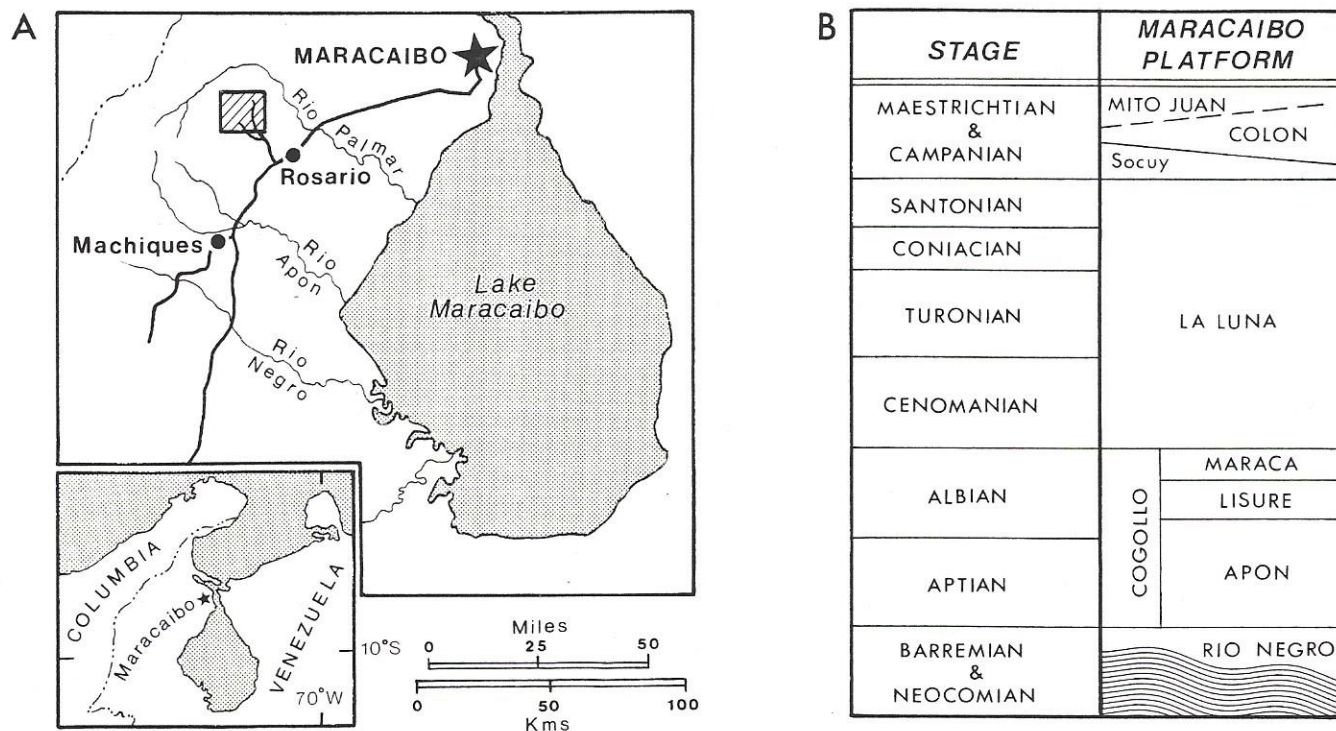


FIGURE 1. A, Outline locality map of north-western Venezuela; collecting sites are within shaded rectangle to NE of Rosario. B, stratigraphy of Cretaceous sediments of the Maracaibo Platform, NE Venezuela (after Gonzales de Juana et al., 1980).

nodosus, *D. stutzeri*, and *D. rotundus*, all of which range from the early to late Aptian. The scarcity of age-indicative fossils in the Cretaceous of the Perija foothills makes it difficult to establish an accurate chronostratigraphic limit between the Aptian and Albian. A single specimen of the early Albian ammonite *Prolyelliceras flandrini* is recorded from Rosarito Quarry in the Machiques Member of the Apon Formation (Renz, 1982: 32).

The fossil fishes from Rosarito Quarry have been recovered from carbonate lenses and concretion-like masses that are said to have formed during deposition, rather than diagenetically (Renz, 1982), and display relatively little compaction; the lenses and "concretions" have suffered some tectonic stress, however, and are prone to shattering upon impact. The paleoenvironment of this part of the Venezuelan carbonate platform (=Maracaibo Platform of authors) during Apon Formation times was probably a shallow shelf sea (Gonzales de Juana et al., 1980). The Cogollo Group, to which the Apon Formation belongs, represents a progradational event which resulted in the partial drowning of much of the Venezuelan carbonate platform during the Aptian-Albian (Martinez and Hernandez, 1992).

Overlying the Cogollo Group is the La Luna Formation (Cenomanian-Santonian), with a fish assemblage that seems typical of the Late Cretaceous. The fishes are preserved in two distinctly different tapho-

nomic situations, suggesting fluctuating changes in bottom environments. Maximum paleodepths of about 600 m were attained over the Venezuelan carbonate platform during the Campanian. The paleoenvironment of the La Luna Formation is interpreted as pelagic, following an episode of regional subsidence, rapid deepening of the shelf sea, and complete drowning of the Venezuelan carbonate platform during the latest Albian-earliest Cenomanian (Martinez and Hernandez, 1992). Pelagic, dark bituminous limestones and shales of the La Luna Formation were deposited in a ramp setting.

In La Luna Quarry, the specimens reported here occur in the lowest exposed section of the La Luna Formation, just above its contact with the Maraca Formation, which is thought to be of late Albian to Cenomanian age (Renz, 1982). The corresponding horizon (Aguada Member) of the La Luna Formation from Trujillo State, southeast of Maracaibo, also has produced "fish remains with vivianite" (Renz, 1982:fig. 62), and ammonites such as *Acanthoceras*, *Sharpeiceras*, *Turritiles*, *Anisoceras*, and *Metoicoceras*, indicating a Cenomanian age. The precise age relations of the base of the La Luna Formation are problematical, however, and from the ammonite data its base appears to become younger farther west. The fossil material described by Weiler (1940) comes from the La Luna Formation of southwestern Venezuela. These disparate and sketchy records collectively suggest that the

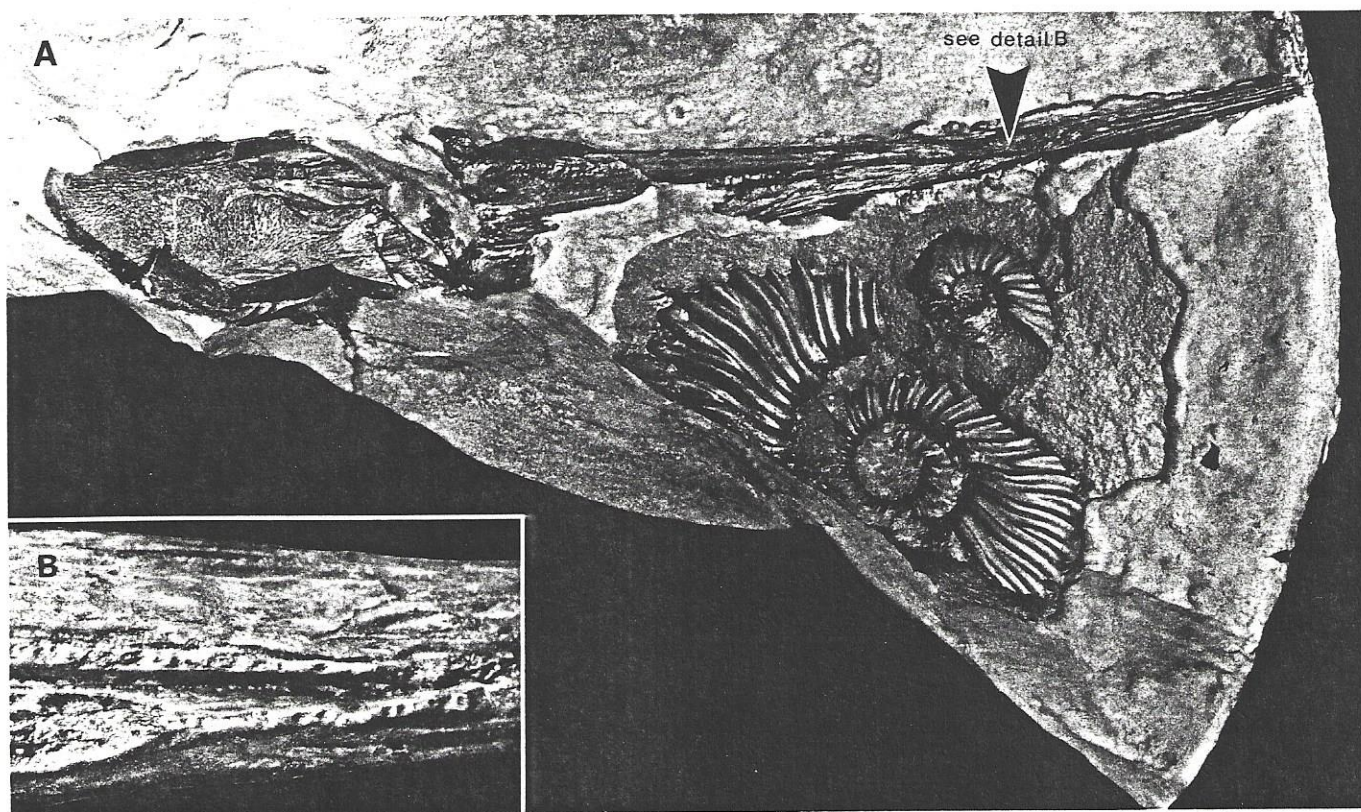


FIGURE 2. A, Rostral part of neurocranium of *Vincitifer* Apon Formation, Rosarito Quarry, Zulua, Venezuela, in ventral view. B, detail of toothed area of rostrum.

La Luna Formation is a potentially productive source of fossil fishes over much or all of its outcrops.

Some of the fossil fish remains from the La Luna Formation occur in platy limestones, as disarticulated fragments including teeth of *Squalicorax*, dentaries of enchodontids, a rostrum of *Belonostomus*, isolated toothplates of *Bananogmius*, and numerous isolated teleost scales and bones. These scattered fish fragments indicate strong current action and sorting but occasionally articulated remains were preserved by rapid sedimentation. For example, large, three-dimensionally preserved fish fossils occur in carbonate lenses and concretions, including an elopoccephalan resembling *Pachyrhizodus*. A large (approx. 1 m long) plethodid (*Bananogmius*?) and some smaller, unidentified elopoccephalan fish skeletons are preserved as compression fossils in a shaly thin-bedded matrix. The La Luna plethodids are the first to be recorded from South America, and if Cenomanian in age, are older than all North American examples. Only one other plethodid (*Plethodus* from the English Albian; Bardack, 1965) is known to be older than the Venezuelan material.

Weiler (1940) described and figured some fragmentary fossil fish remains from equivalent strata from San Cristobal, south-western Venezuela, including an enchodontid which he regarded as a new species of *Cim-*

olichthys (*C. gerthi*); he also referred some isolated scales to ?*Elopopsis* and compared another scale to *Cladocyclus*. Unfortunately, the whereabouts of his material is unknown, and it thus cannot be compared with ours. Enchodontid dentaries recovered from La Luna Quarry have gracile, slender teeth; these are probably referable to *Enchodus* rather than *Cimolichthys*, and closely resemble dentaries of *E. shumardi* Leidy.

Some of the fossil fishes (especially pachyrhizodontids) from the carbonate lenses in the Apon and La Luna formations are preserved with their bodies in three dimensions, as if still bloated after death. Preservation of fine structures such as gill arches is evident even from unprepared material. Some soft tissues may be preserved, but the body is typically infilled with calcite. Their overall appearance is very much like that of specimens in carbonate concretions from the Santana Formation of north-eastern Brazil, especially the pachyrhizodontid *Rhacolepis* (Martill, 1988, 1989). Interestingly, this phenomenon has also been reported in three-dimensional fish fossils from carbonate concretions found in the Lower Cretaceous of Colombia (Weeks, 1953) and identified as *Rhacolepis* (Silva Santos, 1991a). We speculate that some in vivo characteristic of these Lower Cretaceous fishes (e.g., an unusually high lipid content) may have affected early

post-mortem necrolytic processes acting upon their organic remains and may be responsible in part for this curious mode of preservation.

REMARKS ON *VINCTIFER*

Identification of the Venezuelan Material—The presence of the aspidorhynchid *Vinctifer* in the Lower Cretaceous of Venezuela is of biostratigraphic and biogeographic interest (see below). Only a single braincase of an aspidorhynchid has so far been found in the Apon Formation, and its identification rests on the morphology of the snout. It is worthwhile to discuss how we arrived at this identification for the isolated braincase from the Apon Formation (Fig. 2).

At present three aspidorhynchid genera are recognized: *Aspidorhynchus*, *Belonostomus*, and *Vinctifer*. All aspidorhynchids have an elongate rostrum; its structure is complex and provides characters by which the different genera can be distinguished. In *Belonostomus*, the entire rostrum is toothed; the teeth are generally regarded as premaxillary (Woodward, 1895; Bardack, 1968; Dumontet and Wenz, 1979; Taverne, 1981), although the dentition may be partly of vomerine origin. In *Aspidorhynchus*, the teeth are restricted only to the base of the rostrum, but include paired series of several very large fangs (Woodward, 1895; Saint-Seine, 1949). In *Vinctifer comptoni* (the type species, from the Aptian–Albian of NE Brazil), much of the rostrum is edentulous except for short paired series of extremely small teeth located near its base, converging anteriorly, in approximately the same position as the large rostral teeth of *Aspidorhynchus* (Maisey, 1991b). In *V. longirostris* Silva Santos, 1972, from the Aptian of Bahia, there are many small “premaxillary” teeth at the base of the rostrum, but the distal two-thirds of the slender rostrum are edentulous (Silva Santos, 1990). The ventral surface of the rostrum in the Venezuelan aspidorhynchid has a weak dentition of small teeth, arranged in two short series that converge anteriorly as in *V. comptoni*.

Three species of *Vinctifer* have been described: *V. comptoni*, *longirostris*, and *punctatus* (Silva Santos, 1981, 1985a, b, c, 1990, 1991). Of these species, the first two are distinguished by differences in the rostrum and predentary, and in the relative proportions of the flank scales along the body. The last species has been distinguished solely on the basis of scale ornamentation. Among these aspidorhynchids, the Venezuelan example most closely resembles *V. comptoni* in its rostral dentition, but its scale structure is unknown. Other distinguishing features of *Vinctifer*, such as the deep maxilla and dentary, are unknown in the Venezuelan material.

Biostratigraphic Significance—The Apon Formation *Vinctifer* specimen from Venezuela is directly associated with ammonites including *Deshayesites columbianus* (Fig. 2; identification by N. Landman, Dept. of Invertebrates, American Museum of Natural History), demonstrating both an Aptian age and a marine

environment for *Vinctifer*. This is consistent with the presence of *V. comptoni* and *V. punctatus* below a late Aptian ammonite horizon within the Riachuelo and Muribeca formations of the Sergipe-Alagoas Basin (Brito, 1984).

Vinctifer has been utilized as an ad hoc biostratigraphic marker (the “*Vinctifer* biozone”) in several Brazilian Cretaceous basins, for the transition from the local “Alagoan Stage” into the Aptian (Brito and Campos, 1982; Brito, 1984). This local terminology reflects previous work by Asmus and Ponte (1973) who recognized informal lithostratigraphic units within many Early Cretaceous basins in Brazil. Brito and Campos (1982) formalized that work by attaching stage names to the units. The earliest (continental) episode became known as the “Donjoanian Stage.” It supposedly is followed by a lacustrine phase, the “Bahian Stage,” which in turn is followed by an epeiric and evaporitic phase, the transitional “Alagoan Stage.”

The “*Vinctifer* biozone” is a range zone the upper and lower limits of which have not been satisfactorily determined (Maisey, 1991a). In Brazil, only one Early Cretaceous fossil fish assemblage (including *V. comptoni*) has been reported in supposed association with ammonites (of late Aptian to late Albian age), from the upper part of the Riachuelo Formation in the Sergipe-Alagoas Basin (Silva Santos, 1981), but, according to Brito (1984:290), the fishes occur below the ammonite levels, indicating that they pre-date the late Aptian.

The underlying Muribeca Formation (containing *V. punctatus*) is even older (note that according to Brito the Muribeca *Vinctifer* is *V. longirostris*). Brito (1984:290) suggested that the Muribeca Formation “could probably be correlated with the *Dastilbe* level of the Santana Formation” (i.e., the Crato Member), but this would seem to place it below the “Alagoan Stage.”

In the Codo Formation of the Parnaíba Basin, Brito (1984) has reported *Vinctifer* (supposedly *V. longirostris*) below an evaporitic sequence, which ought to place this occurrence well below the “Alagoan Stage” also (within the “Bahian” or even in the “Donjoanian Stage”). According to Silva Santos (1991b:53), the Codo species is *V. comptoni*.

Recent palynological correlative work on the Santana Formation in the Araripe Basin (Pons et al., 1990) suggests a late Aptian to early Albian age for the Crato Member, and a middle to late Albian age for pyrobituminous shales with *Vinctifer* (probably *V. longirostris*) from the Romualdo Member. These shales occur low in the Romualdo Member, well below the levels which produce the famous concretions with *V. comptoni*. According to these palynological data, therefore, all occurrences of *Vinctifer* in the Santana Formation are Albian.

In addition to these records, two other occurrences of *Vinctifer* are suspected from the literature. The first is “*Belonostomus*” *sweeti* from the Toolebuc Limestone of the “Rolling Downs Formation” of Hughenden, Queensland (Etheridge and Woodward, 1892:

pl. 1), now regarded as Albian (Vine and Day, 1965). The second is another "*Belonostomus*" from Equatorial Guinea (Taverne, 1969), the age of which is Aptian or possibly a little older.

Two aspidorhynchid specimens were recently described from James Ross Island in Antarctica (Richter and Thomson, 1989). One of these, a headless specimen designated as the holotype of *Aspidorhynchus antarcticus*, was collected from supposedly Albian strata but may have been reworked from the Upper Jurassic. Its scale histology and flank scale arrangement is consistent with other species of *Aspidorhynchus*. The other specimen (referred to *Aspidorhynchus* sp. by Richter and Thomson, 1989) was collected from an Upper Jurassic (Tithonian) horizon. Its assignment to *Aspidorhynchus* is apparently founded upon histological criteria. Although its flank scales seem closer to those of *Belonostomus* and *Vinctifer*, there is no compelling reason to refer either of these Antarctic specimens to *Vinctifer*.

Known and suspected occurrences of *Vinctifer* may be summarized as follows:

(a) Aptian

- V. comptoni* (Sergipe-Alagoas Basins, Parnaíba Basin)
- V. aff. comptoni* (Maracaibo Platform)
- V. longirostris* (Tucano Basin)
- V. punctatus* (Sergipe-Alagoas Basins)
- ? "*Belonostomus*" sp. (Equatorial Guinea)

(b) Albian

- V. comptoni* (Araripe Basin)
- V. aff. longirostris* (Araripe Basin)
- ? "*Belonostomus sweeti*" (Queensland)

From these data it is evident that the majority of occurrences of *Vinctifer* are Aptian in age, and that Albian records are relatively sparse. This may reflect bias in the stratigraphic record, but alternatively it is possible that the Albian records represent isolated survivals of relict populations.

Cumulatively, these data demonstrate that *Vinctifer* has a stratigraphic range throughout most (perhaps all) the Aptian and Albian of Gondwana, especially in Brazil. The utility of an acrozone spanning such a period of time is certainly limited, and the "*Vinctifer* biozone" does not mark any precise temporal transition from the "Alagoan" into the Aptian stage. It is possible, however, that *Vinctifer* and associated fishes colonized marginal environments within subsiding Gondwanan basins throughout Aptian and Albian times, and that the presence of *Vinctifer* within the Brazilian basins could have paleoecological significance as an indicator of transitional environments prior to the onset of more open marine conditions. The precise timing of these transition events evidently varied from basin to basin, and in general was slightly earlier in marginal basins than in the interior Araripe Basin.

Biogeographic Significance—All the known or suspected occurrences of *Vinctifer* are Gondwanan, and except for "*Belonostomus*" *sweeti*, are essentially re-

stricted to equatorial western Gondwana during the Early Cretaceous. The Venezuelan occurrence represents the most westerly and northerly record of *Vinctifer* in Gondwana. The majority of known or suspected occurrences of *Vinctifer* are tightly clustered within the area of north-eastern Brazil and contiguous west Africa, and the Venezuelan and Australian records are therefore significant range extensions.

Silva Santos (1991a, b) advocated a series of marine connections during the Early Cretaceous, successively linking the Sergipe-Alagoas, Reconcavo-Tucano-Jatoba, Araripe, and Parnaíba basins of north-eastern Brazil, to explain the known distribution pattern of fossil fishes in that region. In his scenario, the marine elements of Cretaceous fish faunas in these interior basins would be derived progressively by dispersal from the early South Atlantic. The southernmost of the supposedly marine assemblages (from near Bahia) is also the oldest (broadly dated as Neocomian; Carvalho, 1982).

Objections to a southerly marine connection such as this have been raised on paleogeographic and other grounds (Silva, 1983), although a non-marine lake system is thought to have extended through the Reconcavo and Sergipe-Alagoas basins during the Hauterivian to Barremian, prior to rifting (Petri, 1987).

A recently published study of foraminiferal biogeography (Koutsoukos, 1992) suggests that surface-water interchange occurred between the Sergipe Basin and a "central North Atlantic-western Tethyan" biogeographic province during the mid- to Late Aptian. This conclusion has profound biogeographical implications for Late Gondwanan ichthyofaunas, and is of particular significance regarding the distribution of *Vinctifer* in Venezuela and Brazil. Koutsoukos (1992:fig. 5) assumed that a direct equatorial connection existed between the North and South Atlantic during the mid- to late Aptian. This is earlier than the Albian to Cenomanian date previously supposed (e.g., Petri, 1987; Szatmari et al., 1987). According to those accounts, the equatorial Atlantic seaway was not developed in the Aptian, precluding any direct oceanic connection between the northern end of the South Atlantic and Caribbean Tethys. Koutsoukos (1992:fig. 5) actually utilized an Albian base-map to plot his Aptian data.

The notion of a connection between the Araripe Basin and the North Atlantic (via the Parnaíba Basin) was advocated by Beurlen and Mabesoone (1969). An alternative model to "explain" the Santana Formation was later offered by Beurlen (1971a, b), who suggested a "Codo-Santana transgression" from the southeast, which he believed was related to the opening of the South Atlantic.

As yet unpublished data now support a southerly post-rift marine transgression from the South Atlantic into Minas Gerais during the Early Cretaceous, rather as Beurlen had supposed but much farther to the west than postulated in any previous models. The precise timing of this event has yet to be established.

During most of the Early Cretaceous the proto-South



FIGURE 3. Paleogeographic sketch map with known and suspected localities of *Vincitifer* in the Early Cretaceous (?=Antarctic aspidorhynchid record discussed in the text).

Atlantic was shallow, with hypersaline conditions north of the Walvis-Rio Grande Rise and anoxic conditions farther south (Reyment and Dingle, 1987). It seems unlikely that the diverse assemblages of Lower Cretaceous fishes from north-eastern Brazil are representative of an established Early Cretaceous South Atlantic ichthyofauna. Most if not all these fishes probably were not adapted to survive in such hostile marine environments. The presence of Tethyan provincial foraminiferans in the Aptian of the Sergipe Basin, and the discovery of *Vincitifer* in Venezuela, so far to the west of its Brazilian occurrences, together offer a provocative alternative scenario, namely that during part of the Aptian, and perhaps also in the Albian, a marine connection existed between some interior and marginal Brazilian basins and the southerly (Caribbean) part of Tethys, extending into the northwestern margin of South America (Fig. 3). The distribution of *Vincitifer* around the margins of northeastern South America during the Early Cretaceous would not necessarily have been continuous.

If "*Belonostomus*" *sweeti* is referable to *Vincitifer*, this fish also had a Pacific distribution that perhaps extended all around the southern margin of Gondwana. At present, however, there is no evidence that *Vincitifer* occurred along the Pacific margins of South America, and its South American distribution may be seen instead as a consequence of an ephemeral epicontinental connection between Caribbean Tethys and the northeastern basins of Brazil.

This hypothesis supposes that an Early Cretaceous (Aptian) arm of shallow marine water extended southward and/or eastward into Brazil (perhaps through the Parnaíba and Araripe basins), providing a corridor along which a highly filtered marine fauna could have reached the interior basins (which lack "typical" invertebrate marine benthos). It remains a mystery how long such a seaway existed, and whether it could have permitted *Vincitifer* and other fishes to enter the interior basin of Araripe during later (Albian) times.

Does the presence of *Vincitifer* in Venezuela represent dispersive counterflow out of central-western Gondwana, or did this fish migrate to the interior from the Pacific and Tethyan margins? The data do not allow us to answer this question, but in either case, the presence of *Vincitifer* in Venezuela as well as Brazil is tantalizing evidence for a transgressive episode originating in the north or north-west of South America during the Early Cretaceous. If we couple this notion with foraminiferal biogeography and the recently recognized Early Cretaceous transgression into Minas Gerais state mentioned above, with a stretch of the imagination it is conceivable that a continuous trans-Brazilian epicontinental seaway existed briefly between Caribbean Tethys and the South Atlantic, bypassing the equatorial land bridge with Africa in the northeast.

At present *Vincitifer* has not been identified from other Tethyan sites. It is an unusual aspidorhynchid and was apparently specialized toward filter-feeding. Its presumed reliance upon a planktonic or nektonic

food supply probably limited its distribution to nutrient-rich marginal shelf environments and shallow seas within Gondwana. Its relative abundance and widespread distribution in western Gondwanan basins provide a measure of its success within this area of endemism, where it was evidently able to tolerate a wide range of salinities ranging from marine to freshwater.

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