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First Records of Fossil Sergestid Decapods and Fossil Brachyuran Crab Larvae (Arthropoda, Crustacea), with Remarks on Some Supposed Palaemonid Fossils, from the Santana Formation (Aptian-Albian, NE Brazil)

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ABSTRACT

A new genus and species of shrimp is described from limestone concretions of the Romualdo Member. These shrimps occur within the matrix of concretions and in the stomach contents of the teleost fish *Rhacolepis*. Based on rostral and carapace characters, it is suggested that these decapods are representatives of the family Sergestidae. Other fossil decapods recovered from the stomach contents of a different fish (*Tharrhias*) are identified as "protozoea" larvae of a brachyuran crab. This new discovery suggests that some brachyurans completed part of their life cycle within a restricted marine or brackish environment in the Araripe Basin. It also indicates that *Tharrhias* was a plankton feeder, and probably did not compete with predators such as *Rhacolepis*, which preferred to eat benthic decapods and small pelagic fishes. The fact that *Rhacolepis* and *Tharrhias* rarely occur in the same horizon suggests that their preferred food sources usually did not occur together. New morphological information is also provided for the supposed palaemonid *Beurlenia* from freshwater strata of the Crato Member. Although this taxon is a caridean decapod, its palaemonid affinity is questionable.

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RESUMO

É descrito um novo gênero e espécie de camarão encontrado em concreções calcárias provenientes do Membro Romualdo. Estes ocorrem também no conteúdo estomacal de peixes teleósteos - *Rhacolepis.* Com base nos caracteres do rostro e da carapaça sugerimos que estes decápodos sejam representantes da Familia Sergestidae. Outros decápodos fósseis foram obtidos do conteúdo estomacal de diferente gênero de peixe - *Tharrhias,* identificados como larva de caranguejo Braquiúro, no estágio "protozoea." Esta nova descoberta sugere que braquiúros poderiam completar seu ciclo vital dentro de um ambiente marinho restrito ou salobro, na Bacia do Araripe. Isto indica também que *Tharrhias* possuía hábito alimentar planctônico e provalmente não competia com *Rhacolepis,* um predador que preferia comer decápodos bentônicos e pequenos peixes pelágicos. O fato de *Rhacolepis* e *Tharrhias* raramente ocorrem no mesmo horizonte sugere que suas fontes de alimentos preferidos normalmente não ocorriam juntas. São dadas novas informações morfológicas sobre *Beurlenia,* um suposto palaemonídeo ocorrente nos depósitos de água doce do Membro Crato. Embora este taxon seja um decápodo carídeo, sua afinidade com palaemonídeo é questionavel.

INTRODUCTION

The Santana Formation of northeast Brazil is famous for its abundant and well-preserved Lower Cretaceous fossil assemblages including vertebrates, insects, and plants (for more details of the fauna and flora, see Maisey, 1991, 1993). It is particularly well known for fossil fishes, especially from limestone concretions in its upper (Romualdo) Member. These fishes are abundant, well preserved, and represent a wide range of taxa including chondrichthyans, coelacanths, and many actinopterygians.

The most informative method of studying these fishes is to dissolve the limestone matrix with dilute formic or acetic acid, usually after embedding the fossil in clear epoxy. This preparation technique reveals the finest details of skeletal anatomy, and may even provide data on associated soft tissues (e.g., muscle, gill lamellae). In some predaceous fishes, the stomach contents are also revealed, providing an opportunity to study predator-prey relationships and reconstruct parts of the trophic network (Maisey, 1994). Phosphatic prey items (e.g., bones, crustacean carapaces) are resistant to the acid, but calcareous items (e.g., molluscan shells) do not survive the preparation method. Besides small fishes and isolated bones, many small crustaceans have been discovered in the stomachs of acid-prepared fish fossils from the Santana Formation (fig. 1).

Decapods have been reported at two distinct levels in the Santana Formation (see next section). In the Romualdo Member, shrimps were found in limestone concretions (Beurlen, 1963), but were not described or named. Fragmentary decapod remains have also been noted in stomach contents of fossil fishes from the Romualdo Member (Maisey, 1991, 1994; Wilby and Martill, 1992; Kellner et al., 1994). Until now, however, no attempt has been made to provide a morphological description of this material. From the Crato Member, much lower in the Santana Formation, Martins-Neto and Mezzalira (1991) described a complete decapod which they named *Beurlenia araripensis* and identified as a palaemonid. Little has been published about Santana Formation decapods, reflecting either their rarity (in the case of *Beurlenia* from the Crato Member, for example) or the difficulty in finding specimens that are morphologically informative (as with the Romualdo Member shrimps).

Here we provide new data about fossil decapods from both the Crato and Romualdo members of the Santana Formation. We describe decapod crustaceans from the Romualdo Member, using specimens obtained during acid preparation of fossil fishes at the American Museum of Natural History. These specimens were recovered both from the matrix surrounding some fish fossils, and from the stomach contents of others. Although fragmentary, this material provides an opportunity to make some morphological observations, identify the decapods, and present some ecological interpretations. New specimens of the supposed palaemonid *Beurlenia* from the Crato Member also are figured and described (figs. 6, 7), supplementing the

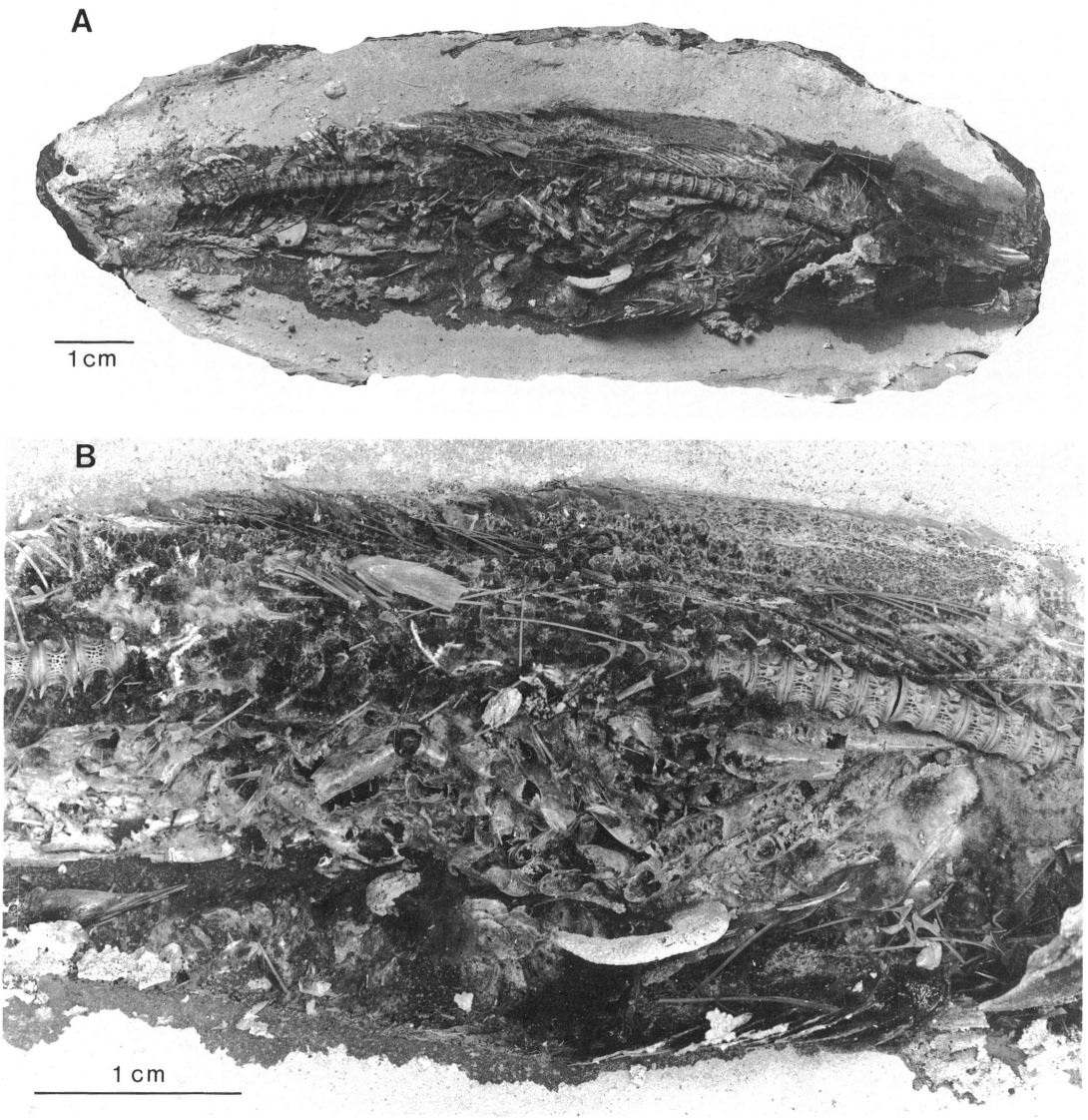

Fig. 1. **(A)** Specimen of the teleost fish *Rhacolepis buccalis,* AMNH DVP 19380, revealing the stomach (parts of which are preserved) completely full of shrimps which are referred here to the new genus *Paleomattea.* One individual with appendages intact (illustrated in fig. 4C) lies within the pylorus and was about to enter the intestine. **(B)** Detail of specimen showing compacted mass of shrimps in the stomach.

data provided by Martins-Neto and Mezzalira (1991).

Stratigraphic Framework

The Chapada do Araripe lies in the interior of northeast Brazil, mostly within the southern part of the State of Ceará (fig. 2). The topography is dominated by the Chapada (plateau), which consists mainly of fluvial sandstones belonging to the Exu Formation (Middle Cretaceous). Below these sandstones, the Santana Formation crops out at

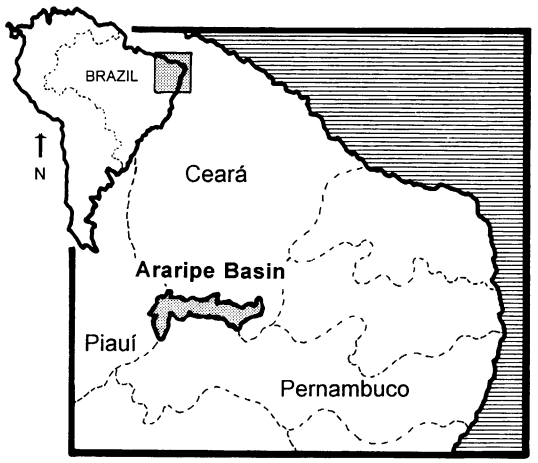

Fig. 2. Outline map to show the location of the Chapada do Araripe.

various sites around the foot of the plateau. The most famous and productive fossil localities lie along its northern border, but fossils are found in many other places around the Chapada.

The Santana Formation is customarily divided into three members. The lowest (Crato) Member is generally regarded as a lacustrine sequence, representing a quiescent phase of basin infilling after a rifting episode (Maisey, 1990). Palynological data (Pons et al., 1990) suggest a Middle to Late Aptian age for the Crato Member. Laminated limestones in these strata have yielded a rich fauna, including several hundred species of insects, as well as fossil spiders, scorpions, fishes, frogs, feathers, and terrestrial plants (Grimaldi and Maisey, 1990; Maisey, 1993). It is from the Crato Member that specimens of *Beurlenia* have been found.

The second unit is the Ipubi Member, which consists mainly of evaporites (gypsum) with some intercalated shales. These shales have yielded conchostracans, small gastropods, and poorly preserved fishes, but no decapods.

The upper part of the Santana Formation is formed by the Romualdo Member. This consists of a heterogeneous sequence of bituminous shales, marls, sandstones, and carbonate sediments. Layers of calcareous concretions occur within oil shales in the middle part of the Romualdo Member. These concretions are the best known source of fossils in the Santana Formation. Bituminous shales near the base of the Romualdo Member are of Middle Albian age (Pons et al., 1990). The concretions are from higher in the succession, and their precise age has yet to be determined. It is unlikely that they are appreciably younger than the bituminous shales, because similar fossil fishes occur in both. Throughout the Romualdo Member there is evidence from ostracods and dinoflagellates of pulsatory marine ingressions (Arai and Coimbra, 1990). Well-preserved decapod fossils described here are associated with fossil fishes in concretions from the Romualdo Member.

Materials and Methods

All decapod remains from the Romualdo Member were obtained following acid preparation of limestone concretions containing fossil fishes. In some cases it was possible to remove decapods from the matrix, especially where they were originally separate from the fish. Specimens removed from matrix were mounted on standard glass microscope slides. Where decapods formed part of the stomach contents in a fish, however, they were usually left in place to avoid damage or destruction during removal. Also, the original trophic relationship was considered of sufficient value to be retained.

The decapod specimens described here have been cataloged and deposited in the Department of Invertebrates at the American Museum of Natural History. Reference is also made to fossil fish specimens from which some of the decapods were recovered. These fishes were originally cataloged by the Department of Vertebrate Paleontology at the same institution; to distinguish between departmental collections, the original catalog numbers of the fossil fishes are here prefixed by DVP. Most of the fishes containing decapod prey have been deposited in the Department of Invertebrates, except for AMNH DVP 19380, which reveals important features of stomach anatomy in *Rhacolepis* (fig. 1).

New specimens of *Beurlenia* (figs. 6, 7) from the Crato Member were prepared mechanically. The fragile condition of their exoskeleton precluded more than local preparation with a needle.

Abbreviations

Institutional

AMNH	American Museum of Natural History
DVP	Department of Vertebrate Paleontology

Morphological

aped	antennal peduncle
asc	antennal scaphocerite
ds	dorsal spine
hs	hepatic spine
per	pereiopod
ple	pleopod
rs	rostral spine
ss	supraorbital spine

A NEW GENUS OF SERGESTIDLIKE DECAPOD FROM THE ROMUALDO MEMBER

Small shrimplike decapods were first noted in Romualdo Member concretions by Beurlen (1963). Some indeterminable fragments were subsequently described by Martins-Neto and Mezzalira (1991). Other fragments were mentioned by Maisey (1991) in matrix associated with fossil fishes and from stomach contents (fig. 1). This occurrence has proven to be an excellent source of fragile decapod fossils, especially following acid preparation of the concretions (Maisey, 1991, 1994; Wilby and Martill, 1992; Kellner et al., 1994). Until now, however, no attempt has been made to describe their morphology. Martins-Neto and Mezzalira (1991) regarded them as indeterminate carideans, but concluded that they did not belong to the family Palaemonidae. The material described below is certainly distinct from *Beurlenia,* and in our view does not represent any caridean family.

No complete specimens of these shrimps have been recovered. Among the material available, however, several partially articulated and incomplete individuals have been studied (fig. 3). These were collected after acid preparation of fishes belonging to the teleostean genus *Rhacolepis* (fig. 5A). One advantage of the acid-prepared decapod material is its preservation in three dimensions, unlike the compressed fossils from the Crato Member. Despite the small size of our sample, we can determine some morphological features with confidence. At the present time, we do not have reason to believe more than one taxon is represented in this sample.

Order Decapoda Latreille, 1803

Suborder Dendrobranchiata Bate, 1888

Family Sergestidae Dana, 1852

Paleomattea, new genus

Diagnosis: Small sergestid with mostly smooth carapace and abdominal segments, lacking keels and grooves; carapace with short rostrum bearing three small spines; small supraorbital and hepatic spines present on carapace; length of sixth abdominal segment almost three times its depth; none of pereiopods enlarged.

Etymology: Greek, *palaios,* ancient; Latin, *mattea,* a delicacy.

Paleomattea deliciosa, new species

Diagnosis: As for species.

Etymology: Latin, *deliciosa,* delicious (self-evident in *Rhacolepis*).

Holotype: AMNH 44985, Department of Invertebrates: carapace and abdominal segments from stomach contents of *Rhacolepis buccalis* AMNH DVP 13696, recovered following acid preparation; Lower Cretaceous, Albian, Romualdo Member, Santana Formation, Chapada do Araripe, Ceará, Brazil (fig. 3B).

Description: The carapace and abdominal pleurae are laterally compressed and smooth and, apart from a small hepatic spine on the lateral surface of the carapace, there is little ornamentation; keels and grooves are absent. The carapace is almost three times longer than its maximum depth. Its dorsal margin is almost straight, except anteriorly where there is a short rostrum which is slightly upturned. In some specimens a small supraorbital spine was observed near the anterior margin of the carapace lateral to the rostrum and just behind the eye (fig. 3B, C, F).

The rostrum of *Paleomattea* is very different from that in *Beurlenia* from the Crato Member, consisting of little more than a raised keel with three or four small spines dorsally, and hardly projecting in front of the carapace (fig. 3B, C, F). A large, spiny rostrum is present in many living and fossil penaeid and caridid decapods, where it probably represents a primitive character. A small rostrum like that of the fossils described here has a

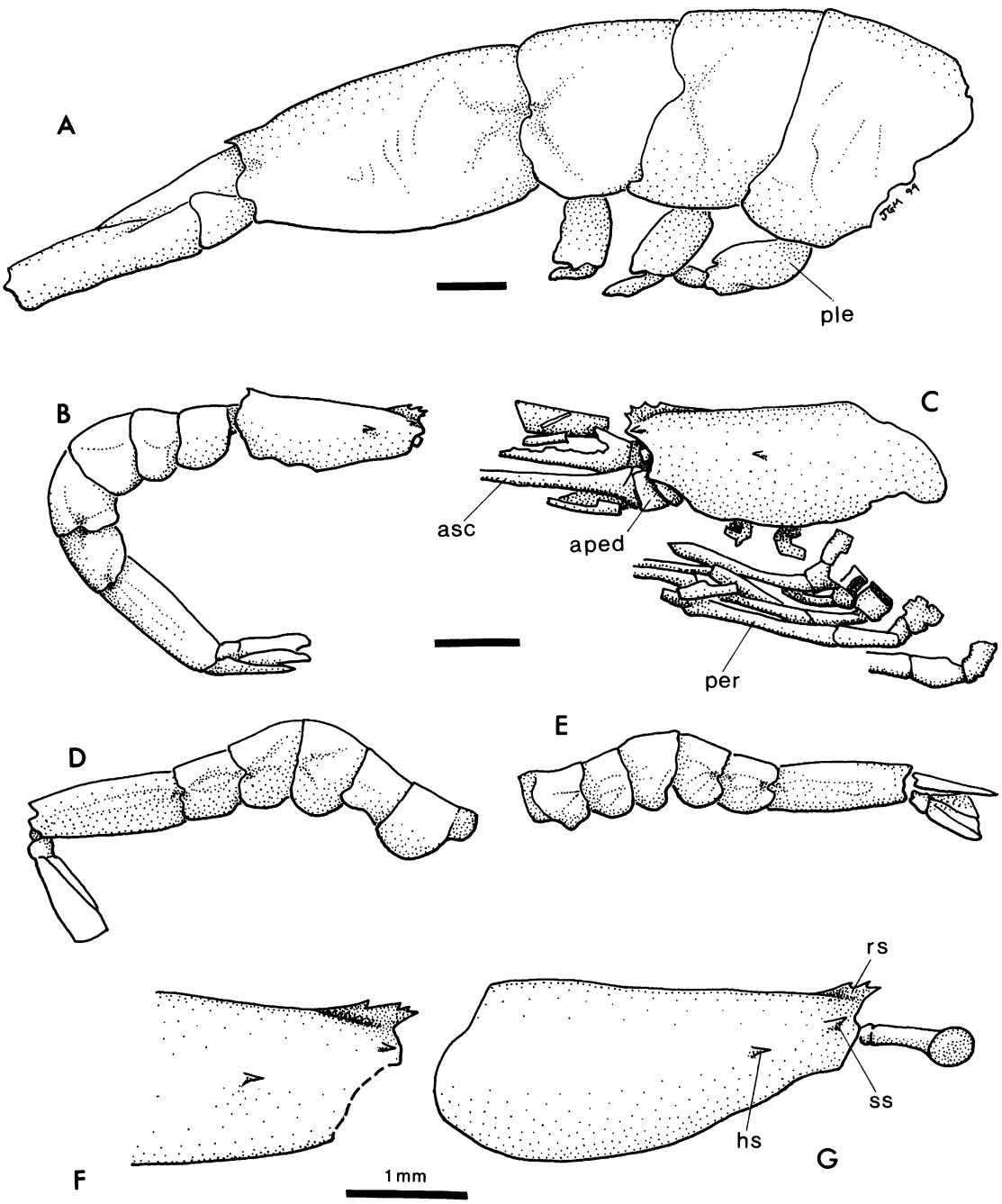

Fig. 3. Fossil and Recent sergestids. Specimen numbers prefixed by DVP refer to the Department of Vertebrate Paleontology (fossil fishes); other numbers refer to Department of Invertebrates. (A–F), examples of the sergestid *Paleomattea deliciosa,* new genus and species from the Romualdo Member of the Santana Formation. Scale bar = 1 mm. **(A)** The largest example, AMNH 44988, recovered from matrix of a concretion during acid preparation; **(B)** the holotype, AMNH 44985, from stomach contents of *Rhacolepis buccalis,* AMNH DVP 13914; **(C)** specimen with parts of appendages intact, AMNH 44989, from stomach contents of *Rhacolepis buccalis,* AMNH DVP 19380 (illustrated in fig. 1); **(D, E)** two abdomens (AMNH 44986 and 44987 respectively) associated with the holotype of *Paleomattea*

more limited occurrence, for example among Recent genera included in the dendrobranchiate family Sergestidae (e.g., *Acetes, Sergestes*). There is a particularly close similarity with the extant *Acetes erythraeus* from South Africa (Kensley, 1972: fig. 10F; see fig. 3G here). The eye stalks have not been observed in any of our material, and were presumably very fragile, but probably were longer than the rostrum. That character would also support inclusion in the family Sergestidae and therefore ought to be verified.

The first five abdominal pleurae in *Paleomattea* are of approximately equal size. Their depth is slightly greater than their length, although the third pleura is deeper than the others. The sixth is more elongated, with a length approximately three times its depth. All the pleurae have a slight overlap with the one behind; there is no "reversed" overlap of the first by the second pleura. Midlateral locking hinge joints are exposed between pleurae 4 and 5, and 5 and 6, but are not observed farther anteriorly. The articulated nature of the Romualdo Member material suggests that concealed hinge joints were present between the anterior pleurae.

According to Burkenroad (1981), exposed hinges between all abdominal pleurae probably represents a primitive pattern among decapods which became modified in certain lineages. There is no well-developed hinge joint between the third and fourth segments in stenopodids, eukyphids (including carideans), and dendrobranchiates (penaeids and sergestids). The anterior hinge joints usually are exposed in members of these groups, but in the Upper Cretaceous penaeid *Sicyonia* from Germany the anterior two are hidden under the pleurae (Marck, 1863). Absence of a hinge joint from all three anterior abdominal pleurae in stenopodids probably represents an autapomorphy of that group. Overlap of the second abdominal segment by the first is regarded by Burkenroad (1981) as a derived character of all dendrobranchiates.

Very little can be said about the appendages of *Paleomattea* from the material available. One specimen (in the stomach of *Rhacolepis buccalis,* AMNH DVP 19380) has proximal parts of the antennules, antennae, and pereiopods (fig. 3C), and in another example (recovered from a concretion after acid preparation) the third, fourth, and fifth pleopods are preserved (fig. 3A). The antennal scaphocerite (asc, fig. 3C) is bladelike, approximately four times longer than its maximum width, and is expanded distally. Both the antennules and antennae are supported by broad, cylindrical peduncles.

Coxae and proximal parts of the pereiopods are known, but their distal extremities have not been observed and it is presently unknown which of them were chelate (in Recent sergestids the first three pereiopods are chelate). From the relatively equal sizes of the ischia it is possible to conclude that none of the pereiopods was enlarged relative to the others, although such an extrapolation from ischium size may be unreliable. Fourth and fifth pereiopods are present (these are reduced in Recent sergestids). The pleopods (ple, fig. 3A) of abdominal segments 3–5 are laterally flattened and leaf-shaped, with very abbreviated distal segments; they appear to have maintained their swimming function. Pleopods of the more anterior abdominal segments have not been observed and it is unknown whether any were modified toward a reproductive function. Pleopods of the sixth abdominal segment form a characteristic tail fan along with the telson.

The absence of "reversed" overlap between the first and second abdominal pleurae in *Paleomattea* rules out affinity with palaemonids or a more general caridean relationship. Overlap of the second abdominal pleura by the first is (according to Burkenroad, 1981)

←

deliciosa, from the stomach contents of *Rhacolepis buccalis,* AMNH DVP 13914; **(F)** anterior detail of carapace in stomach contents of *Rhacolepis buccalis,* AMNH DVP 19380, showing short rostrum, supraorbital spine, and hepatic spine (anterior margin restored); **(G)** carapace of Recent *Acetes erythraeus* from South Africa, showing great similarity with *Paleomattea deliciosa* in rostral morphology and spine arrangement (G after Kensley). Note that the eye stalks are longer than the rostrum (not known in *Paleomattea*).

a dendrobranchiate synapomorphy. Concealed hinge joints between anterior abdominal pleurae apparently represent a shared derived character with some penaeids such as *Sicyonia.* A different derived condition in which the anterior pleurae lack a hinge joint (seen in stenopodids, a different suborder) is not present in *Paleomattea.*

We conclude that *Paleomattea* resembles sergestid dendrobranchiates in several features. Unfortunately, many of these similarities are probably primitive (dendrobranchiate) characters, but we are more confident that rostral morphology of the fossils represents an apomorphic character shared with some modern sergestids. Among Recent sergestid taxa, rostral morphology in *Acetes* is close to that seen in the fossils, with only three dorsal spines on the abbreviated rostrum (fig. 3G). In other Recent sergestids the rostrum lacks a spine or else has only one at its tip (e.g., *Sergestes, Sergia*). The rostrum in most penaeids is much longer and has many dorsal spines, but even in penaeids where the rostrum is short, several dorsal spines are present.

Additional similarities between *Paleomattea* and *Acetes* include the smooth carapace lacking keels or grooves, and the presence of only the supraorbital and hepatic spine. One important difference from *Acetes* is the presence of a full set of pereiopods in the fossils (the last two pairs are absent in *Acetes*; they are present but reduced in other sergestids). This suggests that *Paleomattea* represents an extinct sergestid related to *Acetes,* which has plesiomorphically retained the posterior pereiopods. It would be premature to suggest that *Acetes* and *Paleomattea* are sister taxa on the basis of available data.

If we have correctly identified these decapods as sergestids, then they are the first to be recognized in the fossil record. The oldest dendrobranchiates are of Permo-Triassic age. These are customarily included in the Penaeidae although the relationships of these early forms is not well established (Glaessner, 1969). If penaeids and sergestids are sister groups, they should have an equally long ancestry, and the presence of Lower Cretaceous sergestids would not be unexpected. *Bombur* (from the Triassic and Jurassic of Europe) resembles modern sergestids in its short rostrum, and is similar to *Paleomattea* in having a smooth carapace and elongate sixth abdominal pleura. We suspect, however, that penaeids are not monophyletic when all the fossils are included. It is even possible that the accepted division of dendrobranchiates into penaeids and sergestids is artificial.

No modern dendrobranchiates occur in fresh water, although some are found in brackish environments. Some Triassic penaeids are known from brackish or lagoonal facies, but no brackish-water decapods are known from the Jurassic (Glaessner, 1969: 426).

FOSSIL BRACHYURAN PROTOZOEA LARVAE

It is well known that the majority of decapod crustaceans undergo a series of metamorphoses during ontogeny, passing through distinctive larval stages (e.g., "nauplius, cypris, protozoea, zoea, mysis, megalops," etc.; Gurney, 1942). Some exceptions are noted, particularly among some freshwater brachyurans and astacidean crayfish (which have direct development), and also among certain shrimps and crabs that have various kinds of abbreviated development different from the norm usually seen in a taxon (Gore, 1985). Terminology for various larval stages within the older literature is cumbersome, and has been simplified by more recent workers in the field of decapod development (e.g., Williamson, 1969). The larval term "protozoea" used here is also sometimes referred to as "Stage 1 zoea."

Two larval decapod carapaces were discovered among the stomach contents of a small (approx. 170 mm standard length) specimen of the gonorynchiform fish *Tharrhias araripis,* AMNH DVP 13680 (fig. 5B). One of these larval carapaces is almost complete and is shown in figure 4. The other specimen is slightly damaged. They were first noticed because of their relatively large compound eyes, which are well preserved, and were referred to elsewhere as a "large-eyed decapod crustacean" (Maisey, 1994). The preserved length of the carapaces is slightly less than 2.5 mm including the rostral and dorsal spines. If the spines are excluded, the carapaces are only a little more than 1 mm in length. No appendages are attached, although fragments are littered around in the

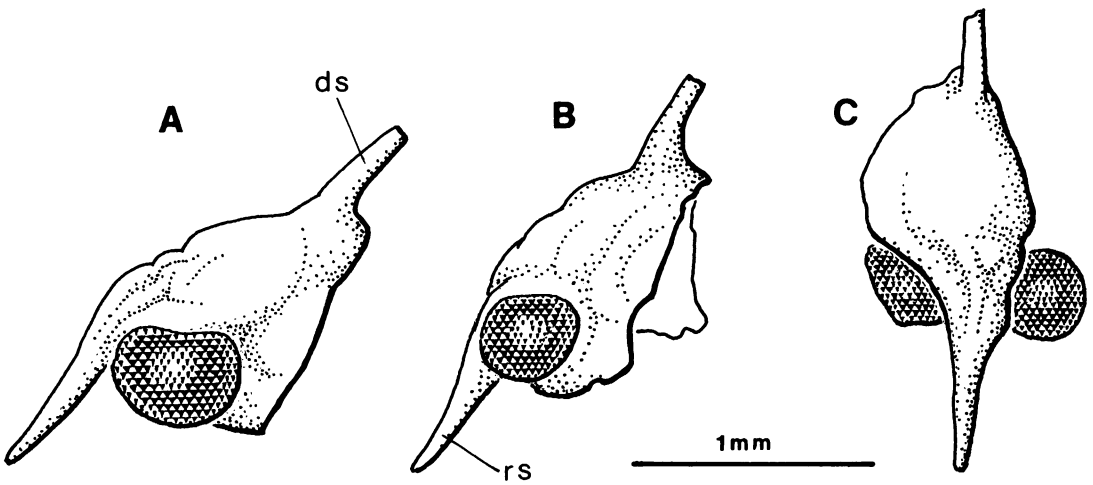

Fig. 4. Carapace of brachyuran "protozoea" larva, AMNH 44990, from stomach contents of *Tharrhias araripis,* AMNH DVP 13680: **(A)** lateral and slightly dorsal view; **(B)** posterolateral view; **(C)** dorsal and slightly oblique view. Scale bar = 1 mm.

stomach region of the fish from which they were recovered.

The most distinctive feature that led to their identification as brachyuran larvae is the dorsal spine (ds, fig. 4). This feature is characteristically absent in adult decapods, and is well developed only in brachyuran "protozoea" and later zoea larvae; in nonbrachyuran decapod larvae a median dorsal spine is not developed, although in anomurans there are short paired spines (Gurney, 1942; Gore, 1985). The distal extremity of the dorsal spine in both our specimens is broken and its original length is unknown, but it was probably at least 1 mm long when complete. The dorsal spine arises close to the posterior margin of the carapace and is directed posterodorsally. It is cylindrical and tapered, but is otherwise featureless.

The rostral spine (rs, fig. 4) is complete, and is approximately 1 mm long. It has a round cross section distally, but is broader and has paired longitudinal furrows proximally, between the eyes. The spine is curved downward gently as it leaves the carapace, but is slightly upturned again distally. Rostral and dorsal spines probably were of about equal length, and both are devoid of serrations.

The carapace is rounded, not laterally compressed, and its dorsal surface is marked by grooves, apparently the larval equivalent of cervical, postcervical, and branchiocardiac grooves in adult decapods. The eyes are bulbous and have a diameter close to 0.5 mm. Their compound lenses are clearly preserved. The fact that the eyes remained attached to the carapace suggests that they were not yet movable.

We conclude that these carapaces represent brachyuran larvae because they possess a single dorsal spine. In modern brachyuran larvae prior to the zoea, the dorsal spine is absent (Gore, 1985: fig. 1), and it is lost again in postzoeal (e.g., megalopa) stages (Gore, 1985: figs. 2, 6, 7). The larva is thought to represent an early zoea ("protozoea") stage because the dorsal spine was not much longer than the rostral spine, and because the eye stalks remained attached to the carapace after ingestion by the fish and even after acid preparation. In the early zoeal stages the eyes are fixed, and the eye stalks become movable only in later zoeal molts ("zoea" of Gurney, 1942). The dorsal spine frequently becomes much longer in successive molts of brachyuran zoea larvae.

The brachyuran *Araripecarcinus ferreirai* is known from a single, almost complete specimen, associated with the fish *Vinctifer* in a Romualdo Member concretion (Martins-Neto, 1987). *Araripecarcinus* was referred to the superfamily Portunoidea because the fifth pereiopod has a flattened and bladelike dac-

tylus distally. This crab is very small, with a carapace less than 10 mm long. It is quite possible that the larva described here pertains to that species, but this cannot be demonstrated. We have refrained from erecting a formal taxon based on such indeterminate larval material.

This discovery of a fossil protozoea larva is significant for several reasons. Firstly, it represents the first recorded instance of a fossil brachyuran larva, and is therefore the oldest known. Secondly, these larvae confirm the presence of brachyurans in the Romualdo Member of the Santana Formation; until now, crabs were represented only by the holotype of *Araripecarcinus ferreirai.*

Thirdly (and perhaps most importantly), this discovery demonstrates that waters within the semienclosed Araripe Basin supported a planktonic community, which was utilized as a food source by some fishes. Micropaleontological data (particularly from dinoflagellates and ostracods) suggest a pulsative marine ingression sustaining a mixihaline environment (Arai and Coimbra, 1990). Brachyuran planktonic larvae were evidently capable of surviving in this environment, despite the general absence of other expected planktonic taxa such as foraminifers. In both anomuran and brachyuran crabs the zoea represents the first free-swimming larval stage, corresponding to the mysis stage in penaeid shrimps; earlier developmental stages of these crabs are passed within the egg (Bliss, 1982). Some brachyurans were thus able to reproduce in the sea which occupied the Araripe Basin.

Fourthly, because zoea larvae characterize the life cycle of many marine decapods, but are atypical of nonmarine taxa, the fossil zoea larvae provide further evidence that the environment was marine to brackish. There are several groups of freshwater brachyurans today (e.g., families Potamidae, Pseudothelphusidae, Trichodactylidae), but modern portunoids are mostly marine. *Callinectes* (blue crabs) can survive in almost fresh water, but do not reproduce there (G. Bishop, personal commun., Oct. 1994). The presence of the supposed portunoid *Araripecarcinus* together with brachyuran zoea larvae, from the same member of the Santana Formation, suggests a marine habitat. The Romualdo Member environment could not have been a "normal" (i.e., open) sea, however, because most pelagic and benthic marine invertebrates such as ammonites, belemnites, brachiopods, sponges, and corals are absent. Instead, the environment (which trophic data from fishes suggest was semienclosed; Maisey, 1994) was able to support only a taxonomically impoverished and highly filtered marine arthropod-pelecypod-gastropod community.

Finally, finding a zoea larva in the stomach of the gonorynchiform fish *Tharrhias* strongly suggests that it was a plankton feeder, and differed in its feeding habits from *Rhacolepis* which was a predator of benthic shrimps and small fishes. *Tharrhias* and *Rhacolepis* possess very different mouthparts; the former has a small subterminal mouth and is toothless, whereas the latter has elongate jaws with many pointed teeth (fig. 5). Elsewhere it has been noted that *Rhacolepis* and *Tharrhias* do not usually occur together in the same horizon (Maisey, 1991, 1994), and it was speculated that this probably had some ecological significance. This suggestion can be expanded by the present observations, because we now have evidence that these fishes were not in direct competition for the same food source. Instead, it may be that their principal food sources were not usually found in the same location (suggesting some local compartmentalization of the environment) or at the same time (suggesting some seasonality or longer-term changes in the environment). These observations offer tantalizing clues about the paleoenvironmental dynamics of the semienclosed sea that occupied the Araripe Basin at that time.

NEW SPECIMENS OF *BEURLENIA ARARIPENSIS* FROM THE CRATO MEMBER

ORDER DECAPODA LATREILLE, 1903

INFRAORDER CARIDEA BURKENROAD, 1963

FAMILY PALAEMONIDAE? RAFINESQUE, 1815

Beurlenia Martins-Neto and Mezzalira, 1991

EMENDED DIAGNOSIS: Palaemonid? with antennae longer than body; antennae and an-

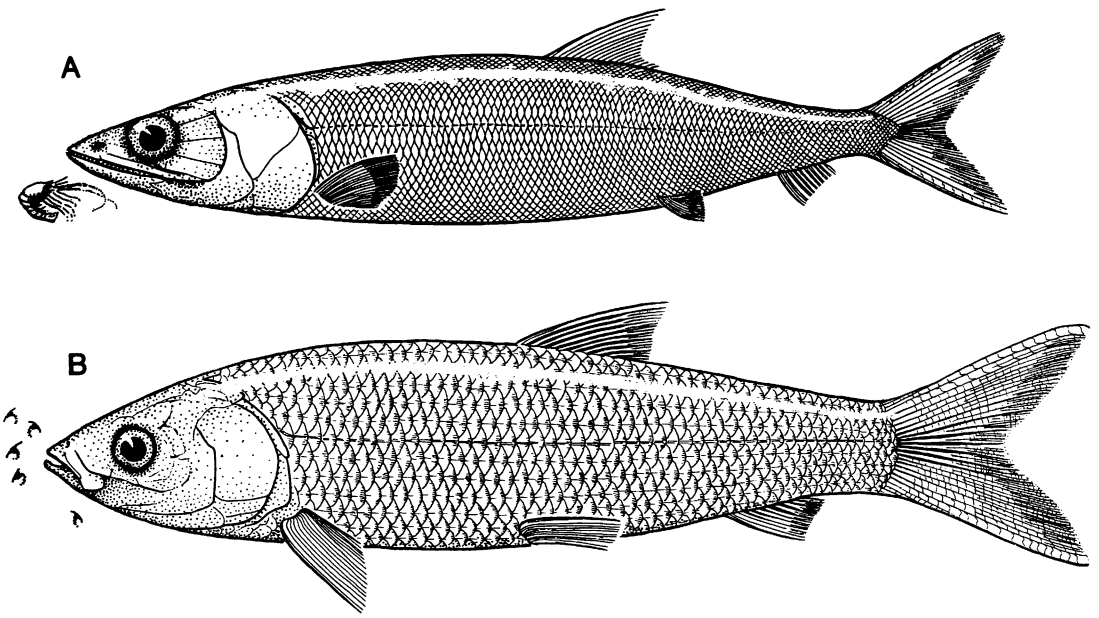

Fig. 5. Outline reconstructions of two fishes from the Santana Formation that preyed upon decapods: **(A)** *Rhacolepis buccalis,* a teleost with elongate, toothed jaws, which ate the sergestid *Paleomattea*; **(B)** *Tharrhias araripis,* a gonorynchiform with a short, edentulous mouth, and which ate planktonic brachyuran larvae.

tennules with two flagellae; antennal scales short; rostrum extending beyond level of antennal peduncles, with six rostral and six postrostral spines dorsally and three rostral spines ventrally; second pereiopod enlarged, chelate; pereiopods posterior to second slender, without chelae; pleopods multisegmented; telson with single apical process, apparently lacking paired spines or setae.

TYPE SPECIES: *Beurlenia araripensis* Martins-Neto and Mezzalira, 1991: 157.

Beurlenia araripensis
Martins-Neto and Mezzalira, 1991

DIAGNOSIS: As for genus.

HOLOTYPE: CD-I-161, Desiree Collection, Rio de Janeiro; complete specimen in laminated lacustrine limestone; Aptian, Santana Formation, Crato Member, Chapada do Araripe, Ceará.

REFERRED MATERIAL: AMNH 44984, 44990, 44991, stratigraphic and locality data as for holotype.

DISCUSSION: *Beurlenia araripensis* was first described by Martins-Neto and Mezzalira (1991) on the basis of a single, almost complete specimen, and its morphology was described in some detail. Certain anatomical features were not well preserved, however. Additional specimens in the Department of Invertebrates, American Museum of Natural History, New York, reveal additional features, especially in the rostral region, presented here (figs. 6, 7).

The largest new specimen (AMNH 44984) is approximately 45 mm overall length, with a carapace length of almost 12 mm excluding the rostrum (18 mm with rostrum; figs. 6A, 7A). Its antennules are approximately 29 mm long, and antenna length was at least 45 mm although the distal extremities are not preserved. These dimensions are slightly greater than those of the holotype, but the two specimens are of approximately equal size. AMNH 44990 represents a slightly smaller individual with an overall length of approximately 35 mm (figs. 6B, 7B), and AMNH 44991 is even smaller (approximately 28 mm overall length; figs. 6C, 7C).

The rostrum is incomplete in the holotype and in AMNH 44990 and 44991, but is com-

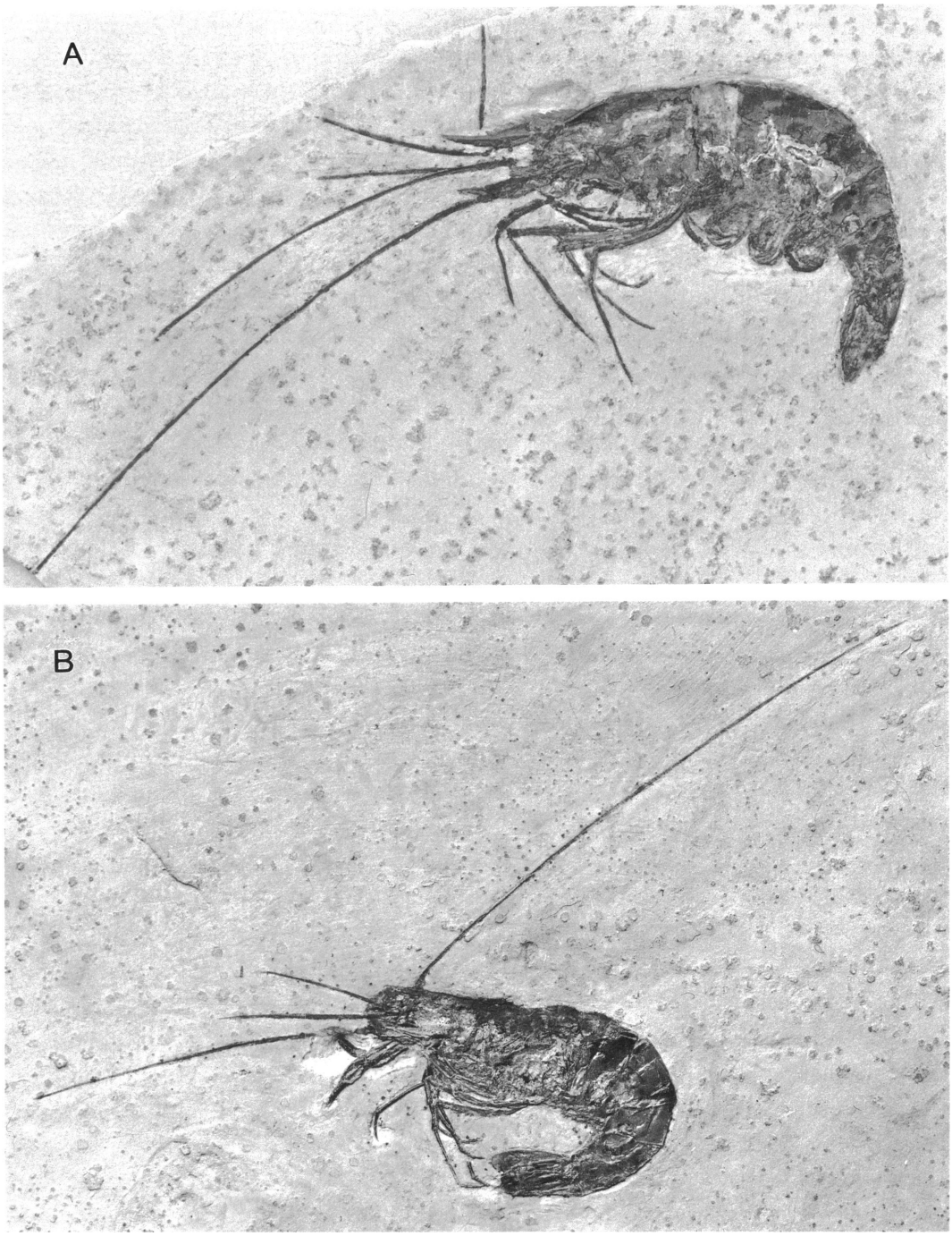

Fig. 6. Specimens of *Beurlenia araripensis*: **(A)** AMNH 44984, × 2.16; **(B)** AMNH 44990, × 2.28; **(C)** AMNH 44991, × 2.05.

pletely preserved in AMNH 44984 (fig. 7A). In this specimen the rostrum arises some 4 mm behind the level of the eye and extends about 6 mm in front of it. The dorsal margin of the rostrum bears six pronounced spines proximally, and there are six more postros-

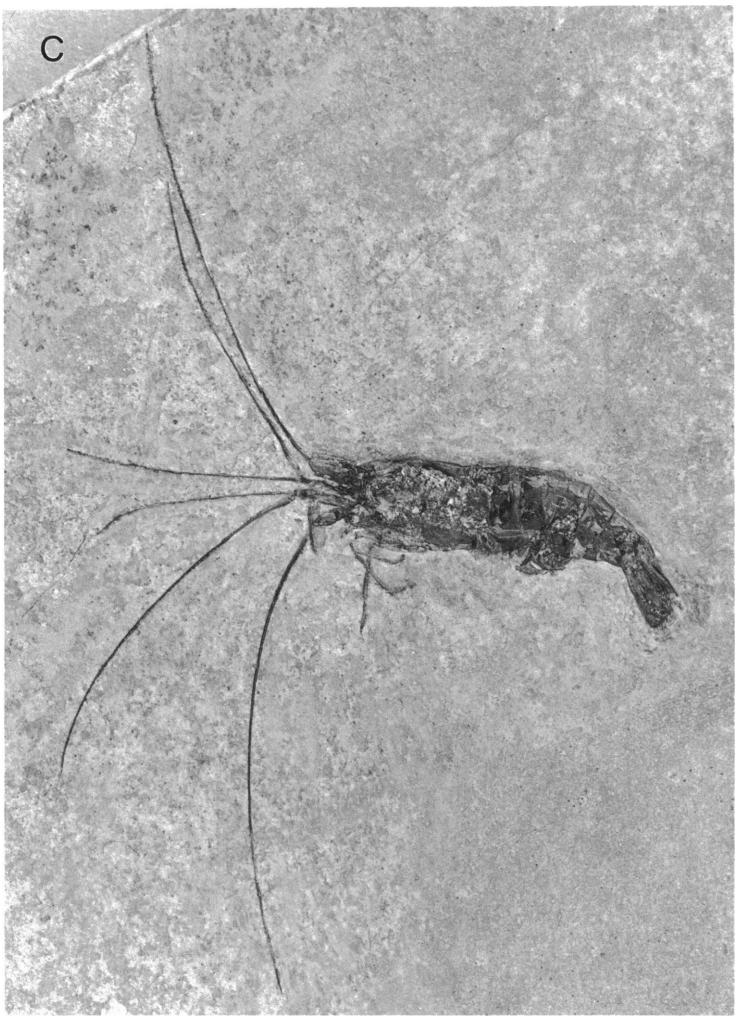

Fig. 6. Continued.

tral spines on the carapace (the posteriormost postrostral spine is very small). Each spine is evenly spaced from the next, giving the rostrum a serrated appearance dorsally. The distal half of the rostrum has no dorsal spines. Ventrally the rostrum has three spines, the first lying almost halfway along the ventral margin, below the anteriormost dorsal spines. The other two ventral spines are located anterior to all the dorsal spines. Rostral morphology in *Beurlenia* is profoundly different from that found in *Paleomattea* from concretions in the Romualdo Member of the Santana Formation.

The second pereiopod is enlarged in comparison with the others (Martins-Neto and Mezzalira, 1991) and in AMNH 44990 its chela is clearly visible. It does not bear a terminal brush of hairs. The third and subsequent pereiopods lack chelae. It is difficult to observe the coxal and basal segments of the pereiopods, but the visible ones seem to lack exopods. Multisegmented pleopods like those of the holotype are visible in AMNH 44984 and 44991.

According to Martins-Neto and Mezzalira (1991) the telson in *Beurlenia* has a single apical "spine," and this is confirmed in both

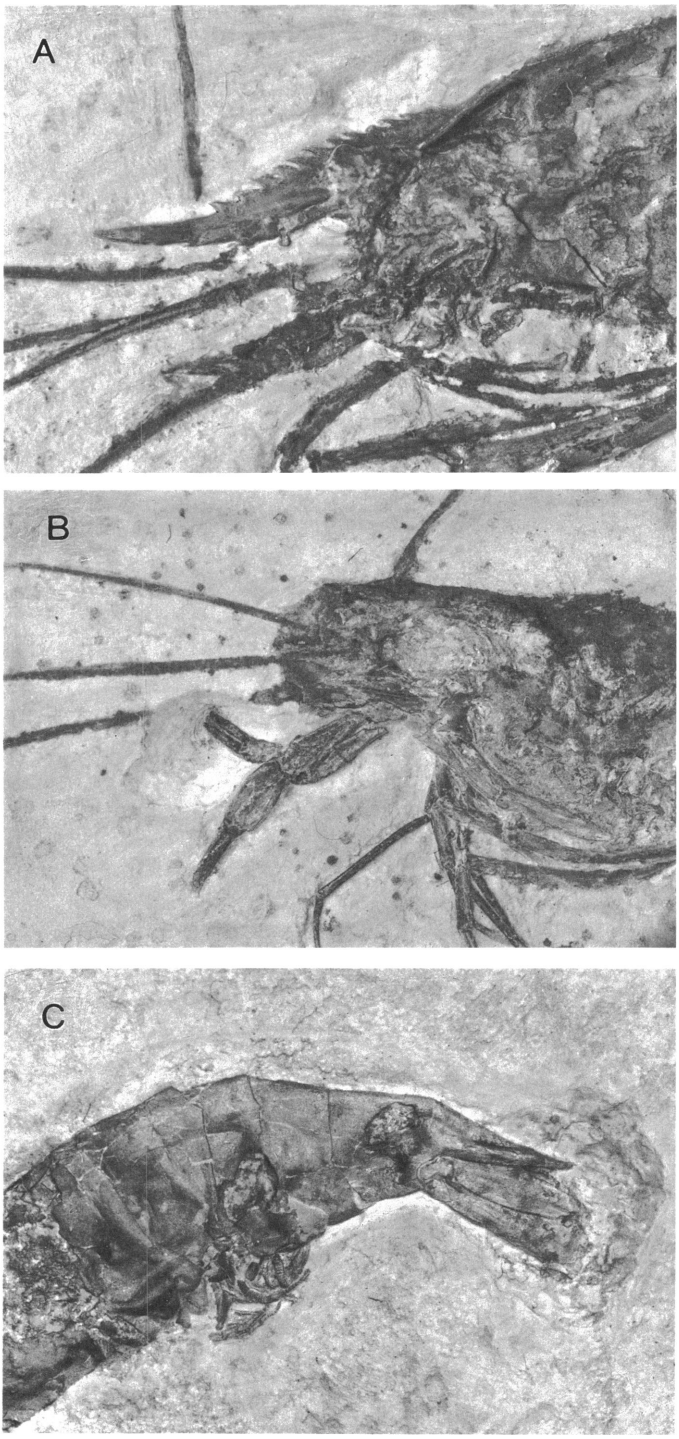

Fig. 7. Details of *Beurlenia araripensis*: **(A)** rostrum of AMNH 44984, × 5.0; **(B)** chelae of AMNH 44990, × 5.8; **(C)** telson of AMNH 44991, × 4.25.

AMNH 44990 and 44991. In actual fact this "spine" is little more than an acuminate median process on the telson, however, not an articulated spine. We have found no evidence for articulated spines or setae on the telson in *Beurlenia.* Among Recent palaemonid decapods, the subfamily Palaemoninae is characterized by two pairs of articulated spines and two or more setae (a fixed median spine may also be present), while the subfamily Pontoniinae has three pairs of articulated spines on the posterior margin of the telson (Kensley, 1972). On this basis, therefore, *Beurlenia* cannot be referred to either of these Recent subfamilies. It is possible that some articulated spines or setae were originally present, but are absent in the fossils because of preservational factors. Absence of articulated spines, if real, would exclude these fossils from the Palaemonidae.

Martins-Neto and Mezzalira (1991) referred *Beurlenia* to the family Palaemonidae (glass prawns). They claimed that the enlarged second abdominal segment, whose pleura overlap both the first and third segment, represents an apomorphic character of Palaemonidae and Udorellidae. This overlap pattern is confirmed in AMNH 44990 and (less clearly) in AMNH 44991. Elsewhere this feature has been cited as a character of all caridean decapods (Glaessner, 1969: 414, 451). If that is true, this character cannot represent a synapomorphy of palaemonids and udorellids only. Burkenroad (1981) also found the same overlap pattern in some Reptantia, where it may have arisen independently.

According to Glaessner (1969), palaemonids are characterized by antennules mostly with three flagellae, having the chelae of the second pereiopods stronger than those of the first, and the absence of exopods on all pereiopods. Triflagellate antennules also occur in some extinct hoplocarids; they are otherwise unknown among phyllocarids and other malacostracan groups, suggesting that they are convergent and apomorphic (Kunze, 1983). According to Martins-Neto and Mezzalira (1991) the holotype of *Beurlenia araripensis* is biflagellate. We have confirmed this condition in AMNH 44991 (fig. 4C), and *Beurlenia* thus lacks the triflagellate antennule condition of most modern palaemonids.

Certain characters shared by *Beurlenia* and Recent palaemonid decapods are phylogenetically informative only at a more general (i.e., caridean) level (e.g., overlap pattern of abdominal segments, relatively large second pereiopod, chelae absent from third and subsequent pereiopods). In *Beurlenia,* exopods are absent from the pereiopods and a terminal brush of hairs on the chelae apparently is absent, as in Recent gnathophyllid and palaemonid decapods. In gnathophyllids the third maxilliped is expanded and leaflike, but it is not expanded in palaemonids. This combination of characters does not unite *Beurlenia* conclusively with palaemonids, because these similarities do not represent apomorphic palaemonid characters. Some features frequently found in Recent palaemonids are absent in *Beurlenia* (e.g., triflagellate antennules, two or more pairs of terminal spines on the telson). Also, characters of the Recent palaemonid subfamilies Palaemoninae and Pontoniinae are either absent (e.g., paired telson spines) or else unknown (e.g., presence or absence of a pleurobranch on the third maxilliped).

Although *Beurlenia* has general caridean features, at present there is no definitive morphological evidence to support its inclusion either within the caridean family Palaemonidae or its Recent subfamilies. If *Beurlenia* is a palaemonid, it is extremely primitive. Among Recent carideans, only members of the Palaemonidae and Atyidae are known to frequent fresh water, and *Beurlenia* lacks characters which would unite it with atyid decapods (a very primitive family). The lacustrine occurrence of *Beurlenia* in the Crato Member of the Santana Formation thus offers circumstantial paleoecological support to the idea that this genus is a palaemonid. It is nevertheless possible that *Beurlenia* is not a palaemonid but belongs instead to some other caridean family that frequented freshwater habitats during the Lower Cretaceous.

CONCLUSIONS

1. Small shrimps recovered from concretions of the Romualdo Member are identified as a new genus and species of sergestid, *Paleomattea deliciosa.* They are the first known fossils referred to the family Sergestidae, and therefore also represent its earliest fossil oc-

currence. These shrimps were abundant and frequently were eaten by the teleost fish *Rhacolepis*; they therefore provided an important base to the trophic system within a shallow sea that occupied the Araripe Basin during Romualdo Member times.

2. Larval brachyurans formed part of the planktonic community during that time, and provided a food source for the gonorynchiform fish *Tharrhias*. The presence of larval brachyurans provides additional evidence for a marine environment. One genus of portunoid crab (*Araripecarcinus*) is known from the Romualdo Member, but we cannot determine whether the larvae described here belong to that genus.

3. Decapods in the stomach contents of *Rhacolepis* and *Tharrhias* suggest that these fishes probably did not compete for the same food source. Many *Rhacolepis* preferred to feed on *Paleomattea,* probably close to the benthic substrate, whereas *Tharrhias* was apparently a plankton feeder and ate (among other things) larval brachyurans.

4. Martins-Neto and Mezzalira (1991) claimed that *Beurlenia araripensis* was a palaemonid decapod, although it lacks several important characters of this group. It is a rare caridean in the lacustrine fauna of the Crato Member. Its freshwater occurrence offers only circumstantial indication of palaemonid affinity, and alternative relationships among carideans should be considered.

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