



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

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 pereopods stronger than those of the first, and the absence of exopods on all pereopods. 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 arripensis* 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 pereopod, chelae absent from third and subsequent pereopods). In *Beurlenia*, exopods are absent from the pereopods 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, *Pa-leomattea 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 *Palaemon*, probably close to the benthic substrate, whereas *Tharrhias* was apparently a plankton feeder and ate (among other things) larval brachyurans.

4. Martins-Neto and Mezzalana (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.

#### ACKNOWLEDGMENTS

We thank Dr. Herbert R. Axelrod for generously providing the fossil specimens on which we based this research. Thanks are extended to Robert Evander for acid preparation of fossil fishes at the American Museum of Natural History, and to William Emerson and Ivy Rutzky for their help with literature on decapods; Ivy also drafted the map. Alexander Kellner took the photograph of *Palaemon* in the stomach of *Rhacolepis*, and Lorraine Meeker prepared the photographs of *Beurlenia*. Useful reviews and comments were provided by Gale Bishop (Georgia Southern University), Sandy Bruce (Northern Territory Museum of Arts and Sciences, Australia), and Alan Harvey (Department of Invertebrates, American Museum of Natural History).

#### REFERENCES

- Arai, M., and J. C. Coimbra  
1990. Análise paleoecológica do registro das primeiras ingressões marinhas na Formação Santana. Atas do 1 Simpósio Bacia do Araripe 1990: 225–239.
- Beurlen, K.  
1963. Geologia e estratigrafia da Chapada do Araripe. XVII Congr. Brasileiro Geol. Publ. SUDENE: 1–47.
- Bliss, D. E.  
1982. Shrimps, lobsters and crabs. Piscataway, NJ: New Century.
- Burkenroad, M. D.  
1981. The higher taxonomy and evolution of Decapoda (Crustacea). Trans. San Diego Soc. Nat. Hist. 19: 251–268.
- Glaessner, M. F.  
1969. Decapoda. Arthropoda 4. Part R. Vol. 2. In R. C. Moore (ed.), Treatise on invertebrate palaeontology. Lawrence: Univ. Kansas Press.
- Gore, R. H.  
1985. Molting and growth in decapod larvae. In A. M. Wenner (ed.), Crustacean Issues 2. Larval growth, pp. 1–65. Rotterdam & Boston: A. A. Balkema.
- Grimaldi, D. A., and J. G. Maisey  
1990. Introduction. In D. A. Grimaldi (ed.), Insects from the Santana Formation, Lower Cretaceous, of Brazil. Bull. Am. Mus. Nat. Hist. 195: 5–14.
- Gurney, R.  
1942. Larvae of decapod crustacea. London: Ray Society.
- Kellner, A. E. W., J. G. Maisey, and R. L. Evander  
1994. Ein besonderes Fossil: die Henkersmalzeit eines Fisches aus der Kreide. Paläontol. Z. 68: 1–3.
- Kensley, B.  
1972. Shrimps and prawns of South Africa. Cape Town: South African Museum.
- Kunze, J. C.  
1983. Stomatopoda and the evolution of the Hoplocarida. In F. R. Schram (ed.), Crustacean phylogeny, pp. 165–188. Rotterdam: A. A. Balkema.
- Maisey, J. G.  
1990. Stratigraphy and depositional environ-

- ment of the Crato Member (Santana Formation, Lower Cretaceous of N.E. Brazil). In D. A. Grimaldi (ed.), *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. Bull. Am. Mus. Nat. Hist. 195: 15–19.
1991. *Santana fossils: an illustrated atlas*. Neptune, NJ: T.F.H. Publications.
1993. Tectonics, the Santana lagerstätten, and the implications for Late Gondwanan biogeography. In P. Goldblatt (ed.), *Biological relationships between Africa and South America*, pp. 435–454. New Haven: Yale Univ. Press.
1994. Predator-prey relationships and trophic level reconstruction in a fossil fish community. *Environ. Biol. Fishes* 40: 1–22.
- Marck, W.  
1863. Fossile Fische, Krebse und Pflanzen aus dem Plattenkalke der jüngsten Kreide in Westphalen. *Palaeontographica* 11: 1–83.
- Martins-Neto, R. G.  
1987. Primeiro registro de decápode na Formação Santana, bacia do Araripe (Cretáceo Inferior), Brasil. *Ciênc. Cult.* 39: 406–410.
- Martins-Neto, R. G., and S. Mezzalana  
1991. Descrição de novos crustáceos (Caridea) da Formação Santana, Cretáceo Inferior do Nordeste do Brasil. *An. Acad. Brasileira Ciênc.* 63: 155–160.
- Pons, D., P. Y. Berthou, and D. A. Campos  
1990. Quelques observations sur la palynologie de l'Aptien Supérieur et de l'Albien du bassin d'Araripe (NE du Brésil). *Atas do 1 Simpósio Bacia do Araripe 1990*: 241–252.
- Wilby, P. R., and D. M. Martill  
1992. Fossil fish stomachs: a microenvironment for exceptional preservation. *Hist. Biol.* 6: 25–36.
- Williamson, D. I.  
1969. Names of larvae in the Decapoda and Euphausiacea. *Crustaceana* 16: 210–213.





Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates*, *Bulletin*, and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: [scipubs@amnh.org](mailto:scipubs@amnh.org)