

THE GONORYNCHIFORM FISH *DASTILBE* FROM THE LOWER CRETACEOUS OF BRAZIL

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ABSTRACT. We examine the preservation, autecology and morphological variation for several characters of the Cretaceous gonorynchiform fish *Dastilbe* from the Lower Cretaceous of Brazil and Africa. More than 83 specimens were examined. We test species validity using characters of the caudal endoskeleton and meristic counts of fin-rays vs length. Evidence provided by fossilized soft tissues and slabs containing large individuals 'freeze framed' in the process of swallowing smaller prey meals, show that *Dastilbe* was predatory, at least as adults, as well as cannibalistic. *Dastilbe* was probably an anadromous fish tolerant of hypersalinity and in Araripe was subjected to frequent mass mortality events. Observations of the otic region indicate that the lagenar statolith is consistently larger than the saccular statolith, hence revealing a primitive actinopterygian condition. For the first time, a lagenar statolith from *Dastilbe* has been cleaved to expose putative annuli-like ridges. Our results clearly show that there is a wide degree of morphological plasticity of the endoskeleton coupled with wide meristic variation, and as such, overall length, fin-ray count and even absence or presence of caudal diastema are not suitable criteria for species recognition in *Dastilbe*. New specimens from the Crato Formation (Aptian) and statistical tests suggest rejection of all species of *Dastilbe* erected subsequent to Jordan (1910). All Brazilian specimens of Lower Cretaceous *Dastilbe* can be assigned to the single species *D. crandalli* Jordan. The African *D. batai* Gayet is also placed within *D. crandalli*.

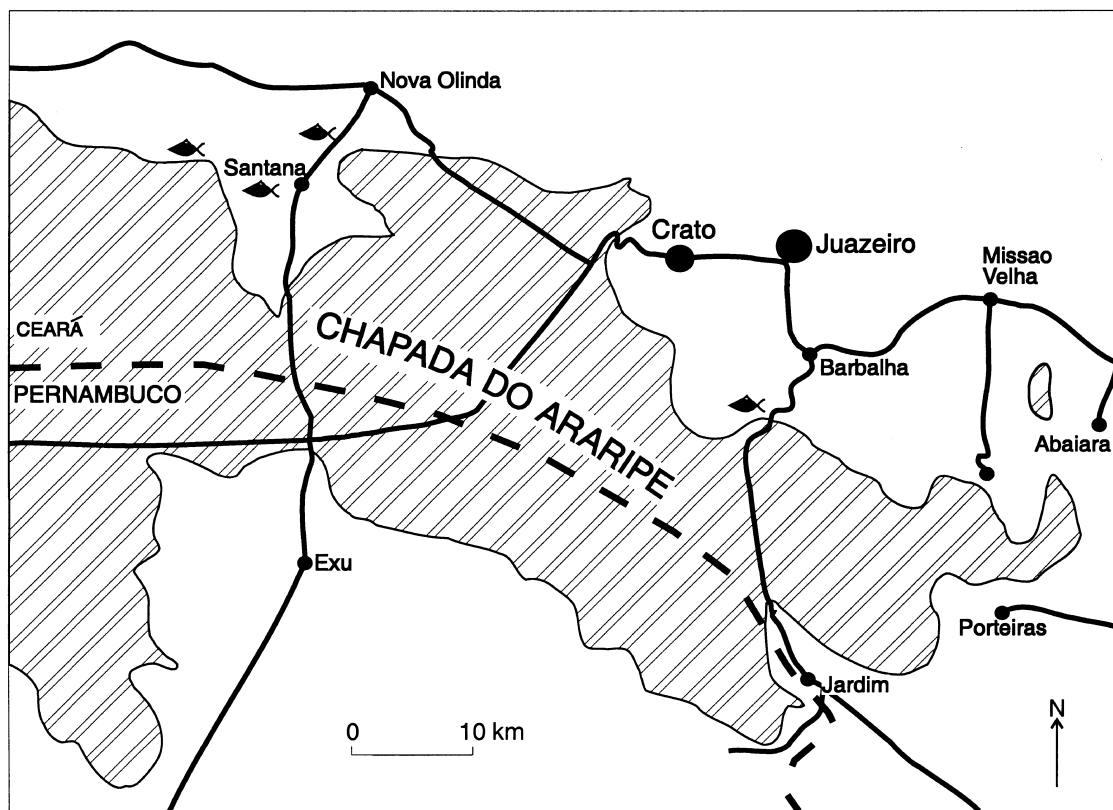
DASTILBE, a primitive gonorynchiform fish, was widespread in Gondwanaland. It occurs in abundance in some Early Cretaceous formations of north-east Brazil and has also been reported from the Lower Cretaceous of Africa (Gayet 1989). In recent cladistic analyses Grande and Poyato-Ariza (1995), Grande (1996), and Poyato-Ariza (1996) placed *Dastilbe* within the order Gonorynchiformes, an extant, morphologically and ecologically diverse assemblage of ostariophysan fishes. Today this order comprises 11 genera of about 50 species. Living gonorynchiforms inhabit both marine and freshwater environments in south-east Asia, Africa and the Indo-Pacific; extinct species are known from the Americas, Europe, the Middle East, Australia and possibly China (Grande 1996). *Dastilbe* appears to be restricted to the Early Cretaceous. Since its discovery by Branner in 1907 (Jordan 1910) *Dastilbe* has been subject to numerous taxonomic interpretations. Jordan (1910) erected the genus and described the type species *D. crandalli* allying it with the European Eocene clupeomorph *Halecopsis*. Taverne (1981) allied *Dastilbe* with the Lower Cretaceous *Aethalionopsis robustus* which he placed in the Gonorynchiformes. Furthermore, he suggested that *Parachanos* and *Dastilbe* might be congeneric (Taverne 1981, p. 974). However, Poyato-Ariza (1996, p. 41) showed that *Parachanos* and *Dastilbe* were indeed distinct at the generic level. Gayet (1989) included *Dastilbe* within a distinct order, Chaniformes. Blum (1991), Duarte and Silva-Santos (1993) and Grande (1996) retained *Dastilbe* within the Gonorynchiformes. Four species of *Dastilbe* have been described. *D. crandalli* from the Riacho Doce Formation (Lower Cretaceous) of Alagoas, Brazil is the type species and was described by Jordan (1910). *D. elongatus* was first described by Silva Santos (1947) on the basis of a single example from the Early Cretaceous Codó Formation of Maranhao (Duarte and Silva Santos 1993). However the first figures of this taxon were provided by Silva Santos (1947) of specimens from the Crato Formation at Sitio Romualdo, near Crato, Ceará. Blum (1991) considered DNPM (Departamento Nacional Producao Mineral, Rio de Janeiro, Brazil) 176-P from the Crato Formation to be a lectotype, presumably because the original specimen from Maranhao had

been lost; *D. morãesi* from the Lower Cretaceous of Minas Gerais was described by Silva Santos (1955); *D. batai* from the Lower Cretaceous of Equatorial Guinea was described by Gayet (1989).

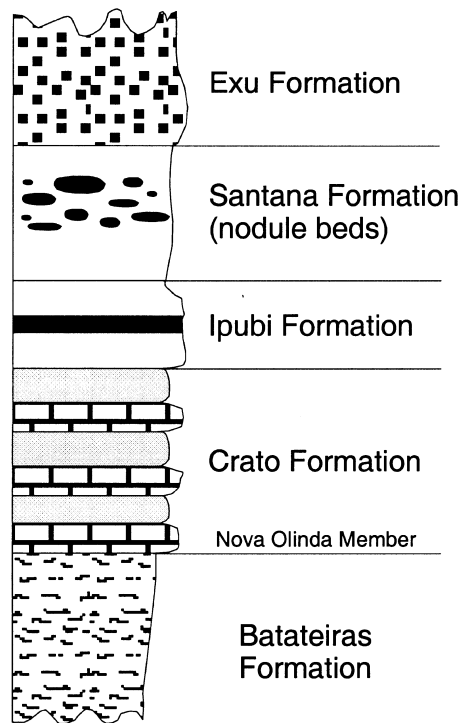
LOCALITY AND STRATIGRAPHY

The analysis provided here is based on the examination of a large number of individuals of a variety of age classes from the Nova Olinda Member of the Crato Formation, Ceará, Brazil. *Dastilbe* is the most abundant vertebrate fossil in the Nova Olinda Member which crops out on the northern, eastern and south-eastern slopes of the Chapada do Araripe (Araripe Basin) in the states of Ceará and Pernambuco (Text-fig. 1). In this basin *Dastilbe* appears to be restricted to the Nova Olinda Member, but it also occurs in a black shale at the western end of the outcrop which may be a lateral equivalent of the Nova Olinda Member at Ipubi and Rancheria (Text-fig. 2). The Nova Olinda Member comprises a sequence of laminated limestones which lacks a benthic fauna, but is rich in insects, plants and rare tetrapods (Martill 1993).

Problems with dating the sediments of the Araripe Basin have been a source of contention amongst stratigraphers, but workers agree that the basin's chronology is closely linked to rifting events associated



TEXT-FIG. 1. Map of the eastern end of the Chapada do Araripe in Ceará and Pernambuco, north-east Brazil. Fish symbols indicate sites where *Dastilbe* has been collected from the Nova Olinda Member of the Crato Formation. Hatching indicates outcrop of the Cenomanian Exu Formation. The Nova Olinda Member crops out on slopes below this unit and in places is obscured by landslips from it.



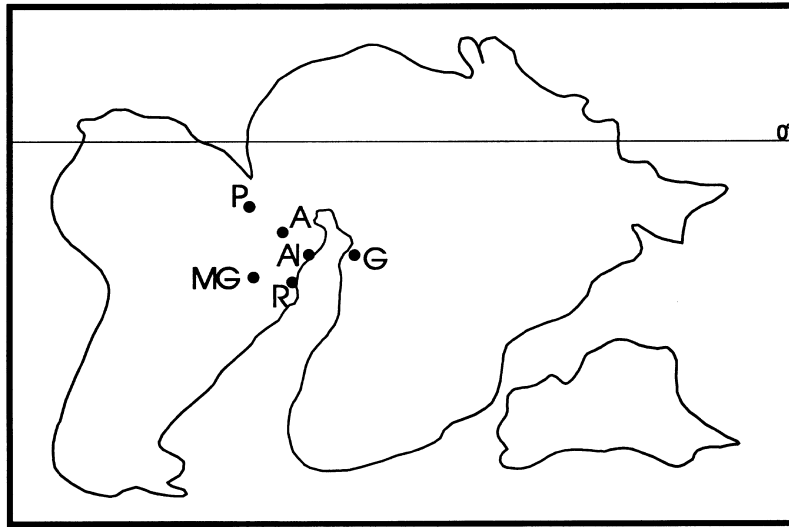
TEXT-FIG. 2. Simplified stratigraphical section showing the position of the Nova Olinda Member within the Crato Formation and its relationship to the famous Santana Formation fossil *konservat Lagerstätte*. *Dastilbe* is known definitely only from the Crato Formation (Aptian) in the Araripe Basin, but the closely related *Tharrhias* is abundant in nodules from the Santana Formation (Albian) above (Maisey 1991; Martill 1993). The Nova Olinda Member is c. 6 m thick. Sediments of the Ipubi Formation are highly variable in thickness, as is the Santana Formation. Despite the variation in thickness, this sequence is typical for most parts of the eastern end of the chapada, except where overlap onto the Precambrian basement occurs.

with the opening of the South Atlantic Ocean during the Mid Jurassic to the Early Cretaceous (Berthou 1990). The youngest surviving sediments are probably Cenomanian (Berthou 1990; Martill 1993) and Pons *et al.* (1990) considered the Crato Formation to be Aptian on palynological grounds. More recently Berthou *et al.* (1994) suggested a latest Aptian to early Albian age for that part of the sequence containing the Nova Olinda Member.

The Crato Formation comprises a diverse suite of sedimentary rocks including oil shales, variegated clays, sandstones and limestones (Martill 1988, 1993). Some marginal environments include quartzite pebble conglomerates and brecciated laminites. The Crato Formation rests conformably on a variety of sedimentary rocks due to previous environmental diversity prior to the development of the Crato lagoon (Martill and Wilby 1993). Salinity levels fluctuated, but were probably elevated during deposition of the Nova Olinda Member.

The Nova Olinda Member comprises a 6–8 m thick sequence of laminated limestones, pisolites and occasionally stromatolites. This basal member of the Crato Formation is mined in the region of Nova Olinda-Santana do Cariri and Tatajuba, and also at Crato. Most of the fossils are obtained by the miners and sold to local dealers.

The majority of this unit is made up of millimetrically laminated limestones with shale partings in the basal metre. *Dastilbe* is extremely abundant in the unit in the region of Nova Olinda and Santana do Cariri, but elsewhere in the Araripe Basin it is less common (see Text-fig. 1). *Dastilbe* has been reported



TEXT-FIG. 3. Simplified reconstruction of Gondwanaland for the Late Albian/Early Cenomanian with sedimentary basins yielding *Dastilbe*. Continental configuration based loosely on Smith *et al.* (1981); locality data from Brito (1984). A, Araripe for *D. crandalli* and *D. elongatus*; Al, Alagoas for *D. crandalli*; G, Equatorial Guinea for *D. batai*; MG, Minas Gerais for *D. morães*; P, Parnaíba for *D. elongatus*; R, Recôncavo for *Dastilbe* sp. Note that we retain a terrestrial link between South America and Africa for the Late Albian.

from the Lower Cretaceous of Maranhão, Alagoas and Minas Gerais in Brazil (Jordan (1910), Silva Santos (1947, 1955), Duarte and Silva Santos (1993)) and near Bata, Equatorial Guinea (Gayet 1989) (Text-fig. 3).

MATERIALS AND METHODS

Materials. Eighty-three examples of *Dastilbe* were examined; the largest sample size analysed to date. Forty-three are housed in the University Museum of Zoology, Cambridge, England (UMZC). Specimen numbers from this collection range from UMZC GN1108 to UMZC GN1127 and UMZC GN1128a to UMZC GN1128t. Some slabs had more than one example on them. The remaining 40 specimens are housed in the School of Earth, Environmental and Physical Sciences, University of Portsmouth. Specimen numbers are UOP 98/1–98/33. Again, some of these slabs contained more than one fish. All were from unspecified horizons within the Nova Olinda Member. The fossils have undergone various degrees of weathering and are preserved on buff-coloured slabs of laminated limestone. Individuals range from 9–210 mm maximum length. Most are complete individuals preserved articulated, but flattened. Few specimens were incomplete due to taphonomic processes. Two were used for scanning electron microscope investigations. Specimens cited (but not examined) in text with abbreviation AMNH are from the American Museum of Natural History, New York, USA.

Methods. Specimens were examined by light microscopy and scanning electron microscopy. Some fossils required matrix removal before examination to reveal diagnostic features. This was achieved by using mounted entomological needles in concert with a fine paint brush to remove thin layers of limestone. In addition, two were coated on one side with polyvinyl butyrol, and the matrix removed by immersion in 10 per cent. acetic acid to reveal the unweathered side. Specimens were then examined using a Wild microscope with attached Zeiss *Camera lucida* drawing arm.

For SEM analysis we used a JEOL JSM-5410LV scanning electron microscope. Specimens were

mounted on flat-topped stubs and sputter coated with gold. Some specimens were examined uncoated in an environmental chamber and examined under low vacuum. Photographs were made using a back scatter detector.

PRESERVATION

At most exposures the Nova Olinda Member is deeply weathered, with specimens of *Dastilbe* appearing dark brown/orange (goethite stained). In unweathered exposures the bones appear black. The bones are preserved in their original biomineral but may be coated in diagenetic pyrite (the weathering of this gives rise to the brown stained specimens in weathered outcrops), or more rarely, surrounded by a halo of dendritic pyrolusite (Pl. 4, fig. 6).

Specimens are usually complete, and mostly preserved lying on their side (Pl. 1, figs 1, 4–5). More rarely specimens may be preserved in a dorso-ventral position (Pl. 2, fig. 7) and some laterally preserved specimens may show displacement of the pelvic and pectoral girdles into a dorso-ventral position (Pl. 4, fig. 4). Some slabs of limestone display several specimens of similar size on the same bedding plane (Pl. 2, figs 5–6). Field excavations of these bedding planes yield hundreds, if not thousands, of specimens on the same surface suggesting mass mortality. The specimens are not usually closely packed, as in other mass mortality fish beds (e.g. Grande 1984). Specimens in which the skull is partly detached from the body are common (12 out of 81 complete specimens) and are indicative of decay during some post-mortem drifting (Pl. 2, fig. 2). Isolated bones as well as isolated portions of articulated material also occur in the limestone matrix (Pl. 2, fig. 5; Pl. 3, fig. 2). Specimens in which the skeleton is associated, but disarticulated, are unknown. This is in marked contrast to famous fish-bearing *konservat Lagerstätten* such as the Eocene Green River Formation (Grande 1984) and the Romualdo Member of the Cretaceous Santana Formation (Martill 1993) where both articulated and disarticulated fishes are abundant. A single example of a rounded mass of *Dastilbe* bones might represent an example of a coprolite or regurgitated bolus (Pl. 3, fig. 4).

Some larger examples of *Dastilbe* are found with smaller examples in their stomachs (Pl. 1, figs 1–2, 4) indicating cannibalistic behaviour. No remains have been found in the stomach region of small individuals.

Preservation of soft tissues

Small (c. 40–50 mm) *Dastilbe* specimens occasionally show preservation of epaxial and hypaxial musculature of the trunk and caudal peduncle. This material commonly appears orange-brown and is unlike the muscle tissue preservation of fishes from the Santana Formation. Muscle fibres can be seen but are somewhat indistinct, although the boundaries between muscle blocks are apparent (Text-fig. 4A). Scanning electron microscopy failed to reveal high fidelity preservation (Text-fig. 4B). The mineral preserving the soft tissues in the weathered specimens is goethite, probably after pyrite. Some specimens show patches of amorphous calcium phosphate, but these do not appear to be preserving soft tissues. Five specimens exhibit muscle tissue preservation (UMZC GN1128g, GN1128l, GN1128o, UOP98/6, UOP98/20). In these specimens the musculature is arranged in typical chevron-shaped myomeres. In UMZC GN1128j a trace of the gut is seen, although no clearly distinguishable gut contents were observed.

Preservation of otoliths

Otoliths only occur rarely *in situ* within fossil fishes, although they may be abundant as isolated microfossils. This apparent rarity might in part be due to a reluctance of curators to allow complete articulated skulls to be dissected, or due to dissolution during acetic acid preparation (Clack 1996). However, it may be the case that the usually aragonitic nature of otoliths allows for their early dissolution during the fossilization process. Ellipsoidal statoliths are present in about half of the *Dastilbe* specimens observed in this study. A lagenar statolith was excised and cleaved to reveal

annuli-like ridges. When present, the posterior-most lagenar statolith was larger than the more anterior saccular statolith (Pl. 4, fig. 1). This primitive actinopterygian configuration of large lagenar statolith and smaller saccular statolith (Coates 1998), supports the supposition proposed by Rosen and Greenwood (1970, p. 15) that the 'ancestor of these two groups' [Gonorynchiformes and ostariophyans] might show a large lagenar otolith. This condition might have been predicted for *Dastilbe* as, in the cladistic analysis of Gonorynchiformes of Grande (1996) *Dastilbe* 'fell out' as being 'primitive' for the group.

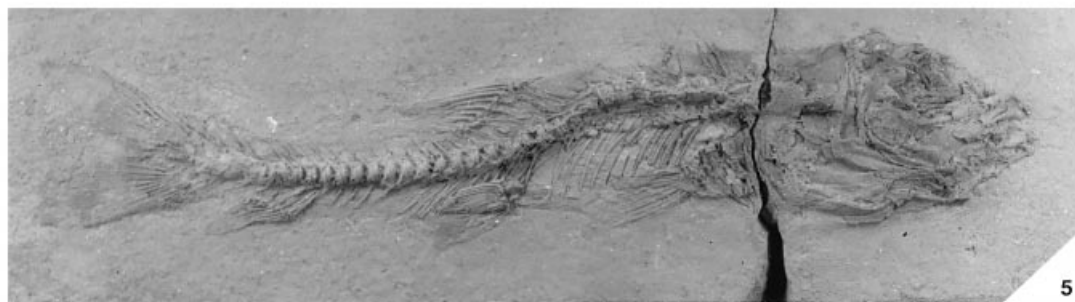
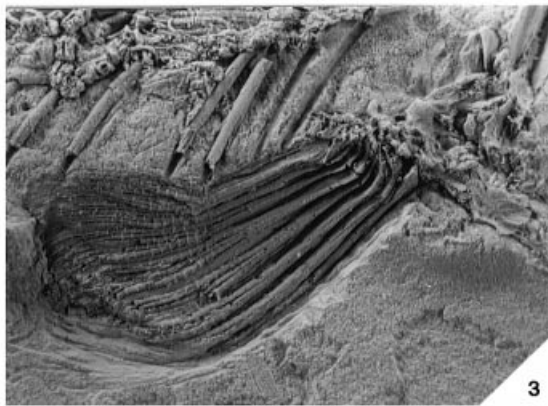
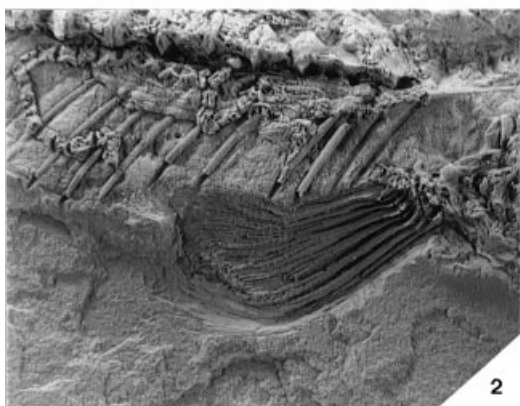
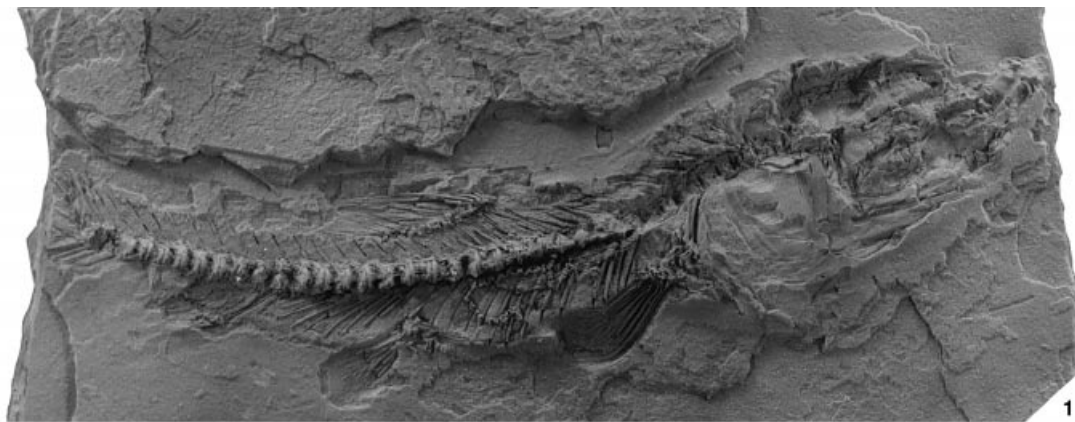
AUTECOLOGY

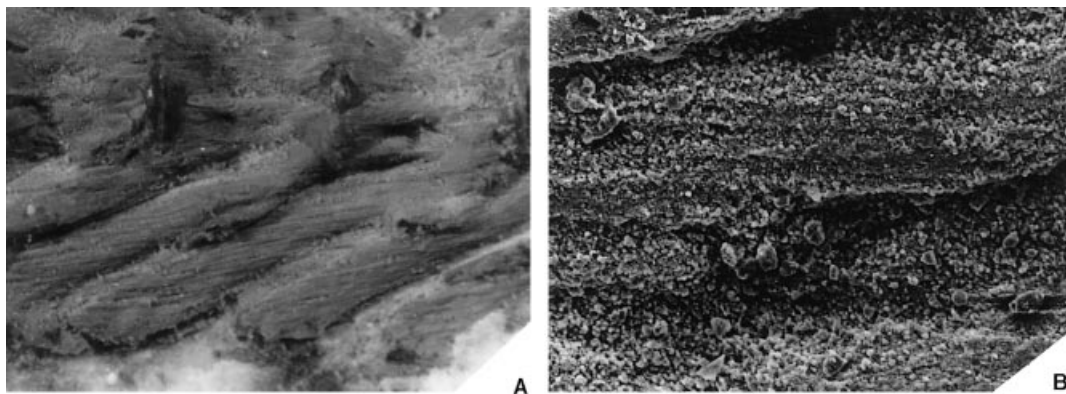
This analysis pertains only to populations of *Dastilbe* from the Nova Olinda Member of the Crato Formation. Populations of *Dastilbe* from other formations may reflect different structures and autecologies. We have attempted to propose a holistic model that explains the distribution and co-occurrence of fossils and sedimentary structures in the Nova Olinda Member. Although *Dastilbe* is the most abundant fish in the Nova Olinda Member of the Crato Formation, two other fish taxa have been reported occurring in the same assemblage; *Cladocyclus* sp. (Maisey 1996) and cf. *Araripelepidotes* sp. (Brito *et al.* 1998), both of which are extremely rare. The salinity tolerance of *Dastilbe* is unclear, but it is widely assumed to have been a freshwater fish (Maisey 1991; Martill 1993). This interpretation of the salinity tolerance of *Dastilbe* is based on the complete absence of typical marine invertebrates in the Crato Formation, the paucity of fish species compared with the slightly younger Santana Formation ichthyofauna of the same basin, and the presence in the Nova Olinda Member of abundant larval ephemeropterans. However, the sediments of the Nova Olinda Member were most probably deposited in a saline basin (Martill 1993; Martill and Frey 1998). Evidence for this is found in salt pseudomorphs and the lack of 'normal' benthic freshwater organisms such as ostracods and freshwater gastropods. The absence of 'normal' shelly aquatic invertebrates in the Nova Olinda Member fossil assemblage is attributed to their absence in the basin, rather than non-preservation. The preservation of otoliths in *Dastilbe* suggests that if ostracods and gastropods had been present, they surely would have been preserved. Of the supposed autochthonous invertebrates, only the larvae of Ephemeroptera are suggestive of the presence of freshwater. Martill (1993) supposed that *Dastilbe* inhabited a surface layer of fresh water supported above a halocline in front of a river entering the Araripe Basin and that disturbance of this surface layer by storm activity would have broken down the halocline and may have been the underlying cause of the mass mortalities. The extant gonorynchiform *Chanos chanos* (the milkfish) of the Indopacific region is euryhaline, and has a 'remarkable' tolerance of hypersaline waters (Herald 1961, cited in Patterson 1984). Hypersalinity of all but the surface waters during deposition of the Nova Olinda Member would explain the rarity, or for most of the time absence, of fishes of either normal marine salinity habit or freshwater habit. A hypersalinity tolerance for *Dastilbe* would allow it to withstand the elevated salinities of the lagoon, and allow it to feed on freshwater organisms in the surface layer.

Dastilbe lacks marginal teeth on the jaws (Pl. 2, fig. 3), even in large individuals (Pl. 1, fig. 5). The presence of small fishes within the guts of only the larger individuals suggests that *Dastilbe* was microphagous on soft-bodied organisms, and perhaps algae until it reached 'maturity'. Only individuals

EXPLANATION OF PLATE 1

Figs 1–5. *Dastilbe crandalli* Jordan 1910; Nova Olinda Member, Crato Formation, Nova Olinda, Ceará, north-east Brazil. 1–3, UOP 98/11; large individual with small specimen of *Dastilbe* within stomach region; $\times 0.9$. 2, close-up of stomach region, showing contorted vertebral column of prey item; $\times 1.4$. 3, close-up of pectoral fin, showing ten pectoral fin rays; $\times 2.5$. 4, UOP 98/34; large example of *Dastilbe* with small *Dastilbe* in mouth. Both specimens identified on basis of caudal endoskeleton and general appearance; $\times 0.9$. 5, UOP 98/7; largest example of *Dastilbe*, with standard length of 180 mm; $\times 0.75$.





TEXT-FIG. 4. Soft tissue preservation in *Dastilbe crandalli* Jordan, 1910. A, light microscope photograph of UMZC GN11280 showing chevron-shape trunk musculature; $\times 12$. B, scanning electron micrograph of UOP98/6 showing muscle fibres but lacking fine detail; $\times 200$.

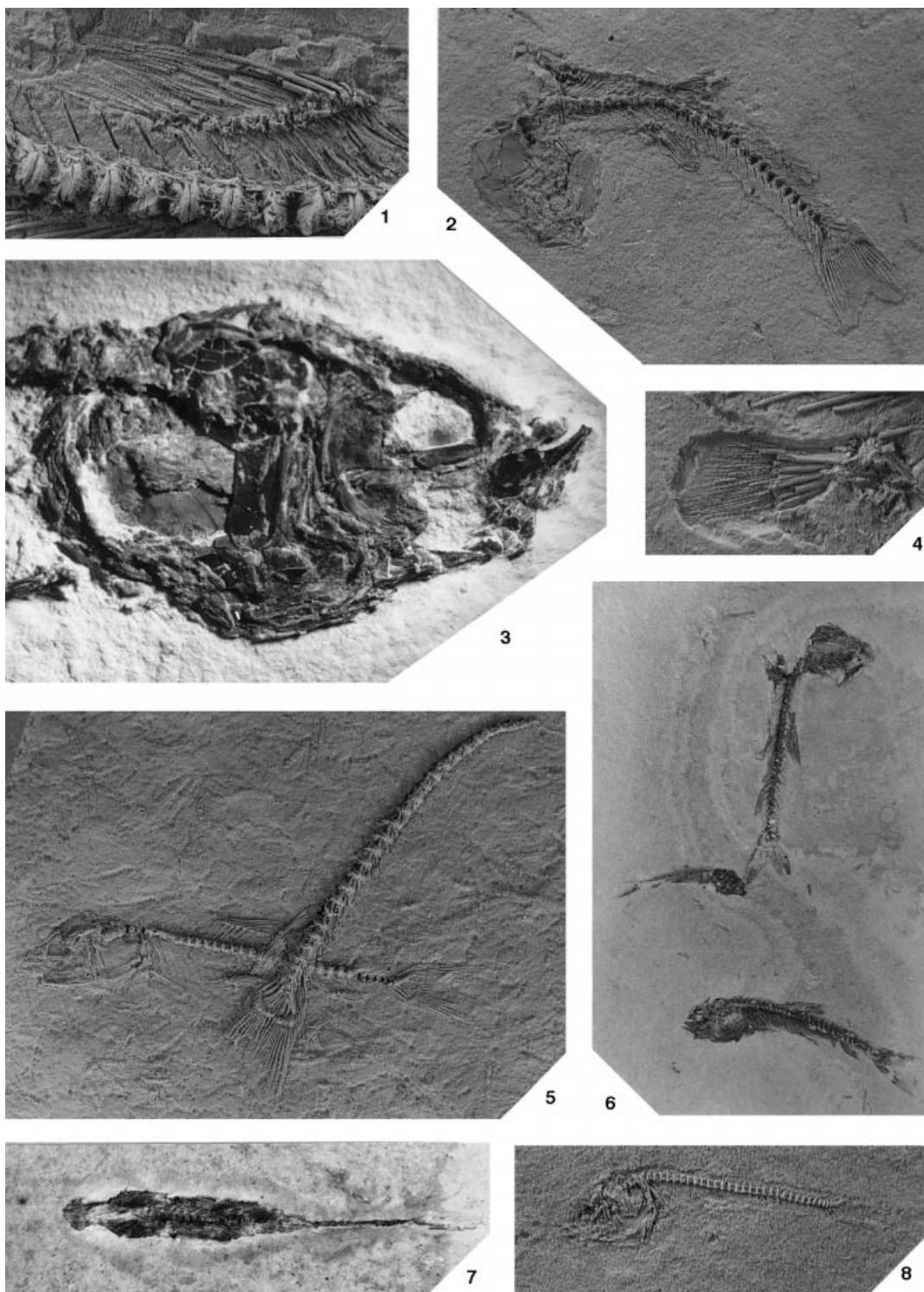
larger than ~ 150 mm standard length appear to have been piscivorous. This is still surprising considering the lack of teeth in large individuals.

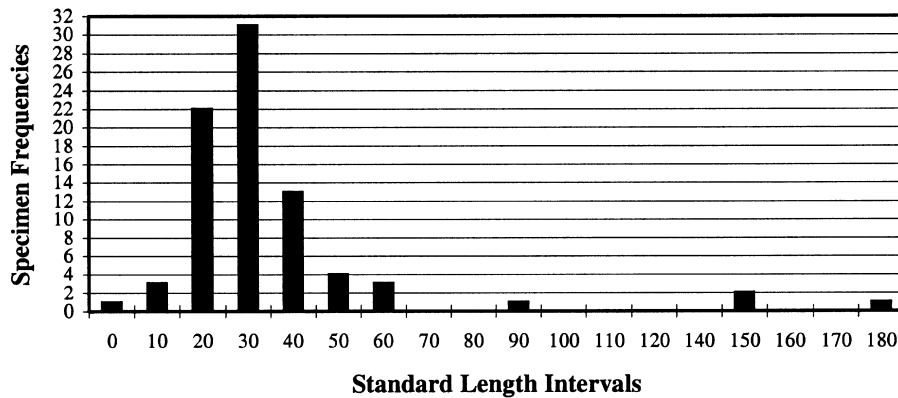
Length distribution data show a unimodal shape with a right skew (Text-fig. 5) although there are no individuals between 65 mm and 92 mm standard length, and between 92 mm and 150 mm standard length. This paucity of 'medium' sized individuals requires explanation. We believe this might indicate a migratory life cycle for this taxon. The 30 mm standard length mode may represent mortalities of individuals of one year old or younger i.e. a juvenile age class, but this cannot be confirmed, whereas the larger, but rarer, individuals presumably represent sexually mature adults. If the populations of *Dastilbe* were non-migratory, the size distribution curve would still be unimodal with a strong right skew, but perhaps more fish in the mid-size range might be expected. We cannot at this stage determine whether *Dastilbe* was anadromous or catadromous, but we speculate that if *Dastilbe* entered slightly hypersaline lagoons for reproduction (low predator numbers in the hypersaline water?) then only young individuals and large, reproductively mature specimens might be present in the lagoon. Mass deaths due to seasonally elevated salinities beyond their salinity tolerance threshold would result in fossil assemblages of young fish not large enough to have left the protective waters of the lagoon, and stray, mature individuals that had failed to leave the lagoon after spawning.

Previous suggestions that *Dastilbe* was a non-marine fish (Maisey 1991; Martill 1993) must be re-examined. At no location do we know of *Dastilbe* occurring with typical Lower Cretaceous non-marine fossils such as unionid bivalves or viviparid gastropods. Neither does *Dastilbe* occur in the basal part of the Nova Olinda Member where conchostracans are abundant.

EXPLANATION OF PLATE 2

Figs 1–8. *Dastilbe crandalli* Jordan, 1910; Nova Olinda Member, Crato Formation, Nova Olinda, Ceará, north-east Brazil. 1, UOP 98/11; dorsal fin showing ten dorsal fin rays or their external moulds; $\times 1.8$. 2, UOP 98/4; complete fish in which the head has partially detached ventrally from the trunk; $\times 1.35$. 3, UOP 98/20; head region showing toothless dentary and premaxilla; $\times 6.5$. 4, UOP 98/11; pelvic fin with nine fin rays; $\times 2$. 5, UOP 98/8; slab with one complete individual and one specimen comprising only the caudal and anal fins with vertebral column; $\times 1.3$. 6, UOP 98/3; part of mass mortality bedding plane assemblage with individuals from two year classes; $\times 0.7$. 7, UOP 98/2; specimen preserved in dorso-ventral attitude with dorsal side displayed, suggesting soft nature of original sediment; $\times 1.2$. 8, UOP 98/10; very small individual lacking all ventrally placed paired fins and anal fin; $\times 2.5$.





TEXT-FIG. 5. Histogram delineating size-frequency distribution of *Dastilbe* specimens from the Nova Olinda Member, Crato Formation. Sample size: 81. Excludes incomplete specimens UMZC GN1127 and UOP98/21.

SYSTEMATIC PALAEOLOGY

Class ACTINOPTERYGII Woodward, 1891

Superorder OSTARIOPHYSI *sensu* Rosen and Greenwood, 1970

Order GONORYNCHIFORMES *sensu* Fink and Fink, 1981

Family CHANIDAE *sensu* Poyato-Ariza 1996

Genus DASTILBE Jordan, 1910

Diagnosis. In addition to the ‘unique combination’ of characters which Poyato-Ariza (1996, p. 44) lists to support his diagnosis for *Dastilbe* we add: dorsal fin with eight to twelve fin-rays situated just anterior to pelvic fins; pectoral fins with nine to thirteen fin-rays latero-ventrally situated; pelvic fins with seven to nine fin-rays; anal fin with eight fin-rays, the first of which is very short; vertebral count 35–39; number of autogenous hypurals variable (five or six), sometimes with hypural 5 bifid. Variations in fin-ray and hypural counts is independent of specific sizes of specimens. Lagenar statolith larger than saccular statolith. Largest individuals in excess of 210 mm standard length. Smallest individual 9 mm.

Dastilbe crandalli Jordan, 1910

Plates 1–4; Text-figure 4

- 1910 *Dastilbe crandalli* Jordan p. 30, pl. 9, figs 9–13.
- 1935 *Dastilbe crandalli* Jordan, 1910; Arambourg, p. 2111.
- 1947 *Dastilbe crandalli* Jordan, 1910; Schaeffer, p. 16.
- 1947 *Dastilbe crandalli* Jordan, 1910; Silva Santos, p. 1.
- 1947 *Dastilbe elongatus* Silva Santos, p. 1, pl. 1, figs 1–4; pl. 2, figs 5–8.
- 1968 *Dastilbe elongatus* Silva Santos, 1947; Silva Santos and Velançã, p. 349.
- 1981 *Dastilbe crandalli* Jordan, 1910; Taverne, p. 973.
- 1984 *Dastilbe elongatus* Silva Santos, 1947; Wenz, p. 277.
- 1989 *Dastilbe batai* Gayet; p. 22, pl. 1, fig. 1.
- 1989 *Dastilbe elongatus* Silva Santos, 1947; Gayet, p. 23.
- 1989 *Dastilbe crandalli* Jordan, 1910; Gayet, p. 23.
- 1990 *Dastilbe elongatus* Silva Santos, 1947; Wenz and Brito, p. 337.
- 1991 *Dastilbe crandalli* Jordan, 1910; Blum, p. 274, unno’d figs on pp. 279–282.
- 1991 *Dastilbe elongatus* Silva Santos, 1947; Blum, pp. 274–283, unno’d figs on pp. 274–275, 279.

- 1993 *Dastilbe elongatus* Silva Santos, 1947; Martill, p. 52, pl. 1.
 1993 *Dastilbe elongatus* Silva Santos, 1947; Duarte and Silva Santos, p. 742, fig. 2c.
 1996 *Dastilbe elongatus* Silva Santos, 1947; Poyato-Ariza, p. 9, fig. 2a.
 1996 *Dastilbe crandalli* Jordan, 1910; Poyato-Ariza, p. 10.
 1996 *Dastilbe batai* Gayet, 1989; Poyato-Ariza, p. 10.
 1996 *Dastilbe minor*? Poyato-Ariza, p. 43.

Revised diagnosis. As for the type species *D. crandalli* (see below).

Type species. *Dastilbe crandalli* (Jordan, 1910). CMNH 5247/91 (from Jordan's description it appears that CMNH 5247/92 is the counterpart, although Jordan did not include it as part of the type specimen). This is a complete specimen from the Muribeca Formation (Aptian, Lower Cretaceous), Riacho Doce, Alagoas, Brazil. Jordan used this specimen as the type of the species, but examined a suite of material for his analysis comprising more than 53 complete specimens and 94 fragments.

Remarks. Specimens of *Dastilbe* examined by Jordan (1910) from the Riacho Doce Formation of the Alagoas Basin had a recorded maximum length of 70 mm and occurred in black shales. Specimens of *Dastilbe* from Maranhão assigned to *D. elongatus* by Silva Santos (1947) were preserved in laminated limestone and reached a length of up to 170 mm, although most were under 70 mm. Silva Santos (1947) did not identify any specific morphological characters that would differentiate *D. crandalli* from *D. elongatus*. The criteria he used for separation of his new taxon appear to have been the different fossil locales and the composition of the matrix, i.e. limestone vs shale. We note that the rules of the ICZN do not allow for the creation of new taxa on these grounds. While we agree that different species may have existed in different sedimentary basins, there is only negative evidence (lack of outcrop) that could be used to show that the populations did indeed live separately. It is possible that these two outcrops, currently separated by a distance of c. 500 km, were previously linked by a series of lakes and rivers to the Alagoas-Sergipe basins via the Reconcavo-Jatoba-Tucano rift system. Therefore, as no skeletal criteria can be found to distinguish these taxa, we reject *D. elongatus* Silva Santos, 1947 and synonymize it with *D. crandalli* Jordan, 1910. In this respect, we agree with Taverne (1981) who first proposed that *D. elongatus* is conspecific with *D. crandalli*, and that two distinct populations of the same species were represented. Taverne's view was later supported by Patterson (1984, p. 135) due to the 'virtually identical' nature of their caudal skeletons. When Silva Santos (1955) erected *Dastilbe morãesi* from the Lower Cretaceous of Minas Gerais, he diagnosed it largely on features that could also be recognized in the type species of the genus, *D. crandalli*. However, he did note that the vertebral count was only 35. Blum (1991, p. 274) cited the vertebral count for the genus *Dastilbe* as being between 36 and 38, whereas Poyato-Ariza (1996, p. 24) quoted 36 to 39. The apparent plasticity in the vertebral count in this genus suggests that this is an unreliable feature for species diagnosis, and accordingly we reject this as a character to distinguish the species *D. morãesi*. Poyato-Ariza (1996, p. 41) noted three additional characters that distinguish *D. morãesi* from other species of *Dastilbe*. These are: anteriorly placed coronoid process; a relatively rounded and expanded angle between the preopercular limbs; and an 'extra' uroneural lateral to uroneural two. We cannot identify these features in the figures given by Silva Santos (1955, pls 1–2) for *D. morãesi*. In addition, in his character matrix Poyato-Ariza (1996, p. 15, character 59 [0]) lists *Dastilbe* as having only two uroneurals. We do not reject *D. morãesi* as a valid taxon, but note that further studies on this fish are required.

The African species *D. batai* was erected by Gayet (1989) for a single specimen with seven fin-rays for the pelvic fins and eight rays in the anal fin. In addition, she noted that the anterior margin of the pelvic fins is situated directly below the anterior margin of the dorsal fin. Although the fin-ray counts overlap with the variation of fin-ray counts found in the Araripe specimens in this study, the pelvic fins are placed more anteriorly than in *D. crandalli*. However, in UOP98/12 the anterior margin of the pelvic fin originates directly beneath the posterior margin of the dorsal fin, whereas in UOP98/15 the anterior margin of the pelvic fin is situated directly below the mid point of the dorsal fin. We thus consider the position of the pelvic fins relative to the dorsal fin to be a variable feature and of little or no diagnostic value. This variability could be due to relative movement of the pelvic girdle during ontogeny or even a post-mortem

taphonomic effect. Accordingly, we also reject *D. batai* Gayet, 1989 as a valid taxon, and synonymize it within *D. crandalli* Jordan, 1910.

Meristic variation

The number of fin-rays and the vertebral count have been used widely by systematists to characterize taxa at a variety of levels, but especially for distinguishing between species. The fin-ray count for the pectoral fins was used by Blum (1991, p. 274) to distinguish between *D. crandalli* and *D. elongatus* from the Nova Olinda Member of the Crato Formation. In particular, he claimed that specimens of *Dastilbe* up to 60 mm long had only ten pectoral fin-rays, which he assigned to *D. crandalli*, whereas specimens up to 200 mm possessed 13 fin-rays and were assigned to *D. elongatus*. Thus Blum considered that length was also a criterion that could be used to distinguish between species. In our study of *Dastilbe* from the Nova Olinda Member, we have acquired individuals of sizes ranging from 9 mm overall length (Pl. 4, fig. 5) to 210 mm overall length (Pl. 1, fig. 5), and have noted the fin-ray counts for the pectoral, pelvic and dorsal fins (Pl. 1, fig. 3; Pl. 2, figs 1, 4; Pl. 3, figs 3, 5–6). It is clear that the fin-ray count for the pectoral fins is variable and independent of length. Pectoral fin-ray counts observed in 18 specimens of *Dastilbe* from the Crato Formation range from as few as nine fin-rays (Pl. 3, fig. 3) to as many as 13 (Pl. 4, fig. 4). More than half of these specimens possess ten pectoral fin-rays (Pl. 1, fig. 3). Blum (1991) considered that those specimens with ten fin-rays represent individuals of the shorter species *D. crandalli*. However, several of the specimens we examined possessing ten pectoral fin-rays were individuals longer than 60 mm total length, including one individual of 210 mm total length (our largest example; Pl. 1, fig. 5).

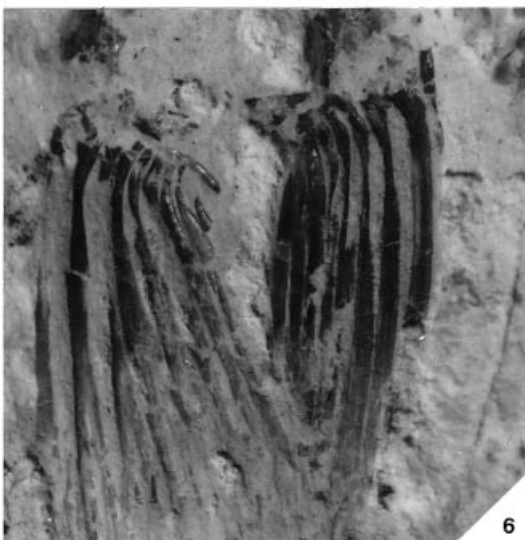
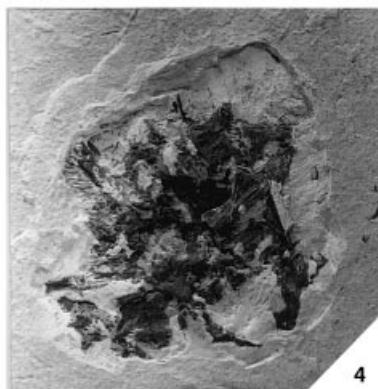
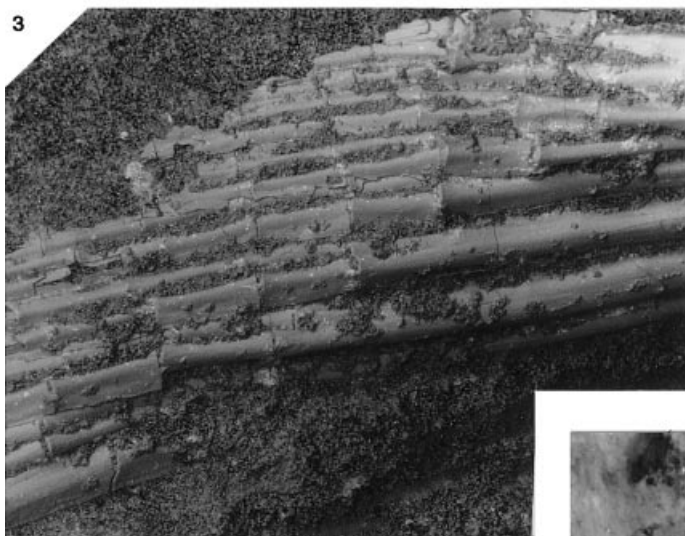
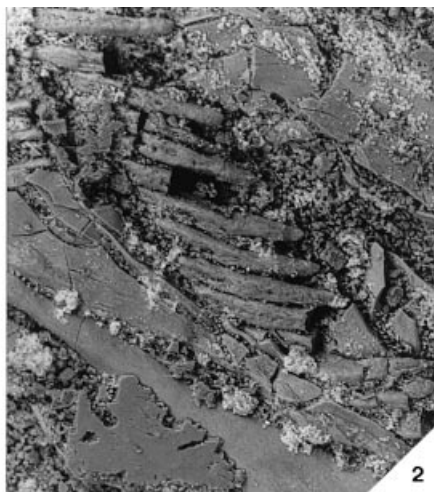
We found only a single individual (UOP 98/23) with 13 pectoral fin-rays (Pl. 4, fig. 4), although we found several specimens with 11 or 12. However, these individuals were smaller than the 60 mm size limit for *D. crandalli*, and therefore would, if such features are species diagnostic, represent a species distinct from either *D. crandalli* or *D. elongatus*. Poyato-Ariza (1996, p. 41) also noted intermediate pectoral fin-ray counts of 11 and 12 for *Dastilbe*. Because of the continuous variation in pectoral fin-ray count between nine and 13 regardless of total length, we conclude that pectoral fin-ray count cannot be used as a reliable indicator for species determination for the genus *Dastilbe*.

Endoskeletal variation

Besides the meristic features discussed above, Poyato-Ariza (1996) used two caudal characters to differentiate *D. crandalli* from the type locality of Riacho Doce from *D. elongatus*, *D. batai* and the so-called *D. elongatus* from the Araripe Basin: these characters are: (1) hypurals more inclined posteriorly and, (2) hypurals two and three articulate throughout their length resulting in absence of the caudal diastema. The degree of plasticity is taken to extremes in UOP 98/20 (Pl. 4, fig. 2) where only one uroneural is present when other specimens usually show two. In this specimen the uroneural possesses an antero-ventrally directed posterior process which appears to be fused to the posterior margin of ural centrum two. This could be teratological in this instance. The supposed increased inclination of posterior

EXPLANATION OF PLATE 3

Figs 1–6. *Dastilbe crandalli* Jordan, 1910; Nova Olinda Member, Crato Formation, Nova Olinda, Ceará, north-east Brazil. 1–2, UMZC GN1128a; scanning electron micrographs of uncoated specimen under low vacuum. 1, caudal endoskeleton showing hypurals 1–5, with the fifth hypural bifid; $\times 5$. 2, probable gill rays of the right side; $\times 200$. 3, UOP 98/20; scanning electron micrograph of uncoated specimen under low vacuum of pectoral fin showing nine fin-rays; $\times 6$. 4, UOP 98/21; circular aggregate of cf. *Dastilbe* bones of possible coprolitic origin; $\times 1$. 5, UMZC GN1128m; scanning electron micrograph of uncoated specimen under low vacuum of pectoral fin showing 12 fin-rays; $\times 5$. 6, UOP 98/15; paired pectoral fins both with 11 fin-rays; $\times 12$.



hypurals in *D. crandalli* from Riacho Doce given by Poyato-Ariza (1996, p. 40) is not supported by the figures given by Silva Santos (1947, pl. 2, figs 5–6) where it appears that the hypurals of *D. elongatus* are slightly more steeply inclined. This inclination may be variable according to the number of hypurals present.

Caudal diastema. Poyato-Ariza (1996, p. 40) stated that although the number of epurals and uroneurals may vary, the absence of a caudal diastema is a feature that may be used to distinguish between species, and hence he considered that *D. crandalli* from Riacho Doce is distinct from *D. crandalli* and *D. elongatus* from Araripe on the basis that *D. crandalli* from Riacho Doce lacks a caudal diastema. However, we have found that the caudal diastema is also absent in many examples of *Dastilbe* from Araripe (e.g. UOP 98/8a, UOP 98/6) (Pl. 3, fig. 1). In addition, the size of the diastema appears to be somewhat variable, i.e. there may be a complete diastema extending from the base of the hypurals to their posterior termination, or an incomplete diastema which commences at a position somewhat posterior to the base of the hypurals resulting in a shortened diastema (Text-fig. 9). Examples of *Dastilbe* with near complete caudal diastemas are given by Blum (1991, p. 281). Therefore, this character appears to be of little or no diagnostic value for species determination, and as such, we consider *D. elongatus* to be indistinguishable from the Riacho Doce species *D. crandalli*. Of our sample, only two specimens, UOP 98/32a, and UMZC GN11281 have a distinct caudal diastema.

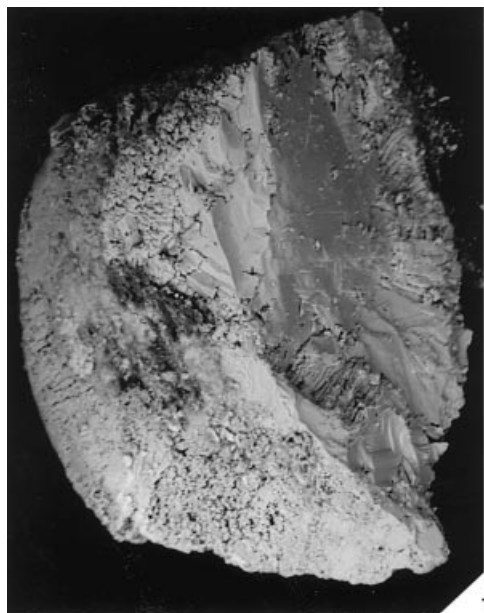
Hypurals. Blum (1991, p. 274) stated that *Dastilbe* has six hypurals but Poyato-Ariza (1996, p. 31) noted that Blum (1991, p. 279) showed only five hypurals in the caudal skeleton of *D. crandalli*. However, Poyato-Ariza still maintains that the hypural count for *Dastilbe* is six and supposes that in young or small specimens, weak ossifications and lack of preservation may result in absence of small bony elements. Whilst this may be the case, we note that in many of even the smallest examples of *Dastilbe* (smallest c. 9 mm long) bones much smaller than the hypurals are present (Pl. 2, fig. 8; Pl. 4, fig. 5) on the same specimen. We have noted specimens of *Dastilbe* from Araripe in which there are five, six or a bifid fifth hypural as seen in UMZC GN1128a (Pl. 3, fig. 1). Electron microscopy of the caudal endoskeleton of the specimen suggests that the putative hypural six was perhaps connected to the lower ramus of hypural five proximally. No distinct separation between the rami of putative hypural five is seen which might support Poyato-Ariza's interpretation. Once again, this character appears to be somewhat plastic and of dubious value for diagnosing species of *Dastilbe*.

STATISTICAL ANALYSIS

The following analysis of *Dastilbe* was based on specimens from the Araripe Basin and includes meristic fin-ray counts of the dorsal, pectoral, and pelvic fins. Anal fin-ray counts were excluded because of the relatively poor preservation of these elements in the majority of specimens (but see Pl. 4, fig. 3, UOP98/26

EXPLANATION OF PLATE 4

Figs 1–6. *Dastilbe crandalli* Jordan, 1910; Nova Olinda Member, Crato Formation, Nova Olinda, Ceará, north-east Brazil. 1, UMZC GN1128m; scanning electron micrograph of uncoated specimen under low vacuum of excised lagenar statolith; $\times 210$. 2, UOP 98/20; scanning electron micrograph of uncoated specimen under low vacuum of fused uroneurals 1 and 2 with antero-ventrally directed posterior ramus which appears to fuse with posterior margin of ural centrum two; $\times 4.5$. 3, UOP 98/26; well preserved anal fin; $\times 6$. 4, UOP 98/23; specimen in which the pectoral fins, each with 13 rays, are twisted into a ventro-dorsal position (as viewed); $\times 2.5$. 5, UOP 98/1; the smallest fish encountered during this project with overall length of 9 mm. 6, UOP 98/33; specimen forming nucleus to dendritic outgrowth of pyrolusite; $\times 2.8$.



1



2



3



4



5



6

TABLE 1. List of *Dastilbe* specimens examined in this study. Sample size: 83.

Specimen number	Side observed	Standard length (mm)	Pectoral fin-ray count	Dorsal fin-ray count	Pelvic fin-ray count
GN1108	L	41	—	—	—
GN1109a	L	30	—	—	—
GN1109b	R	28	—	11	8
GN1110	L	26	—	—	—
GN1111	R	31	—	—	—
GN1112a	L	33	—	—	8
GN1112b	R	23	—	9	—
GN1113a	R	32	9	—	—
GN1113b	R	29	—	8	—
GN1111	R	40	—	—	—
GN1115	R	45	9	9	—
GN1116	L	37	—	—	—
GN1117	R	27	—	—	—
GN1118	L	27	—	—	—
GN1119	L	32	—	—	—
GN1120	R	30	10	—	8
GN1121	R	34	—	9	—
GN1122	R	33	—	—	—
GN1123	L	42	—	—	—
GN1124	L	32	—	9	—
GN1125	R	26	—	—	—
GN1126	R	23	—	9	—
GN1127	L	N/A	—	—	—
GN1128a	R	27	—	—	—
GN1128b	L	31	10	10	7
GN1128c	R	31	—	—	—
GN1128d	L	22	—	10	8
GN1128e	R	34	—	—	—
GN1128f	R	39	—	10	—
GN1128g	L	37	10	—	8
GN1128h	L	32	11	—	—
GN1128i	L	28	—	—	—
GN1128j	R	31	10	—	—
GN1128k	L	27	—	—	—
GN1128l	R	34	—	10	8
GN1128m	R	36	12	—	8
GN1128n	L	32	10	10	8
GN1128o	R	23	—	—	—
GN1128p	R	29	10	—	—
GN1128q	L	38	—	—	8
GN1128r	R	35	11	—	8
GN1128s	L	28	10	10	—
GN1128t	L	35	—	—	—
UOP98/1	R	9	—	—	—
UOP98/2	D	48	—	—	—
UOP98/3a	R	22	—	—	—
UOP98/3b	L	40	—	11	—
UOP98/3c	R	45	—	10	—
UOP98/4	R	59	—	10	—
UOP98/5	L	25	—	10	8
UOP98/6	R	27	—	—	—
UOP98/7	R	180	10	12	10

TABLE 1. (*Continued*)

Specimen number	Side observed	Standard length (mm)	Pectoral fin-ray count	Dorsal fin-ray count	Pelvic fin-ray count
UOP98/8a	R	30	—	—	—
UOP98/8b	L	35	—	10	8
UOP98/9a	R	33	—	10	8
UOP98/9b	R	29	—	—	—
UOP98/10	L	11	—	—	—
UOP98/11	L	30	—	—	—
UOP98/12	R	150	10	12	9
UOP98/13	R	37	—	10	—
UOP98/14	R	42	—	—	—
UOP98/15	L	60	11	—	9
UOP98/16a	L	29	—	—	—
UOP98/16b	R	34	—	10	—
UOP98/17	R	45	—	—	—
UOP98/18	L	20	—	10	—
UOP98/19	L	22	—	—	—
UOP98/20	R	43	—	—	9
UOP98/21	N/A	N/A	—	—	—
UOP98/22	R	14	—	—	—
UOP98/23	L	155	13	—	8
UOP98/24	L	60	—	—	—
UOP98/25a	R	39	—	10	7
UOP98/25b	L	14	—	—	—
UOP98/26	R	92	—	11	—
UOP98/27	L	65	—	12	—
UOP98/28	R	45	10	—	8
UOP98/29	R	38	10	—	—
UOP98/30	R	52	—	10	—
UOP98/31	L	40	—	10	8
UOP98/32a	L	45	—	10	8
UOP98/32b	L	50	—	—	—
UOP98/33	L	51	—	10	8

for a well-preserved example). Data analysis and statistical tests were conducted using *Excel* version 5.0 and accuracy checked by *Statistica* version 5.1. Specimens used for this analysis are listed in Table 1, and from this, 46 complete, articulated individuals were used for statistical testing. In some cases bony elements were missing, but external moulds were present. Presumably the missing elements were present on the counter slab, and where a distinct external mould was preserved, these were included in the analysis. Meristic counts of fin-rays are presented in Tables 2–4. The results of these analyses are listed in Table 5. The standard length (measured from anterior-most part of rostrum to distal margin of posterior-most hypural) of the shortest individual was 7 mm (Pl. 4, fig. 5) and *c.* 180 mm for the largest (Pl. 1, fig. 5). The shape of the overall distribution was normal with a right skew caused by a few very large specimens (Text-fig. 5). To reduce the skew effect generated on the main data cluster by outlier specimens, Tukey's outlier exclusion formula was utilized separately on each fin-ray group. Outliers for pectoral fin study were specimens shorter than 10 mm and longer than 66 mm. The same outliers were used for the dorsal fin study, but for the pelvic fin analysis, specimens shorter than 15 mm and larger than 63 mm were considered outliers. Median individuals were 33 mm standard length. The most common individuals (mode) were 32 mm standard length which is within the *D. crandalli* size range of Blum (1991). Specimens

TABLE 2. *Dasylabe* Specimens with observable pectoral fin-rays or external moulds. Sample size: 18.

Specimen number	Side observed	Standard length (mm)	Pectoral fin-ray count
GN1113a	R	32	9
GN1115	R	45	9
GN1128s	L	28	10
GN1128p	R	29	10
GN1120	R	30	10
GN1128b	L	31	10
GN1128j	R	31	10
GN1128n	L	32	10
GN1128h	L	32	11
GN1128r	R	35	11
GN1128m	R	36	12
GN1128g	L	37	10
UOP98/7	R	180	10
UOP98/12	R	150	10
UOP98/15	L	60	11
UOP98/23	L	155	13
UOP98/28	R	45	10
UOP98/29	R	38	10

above 60 mm and therefore meeting the *D. elongatus* size criterion of Blum (1991) were also observed (Pl. 1, fig. 4).

Pectoral fin-ray count vs standard length. A frequency histogram of length vs pectoral fin-ray number (Text-fig. 6A) exhibited a normal distribution about an average of ten pectoral fin-rays represented by 11 specimens. Neither Poyato-Ariza (1996) nor Blum (1991) discovered specimens with nine pectoral fin-rays. However, UOP 98/20 (Pl. 3, fig. 3) exhibits nine pectoral fin-rays. Clearly, a range of fin-ray counts exists within *Dasylabe* from the Crato Formation. Using Blum's criteria for species recognition, these specimens would constitute distinct species. The largest specimens we examined, including UOP 98/12 and UOP 98/7, had fewer than 13 pectoral fin-rays (Pl. 1, figs 1, 5) but were well above the minimum total length for *D. crandalli* (i.e. up to 60 mm total length) of Blum (1991). In fact, only one specimen (UOP98/23) (Pl. 4, fig. 4) out of 81 individuals measured met the criteria for Blum's species-placement hypotheses erected for the larger examples of *D. elongatus*. A correlation coefficient analysis of pectoral fin-ray count vs standard length does not support Blum's (1991) method of species determination. Four specimens equal to or shorter than 60 mm (Table 2) have more than ten pectoral fin-rays, whilst UOP 98/12 (standard length 150 mm), and UOP98/7 (standard length 180 mm) have only ten pectoral fin-rays each. Correlation coefficients were calculated both with and without outlier specimens (UOP 98/7, UOP98/12, and UOP98/23) which were well outside the primary data cluster (Text-fig. 6B). Both correlation coefficients of 0.302 (all 18 specimens included) and 0.151 [three largest specimens (outliers) were excluded leaving 83 per cent. of the data group] gave insignificant results when tested to 95 per cent. confidence, i.e. 'r' values were less than 0.468 and 0.513 respectively (Table 5). These results clearly show that a positive relationship between length and pectoral fin-ray numbers as proposed by Blum 1991 is not supported.

Dorsal fin-ray count vs standard length. Dorsal fin-ray counts for the specimens tested also show a strong normal distribution with 19 out of 31 specimens (>60 per cent.) possessing ten dorsal fin-rays (Text-fig. 7A). Unlike pectoral fin-rays which have been analysed by Blum 1991 and Poyato-Ariza 1996, dorsal

TABLE 3. *Dastilbe* Specimens with observable dorsal fin-rays or external moulds. Sample size: 31.

Specimen number	Side observed	Standard length (mm)	Dorsal fin-ray count
GN1109b	R	28	11
GN1112b	R	23	9
GN1113a	L	45	10
GN113b	R	29	8
GN1115	R	45	9
GN1121	R	34	9
GN1124	L	32	9
GN1126	R	23	9
GN1128b	L	31	10
GN1128d	L	22	10
GN1128f	R	39	10
GN1128l	R	34	10
GN1128n	L	32	10
GN1128s	L	28	10
UOP98/3b	L	40	11
UOP98/3c	R	45	10
UOP98/4	R	59	10
UOP98/5	L	25	10
UOP98/7	R	180	12
UOP98/8b	L	35	10
UOP98/9a	R	33	10
UOP98/12	R	150	12
UOP98/13	R	37	10
UOP98/16b	R	34	10
UOP98/18	L	20	10
UOP98/25a	R	39	10
UOP98/26	R	92	11
UOP98/27	L	65	12
UOP98/30	R	52	10
UOP98/31	L	40	10
UOP98/33	L	51	10

fin-ray studies have not been published previously for *Dastilbe*. These new data reveal a strong positive relationship for length vs dorsal fin-ray numbers (Text-fig. 7B). The correlation coefficient of 0.685 which exceeds the 'r' value of 0.356 needed to satisfy the 95 per cent. confidence requirement is easily attained (Table 5). Although the correlation coefficient drops significantly to 0.419 when large outlier specimens (i.e. UOP 98/7, UOP98/12 and UOP98/26) were excluded (leaving 90 per cent. of the primary data group), the result is still significant with 95 per cent. confidence, i.e. higher than 0.375. One problem in counting the dorsal fin-rays on *Dastilbe* was the lack of observability of the first few anterior rays of the dorsal fin in many of its smaller representatives. In larger individuals such as UOP98/26, these anterior fin-rays are short, recurved and overlapping as in smaller specimens, but were easier to distinguish with certainty due to their higher degree of ossification. This problem is not seen when counting pectoral and pelvic fin-rays in either small or large individuals because the anterior fin-rays of these fins are not normally imbricated.

Pelvic fin-ray count vs standard length. Pelvic fin-ray numbers were analysed to determine if larger specimens would also exhibit higher fin-ray numbers as seen in the length vs dorsal fin-ray analysis. Again,

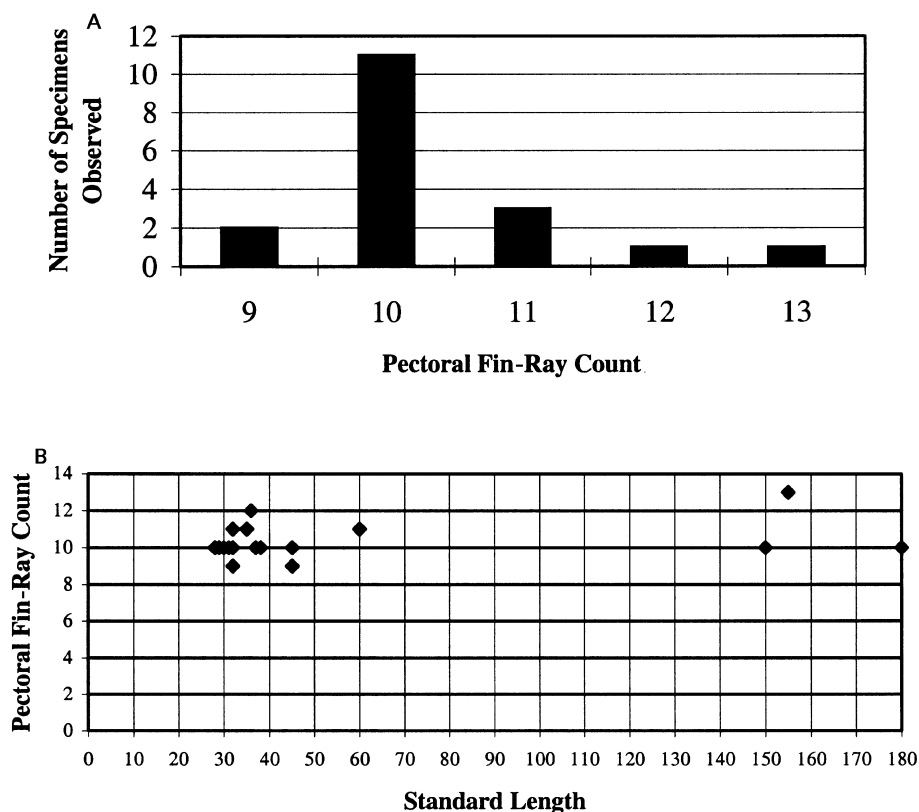
TABLE 4. *Dastilbe* specimens with observable pelvic fin-rays or external moulds. Sample size: 24.

Specimen number	Side observed	Standard length (mm)	Pelvic fin-ray count
GN1109b	R	28	8
GN1112a	L	33	8
GN1120	R	30	8
GN1128b	L	31	7
GN1128d	L	22	8
GN1128g	L	37	8
GN1128l	R	34	8
GN1128m	R	36	8
GN1128n	L	32	8
GN1128q	L	38	8
GN1128r	R	35	8
UOP98/5	L	25	8
UOP98/7	R	180	10
UOP98/8b	L	35	8
UOP98/9a	R	33	8
UOP98/12	R	150	9
UOP98/15	L	60	9
UOP98/20	R	43	9
UOP98/23	L	155	8
UOP98/25a	R	39	7
UOP98/28	R	45	8
UOP98/31	L	40	8
UOP98/32a	L	45	8
UOP98/33	L	51	8

a normal distribution is encountered with 18 out 24 individuals (75 per cent.) having eight pelvic fin-rays (Text-fig. 8A). Of the smaller specimens within the primary data cluster, only UOP 98/20 had a pelvic fin-ray count exceeding eight. But, three out of the four large outlier specimens (i.e. UOP98/7, UOP 98/12 and UOP98/23) had nine or even ten pelvic fin-rays. Again, as with the test results for dorsal fin-rays, a

TABLE 5. Results of correlation coefficient [r] analysis on pectoral, dorsal and pelvic fin-rays of *Dastilbe* from the Crato Formation, Brazil.

Fin-ray count analysed	Sample size [n] with degrees of freedom [n - 2]	Correlation coefficient [r] including all specimens	Correlation coefficient [r] excluding larger outlier specimens	Correlation coefficient [r] significant with 95 per cent. confidence
Pectoral	16	0.302	—	0.468
Pectoral	13	—	0.151	0.513
Dorsal	29	0.685	—	0.356
Dorsal	26	—	0.419	0.375
Pelvic	22	0.634	—	0.406
Pelvic	19	—	0.424	0.432



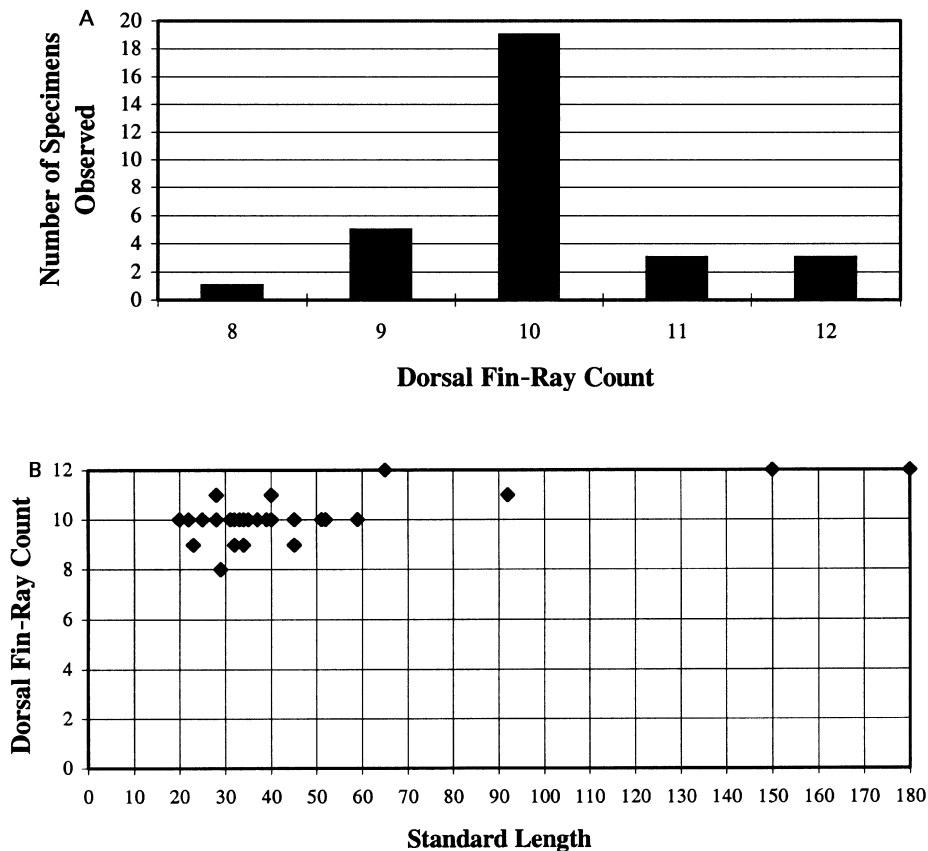
TEXT-FIG. 6. A, histogram of pectoral fin-ray counts for *Dastilbe* from the Crato Formation, Brazil. Counts taken from complete specimens with distinct fin-rays or external moulds. Sample size: 18. B, scatterplot distribution of pectoral fin-ray count vs standard length in 18 *Dastilbe* specimens.

strong positive relationship exists between length and number of fin-rays, at least when outlier specimens are incorporated (Text-fig. 8B). This is supported by an 'r' value of 0.634 (all specimens included). The relationship ceases to exist with 95 per cent. confidence, i.e. the 'r' value drops to 0.424 (Table 5) when the outlier specimens (UOP 98/7, UOP98/12, and UOP98/23) are removed and only 88 per cent. of the main data cluster remains for trend analysis.

From the data, it appears that there may be a positive relationship between length and dorsal/pelvic fin-rays, especially with the inclusion of specimens which are clearly outside the main data cluster, but again, problems remain. Results from the length vs pectoral fin-ray data do not support a significant positive correlation between length and pectoral fin-ray number which could corroborate the trend in dorsal and pelvic fin-rays even with the inclusion of the larger outlier specimens.

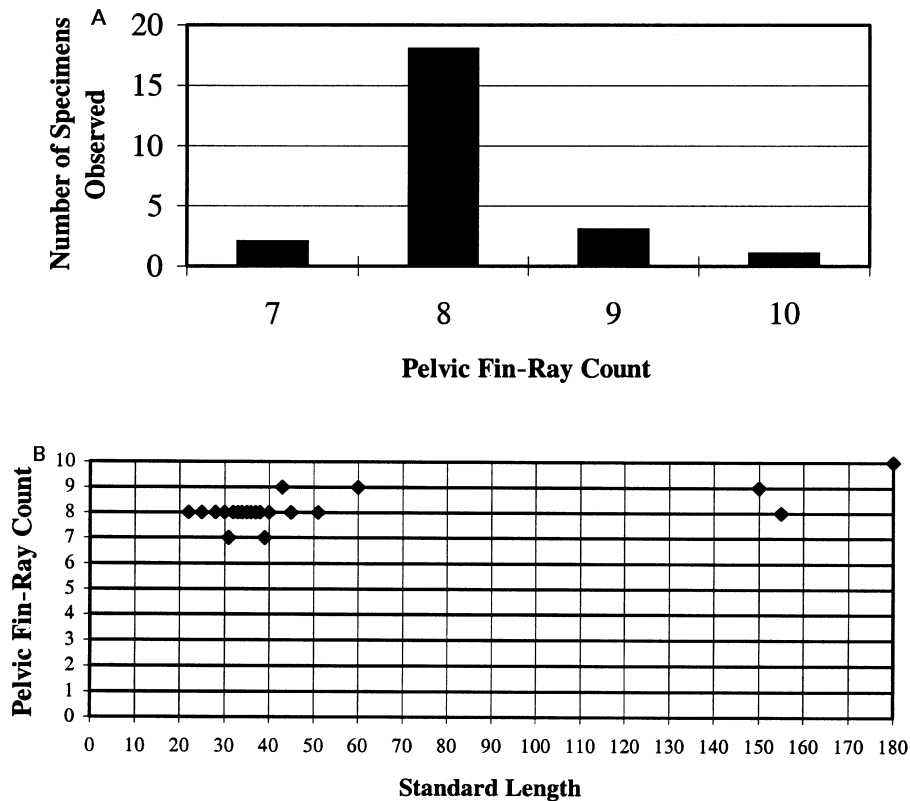
CONCLUSIONS

From the results of our analysis on the meristic counts of fin-rays vs standard length it is clear that the fossil populations of *Dastilbe* from the Crato Formation represent a single cohort. The degree of variation



TEXT-FIG. 7. Dorsal fin-ray counts for 31 specimens of *Dastilbe* from the Crato Formation, Brazil. A, histogram of dorsal fin-ray counts taken from complete specimens with distinct fin-rays or well defined external moulds. B, scatterplot distribution of dorsal fin-ray count vs standard length in *Dastilbe*.

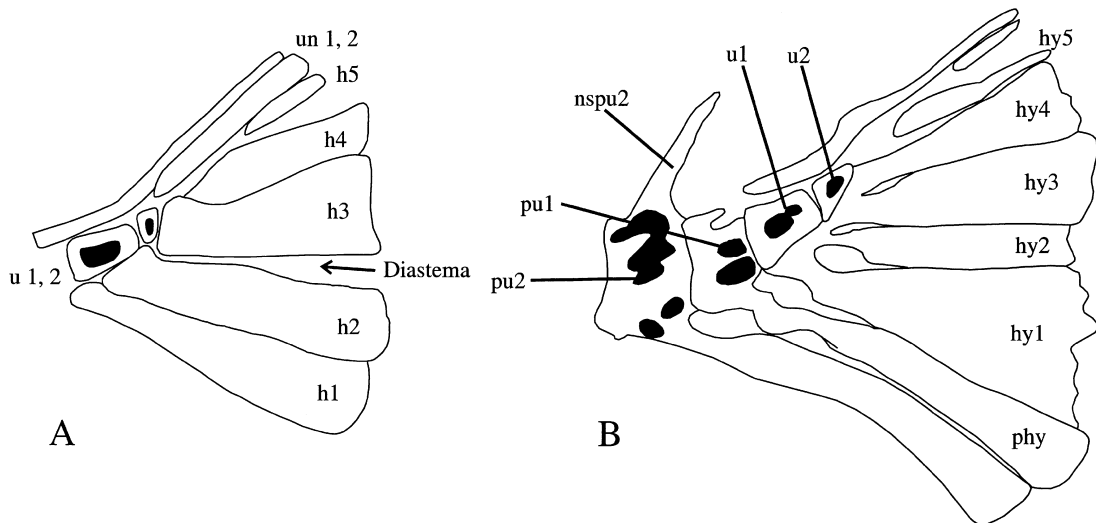
of fin-ray count shows a strong normal distribution around a mean of ten-rays for the pectoral fins, ten for the dorsal fins and eight for the pelvic fins. Although there is a statistically significant difference between the fin-ray counts of the dorsal and pelvic fins of small and large examples of *Dastilbe*, this is attributable to the influence of larger individuals on the small data set (only four over 65 mm for dorsal and pelvic, three for pectoral). Those examples of large individuals where we were able to count the pectoral fin-rays clearly show a wide degree of variation in fin-ray count that is unrelated to length. In addition, the caudal diastema is large and conspicuous in some specimens but absent in many, and only slightly apparent in a few (Text-fig. 9). Thus there is continuous variation in this feature. There is no positive correlation between the presence or absence of a caudal diastema and fin-ray count or overall standard length. The number of hypurals varies between five and six, but where six are present, this is sometimes due to a bifid hypural five which, during decay, had undergone separation of the rami. Thus we can only recognize a single species of *Dastilbe* in the Crato Formation and it does not differ from populations of the type species *Dastilbe crandalli*. Therefore all specimens of *Dastilbe* from Araripe examined here are referred to *D. crandalli* and we synonymize *D. elongatus* Silva Santos (1947) with *D. crandalli*. *D. morães*



TEXT-FIG. 8. Pelvic fin-ray counts in 24 specimens of *Dastilbe* from the Crato Formation, Brazil. A, histogram of pelvic fin-ray count vs standard length. B, scatterplot distribution of pelvic fin-ray count vs standard length.

Silva Santos (1955) is known only from a few specimens from the Lower Cretaceous of Minas Gerais, and its original diagnosis does not distinguish it from our revised diagnosis of *D. crandalli*. The same is true for the African *D. batai*, and as such, we consider that no criteria have been found to satisfactorily define more than one species of *Dastilbe*.

It is clear that where meristic counts are used in species diagnosis on small data sets, many different species will be recognized. An alternative to our 'lumping' strategy, would be to recognize, at least for the Crato Formation, the sympatric existence of at least five species of *Dastilbe* based on pectoral fin-ray count alone. Only four of our specimens (UMZC GN1128b, GN1128n, UOP98/7, and UOP98/12) allowed us to count the fin-rays of all three target fins. In these four specimens, which all had a pectoral fin-ray count of ten, none had constant fin-ray counts for the other fins. For example, the dorsal fin-ray counts for these specimens were nine and ten for the first two specimens with the last two sharing 12 dorsal fin-rays. The counts are less consistent for the pelvic fin-rays with all specimens possessing different counts ranging from seven to ten rays. Thus we would have to recognize three additional sympatric species. If this were also the case for pectoral fin-ray counts of nine, 11, 12 and 13 pectoral fin-rays, there could be as many as 15 morphospecies. Systematists using meristic counts of fin-rays should be very wary of erecting taxa on such criteria, especially when using data sets comprising a single specimen or only a few individuals.



TEXT-FIG. 9. Diagrammatic sketches of the proximal caudal endoskeleton of *Dastilbe* from the Crato Formation, Brazil. Two conditions are illustrated. In A, there is a diastema between hypurals two and three. In B, hypurals two and three are articulated along their entire margins. Gradations are seen between these two conditions. A, based on specimen UOP 98/3a, B, based on specimen UMZC GN1128h. hy, hypural; nspu, neural spine of preural; phy, parahypural; pu, preural; u, ural; un, uroneural.

Acknowledgements. Research for this paper began as an undergraduate biology project supervised by Dr Mike Coates (University College, London). We thank the staff of the University Museum of Zoology, Cambridge for loan of specimens; Dr Mike Coates kindly read the manuscript and provided useful comments. Special thanks go to Dr Adrian Lister (University College London) for helpful discussions on statistical analyses, and to Dr Poyato-Ariza and an anonymous referee whose comments greatly improved the manuscript. We also thank Dr Paulo Brito for comments on a preliminary manuscript, and his help in the field; Mr Bob Loveridge (University of Portsmouth) for photography, Mark Turmaine (Department of Anatomy, University College London) for technical assistance on SEM and development of SEM photos and Mr Simon Brookes (Portsmouth) for help with diagrams.

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Typescript received 30 June 1998

Revised typescript received 28 January 1999