Cretaceous Research 33 (2012) 183–188

Contents lists available at SciVerse ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Ptychodus decurrens Agassiz (Elasmobranchii: Ptychodontidae) from the Upper Cretaceous of India

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ARTICLE INFO

Article history:
Received 17 January 2011
Accepted in revised form
16 September 2011
Available online 22 September 2011

Keywords:
Ptychodontidae
Ptychodus decurrens
Late Cretaceous
Cauvery Basin
India

ABSTRACT

Although a very high invertebrate faunal diversity is known from the outcrops of the Ariyalur group in the Cauvery Basin, southern India, little is known about its vertebrate fauna. Recent fieldwork in the badland exposures of the Karai Formation (Upper Cenomanian–Lower Turonian) near Garudamangalam in the basin has yielded two teeth belonging to the Late Cretaceous shark *Ptychodus decurrens* (Ptychodontidae). The fossil record of *Ptychodus decurrens* from the southern continents is very poor, being known from a single Late/Middle Albian occurrence in Australia. This finding documents the first record of fossil *P. decurrens* in India and second from a Gondwanan landmass, and provides the first evidence of a cosmopolitan, Pangaean, distribution of the species during the Albian–Turonian and additional insights into the palaeoecology of the Cauvery Basin during the deposition of the Karai Formation.

1. Introduction

Ptychodus is a highly specialized extinct genus of the family Ptychodontidae (Elasmobranchii). It is characterized by distinctive grinding-type (durophagous) dentition and is known from the Albian–Campanian (112–70 Ma) stages of the Cretaceous Period (Cappetta, 1987). It has a global distribution and is well represented in the fossil record by isolated teeth, fragments of dentition, calcified vertebral centra, denticles and associated fragments of calcified cartilage (Cappetta, 1987; Johnson and Lucas, 2003; Hamm, 2008, 2010; Shimada et al., 2009, 2010).

The fossil record of *Ptychodus* is diverse and well documented from the Laurasian continents, with reports known from North America (Macleod, 1982; Cappetta, 1987; Welton and Farish, 1993; Everhart and Caggiano, 2004; Blanco-Piñón et al., 2007; Hamm, 2008), Europe (Herman, 1975; Cappetta, 1987; Trbušek, 1999; Niedźwiedzki and Kalina, 2003) and Asia (Cappetta, 1987; Radwański and Marcinowski, 1996; Cuny, 2008). By contrast, the record from the Gondwanan continents is relatively poor, with reports coming from South America (Reinhart, 1951; Wenz, 1972; Brito and Janvier, 2002) and Africa (Cappetta, 1987; Antunes and Cappetta, 2002). Cretaceous elasmobranchs are rare in India with only a few reports coming from the Upper Cretaceous deposits of peninsular India. These include lamniformes from the Cenomanian–Turonian (99.6–89.3 Ma) Bagh Beds of the Narmada Valley (Verma, 1965) and batoids from the Maastrichtian (70.6–65.5 Ma) Deccan infra- and intertrappean sediments of Jabalpur, Pisdura, Marepalli, Nagpur, Asifabad and Kisalpuri in peninsular India (Jain and Sahni, 1983; Courtillot et al., 1986; Prasad and Cappetta, 1993; Khosla et al., 2004; Verma, 2008). Stoliczka (1873) noted the occurrence of *Ptychodus* in Cretaceous deposits of the Cauvery Basin, but he did not describe the specimens. We report here a definitive occurrence of a ptychodontid in the Karai Formation of this basin and discuss its palaeoecological and palaeobiogeographical implications.

2. Geographic and stratigraphic setting

The fish remains described herein were recovered from the Karai Formation (Late Cenomanian–Early Turonian) of the Uttattur Group in the Cauvery Basin. This basin contains a thick accumulation of Cretaceous–Palaeocene sediments (ca. 6 km) with an approximate aerial extent of 25,000 km^2, resting on the Archaean granites along the southeast coast of the Tamil Nadu, southern India

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doi:10.1016/j.cretres.2011.09.014

(Yadagiri and Govindan, 2000). The basin is considered to be a rift basin that developed in response to the Late Jurassic–Early Cretaceous separation of the Indian subcontinent from Australia and Antarctica (Veevers et al., 1991). These sediments record transgressive and regressive cycles that occurred throughout the depositional history of the basin and represent a variety of palaeoenvironments, including shallow marine, estuarine, lagoonal and fluvial/lacustrine (Tewari et al., 1996; Sundaram et al., 2001).

The Cretaceous sedimentary succession of the basin is well-exposed in five isolated outcrops in the Pondicherry, Vridhachalam, Ariyalur, Tanjavur and Sivaganga areas. The outcrops at Ariyalur are the largest and contain an easily accessible well-preserved sedimentary sequence that includes the Uttattur, Trichinopoly and Ariyalur groups, which have traditionally been distinguished based on lithology and fossils (Blanford, 1862; Tewari et al., 1996; Sundaram et al., 2001).

The Uttattur Group, representing the basal most marine transgressive unit of the succession of basin, overlies the Archaean basement along its western margin and unconformably underlies the basal marine regressive phase of the succeeding Trichinopoly Group. The Uttattur Group attains a maximum thickness of some 820 m (Sundaram et al., 2001). Sundaram et al. (2001) subdivided the Uttattur Group into four formations in chronological order: Terani, Arogyapuram, Dalmiapuram and Karai formations (Table 1).

The Karai Formation is the uppermost unit of Uttattur Group. It contains dirty brown to rust-yellow clays, silty clays, sandy clays, siltstones, calcareous sandstones, phosphatic nodules and superficial concentrations of gypsum. It yields abundant remains of oysters, ammonites, belemnites and foraminifers (Ayyasami, 2006). Based on the presence of the ammonite *Mammites conciliatum* and *Pseudaspidoceras footeanun* assemblages zones, a Cenomanian–Early Turonian age has been suggested for the topmost part of the Uttattur Group (Phansalkar and Kumar, 1983). Venkatachalapathy and Ragothaman (1995) suggested a similar age based on the foraminiferal assemblage *Praeglobotruncana*, *Rotalipora* and *Helvetoglobotruncana*. Narayanan (1977) inferred an Early Turonian age from the presence of the foraminiferal *Marginotruncana helvetica–Marginotruncana sigali* Assemblage Zone. Recently, based on the occurrence of the ostreiid *Rynchostreon suborbiculatum* Zone within the Karai Formation, Ayyasami (2006) proposed an Early Turonian age for this formation.

The Karai Formation consists of beds that accumulated in an offshore, highstand depositional environment. The sediments of the lower part of the formation conformably overlie the Dalmiapuram Formation, which was deposited during a transgressive phase in a shallow marine bay (Sundaram et al., 2001). Based on the abundance of belemnites, ammonites and planktic foraminifera, a deep neritic environment close to the shelf edge in a warm climate is inferred for the mid–upper part of the formation, which consists essentially of gypsum-rich clays and shales. The top of the formation reflects the beginning of a marine regression, an event marked by a sudden, sharp reduction in abundance of planktic foraminifera (Venkatachalapathy and Ragothaman, 1995).

The fish remains described here are surface finds, collected from the badland exposures of the middle part of Karai Formation

Table 1
Lithostratigraphic classification of Uttattur Group, Cauvery Basin (Sundaram et al., 2001).

Group	Formations	Age
Uttattur	Karai	Early
	Dalmiapuram	Turonian
	Arogyapurum	to
	Terani	Albian

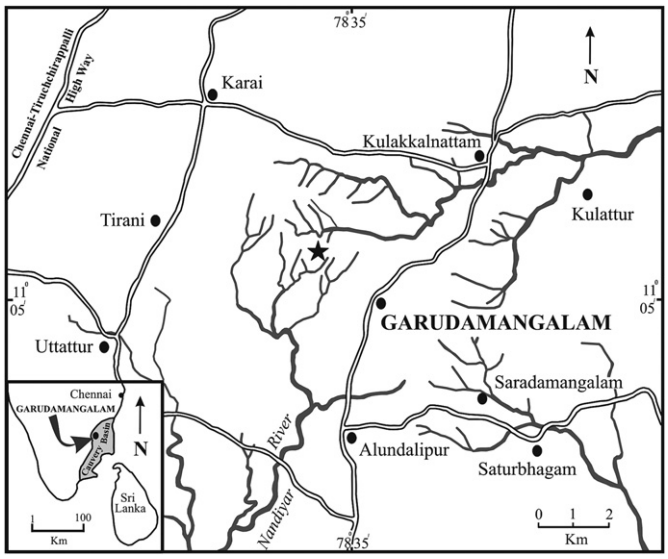

Fig. 1. Location map of the site yielding *Ptychodus decurrens* marked by a star. Inset location map of the Cauvery Basin, Tamil Nadu, southern India.

located some 2.3 km northwest of the village of Garudamangalam, Ariyalur District, Tamil Nadu (Fig. 1). The fish-bearing horizon is thick, and consists of gypsiferous and sandy clays. The fish remains are represented by isolated teeth, scales and vertebrae. The specimens are housed in the Palaeontological Laboratory, Indira Gandhi National Open University, New Delhi, their numbers being prefixed by PL/IGNOU.

3. Systematic palaeontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Subcohort Neoselachii Compagno, 1977
Order *incertae sedis*
Family Ptychodontidae Jaekel, 1898
Genus *Ptychodus* Agassiz, 1835

Ptychodus decurrens Agassiz, 1843
Figs. 2 and 3

Material. PL/IGNOU/101, isolated anterolateral tooth (Figs. 2A, 3A–F); PL/IGNOU/102, isolated tooth (Figs. 2B, 3G–L).

Description. PL/IGNOU/101 is an isolated tooth. Its crown is bilaterally symmetrical and rectangular, possibly indicating that it is one of the anterolateral teeth in the *Ptychodus* jaw (Woodward, 1887; Dilbey, 1911). In occlusal view, the crown is low, broad, slightly inflated, rectangular in shape with gently rounded corners, and projected linguo-distally. The labio-distal margin is rounded. The triturating zone is ornamented by 13 strong, coarse straight to wavy transverse ridges. The marginal area of the tooth is ornamented with much finer anastomosing ridges, which bifurcate on their mesio-distal ends and reach the crown perimeter. There are numerous longitudinal fine ridges on the labial tooth edge perpendicular to the transverse ridges. At the lingual margin, the ridges are bifurcated and branched into numerous finer anastomosing ridges that extend to the edge of the crown. The crown of the tooth overhangs a short, weakly bilobed root. The root is massive, smaller than the crown and pierced by many foramina along the crown-root contact. A shallow labio-lingually

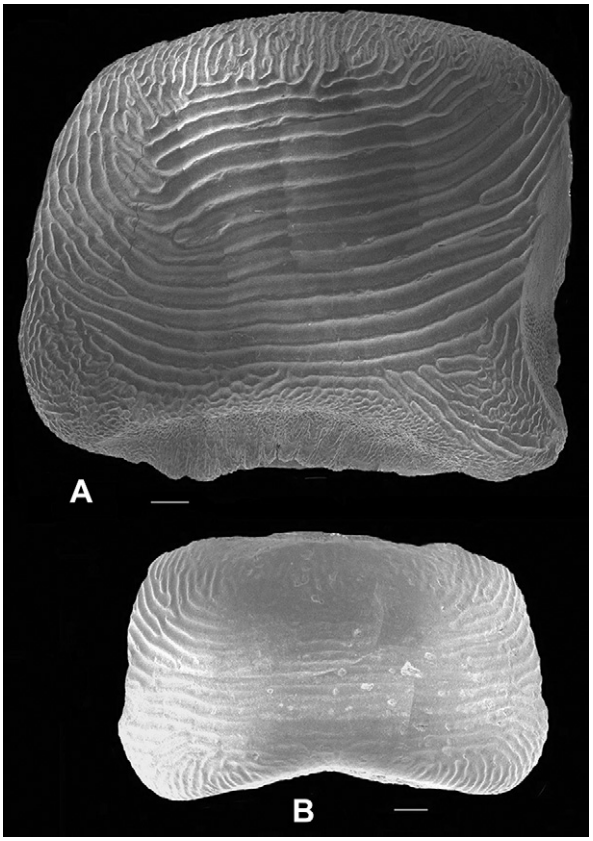

Fig. 2. Scanning electron micrographs of *Ptychodus decurrens* teeth. A, PL/IGNOU/101 and B, PL/IGNOU/102 in occlusal views. Scale bar represents 1 mm.

oriented groove divides the root into two weak lobes. The lingual margin is concave and smoothly indented, making a lingual sulcus that may have accommodated the labial margin of the preceding crown of the tooth. The labial margin is convex having a labial protuberance.

PL/IGNOU/102 is an isolated tooth from the anterior file. It is mesio-distally elongate and labio-lingually narrow, with the lingual margin greatly overhanging the root. The crown is low, weakly inflated, and rectangular in occlusal view with rounded corners. Some breakage has occurred in the labial, mesial and distal margins of the tooth. The crown of the tooth is extensively abraded and pitted, possibly owing to weathering; it is ornamented by 10 coarse, well-developed, straight to sinuous transverse ridges, perpendicular to the mesial and distal crown margins. These ridges abruptly branch into ever smaller ridges on the marginal mesio-distal areas of the crown. The labial and lingual margins bear numerous fine ridges oriented perpendicular to the crown. The crown is larger than the root and overhangs it on all sides. Its lingual margin is concave, having a well-developed lingual sulcus, whereas the labial margin is convex and the labial protuberance is broken. The root is massive, inclined lingually, and pierced by a number of well-preserved foramina which are open at the level of the collar.

Dimensions. PL/IGNOU/101 measures 13.5 mm in length mesio-distally and 10.5 mm in width labio-lingually. The crown is 6 mm high measured from the base of enameloid and the root extends 3.5 mm below the base of crown. PL/IGNOU/102 measures 11 mm in length mesio-distally and 7 mm in width labio-lingually. The crown is 4.1 mm high measured from the base of enameloid. The root extends 3 mm and 5.9 mm below the base of crown lingually and labially, respectively.

Comparison. The teeth of *Ptychodus decurrens*, including the new material described here, are characterized by weakly inflated, low, rounded and broad crowns, and a unique crown pattern that distinguishes them from all the other genera of ptychodontids (Woodward, 1887; Williamson et al., 1991, 1993; Cicimurri, 2001). *Ptychodus* is represented by both low and high crowned species. PL/IGNOU/101 and 102 are low-crowned forms that differ from the high-crowned species (*Ptychodus anonymus*, *P. mortoni*, *P. mammillaris*, *P. occidentalis* and *P. whipplei*) in having a much larger occlusal surface relative to the base of the tooth, a low, flat crown, and coarse transverse ridges that cross the medial area of the crown (Williamson et al., 1991, 1993; Hamm, 2008). Among the low crowned species (*P. decurrens*, *P. marginalis*, *P. polygyrus*, and *P. latissimus*), the morphology of our specimens closely corresponds to that of *P. decurrens* in having transverse ridges on the entire crown surface, radiating ridges at the mesial and distal margins, and parallel anatomosing ridges on the labial margin. In contrast, *Ptychodus marginalis* and *P. polygyrus* have a concentric pattern of transverse ridges on the crown surface (Woodward, 1911; Hamm, 2010). *Ptychodus latissimus* differs from our specimens in having thick, widely spaced, and parallel transverse ridges restricted to the central portion of the crown. In this species, the transverse ridges do not bifurcate into numerous finer anastomosing ridges in the marginal area; rather the marginal area is wider than the central portion and is covered by irregular and coarse enameloid granulations (Niedźwiedzki and Kalina, 2003). *Ptychodus rugosus* differs from our specimens in possessing a crown covered by discontinuous transverse ridges and a well-developed marginal area ornamented with thin, concentric, enameloid ridges (Macleod, 1982). On account of the close similarity of the dental features of PL/IGNOU/101 and 102 to those of *P. decurrens*, we attribute the teeth from the Karai Formation to this species.

4. Discussion

The specimens of *P. decurrens* reported here not only attest to the presence of durophagous sharks, but also provide additional insights into the environmental conditions that prevailed during the deposition of the Karai Formation. The putative prey of *P. decurrens* has been previously suggested to be animals with hard shells, such as molluscs, crustaceans, and echinoderms (Kauffman, 1972; Williamson et al., 1991). The shallow marine setting of the Karai Formation provided habitats for a wide array of macro-invertebrates, including ammonites, bivalves, belemnites, echinoderms, and brachiopods (Stoliczka, 1871; Ayyasami, 2006), which may have served as prey for the sharks. The specimens of *P. decurrens* occur in association with a diverse ichthyofauna comprising of squaliform, hexanchiform and lamniform sharks, and ichthyosaur remains in the Karai Formation (Underwood et al., 2011).

On the basis of the flat nature and low height of the crown, *P. decurrens* is considered to be a basal form of *Ptychodus*, from which all later ptychodontids evolved (Herman, 1975; Hamm, 2008). This species first appeared in the Middle/Late Albian and diversified during the Late Cenomanian–Early Turonian (Herman, 1975; Williamson et al., 1991; Siverson, 1999). Prior to this report, its occurrence was restricted to the Laurasian continents and Australia. *P. decurrens* has a wide geographic distribution across the Laurasian continents, where it is known from Late Albian, Cenomanian and Turonian deposits in North America and Europe. In North America, it has been reported from the Turonian of Mexico (Alvarado-Ortega et al., 2006), the Upper Cenomanian–Lower Turonian of Nebraska (Williamson et al., 1991), Arizona (Williamson et al., 1993), and the Middle Cenomanian–Middle Turonian of South Dakota (Cicimurri, 2001). It is also known from

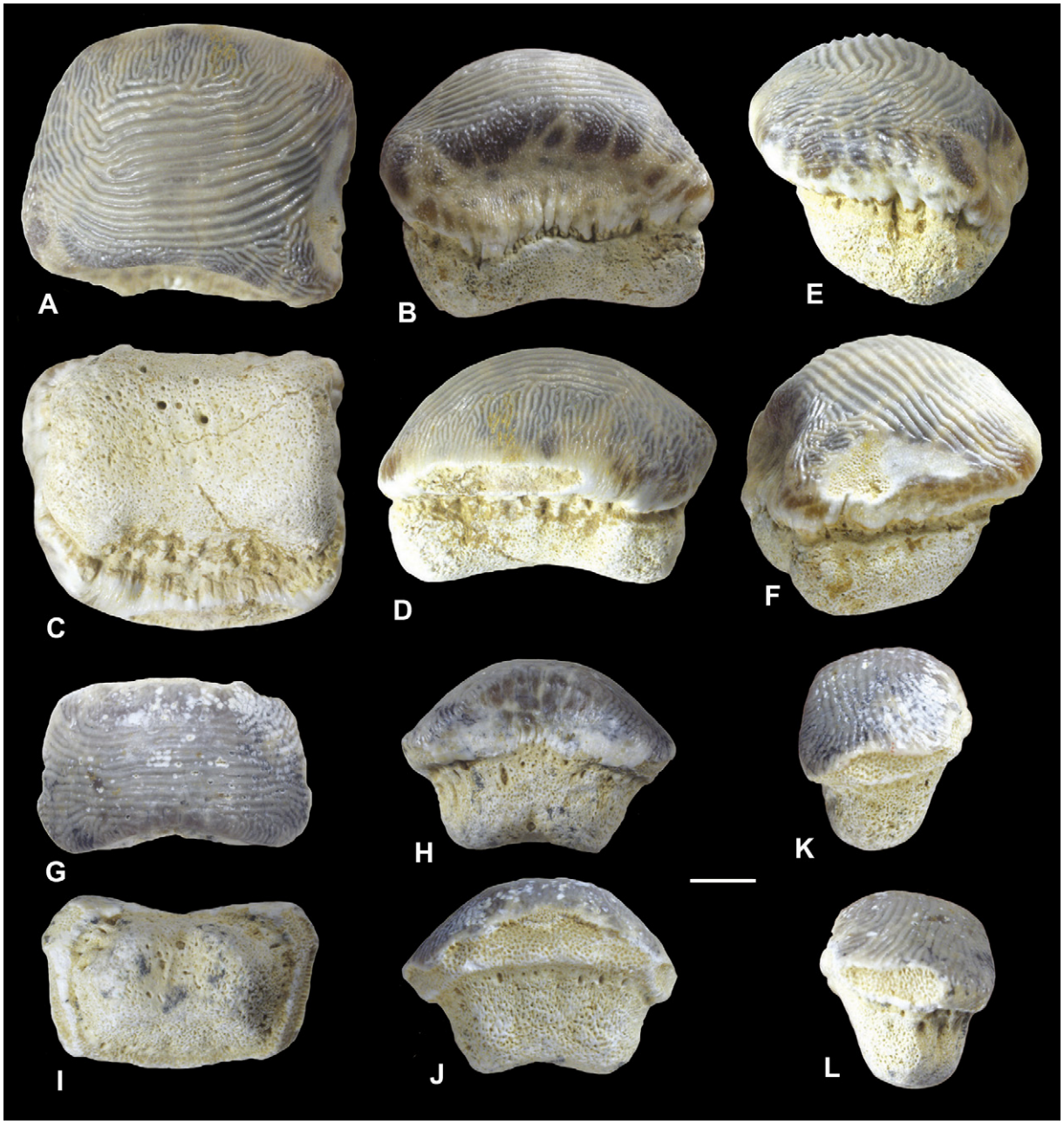

Fig. 3. Photomicrographs of *Ptychodus decurrens* teeth. A–F, PL/IGNOU/101 in A, occlusal, B, lingual, C, basal, D, labial, E, distal, and F, mesial views. G–L, PL/IGNOU/102 in G, occlusal, H, lingual, I, basal, J, labial, and K, L, lateral views. Scale bar represents 3 mm.

the mid Late Turonian beds in Greenland (Hoch, 1992). In Europe, *P. decurrens* has been documented from the Upper Albian–Turonian in France, Belgium and Great Britain (Woodward, 1911; Herman, 1975), the Upper Cenomanian of Bohemia Czech Republic (Trbušek, 1999) and the Upper Senonian of northern Italy (Cappetta, 1987). Among the Gondwanan landmasses, it has only been reported from Middle/Late Albian deposits in Western Australia (Siverson, 1999) (Fig. 4).

The Late Cenomanian–Early Turonian occurrence of *P. decurrens* in southern India has several palaeobiogeographical implications. Firstly, it represents only the second occurrence of the species from a Gondwanan landmass, and the first from the Indian subcontinent, supporting a cosmopolitan distribution for the species in both Laurasian and Gondwanan landmasses during the mid Cretaceous (Albian–Turonian). Secondly, the records of *P. decurrens* from North America, Europe, Australia and India, indicate that uninterrupted dispersal could occur throughout the Tethyan Sea. However, the majority of *P. decurrens*-yielding localities are at high palaeolatitudes in both hemispheres, suggesting an "antitropical" distribution (Underwood et al., 2011) and a preference for cooler waters.

The temporal occurrences of *P. decurrens* also have implications for reconstructing its dispersal history. The Middle/Late Albian occurrence of the species in Western Australia currently represents the oldest record, which may suggest that the species might have migrated from the Southern Hemisphere to the Northern Hemisphere via Tethyan Sea margins. Report of *Ptychodus* sp. from the Senonian of Brazil (Cappetta, 1987) along with this report from India may provide further support for such a mode of dispersal. However, the age of the Australian material is a little uncertain: it

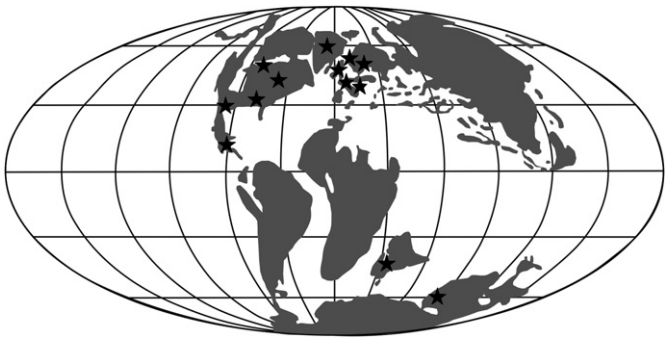

Fig. 4. Map showing the position of continents during the Late Cretaceous at around 94 Ma (Scotese, 2001) and the distribution of *Ptychodus decurrens* in Albian–Turonian strata.

could be younger Cenomanian (Siverson, 1999). If so, the polarity of the reconstructed dispersal pattern could be reversed, as a result of the record of a single tooth of *Ptychodus* sp. aff. *P. decurrens* from Texas dated as Late Albian (Meyer, 1974).

The overall stratigraphic range of *P. decurrens* is Albian–Turonian in both Gondwana and Laurasia. Although the place of origin of the ptychodontids cannot be conclusively determined at present, it is clear that it had a Pangaean distribution. Its apparent absence during the Late Cretaceous from other parts of Gondwana may well reflect limited field investigations in those areas.

5. Conclusions

P. decurrens was known previously mainly from the Albian–Turonian of North America and Europe, with the exception of a single report from Australia. Our record of this species in Late Cenomanian–Early Turonian deposits in southern India extends its geographic range within the Gondwanan landmasses. Very recently, a small vertebrate assemblage comprising remains of sharks and ichthyosaurs has been described from the Karai Formation (Underwood et al., 2011). Our report of durophagous *P. decurrens* further adds to our knowledge of the diversity of vertrbrate remains in the Karai Formation and provides additional data for palaeoenvironmental and palaeoecological reconstructions. Its occurrence on the Indian subcontinent during the Late Cenomanian–Early Turonian indicates a wide spatial, probable Pangaean distribution for the taxon. The teeth were recovered from deposits that contain abundant invertebrates, such as bivalves, ammonites, and belemnites, which were likely prey for *P. decurrens*. During the last three decades, the fossil record from Late Cretaceous deposits of the Indian subcontinent has improved dramatically, with reports of many new taxa from the continental Deccan infra- and intertrappean beds (ostracods; charophytes; eutherian, gondwanatherian and haramiyidan mammals; abelisaurid and titanosaurid dinosaurs; pelomedusid turtles; leptodactylid, ? hylid and ranoid frogs; madtsoiid and nigerophiid snakes; and anguimorph lizards) of great evolutionary and palaeobiogeographical significance (Prasad and Sahni, 2009). With the recent discovery of elasmobrachs and ichchthyosaurs (Underwood et al., 2011) and the present find of *P. decurrens* in the Karai Formation, gaps in the marine Cretaceous vertebrate fossil record of India are gradually narrowing.

Acknowledgements

We thank an anonymous referee, Dr. Gilles Cuny (University of Copenhagen, Denmark) and Mr. Shawn A. Hamm (University of Texas at Dallas, Texas) for critically reviewing the manuscript. This research was supported by funds from the Department of Science and Technology (DST) (Project No.SR/FTP/ES-33/2008) and Council of Scientific and Industrial Research (Award No. 09/100(0148)2K8-EMR-I), Government of India, New Delhi to OV in the form of a Fast-Track Research Project and Research Associateship, respectively; DST project grant No. SR/S4/ES-24/2002 and J C Bose National Fellowship to GVRP; a DST project grant No. SR/FTP/ES-46/2009 and UGC-SAP financial assistance from the Department of Geology, University of Jammu, to VP; and a Linnaean Society Percy Sladen memorial grant to AG.

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