ABSTRACT

Investigations in Blastoid Phylogenetics, Speciation, and the Sedimentology of an Echinoderm-defined Stratotype

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This dissertation addresses questions on blastoid (*Deltoblastus*) speciation and phylogeny, as well as investigation of the sedimentology of an echinoderm-defined (*Marsupites*) stratotype. *Deltoblastus* is a genus of Permian blastoid comprised of 15 species which differ based on thecal morphology. Investigation into described species revealed three new species, which are described based on characteristics that distinguish individuals from established morphotypes. Enhancing understanding of the genus is the construction of a character matrix containing all known species. Differences in characters provide evidence for unique thecal morphologies.

In addition, *Deltoblastus* is characterized using phylogenetic and clustering methods. Parsimony analysis allows construction of a phylogeny of the genus, with *Schizoblastus sayi* serving as the primary outgroup. Neighbor-joining cluster analysis together with Principal Components Analysis support clade associations and demonstrate the unique morphologies of *Deltoblastus* species. Despite demonstrating distinct separation of *Deltoblastus* from possible sister genera, parsimony analysis fails to

completely discern *Deltoblastus* species relationships. Supporting analyses aid in differentiation, and suggest separation of *D. molengraaffi* and *D. sebotensis* into a new genus. Whereas it has been put forward that *Schizoblastus*, among others, is the sister genus of *Deltoblastus*, this study fails to discern among the many genera which is the true sister group.

While investigating an echinoderm-defined stratotype exposure outside of Waco, Texas, a new species of *Gyrolithes* was discovered. This helical marine trace fossil occurs in beds of the Austin Chalk. The new ichnospecies *Gyrolithes texanus* is characterized by unique morphology and wall construction. This discovery expands the current geographic and environmental range of *Gyrolithes*, extending this ichnogenus into the chalk-dominated beds of the Cretaceous of Texas. Irregular bedding features from the *Gyrolithes* locality indicate this section of the Austin Chalk was deposited within a storm-dominated depositional regime, interspersed with periods of quiescence which allowed for firm ground formation and colonization by the trace maker. *Gyrolithes* is associated with marginal marine settings but is not associated with storm deposits; therefore, this discovery constitutes an expansion of environment for this ichnogenus.

Although seemingly disparate, these studies prove insightful to the development of echinoderm paleontology. These investigations are described in detail within.

Investigations in Blastoid Phylogenetics, Speciation, and the Sedimentology of an Echinoderm-defined Stratotype

by

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A Dissertation

Approved by the Department of Geology

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CHAPTER ONE

Introduction

Paleontology, as a field, encompasses many subdisciplines and employs a plethora of techniques to answer fundamental questions about the history of life on Earth. This dissertation uses a few of these techniques to answer three underlying questions.

The first question: How do we identify blastoid species? To answer this, an in-depth analysis of two major collections of *Deltoblastus*, a diverse genus with many species, and one particularly noted from its large abundance in the Permian beds of Timor, was undertaken, with the intent to measure and characterize these species with their many morphologies. As these observations progressed, it became apparent that three new species were present within these collections, and chapter two illustrates the process of observing, describing, and comparing new morphologies to past species, and the disparity in form which can exist within a single genus.

The second question was more complex than the first: How do we distinguish between species displaying diverse morphologies and closely related genera? To address this issue, *Deltoblastus* was once again employed. The diversity of morphologies demonstrated by the species contained within this genus complicates traditional methods employed by the discipline, an issue further exacerbated by the many proposed sister genera exhibiting similar morphologies. Chapter three illustrates the challenges to addressing this question, and shows that, in this instance, a multifaceted approach performs better than the standard.

The third question followed an ichnological and sedimentological approach: What can behavioral and depositional evidence tell us about a lithologically defined member of which the upper limit is designated by the presence/absence of a single echinoderm species? This question turned out to be complex and very informative. Both ichnology and sedimentology are overlooked in geology for what is often described as circumstantial evidence of environment, whereas other methods and disciplines give more concrete results. While it is true that individual observations are commonly only minor details with multiple interpretations open to them, many observations can lead to strong inferences and inductive reasoning. Using Occam's razor, we can then infer that many observations with overlapping explanations lead to simple, strongly supported results. In chapter four, this is exactly the case. Investigation into the many details present in the Austin Chalk, a formation well known in Texas for its coccolithophorian chalk bluffs and exposures, which contains members defined by total range of a single echinoderm species, demonstrates complex sedimentological history in a single outcrop leading to a new ichnospecies being described.

With these ideas in mind, it is important to remember that all sciences are, in essence, a work in progress, constantly being refined, and improving with age. Paleontology is a particularly complex field, caught between the disciplines of biology and geology, often relying on indirect evidence for support of hypotheses. Those challenges have improved the field rather than detracting from it, and paleontology continues to supply science with unique and insightful views into life of the past.

CHAPTER TWO

Three New Species of *Deltoblastus* Fay from the Permian of Timor

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Abstract

Deltoblastus is a genus of Permian blastoid comprised of 15 species, each differing based on subtle thecal morphology differences. Three new species are introduced here, based on characteristics present which distinguish individuals from established morphotypes. In order to guarantee a more complete understanding of the genus, a complex character matrix containing all 15 named and three new species was created, defining all species based on the presence or absence of 30 unique traits. Differences in character compositions give evidence for unique thecal morphologies, supporting the three new species which are proposed.

Introduction

Blastoids are a class of extinct marine echinoderms, characterized by five-fold symmetry, small columnar stems, and small theca. *Deltoblastus* Fay is a genus of Schizoblastid blastoid, composed of 15 species, characterized by elongate deltoid plates and diminished basal plates which are often invaginated. *Deltoblastus* is one of many radiating blastoid genera in the Permian, and the only member of family Schizoblastidae outside of the Early Carboniferous [1]. Recent investigation into the collections at Baylor University and the Natural History Museum of London (NHMUK) yields *Deltoblastus* specimens not ascribable to named species due to significant differences in theca morphology. These specimens are herein assigned to new species within *Deltoblastus*, and description of these is the purpose of this paper.

Geologic Setting

Deltoblastus is a Permian genus, primarily constrained to the island of Timor, with a few examples from Australia, Oman, and eastern Russia. The Permian *Deltoblastus* assemblages range from the Early to Middle Permian [2, 3, 4] and the abundance of this genus, particularly in the Timorese deposits, likely represents unique conditions favorable to *Deltoblastus* proliferation, as numbers of preserved Deltoblastus far exceed expected if only preservation effects were at work [2]. The *Deltoblastus* species described in this paper originate from Permian Timorese deposits. These deposits are heterogeneous, and have presented a complex problem for geologists for decades. Recent interpretations suggest this region is dominated by a shallow mixed marine carbonate and volcanics succession, while in some areas it is a thin bedded siliciclastic succession [2]. While traditional interpretations have placed the carbonate and volcanic succession as allochthonous, recent revision places both successions as autochthonous within a lithologically heterogeneous basin complex [2].

Methods

Investigation into these *Deltoblastus* species involved a detailed study of important thecal characters presented by the specimens. Initial visualization of the defining characters separating *Deltoblastus* species was attained using a detailed presence-absence character matrix, whose construction was based on information from original species descriptions and plates [5, 6, 7, 8, 9] and the suspected new species were added to this matrix (Table 2.1). Further evaluation of species of merit was attained from individual examination and comparison to electrotypes, published descriptions, and

detailed figures. Character choices were based on observed attributes and those defined as unique to species by previous researchers [5, 6, 7, 8, 9]. No permits were required for the described study, which complied with all relevant regulations. Specimen coating (where applied) was performed via ammonium chloride sublimation.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoobank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:E4D8639C-95B8-4F21-8B1F-E45C2342AFF9. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS. Specimens studied can be found at the following repositories: National Museum of Natural History, Smithsonian Institution: USNM 594945, USNM 594946, USNM 594947; Natural History Museum of London: NHMUK e59727, e59734, e59209, e59210, and e59212.

Table 2.1. Table of *Deltoblastus* binomial character matrix. See 'Remarks' for a thorough comparison of thecal characters of proposed new species to established species. Question marks (?) used when character was indeterminate. RDSutureRelief= Relief on the thecal surface of the radiodeltoid suture, 1= depressed, 0= flush/no relief; AmbSummitHabit= shape of the ambulacral groove at summit truncation, 1= pointed/rounded, 0= linear; AnusShape= shape of the anal opening, 1= triangular, 0= ovoid; AmbInd= indentation of the ambulacral groove, 1= depressed, 0= flush; MaxDeltWidth= position of the maxium width of the deltoid plate, 1= above radiodeltoid suture, 0= at the radiodeltoid suture; BrachioleAttachment= shape of the brachiole attachment point, 1= pointed, 0= ovoid; AmbFurrCurv= curvature of the ambulacral furrow, 1= curved, 0= straight; AmbW= ambulacral width, 1= medium/wide, 0= thin; AmbShape= ambulacral groove shape, 1= lancet, 0= linear; AmbLipIndrawing= severity of indrawing of the ambulacra at the radial lip, 1= significant, 0= slight/none; Periphery= position of the periphery on the theca, 1= low/adoral, 0= high/oral; DeltRadOverlap= presence of overlap of the deltoids/radials, 1= present, 0= absent; DeltoidInflation= inflation of the deltoid plate, 1= significant inflation, 0= none; LipExtension= extension of the radial lip adorally, 1= extended, 0= none; InvBasPresence= invagination of the basal plates, 1= invaginated, 0=none/protruding; RadAmbEdgeInfl= inflation of the radial plate along the contact with the ambulacral groove, 1= inflated, 0= depressed/inverted; LancExp= exposure of the lancet, 1= exposed, 0= not exposed; ThecaShape= overall shape of the theca in profile view, 1= globose, 0= ovoid; DeltAmbEdgeInfl= inflation of the deltoid plate along the contact with the ambulacral groove, 1= inflated, 0= none; OralTap= tapering of plates approaching the oral surface, 1= severe, 0= slight/gradual; DistRCurve= curvature of the distal (adoral) end of the radial plate, where flat and concave growth of this plate is the most common observed outside this genus, 1= flat/convex, 0= concave; MouthShape= shape of the oral openings, 1= slit, 0= ovoid; RDSutureShape= shape of the radiodeltoid suture, 1= pointed, 0= horizontal; Ornamentation= presence of theca ornamentation, 1= ornamented, 0= smooth; BPlateW= width of the basal plates, 1= wide, 0= small; RDSutvsPer= position of the radiodeltoid suture versus position of the periphery, 1= suture at or above periphery, 0= suture below periphery; RAmbSlope= degree of incline between radial plate and ambulacral groove, 1= shallow/horizontal, 0= steep; DeltExt= extension of the deltoids above the oral surface, 1= no extension, 0= ridge/comb/point; RadialInflation= inflation of the radial plate, 1= inflated, 0= depressed/flat; AmbFurrows= number of ambulacral furrows in 5mm, 1= >14, 0= ≤14.

Characters	*D. molengraffi*	*D. sebotensis*	*D. timorensis*	*D. globosus*	*D. jonkeri*	*D. somoholensis*	*D. verbeeki*	*D. delta*	*D. elongatus*	*D. subglobosus*	*D. magnificus*	*D. batheri*	*D. pseudodelta*	*D. permicus*	*D. ellipticus*	*D. beaveri n. sp.*	*D. ewini n. sp.*	*D. elevatus n. sp.*
ThecaShape	0	1	0	1	0	1	1	0	0	1	1	1	1	1	0	0	1	0
LipExtension	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
InvDeltPresence	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
AmbShape	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Periphery	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
RDSutvsPer	1	1	0	0	1	1	1	0	0	0	1	1	0	0	0	1	0	0
RDSutureShape	1	1	1	0	1	1	0	1	1	0	1	1	1	0	0	1	1	0
RDSutureRelief	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	1
AmbInd	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	0
RAmbSlope	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0
Ornamentation	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0
AmbFurrows	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
AmbLipIndrawing	1	0	1	1	1	0	0	1	0	1	0	0	1	1	0	1	1	0
DistRCurve	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0
DeltExt	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AmbSummitHabit	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
AnusShape	0	0	0	0	1	0	?	1	?	1	0	0	?	0	1	1	0	?
MouthShape	1	1	1	1	1	1	?	0	?	0	0	1	?	1	1	0	?	1
BrachioleAttachment	0	0	1	1	0	?	0	1	1	1	?	1	?	1	1	?	?	?
BPlateW	1	1	0	0	0	?	0	1	0	0	1	0	?	0	0	1	0	0
AmbW	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
AmbFurrCurv	0	0	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0
OralTap	0	0	0	0	1	1	1	0	0	1	1	1	1	1	0	1	1	0
DeltRadOverlap	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?
LancExp	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
DeltoidNum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
MaxDeltWidth	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
DeltoidInflation	1	0	1	1	1	0	0	0	0	1	0	0	0	1	1	0	0	1
RadialInflation	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
DeltAmbEdgeInfl	1	1	1	0	1	1	1	1	1	0	1	1	1	0	1	1	0	0
RadAmbEdgeInfl	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0

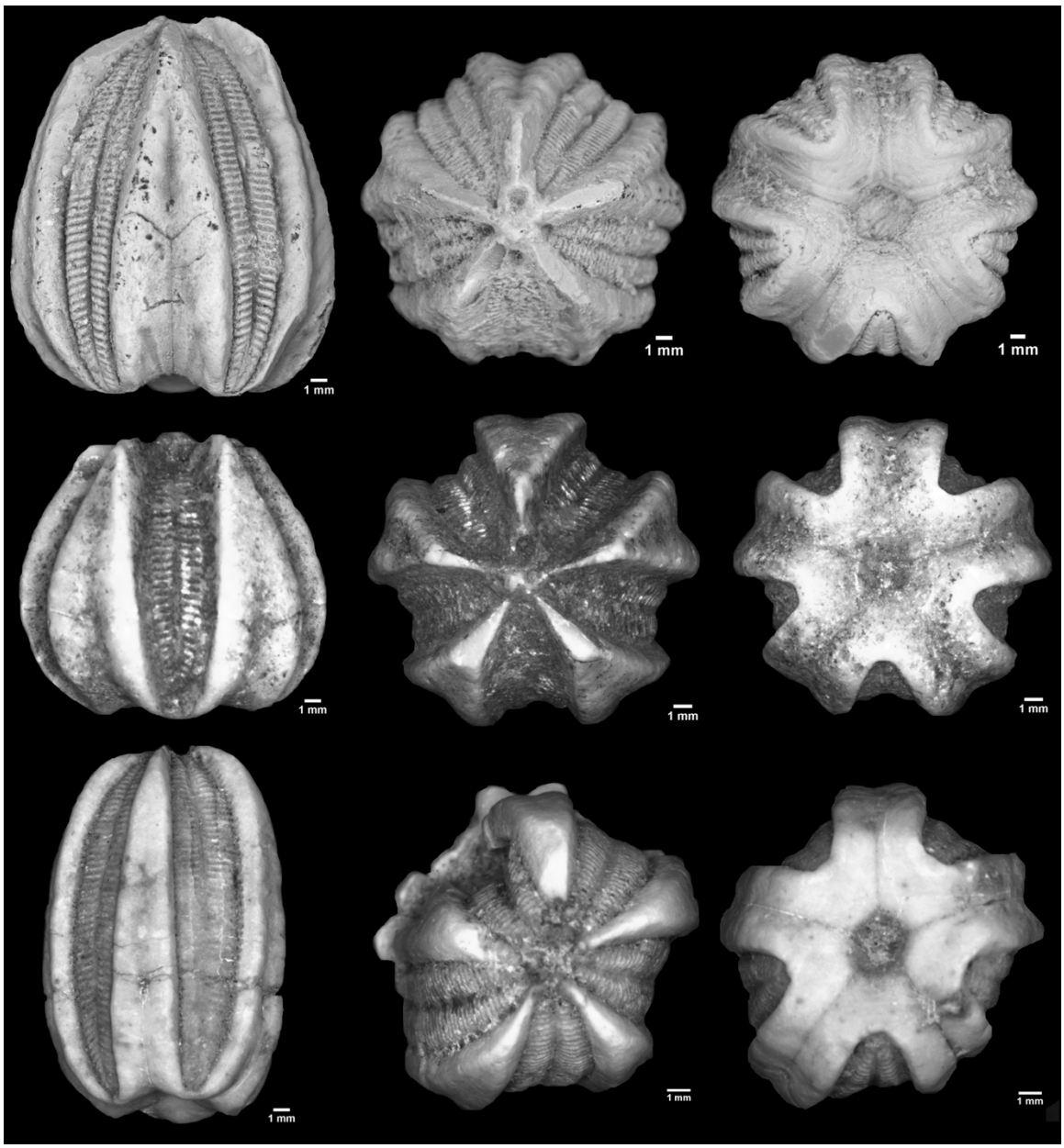

Figure 2.1. Staged photographs of new *Deltoblastus* species. Top) *Deltoblastus beaveri* sp. nov (left-to-right: theca, oral, and basal views), coated via ammonium chloride sublimation to maximize visibility of features*;* Middle) *Deltoblastus ewini* sp. nov (left-to-right: theca, oral, and basal views), uncoated, as per NMUK requirements*;* Bottom) *Deltoblastus elevatus* sp. nov (left-to-right: theca, oral, and basal views), uncoated, as per NMUK requirements.

Systematic Paleontology

Class Blastoidea Say, 1825
Family Schizoblastidae Etheridge and Carpenter, 1886

Genus *Deltoblastus* Fay, 1961

Type species— *Schizoblastus delta* var. *elongata* Wanner, 1924

Deltoblastus beaveri new species
urn:lsid:zoobank.org:act:CD3D10DA-D55E-42E5-9279-D21344BDA107
(Fig. 2.1 a-c)

Derivation of name

Named for Dr. Harold H. Beaver, Professor Emeritus (1978-1994), Baylor University.

Type specimen

USNM 594945.

Diagnosis

Deltoblastus beaveri sp. nov. possesses a subellipsoidal calyx, higher-than-wide. Large, rounded triangular anal opening, separate from small ovoid oral openings. Prominent deltoid septa are broken in holotype, appearing to extend into a ridge or comb structure. The deeply invaginated basal plates are wide for *Deltoblastus*, and distal radial curve approaching basals is convex in shape. Elongate ambulacra are wide and lancet shaped, in a shallow depression. Ambulacral lips are strongly indrawn, emphasizing the convex radial curve approaching the basal plates. Radials are extended, exceeding the

length of deltoids, an oddity for *Deltoblastus*. Radiodeltoid suture is flush to theca and is v-shaped, pointing distally. No ornamentation is observable, barring growth striae. Subdued deltoid ridges with minor inflation along length of ambulacra, with a shallow slope to the ambulacral groove. Ambulacral furrows number 10-12 in 5mm length, and are slightly arcuate in shape.

Description

Subellipsoidal theca, lacking ornamentation. Growth striae present, but shallow and hard to discern. Deeply invaginated basal plates. Cross-section is roughly a rounded decagon, with indented ambulacral groves. Theca height ~1.2 times that of theca width at greatest points. Radial length exceeds that of deltoid length. Deltoid 1.5 times wider than an ambulacrum at radiodeltoid suture. Ambulacra indented and wide, with ten to twelve furrows in 5mm length. Ambulacra length greater than two times the deltoid length, and nearly the length of the theca. Radials and deltoids inflated along ambulacrum edges, adorally becoming shallow crests or peaks. Radio-deltoid suture pointed basally, with theca periphery well below suture.

The small basal plates form a steep sided, truncated cone (Fig. 2.1 c). Invagination depth is 1/5th total theca height. Basal plate diameter is 1/7th total theca diameter.

Radial plates are higher than wide, and constitute more than ½ the height of the entire theca. Ambulacral lips are narrow, extending downward from theca, and tapering inward towards basals. Interradial seam is in a shallow depression, and is easily visible. Radiodeltoids from the exterior of the theca in a slightly convex arc. Radiodeltoid suture is pointed, downward facing, and is flush with plates. Suture is located at about ½ height

of theca. Theca periphery falls well below the suture, and is present about ¼ of the height of the theca. Deltoids at radiodeltoid suture exceed ambulacral width by about 3x. Deltoid is indented through the center, and tapers to an extended crest or comb orally. Where crests meet, theca comes to a point.

Slope to the ambulacral sinus is at a shallow angle, but falls to a somewhat deep groove. Ambulacral furrows are regular, about 14 in 5 mm, and fall in 2 inflated ridges running nearly the length of the theca. Individual furrows are linear to slightly curved. Overall, ambulacra are lancet shaped, and come to a rounded point basally and a sharp point orally.

Anal opening is large and teardrop shaped, easily discernible from the small, circular-to-ovoid oral openings.

Remarks

D. beaveri sp. nov. has many features which set it apart from the many established species of *Deltoblastus*. *D. beaveri* has a radial length-to-deltoid length ratio in excess of 1, meaning it possesses elongate radials, atypical of all other *Deltoblastus* species [4]. The deltoid length-to-ambulacrum length ratio of *D. beaveri* sp. nov. is too small for it to conform to the standards set for *D. molengraaffi* [4] or *D. sebotensis* [4], which have a 3:1 or greater ratio. With wide ambulacra, *D. beaveri* sp. nov. does not conform to the thin lancet-shaped ambulacra or ornamentations present on *D. timorensis* [4], *D. globosis* [4], *D. somoholensis* [4], *D. jonkeri* [4], *D. delta* [4], *D. elongatus* [4], *D. subglobosus* [4], *D. magnificus* [4], *D. batheri* [4], or *D. pseudelta* [4]. The position of the periphery of *D. beaveri* is well below the radio-deltoid suture, indicating it is unlikely

to be the same species as *D. verbeeki*, which commonly has the periphery at the radio-deltoid suture [4]. The elongate radials in this specimen set it apart from all other *Deltoblastus* species known.

Occurrence

Permian of Timor.

Deltoblastus ewini new species

urn:lsid:zoobank.org:act:E8C5BB71-E9F1-475C-8081-C5E0BA918208

(Fig. 2.1 d-f)

Derivation of name

Named for Dr. Timothy A. M. Ewin, Curator of Echinoderms (2008- Present), Natural History Museum of London.

Type specimen

NHMUK e59727, e59734, e59209, e59210, and e59212.

Diagnosis

Deltoblastus ewini sp. nov. is an obtusely globose species. *D. ewini* posseses shortened radials with a low-lying periphery, and pointed radiodeltoid suture falling above periphery. Pronounced inflation of deltoid ridges along ambulacral groove merges to become bladed peaks adorally. Long and wide petaloid ambulacra extend length of theca, and are strongly indrawn basally. Ornamentation absent.

Description

Overall shape of *D. ewini* is extremely globose, tapering adorally. Theca not ornamented, excepting minor growth striae on a few specimens. Theca height is exceeded by theca width at greatest points, lending a globose shape to the theca. Anus is teardrop-to-oval shaped.

Radial length is greatly exceeded by deltoid length, ~1.6x. Deltoid 1.5 times wider than ambulacra at radio-deltoid suture.

Ambulacra are deeply indented and wide, with ten to twelve furrows in 5 mm of length. Ambulacra length is two times the deltoid length, and extend nearly the length of the theca. Ambulacra are petaloid in shape, wider towards the base of the theca, with basal ends indrawn. Oral end of ambulacra appear truncated, ending abruptly at oral surface.

Radials and deltoids produce raised ridges along length of ambulacra, and are slightly depressed through the center of the plates. Orally, deltoids become pointed peaks or crests. Radio-deltoid suture is pointed in a v-shape towards the basals, and is placed at or slightly above the periphery. Deltoids are triangular in shape, widest at the radio-deltoid suture. Elevation of deltoids above ambulacra is greatest near oral surface. Overall, radial plates are strongly convex. Ambulacral extension into radial plate nearly bifurcating, with 2/3 dominated by ambulacral presence. Radial-radial suture barely visible, creating slight depression.

Basal plates are small, and only shallowly invaginated.

Remarks

The extreme globosity of this species sets it apart from other named species of *Deltoblastus*. Initial observation of *D. ewini* sp. nov. would lead to the diagnosis of *D. globosus* [4]; yet, the pointed radio-deltoid suture, which is more akin to that observed on *D. jonkeri* [4], excludes this diagnosis. *D. jonkeri*, with an average radial/deltoid length

ratio of greater than 0.5 [4], possesses radials that are too long and is, on average, too elongate in overall shape to be a viable alternative species assignation.

Occurrence.

Neoetpantoekak and Basleo localities, Sonnebait Series, Timor, Permian.

Deltoblastus elevatus new species

urn:lsid:zoobank.org:act:1C241EE2-76ED-4CB3-AD57-C38AC7E27122

(Fig. 2.1 g-i)

Derivation of name

Named for the extreme length of the deltoids; from Latin *elevo*, meaning elevated.

Type specimen

USNM 594946.

Paratype

USNM 594947.

Diagnosis

Deltoblastus elevatus sp. nov. possesses an extremely elongate, ellipsoidal theca. Ambulacral indentation is shallow, with wide, petaloid ambulacra extending the length of the theca. Deltoids are extremely elongated for *Deltoblastus* and narrow. Radio-deltoid suture horizontal, and is placed well below the periphery. Radials short, less than half the length of deltoids. Deltoid length greater than 4.5x deltoid width at radio-deltoid suture.

Description

Overall form of *Deltoblastus elevatus* resembles an elongate ellipsoid, which very slightly tapers adorally. Theca width is half that of theca height at greatest points. Theca lacks ornamentation and growth striae. Deltoid length exceeds radial length by a factor of 2.

Deltoid width is equal to ambulacral width at radio-deltoid suture. Deltoids elongate, and slightly tapering orally. Deltoid length exceeds deltoid width at greatest points by a factor of 4.5. Deltoids are raised above ambulacral surface, creating a narrow, steep-sided platform. Deltoids sharply indrawn at oral surface and produce narrow crests.

Ambulacra are shallowly indented and wide, with ambulacral side furrows in excess of 13 per 5 mm of length. Side furrow surface is slightly convex. Ambulacral length is 1.3x that of deltoids, with ambulacra extending the length of the theca. Radials and deltoids produce a raised platform along the length of the ambulalcra.

Radio-deltoid suture near horizontal, with periphery well above. Radials short, strongly influenced by ambulacral extension. Radial plates sharply convex, almost at right angle. Radial-radial suture is barely visible, flush with plate surface.

Reduced, invaginated basal plates are slightly depressed from radial surface. Radial-basal plate margin sharply contrasts with radial platform.

Remarks

D. elevatus sp. nov. is similar in basic form to *D. ellipticus*, with ambulacral side furrows in excess of 13 per 5 mm of length; however *D. elevatus* possesses extremely elongate deltoids, whose length is greater than 4.5x the width of the deltoids at the radio-deltoid suture, far in excess of the 2.4x-2.8x required for *D. ellipticus*, or the 3x required

for *D. elongatus* [4]. No other *Deltoblastus* species displays such distinctly elongate deltoids or morphology.

Occurrence

Basleo locality, Timor, Permian.

Conclusions

Deltoblastus morphology is complex but defining characters important to species differentiation can be resolved using simple visualization techniques. This paper used data taken from the original works on *Deltoblastus* species to establish a character matrix that can be used to ascertain species affinities based on simple metrics. Three new species of *Deltoblastus* are resolved using this approach, with each demonstrating a unique morphology. *Deltoblastus beaveri* is unique in its possession of shortened deltoids and elongated radials. *Deltoblastus ewini* demonstrates extreme globosity, with shortened radials and wide ambulacral grooves. Finally, *Deltoblastus elevatus* displays the opposing extreme, with pronounced elongation of the theca, especially of the deltoid plates.

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CHAPTER THREE

Phylogenetic Analysis of Blastoid Genus *Deltoblastus* Fay

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Abstract

Deltoblastus, an abundant and diverse blastoid genus known primarily from the Permian of Timor, is characterized using phylogenetic and clustering methods. Parsimony analysis, operating under heuristic TBR methods and Fitch assumptions, allows construction of a well-constrained phylogeny of the genus, with *Schizoblastus sayi* serving as the primary outgroup member of family Schizoblastidae. Neighbor joining cluster analysis (NJCA) together with Principal Components Analysis (PCA) supports phylogenetic clade associations, and demonstrates the unique morphologies of *Deltoblastus* species. Despite demonstrating distinct separation of *Deltoblastus* from possible sister genera, parsimony analysis fails to completely discern *Deltoblastus* species relationships. Supporting analyses (NJCA and PCA) aid in differentiation, and support possible separation of *D. molengraaffi* and *D. sebotensis* into a new transitional genus. While it has been put forward that *Schizoblastus*, among others, is the sister genus of *Deltoblastus*, this study fails to discern among the many genera which is the true sister group.

Introduction

Blastoids compose an extinct class of stalked marine echinoderm characterized by pentaradial symmetry, small theca, and shortened, and occasionally absent, columnar stems. Number and arrangement of thecal plates among the blastoids is highly conserved, with morphologic variations relying primarily on dimensional changes within the individual plates' structures. Ranging from the Silurian through Permian, blastoids reach their peak in diversity in the Mississippian, and decrease in number until the Permian, when a short resurgence in diversity precedes the class' extinction. *Deltoblastus* Fay [1], the focus of this study, constitutes one of the last genera of this now-extinct clade, and is unique in its high local abundance where it is found and the diverse range of forms,

which are currently ascribed species status. Perhaps because of this large diversity in form, is has long been suspect that *Deltoblastus* species may constitute a series of environmental adaptations rather than separate species. It has yet to be demonstrated that a continuum exists, however, among the many named species of *Deltoblastus*.

With 20 species (including Jansen's overlooked members) [2, 3, 4, 5, 6, 7], *Deltoblastus* Fay is one of several radiating blastoid genera from the Permian, and is restricted in provenance. Primarily known from deposits on the island of Timor, limited occurrences of this genus are reported from Australia, Oman, and eastern Russia. Thousands of specimens of the genus exist in major museum collections (e.g., Natural History Museum of London, Smithsonian Natural History Museum, Chicago Field Museum), the most important being Naturalis (Netherlands), which reports over 15,000 specimens, including 17 holotypes (Table 3.1). Three other species of *Deltoblastus* are known, with one holotype housed within the Natural History Museum of London (NHMUK), and the other two housed in the Smithsonian Institute's National Museum of Natural History (USNM). Many smaller collections also exist at museums and major research institutions around the world. A notable mention should be made of the Beaver collection currently housed within Baylor University's Department of Geology, which has over 800 specimens, including a diverse array of species and localities from Timor, and from which two of the most recent described species of *Deltoblastus* were described [6] (now housed in USNM). All occurrences of *Deltoblastus* are dated to the Late Permian [6, 7, 8, 9]. Due to the complex geology of Timor, detailed stratigraphic and geographic data for holotype material is often unavailable [7] (see [6] for a more thorough discussion of this problem).

Originally attributed to the Mississippian genus *Schizoblastus* Etheridge and Carpenter 1886 [10], Bather [2] described two species from Timor, *S. delta* and *S. timorensis*. In two manuscripts on Timorese blastoids and echinoderms, eight species and five subspecies were described by Wanner [3, 4], also being attributed to *Schizoblastus*. Jansen [5] added an additional species, *S. crassus*, and subspecies, *S. verbeeki* var *elongata* (Table 3.1). Recognizing morphological differences in the older (Mississippian-age) North American genus *Schizoblastus* and the younger (Permian) Timorese fauna, Fay [1] established the new genus *Deltoblastus* to include all of Wanner and Bather's named Timorese *Schizoblastus* species (*D. molengraaffi, D. timorensis, D. jonkeri, D. somoholensis, D. verbeeki, D. delta, D. magnificus, D. batheri, D. pseudodelta,* and *D. permicus*) and raised five subspecies (*D. sebotensis, D. globosus, D. elongatus, D. subglobosus,* and *D. ellipticus*) to species, while also defining a hierarchy of character states (Figure 1). When designating *Deltoblastus* species, Fay overlooked Jansen's [5] species and subspecies, and Jansen's material has continued to be overlooked since publication. While labelled for the duration of this study with the "*Schizoblastus (Deltoblastus)"* genus placeholder, these species are suggested for proper reassignment once type specimen information becomes available. In the context of Fay's reassignment of other *Schizoblastus* species as *Deltoblastus*, Jansen's [5] subspecies are recognized for this analysis as distinct operational taxonomic units. Since Fay's work, *Deltoblastus* has not been subject to evaluation as a genus, nor have the member subspecies been evaluated to demonstrate legitimacy of Fay's elevation of the subspecies members to species. Three additional species have since been added to *Deltoblastus* [6] based on distinct morphological differences: *D. beaveri*, *D. elevatus*, and *D. ewini*; however, no

formal evaluation of the genus was performed, despite this work containing a detailed character matrix of known *Deltoblastus* species. Evaluation of *Deltoblastus* species assignments, along with testing the stability of the relationship of *Deltoblastus* to proposed sister genera, prompted this research.

Table 3.1. Current and past designations of all ascribed and appropriated *Deltoblastus* species. Note those by Jansen [5] are currently assigned to *Schizoblastus*. Fay's [1] redesignation of species to *Detlobastus* raised all of Wanner's [2] subspecies to species, but did not give an explanation as to why.

Genus	Species	Original Species Designation	Described by	Reassigned by
Deltoblastus	*delta*	*Schizoblastus delta*	Bather, 1908	Fay, 1961
Deltoblastus	*timorensis*	*Schizoblastus timorensis*	Bather, 1908	Fay, 1961
Deltoblastus	*molengraaffi*	*Schizoblastus molengraffi*	Wanner, 1924	Fay, 1961
Deltoblastus	*sebotensis*	*Schizoblastus molengraaffi sebotensis*	Wanner, 1924	Fay, 1961
Deltoblastus	*globosus*	*Schizoblastus timorensis globosa*	Wanner, 1924	Fay, 1961
Deltoblastus	*jonkeri*	*Schizoblastus jonkeri*	Wanner, 1924	Fay, 1961
Deltoblastus	*elongatus*	*Schizoblastus delta elongata*	Wanner, 1924	Fay, 1961
Deltoblastus	*subglobosus*	*Schizoblastus delta subglobosus*	Wanner, 1924	Fay, 1961
Deltoblastus	*magnificus*	*Schizoblastus magnificus*	Wanner, 1924	Fay, 1961
Deltoblastus	*batheri*	*Schizoblastus bather*	Wanner, 1924	Fay, 1961
Deltoblastus	*pseudodelta*	*Schizoblastus pseudodelta*	Wanner, 1924	Fay, 1961
Deltoblastus	*permicus*	*Schizoblastus permicus*	Wanner, 1924	Fay, 1961
Deltoblastus	*ellipticus*	*Schizoblastus perimicus elliptica*	Wanner, 1924	Fay, 1961
Deltoblastus	*somoholensis*	*Schizoblastus somoholensis*	Wanner, 1924	Fay, 1961
Deltoblastus	*verbeeki*	*Schizoblastus verbeeki*	Wanner, 1924	Fay, 1961
Schizoblastus	*crassus*	n/a	Jansen, 1934	n/a
Schizoblastus	*verbeeki elongata*	n/a	Jansen, 1934	n/a
Deltoblastus	*beaveri*	n/a	Morgan, 2015	n/a
Deltoblastus	*elevatus*	n/a	Morgan, 2015	n/a
Deltoblastus	*ewini*	n/a	Morgan, 2015	n/a

Phylogenetically, the placement of *Deltoblastus* has been subject to debate since its inception. Originally considered part of *Schizoblastus* [2], *Deltoblastus* was raised to genus status by Fay [1], who considered *Schizoblastus* to be a sister genus, and possibly

the parent genus [1]. However, the sisterhood of *Schizoblastus* was put into question when *Orbiblastus* [11] was proposed as the possible parent genus [12], and part of the larger family of Schizoblastidae. The illustrations provided by Fay [12; p. S395] demonstrate hypothetical possible or inferred relationships, and exclude *Schizoblastus* from the *Deltoblastus* lineage, despite its inclusion within the same family. Within this proposed phylogeny, *Auloblastus* [13] is the first Schizoblastid of the *Deltoblastus* ancestry, giving rise to two genera, *Lophoblastus* [14] and *Orbiblastus*. *Orbiblastus* then later gives rise to *Deltoblastus*. This phylogenetic framework went unquestioned in the literature until Waters and Horowitz [15], who proposed a revision to blastoid orders based on spiracle structure. This revision redefined the Schizoblastidae as composed of five genera: *Schizoblastus*, *Auloblastus*, *Deltoblastus*, *Lophoblastus*, and *Orbiblastus*. Bodenbender [16] later used an extensive character matrix combined with crystallography of plates to calculate blastoid genera relationships. This analysis hypothesized that *Deltoblastus* was not related to *Orbiblastus*, but perhaps descended from a completely different lineage, as Schizoblastidae was suspected of composing a polyphyletic family. Following this analysis, and relying on much of the same data, Bodenbender and Fisher [17] completed an analysis of the stratocladistic relationships of blastoids. Their analysis presented many different possible phylogenies, the most notable based on stratocladistic principles. This analysis hypothesized that the sister genus of *Deltoblastus* is *Heteroblastus* [10], a genus belonging to family Granatocrinidae. These genera were then sister to *Astrocrinus* [10] member of Astrocrinidae. Other members of this new hypothesized clade included *Schizoblastus*, *Orbiblastus*, and *Lophoblastus*. It should be noted, however, that a strict consensus tree of this analysis produced a vast

polytomy for the blastoids. Sumrall and Brochu [18] produced a rebuttal to the earlier [17] stratocladistic analysis, and the resultant Adam's consensus suggests a different clade for *Deltoblastus* as well, with *Heteroblastus* and *Schizoblastus* forming the two closest genera. Most recently, *Pinguiblastus* [20] was proposed as a potential sister genus to *Deltoblastus*, based on shared morphological characters [20].

Methods

Phylogenetic analysis of *Deltoblastus* was undertaken to establish an understanding of *Deltoblastus* species relationships, and to compare these species to the proposed nearest evolutionary genera. It has been postulated that the Chinese *Pinguiblastus* [20] is the more direct ancestor over the North American genus *Schizoblastus* [1, 21]. Other authors have hypothesized that varying other genera, including *Lophoblastus*, *Orbiblastus*, and *Heteroblastus*, could also pose close relationships with *Deltoblastus*, and are therefore included in this analysis. Using characters measured from original publications and redescriptions [3, 4, 5, 6, 10, 11, 13, 21, 22], a binomial matrix summarizing species' attributes was developed, with each species represented as a distinct operational taxonomic unit (OTU). For all species excepting those of *Deltoblastus*, only type specimens defining the genus were used, limited to one representative per genus. Primary data are derived from traits observable in the original published plates of paratypes and holotypes, with secondary information coming from published species descriptions. To avoid biases leading to artificial polarization of the data, *Deltoblastus* species' characters were measured in a random order, and the ancestral members, *Schizoblastus*, *Orbiblastus*, *Lophoblastus*, *Heteroblastus*, *Astrocrinus*, and *Pinguiblastus*, measured last. The data are randomly

organized into the data matrix, *i.e.*, there was no intentional ordering of measured characters, and these data can be observed in Table 3.2.

In addition to the principal matrix developed for *Deltoblastus*, data were taken from Bodenbender's [16] discussion of crystallography within blastoids. Taken directly were the characters for *Schizoblastus*, *Orbiblastus*, *Lophoblastus*, *Heteroblastus*, and *Astrocrinus*. As each individual member of *Deltoblastus* was included in the matrix developed for this manuscript, characters for the *Deltoblastus* species were each tabulated according to the original parameters of Bodenbender [16]. *Pinguiblastus* was not described until after the publication of Bodenbender's work, therefore characters for *Pinguiblastus* were calculated from the original parameters in the same manner as *Deltoblastus* species [20]. As PAST does not recognize in a character matrix, question marks (?) were inserted into the original Bodenbender [16] dataset as placeholders, and were used in the same fashion for all species and genera tabulated for this analysis.

Once these data are collected, they are subjected to parsimony analysis, and resulting cladograms interpreted with respect to the data. Parsimony analysis is performed using the program PAST [23], using heuristic tree bisection and reconnection, Fitch optimization, and reordered 50,000 times. Analyses were conducted three times: once using the matrix derived for *Deltoblastus* species [6] (Figure 1), secondly using the original Bodenbender [16] matrix with additions of the *Deltoblastus* species and *Pinguiblastus* (Figure 3.2), and finally using a combined matrix of both the *Deltoblastus* characters and Bodenbender's [16] original ninety-four characters (Figures 3.3, 3.4). Evaluation of trees relied on resolution and the ability to separate *Deltoblastus* species

from other potential genera. As parsimony often produced more than one most parsimonious tree, strict consensuses were used by default.

Neighbor joining cluster analysis (NJCA) and Principal Components Analysis (PCA) are employed to compare whether species associations agree with those of parsimony analysis, and to evaluate overall similarity of *Deltoblastus* species (Figures 3.5, 3.6). Operating under Euclidean distance assumptions, NJCA is used to evaluate the data matrix. As this analysis evaluates absolute similarity, results are not always congruent with parsimony, but when both analyses are in agreement, resulting clusters are considered to be particularly significant [24]. Variances within and between clusters often can be insightful, especially when underscoring characteristics not emphasized in parsimony analysis. Although not influencing similarity results, *Schizoblastus*, *Orbiblastus*, *Lophoblastus*, *Heteroblastus*, *Astrocrinus*, and *Pinguiblastus* are included to show overall genus dissimilarity from *Deltoblastus* species. PCA, in contrast, often is used to distinguish noise from useful data signals within a data set. PCA is also performed using the combined dataset, using the first two principal components axes, as these likely contain the most relevant data for differentiating species and genera within this study.

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard

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Table 3.2. Combined matrix of blastoids characters used for parsimony analyses, NJCA, and PCA. “Morgan Char #” indicates which character from Morgan [6] was used, and “Bodenbender Char #” indicated a character from Bodenbender [16]. Refer to these works for a more complete review of these character designations. Bodenbender characters for *Schizoblastus*, *Lophoblastus*, *Heteroblastus*, and *Orbiblastus* come from Bodenbender [16].

	Astrocrinus tetragonus	***Deltoblastus batheri***	***D. beaveri***	***D. delta***	***D. elevatus***	***D. ellipticus***	***D. elongatus***	***D. ewini***	***D. globosus***	***D. jonkeri***	***D. magnificus***	***D. molengraffi***	***D. permicus***	***D. pseudodelta***	***D. sebotensis***	***D. somoholensis***	***D. subglobosus***	***D. timorensis***	***D. verbeeki***	***Heteroblastus cumberlandi***	***Lophoblastus inopinatus***	***Orbiblastus hoskynae***	***Pinguiblastus tushansis***	***Schizoblastus sayi***	***S. (D.) crassus***	***S. (D.) verbeeki elongata***
Morgan Char 1	1	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	1	0	1	0	0	1	1	0	1	0
Morgan Char 2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1
Morgan Char 3	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1
Morgan Char 4	0	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	0	0	0	0	1	1
Morgan Char 5	0	1	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1	1	1	0	0	0	0	0	0	1
Morgan Char 6	0	1	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	1	0	1	1	1	0	0	1
Morgan Char 7	1	1	1	1	0	0	1	1	0	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	0	1
Morgan Char 8	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0
Morgan Char 9	1	1	0	1	0	1	1	1	0	0	1	0	1	1	0	0	1	0	1	0	0	1	0	0	1	0

	Astrocrinus tetragonus	*Deltoblastus batheri*	*D. beaveri*	*D. delta*	*D. elevatus*	*D. ellipticus*	*D. elongatus*	*D. ewini*	*D. globosus*	*D. jonkeri*	*D. magnificus*	*D. molengraffi*	*D. permicus*	*D. pseudodelta*	*D. sebotensis*	*D. somoholensis*	*D. subglobosus*	*D. timorensis*	*D. verbeeki*	*Heteroblastus cumberlandi*	*Lophoblastus inopinatus*	*Orbiblastus hoskynae*	*Pinguiblastus tushansis*	*Schizoblastus sayi*	*S. (D.) crassus*	*S. (D.) verbeeki elongata*
Morgan Char 10	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	1	0	0	0
Morgan Char 11	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	1	1	0	0
Morgan Char 12	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	0	0
Morgan Char 13	0	0	1	1	0	0	0	1	1	1	0	1	1	1	0	0	1	1	0	1	0	1	0	1	1	0
Morgan Char 14	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	1	0	0	1
Morgan Char 15	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	0	1	1	1	0	0	0
Morgan Char 16	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0	0
Morgan Char 17	0	0	1	1	?	1	?	0	0	1	0	0	0	?	0	0	1	0	?	1	0	0	0	0	?	?
Morgan Char 18	1	1	0	0	1	1	?	?	1	1	0	1	1	?	1	1	0	1	?	1	?	0	1	1	?	?
Morgan Char 19	?	1	?	1	?	1	1	?	1	0	?	0	1	?	0	?	1	1	0	?	?	0	1	0	?	?
Morgan Char 20	0	0	1	1	0	0	0	0	0	0	1	1	0	?	1	?	0	0	0	0	0	0	0	0	?	?
Morgan Char 21	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	0	0	1	0	1	0
Morgan Char 22	1	0	1	1	0	1	1	1	1	1	1	0	1	1	0	0	1	1	1	?	?	0	1	0	?	?
Morgan Char 23	0	1	1	0	0	0	0	1	0	1	1	0	1	1	0	1	1	0	1	1	0	0	0	1	0	1
Morgan Char 24	?	1	?	1	?	1	1	?	1	1	1	1	1	1	1	1	1	1	1	?	0	?	0	1	?	?
Morgan Char 25	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Morgan Char 26	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	1	1	0	0	0
Morgan Char 27	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Morgan Char 28	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0
Morgan Char 29	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Morgan Char 30	1	1	1	1	0	1	1	0	0	1	1	1	0	1	1	1	0	1	1	1	0	0	0	0	1	1
Morgan Char 31	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1
Bodenbender Char 1	1	0	0	1	1	1	1	0	1	1	0	1	1	1	1	1	0	1	0	1	1	1	1	1	0	0
Bodenbender Char 2	1	0	0	1	0	0	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	1	1	0	0
Bodenbender Char 3	0	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	6	5	6	6	6
Bodenbender Char 4	?	2	2	2	2	2	2	2	2	2	2	2	2	2	?	2	2	2	2	?	?	?	0	1	2	?
Bodenbender Char 5	1	1	?	1	?	1	?	?	?	?	?	1	?	?	1	?	?	1	1	1	1	1	1	1	?	?
Bodenbender Char 6	2	2	?	?	?	2	?	?	?	?	?	2	?	?	?	?	?	?	2	?	3	3	?	2	?	?
Bodenbender Char 7	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	Astrocrinus tetragonus	*Deltoblastus batheri*	*D. beaveri*	*D. delta*	*D. elevatus*	*D. ellipticus*	*D. elongatus*	*D. ewini*	*D. globosus*	*D. jonkeri*	*D. magnificus*	*D. molengraffi*	*D. permicus*	*D. pseudodelta*	*D. sebotensis*	*D. somoholensis*	*D. subglobosus*	*D. timorensis*	*D. verbeeki*	*Heteroblastus cumberlandi*	*Lophoblastus inopinatus*	*Orbiblastus hoskynae*	*Pinguiblastus tushansis*	*Schizoblastus sayi*	*S. (D.) crassus*	*S. (D.) verbeeki elongata*
Bodenbender Char 8	1	1	?	?	?	1	?	?	?	?	?	1	?	?	?	?	?	?	1	?	1	?	?	0	?	?
Bodenbender Char 9	0	1	?	?	?	1	?	?	?	?	?	1	?	?	?	?	?	?	1	?	0	?	?	1	?	?
Bodenbender Char 10	3	2	2	3	2	2	2	?	3	3	2	3	2	?	?	2	2	3	2	3	2	2	2	3	2	?
Bodenbender Char 11	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	?
Bodenbender Char 12	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	?
Bodenbender Char 13	?	2	2	2	2	2	2	2	2	2	2	?	2	2	?	?	2	2	2	2	?	?	2	2	2	?
Bodenbender Char 14	0	0	0	0	0	0	0	0	0	0	?	?	0	?	?	?	?	?	0	?	?	?	?	?	1	0
Bodenbender Char 15	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	1	?	?
Bodenbender Char 16	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?
Bodenbender Char 17	0	1	0	1	1	1	?	1	1	1	1	1	1	1	?	1	?	1	1	1	1	1	1	1	1	?
Bodenbender Char 18	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	?	?
Bodenbender Char 19	0	?	?	1	?	?	?	?	1	1	?	1	?	?	1	?	?	1	1	1	1	1	1	1	?	?
Bodenbender Char 20	?	?	?	0	?	?	0	?	0	0	?	0	?	?	0	?	?	0	0	0	0	0	0	1	?	?
Bodenbender Char 21	0	3	3	3	3	3	3	3	3	3	3	0	3	3	0	3	3	3	3	0	1	0	0	0	3	3
Bodenbender Char 22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Bodenbender Char 23	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	?	0	?	1	0	0	0
Bodenbender Char 24	?	3	3	3	3	3	3	3	1	1	3	3	3	3	3	3	3	1	3	1	?	2	1	1	3	3
Bodenbender Char 25	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0	1	0	0	1	1	2	1	0	0
Bodenbender Char 26	2	2	1	2	1	1	2	1	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	?	?
Bodenbender Char 27	3	3	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3	2	3	1	3	3	3
Bodenbender Char 28	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	?
Bodenbender Char 29	?	1	1	1	1	1	0	1	0	1	1	1	1	0	0	0	1	1	1	1	1	?	0	?	1	1

	Astrocrinus tetragonus	*Deltoblastus batheri*	*D. beaveri*	*D. delta*	*D. elevatus*	*D. ellipticus*	*D. elongatus*	*D. ewini*	*D. globosus*	*D. jonkeri*	*D. magnificus*	*D. molengraffi*	*D. permicus*	*D. pseudodelta*	*D. sebotensis*	*D. somoholensis*	*D. subglobosus*	*D. timorensis*	*D. verbeeki*	*Heteroblastus cumberlandi*	*Lophoblastus inopinatus*	*Orbiblastus hoskynae*	*Pinguiblastus tushansis*	*Schizoblastus sayi*	*S. (D.) crassus*	*S. (D.) verbeeki elongata*
Bodenbender Char 30	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	?	?	0	0
Bodenbender Char 31	?	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	?	1	1	2	1	2	2
Bodenbender Char 32	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	?	0	0	0	0	1	1
Bodenbender Char 33	1	1	1	1	0	1	1	0	?	0	?	0	1	1	0	?	1	1	0	?	1	0	1	?	1	1
Bodenbender Char 34	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0
Bodenbender Char 35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0
Bodenbender Char 36	0	0	?	0	?	0	0	?	0	0	?	0	0	?	0	?	0	0	0	0	0	0	?	0	0	?
Bodenbender Char 37	0	0	?	?	?	0	?	?	0	0	?	0	1	?	0	?	?	0	0	0	0	0	?	0	?	?
Bodenbender Char 38	?	0	?	?	?	1	?	?	0	?	?	1	1	?	1	?	?	1	0	1	1	0	?	0	?	?
Bodenbender Char 39	?	1	?	?	?	1	?	?	1	?	?	1	1	?	?	?	?	?	1	1	1	1	?	1	?	?
Bodenbender Char 40	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
Bodenbender Char 41	?	0	?	?	?	0	?	?	0	0	?	0	0	?	?	?	?	0	0	0	0	0	0	0	?	?
Bodenbender Char 42	1	0	?	?	?	0	?	?	0	0	?	0	0	?	?	?	?	0	0	?	1	?	0	?	?	?
Bodenbender Char 43	?	1	?	?	?	1	?	?	1	?	?	1	1	?	?	?	?	1	1	1	1	1	1	0	?	?
Bodenbender Char 44	?	1	?	?	?	1	?	?	1	?	?	1	1	?	?	?	?	1	1	1	1	1	?	1	?	?
Bodenbender Char 45	?	0	?	?	?	0	?	?	?	?	?	0	0	?	?	?	?	?	?	?	1	1	0	2	?	?
Bodenbender Char 46	1	1	?	1	?	0	?	?	1	?	?	1	0	?	?	?	?	?	?	?	0	1	1	0	?	?
Bodenbender Char 47	0	1	?	?	?	1	?	?	1	1	?	1	1	?	?	?	?	1	1	?	0	0	1	1	?	?
Bodenbender Char 48	1	1	?	?	?	1	?	?	?	?	?	0	1	?	?	?	?	?	1	?	1	0	0	1	?	?
Bodenbender Char 49	?	0	?	?	?	0	?	?	?	?	?	1	0	?	?	?	?	?	1	?	1	0	0	1	?	?
Bodenbender Char 50	0	1	?	?	?	0	?	?	?	?	?	0	0	?	?	?	?	?	1	?	0	0	0	0	?	?
Bodenbender Char 51	0	0	?	?	?	0	?	?	?	?	?	0	0	?	?	?	?	?	?	?	0	0	0	0	?	?

	Astrocrinus tetragonus	*Deltoblastus batheri*	*D. beaveri*	*D. delta*	*D. elevatus*	*D. ellipticus*	*D. elongatus*	*D. ewini*	*D. globosus*	*D. jonkeri*	*D. magnificus*	*D. molengraffi*	*D. permicus*	*D. pseudodelta*	*D. sebotensis*	*D. somoholensis*	*D. subglobosus*	*D. timorensis*	*D. verbeeki*	*Heteroblastus cumberlandi*	*Lophoblastus inopinatus*	*Orbiblastus hoskynae*	*Pinguiblastus tushansis*	*Schizoblastus sayi*	*S. (D.) crassus*	*S. (D.) verbeeki elongata*
Bodenbender Char 52	0	0	?	?	?	0	?	?	0	?	?	0	0	?	?	?	?	?	?	?	0	0	0	0	?	?
Bodenbender Char 53	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1	0	0	0	1	2	1	0	2	0	0
Bodenbender Char 54	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bodenbender Char 55	?	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	?
Bodenbender Char 56	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	?
Bodenbender Char 57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0
Bodenbender Char 58	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	1	0	0	0	1	0	0	0	0	0	0
Bodenbender Char 59	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	0	0	?	0	0	0	1	1	0
Bodenbender Char 60	1	1	1	1	0	1	1	1	1	1	1	1	1	0	?	0	1	0	1	1	0	0	0	0	0	0
Bodenbender Char 61	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bodenbender Char 62	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Bodenbender Char 63	1	1	1	1	1	1	1	1	1	1	1	1	1	0	?	0	1	1	1	?	1	1	0	1	0	1
Bodenbender Char 64	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	1	?	0	1	0	0
Bodenbender Char 65	2	1	1	1	1	1	1	1	1	1	1	1	1	?	?	?	1	1	1	?	1	1	2	1	1	1
Bodenbender Char 66	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?
Bodenbender Char 67	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?
Bodenbender Char 68	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	1	?	?	?
Bodenbender Char 69	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	1	1
Bodenbender Char 70	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	2	0	1	2	2	1	1
Bodenbender Char 71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bodenbender Char 72	?	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	1	?	0	?	0	0
Bodenbender Char 73	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

	Astrocrinus tetragonus	*Deltoblastus batheri*	*D. beaveri*	*D. delta*	*D. elevatus*	*D. ellipticus*	*D. elongatus*	*D. ewini*	*D. globosus*	*D. jonkeri*	*D. magnificus*	*D. molengraffi*	*D. permicus*	*D. pseudodelta*	*D. sebotensis*	*D. somoholensis*	*D. subglobosus*	*D. timorensis*	*D. verbeeki*	*Heteroblastus cumberlandi*	*Lophoblastus inopinatus*	*Orbiblastus hoskynae*	*Pinguiblastus tushansis*	*Schizoblastus sayi*	*S. (D.) crassus*	*S. (D.) verbeeki elongata*
Bodenbender Char 74	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Bodenbender Char 75	2	0	1	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Bodenbender Char 76	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	0	0
Bodenbender Char 77	?	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	?	1	1	0	1	0	?
Bodenbender Char 78	0	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1	?	?	?	1	1	1	1	1	?	?
Bodenbender Char 79	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	0	0	0	0	?	?
Bodenbender Char 80	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	0	0	0	0	?	?
Bodenbender Char 81	2	?	?	?	?	?	?	?	?	?	?	?	0	?	1	2	?	?	?	?	?	?	0	?	?	?
Bodenbender Char 82	?	?	?	0	?	0	0	0	0	0	?	0	0	?	0	?	0	0	0	?	0	0	0	0	?	?
Bodenbender Char 83	0	1	1	1	0	0	1	0	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1	1	1
Bodenbender Char 84	?	2	0	0	?	?	0	?	0	0	0	0	3	3	?	2	?	0	0	3	0	?	0	3	0	0
Bodenbender Char 85	3	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2	0	0	1	0	0	0
Bodenbender Char 86	1	1	1	1	0	1	0	0	1	0	1	1	0	0	1	0	1	1	1	1	1	1	1	1	0	1
Bodenbender Char 87	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0	0	1	0	0	0
Bodenbender Char 88	?	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	?	2	2	1	1	1	1
Bodenbender Char 89	?	1	1	1	2	1	1	1	2	1	1	1	2	1	1	1	1	1	1	?	0	1	0	2	1	1
Bodenbender Char 90	?	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0	2	2
Bodenbender Char 91	?	0	0	0	0	0	0	0	0	1	0	0	0	0	?	?	0	0	0	?	1	2	0	2	0	0
Bodenbender Char 92	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	2	?	0
Bodenbender Char 93	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	?	?
Bodenbender Char 94	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	?	?	1	?	?

Results

Cladograms produced by parsimony analysis of *Deltoblastus* species demonstrate multiple core clades supported by transitional species, as well as unresolved placements of two contained species (Figures 3.1, 3.2, 3.3, 3.4). In the best resolved phylogeny (Figure 3.3), there is a core polytomy, two subclades, and multiple transitional species. Within the combined dataset results, only *Heteroblastus* is questionably placed within the center of *Deltoblastus*, possibly demonstrating the long branch effect. When this branch is investigated using a phylogram (Figure 3.4), it becomes clear that *Heteroblastus* is many steps removed from the surrounding species, and long branch is the likely cause. Among the three different database approaches used (Bodenbender (revised), Morgan, and Combined) the Combined database appeared the best resolved (Figure 3.3). This phylogeny demonstrates a core polytomy, but proves superior at separating the different genera from *Deltoblastus* and possible sister genera, excepting *Heteroblastus*. This provides the best support for the use of the combined database, as it would be expected that there would be many differences between *Deltoblastus* species and its sister genera based on time gap alone. The structure observed in parsimony analysis results are supported by NJCA (Figure 3.5), except for the placement of *Heteroblastus*, which is separated from the core cluster of *Deltoblastus*. PCA corroborates these results (Figure 3.6), and separates well the core *Deltoblastus* species from possible sister genera along the first principle component axis. Within both NJCA and PCA, two *Deltoblastus* species, *D. molengraaffi* and *D. sebotensis*, are separated out from the core group of Deltoblastus species, and show more similarity with proposed sister genera. This co-agreement is considered significant, is discussed below.

Discussion

The initial goal of this study was to demonstrate the correct assignment of currently ascribed species to *Deltoblastus*, and, barring that, to move any dissimilar species from the genus. The results of parsimony analysis indicate that although absolute relationship within the genus may not be completely resolved, *Deltoblastus* species compose a distinct and stable clade. There are a series of smaller clades within *Deltoblastus*, and it is possible that variations within these may represent environmental relationships, as many, such as that *D. ellipticus*, *D. elevatus*, and *D. permicus*, have varying morphologies.

One important mention that should be made here is the placement of *D. molengraaffi* and *D. sebotensis*. These species possesses a very unique profile, including smooth theca and thin, linear ambulacra. With their consistent basal placement and many step separation shown in the phylograms, NJCA, and PCA, it is possible *D. molengraaffi* and *D. sebotensis* actually represent a separate genus from *Deltoblastus*. Further investigation into these species is needed to determine whether these differences constitute separate genus assignment.

The placement of *Heteroblastus* as sister genus to *Deltoblastus* is suspect given the results of these analyses. In the majority consensus cladogram based on the combined dataset (Figure 3.3), *Heteroblastus* invaded the *Deltoblastus* clade at the point of the core polytomy, raising concerns over the long branch effect possibly influencing the determination of clade relationships. NJCA and PCA were much more successful at separating out sister genera from *Deltoblastus* species, placing *Heteroblastus* as distinctly dissimilar, especially in NJCA (Figure 3.5). The results of these analyses do not indicate

a specific genus as being consistently close enough to *Deltoblastus* to merit sister genus status, but rather show that there is more to be resolved before such a relationship can be determined.

Comparison to Past Phylogenies. Comparison of the most well resolved phylogeny (Figure 3.3) with that of previous authors [17] does not change the current understanding of *Deltoblastus* species relationships. While demonstrating species relationships within *Deltoblastus* very well, the relationships between *Deltoblastus* and other genera are not greatly understood. In moving towards understanding a greater evolutionary relationship it is important to know which species within a genus offer the most insight into basal evolutionary similarity. This analysis demonstrates that *D. molengraaffi* and *D. sebotensis* may represent a separate genus, and alternatively these species may be the best representatives of *Deltoblastus* when comparing it with other genera. In addition to these observations, while early phylogenies were developed based on easily recognized traits, more recent approaches are too generalized to offer resolution at the species level. This analysis demonstrates that a combined approach, linking broad relationships and species details, may offer insight into the highly variable and complex morphology present within *Deltoblastus* captured in a more comprehensive phylogeny (Figure 3.2).

Drivers of Deltoblastus *Diversity*. The diversity of morphotypes present within *Deltoblastus* presents a unique problem, and one without a clear answer. Previous authors [1, 2, 3, 4] did not discuss possible diversification routes and drivers, and this is likely due to the lack of detailed stratigraphy, locality data, and questionable species

designations in large collections. These problems need to be rectified before any diversification hypotheses can be put forward.

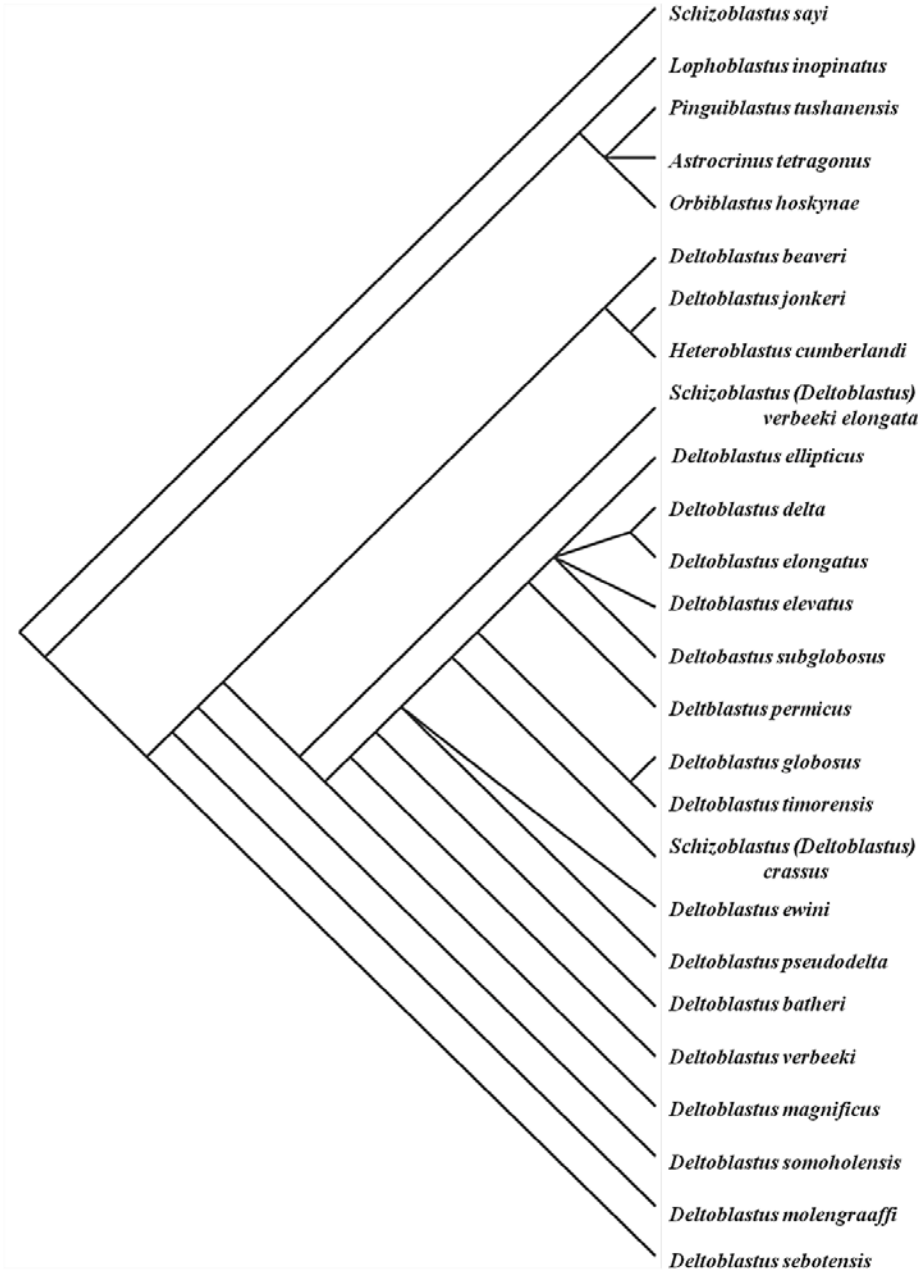

Figure 3.1. Cladogram of Morgan [6] Data parsimony analysis. Heuristic tree bisection and recombination (H-TBR), Fitch assumptions. 50,000 reorderings. Tree Length (TL): 115. Most Parsimonious Trees (MPTs): 2. Consistency Index (CI): 0.2609. Retention Index (RI): 0.632.

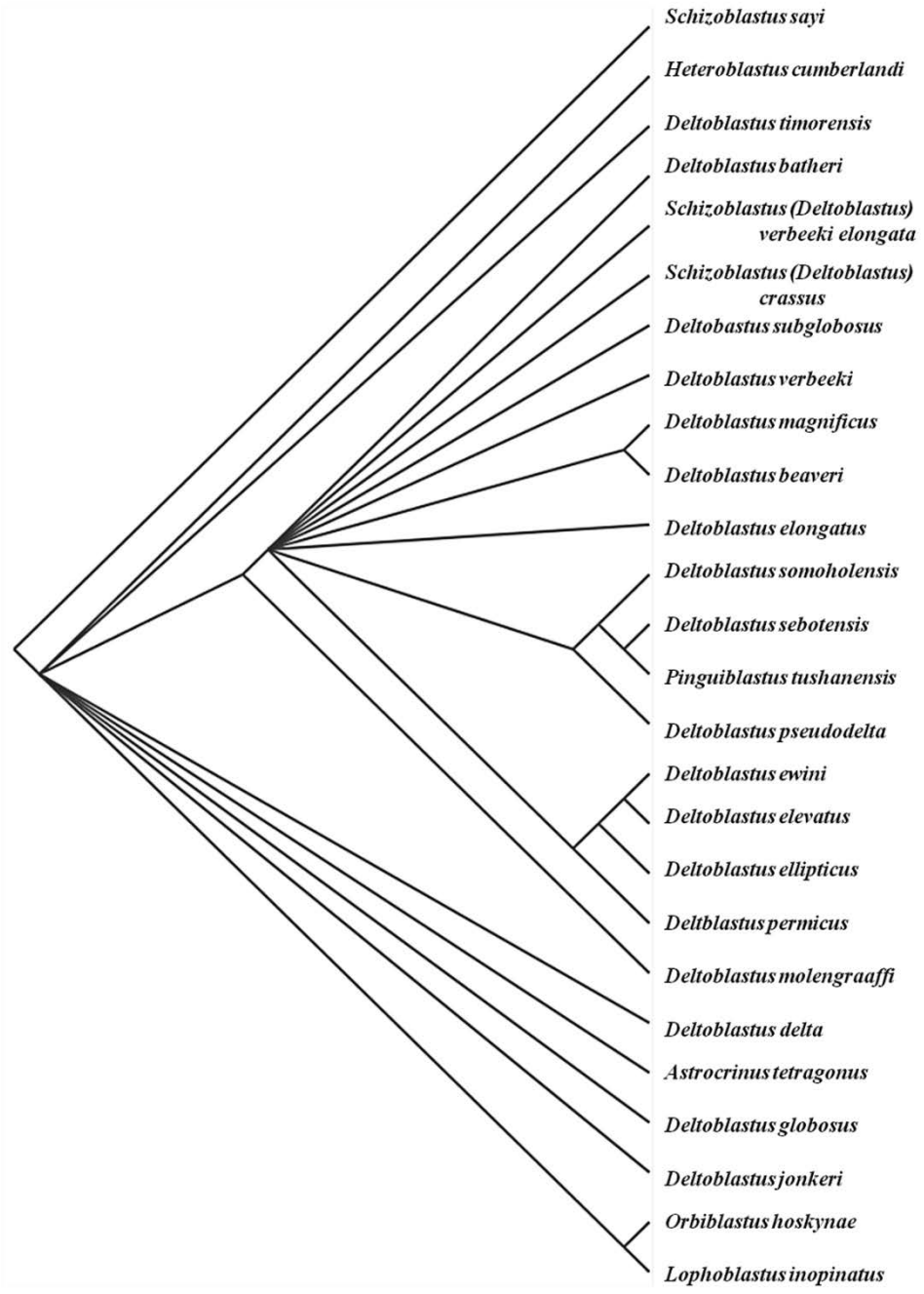

Figure 3.2. Cladogram of Bodenbender [16] Data parsimony analysis. Heuristic tree bisection and recombination (H-TBR), Fitch assumptions. 50,000 reorderings. Tree Length (TL): 182. Most Parsimonious Trees (MPTs): 501. Consistency Index (CI): 0.4845. Retention Index (RI): 0.9141.

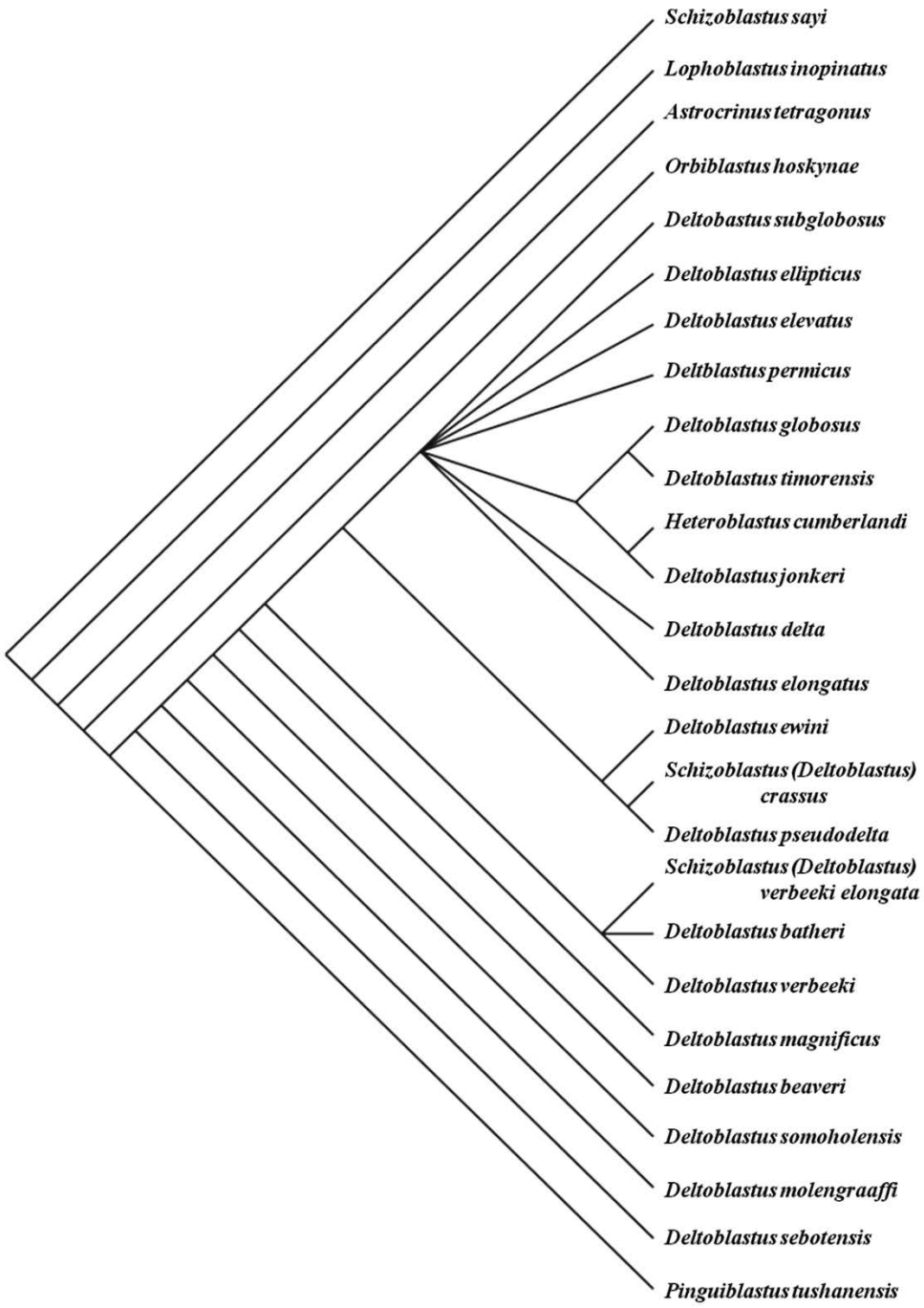

Figure 3.3. Cladogram of Combined Data parsimony analysis. Heuristic tree bisection and recombination (H-TBR), Fitch assumptions. 50,000 reorderings. Tree Length (TL): 319. Most Parsimonious Trees (MPTs): 2. Consistency Index (CI): 0.3686. Retention Index (RI): 0.454.

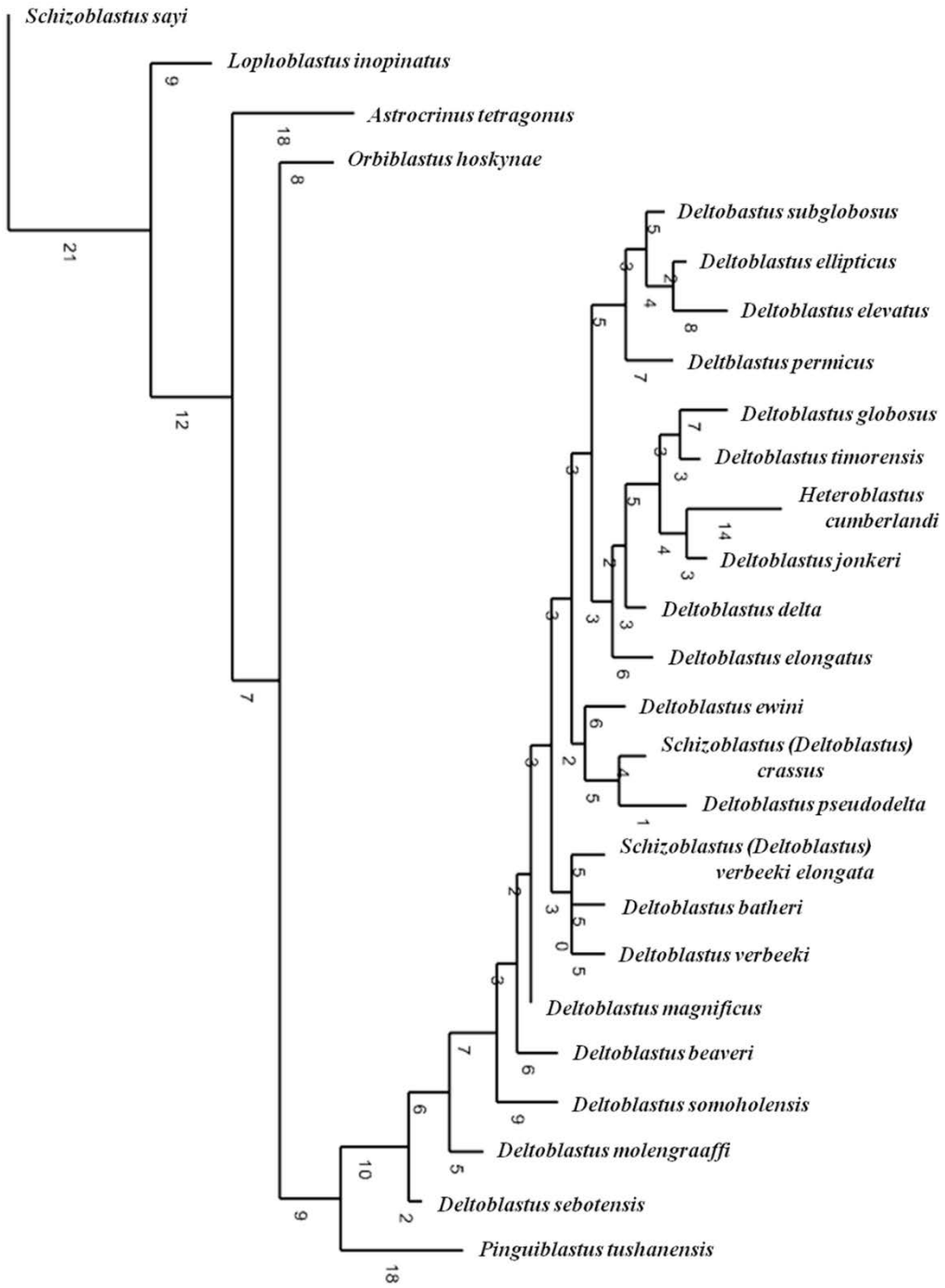

Figure 3.4. Phylogram of Combined Data parsimony analysis with branch lengths. Heuristic tree bisection and recombination (H-TBR), Fitch assumptions. 50,000 reorderings. Tree Length (TL): 319. Most Parsimonious Trees (MPTs): 2; first tree displayed. Consistency Index (CI): 0.3686. Retention Index (RI): 0.454.

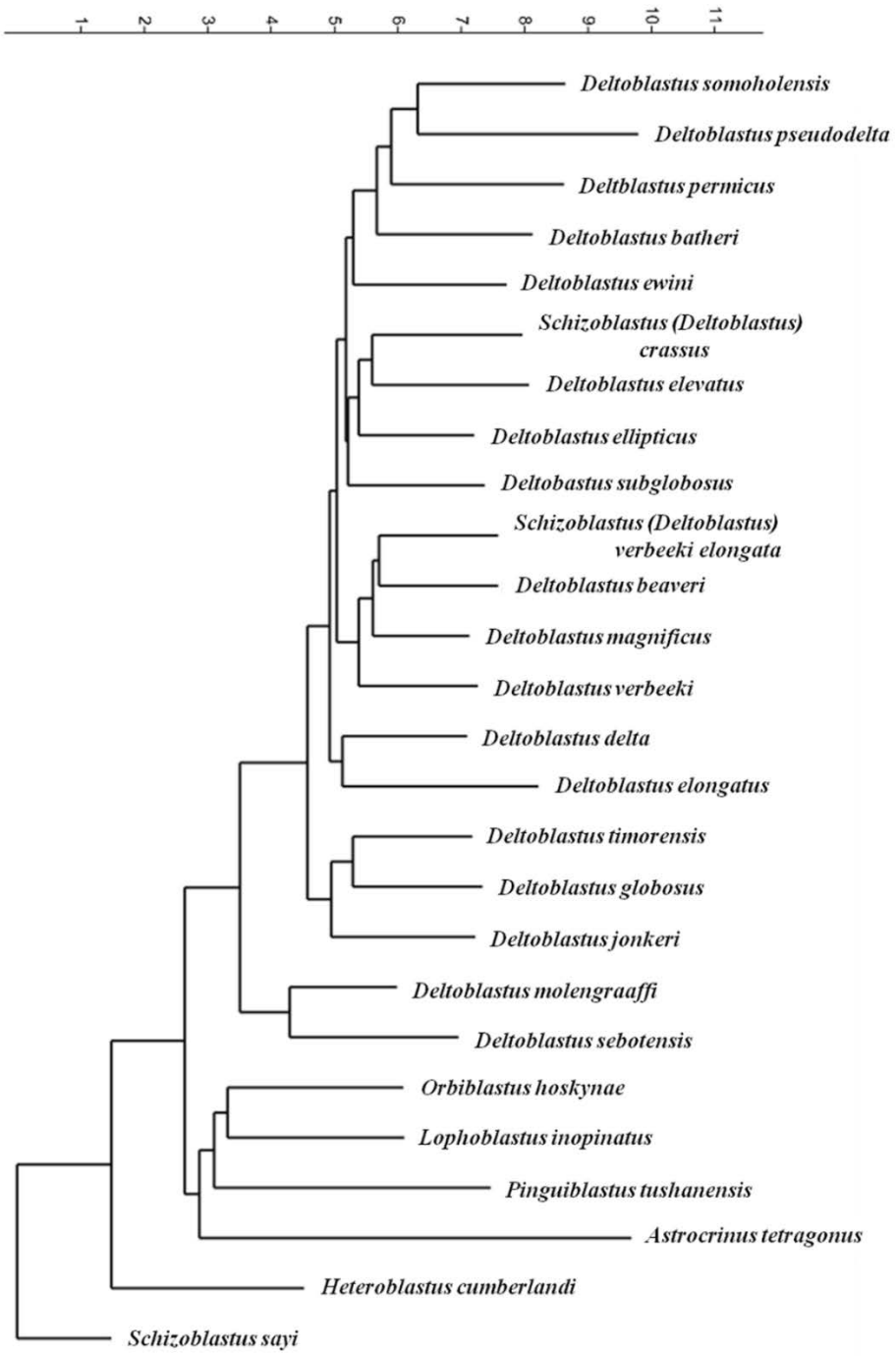

Figure 3.5. Neighbor Joining Cluster Analysis (NJCA) of Combined Data with *Schizoblastus* serving as an outgroup. Scale is similarity by percent. Note basal placement and separate clustering of *D. molengraaffi* and *D. sebotensis*. Proposed sister genera cluster separately from *Deltoblastus*.

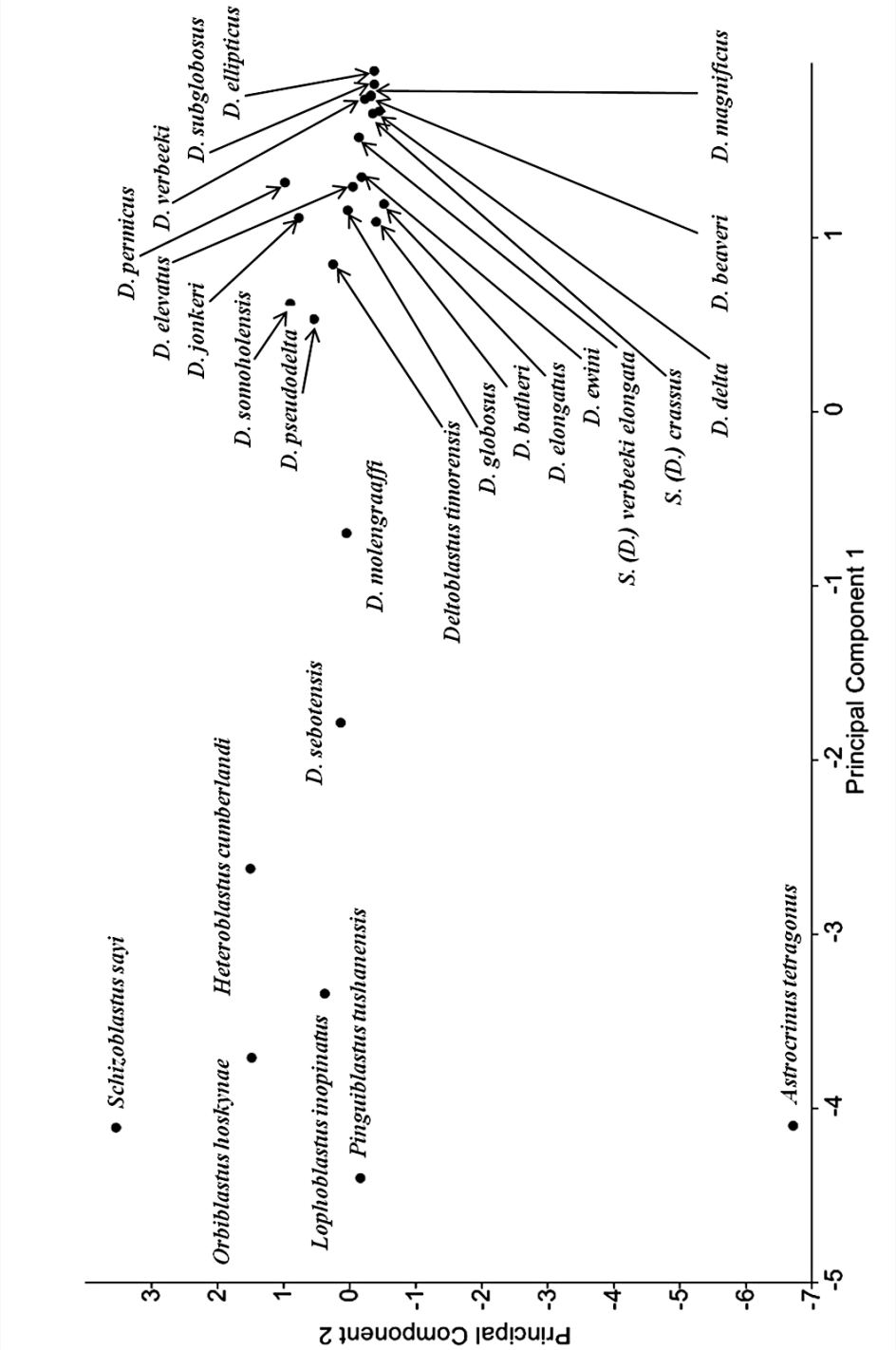

Figure 3.6. Principal Components Analysis (PCA) of Combined Data. Arrows, when used, indicate true placement of species. Separation of genera and species occurs primarily along principal component axis 1. Majority of *Deltoblastus* species (assigned and appropriated) cluster strongly on the right. Note distinct separation and middle placement of *D. molengraaffi* and *D. sebotensis.*

Conclusions

Species relationships within *Deltoblastus* are complex. Simplified older phylogenies [1] fail to describe the full breadth of morphologic variation present. Despite a complex character matrix, many of Deltoblastus' relationships are unresolved, as demonstrated by the presence of a core polytomy and many transitional members (Figure 3.3). Some species possibly serve as either transitional members or ancestral morphologies connecting larger clades within *Deltoblastus*. Further phylogenetic analysis inclusive of data beyond those of holotypes, paired with detailed stratigraphic and geographic information, may help resolve these complexities.

Realizing how little is known about the stratigraphy of Timor [7] and geographic relationships between *Deltoblastus* species, it is impossible to make any concrete determinations related to the order of species appearance and ecological drivers of *Deltoblastus* speciation. Further research into species ontogeny, regional ecology, and family level (Schizoblastidae) biogeographic distributions may clarify why this genus became so diverse shortly before blastoid extinction.

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CHAPTER FOUR

A New Ichnospecies of *Gyrolithes* from the Austin Chalk, Upper Cretaceous, Texas, USA

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Abstract

Gyrolithes, a helical marine trace fossil, occurs in beds of the Austin Chalk near Waco, McLennan County, Texas. The new ichnospecies *Gyrolithes texanus* is characterized by unique morphology and wall construction. This discovery expands the current geographic and environmental range of *Gyrolithes*, extending this ichnogenus into the chalk-dominated beds of the Cretaceous of Texas. Irregular bedding features from the *Gyrolithes* locality indicate this section of the Austin Chalk was deposited within a storm-dominated depositional regime, interspersed with periods of quiescence which allow for firm ground formation and colonization by the trace maker. *Gyrolithes* is associated with marginal marine settings is not with storm deposits; therefore, this discovery constitutes an expansion of environment for this ichnogenus.

Introduction

Gyrolithes Saporta [1] ranges from the Cambrian [2] through Recent, with the majority of ichnospecies appearing since the Permian [3; 4]. With large vertical burrow helices, *Gyrolithes* is discernible from the similar corkscrew-shaped burrow *Lapispira* Lange [5] in that *Gyrolithes* possesses only a single spiral burrow versus the smaller-scale doublet of *Lapispira*. Recent critical review of *Gyrolithes* [4] extensively redefines the morphologic parameters of the included ichnospecies, removing the dependence on

ornamentation and wall margin characteristics, and emphasizing the width of the burrow versus the radius of the whorls. This redefinition leads to the reduction of recognized ichnospecies within *Gyrolithes* from 19 to 13 ichnospecies, including: *G. cycloides, G. saxonicus, G. davreuxi, G. polonicus, G. mexicanus, G. lorcaensis, G. marylandicus, G. nodosus, G. krameri, G. variabilis, G. suprajurassicus, G. krymensis,* and *G. okinawaensis*. These species vary based on whorl radii and burrow width, but chronostratigraphy, substrate, wall possession and composition, as well as internal burrow structure as also taken into account when determining viability of *Gyrolithes* ichnospecies. This updated format is used for species identification and followed in this manuscript.

The discovery of *Gyrolithes* in the Upper Cretaceous Austin Chalk prompted this research. Unique morphologic parameters and expansion of the geographic range of *Gyrolithes* indicates a new ichnospecies identity.

Geologic Setting

The *Gyrolithes* are found *in situ* in biomicritic, calcareous chalk layers of the Austin Chalk. Multiple specimens are found along the exposures of the Austin Chalk at White Rock Creek, just north of Waco, McLennan County, Texas (Figure 4.1). This outcrop is about 150 kilometers south of Dallas, Texas, and about 170 km north of Austin, Texas. GPS coordinates of the creek bed are 31.63° N, 97.12° W. The Austin Chalk in this area is Upper Cretaceous (Santonian) in age (Figure 4.2). *Marsupites testudinarius* is a crinoid which is stratigraphically restricted to the Dessau member of the Austin Chalk Fm, has a last occurrence coincident with the evolutionary transition of the belemnite *Gonioteuthis granulate* to *G. granulataquadrata*, as well as the first

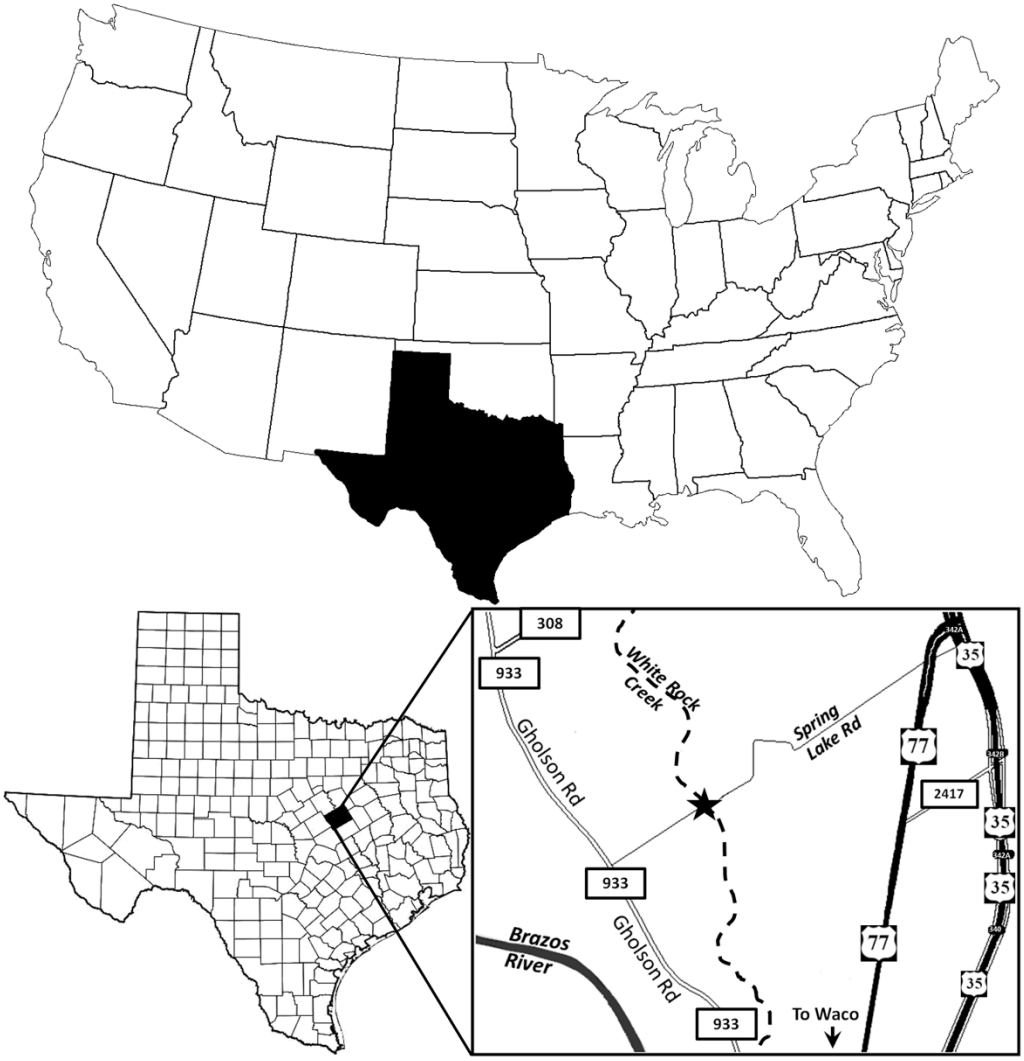

Figure 4.1. Location of field locality exposing *Gyrolithes.* Star indicates location of *Gyrolithes texanus* isp.n. exposure along White Rock Creek, McLennan County, Texas. See Fig. 2 for stratigraphy of creek bed.

appearance of the ammonite *Placenticeras bidorsatum*. *Marsupites* fossils found in association with *Gyrolithes* in White Rock Creek support the age and unit designations [6]. The Austin Chalk at White Rock Creek is characterized by alternating layers of biomicritic chalk and marl, with chalk layers averaging 1 m in thickness (Figure 4.2). Chalk layers are micritic with regular bedding, transitioning abruptly to irregularly bedded chalks. The contact between chalks and overlying marls is gradational. Marls are cross bedded locally and substantially thinner than chalk units, averaging 0.1 to 0.2 m. Historically, the Austin Chalk has been interpreted as an open marine, outer-shelf depositional environment [e.g., 7; 8].

Observations

Gyrolithes in White Rock Creek is typically found exposed on the underside of overhanging chalk ledges (Figures 4.2, 4.3). No examples were found in this locality where *Gyrolithes* extends into the underlying cross-bedded marl horizons. Similarly, none of the associated *Thalassinoides* Ehrenberg [9] or *Ophiomorpha* Lundgren [10] extends into the marl beds.

Irregular bedding with symmetrical ripples is observed in White Rock Creek (Figure 4.2). These ripples range from small (5 –10 cm in height, 10 –20 cm wavelength) to very large (30 –100 cm in height, up to 7 m wavelength), and are restricted to the chalk units. Beds with the largest ripples form the base of the irregularly bedded sections, grading upwards into beds with smaller ripples, which are overlain by cross-bedded marls. Bedding below the large ripples is undisturbed, and contains the *Gyrolithes*, *Thalassinoides*, and *Ophiomorpha* (Figure 4.3). Marl units lack evident burrowing. Clasts of variable size are found throughout the marl beds, and are typically imbricated and

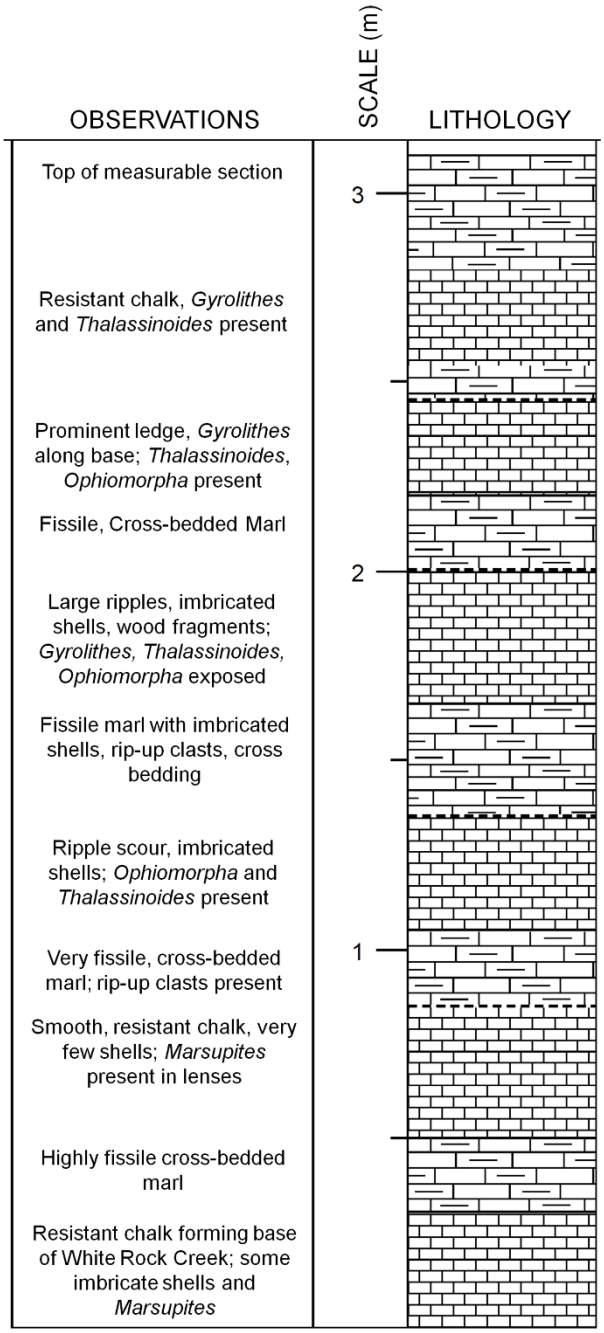

Figure 4.2. Stratigraphic section for type exposure of *Gyrolithes* at White Rock Creek. Note regularly alternating beds of chalks and marls. Primary *Gyrolithes* exposures in chalk beds at 2 m height from creek bed.

angular (Figure 4.3). Cross bedding dominates the marl units, and ends abruptly with a sharp contact formed between the top of the marl and bottom of the next overlying chalk. Multiple cycles of this type are observable at White Rock Creek (Figure 4.2).

Body fossils observed in White Rock Creek include fragmented *Inoceramus* and other bivalves, imbricated shells, and small carbonized plant debris (Figure 4.3). Storm-fill burrows (tubular tempestites) *sensu* Tedesco and Wanless [11] of *Thalassinoides* and *Ophiomorpha* in-filled with *Marsupites* are also observed. *Marsupites* in this locality are restricted to these infilled burrows and occasionally observed in debris lenses which are associated with the fragmented and imbricated shells described above. These observations are unique to the Waco-area exposures of the Austin Chalk.

Systematic Ichnology

Ichnofamily Gyrolithidae Vialov [12]

Ichnogenus *Gyrolithes* Saporta [1]

1884 *Gyrolithes* Saporta. [1]

1927 *Xenohelix* Mansfield. [13]

1969 *Conispiron* Vialov. [12]

non 1982 *Gyrolithes triassica* n. ichnosp.: Yang and Sun, p. 373, pl. 2, fig. 3 [14] (= *Gyrolithes triassica* Yang et al., [15], p. 203, pl. 19, figs. 3, 4).

1994 *Spirocircus* Mikuláš and Pek. [16]

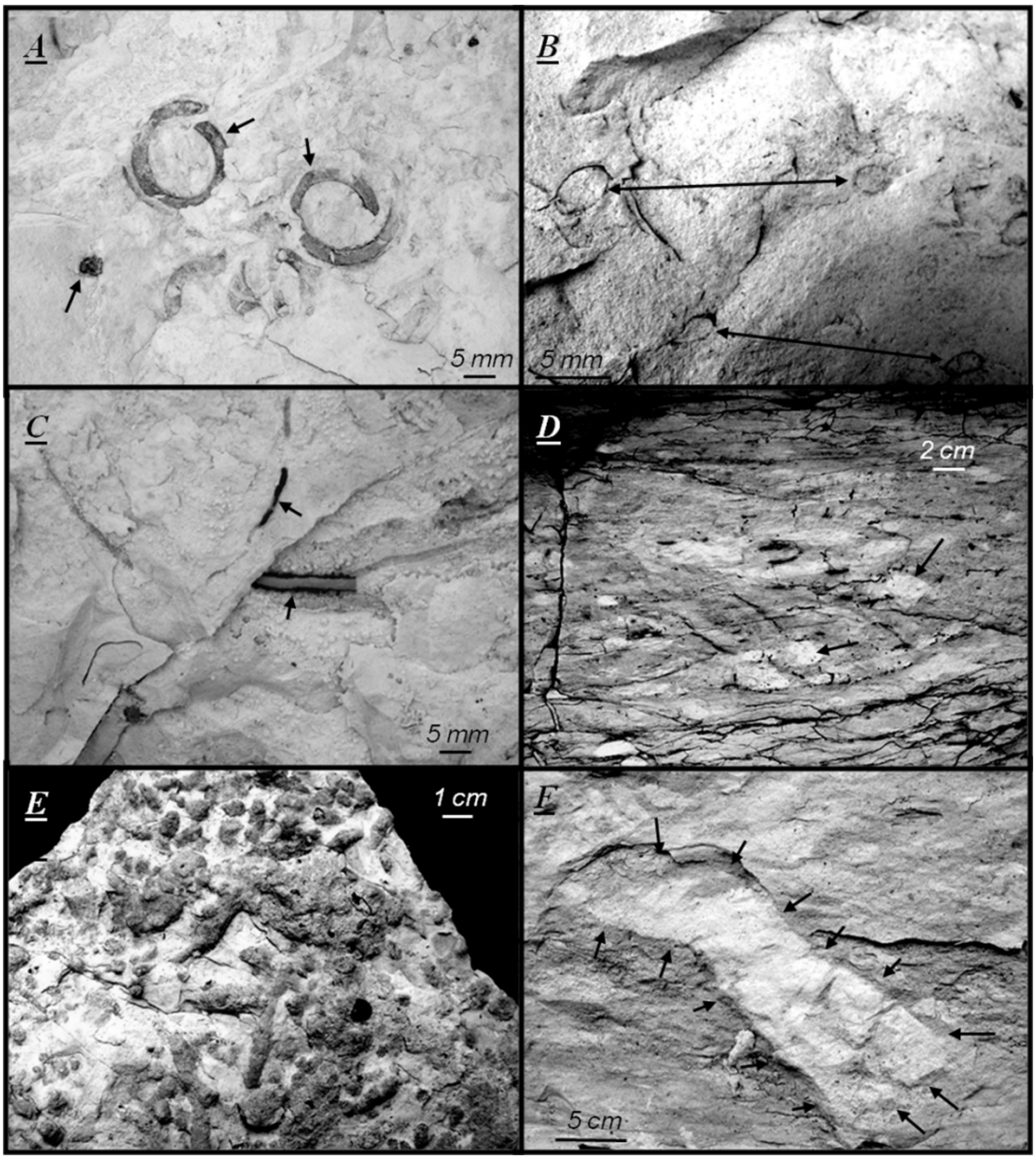

Figure 4.3. Observations from White Rock Creek, Waco, Texas. ***A****:* An *in situ* example of *Gyrolithes* exposed on an overhanging ledge. A small *Ophiomorpha* is to the left of the *Gyrolithes*. ***B****:* Exposed cross sections through *Gyrolithes* (pair indicated by arrows). ***C****:* Various *Ophiomorpha* (lower arrow) and *Thalassinoides* (upper arrow). ***D****:* Cross bedded marl unit, with lenses of debris and rip-up clasts (indicated by arrows). ***E****:* Slab containing storm-fill burrows of *Thalassinoides*, in-filled with *Marsupites* crinoid debris. ***F****:* Large rip-up clast from the top of a chalk unit (edges indicated by arrows; note angular shape).

Diagnosis

Rarely branched, spiraled burrows; helix vertical, consisting of dextral, sinistral or reversing coils, which are not in contact (*sensu* Uchman and Hanken [4]; modified from Bromley and Frey [17].

Gyrolithes texanus isp.n.

Material

One limestone slab, approximately 15 x 15 x 5 cm (length, width, and height) containing three specimens of *Gyrolithes* in both dextral and sinestral orientations. Specimens are housed in the Texas Natural Science Center, Non-vertebrate Paleontology Laboratory, Austin, Texas.

Holotype

NPL 2014-006 (Figure 4.4).

Occurrence

Austin Chalk, McLennan County, Texas, USA.

Etymology

Latinisation of Texas, the state of discovery.

Diagnosis

Smooth *Gyrolithes* with a wall, often glauconitic. Burrow is 4–8 mm wide; radius of whorls is 9–23 mm.

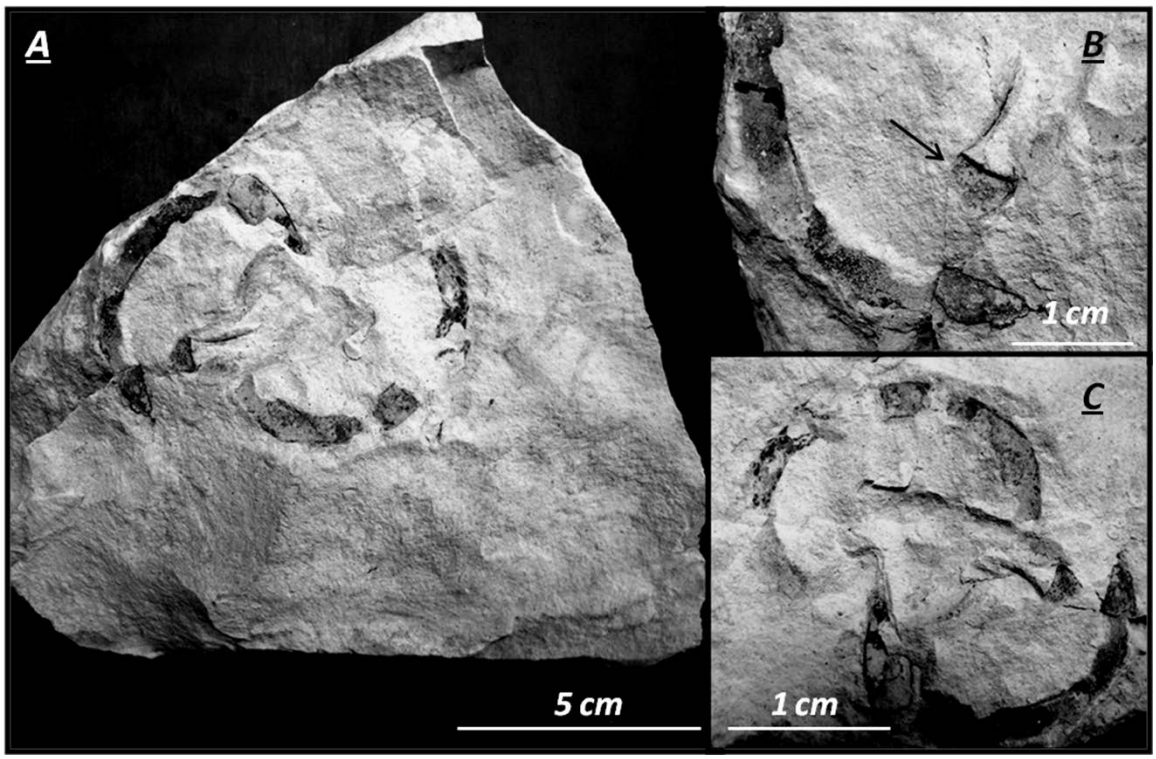

Figure 4.4. *Gyrolithes texanus* isp.n. from the Austin Chalk, Waco, Texas (NPL 2014-006). ***A***: Specimen is 15 cm across at widest part. Specimen contains three sets of *Gyrolithes*, overlapping, and displaying both dextral and sinistral whorls. B: Magnified section of specimen displaying pelleted wall structure (arrow). C: Slightly magnified and rotated view demonstrating overlapping nature of whorls with variable wall textures.

Description

Vertical helix (corkscrew shaped) burrows typically found in calcareous limestone chalk. Both dextral and sinistral whorls observed. Smooth-sided burrow with a green glauconitic wall is filled with calcareous material consistent with matrix; in this case, a biomicritic calcareous chalk. Cross section is ellipsoidal to triangular, with variable wall thickness, less than 0.5 mm. Triangular shape of burrow may be due to compression after burial. Wall is typically smooth, but is occasionally partially-to-completely pelletized. Small grooves can occasionally be observed under magnification.

Wall thickness is variable, depending on structure, ranging from 0.5 to 1.0 mm. Composition of the wall is glauconitic, and in some specimens small pyrite rhombs are present.

Twelve specimens of this ichnospecies were measured, primarily *in situ* as the nature of the exposures often makes extraction of specimens difficult. Format for the taking of measurements is based on the most recent review and recommendations to *Gyrolithes* [4]. The majority of the *Gyrolithes texanus* specimens are 5–6.5 mm wide (mean value 6 mm), with a minimum of 4 mm and maximum of 8 mm. The helical whorls are circular in outline. The radius of the whorls is highly variable and independent of burrow width. Whorl radii vary from the smallest 9 mm to the largest 23 mm, with the majority between 15 to 23 mm. Due to apparent reworking of sediments at the source locality (*see* Environmental Associations), the total screw height and whorl inclination variability are unknown. The largest observed screw was in poor condition and incomplete but is an estimated 24 centimeters long. *Gyrolithes* specimens are often found near *Thalassinoides* and *Ophiomorpha* in White Rock Creek (Figures 4.2, 4.3).

Remarks

The morphometric parameters of *Gyrolithes texanus* are significantly different from all other smooth sided *Gyrolithes* ichnospecies, and the possession of a wall sets this ichnospecies apart from other similarly shaped ichnospecies. The large whorl diameter combined with small burrow width is unique to *G. texanus*, and distinguishes this as a new ichnospecies.

The closest ichnospecies in form to *G. texanus* is *G. polonicus* Fedonkin [2] a Cambrian- and Ordovician-specific ichnospecies possessing perpendicular striations. The

large time-gap and lack of internal striae exclude *G. polonicus* as a possible alternative. The second closest ichnospecies to *G. texanus* is *G. davreuxi* Saporta [1] which possesses burrows typically 2x wider than *G. texanus*, with no overlap in burrow radii between ichnospecies. In addition, while *G. texanus* and *G. davruexi* share possession of a wall, they differ in wall structure, as *G. davreuxi* has a wall which typically is either completely smooth or possesses intricate small sinuous swirls. *G. texanus* has a smooth to pelleted wall, but no sinuous shapes are apparent in any observed specimens; however, small striae have been observed. *G. saxonicus* Häntzschel [18] is the only other ichnospecies with similar dimensions to *G. texanus*, but *G. saxonicus* is both larger and lacks a wall and therefore cannot be considered a viable alternative.

Significance

Environmental Associations

The discovery of *G. texanus* is significant in that it expands the environments with which this ichnospecies is associated. Previous investigations have interpreted the Austin Chalk as an open marine, outer-shelf depositional environment [e.g., 7; 8]. Fragmented *Inoceramus* and other bivalves, imbricated shells, plant debris, and rip-up clasts (Figure 4.3) observed at White Rock Creek suggest episodic disruption, with quiescent periods of bioturbation, colonization of bivalves, and firm-to-hard ground formation. Firm grounds are evidenced by the presence of variably-sized angular rip-up clasts composed of the underlying chalk units found within the cross-bedded marl units (Figure 4.3). Storm-fill burrows (tubular tempestites) *sensu* Tedesco and Wanless [11] of *Thalassinoides* and *Ophiomorpha* in-filled with *Marsupites* and bivalve fragments further support storm assertions (Figure 4.3). Lack of burrows within rippled and cross-bedded layers suggests

that the disruption was continuous or too changing in nature to allow for colonization, which is typical of storm dominated regimes. The presence of *Ophiomorpha*- and *Thalassinoides*-type burrows, which are typical of shallow-shelf environments [19], with *G. texanus* and associated features in the Austin Chalk of central Texas are indicative of shallow shelf deposition, dominated periodically by storm events. *Gyrolithes* is historically interpreted as occupying marginal marine settings, including those with severe salinity fluctuations [20; 21; 22; 23; 24]. These interpretations coincide with observations of *Gyrolithes* and related burrows found in tidal flat deposits [24; 25; 26; 27; 28]. While the Austin Chalk does not show evidence of severe salinity or temperature fluctuations, preference for marginal, stressed environments by *Gyrolithes* in concert with periodic storm deposition supports reinterpretation of the Austin Chalk as a shallow marine deposit. This evidence suggest revision of depositional environment for the Austin Chalk.

Possible Trace Makers

The occurrence of *Gyrolithes* has been reported from Cambrian through Recent, with the majority of species occurring after the Permian. *Gyrolithes* ichnospecies have been interpreted as crustacean burrows [17; 21], and are regularly associated with *Thalassinoides* and *Ophiomorpha* [4]. *Gyrolithes* are also attributed to worms [25; 29; 30] and hemichordates [27; 28]. The small striae and occasional pellets observed within the wall of *G. texanus* (Fig. 4B), in addition to a preference for stiff muds in stressed environments suggests thalassinidean shrimp as the most probable trace maker [24; 31].

Conclusions

Gyrolithes texanus is a new and unique form of *Gyrolithes*, and differs substantially from other members of the ichnogenus based on whorl radius and burrow width. Close association of *G. texanus* with *Thalassinoides* and *Ophiomorpha* within White Rock Creek support previous assertions of a possible crustacean trace maker, although others have been suggested. In addition, depositional features present within White Rock Creek, including tubular tempestites, rip-up clasts, cross-bedded marls, large-scale ripples, and imbricated shells indicate a dynamic depositional environment dominated by storm events.

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CHAPTER FIVE

Conclusions

This dissertation initially intended to focus on blastoid speciation and diversity near the end of the Paleozoic. While examining local exposures for other echinoderms, depositional environments became a concern. Investigation into these areas of interest led to changes in subject matter and many questions concerning the phylogeny, speciation, and environments defined by blastoids and related clades. Using small, focused studies, this dissertation followed the clues and inferences available within the fossils and associated depositional structures. Although the ultimate conclusions are summarized below, these are discussed in detail within the individual chapters.

When addressing the observation of blastoid species (chapter two), it was determined that although *Deltoblastus* is a complex genus with many subtle morphological differences, it is possible to separate our distinct morphologies based on classical comparative anatomy coupled with detailed observations. Using these methods, three new species of *Deltoblastus* were established: *Deltoblastus beaveri*, *Deltoblastus elevatus*, and *Deltoblastus ewini*. Following these determinations is the need to evaluate the genus and species as a whole, a study which requires access to the type specimens, which are currently unavailable. It is expected that once access to these is granted, further analysis will support the initial results of this study.

While comparative anatomy does provide insight into *Deltoblastus* speciation, it is also necessary to determine whether this genus is well supported, and to see if proposed sister genera provide insight into the structure of this genus. Chapter three

addressed this question, as *Deltoblastus* species, established, new, and appropriated (awaiting reassignment), were compared to representatives of sister genera. This study demonstrated that while it is still unclear which proposed genus sisters *Deltoblastus*, the species contained within the genus are well separated using cladistics, neighbor joining cluster analysis, and principal components analysis. In addition, it has been recommended that two species, *Deltoblastus molengraaffi* and *D. sebotensis*, be investigated for potential reassignment to a new blastoid genus.

In addressing the unique question of whether sediments and trace fossils can be important in the interpretation of apparently simple environments, it became clear that these traits can absolutely modify entrenched ideas. Chapter four demonstrates that exposure of White Rock Creek had many subtle but definitive characteristics which led to a total reinterpretation of the depositional regime of the Austin Chalk in the Waco area. Sedimentological clues, including imbricated and shattered shells, tubular tempestites, and large ripples and hummocks, indicate an environment that was anything but tranquil and deep basin. This study concludes that these features indicate a storm-deposited chalk, with interperiods of quiescence.

As this dissertation shows, paleontology as a science is expanding, complicated, and well poised to address the many complexities of biological history on the Earth. By perching on the crossroads of biological and geological sciences, this field draws from a vast array of information, allowing for investigation into many different problems and providing insight into questions other fields are unable to address.

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