EVALUATING THE ICHNOFOSSIL *TEREDOLITES* AS AN INDICATOR OF SALINITY AND PALEOENVIRONMENT

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ABSTRACT

The ichnogenus *Teredolites* and Teredolites Ichnofacies is an accepted proxy for marine influence in paralic to open marine depositional environments (EOD). Actualistic approaches and the process-ichnologic framework allow independent analysis of both quantitative and semiquantitative data to interpret the physicochemical conditions of a given EOD when *Teredolites* are present. Measurements collected in modern EOD and Jurassic–Eocene successions produce a spatially and temporally robust dataset of 14,137 borings from 17 tracemaking genera. Life history strategies of extant tracemakers are reflected in Mesozoic borings, which allow reconstruction of paleosalinity. Trends extrapolated indicate four ecotones in modern paralic to nearshore EOD, which can be identified into the Late Cretaceous. These zones display variation in boring metrics, densities, and relative composition of *Teredolites* ichnospecies. Zone 1 represents upper estuarine to tidally modified fluvial successions with salinities from 0.5–10 ppt (oligohaline to alpha-mesohaline). Zone 2 represents upper to central estuarine successions with salinities from 10–19 ppt (beta-mesohaline to lower polyhaline). Zone 3 represents central to lower estuarine succession with salinities from 15–30 ppt (beta-mesohaline to euhaline). Zone 4 represents backshore to open marine successions with salinities from 20–30+ ppt (polyhaline to euhaline). Boring metrics compared against identified fossil genera suggest high species richness in the Western Interior Seaway coincided with physical adaptations to compensate for interspecific competition—differences in reproduction style and media preferences at time of settlement—by the Late Cretaceous.

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INTRODUCTION

Teredolites, the ichnogenus of flask-shaped borings within woody media (endoxylic) in paralic and marine settings are produced by teredinid and pholadid clams (Class: Bivalvia, superfamily, Pholadoidea) (Laymerie 1842; Kelly and Bromley 1984). *Teredolites* and associated woody material are commonly used as indicators of marine flooding surfaces and transgressions in Jurassic and younger paralic and fluviodeltaic sequences (e.g., Savrda 1995; Gingras et al. 2004; Vahldiek and Schweigert 2007). Studies of modern, nearshore driftwood distribution (Hinojosa et al. 2010) and tracemaker larval dispersal (e.g., Nair and Saraswathy 1971; MacIntosh et al. 2012) reflect a nearshore retainment in brooding species due to passive dispersal capability of both larvae and adults, requiring either driftwood transport or repetitive recruitments—lateral movement over multiple generations—for extrabasinal dispersal (Hoagland and Turner 1981). Recent investigations into deep-sea species provide a source-to-sink perspective of wood transport from the intertidal to hadal zones (Haga and Kase 2011; Voight et al. 2019) with wood accumulating in topographically complex, localized retention zones, such as submarine canyons (Hinojosa et al. 2011; Romano et al. 2014; Voight 2015).

The goal of this research is to utilize a process-ichnology-driven approach to evaluate the environmental factors that control size, abundance, and distribution of modern pholadoidean bivalves as analogs for *Teredolites* in Mesozoic and Cenozoic strata to better interpret paleoenvironmental conditions and trends in salinity patterns in ancient transitional zone—paralic and shallow marine—deposits. Euhaline burrowing organism diameters are heavily influenced by salinity, and maximum-boring diameters within a given sample are suitable proxies for salinity stress (Timmer 2017). Hence, the objectives of this study are to: (1) create a database from an extensive literature review of environmental preferences of modern teredinid and pholadid species that produce *Teredolites*; (2) establish statistical trends for salinity, reproductive strategy, and media type preferences of modern *Teredolites*; and (3) conduct outcrop studies of *Teredolites* in Cretaceous Western Interior Seaway (CWIS) deposits of Utah and Colorado to apply the trends synthesized from the database by using boring size and abundance to determine salinity trends. We hypothesize that Size-Diversity Index (SDI) is an indicator of salinity concentrations in Mesozoic and Cenozoic strata under the assumptions that: (1) *Teredolites* occurrences imply a strong marine influence on depositional systems; (2) boring size indicates residence time in tolerable salinities such that diminutive boring densities represent unfavorable conditions and larger boring densities reflect higher salinities or reduced salinity stress; (3) the temporal scale of marine incursion when *Teredolites* are abundant reflect appropriate salinities to allow reproductive success and subsequent recruitment; and (4) temperature provides a secondary control on tracemaker species occurrence so that paleoclimatic reconstructions are equally important to ichnogeneric modeling of facies associations. We contend that *Teredolites* should be viewed as locally derived within depositional systems where larval modes and media availability reflect local-to-regional seasonally stable temperature, salinity, and constant wood supply.

BACKGROUND

Previous Work

The Pholadoidea are a highly diverse and specialized group of bivalves that bore by mechanical means in consolidated and semiconsolidated media (Fig. 1). Early studies concerning the physiology and systematics of wood-boring groups expressed the need for schema to properly classify identifiable features to the generic and species level, which commonly vary between communities with respect to local environmental parameters reflecting the plasticity of the group's genome (Turner 1954, 1966, 1971). Recent works have focused on: (1) the molecular phylogeny of the Teredinidae (Distel et al. 2011; Shipway 2013; Shipway et al. 2016) and Xylophagainae (Voight 2009; Romano et al. 2014; Voight 2015, Voight et al. 2019); and (2) their uses as a model for competition in ephemeral media (MacIntosh et al. 2012, 2014; Nishimoto et al. 2015). Identification to species level within the Teredinidae is prescribed based on the characteristics of the valves, pallets (bladelike structures used to plug the boring aperture when siphons are retracted), and reproductive style (Turner 1966). Diagnosis within the Pholadidae is based on shell morphology and the presence and morphology of accessory plates (i.e., protoplax, mesoplax, metaplax, siphonoplax, and hypoplax; Fischer 1858). Identification to species level is exceedingly difficult due to the alteration of hard parts by environmental parameters, media overcrowding, mechanical abrasion, and diagenesis (Turner 1954, 1966; Robin et al. 2018). If all necessary diagnostic characters are unavailable, identification to the family level is only possible (Turner 1966).

The fossil record of this group is generally poor and rarely figured (Stolicza 1871), and early works have been difficult to locate (Warren 1934; Moll 1941). Hence, the boring *Teredolites* provides the best evidence of timing and dispersal in the rock record. The first appearance datum (FAD) for the Pholadoidea is via *Teredolites* in Lower Jurassic (Pleinsbachian) marine deposits from the Tethys Sea (Kelly 1988a; Vahldiek and Schewigert

2007; Mayer 2010). A younger FAD of body fossils (Pholadidae, *Opertochasma*) in the Late Jurassic (Kimmeridgian–Tithonian) was described by Cragin (1905) from the Malone Formation. The oldest confirmed pallets of the Teredinidae (Bankiinae) are from the Late Cretaceous (Santonian) of New Zealand described by Mckoy (1978) and are segmented. The appearance of derived pallets before unsegmented (plesiomorphic) pallets suggest that they appear much earlier in the rock record (Robin et al. 2018). Woodward (1880) briefly mentioned pallets from the Lower Cretaceous Greensand of Blackdown, England, with no description and no supplemental information provided. Distel et al. (2011) provided the first molecular phylogenetic topology of the Pholadoidea, onto which Robin et al. (2018) plotted the FAD for diagnostic morphological synapomorphies. This updated topology generally agrees with the temporal distribution and suggested FAD of subfamilies, genera, and *Teredolites* figured in Kelly (1988A, *text-fig.* 18). Divergence time estimates calculated by Lee et al. (2019) show the timing of divergence of subfamily nodes and should serve as a generalized visualization for the appearance of key characters of the Teredinidae.

Ichnological assessments were formalized by Kelly and Bromley (1984) due to inconsistency in terminology of both borings and related features: (1) calcite linings; (2) retrusive caps; and (3) surficial morphology (i.e., scratches from boring and wood-grain pattern) (e.g., Bartsch 1930; Savrda and Smith 1996). Fecal ‘chimneys’ and peloidal linings have been described as an alternative to calcite linings in some xylophagainids as a possible means to limit sulfide exposure (Purchon 1941; Voight et al. 2019, Clade I, *text-fig.* 4; J.A. Voight personal communication 2019), but their presence in the fossil record is, as yet, unknown. In general, studies on the mechanics of boring behaviors and paleoethological signatures are numerous (e.g., Miller 1924; Duval 1963; Turner 1966; Ansell and Nair 1969; Ekdale and de Gilbert 2010). For example, Savrda and Smith (1996) interpreted the branching behavior in *Teredolites longissimus* as a response to media overcrowding.

Recent ichnological research has focused on such quantitative approaches as process ichnology to quantify the effects of physicochemical stressors (e.g., hydraulic energy, salinity, sedimentation rates, and media consistency) on marine organismal interactions (Gingras et al. 2011; Hasiotis and Platt 2012). Process ichnology combines ichnofacies and ichnofabric analyses with the Bioturbation Index (BI; Taylor and Goldring 1993), and Size-Diversity Index (SDI; Timmer 2017) to provide proxies for environmental conditions. Size-Diversity Index is the product of the maximum burrow diameter and number of ichnogenera present in a given stratigraphic interval (Timmer 2017). Two types of salinity-size trends were identified in a review paper by Gingras et al. (2011): (1) facultative diminution, in which organisms maximize their surface area to volume ratio to maximize efficiency in osmotic and ionic regulation, typically in brackish and/or warm, dysoxic conditions; and (2) enforced diminution, a decrease in body size as a response to physicochemical stresses, typically in oligopoikilohaline (i.e., low, fluctuating salinities) or very warm environments as a result of higher-than-normal metabolic or mortality rates. Facultative diminution produces a greater number of juvenile to subadult tracemakers that result in diminutive traces constituting the majority of an ichnological suite. Size diminution is not equal across the *Teredolites* ichnogenus; tracemakers of *T. longissimus* are able to control their boring environment when prevailing physicochemical conditions are unfavorable in the water column by sealing the entrance of the borings with pallets (e.g., Turner 1966; Nair and Saraswathy 1971). Within the same ichnospecies, diminution is partly controlled by the style of reproduction used, with larviparous species having an overall lower body volume (Cragg et al. 2009). The development of pallets within the Teredinidae make physiological adaptations to environmental stressors less relevant, with the main control on *T. longissimus* boring size being: (1) media overcrowding; (2) hydraulic energy; and (3) reproductive style. Pallets (if present in the borings) may allow determination of species composition and reproduction types within a sedimentologic and paleoecologic framework by comparing the lithologies and facies associations in which specific pallet morphologies (i.e. segmented or nonsegmented) occur (e.g., Voight 2015; Robin et al. 2018).

Salinity Classification

The Venice System (Venice System 1959) is the most widely applied salinity classification system to bin salinity ranges in aquatic systems, constructed for universal use in brackish water systems. Salinity bins (Fig. 2A) can be considered dynamic as to describe waters experiencing frequent mixing (i.e., poikilohaline) and waters of constant salinity concentrations (i.e., homoiohaline) (Venice System 1959). The term mixoeuhaline is used to avoid “brackish” when describing diluted sea water to prevent descriptive ambiguity in the nomenclature. The Venice System has been subject to criticism due to its static, descriptive nature (e.g., Bulger et al. 1993; Attrill and Rundle 2002) and is built upon mean salinity values for a given area (Venice System 1959). The static nature of the Venice scheme is best suited to homoiohaline waters, but its application proves ambiguous in poikilohaline, tidally modified estuaries (e.g., Boesch 1977; Chainho et al. 2006). Bulger et al. (1990, 1993) conducted a statistical analysis of salinity gradients within estuarine systems through use of Principle Component Analysis to determine salinity zones used, in common, by 317 species (Fig. 2B). They determined that, while the lower and upper limits of the mixoeuhaline zone are shared in both schemes, the Venice System is more appropriately applied to hydrographic boundaries, rather than biogeographic boundaries.

Poikilohalinity and estuarine mixing arise from high-frequency changes in marine and freshwater input as a result of tidal forcings and seasonality. Seasonality is a consideration in monsoonal, subtropical climates in which fluvial-system-derived mouthbar sandbodies are deposited by major freshwater floods in the wet season and are reworked by tides and marine organisms during the dry season, such as seen in modern Moreton Bay, Queensland, Australia (e.g., Hasiotis et al. 2015). Variation in salinity has been shown to play the largest role in the composition of benthic communities in poikilohaline estuarine environments, with generally lower variability in salinities (homoiohalinity) in the most proximal and distal portions of estuarine systems, allowing mean salinity values to be the primary control on community structure (Taupp and Wetzel 2014). Multivariate methods expanded upon by Christensen et al. (1997), Greenwood (2007), and Guenther and MacDonald (2012) were used to develop a sensitivity index of species in the Gulf of Mexico to variations in freshwater influx and zonation of estuarine nekton communities with respect to salinity. The pitfalls with both models are the reliance on mean salinity values, where high variability in physicochemical environmental factors limits species richness and distribution in mixoeuhaline estuarine systems (Atrill and Rundle 2002). The high degree of physiological stress is exemplified in the fossil and ichnologic record, with high-ichnodiversity colonization of estuarine systems not occurring prior to the Late Cretaceous (e.g., Pemberton and Wightman 1992; MacEachern et al. 2007).

In general, estuarine community patterns only coincide with the Venice System in the oligohaline zone, which was identified by Khlebovich (1979) as the critical lower salinity boundary (5 to 8 ppt; alpha mesohaline) beyond which limnetic hydrobionts and marine fauna could not extend without adaptations for hypertonic regulation. Hypertonic regulation allows marine organisms to live in very low salinities as adults while requiring elevated salinities for seasonal reproduction, a pattern which is exhibited by tracemakers in monsoonal climates (i.e. *Bankia*, *Nausitora*, and *Psiloteredo*), such as in India and Southeast Asia.

Life History and Environmental Factors

The primary factors controlling the distribution of marine organisms include: salinity, temperature, water depth, dissolved oxygen, and turbidity (e.g., Ekdale 1988; MacEachern et al. 2007; Hasiotis and Platt 2012). Nair and Saraswathy (1971) identified 20 primary factors (Table 1), and the interaction between them, responsible for controlling the occurrence of teredinids in a given area. Temperature, salinity, and water depth are the primary factors that control the distribution of modern pholadoidean ecotones, and result in a shift in species composition (Fig. 3) or reproductive strategies as to best exploit ephemeral media (e.g., Voight et al. 2019). Wood borers are most dominant in tropical waters, and are absent only from polar waters, where wood supply is not adequate as to support their distribution (Turner 1966; Nair and Saraswathy 1971). For example, compilation of teredinid biogeographic ranges (Turner 1954, 1955, 1966, 1971) and their distribution (Hoagland and Turner 1981) showed that ~ 2/3 of the 60 valid species are tropical with at least six species being circumtropical. Teredinids belonging to genera with fewer than six species are mostly tropical and have very narrow distributions. Seventy species belonging to the Xylophagaidae are found at most latitidues except for those south of Deception Island (~62ºS). They occur only in deep water and are considered euhaline (e.g., Voight 2015).

Wood supply is most readily available in mangrove habitats where roughly a third of teredinid species occur, enhancing productivity in these systems via nutrient recycling while processing more than half of the wood produced (Cragg et al. 2009; Hendy et al. 2013; Voight 2015). Species specializing in, or distributed within, mangrove habitats (Voigt 2015) prefer the same salinity ranges as their host species (Fig. 3; Leonel et al. 1998; Voight 2015). Mangroves are tolerant of a wide range of salinities with optimal growth occurring at different salinities between species and localties. The black mangroves *Avicennia* and *Aegiceras* collected from Sydney, New South Wales, Australia, showed optimal growth between 20–40 practical salinity units (PSU; roughly equivalent to parts per thousand (ppt), Zimmerman 2005) (Clarke and Hannon 1970), and *Avicennia marina* had optimal growth at 15.4 PSU along the Gujarat Coast, India (Patel et al. 2010). *Avicennia germinans*, *Leguncularia racemosa,* and *Rhizophora mangle* all occur in soil salinities between 10–60 ppt along the coast of San Andrés Island (in the Caribbean Sea); *L. racemosa* and *R. mangle* dominated oligohaline localties, while *A. germinans* dominated euhaline environments (Rodríguez-Rodríguez et al. 2018). Occurrences of *Bankia rochi*, *Dicyathifer manni*, *Nototeredo globosa,* and *Teredo biparitius* in mangrove environments of Papua New Guinea were restricted to salinities between 10–30 ppt with mortality at 1 ppt (Rayner 1979). The mangrove specialist *Bactronophorus thoracites* associated with the orange mangrove *Bruguiera* was collected in mesohaline waters (16 ppt) at Little Andaman, India (Das and Dev Roy 1984), and associated with the red mangrove *Rhizophora stylosa* on the Burrup Peninsula, Western Australia, Australia (Brearley et al. 2003). The salinity tolerances of *B. thoracites* have yet to be evaluated. *Dicyathifer manni* along the Burrup Peninsula was associated with *Rhizophora*, *Avicennia*, and *Bruguiera* (listed in decreasing abundance); *Bankia rochi* was most prevalent in *Avicennia* (Brearley et al. 2003). *Terminalia arjuna* (a white mangrove) can survive soil salinities between 3.85–9.35 ppt (Tomar and Gupta 1985), preferring hammocks (i.e., raised mounds) and terrestrial areas inundated during wet seasons.

When multiple species co-occur in the same geographic area, one species tends to outcompete others to some spatial extent due to environmental factors, hydrography, reproductive modes, temperature, and/or larval settlement patterns (synchronous or staggered) (Scheltema 1971; Hoagland and Turner 1981; MacIntosh et al. 2014). The distribution of the Teredinidae in Japanese coastal waters suggest that larval distribution of *Lyrodus pedicellatus* (long-term larviparous species) is confined to the vicinity in which the adults live, providing a dispersal limitation in areas where they compete syntopically (i.e., coexist and compete for boring space in the same geographic area) with *Teredo navalis* (Tsunoda 1979). Test panels deployed by Tsunoda (1979) in Japanese coastal waters had some localties dominated by *T. navalis* that contained very low densities of settled individuals (<100) after a 30-day immersion period. Localties with two or more species had much larger densities per panel where brooding species (65–2282 borings) and mixed-reproduction populations (28–816 borings) were found. Monthly trends in brooding species show a depauperate primary settlement occurring in the early summer months followed by a much larger settlement in late summer and early fall; the fall settlement population being offspring of those from the early summer settlement.

Maximum boring densities and sizes occur in salinities ranging from 15–35 ppt (mesohaline–euhaline; e.g., Borges et al., 2014). The relationship between size and salinity is substantially important as many teredinid species grow between 10–60-mm long, reaching sexual maturity between 10–20 mm in length within 4–8 weeks of settlement (e.g., Nair and Saraswathy 1971). MacIntosh (2015) observed that oviparous species (*Bankia carinata)* and brooding species (*Teredo parksi*) had similar fecundities after reaching sexual maturity under 40 mm in length; clutch sizes for *B. carinata* reaching up to $3x10^6$ in individuals measuring 100 mm in length. Boring diameter in these groups is variable and based on the number of individuals on a given piece of wood; crowded media have smaller diameters and longer individuals (MacIntosh 2015). In temperate and tropical waters, maximum growth rates and higher fecundity result in rapid growth, with some species reaching sexual maturity within 2–4 weeks. Most species can inhabit waters with salinities as low as 5 ppt (oligohaline) for short periods of time, but importantly cannot reproduce when exposed to such low salinities (Nair and Saraswathy 1971).

Species belonging to *Lithoredo*, *Nausitora*, and *Psiloteredo* preferentially inhabit waterbodies with salinities as low as 0.5–5 ppt (oligohaline) but are unable to either survive or reproduce when exposed to euhaline (30–40 ppt) or hyperhaline salinities (> 40 ppt). *Lithoredo* is geographically restricted to tropical fluvial-tidal systems in southeast Asia (India, Myanmar, and the Philippines; Nair and Saraswathy 1971; Shipway et al. 2019a), *Nausitora* is pantropical, and *Psiloteredo* inhabits tidally influenced fluvial environments and restricted embayments with marine connections (Turner 1966; Lopes and Narchi 1993; Taylor 1993; Rojas and Severeyn 2000). *Psiloteredo healdi* has been shown to dominate zones proximal to mangrove forests along Lake Maracaibo, Venezuela, preferentially inhabiting freshly available media from dead mangroves in salinities from 0–20 ppt (fresh to polyhaline; Laval et al. 2003), limiting competition with *B. fimbriatula* in *Rhizophora* (Rojas and Severeyn 2000). *Psiloteredo healdi* inhabits proximal paralic (marine-influenced fluvial) environments with salinities of 0–2 ppt (fresh to oligohaline) along the Rio Comprido, Brazil, with populations sharply declining toward the river mouth where *N. fusticulus* becomes increasingly abundant with increasing salinities (2–5 ppt and higher) (Fig. 4; Lopes and Narchi 1993).

Larviparous teredinids reproducing in oligo–mesohaline salinities (0.5–18 ppt) are few, including *Teredo bartschi*, *T. navalis,* and *T. poculifer*; the latter exhibiting reduced activity at salinities > 15 ppt (mesohaline). *Teredo navalis* has been suggested to resume breeding activity in salinities > 9 ppt in Chesapeake Bay (NEMESIS) but has been shown to reduce activity at 18 ppt (mesohaline-polyhaline boundary) with a lower lethal limit of 10 ppt elsewhere (M'gonigle 1928; Imai et al. 1950).

Studies on paralic and estuarine teredinid distributions (e.g., Rayner 1979; Lopes and Narchi 1993; Maldonado and Skinner 2016) provide excellent data to examine the distribution of modern wood borers at high resolution. Rayner (1979) studied the percent composition of species along the Gonema River and within Macfarlane Harbour, Papua New Guinea. He observed the dominance of oviparous species in proximal reaches with an increasing interaction with larviparous species within the upper estuary at the onset of the wet season. This indicates that reproduction seasonality for larviparous species takes place during the dry season with settlement in the transitional dry-wet season. Lopes and Narchi (1993) studied the species composition and occurrence densities with respect to salinity variations from *in situ* media over one wet and two dry seasons in the Escuro and Comprido rivers at Praia Dura, Sao Paulo, Brazil (Fig. 4). Oviparous species dominate at all localities with the greatest contribution provided by *Nausitora fusticulus*. While salinity tolerances of this species have yet to be measured, members of the genus can tolerate salinities as low as 0.62 ppt but must reproduce in mesohaline salinities (5–18 ppt), with highest survivorship of larvae in 11.2–14.5 ppt. There is no embryonic development in salinities < 4.26 ppt (Nair and Saraswathy 1971; Rayner 1979). Maldonado and Skinner (2016) examined the distribution of communities in the coastal waters of Rio de Janiero, Brazil, ~ 65 km northeast of the study area of Lopes and Narchi (1993), recording the number of individuals present in a given panel at multiple localities along the coast. Larviparous species dominate sites within the bay, whereas oviparous species become more prevalent in areas with more connectivity to the Atlantic (Fig. 5). These studies reinforce the consensus that oviparous species tend to dominate environments with oligohaline to lower mesohaline mean salinities, whereas larviparous species tend to dominate upper mesohaline to euhaline salinities.

The relationship between boring size, boring density, and salinity is of particular importance in paleoenvironmental and sequence stratigraphic analyses with respect to the salinities required in modern environments for: (1) species survival; (2) reproduction; and (3) survival of larvae. The survival of larvae being of primary significance as larvae are much more susceptible to mortality driven by salinity stress than adults, requiring a much narrower salinity range than adults. The narrow range of larval salinity tolerances is suggested to be the most important limiting factor in teredinid distributions (Rayner 1979). Desirable salinity ranges for survival and reproduction are exemplified by high boring densities occurring with a decrease in boring metrics (diameter and volume), where competition for space limits continued growth resulting in stenomorphism, branching, and tunnel-diameter maintenance (e.g., Nair and Saraswathy, 1971; Savrda and Smith 1996).

Problems associated with a sessile lifestyle specialized to exploit ephemeral media have resulted in efficient boring and reproductive strategies to cope with: (1) low dispersal capability of adults; (2) sympatric competition; and (3) the rapid decay and fragmentation of submerged wood. The affinity of wood borers with respect to degradational state of media investigated by Nishimoto et al. (2015) indicate that the Pholadidae are most prevalent in freshly exposed wood in Tanabe Bay, Japan. Highly specialized species, such as *Martesia striata*, have a suite of adaptations to bore into freshly exposed media: noncork bark (Turner 1954); living mangroves

(Boyle and Turner 1976); PVC piping (Morton 1971); and soft clay (Turner 1954, 1955). As exposure time and degradation increased, Nishimoto et al. (2015) showed that teredinids became dominant and outcompeted pholadids.

Three modes of reproduction are utilized by the Pholadoidea to facilitate dispersal of larvae in a spatiotemporal framework, whether to maximize philopatric recruitment to exploit a constant media supply, or to broadcast young to maximize species dispersal. Ovipary is external fertilization of gametes with a planktonic development stage of 20 or more days (Nair and Saraswathy, 1971; Culliney, 1975). Short-term larvipary is when larvae are retained in the water tubes of the parental gills and released at the straight-hinge veliger stage. Long-term larvipary is similar, with larvae retained in the gills but released as competent pediveligers (i.e., ready to settle immediately; Nair and Saraswathy, 1971; Calloway and Turner, 1988). All three modes signify different life-history strategies, which relate to exploitation of differing environmental conditions. Brooding species exhibit reduction of the lateral pallet segmentation, which reduces retention of newly released larvae. Releasing larvae ready for settlement allows dominance in estuarine and upper estuarine settings by restricting offspring to the same environment, or to laterally adjacent environments that likely have similar physicochemical conditions (Giangrande et al. 1994; Distel et al. 2011; MacIntosh et al. 2014; Voight 2015). Species that brood young (larviparous) have much larger distributions than those with planktonic larvae (oviparous), which stands in stark contrast to generalizations of dispersal patterns in other groups in which ovipary is correlated to larger biogeographic ranges (Hoagland and Turner, 1981).

Estuarine hydrobionts frequently develop complex larval swimming and sinking behaviors that allow them to be carried in such a way as to preferentially reduce overall drift distances to keep them close to natal habitats (Zhang et al. 2015). In vertically stratified estuaries, denser water must move upstream along the bottom. For example, croaker larvae, *Micropogon undulatus*, are transported upstream along the bottom of Chesapeake Bay by the net upstream transport of denser, more saline bottom waters (Wallace 1940); salinities can vary 1–15 ppt (oligohaline to mesohaline) between surface and bottom waters in river-dominated and microtidal estuaries (i.e. Schroeder et al. 1990; Xu et al. 2008). Bottom-water transport also supports that the settlement preference for teredinid larvae below the mudline is partially forced rather than chosen, with the majority of individuals settling within higher density gradients and outliers settling in lower gradients due to fine-scale changes in turbulence or relative vorticity (Nair and Saraswathy 1971). Variation in the distances traveled by larvae are likely impacted heavily by time spent in planktonic stages and the location of source populations. Larvae of the Atlantic Surf Clam can travel over 100 km during a one-month larval duration in open shelf waters, whereas oyster larvae in estuaries along the east coast of the United States travel only 10–30 km, despite having a similar larval duration (Zhang et al. 2015). The larvae of *Teredo navalis* and *Psiloteredo megotara* can detect suitable media for settlement via waterborne chemical cues, and significantly greater recruitment occurs in areas with higher densities of accumulated wood than those with isolated logs and flotsam (Toth et al. 2015). On a basin-wide and larger scale, tracemaker communities of *Teredolites* linked by larval dispersal and adult rafting create a diverse metacommunity where environmental factors and life history characteristics regulate a given species ability to become established in new habitats and compete with other wood borers (MacIntosh et al. 2012, MacIntosh 2015).

Temperature plays a major role in the demographics of species occurring in temperate waters (Nair and Saraswathy 1971), best illustrated by the dominance of *Bankia gouldi* in the waters of Chesapeake Bay (Scheltema and Truitt 1954), where winter temperatures restrict the ranges of *Teredo navalis, T. megotara,* and *T. sigerfoosi* to the distal margins of the bay and offshore, preventing populations from becoming established in the inner bay. Recruitment and settlement in temperate waters occurs primarily in warmer months, whereas reproduction and recruitment may occur year-round in tropical water (Nair and Saraswathy 1971, MacIntosh 2015).

Media classification and preservational modes

Teredolites occur in a variety of woodgrounds with varying degrees of preservation due to degradation, bioerosion, and diagenetic alteration. Bromley et al. (1984) coined the term ‘woodground’ for laterally continuous xylic media (i.e. peats, coals) as the archetypal media for the Teredolites Ichnofacies. *Teredolites* occurring in woodgrounds are inherently autochthonous, boring *in situ* during the early stages of the development of back barrier embayments and tidal channels after media exhumation (Bromley et al. 1984). Savrda et al. (1993) built upon this model to generate a suite of woodground subtypes to: (1) describe the degradational state of wood when occurring as isolated entities; (2) describe the degree of bioerosion; and (3) differentiate between allochthonous (isolated, reworked log ground) and autochthonous (*in situ* log ground and woodground) xylic media. Well-preserved log grounds, relict log grounds, and ghost log grounds are classified with respect to depositional and/or diagenetic fragmentation and the relationship of borings with respect to the degradational state of the media (Savrda et al. 1993). Reworked *Teredolites*—where only the boring remains because the wood has degraded—include occurrences of isolated calcite linings or infilled borings with complete disintegration and absence of media (Savrda et al. 1993).

The distribution of *Teredolites* within sedimentary successions is generally considered to be a function of hydraulic transport of xylic media (i.e. allochthonous flotsam) and an inherent relationship between sea-level dynamics and influx of xylic media into marine systems. The relationship between media influx and sea-level dynamics is well documented in the rock record (e.g., Savrda 1991, 1995; Savrda et al. 1993; Tewari et al 1998) and in modern systems (e.g., Gingras et al. 2004; Hinojosa et al. 2010). Allochthonous xylic media containing *Teredolites* is most commonly found in sediments deposited during the transgressive systems tract (TST), deposited along transgressive surfaces of erosion (TSE), and along marine flooding surfaces (MFS). Concentration of media in these intervals is due to: (1) concentration or exhumation associated with ravinement; (2) inundation of the coastal plain by marine waters; and/or (3) concentration of flotsam associated with sediment starvation (e.g., Savrda et al. 1993).

MATERIAL AND METHODS

Material for this research comes from both previously published studies on *Teredolites clavatus* and *T. longissimus* occurrences and newly collected material. Both sources span from the modern to the Lower Jurassic (Pleinsbachian) (Table 2–4) in order to produce a database for statistical analysis to determine what, if any, *Teredolites*-based paleoenvironmental trends exist in the geologic record (Table 5). Abbreviations used in this study include: $\boldsymbol{\sigma}^2$, variance; **CO**, Colorado; **CWIS**, Cretaceous Western Interior Seaway; **EOD**, Environment of Deposition; **FHSM**, Sternberg Museum of Natural History; **Fm**, Formation; **HST**, highstand systems tract; **IBGS**, IchnoBioGeoScience Research Group; **KS**, Kansas; **KUMIP**, University of Kansas Museum of Invertebrate Paleontology; **KUPB**, University of Kansas Paleobotany Collection;

LACMIP, Los Angeles County Museum of Invertebrate Paleontology; **LST**, lowstand systems tract; **Mbr**, Member; **MFS,** Marine Flooding Surface; **NHMLA**, Natural History Museum of Los Angeles County; **S.D.**, standard deviation; **SMNH**, Sternberg Museum of Natural History; **Ss**, Sandstone; **TSE,** transgressive surface of erosion; **TST,** transgressive systems tract; **UT**, Utah; **VA**, Virginia; **YPM IP**, Yale Peabody Museum Invertebrate Paleontology Collection. Key to fossil collection nomenclature (after Hammersburg *et al.* 2018): XX-Y-ZZZ [XX: Collector and Donor (CB: Caldwell Buntin, JP: Jon Pancost); Y: facies association; ZZZ: speciman number (Table 5)].

Samples observed and/or collected from outcrop were derived from Upper Cretaceous coastal plain and delta plain to shallow-marine to open marine shelfal deposits (Fig. 6, Table 4, 5), which contain all woodground types (Savrda et al. 1993) from stratigraphic units in KS, CO, and UT (Table 5). Additional material from Cretaceous and Paleogene deposits were measured from samples provided by or photographed from: (1) NHMLA, samples from the Barremian–Aptian Lower Chickabilly Member, Budden Canyon Formation at North Fork Cottonwood Creek, Ono, CA; (2) KUMIP, samples from the Turonian Carlile Shale, and Coniacian–Campanian Smoky Hill Chalk Member, Niobrara Chalk, Logan, Hodgeman, and Russell counties, KS; (3) samples from the Turonian Carlile Shale and unrecorded stratigraphic data, Russell County, KS; and (4) IBGS, samples from the Campanian Williams Fork Formation, Mesa County, CO; the Maastrichtian Prince Creek Formation, North Slope, Alaska; Priabonian Dir Abu Lifa Member, Qsar El-Sagha Formation, Faiyum Depression, Egypt; and the Paleocene-Eocene La Meseta Formation, Seymour Island, Antarctica. Facies associations were established from a combination of field observations, discussions with researchers who have worked on the stratigraphy discussed, and an extensive literature search (see Table 5).

Modern boring-bearing wood was collected from EOD that include tidal channelforms, and the foreshore and upper shoreface. Borings were measured, and tracemakers identified when possible. Collection localities include: (1) Cabretta and Nannygoat keys, Sapelo Island, Georgia; (2) Delaware Beach, Delaware; (3) Broad Bay, Lafayette River, and Virginia Beach, Virginia; and (4) Saint-Laurent-sur-Mer, Normandy, France. Salinity was measured as parts per thousand in the field using a handheld salinity refractometer independent of the timing of the tides. Data from Maldonado and Skinner (2016) from the Ilha Grande Bay was used to examine the distribution of species by reproductive type in the proximal to distal estuary at: (1) Rio Barcuy Estuary at Ilha Grande Bay (estuarine to upper estuarine); (2) Angra dos Reis (distal estuary); (3) Ponta Leste (interdistributary bay), Abraão; and (4) Ilha de Amarração (foreshore to lower shoreface; see Fig. 5). Data from Lopes and Narchi (1993) was used to examine species, reproduction style, and boring density with respect to salinity between sites in the Escuro and Comprido rivers at Praia Dura, Sao Paulo, Brazil (see Fig. 4). Data was retabulated to regress mean salinity at low tide onto occurrence densities between sites. The resulting regression equation was used as a predictor of paleo-salinity based on the characteristics of our fossil data.

Specimens were measured in the field using a metric ruler (1.0-mm accuracy), in the laboratory with digital Vernier calipers (0.01-mm accuracy), and by calibrated line measurements in ImageJ (0.001-mm accuracy). Long or sinuous traces were measured by the summation of branch lengths. Specimens examined by hand sample or at outcrop were photographed with a Canon 5D DSLR camera or with a Nikon DXM1200 digital camera mounted to a Nikon SMZ1000 stereomicroscope. Images were processed with ImageJ version 1.52a to measure individual boring diameter and length (if applicable).

Ancient and modern *Teredolites* specimens were organized into a data set of 14,137 measurements. *Teredolites* were identified to the ichnospecies level and assigned a rank (1, 2) per Kelly and Bromley (1984), while the medium was assigned a woodground preservation type *per* Savrda et al. (1993) and ranked with increasing degree of degradation (1: Xylic Peatgrounds; 2: Well-Preserved Log Grounds; 3: Relict Log Grounds; 4 Ghost Log Grounds; 5: Reworked *Teredolites*). Facies associations were assigned coded rankings from the most distal (1, open marine) to most proximal (21, i.e., most landward). Co-occurring trace fossils within the same medium and within the same bedding planes were recorded and assigned a diversity rank (1–7) by the relative number of ichnogenera present. SDI was calculated as the product of the maximum boring diameter in a sample by the diversity rank along the bedding interval in which the sample was located. Systems tracts were assigned to samples based on their stratigrphic occurrence using sequence stratigraphic observations of Van Wagoner et al. (1991), Yoshida (2000), Willis (2000), Pattison et al. (2007), Hoffmeister (2011), and others. Systems tracts were compared against woodground preservation types, boring densities, SDI, and boring metrics to determine sequence stratigraphic relationships. These data were analyzed to determine the effects contributing to variations in size ranges, boring densities, and lateral abundance of occurrences to interpret salinity ranges within facies associations using the modern trends of salinity-size relations as a proxy for the physiological requirements of the progenitors of *Teredolites* in the CWIS.

One-Way Model I Analysis of Variance (ANOVA), Two-Way Model I ANOVA, Mixed Model Nested ANOVA, and Factorial ANOVA were used to evaluate differences among mean and maximum boring diameters between: (1) facies association; (2) *Teredolites* ichnospecies; (3) woodground preservation type; (4) ichnocoenoses; and (5) boring densities. One-Way Model I

ANOVA were used to determine differences in boring densities per sample due to: (1) ichnospecies; (2) ichnocoenoses; and (3) woodground preservation type. Two-Way Model I ANOVA were used to determine the effects of boring densities due to ichnospecies covarying with mean diameters. Mixed Model Nested ANOVA was used to determine the effects of: (1) maximum diameters due to ichnospecies within facies associations; (2) mean boring diameters due to woodground types within facies associations; and (3) mean boring diameters due to ichnocoenoses within facies associations. Significant ANOVAs were superseded by Tukey's Pairwise Comparisons, *a posteriori*. Factorial ANOVA was used to determine differences between facies associations with respect to woodground types, ichnospecies, and the interaction between both causal variables. More robust models were not frequently used on the full data set (only on grouped data) due to significant differences in variance caused by unequal sample sizes and data transformation (e.g., Underwood, 1997; Filho et al. 2008). Since the assumption of homogeneity was not met for these data, Welch's F test was performed and is provided in One-Way ANOVA reporting. Statistical analyses were completed using Minitab® version 19.1.

SYSTEMATIC ICHNOLOGY

Excavation of borings in xylic substrates by wood-boring bivalves results in various morphotypes (Kelly 1988a). Variations in tracemaker musculature and shell morphology directly influence motion during excavation (Ansell and Nair 1969). Although the relationship between ichnotaxa and biological taxa is generally indiscernible, ichnotaxa may express morphologies indicating key character traits of their producers such that biotaxonomic affinity can be ascertained (Bertling et al. 2006). Recently, substrate type was rejected as an ichnotaxobase for clavate borings occurring in wood (Donovan and Ewin, 2018) although this view was rejected by Melnyk et al. (2020), as media type does provide paleontologic, paleoethologic, and taphonomic insight.

Hence, we contest the argument that the *Apectoichnus longissimus* and *Teredolites clavatus* vary markedly in their forms and reject the assumption that morphology is not a valid ichnotaxobase (Donovan 2018). The mechanical action used to excavate boreholes is directly influenced by valve and tissue morphology, directly influencing boring morphology. Similar motions observed in *Martesia* and *Petricolaria pholadiformis* (Veneridae) produce clavate borings *sensu* Kelly and Bromley (1984) and the similar motion made by the Xylophagaidae and Teredinidae produce *Apectoichnus longissimus* (Ansell and Nair 1969). Sinuous, clavate borings can commonly transition into long, sinuous borings (Fig. 2) by the extinct tracemakers *Goniochasma*, *Terebrimya*, *Teredina*, *Turnus*, and *Xylophagella* (Kelly 1988a) due to variations in boring densities within a given medium or due to the ichnogenetic stages their borings record. Such borings vary larkedly in their length ratios from 1.25:1 to 11.4:1 and can either be oriented parallel or perpendicular to the grain of wood and provide an intermediate morphology between *Apectoichnus longissimus* and *Teredolites clavatus*. Such intermediate or transitional boring metrics accompanied by directional changes negate significant differences in morphology as a valid ichnotaxobase to partition these borings at the ichnogeneric level.

Ichnogenus *Teredolites* Laymerie, 1842

Type ichnospecies.—Teredolites clavatus Laymerie, 1842

Diagnosis.—Flask-shaped borings in xylic medium, tapering evenly from anterior to posterior; neck region connected to main chamber; more or less circular to ovate in cross section at all levels (Fig. 7) (after Kelly and Bromley 1984).

Remarks.—Boring apertures commonly oriented vertically to slightly oblique in heavily bored media. Borings are more or less smooth, occasionally bearing surficial morphology (mostly wood-grain texture; rarely scratches produced by boring), calcite linings, and siphonoplax impressions (rare). Boring axis is straight, sinuous, or contorted to branched. Sudden changes in boring axis result in constriction or branching as a response to medium overcrowding and/or disturbance of the aperture regions (e.g., due to predation) (Miller 1924; Savrda and Smith 1996). Calcite linings were informally designated as "Teredolithus" by Bartsch (1930) and may include retrusive caps (Turner 1954, Savrda and Smith 1996). *Teredolites* is distinguished from *Asthenopodichnium* (Fig. 8) by lacking a shallow groove or pouch-like shape that occurs on the upper surface of the medium. *Teredolites* is considered a dwelling trace (domichnia) attributed to pholadoidean bivalves. *Teredolites* differ from *Gastrochaenolites* by occurring in xylic media, rather than in semiconsolidated to hardground media. Extant tracemakers are found in a variety of marine-influenced environments, requiring oligohaline to hyperhaline (rarely fresh) conditions for survival.

Range.—Jurassic (Pleinsbachian)–recent.

Teredolites clavatus Laymerie, 1842

Type specimen.—Untraced, Laymerie 1842 (Kelly and Bromley 1984).

Diagnosis.—Clavate-shaped borings in wood, coal, or amber with circular aperture and circular to ovate cross section. Borings perpendicular to grain in xylic media. Mean width/length ratios 1:2.70 (n=8873).

Remarks.—Boring diameters increase in size gradually towards the posterior, with a maximum diameter just before a hemispherical distal termination. Extant tracemakers include pholadids and the venerid *Petricolaria pholadiformis*. Minute borings (0.1–0.3 cm) may reflect an intermediate phase into *T. longissimus* as 'unprogressive borings' (Savrda et al. 2005) by *T. longissimus* larval tracemakers (ichnogenetic stages; Z. Belaústegui personal communication 2020). Two generalized morphologies (see Fig. 7) exist within *T. clavatus* that are directly correlated to body plan (Kelly 1988a): (1) short borings relative to shell length with a low width to length ratio (Type I, Fig. 7A, B, E), belonging to *Barnea, Lignopholas, Martesia, Opertochasma, Turnus,* and *P. pholadiformis*; and (2) long borings relative to shell length with progenitors having a vermiform body plan (Type II, Fig. 7C, D, F), such as in *Teredina*, *Turnus*, *Xylophagella*, and the Xylophagaidae. The Type II borings remain perpendicular with the woodgrain of associated media and commonly transitions into *T. longissimus* in densely bored media.

Range.—Jurassic to recent.

Teredolites longissimus Kelly and Bromley 1984

Diagnosis.—Elongate clavate borings with axis primarily aligned perpendicular to grain of xylic media (Fig. 9) with a mean width:length ratio of 1:4.97 (n=3901). Borings may contain surficial morphology, calcite linings, branching, siphon impressions, and/or constrictions.

Remarks.—Extant tracemakers include the bankiinids (Fig. 9D, E), teredinids, and xylophagids. Calcite linings within *T. longissimus* may be used for preliminary assessment of tracemaker affinity: Teredinidae (all can produce linings) vs. Pholadidae (only some genera, species) (see Haga and Kase 2011, table 1). For example, the siphonal region is thickened with calcite linings produced by the Teredinidae as a reinforcement against wear from pallet forcing. The lining in borings of the Teredinidae may exhibit retrusive caps that record the cession of boring activity and transformation to complete filter-feeding behavior (Turner 1966; Savrda and Smith 1996; Evans 1999; Savrda et al. 2005).

The recent reassessment of *T. longissimus* to *Apectoichnus* igen. by Donovan (2018) based on a longer boring length than Type 1 *T. clavatus* (*sensu* Kelly and Bromley, 1984) only prolongs the nomenclatural disarray experienced by this group in the literature. *Teredolites longissimus* and Type 2 *T. clavatus* share a vermiform body plan and likely xylophagy, the retainment of boring orientation in *T. longissimus* bears ecological significance in the ethnogenesis of and compensation for the vermiform body plan. The diagnosis of Donovan (2018) would lump Type 2 *T. clavatus* into *Apectoichnus isp.* as an oversimplification, being "mostly straight to contorted," regardless of orientation with wood grain. Differences in the ichnogenetic stages of *Teredolites* tracemakers may result in both ichnospecies, such as borings produced by *Turnus*. *Turnus* produces *T. clavatus* (Fig. 7E) until boring diameters exceed 1 cm and borings become long, sinuous, and oriented parallel to the woodgrain, which would characterize them as *T. longissimus* (Fig. 9A). Binning effectively dampens the significance of boring morphology, ichnogenetic stages, and orientation, making inferences into community structures difficult for both ichnospecies *sensu* Kelly and Bromley (1984). We, therefore, retain *T. longissimus* as an ichnotaxon.

Range.—Jurassic (Pleinsbachian)–recent.

Fossil and Modern Trace Associations (Ichnocoenoses) with *Teredolites*

Occurrences of trace fossils associated with *Teredolites* in fossilized xylic media studied in CO, KS, and UT include: *Asthenopodichnium, Apectoichnus* indet., cf. *Psilonichnus*. *Asthenopodichnium,* in general, were most abundant in deposits interpreted as: tidal inlet channels (30.89%); tidally influenced fluvial channels (24.39%); tidal channels (11.38%); estuarine (9.85%); upper estuarine (7.31%); distal tidal-fluvial channels (6.50%); estuarine tidal sand bars (6.05%); and proximal tidal-fluvial channels (3.25%). Only one sample contained *Apectoichnus* indet. co-occurring with *Teredolites* from the Carlile Shale (open marine; SE ¼ Sec. 36 T. 215, R. 26W on tributary to Pawnee River, 14 mi. WNW of Jetmore, KS). Observations of trace fossils in the same bedding plane as *Teredolites* in the Mesaverde Group (Table 5) did not show evidence of association with xylic media, with the exception of cf. *Psilonichnus*. *Piscichnus* was infrequently observed directly overlying *Teredolites*-bored media in the Castlegate Sandstone at Blaze Canyon, Utah. *Thalassinoides* was frequently associated with xylic peatgrounds, with burrows occurring within coals and in carbonaceous drapes.

Modern wood bored by *Bankia gouldi* collected from the Lafayette River, VA, were also found associated with wood that contained borings by other marine and terrestrial animals, such as: (1) polychaete worms (ichnotaxon *Caulostrepsis*); (2) gastropods (ichnotaxon *Radulichnus*); (3) beetles (ichnotaxon *Paleobuprestis*); or (4) termites (Isoptera: Rhinotermitidae; boring nests in open nomenclature). *Arenicolites* produced by *Nereis sp.* was frequently observed in sediments associated with those xylic media at low tide.

Borings by other marine organisms associated with wood at Nannygoat and Cabretta keys, Sapelo Island, Georgia (and EOD), containing *T. longissimus* (*Bankia carinata*) include: 1) *Petricolaria pholadiformis* (venerid bivalve), and *Barnea truncata* and *Martesia cuneiformis* (pholadid bivalve) that produce *T. clavatus* in wood found in tidal inlet channel and upper shoreface environments; and 2) limnorinid (isopod) borings (*Apectoichnus lignummasticans*) in wood found in tidal inlet channel and spit environments.

Organisms associated with xylic media containing *T. clavatus* include: (1) cf. *Psilonichnus*, upper shoreface; (2) limnorinid (isopod) borings, distal tidal inlet channel, spit; (3) *Rogerella*, upper shoreface and salt marsh firmground; and (4) *T. clavatus* produced by *Petricolaria pholadiformis* (venerid bivalve) in exhumed saltmarsh firmground. The latter occurred with the ichnogenus *Siphonichnus*, which was also made by *P. pholadiformis* in firmground of exhumed relict marsh.

Organisms and their traces in sedimentary environments containing *Teredolites*-bored wood include: (1) upper shoreface—*Onuphis* (polychaete worm), ichnogenus *Skolithos*; *Callianassa* (shrimp), ichnogenus *Ophiomorpha; Balanoglossus* (peanut worm), ichnogenus *Rosselia;* indet. Amphipoda (amphipod), cryptoturbation; (2) relict salt marsh—*P. pholadiformis*, ichnogenera *Gastrochaenolites* and *Siphonichnus*; *Oliva* (burrowing gastropod), indet. repichnia; and (3) tidal inlet channel—*Callianassa*, ichnogenus *Ophiomorpha*; indet. Elasmobranch (rays), ichnogenus *Piscichnus.*

RESULTS OF STATISTICAL ANALYSES

A total of 14,137 borings within 368 occurrences were measured; 203 occurrences were *Teredolites clavatus* (55%) and 165 occurrences were *T. longissimus* (45%) found within 21 facies associations (Table 5). Size-frequency analysis yields a mean *Teredolites* boring diameter of 0.67 cm (S.D. = 0.536 cm, $\sigma^2 = 0.288$), mode of 0.40 cm, median of 0.59 cm, minimum of 0.03 cm, maximum of 6.88 cm, and skewness of 2.70. Metrics for *T. clavatus* are: mean width and length = 0.63 x 1.97 cm (0.51 cm, ± 0.51 cm; respectively), mode of 0.5 x 1.5 cm, median of 0.49 x 1.57 cm, minimum of 0.08 x 0.1 cm, maximum of 5.00 x 12.43 cm, and an average W:L ratio of 1:2.91. Metrics for *T. longissimus* are: mean width and length = 0.7 x 3.59 cm (0.57 cm, ± 2.85 cm; respectively), mode of 1.0 x 8.0 cm, median of 0.59 x 2.8 cm, minimum of 0.06 x 0.20 cm, maximum of 6.81 x 30.6 cm, and a W:L ratio of 1:4.97.

Individual measurements follow a right-skewed, unimodal distribution with a peak in the range of 0.25–0.55 cm and a modal group between 0.3 and 0.4 cm. Group means best fit a loglogistic distribution with untransformed values, and follow a normal distribution with the following Johnson Transformation Function:

$$-1.15993 + 1.02744 \times \operatorname{asinh}[(x - 0.365572) \div 0.245016]$$

Collection of measurements on boring length were exceedingly difficult at outcrop due to the sinuous nature of borings compounded by high boring densities. Borings are frequently intertwined or change direction, easily obscured by neighboring *Teredolites,* or by directional changes into the medium. The lack of paired width and length data prevents the statistical determination of stenomorphism (Fig. 7F, 9B), which must be qualitatively determined from images at outcrop or in hand sample as smaller than expected sizes. Simple Linear Regression analysis metrics from *T. longissimus* produced by *Bankia gouldi* in the Lafayette River, Norfolk, VA (~9 ppt) yield the following regression equation for length upon diameter:

$$L = -6.27 + 19.79d$$

where L is boring length and d is boring diameter.

Teredolites occurrence frequencies with respect to facies associations (Fig. 10) follow multimodal distributions at the ichnogenus and ichnospecies level and percent contribution of each facies association with respect to occurrence frequency (Table 5). Greatest frequencies of *Teredolites* occur in open-marine environments, tidal-inlet channels, distal tidal-fluvial channels, and tidally influenced fluvial channels. Mean and maximum boring sizes with respect to facies association vary considerably (Fig. 10A). SDI values calculated for the ichnogenus *Teredolites* (313 group occurrences) are unimodal. SDI display a mean of 3.820 (S.D. = 4.255, $\sigma^2 = 18.104$), mode of 0 (85), median of 2.574, minimum of 0.000, maximum of 21.825, and skewness of 1.44.

Occurrence data for *T. clavatus* yield a trimodal distribution with the greatest occurrence frequencies in tidal-inlet channels, distal tidal-fluvial channels, tidal channels, and tidally influenced fluvial channels. The size-frequency distribution (Fig. 11) for maximum boring diameter is right-skewed and unimodal with the greatest size frequency occurring at 0.75–1.25 cm (40%). Size-frequency distribution for mean boring diameter is unimodal with a grand mean of 0.82 cm (Fig. 11B). The greatest frequencies of mean boring sizes occur between 0.37–0.62 cm (65%) and 1.37–1.62 cm (11%). SDI values calculated for *T. clavatus* (168 group occurrences) are unimodal. SDI display a mean of 3.946 (S.D. = 4.007, $\sigma^2 = 16.054$), mode of 0 (39), median of 3.043, minimum of 0.000, maximum of 18.579, and skewness of 1.35.

The frequency distribution for *T. longissimus* with respect to facies association is trimodal with the highest occurrences in open marine, distal tidal-fluvial channels, and tidally influenced fluvial channels. The size-frequency distribution for maximum boring diameters is right-skewed and unimodal with greatest frequencies occurring at 0.75–1.25 cm and 2.75–3.25 cm (Fig. 11C). Mean boring size frequencies are bimodal with peaks at 0.37–0.62 cm (48%) and 1.85–2.12 cm (5%), and a grand mean of 0.89 cm. SDI values calculated for *T. longissimus* (145 group occurrences) are unimodal. SDI display a mean of 3.673 (S.D. = 4.535, $\sigma^2 = 20.567$), mode of 0 (46), median of 1.956, minimum of 0.000, maximum of 21.825, and skewness of 1.54.

Borings observed at outcrop were commonly found in all woodground types with the exception of the category Reworked *Teredolites,* which were only observed in the Upper Cretaceous Castlegate Sandstone and in museum specimens from the Upper Cretaceous Carlile Shale and Oligocene Qsar al Sagha Formation. When characteristics concerning media preservation state are combined from Savrda et al. (1993) and Nishimoto et al. (2015) and applied to our dataset, *T. clavatus* are far more abundant than *T. longissimus* in each preservation state, apart from xylic peatgrounds where both are equally abundant (Table 6; Fig. 12–14). Sample sizes for Reworked *Teredolites* were too small in this study to provide reliable statistical analyses (*n* = 23), however, Bonferroni's pairwise comparison does show that this media type trends to sharing means with all other media types.

Analyses conducted on boring diameter and length show significance at the ichnospecies and facies association level. One-Way ANOVA (Table 7) show a significant effect on boring diameter at the ichnospecies level, facies association level, between woodground types, and between associated ichnocoenoses. One-Way ANOVA show significant effects of boring length (Table 7) between ichnospecies, facies associations, and woodground preservation types. Simple linear regression yields a positive correlation between the diameter and length of borings for both ichnospecies, *T.c.:* $p < 0.000$, $r^2 = 82.94\%$; *T.l.*: $p < 0.000$, $r^2 = 79.82\%$. Regression equation of boring diameter (d) upon boring length (L) for log transformed data is as follows:

$$T.\ clavatus: \ln(d) = 0.36832 \times \ln(L)$$

$$T.\ longissimus: \ln(d) = 0.20224 \times \ln(L)$$

Significant effects on group mean boring diameters are observed with the following factors in One Way ANOVA (Table 7): facies association; woodground preservation type; and ichnocoenoses. Significance is approached when group mean boring diameters are compared to all *Teredolites* ichnospecies and facies associations. The effect of boring densities and ichnospecies is nonsignificant when compared to mean boring diameter. Hierarchical ANOVA explain additional variance in group mean boring diameters (Table 8) when woodground preservation type and ichnocoenoses are nested within facies associations.

Multiple linear regression on mean diameters of all *Teredolites* show that maximum boring diameters, densities, facies association, and ichnospecies are significant predictors of group mean boring diameters ($F_{9,\,320} = 90.41$, $p < 0.000$, $r^2 = 71.77\%$). Individual predictors show that maximum boring diameters (t = 13.56, $p < 0.000$) and the interactions between maximum boring diameters (d_{max}^2) (t = –8.21, $p < 0.000$), maximum diameters with boring densities (t = –4.39, $p < 0.000$), and boring densities with proximodistally ranked facies associations (t = 1.98, $p < 0.05$) are significant predictors of group mean boring diameter. The regression equations for natural log transformed group maximum boring diameters are as follows:

Teredolites clavatus

$$-1.4297 + 0.8449X_1 - 0.1359X_2 - 0.00249X_3 - 0.07538X_1 \times X_1 - 0.001574X_1 \times X_2 + 0.00185X_1 \times X_3 + 0.000093X_2 \times X_3$$

Teredolites longissimus

$$-1.2904 + 0.7884X_1 - 0.001359X_2 - 0.00249X_3 - 0.07538X_1 \times X_1 - 0.001574X_1 \times X_2 + 0.00185X_1 \times X_3 + 0.000093X_2 \times X_3$$

Where, for any given sample: X_1 is the maximum boring diameter, X_2 is the number of borings present, and X_3 is the coded value of ranked facies association in which the sample occurs.

One-Way ANOVA on group maximum boring diameters (Table 7) show significant variance when compared to facies association, ichnocoenoses, and woodground preservation type (Table 7). The effect of *Teredolites* boring densities and ichnospecies show no significance when compared to group maximum boring diameters but the effect of woodground preservation trends towards significance when nested within facies associations (Table 8). Additional variance is explained when ichnocoenoses and woodground preservation type are nested within facies association, although the effect for woodground is no longer significant when nested.

Significant factors accounting for differences in boring density (Table 8) include: ichnocoenoses; ichnospecies; and woodground preservation type. Boring densities are affected when *Teredolites* ichnospecies covary with group mean diameter, but the effect of group maximum diameter is no longer significant when nested (Table 8). The effect of facies associations approaches significance when compared to maximum and mean boring diameter, although the relationships are inversely related to boring density (Fig. 10, 15). Simple linear regression on boring density show a negative effect on group mean boring diameters as density increases with a significant regression of: $F_{1,\,297} = 31.48$; $p < 0.000$; with $r^2 = 17.49\%$. The regression of boring density onto mean boring diameters yields the following regression equation:

$$T.\ clavatus\text{: } \ln(N) = 0.753 + -0.725\ln(\mu d)$$

$$T.\ longissimus\text{: } \ln(N) = 3.255 + -0.725\ln(\mu d)$$

where N denotes the number of *Teredolites* present and μd is the mean boring diameter in a given sample. Group mean boring diameters decrease –0.743 cm per boring present. Maximum boring diameter (d_{max}) has a nonsignificant, positive effect on boring density, $F_{1,328} = 2.18$, $p = 0.141$, $r^2 = 0.66\%$, yielding the regression equation:

$$\ln(N) = 0.736 + 0.0923\ln(d_{max})$$

Analyses on coded facies association data yield significance (Table 7) when compared to woodground preservation type and ichnocoenoses; no significance arises in One-Way ANOVA compared to ichnospecies. The interaction between ichnospecies and woodground, however, is significant with respect to facies association (Table 8).

One-Way ANOVA analyses on systems tracts (Table 7, 9) show significance between boring densities, boring metrics, woodground preservation types, and ichnocoenoses. Percent contribution of *Teredolites* within systems tracts shows the highest densities to occur in lowstand and transgressive systems tracts with little contribution from highstand systems tracts (Table 9).

Linear regression performed on mean salinity at low tide with respect to number of individuals present at each modern site sampled at Rio Comprido near Praia Dura, Sao Paulo, Brazil (Fig. 17; data from Lopes and Narchi 1993), yields the regression equation:

$$PPT\ (mean) = -3.43 + 0.03990N$$

where *N* is the number of *T. longissimus* borings in a given sample. This regression equation will be used as a predictor of salinity against our dataset of ancient examples (Fig. 18).

SDI for *Teredolites* at the ichnogenus and ichnospecies level (Fig. 19) is high in facies associations interpreted to have had a high level of connectivity to open marine systems or mixing by tidal processes. SDI for the ichnogenus is highest in facies associations interpreted as distal lower shoreface. SDI for *T. clavatus* is highest in facies associations interpreted as distal lower shoreface, upper estuary, and tidally influenced channels. SDI for *T. longissimus* is highest in MFS overlain by facies associations interpreted as braided fluvial channels, upper estuarine, and distal lower shoreface. SDI is lowest at the ichnogenus level within facies associations interpreted as fluvial channel and foreshore. SDI is lowest at the ichnospecies level in facies associations interpreted as foreshore and backshore, mouth bars, and proximal tidal-fluvial channels.

DISCUSSION

Findings from this study indicate that the diameter, length, boring density, and SDI of *Teredolites* can serve as predictors of paleosalinity from the rock record that can help clarify paleoenvironmental interpretations to the subenvironment level in shallow-marine to transitional continental environments, based on the distribution of modern tracemakers and their borings. The settlement patterns interpreted from boring metrics and SDI reflect population settlement trends of *Teredolites* tracemakers in the transitional zone—paralic to upper estuarine, central estuarine, lower estuarine—to open marine environments, with *T. clavatus* being slightly more abundant than *T. longissimus.* While the occurrence of *Teredolites* is intuitively controlled by the availability of suitable media, variations in boring size, density, and taxonomic and ichnotaxonomic affinities can be reconciled when accounting for salinity, life history strategies, woodground character, and ichnocoenoses.

Results of this research are also important for identifying sequence stratigraphic position, flooding surfaces, and autogenic versus allogenic controls on deposition in ancient deposits that record the influx and transport of terrigenous woody media from coastal plain to open marine EODs. Variations occurring within *Teredolites*—ichnospecific affinity, morphometrics, boring densities, woodground preservation character, and ichnocoenosis affiliations—can serve as proxies to better interpret the history of transitional depositional systems and location relative to the paleoshoreline. This application can also be used for better predictability of sandbody-shale abundance, distribution, and geometries, which are important to the petroleum industry.

Effect of *Teredolites* Ichnospecies on Boring Metrics

Basal families within the Pholadoidea (Pholadidae) and Veneridae (Veneroidea) generally produce *T. clavatus*, whereas *T. longissimus* is produced by the more derived members of the Teredinidae and Xylophagaidae (see Fig. 1). Differences in the physiology, shell morphology, life-history strategies, and media preferences of these families are reflected at the ichnospecies level with significant contributions to differences between overall boring diameters, lengths, and densities. When combined with woodground preservation type, ichnospecies trends show preferences for settlement in different environments (i.e., facies associations) and media fragmentation state (Fig. 10, 12–14, 16). Significant differences between ichnospecies with respect to boring diameter is suggested in unsummarized metrics (i.e., all borings independent of sample density and neighboring borings, but statistical power (i.e., high r^2 values) is lost in summarized data (Table 7). Summarizing results in nonsignificant ANOVAs, increases our Type II error rate for differences in mean and maximum boring diameters due to the effect of ichnospecies.

Distinct life history differences are shown in significant ANOVAS: (1) at the ichnospecies level between boring diameters and lengths, boring density, facies associations, and woodground preservation type; and (2) in *Teredolites* sample density with respect to ichnospecies, mean boring diameters, woodground preservation type, and ichnodiversity. Findings indicate that group-diameter metrics and boring densities are a more suitable metric when treated singly than combined (SDI) to constrain variance due to the low number of ichnogenera within the Teredolites Ichnofacies, as well as the high fecundity of pholadoideans coupled with localized larval retention of tracemakers in estuarine settings.

The relationship between boring morphometrics at the ichnospecies level may be explained by differences in tracemaker body plan within *T. clavatus* and tracemaker reproductive strategies within *T. longissimus*. *Teredolites clavatus* vary with respect to the body-to-shell length ratio of their respective tracemakers, resulting in pronounced differences in body volumes between Type I and II morphologies within *T. clavatus*. The low abundance of large W:L relationships in *T. clavatus* is reflected in the low abundance of Type II borings in the Mesaverde Group, with the exception of the Neslen Formation (see Table 4).

Differences in boring densities of *Teredolites* ichnospecies between media preservation types suggests a degree of independence from the sole availability of appropriate media at the time of settlement (Fig. 12–14). Increasingly right-skewed size frequencies coincide with increasing woodground degradation, and illustrate that settlement was more likely to occur in media immersed for longer periods of time (e.g., Nair and Saraswathy 1971; Toth et al. 2015). Settlement preferences with respect to media immersion time or degradation illustrated selective settlement of larvae, differences in community composition, media reworking and transport, or seasonal differences in lower boundary layer circulation that affected larval transport.

Differences in boring metrics (diameter and length; Fig. 10) between ichnospecies are also likely physiological, with both ichnospecies equally effected by media overcrowding and salinity resulting in stenomorphism (e.g., Clapp 1923; Savrda et al. 1993). For example, the tracemakers of *T. clavatus* cease all boring activity and accessory plates are formed when sexual maturity is reached (deterministic growth; i.e., stop growing), making inferences of environmental factors from boring metrics difficult to interpret in the rock record. The tracemakers of *T. longissimus* frequently display changes in species composition across environments (i.e., Rayner 1979; Lopes and Narchi 1993; MacIntosh 2015), which also reflect changes in body volume with respect to reproduction style (i.e., boring metrics; Cragg et al. 2009). While length measurements were infrequently collected, Rojas and Severeyn (2000) demonstrated that there is only a 12% loss in statistical power when diameter is used to calculate boring volume rather than length, being able to satisfactorily predict volume in 85% of borings.

The effect of media overcrowding is strongly correlated to diameter, with increasing boring densities within a given medium resulting in a decrease in mean boring diameter and an increase in maximum boring diameter (i.e., few larger diameter borings)(Fig. 15). Space limitation is of particular importance as the ranges between boring-diameter size classes can be used to distinguish the timing of settlement for individual borings, where the largest borings within a cluster of stenomorphic borings would have been the primary colonizers (Fig. 21). The principle growth of primary colonizers would not have been restricted by adjacent borings, although the effect of subsequent space limitation cannot be observed in the fossil record because settlement events can not be directly observed and recorded as in modern studies.

Ichnospecies and body fossils.—The identification of tracemakers provides substantial insight into expected boring metrics in a given environment and, by inference, can aid in identifying ancient environments and paleoenvironmental evolution. Tracemaker affinity can be inferred in ancient deposits using boring morphologies and permineralized hard parts or internal molds to understand changes in species composition across depositional environments and also within a sequence stratigraphic framework. While well-preserved body fossils are preferred for identification, weakly preserved molds of valves, accessory plates, and/or pallets can also be used to identify tracemakers to the subfamily or generic level. Such features are generally rare, but may be associated with finer grained lithologies (i.e. sandy siltstone to fine silty sandstone). Identification with respect to boring morphometrics follows the intra-ichnospecific variation within *T. clavatus* (Kelly 1988a) with respect to wood-boring pholadid genera: (1) tear-drop-shaped borings similar to *T. clavatus* (Type I) were made by *Barnea*, *Martesia*, and *Opertochasma*; (2) long, thin *T. clavatus* similar to *T. longissimus* (Type II) were made by

Teredina and *Xylophagella*; and (3) Type II linguoid-shaped borings equal in diameter from the opening to the chamber similar to *T. clavatus* were made by *Turnus*.

Borings containing hard parts in our study similarly follow such observations (Fig. 7). Borings created by *Terebrimya* and *Xylophomya* were not observed in this study, both having a poor fossil record, and are likely synonymous with *Xylophagella* (Stephenson 1952, Kelly 1988a, Insole et al. 1998, Kirkland 1996); however, they are assumed to have produced *T. longissimus* (e.g., Donovan and Isted 2014). Evidence for the construction, or lack thereof, of accessory plates is occasionally visible on the anterior surface of the boring in *T. clavatus,* and on the ventral and dorsal surfaces in the case of *Teredina* (Fig. 22). Horizontal exposures of borings belonging to *Teredina jeffersoni* and *Teredina neomexicana* posterior to the valves show the metaplax as a convex ridge on the dorsal surface of the siphonoplax, and hypoplax as a concave gutter. Specimens of *Teredina neomexicana* from the Carlile Shale (FHSM IP-1520, 1800-1802) also show that this species had apophyses and a mesoplax that were not described by Whitfield (1902). Vermiform *Teredolites* bearing similar concamerations to *Teredina neomexicana* from the Upper Cretaceous Castlegate Ss and Neslen Fm are likely to belong to this genus, although valve material has yet to be studied to confirm this interpretation.

Teredolites clavatus bearing surficial morphology (bioglyphs) may, in some cases, infer the tracemaker was still in an active boring stage at the time of burial where the anterior slope was not yet covered by the callum, preserving some insight into shell morphology. Surficial morphologies preserving morphological information may contain: (1) the angle of inflection between the anterior slope and disk (Bromley et al. 1984, *text-fig.* 6D); (2) the presence of shieldlike siphonoplax where it inserts over the posterior slope, as in *Teredina personata;* and (3) the presence of a pronounced, recurved anterior slope that may produce a circular, concave pit in the boring terminus, as in borings associated with *Xylophagella*. Inferences must be drawn carefully, as the Pholadinae do not produce a callum, and *Xylophagella* does not produce accessory plates. Associated borings for *Xylophagella* may become transitional between *T. clavatus* and *T. longissimus*, particularly in overcrowded media (Fig. 7F).

Within the Teredinidae, some variation exists in the posterior of the boring, which pertain to both pallet and siphonal morphologies. The most readily occurring variation are the siphon impressions at the boring apertures, which can be of some use in identification at the generic level. Species with long, separated, and protractile siphons (e.g., *Lyrodus*, *Teredo*, and *Teredothyra)* may produce a thickened, partial to fully divided median at the most posterior end of the boring (Turner 1966). When these siphonal divisions occur, the larger and smaller apertures belong to the excurrent and incurrent siphon, respectively. Surficial morphology at, or the weakly preserved impression of, the pedal gape could theoretically provide some insight into taxonomic affinity. In most teredinids, the angle of inflection between the anterior slope and disc is typically > 90°; occurrences of *Nototeredo knoxi* have been shown to have an angle at 90° (Kumar et al. 2011). Teredinids with flattened pallets (e.g., *Teredora, Nototeredo, Teredothyra*) are known to produce concamerations (i.e., ribs) (Cvancara 1970) against which the pallets rest (Turner 1966), or as an equilibrichnia response to media degradation (Savrda et al. 2005). Species with unsegmented pallets may produce a thickened calcite lining near the boring aperture to compensate for slower pallet growth compared to the rest of the body (Turner 1966).

Pallets are frequently absent in the rock record not only due to their extreme fragility, but also due to taphonomic bias relating to the ‘calcite vs. aragonite seas’ paradigm where aragonitic pallets would be highly unstable in calcitic seas of the late Mesozoic (Robin et al. 2018). When preserved, pallets are typically permineralized and rarely as mold casts (Cvancara 1970).

Unsegmented pallets from the Castlegate Sandstone (Fig. 23) in Horse Canyon, UT, are preserved as casts in two borings in sample CB-HC-017, collected from a woody lag along the base of a tidally influenced channel fill. Shell material was not preserved in this sample, although the casts bear resemblance to pallets belonging to *Teredo* or *Lyrodus.* Age-equivalent (late Campanian), unsegmented pallets were recently described by Serrano-Brañas et al. (2019) from the Cerro del Pueblo Fm in Coahuila, Mexico, similarly preserved by sediment infill of their respective borings. The presence of Mesozoic-age, unsegmented pallets implies that the adaptation to larval brooding is also extended temporally from the Eocene (Deshayes 1860) to the Late Cretaceous (Campanian). The presence of these pallets in the Campanian supports node calibrations of Distel et al. (2011), and is within the confidence interval for the divergence time estimates of *Teredo* and *Lyrodus* from *Bankia* of Lee et al. (2019).

The identification of tracemakers to family level or higher, when possible, is of importance to calibrate for the delineation of lateral ecotone boundaries, and to determine trends in boring metrics with respect to stacking patterns. Undescribed valve material (YPM IP 393493) possibly belonging to *Teredora* or *Teredothyra* from the Upper Cretaceous Carlile Shale (Turonian) are attributed to *T. longissimus,* bearing calcite linings with exaggerated annulations (Fig. 24)Samples in the KU IBGS, KU MIP, SMNH, and YPM IP collections were collected from the Sego Sandstone Member of the Mancos Shale and from the Fairport Chalk and Turner Sandy mbrs of the Carlile Shale. They have a known paleogeographic range in deposits from Black Mesa, Arizona, to Butte Co., South Dakota during the Turonian, and are found to occur in deposits in Emory Co., UT, by the Campanian. Similar boring linings have been described from the Mancos Shale (Kirkland 1996), the Fort Hays Limestone Mbr of the Niobrara Chalk (Frey 1972), and Pierre Shale (c.f. *Teredo globosa* Meek; Meek and Hayden 1876. Annulated borings described by Kirkland (1996) are found in the same marker bed as *Terebrimya sp.* (Black Mesa Marker Bed 10), however vales on YPMIP 393493 differ from *Terebrimya* in having a high posterior slope and lining annulae of *Terebrimya* are discrete and closely packed. Annulations attributed to this species of teredinid are found throughout the entire length of the calcite lining, whereas those of *Teredo selliformis* and material described from the Paleocene to recent (e.g., *Nototeredo globosa*, Cvancara 1970) only exhibit such structures in the aperture region where the siphons and pallets are located.

Although the use of calcareous linings or siphon impressions are not traditionally used for zootaxonomic identification, they do bear significance for identifying species that produce *Teredolites* (Savrda and Smith 1996). For example, Turner (1966) alluded to the use of calcareous linings to identify species as well as evolutionary trends when body-fossil material is present. Although annulations in calcite linings are most likely attributed to behavior (C.E. Savrda personal communication 2020), exaggerated concamerations are produced by species with flattened pallets, such as *Nototeredo*, *Teredora*, or *Teredothyra*, which occur in euhaline (fully marine salinity) environments. Siphons of *Teredothyra* are long and separated, whereas those of *Nototeredo* are only partially separated, whereas the siphons of *Teredora* are united except at the tip (Turner 1966). Thus, *Teredolites* that contain exaggerated annulations from this study are interpreted to belong to *Teredothyra* and developed in euhaline depositional environments, as do the borings of modern species within the genus. Future discoveries of additional material with well-documented lithologic descriptions will further help interpret the physiological requirements of this organism. Future studies on fossil material and surficial morphological character states of *Teredolites* will help delineate regional ecotone boundaries (e.g., salinity boundaries).

Synthesis of features herein suggests high species richness during deposition of the Mesaverde Group, with contributions from all three subfamilies of tracemakers. Body fossils and boring morphometrics confirm the presence of: *Opertochasma sp.*, *Teredina sp.*, *Xylophagella sp.*, and an undescribed species of *Teredo* or *Lyrodus* in the Desert Mbr. and Castlegate Ss. Additional borings with surficial morpholgy recording separated siphons at boring apertures provide additional evidence of tereninid tracemakers (i.e., *Lyrodus*, *Teredo*, or *Teredothyra*) in the Desert Mbr and Castlegate Ss at Nefertiti and Horse Canyon, respectively. High volume borings within the MFS in the Castlegate Ss suggest the presence of bankiinid tracemakers. Additional valve material in the Neslen Fm confirms the existence of tracemakers *Teredina sp.* and *Opertochasma sp.* Boring morphometrics and identifiable features based on boring morphologies suggest additional contributions by teredinids and *Turnus sp.* Representation of multiple genera within the Mesaverde Group is consistent with species richness seen in modern paralic poikilohaline to tropical and subtropical euhaline marine environments.

Ichnospecies, boring density, and lithofacies occurrence.—*Teredolites* found within woody lags or in scattered xylic media along channel bases may not be entirely allochthonous and should be considered at least parautochthonous based on the occurrence of larval-size borings (i.e., ichnogenetic stages) and the distribution of boring sizes (Fig. 21) and their densities. Designation of allochthonous media does not necessarily facilitate designation of *Teredolites* as similarly sourced, assuming *a priori* that media rapidly deteriorates and is likely to be settled, given its presence is within a marine-influenced environment. Xylic media in modern systems lacking mangrove communities is inherently allochthonous, but may include autochthonous *Teredolites* as suggested by Tsunoda (1979). Boring densities and the distribution of *Teredolites*' size classes within a sample or a surface reflect suitability of the ambient environment for reproduction to have occurred and survival of larvae until settlement. The clustering of allochthonous xylic media via ravinement or sediment starvation would have produced viable colonization surfaces for larval settlement (autochthony) prior to burial. Hence, parautochthonous to autochthonous colonization of allocthonous material is inherently interrelated.

Autochthonous occurrences of *T. longissimus* in the rock record on surfaces bearing woody lags (i.e., composite log grounds) and laterally continuous log grounds may be interpreted based on boring size and density trends. For example, autochthonous *T. longissimus* may exhibit: (1) low densities of large boring sizes (Fig. 9C); (2) greater densities of smaller boring sizes with W:L ratios >1:8 that reflect normal growth in reasonably uncrowded media; (3) stenomorphic borings (low W:L ratio) that reflect the effect of stepwise settlement based on two or more groups of smaller boring size classes; and/or (4) little to no settlement by groups 0.5–2 mm diameter with a low W:L ratio in heavily bored media (Fig. 9B, i.e. ichnogenetic stages). *Teredolites clavatus* occurring in such surfaces alongside *T. longissimus* are typically isolated or in small clusters, and diminutive in size (< 1 cm diameter).

Boring density may play a larger role in controlling boring metrics than our assumption of volume vis-á-vis reproduction style, based on the case of extant *Bankia gouldi* in Chesapeake Bay (Scheltema and Truitt 1954). Trends seen in population densities of *B. gouldi* between subenvironments in Chesapeake Bay are similar to findings of Lopes and Narchi (1993). The size distribution and population densities of *B. gouldi* in the Chesapeake Bay vary considerably between sites with respect to salinity. Occurrences of *B. gouldi* in water measuring 19 ppt at Broad Bay, Virginia Beach, VA, occur in high densities (90–150 borings per sample) with low maximum and mean diameters (stenomorphic) and exhibit multiple boring size classes via repetitive recruitment in polyhaline salinities. A maximum boring length of 4.5 cm suggests a boring period of 3–9 months (Scheltema and Truitt 1954). Borings belonging to the same species in mesohaline waters (~9 ppt) from intertidal muddy margins of the Lafayette River, VA (Fig. 9C–E), occur in low density (23–50 borings per sample) but only exhibit a single settlement event per sample, having much larger maximum and mean diameters. Maximum boring lengths of 24.6 cm suggest a boring period of 4–12 months for this species (Scheltema and Truitt 1954). While the lethal lower limit has yet to be established for larval of *B. gouldi*, ~9 ppt is likely the lower limit for this species (Fig. 3), which is only applicable to adults, acting as a control against settlement in lower salinities as illustrated in *Lyrodus* (Roch, 1940). Such examples may be more likely in temperate climates, where less competitive pressure occurs between species.

Larval settlement is most dense in woody lags if assuming ambient salinities are meso- to polyhaline, where larvipary is more likely to have occurred (Nair and Saraswathy, 1971). Dense occurrences of ichnogenetic stages alongside morphologies *sensu* Kelly and Bromley (1984) are considered autochthonous and are most easily recognized in laterally continuous surfaces bearing mono-ichnospecific populations of *Teredolites,* such as the Lower Chesterfield coal zone and overlying channels in the Neslen Formation at East Canyon, UT. Such surfaces suggest sympatric competition had likely reached equilibria with both local environmental factors and degree of media fragmentation (e.g., Hinojosa et al. 2010).

The absence of ichnogenetic stages in composite log grounds can be explained by the combined effects of taphonomic bias against small boring size, media availability, and the ability for larvae to relocate when faced with competitive pressure to settle on adjacent media (e.g., Toth et al. 2015). Miniscule borings were suggested by Savrda et al. (2005) to be unprogressive, where the respective tracemaker perished due to competition in heavily crowded media. Their diminutive size, however, approaches those of modern postpediveliger to metamorphosed juvenile pholadoideans (200–500 microns; i.e., Culliney 1975; Mann and Gallagher 1984; Calloway and Turner 1988). *Teredolites* with ichnogenetic morphotypes in this study (0.05–2 mm diameter borings) were typically found in well-preserved to relict-log grounds bearing only one, and occasionally two, larger size classes (e.g., 2–4 mm or greater in diameter) with ample space available on the woodground. This records the ichnogenetic stages (see Ichnogeny, Belaústegui et al. 2017, 2020) from the postmetamorphosis borings of pediveligers through the juvenile stage (Example 2, Belaústegui et al. 2017; Stage A, Belaústegui et al. 2020) with tracemakers perishing due to burial rather than from competition.

Allochthonous occurrences of *Teredolites* can be interpreted from highly diverse populations of *Teredolites* that include multiple ichnospecies, boring size ranges and densities, and their comparison to occurrence metrics from laterally or vertically adjacent facies associations, or isolated occurrences of *Teredolites* (i.e., reworked *Teredolites*). Xylic media with allochthonous *Teredolites, a posteriori*, were often exposed to a variety of larval dispersal patterns, salinities, transport mechanisms, and states of fragmentation. The presence of mixed populations (i.e., ichnospecies, boring sizes, boring densities) allows for the interpretation of different settlement periods used by the wood-borer community, evidence for media transport, and identification of the dominant ichnospecies type based on occurrence frequencies (e.g., Hoagland and Turner, 1981). Examples of allochthonous *Teredolites* occur in condensed sections (TSE and MFS) or in successions interpreted as shoreface, tidal inlet, and/or delta front deposits where reworked and transported xylic media would be likely to accumulate. *Teredolites* occurring in EODs seaward of the fair-weather wave base are considered allochthonous where cyclonic eddies and other advective forces transport woody flotsam away from the upper shoreface (e.g., Huntley et al. 2015; D'Asaro et al. 2018), although this 'garbage-can' designation is only appropriate because lateral and vertical distribution of modern open marine species are understudied in open marine surfuce waters. Designating occurrences in open marine EOD seaward of the shelf break as allochthonous should be done with caution, as evidence for specialized open marine guilds suggests novel adaptations in modern species for media preference in surface waters and reproduction strategies in deep-water EOD (i.e., Edmondson 1959, 1962; McKoy 1980; and Voight 2015).

Facies Association Trends and EOD Variations on *Teredolites* Morphometrics

Differences in size, density, and SDI zonation patterns in paleontological data from ancient deposits and facies associations interpreted to represent different parts of estuarine environments roughly follow trends of multivariate analyses of modern estuarine communities with respect to SDI, salinity, and community structures (Fig. 20) (e.g., Rayner 1979; Bulger et al. 1990, 1993; Hauck et al. 2009; Taupp and Wetzel 2014). Fossilized xylic media containing *Teredolites* is most dense along TSE-MFS that truncate conterminous facies associations, making the location of continuous occurrences of fossilized *Teredolites* relatively predictable at the outcrop scale. This predictability of laterally continuous *Teredolites* can help to correlate TSE-MFS across discontinuous outcrop belts based on the character of these surfaces. The distribution of *T. longissimus* tracemakers in modern systems implies that the signature of oviparous species in the rock record should be recorded by an increase in boring volume (and thus length and diameter) from a distal to proximal position within marine to transitional continental environments associated with increasing fluvial influence until dominated by freshwater. Significant effects of EOD (facies association) on mean and maximum boring diameters within the ichnospecies *T. longissimus* fossil dataset suggests similar patterns of environmental partitioning with respect to niche diversification in Mesozoic strata.

Fossil *Teredolites* are found to increase in boring size (length, diameter) in corresponding facies associations that represent proximal environments (i.e. tidally influenced fluvial channels) followed by a sharp decrease in upper estuarine facies associations, similarly to trends seen in modern systems (i.e., Rio Comprido, Brazil; Strait of Maracaibo, Venezuela) where larviparous and oviparous species interact (Fig. 10, 12). High densities of *T. longissimus* occurring in proximal EOD (Fig. 16; tidally influenced fluvial facies associations) coincide with the largest maximum boring diameters recorded with only modest mean diameters (Fig. 10D). Larger boring densities of with greater volumes are interpreted to have occurred in oligohaline to mesohaline conditions due to the generalized specialization of oviparous tracemakers (i.e. *Nausitora dunlopei*) to exploit this range of salinities.This results in high postsettlement mortality rates in the intertidal zone, which minimizes competition for space. Facies associations that represent deposits of lower to upper estuarine environments display fluctuations in the relative increase and decrease in boring densities and diameters, with an increase in central to upper estuarine environments and a decrease in central to lower estuarine environments. Mean boring diameters in central and upper estuarine environments increase in size with respect to moderate maximum diameters (e.g., 30–40 mm) and also exhibit a low mean boring density (e.g., *T. clavatus* 25–40 borings/sample; *T. longissimus* 10–20 borings/sample). Thus, the tracemakers of *T. longissimus* experienced little competition in these environments with respect to other wood borers, as mean boring diameter is in general negatively affected by boring density (Fig. 15). Lower to central estuarine environments exhibit decreasing boring diameters and densities with increasing abundances of marine indicators and increasing diversity and abundances of marine traces (i.e., more seaward). The greatest occurrences of borings coincide with large maximum boring diameters, with a basinward increase in mean boring diameter. These relationships illustrate that settlement of tracemakers from the lower estuary was heavily affected by tidal effects as they exhibit preferences for higher and more stable salinities (i.e., stenohaline). Increased ichnodiversity and abundances in facies associations representative of shoreface and open marine environments reflects abundant settlement and growth under normal marine salinities.

Trends combined from analyses within univariate space on the rock record data—primarily from the CWIS—suggest the presence of at least four ecotones or diversity gradients (conservatively), based on the abundance of ichnotaxa, boring size, and boring density of *Teredolites* across laterally occurring facies associations (Fig. 20). Zone 1, composed of facies associations 16–20 (bayhead deltas, distal tidal fluvial, tidally influenced fluvial, proximal tidal fluvial environments), includes low-density occurrences of borings with a low SDI in *T. longissimus*, a high SDI in *T. clavatus* decreasing distally, and high mean and maximum boring diameter increasing distally within this zone. Zone 2, composed of facies associations 12, 21, and 13–15 (estuary, estuarine tidal sand bar, tidally influence estuarine valley fill, and upper estuary environments), has higher SDI and increased boring densities compared to zone 1, but exhibits a decrease in maximum and mean boring diameters. Zone 3, composed of facies associations 5–11 (upper shoreface, backshore, tidally modified delta, mouth bar, tidal inlet channel, tidal channel, and sandy tidal flat environments), contains slightly lower SDI, boring densities, and maximum and mean boring diameters compared to zones 1 and 2, decreasing distally within the zone itself. Zone 4, composed of facies associations 1–4 (shelf, offshore transition, lower shoreface, and distal lower shoreface environments), contains similar boring densities as Zone 1, but with lower maximum and mean boring diameters and SDI compared to zones 2 and 3. While the SDI zonation of *Teredolites* follows similar trends compared to those determined by Hauck et al. (2009) for a modern barrier island–embayment system, the SDI of EOD interpreted to be lower estuarine is much lower than expected in our study due to low maximum boring diameters of *Teredolites* rather than ichnodiversity. Gaussian curves fit onto the facies association occurrence data do not perfectly approach normality, but do show a strong central tendency. Right-skewed densities in Zone 2 are not unexpected when compared to similar modern environments where species abundances do occasionally exhibit higher population densities near one end of their biogeographic range (e.g., Brown, 1984; Greenwood, 2007).

Boring diameter and density variations in *T. longissimus* between facies associations (Fig. 10) suggest tracemaker preferences and/or salinity requirements varied between EOD. The overall increase in boring diameters in increasingly proximal facies associations (landward) across ungrouped data, along with mean and maximum boring diameters, densities, and SDI for *T. longissimus* indicate environmental preferences likely coincided with differing reproductive modes. Differences in reproductive modes by the tracemakers of *T. longissimus* (i.e., teredinids) can be inferred from morphometrics, except within stenomorphic borings, as they are not as readily susceptible to enforced diminution from physicochemical stressors as are the pholadids. High densities of borings in Zone 1 occurring with very high maximum diameters and relatively high mean boring diameters suggests that physicochemical controls (e.g., salinity stress) effected larval settlement patterns in these depositional environments, with decreasing settlement densities in most landward environments. This indicates that stenomorphism (i.e., small boring diameters within densely bored media) is unlikely in proximal facies associations due to increased freshwater input diluting salinitie beyond the lower lethal limit for larval survival.

Teredolites from facies associations interpreted as upper estuarine to tidally modified fluvial successions (Zone 1)—tidal-fluvial channels (Neslen Fm, Qsar al Sagha Fm), tidally influenced fluvial deposits (Castlegate Ss), and bayhead delta deposits (Dakota Ss) in more landward EOD—exhibit a sharp increase in boring densities, higher SDI, and a decrease in maximum and mean boring diameters. This pattern is consistent with that of the patterns exhibited by *Bankia gouldi* in alpha-mesohaline salinities of Chesapeake Bay, VA (see Fig. 3), with increasing freshwater and decreasing seawater influence. Accessory traces in this zone (Table 5) primarily include bivalve resting traces with minor contributions by gastropods, decapods, and vertebrates. *Teredolites* metrics and the low diversity of accessory traces suggests these successions were deposited under oligohaline to alpha-mesohaline paleosalinities (~0.5–10 ppt) when compared to the loadings of Bulger et al. (1993; Fig. 2) and reflect the relative effect of the alpha-/beta-mesohaline boundary as endpoint salinities for many teredinid species (Fig. 3). *Teredolites longissimus* from these environments are interpreted to have been primarily produced by oviparous tracemakers (i.e. *Bankia*), with minor contributions from larviparous tracemakers.

Teredolites from facies associations interpreted as estuarine deposits (Zone 2)—estuarine (uppermost lower Castlegate Ss. and Chatton Fm.), and estuarine tidal sand bars (Sego Ss.)—exhibit a sharp increase in boring densities, higher SDI, and a decrease in maximum and mean boring diameters compared to Zone 1. Increasing diversity in marine traces attributed to annelids, anthozoans, bivalves, decapods, polychaetes, and xiphosurids occur in this zone, resulting in increased SDI values despite moderately low, maximum boring diameters. and (Table 5). Rapid changes in community structure have been shown to be common in modern benthic communities (Greenwood 2007), and can greatly affect SDI values between conterminous subenvironments. This suggests a boundary defined by the lower salinity limits for euryhaline tracemakers at the alpha-mesohaline and beta-mesohaline boundary (Fig. 3). Increasing *Teredolites* boring densities, decreasing diameters, and increasingly marine accessory traces suggest an increase from oligo- to alpha-mesohaline salinities landward to beta-mesohaline to lower polyhaline salinities (~10–19 ppt) seaward, with a greater contribution by larviparous tracemakers, suggested by the presence of the Teredinine (*Teredo* + *Lyrodus* clade) in the lower Castlegate Ss (Fig. 23) with minor contributions by patchy occurrences of *T. clavatus* Type I and Type II (cf. *Teredina* and *Xylophagella*, respectively).

Teredolites from facies associations interpreted as lower estuarine to proximal shoreface deposits (Zone 3)—tidal flats (Sego Ss and Neslen Fm), tidal channels (Castlegate Ss), tidal inlet channels (Desert Mbr, Blackhawk Fm), mouth bars (Panther Tongue), backshore (Desert Mbr., Blackhawk Fm.), and tidally modified deltas (Sego Ss, UT; Castlegate Ss, CO only)—display bimodal tendencies with both left-skewed (distal) and right-skewed (proximal) peaks with respect to boring diameter and length. *Teredolites longissimus* diameter and length are typically stenomorphic with high boring densities in EOD that reflect estuarine conditions. A decrease in boring densities with increasingly marine EOD coincide with decreasing SDI, boring diameter, and length. Modest increases in boring diameter in tidally modified deltaic EOD likely reflect deposition and retention of xylic media near to shore. Metrics of *T. clavatus* follow a similar pattern, although they exhibit a sharp increase of boring diameters in backshore EOD, coinciding with relatively low SDI and boring densities. Bimodality likely reflects the landward boundary and the distal edge of a euhaline community between zones 3 and 4. Accessory ichnotaxa become increasingly marine with contributions by elasmobranchs and bioturbators represented by trace fossils in the Skolithos Ichnofacies in this interval (Table 5), due to increasing salinity. We interpret this zone to have been deposited in prevailing beta-mesohaline to upper polyhaline salinities (~15–30 ppt). Autochthonous *Teredolites* in this interval would likely have been created by a mixture of landward communities and endogenous recruits from adjacent marineward regions (e.g., Zhang et al. 2015).

Teredolites from facies associations interpreted as lower shoreface to offshore and distal deposits (Zone 4)—lower shoreface, distal lower shoreface (distal Desert Mbr., Blackhawk Fm., Castlegate Ss., UT, Budden Canyon Fm.), offshore transition (Kennilworth Mbr., Blackhawk Fm.), and open marine environments (Anchor Mine Tongue, Birket Qarun Fm., Carlile Shale, Greenhorn Limestone, Niobrara Limestone, and Sego Ss)—display decreasing metrics along a proximal (landward) to distal (deep water) transect relative to the paleoshoreline (boring size and density, SDI). Additional ichnotaxa indicative of the Skolithos and Cruziana ichnofacies reflect fully marine and storm-dominated conditions (Table 5). Paleosalinites for these environments were euhaline (30 + ppt).

Low sample sizes in zone 4 EOD in highstand systems tracts and transgressive-regressive cycles is due to the greater likelihood for xylic media to be retained in nearshore environments (Hinojosa et al. 2010). While xylic media can be transported over long distances, the likelihood of discovery is low in offshore EOD due to the complex relationship between buoyancy, current transport, and the clustering of floatsam along density fronts and impacted by gyres (D’Asaro et al. 2018).

Teredolites *and the Desert Sequence Boundary.*—The Desert Sequence Boundary between Nefertiti (most proximal location; landward), Tusher Canyon, and Horse Canyon (most distal location; seaward) records a shift from a highstand to lowstand systems tract demarcated by a laterally continuous surface expressing the Glossifungites Ichnofacies (Van Wagoner et al. 1991, 1998). Log grounds containing *Teredolites* occurring at this surface in the D4 and D5 parasequences show a basinward increase in mean diameter and boring density (Fig. 25) to the southeast, relative to paleoflow and the interpreted location of the paleoshoreline (Pattison 2019). Variations in boring density along this gradient also change with respect to ichnospecies: *T. clavatus* exhibits highest densities in Tusher Canyon, whereas *T. longissimus* are commonly stenomorphic while retaining the same (background-level) densities in all three localities. Additionally, log grounds containing *Asthenopodichnium* along this same surface decrease in abundance basinward, being most abundant at Nefertiti, absent at Tusher Canyon, and rare at Horse Canyon. The basinward changes in the abundance of *Asthenopodichium* illustrate that woody media was likely rafted downstream to environments with higher, more desirable salinities that facilitated increased colonization of *T. clavatus* tracemakers, excluded colonization of *Asthenopodichnium* tracemakers, and subsequently overprinted *Asthenopodichnium* during settlement and growth of *T. clavatus* tracemakers. Similar observations on *Teredolites* ichnospecies composition, boring metrics, and boring densities have been observed along the MFS directly overlying the Sunnyside Member of the Blackhawk Formation basal sequence boundary (e.g., King et al. 2018).

The trends of boring metrics and densities within each locality containing the Desert Sequence Boundary suggest that media found along these transgressive surfaces were exposed to marine waters for short-time periods prior to burial, given that pholadids are adapted to colonize more freshly available media. Increased relative boring densities of *T. clavatus* at Tusher Canyon suggest high exploitation (with the presence of ichnogenetic stages) and limited dispersal distances between accumulated media along this boundary. The straight-line distance between these sites (10–13 km) is sufficient to limit larval dispersal in estuarine environments (e.g., ~10–30 km, Zhang et al. 2015). *Teredolites clavatus* along this surface exhibited a coupling of short dispersal and high exploitation—termed a Phalanx Effect (Holyoak et al. 2005)—that allowed them to suppress competition with *T. longissimus* tracemakers. Low-density occurrences of *T. longissimus* as stenomorphs suggests high competitive pressure during settlement, given that the presence and intensity of other wood borers is an important factor in the distribution of *Teredolites* (Table 1; Nair and Saraswathy 1971). In this context, the larvae of *T. longissimus* tracemakers would have had limited media selection if high densities of borings occupied by *T. clavatus* prevented teredinid pediveligers from having direct access to media.

Similar effects in community competition have been recognized in shallow-marine and coastal marine ecosystems that experience high-magnitude disturbances (e.g., earthquakes, major freshwater discharge events; Resh et al. 1988), which result in high species richness immediately following the disturbance (i.e., Treneman et al. 2018), followed by low species richness (Pemberton and MacEachern 1997) related to the generalized life history strategies of primary colonizers, becoming outcompeted by more specialized species as communities reach dynamic equillibrium. This pattern suggests that ancient *Teredolites* tracemaker communities provide additional insight into local and regional processes when viewed as a proxy for patch dynamics within a metacommunity framework (e.g., MacIntosh et al. 2014), and that *Teredolites* may also serve as a proxy for disturbance theory (e.g., Hutchison 1953; Wilson 1994).

Teredolites *and the lower Castlegate Ss.*—In the lower Castlegate Ss section at Tusher Canyon, *Teredolites* occurs within woody lags along and just above the Castlegate sequence boundary that display variation in boring size and densities (Fig. 21) similar to the expression along the Desert sequence boundary, some of which overprint *Asthenopodichnium*-bored media.

Below this surface, isolated, high-sinuosity, tidally influenced, heterolithic channels of the Desert Mbr. contain *Teredolites*-overprinted *Asthenopodichnium*-bored media. Above the sequence boundary, multistory braided fluvial channels contain *Asthenopodichnium*-bored media which locally contain *Teredolites* borings. Woody media above the Castlegate sequence boundary are preserved as relict log-grounds with a NNE to SSW orientation of large woody media (Hoffmeister 2011), parallel to the paleoshoreline. *Teredolites* within Castlegate lags display morphologies of both ichnospecies, with a decrease in the occurrence of stenomorphic morphologies. Localized lags likely represent small-scale floodbacks foreshadowing the transition from a lowstand to transgressive systems tract during the later stages of valley fill, whereas the overlying sheet sandstones record a landward shift in facies and lowering of base level (Pattison 2019). Accumulation of media containing *Teredolites* within the uppermost Desert heterolithic packages and in the Castlegate Ss indicate that an influx of waters from the marine system occurred within the heterolithic channel fills, whereas braided channel fills above this interval containing isolated woody media bored only by *Asthenopodichnium* reflecting either purely freshwater conditions, rapid burial, or deposition above the mean high tide line. Facies changes in the lower Castlegate SS suggest decreasing slope gradients and discharge due to the initial relative rise in sea level before the Buck Tongue transgression, which is expressed by a transgressive surface on the top lower Castlegate Ss (Pattison 2019, 2020) that also contains exclusively *Teredolites*-bored wood.

Changes in relative sea level can be quantified by the presence of *Teredolites* and the preservational state of the media in which they are found (Savrda 1991). Rapid burial likely occurred along woody lags in heterolithic facies, suggested by the prevalence of relict log-grounds—buried prior to significant biochemical degradation (Savrda et al. 1993)—and the relatively low densities of tracemakers in a given sample. Inundation of the coastal EOD during transgressive episodes provided an influx of woody media into marine systems and an increase in niche space for wood-borers to exploit (Savrda 1991). If the media along these lags had been exposed to the water column for longer periods of time, then they would have inherently contained higher boring densities and increasingly stenomorphic morphologies. *Teredolites* in the uppermost lower Castlegate Ss at Tusher Canyon in tidally influenced heterolithics and estuarine deposits underlying the Buck Tongue (Yoshida, 2000, *fig. 10A*) exhibit no statistical significance in occurrence metrics with respect to boring diameter and density along the Desert–Castlegate interval. Significance arises at the ichnospecies level along sequence boundaries in the Desert–Castlegate–Buck Tongue interval, where *T. clavatus* occurs more frequently along major sequence stratigraphic surfaces.

Several issues arise with the use of a generalized proximal-to-distal characterization of facies association data recorded in the lower Castlegate Ss at Tusher and Horse canyons via heterolithic facies associations containing woody lags and bounded by sheet sandstones, indicaing marine influence and tidal mixing. The first is the effects of poikilohalinity (e.g., tidal influence) and estuarine mixing that create overprinted ichnocoenoses due to seasonal fluctuations in freshwater input (e.g., Flaig et al. 2016). The other is increased salinities related to autogenic processes, such as delta-lobe switching, and allogenic processes, such as tectonism or eustacy. Delta-lobe switching would increase the salinity and produce greater stenomorphism of *Teredolites* in the area that once received freshwater and sediment, producing an apparent rise in sea level. Eustatic sea-level rise or fall would shift communities of *Teredolites* and associated ichnocoenoses landward or seaward, respectively.

Teredolites *and coal seams.*—Laterally continuous occurrences of sand-filled *Teredolites* present along the upper surface of coal seams exhibit borings with very large diameters and low relative densities compared to facies associations that do not overlie xylic peatgrounds interpreted to represent shallow marine environments. Borings along these surfaces record transgression of paleomires, under increased marine influence in the early stages of marine deposition that constitute the Teredolites Ichnofacies (see Bromley et al. 1984). These types of occurrences are significant because they record true MFS-TSE based on the characteristics of the coal and overlying marine deposits. *Asthenopodichnium*, *Piscichnus*, *Rosselia*, and *Thalassinoides* occurring in the beds directly overlying the coal indicate that they were deposited in a fully marine environment.

Freshwater occurrences of Teredolites.—Autochthonous occurrences reported in the literature of *Teredolites* within stratigraphic successions interpreted to have no marine influence are problematic. These require scrutiny due to the relationship of modern species to salinity tolerances—larvae, adults, and adults with respect to reproduction—and geographical distributions of species-poor genera. Studies on modern species that produce *Teredolites* ubiquitously demonstrate a connection with marine salinities in their distribution within a given system. For example, larvae that are transported to the most landward reaches of coastal river systems still require certain salinities for survivorship to settlement (Scheltema and Truitt 1954), display higher densities with increasing salinities, and display behavioral partitioning of resources to reduce competition with other species (Fig. 3; Lopes and Narchi 1993; Khlebovich and Aladin 2010). *Psiloteredo healdi* in these paralic environments preferentially inhabit dead xylic media as a response to limit competition in poikilohaline environments with other wood borers, and are known to inhabit EOD having salinities as high as 20 ppt (e.g., Rojas and

Severeyn 2000; Laval et al. 2003). This indicates that *P. healdi* is not a freshwater specialist (*contra* Shipway et al. 2019b; see Rojas and Severeyn, 2000), but rather it's distribution within specific salinities is enforced via syntopic competition. Likewise, genera inhabiting low salinity systems (< 5 ppt, e.g., *Lithoredo* and *Nausitora*) with restricted connections to marine waters are limited to species-poor genera (with less than seven species); however, *Nausitora* requires increased salinities for reproduction and survival of larvae (e.g., Khlebovich and Aladin, 2010; Voight, 2015). Embryonic development of the euryhaline *Nausitora hedleyi* is optimal when salinity range between 11–14.5 ppt, with abnormal segementation or mortality occurring above or below this range (Nair and Saraswathy 1971). Specialization in *Lithoredo* to inhabit hardgrounds could similarly be a mechanism to reduce competition with *Nausitora* in limnetic to alpha-oligohaline salinities, as seen in *Psiloteredo*. Reproduction requirements of *Lithoredo* have yet to be evaluated, however, reproduction likely occurs in the dry season when salinities increase, as do for members of the Neritidae, which are observed in the same EOD as *Lithoredo* (Shipway et al. 2019b). More importantly, such specialized species are prone to die with mean sea-level rise, being unable to survive fully marine salinities (Voight, 2015), which would cause extinction of this species.

The description of Eocene freshwater occurrences of *Teredolites* by Plint and Pickerill (1985) from the middle Eocene Bracklesham Fm was questioned by MacEachern et al. (2007), as the deposits were in close proximity to a paleoshoreline that exhibited major transgressive-regressive cycles. We agree with the position taken by MacEachern et al. (2007): log-ground occurrences of Plint and Pickerill (1985) were certainly allochthonous, carried landward and deposited along a flooding surface. Lignite occurrences, which are autochthonous, record transgression, exhumation of peatgrounds and exposure to marine salinities, and boring in a marine environment. The overlying fluvial channel deposits may have scoured and reworked any marine deposits that may have overlain the coal. The log-ground descriptions of *T. longissimus* and boring density within Plint and Pickerill (1985, *text-fig. 4*) are consistent with boring diameter and density metrics of modern *Bankia gouldi* borings produced in 19 ppt water in Broad Bay, VA, as well as fossil occurrences in tidally influenced fluvial channel deposits in the Desert Mbr, Blackhawk Fm, lower Castlegate Ss, and Neslen Fm (see Fig. 10; Appendix 1). Our interpretation of the borings in Plint and Pickerill (1985) as stenomorphic based on their size and density illustrate: (1) settlement occurred within a single season; (2) salinity was more than optimal for larval survival; (3) competition for space provided greater physiological stress than the ambient environment; and (4) the correlation between increased media transport, localized media retention, and transgression provided a viable mechanism to deposit borings landward of their original environment. The Eocene examples of *Teredolites* demonstrate that they do not make this trace fossil a proxy for freshwater (limnetic–oligohaline) conditions.

Media Preservation Character

Size-frequency relations (Figs. 11–13, 15) show that the interaction between ichnospecies composition and woodground type are correlated to mean boring diameters and boring density within media preservation state. Boring density is roughly additive across different log-ground types with increasing degradation, likely due to longer immersion periods and subsequent exposure to settlement by wood borers. Exposure to settlement is seen in the minimum and 1st quartile values in each media type (except reworked *Teredolites*), recording ichnogenetic stages within postpediveliger to diminutive borings and reproductive size ranges, respectively, when compared to modern species (Table 6). While ichnogenetic stages are not present in each sample, *Teredolites* settlement can occur and be recognized in all marine-influenced EOD, regardless of wood preservation, with the exception of reworked *Teredolites*. Preservation of ichnogenetic stages in reworked *Teredolites* is affected by taphonomic bias—removal during reworking or being too small to infill—like other surficial borings in xylic media (e.g., Gingras et al. 2004). Our data reflects similar significance between ichnospecies composition and woodground preservation type as shown by Nishimoto et al. (2015), with a decrease in percent composition of Type I *T. clavatus* and an increase in Type II *T. clavatus* and *T. longissimus* as the degradational state increased from well-preserved to poorly preserved log grounds.

Positive skewness in size-frequency distributions of diameter with respect to woodground preservation type reflects the influence of increasing larval recruitment provided with increased media immersion time in the marine environment. Multimodality of boring diameters in xylic peatgrounds—and well-preserved log grounds for *T. longissimus*—occurring with relatively lower densities when compared to more heavily degraded media (i.e., relict and ghost log grounds) suggest rapid burial after exhumation. Increasing exposure periodicity to multiple settlement events likely resulted in size diminution where competition for space acted as a control on mean boring diameter. Modal values in xylic peatgrounds suggest an average of two settlement events before burial on the basis of size classes: *T. clavatus*, 6.5 mm, 8.6–10 mm; *T. longissimus,* 3.4–3.6 mm, 5.0–5.7 mm. These peatgrounds were likely exposed to a marin-influenced water column for an average of 1–18 months prior to burial to have allowed these settlement events under the assumption that reproduction occurred seasonally (see Background section). Many modern *Teredolites* tracemakers in tropical and subtropical climates—where species richness is generally high—have multiple settlement events in a given season and partition reproduction seasonality to avoid high competitive pressure during settlement (e.g., Nair and Saraswathy 1971; Rayner 1979).

Boring densities display a multiplicative relationship between each woodground type, increasing ~2–4% between media preservation types (Table 6). Increased immersion time is apparent in more degraded media with size-frequencies being increasingly right skewed and unimodal in relict and ghost log grounds. Rapid increases in boring densities—and thus increased exposure settlement events—resulted in an increased frequency of stenomorphic forms in these media types, frequently masking the presence of larger borings in the data analysis. Unimodal values for these woodground preservation types suggest: (1) stenomorphic *T. longissimus* produce boring diameters averaging 1 mm, similar to sizes reached by modern stenomorphic forms (i.e., *Teredo navalis*, Clapp 1923 *text-plate IV*); (2) the larger interquartile range of *T. longissimus* reflects rapid growth in juvenile borers to outcompete other borers in the same media, facilitating a shorter juvenile period to reach reproductive sizes as quickly as possible (Voight 2015); and (3) cessation of boring activity in *T. clavatus* occurred after reaching a modal boring diameter of 4–5 mm. This is similar to sizes at which modern species of *Teredolites* tracemakers cease boring activity in overcrowded media (< 5 mm in shell length for *T. clavatus* tracemakers; shell height:length ratio of 1.4–2.7), and up to 50-mm boring diameter in soft media (shell height:length ratio of 1.7–2.3) (Turner 1954), such as in *Opertochasma sp.* observed in the middle part of the Neslen Fm in East Canyon (48.62 mm).

Bulk data analysis indicates that, while Savrda et al. (1993) does provide useful classification of woodground types, relict and ghost log grounds do not provide a reliable proxy for the original state of the wood. Rather the classification of woodground types is a qualitative measure of immersion period and taphonomy as independent factors. The division between relict and ghost log-ground assignment was frequently arbitrary in heavily weathered Mesaverde Group examples, especially in finer grained lithologies. We agree with the importance of both the degradational state and degree of bioerosion for a given sample, as both impact the composition of woodborers (Nishimoto et al. 2015) and the general morphology of borings. The morphology of borings is impacted by boring densities where competition for space is increased in densely bored logs, resulting in stenomorphic borings. Stenomorphic borings are especially present in facies associations that represent estuarine EOD, which are conducive to decreasing boring sizes for *T. longissimus* (Fig. 10C, D). The relative consistency of *T. clavatus* diameters and densities in estuarine EOD is more likely a function of settlement with respect to media quality rather than environmental factors, where Type I borings are more prevalent in well-preserved and relict log grounds. The greater abundance in Type I borings in these facies associations reflect diminution controlled by determinate growth rather than media overcrowding (e.g., Savazzi 2005).

Media Character and Sea-Level Dynamics.—The effects of tidal influence and development of surfaces producing condensed woody lags containing allochthonous media are more likely to occur on large scales within TST. Media along condensed sections, such as lags, provide theoretical ‘hot-zones’ for settlement as long as they are not immediately buried. Available media would be subject to settlement in a similar manner xylic peatgrounds exhumed during transgression and exposed to marine salinity. Wood-boring bivalves were free to exploit these retention zones via philopatric larval recruitment in brooding populations, or endogenous recruitment from bidirectional dispersal in increased salinities along transgressive surfaces (Savrda 1991).

Previous workers have suggested a correlation between the accumulation of log grounds and sea-level dynamics based on research in Cretaceous and Cenozoic marine EOD (e.g., Savrda and King, 1993; Savrda et al., 1993; Savrda et al., 2005). Within the context of our study area, log grounds are most abundant in TST underlying incised valley fills of the Desert Mbr., Blackhawk Fm., and along MFS within the Neslen Fm. These examples show that media availability for *Teredolites* (Fig. 26) is controlled by exhumation and concentration of media during ravinement, and increased input of media during transgressive inundation of the coastal plain. Differences between these two processes are illustrated by the abundance of woodground types within each formation (Fig. 26). The Neslen Fm has a much greater contribution of ghost log grounds and xylic peatgrounds with abundant, laterally extensive *Teredolites* caused by flooding by marine waters, recording the allogenic processes of sea-level rise (MFS). Woodgrounds like this differ from numerous instances of *Teredolites* in wood found in Neslen Fm channel lags. These result from autogenic processesses that include recurrent development of peat swamps, splaying, and the incision, migration, and abandonment of distal tidal-fluvial channels or tidally influenced channels located proximal to the paleoshoreline and connected to and influenced by marine waters. Woodgrounds in the Desert Mbr of the Blackhawk Fm are due mostly to inundation of the coastal plain with some ravinement. The increase in ghost log grounds in the Neslen Fm may have been controlled by the higher abundance of *T. longissimus*, whose tracemakers are more efficient at both boring and processing media (xylophagy).

Higher boring densities in environments prone to increased tidal-current velocities supports the application of disturbance theory to *Teredolites*: influx of xylic media into marine environments is inherently related to environmental disturbance. Adaptations to rapidly exploit freshly available media would have resulted in adaptations to produce sustainable source populations where tidal fluxuations are highest to maximize larval transport within a given system. Such adaptations would result in sink communities in more quiescent, slack-water settings, perhaps in lagoonal and central estuarine EOD.

Overprinted Asthenopodichnium*-bored media.—Asthenopodichnium* (Fig. 8), freshwater mayfly borings in xylic media (e.g., Uchman et al. 2007; Moran et al. 2010), was commonly observed in high densities where it constituted the only traces within a given medium. *Asthenopodichnium* overprinted by *Teredolites* occurred infrequently and with low sample densities in the Mesaverde Group. Modern examples of overprinted communities containing beetle and termite borings occurring in woody media from Lafayette River, VA, illustrate transport of terrestrial media bored by freshwater aquatic traces into marine systems, where they are more likely to be recorded in well-preserved and relict log grounds. The absence of *Teredolites* in modern examples of terrestrial media bored by freshwater aquatic tracemakers in well-preserved log grounds mirrors observations from the Mesaverde Group, suggesting media had not been exposed to settlement by pholadoideans after exposure to marine environments prior to burial.

Statistical significance arises between *Teredolites*' boring metrics and *Teredolites'* borings metrics overprinting *Asthenopodichnium* in relict and ghost log grounds. All samples containing both boring types were found along sequence boundaries, TSE-MFS, and in estuarine EOD. Samples containing both ichnogenera were also recovered from LST and TST sequences within the Castlegate Ss, Sego Ss, and Neslen Fm. Higher stream gradients in the LST result in greater amounts of bank erosion upstream and delivery of wood into rivers with subsequent downstream transport (e.g., Savrda et al. 1993; Hinojosa et al. 2010), increasing the likelihood of both *Asthenopodichnium* and *Teredolites* occurring in the same medium. The transport of allochthonous xylic media could occur over long distances in estuarine settings as flotsam in hypopycnal flow regimes. This interpretation is supported by the distribution of *Asthenopodichnium*-bored wood along the Desert Sequence Boundary.

Boring diameters of *T. longissimus* not overprinting *Asthenopodichnium* remain larger than those borings overprinting *Asthenopodichnium* (Fig. 28) in EOD interpreted to be more proximal (tidally modified fluvial, distal tidal-fluvial channels), but subsequently become larger in estuarine EOD. Larger borings in more proximal EOD show the typical pattern of proximal occurrences. A decrease in *Teredolites* boring diameters overprinting *Asthenopodichnium* may indicate: (1) *Asthenopodichnium*-bearing wood was actively transported into marine-influenced systems; (2) *Teredolites* tracemakers exhibited a shorter growth period, where media containing both ichnogenera is more prone to transport, with growth occurring shortly after being settled; and/or (3) that bioeroded media is more susceptible to hydraulic transport and burial. Dense bioerosion via *Asthenopodichnium* before transport down dip could decrease overprinting of *Teredolites* progenitors, where larvae potentially possessed the ability to select media, as in modern systems (Toth et al. 2015).

Teredolites and Ichnocoenosis Affiliations

An ichnocoenosis is an assemblage of ichnotaxa (proxy for ichnodiversity) produced by a community of tracemaking organisms used to interpret the physicochemical parameters of the surrounding environment at the time of deposition (e.g., Ekdale 1988; Hasiotis, 2004, 2008). Ichnocoenoses for this study included traces occurring along the same bedding planes directly associated with the *Teredolites*-bearing xylic media. Statistical significance arises between mean boring diameter and the effect of ichnodiversity nested within facies associations, reflecting similarities between the ranked diversity of a given benthic community, *Teredolites* boring densities, and the physicochemical properties of the ambient EOD (Fig. 10A). This relationship suggests that isolated occurrences of *Teredolites* may be more locally derived than suggested in the allochthonous-autochthonous Savrdian framework (e.g., Savrda et al. 1993). *Teredolites* tracemakers occurring in depauperate ichnocoenoses—for example, associated with higher depositional energy, poikilohalinity, or variably oxygenated conditions—would have grown to normal, or near normal diameters at normal to slowed growth rates (e.g., Nair and Saraswathy, 1971; Shchepetkina et al., 2018; Shipway et al., 2019). The lateral offset between *Teredolites* diameters and ichnodiversity (dimensionless) reflects: (1) fluctuating salinity gradients in intertidal to estuarine strata; (2) low ichnodiversity along mixing fronts and along event beds; and (3) the disparity between motile and media-restricted tracemakers.

Traces included in the Teredolites Ichnofacies are also impacted by the preservation of log grounds and include: *Asthenopodichnium* and *Apectoichnus lignummasticans* (e.g., Gingras et al. 2004; MacEachern et al. 2007; Melnyk et al., 2020). *Thalassinoides* is an uncommon constituent of the Teredolites Ichnofacies in xylic peatgrounds *per* Bromley et al. (1984). Overprinted xylic assemblages—wood initially bored by terrestrial, than freshwater borers, and later bored by marine borers—were rare in this study. Well-preserved log grounds, relict log grounds, ghost log grounds, and xylic peatgrounds all exhibited low ichnodiversity. Preservation of *Apectoichnus lignummasticans* was restricted to well-preserved log grounds in modern samples and in museum specimens (e.g., KUPBC KC-5-L) (Fig. 27). Neo- and palichnological occurrences of *A. lignummasticans* illustrate the preservation potential of taphonomic bias against diminutive surficial traces being less likely to be infilled or destroyed during hydraulic transport (e.g., Gingras et al. 2004).

Trace-fossil assemblages in the proximal part of Zone 1 (proximal tidal-fluvial channels) display distally increasing ichnodiversity and abundances of a mixed *Cylindrichnus-Siphonichnus* ichnocoenosis. Traces in this ichnocoenosis record deposit- and suspension-feeding strategies. Proximal (landward) tidally influenced fluvial channels in the Neslen Fm are composed of low densities of bivalve, crustacean, and vermiform traces including *Diplocrateron*, *Ophiomorpha*, *Rhizocorallium*, and *Siphonichnus*. Tidally influenced fluvial deposits from the lower Castlegate Ss have similarly low ichnodiversity with uncommon traces likely produced by: bivalves (*Siphonichnus*); crustaceans (*Thalassinoides*); and vermiform organisms (*Cylindrichnus*). Terrestrial traces record overprinting within log grounds (*Asthenopodichnium* overprinted by *Teredolites*) and subsequent subaerial exposure after deposition (dinosaur tracks and rhizoliths) in overlying planar- and convolute-bedded sandstones.

Traces in the *Cylindrichnus-Siphonichnus* ichnocoenosis represent a depauperate Skolithos Ichnofacies, occurring as uncommon accessory traces in strata containing *Teredolites. Teredolites* infrequently contain Type I *T. clavatus* and are dominated by heavily crowded to stenomorphic Type II *T. clavatus* and *T. longissimus* that rarely exhibit ichnogenetic stages. Infrequent occurrences of ichnogenetic stages suggests that tidally modified channels in the Neslen Fm and Castlegate Ss were heavily subjected to tidal input with minor to moderate fluvial influence, although the Neslen Fm shows higher amounts of tidal modification with tidal-bar forests bounded by double mud drapes containing tidal bundles. Tidally modified channelized deposits are suggested to have been within 2–5 km of the paleoshoreline during lower Castlegate Ss deposition (Pattison 2019). Facies associations from both formations commonly contain overprinted *Asthenopodichnium* by *Teredolites,* suggesting proximity to limnetic environments and seasonal variation in fluvial discharge that provide increases in salinity to also allow bioturbation by marine organisms (e.g., Gingras 1999; Flaig et al. 2016).

Trace-fossil assemblages in the distal part (marineward) of Zone 1 (distal tidal-fluvial channels) display increasing ichnodiversity and abundances in a *Rhizocorallium* ichnocoenosis. This ichnocoenosis record deposit- and suspension-feeding strategies, and locomotion behaviors. Distal tidally influenced fluvial channels in the Neslen Fm display traces produced by: anemones (*Bergaueria*); bivalves (*Lockeia* and *Siphonichnus*); crustaceans (*Rhizocorallium* and *Rusophycus*), gastropods (*Aulichnites*), vermiform animals (*Cylindrichnus*, *Rhizocorallium, Teichichnus*), sting rays (*Piscichnus*), and terrestrial vertebrates (vertebrate swim tracks). Distal tidal-fluvial channels in the Neslen Fm exhibit a higher mud-to-sand ratio and increasing tidal modification with more abundant and thicker mud drapes than more proximal tidal-fluvial channels (Murphy 2017). The presence of euryhaline traces likely produced by anemones, stingrays, and mixed components of the Skolithos-Cruziana ichnofacies (mixoeuhaline indicator, i.e. Pemberton and Wightman 1992; Flaig et al., 2016) suggests increasing salinity and decreasing fluvial influence along the sediment-water interface. Increasing salinity is also suggested by the increased abundance of *T. clavatus* preserved in woody media. The relative abundance of *T. clavatus* is nearly 50% lower than that of *T. longissimus* and coincides with a greater abundance of relict and ghost log grounds. The lack of *T. longissimus* in well-preserved log grounds—only associated with *T. clavatus*—suggests that tracemakers of *T. longissimus* were not primary colonizers of allochthonous media (e.g., Nishimoto et al. 2015).

Trace-fossil assemblages in Zone 2 (central to upper estuarine successions) display higher ichnodiversity and abundances of a *Teichichnus–Cylindrichnus* ichnocoenosis reflecting increasing marine salinities and diverse ethologies, alongside *Teredolites* occurrences. Traces in this ichnocoenosis record deposit- and suspension-feeding, resting, dwelling, and locomotion behaviors. Estuarine deposits contain traces likely produced by: anemones (*Bergaueria* and *Conichnus*); crustaceans (*Limulichnus, Ophiomorpha*, *Rhizocorallium,* and *Thalassinoides*); and vermiform organisms (*Cylindrichnus, Diplocrateron, Phycodes, Planolites, Skolithos,* and *Teichichnus*). Alluvial plain deposits containing peatgrounds flooded by a rise in sea level to produce a MFS-TSE were subsequently exposed to marine estuarine environments in which the underlying peatgrounds recorded *Thalassinoides* and *T. clavatus* and *T. longissimus,* whereas overlying beds contained a higher ichnodiversity of the *Teichichnus–Cylindrichnus* ichnocoenosis. This ichnocoenosis reflects increasing diversity within a mixed Skolithos-Cruziana ichnofacies. Marine overprinting of *Asthenopodichnium* bored wood by *Teredolites* indicate propagation of fluvial discharge of wood downdip.

Trace-fossil assemblages in Zone 3 (lower estuarine to foreshore facies associations) display a *Teichichnus–Cylindrichnus* ichnocoenosis, but with greater variation in diversity and abundances. This ichnocoenosis record deposit- and suspension-feeding, resting, dwelling, and locomotion behaviors. Sandy tidal flats exhibited abundant crustacean burrows (*Ophiomorpha*), rare bivalve traces (*Siphonichnus*), and rare evidence of overprinting during subaerial exposure (rhizoliths). This suggests an intertidal to supratitdal regime along the sandy margins of tidal channels and tidal inlets and physiochemically stressed conditions in channel forms, which can become oxygen poor at times of lower tidal influence. Tidal channels and tidal inlet channels contained sparse bioturbation produced by: vermiform organisms (*Cylindrichnus* and *Teichichnus*). Tidal inlet channels contained much higher densities of traces occurring alongside *Teredolites.* Mouth bars rarely contained traces produced by crustaceans (*Ophiomorpha*), suggesting extremely stressed conditions. Mouth bars are frequently inundated with large amounts of suspended sediments and prone to fluctuating salinities (Gingras et al. 1998; Flaig et al. 2016). Tidally modified deltaic deposits contained the greatest ichnodiversity with contributions from the Cruziana Ichnofacies: anemones (*Bergaueria*); crustaceans (*Crossopodia, Limulichnus*; and *Ophiomorpha*); vermiform organisms (*Gordia, Phycodes,* and *Rosselia*); sting rays (*Piscichnus*); and terrestrial vertebrates (vertebrate swim tracks).

Trace-fossil assemblages in Zone 4 (lower and distal lower shoreface, offshore transition, and shelf) were not extensively studied in outcrop, as the majority of *Teredolites* samples from these EODs were measured from museum specimens or are from the literature. Trace-fossil assemblages observed at outcrop as well as those described in previous studies (e.g., Hattin 1962; Frey 1972; Reolid et al. 2016) indicate a mixed Skolithos-Cruziana ichnofacies as well as a Cruziana Ichnofacies for more distal environments. For example, lower shoreface and distal lower shoreface deposits of the Desert Mbr and lower Castlegate Ss at Sagers Canyon (e.g., Van Wagoner et al. 1991; Pattison et al. 2007; Pattison 2019) display bioturbation by anemones (*Bergaueria*), crustaceans (*Ophiomorpha, Rhizocorallium,* and *Thalassinoides*), echinoids (*Scolicia*), and vermiform organisms (*Palaeophycus*, *Planolites,* and *Skolithos*).

IMPLICATIONS

Teredolites occur in a variety of marine-influenced environments recording evidence of salinity preference, competition, and niche diversification in tracemakers, as well as the physicochemical factors of the EOD in which this trace occurs. Comparative analysis on the ichnogenus *Teredolites* reveals that spatial trends between boring size, boring densities, woodground type, and facies association occurrence densities follow trends in the abundance and distribution of modern tracemaker species that produce *Teredolites*. Large-scale analyses on ichnofossil morphometrics were used to model paleosalinity and ichnological ecoclines across a continuum of EOD (Fig. 20) based on: (1) occurrence densities; (2) ichnotaxonomy; (3) woodground preservation type; (4) ichnocoenoses; and (5) community structures of extant species.

Zonation is typified by the following facies associations and laterally adjacent subenvironments. Zone 1 is a tidally modified fluvial zone and transgressive surfaces composed of *Teredolites* with high boring volumes associated with a low ichnodiversity with paleosalinities interpreted to range between 0.5–10 ppt. Zone 2 is an upper estuarine zone with boring densities, diameters, and moderate to high ichnodiversity increasing distally (seaward) with salinities interpreted to range between 10–19 ppt. Zone 3 is a central to lower estuarine zone with highly variable boring metrics, densities, and ichnodiversity with paleosalinities interpreted to range between 15–30 ppt. Zone 4 is a backshore to open marine zone recording local and regional morphometric trends based on community structure, with paleosalinities interpreted to range between 20–30+ ppt.

Studies on modern occurrences of *Teredolites* and/or their tracemakers are of most use when salinities are recorded alongside species composition, densities, and boring metrics (length and diameter). Data modified from Rayner (1979) and Lopes and Narchi (1993) (Fig. 3, 17, 18) were used to model predicted salinities, but this data only provides a reliable basis for oligohaline to mesohaline occurrences in tropical environments with high species richness. While palichnological data herein was sufficient to recognize trends suggesting paleosalinity gradients, resolution will be greatly improved when more detailed salinity data are collected and reported in studies of modern *Teredolities* tracemakers.

Xylic media containing *Teredolites* was inherently exposed to marine conditions for settlement by *Teredolites* tracemakers prior to burial, as shown by the presence of borings exhibiting ichnogenetic stages (Belaústegui et al. 2020). The increase in media degradation inferred by media preservation type coincides with higher boring densities and a greater likelihood of stenomorphism, both of which occur with increasingly marine-influenced strata. Well-preserved log grounds containing low densities of large borings indicate a decrease in marine influence where reduced salinities inhibited local settlement and preferentially provided habitat for euryhaline tracemakers. For example, tracemakers using high fecundity as a bet-hedging strategy can create a sustainable source population in highly diverse wood-boring communities (i.e. *Psiloteredo healdi*, Fig. 4; Lopes and Narchi 1993), a behavior that generally coincides with specific media preferences during settlement (e.g., Rojas and Severeyn, 2000; Nishimoto et al 2015). The larvae of those tracemakers are primarily emigrants to downstream environments where low intraspecific competition neither controls nor masks population connectivity (i.e. *Bankia gouldi* in Chesapeake Bay; see Zhang et al. 2015). Landward increases in boring densities between the EOD studied reflect that specialization to inhabit reduced salinities was well established by the Late Cretaceous, exemplified by the pronounced increase in density and boring diameters in Zone 1 EOD (Fruitland Fm; Hutchinson and Kues 1985). Extant species of *Teredolites* tracemakers specialized in colonizing oligohaline environments in are typically intolerant of mesohaline or greater salinities and show sharp population declines along such mixing fronts, as well as where competitive stress is high in areas containing multiple tracemaker species (Fig. 3, 4; MacIntosh et al. 2014). The adults, however, need mesohaline or greater salinities to initiate the reproduction cycle (i.e., gametogenesis), and the larvae need increased salinities for survival to settlement. Once they have settled and commenced boring, the larvae can tolerate lower salinities, depending on species.

Inferences drawn from niche partitioning in modern species (e.g., media preferences, salinity preferences, salinity preferences coinciding with reproduction strategies) with respect to settlement inferred from fossilized *Teredolites* is suggested by the overall increase in boring diameters and boring densities, as well as greater overprinting of media containing *Asthenopodichnium* in proximal EOD. Future actuopaleontologic studies should focus on modeling fossil species salinity tolerances in context to competition with other species within the same EOD rather than treating each species occurrence independently from the other co-occurring species. Species specialized in inhabiting oligohaline–polyhaline salinities inhabit specific salinities as a response to competitive stress; the range of salinities occupied varies depends on the number of species present in a given EOD. For example, *Psiloteredo healdi* in southeastern Brazil are successful in a narrow range of salinities ($\leq$ 2 ppt) but face high competitive pressure and population declines where it interacts with other specialized species in oligohaline salinities (i.e. *Nausitora fusticulus*; Lopes and Narchi 1993). *Psiloteredo healdi* occupies larger salinity ranges (≥20 ppt) in Lake Maracaibo, Venezuela, where low competitive pressure with *Bankia fimbriatula* does not limit their distribution in proximal EOD.

A key implication of this study is that occurrences of *Teredolites* in sedimentary successions can be used as indicators of marine influence and paleosalinity proxy. *Teredolites* within the lower Castlegate Ss, west of Green River, UT, reinforces previous interpretations of marine influence (e.g., Yoshida 2000; Pattison et al. 2007; Pattison 2019) on strata previously interpreted to be strictly fluviatile (e.g., Plint and Pickerill 1985; Van Wagoner et al. 1991; Van

Wagoner 1998; Yoshida et al. 1998). Other stratigraphic units interpreted as purely freshwater will most commonly: (1) contain *Teredolites* and other marine ichnotaxa along TSE-MFS or other high-order frequency surfaces; (2) contain tidal indicators; (3) be within close proximity to a paleoshoreline: and/or (4) contain marine skeletal debris (e.g., Plint and Pickerill 1985; MacEachern et al. 2007; Shipway et al. 2019b). The occurrence of *Teredolites* strata with little or no other evidence of marine influence should not be overlooked because these traces are indicators of proximity to the paleoshoreline, influx of marine waters into the fluvial systems, tidal influence, and/or a marine flooding surface and transgression.

Freshwater examples of autochthonous *Teredolites* in the rock record are unlikely based on the physiology and distribution of modern tracemakers. If they had ever existed, species in tropical and monsoonal paleoclimates, like their modern counterparts (e.g., *Psiloterdo healdi*), could have tolerated low salinity conditions (i.e., limnetic and alpha-oligohaline; 0.5–2 ppt) but still required marine influence (i.e., mesohaline and/or polyhaline salinities; 5–18 ppt and 18–30 ppt) to successfully reproduce (e.g., Khlebovich and Aladin 2010). For example, such species-poor genera of tracemakers, like *Teredina* (four species only), occur in lower delta plain deposits of the Fruitland Fm (*T. neomexicana*, Campanian, Kues 1983; Hutchinson and Kues 1985) and in tidal flat and marsh deposits of the Epernay Fm (*T. oweni*, Thanetian, lower Paleogene; Aubry et al. 2005). These species may be indicative of EOD with salinity ranges that varied from 0.5–2 ppt in the wet season and 5–18 ppt to 18–30 ppt in the dry season in the Fruitland Fm and Epernay Fm.

Occurrences of *Teredolites* across mappable surfaces, such as the Desert Sequence Boundary (Pattison 2019), show the tendency for bioeroded media to be more susceptible to hydraulic transport. Occurrence metrics and boring densities within similarly mappable erosional surfaces produced by transgression or episodic flooding (e.g., King et al. 2018) may provide insight into paleoenvironmental disturbances and community succession using a framework within the Intermediate Disturbance Theory, given that this media-controlled ichnotaxon fits the assumptions of Hutchison (1953) (see Effects of Facies Association). Increased densities of Type I *T. clavatus* at Tusher Canyon along the Desert Sequence Boundary show that tidal influences—evidenced by herringbone cross lamination, tidal rhythmites, and double mud drapes—could have been sufficient to carry larvae landward (e.g., Narváez et al. 2012). Very low densities of *T. longissimus* along this surface suggest persistence, but the greater colonization abilities and deterministic growth of *T. clavatus* tracemakers allowed them to dominate those heavily disturbed surfaces that comprise the Desert Sequence Boundary.

A major implication of this research is that *Teredolites* can serve as a predictor of paleosalinity in shallow-marine to continental systems, helping to clarify proximity to a paleoshoreline and refine subenvironment interpretations. Applying the method proposed here increases our ability to identify sequence stratigraphic surfaces and autogenic versus allogenic controls on deposition. Ultimately, characteristics of *Teredolites* in the rock record provide a unique tool to refine paleoenvironmental interpretations for a given stratigraphic interval, assisting with better prediction of sandbody-shale abundance, distribution of facies, and geometries of architectural elements, which are all important to the petroleum industry (e.g., Van Wagoner et al., 1991; Pemberton and Wightman, 1992; MacEachern et al., 2007; Gingras et al., 2011; Flaig et al., 2019).

CONCLUSIONS

Statistical analysis of a rich dataset of actuopaleontologic observations, morphometrics. and occurrences of *Teredolites* and their tracemakers from the literature and CWIS outcrop were used to model their spatial and temporal variations to reconstruct paleosalinity, physicochemical conditions, and faunal communities. *Teredolites* are related to marine systems through media exploitation, feeding, dwelling, reproductive preferences, and the interaction with other wood borers in a given medium. Wood-boring bivalves are unique in that their valve morphologies and body plan can be reconstructed semiquantitatively by their boring morphologies and presence or absence of indicative features (e.g., boring linings, posterior annulae, and accessory plates).

Extant tracemakers of *Teredolites* are present in a variety of EOD, all occurring in facies associations displaying some degree of marine influence and salinity. Such tracemaker preferences are evident in large-scale analyses and reveal size-density-diversity gradients in ancient EOD, and include changes in ichnotaxa and ichnodiversity producing four primary zones in paralic to open marine deposits. Zone 1 represents upper estuarine to tidally modified fluvial successions with salinities from 0.5–10 ppt (oligohaline to alpha-mesohaline). Zone 2 represents upper to central estuarine successions with salinities from 10–19 ppt (beta mesohaline to lower polyhaline). Zone 3 represents central to lower estuarine successions with salinities from 15–30 ppt (beta mesohaline to euhaline). Zone 4 represents backshore to open marine successions with salinities from 20–30+ ppt (polyhaline to euhaline). These zones display variation in boring metrics, densities, and relative composition of *Teredolites* ichnospecies.

Zonation trends are not evident along major sequence stratigraphic surfaces (e.g., sequence boundaries and flooding surfaces) or accumulations of media produced by sediment starvation. Such surfaces record a disturbed *Teredolites* assemblage dominated by *T. clavatus* and uncommon, stenomorphic *T. longissimus.* Repetition of this type of assemblage within TSE-

MFS and sequence boundaries in the Blackhawk–Castlegate stratigraphic interval suggests that condensation of allochthonous woody media may, in some cases, bear autochthonous *Teredolites* where high fecundity and exploitation may outpace sedimentation rates and media burial.

Understanding the morphometrics and occurrences of *Teredolites* is important for identifying sequence stratigraphic position with respect to the paleoshoreline, flooding surfaces, and autogenic versus allogenic controls on deposition of marine-influenced deposits. This then leads to better predictability for sandbody-shale abundance, distribution, and geometries.

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FIGURE CAPTIONS

FIG. 1.—Appearance datum and relationships of wood-boring pholadoideans.

FIG. 2.—Salinity classification schemes. **A**) Venice Salinity Classification System (Anonymous, 1959). **B**) Biologically Based Estuarine Salinity System (Bulger et al. 1990, 1993).

FIG. 3.—Salinity ranges of *Teredolites* tracemakers from the literature with respect to salinities at which some reproduce as well as their larval salinity requirements See text for references.

FIG. 4.—Reanalyzed data from Lopes and Narchi (1993): **A**) Species abundances and composition between sampling sites; **B**) Number of tracemakers with respect to reproduction types between sampling sites; **C**) Number of teredinids between sampling sites by species and reproduction style with respect to salinity at low tide.

FIG. 5.—Reanalyzed data of Maldonado and Skinner (2016). **A**) Sample localities in Ilha Grande and Sepetiba bays, Rio de Janeiro, Brazil. A-A' used in analyses. Cross section analysis of teredinid distributions by: B) species, blue (solid) = *Teredo furcifera*, red (dash) = *T. bartschi*, green (dash) = *Lyrodus floridanus*, pink (dash) = *Bankia gouldi*, Black (dash) = *B. fimbriatula*, Yellow (solid) = *B. destructa*, blue (dash) = *Nototeredo knoxi*; C) reproduction type (ovipary, short-term larvipary, and long-term larvipary), D) reproduction type (ovipary, larvipary), and E) percent contribution by reproduction type. **C – E)** blue = long term larvipary, green = short term larvipary, red = ovipary, purple = larvipary (binned).

FIG. 6.—Idealized diagram of conterminous environments of deposition sampled in this study. See Table 5 for key to facies associations.

FIG. 7.—*Teredolites clavatus* and variations in morphology with respect to tracemaker affinity (Kelly 1988). **A**) *Barnea* **B**) *Martesia*, **C**) *Xylophagella*, **D)** *Teredina*, **E**) *Turnus*, **F**) *Teredina.*

FIG. 8.—*Asthenopodichnium* (As), Desert Mbr, Blackhawk Fm occurring with: **A**) *Teredolites clavatus* (Tc); and **B**) *Teredolites longissimus* (Tl).

FIG. 9.—*Teredolites longissimus*. **A**) Lower Chickabilly Mbr., Budden Canyon Fm. (Cretaceous: Barremian–Aptian), Ono, California; **B**) Birket Qarun Fm. (Eocene: Priabonian), Fayum, Egypt; **C**–**E**) Lafayette River, Norfolk, VA; **D**) *in situ* pallets of *Bankia gouldi* sealing boring aperture (cl: calcite lining, es: excurrent siphon, is: incurrent siphon, pa: pallet); and **E**) boring containing the tracemaker *B. gouldi*.

FIG. 10.—Boring metrics with respect to Facies Association. **A**) *Teredolites* maximum and mean diameters with maximum of ichnotaxa present, **B**) *T. clavatus* maximum and mean boring diameters, **C**) maximum and mean boring length for *T. clavatus* and *T. longissimus*, **D**) *T. longissimus* maximum and mean boring diameters.

FIG. 11.—Size frequency distributions for the ichnogenus *Teredolites*, *T. clavatus*, and *T. longissimus*.

FIG. 12.— Statistical summary plot of boring diameter size-frequency between woodground preservation types for *T. clavatus.*

FIG. 13.— Statistical summary plot of boring diameter size-frequency between woodground preservation types for *T. longissimus.*

FIG. 14.—Statistical summary plot of boring diameter size-frequency between woodground preservation types for the *Teredolites* ichnogenus.

FIG. 15.— Line plot of simple linear regression illustrating the relationship between boring density, mean, and maximum diameter within a sample.

FIG. 16.—Frequency of *Teredolites* occurrences by Facies Association. **A**) *Teredolites isp.*, **B**) *T. clavatus,* and **C**) *T. longissimus.*

FIG. 17.—Mean salinity and number of teredinids among sites, modified from Lopes and Narchi (1993).

FIG. 18.—Contour plot of predicted salinity values on fossil data from *T. longissimus* in mixoeuhaline environments using maximum boring diameter, number of *Teredolites* borings per sample, and mean salinity at low tide from Lopes and Narchi (1993).

FIG. 19.—Size Diversity Index (SDI) of *Teredolites* with respect to facies associations.

FIG. 20.—Zonation of *Teredolites* populations within an idealized tide and wave-dominated estuarine system.

FIG. 21.—Variation in boring sizes within a single cluster of *Teredolites*. **A**, **B** illustrate: Size 1, final stage of development showing *T. clavatus* morphology *sensu* Kelly and Bromley (1984); Size 2, roughly hemispherical borings showing some elongation, anterior and posterior diameters no longer equal; Size 3, simple, hemispheric borings < 1 mm in diameter. Scale bar 1 cm.

FIG. 22.—KUPB 0055115, *Teredolites clavatus* bearing fossilized hard parts of *Teredina jeffersoni*. **A, B**) posterior of boring with accessory plates, **C, D**) anterior of boring with accessory plates along posterior margin of valves, **E, F**) anterior margin of valves bearing

accessory plates. As= anterior slope, c= callum, dec= dorsal extension of the callum, hp= hypoplax, ms= mesoplax, mt= metaplax, sp= siphonoplax. Scale bars 5 mm.

FIG. 23.—KUIBGS CB-HC-001, *T. longissimus* from the Castlegate Sandstone with *in situ* pallets preserved as molds.

FIG. 24.—*Teredolites* with annulated boring linings from Cretaceous strata. **A**, **B**, and **F)** Fairport Chalk Member, Carlile Shale; **D**) Sego Sandstone; and **C**, **E**, **G**) Turner Sandy Member, Carlile Shale.

FIG. 25.—Measurements (cm) of *T. clavatus* and *T. longissimus* along the Desert Sequence Boundary at Nefertiti, Tusher Canyon, and Horse Canyon: **A, B**) mean diameter; **C, D**) maximum diameter; **E, F**) boring density per sample.

FIG. 26.—Contribution of woodground preservation types in transgressive systems tracts within incised valley fills of the Desert Member, Blackhawk Formation and marine flooding surfaces in the Neslen Formation.

FIG. 27.—KUPB KC-5-L (no ID), specimen from the Fairport Mbr, Carlile Shale (Cretaceous: Turonian) from Hodgeman Co., Kansas containing shrinkage cracks (blue), *T. clavatus* (black) and *Apectoichnus* indet. (red). Scale bar 0.5 cm.

FIG. 28.—*Teredolites* boring diameters when occurring with and without *Asthenopodichnium*. **A)** mean diameter, **B**) maximum diameter.

TABLE CAPTIONS

TABLE 1.—Environmental factors affecting natural populations of shipworms. Modified from Nair and Saraswathy (1971).

TABLE 2.—Factors and explanation of palichnologic dataset.

TABLE 3.—Factors and explanation of modern *Teredolites* and tracemaker dataset.

TABLE 4.—*Teredolites*-bearing formations and number of occurrences used in this study.

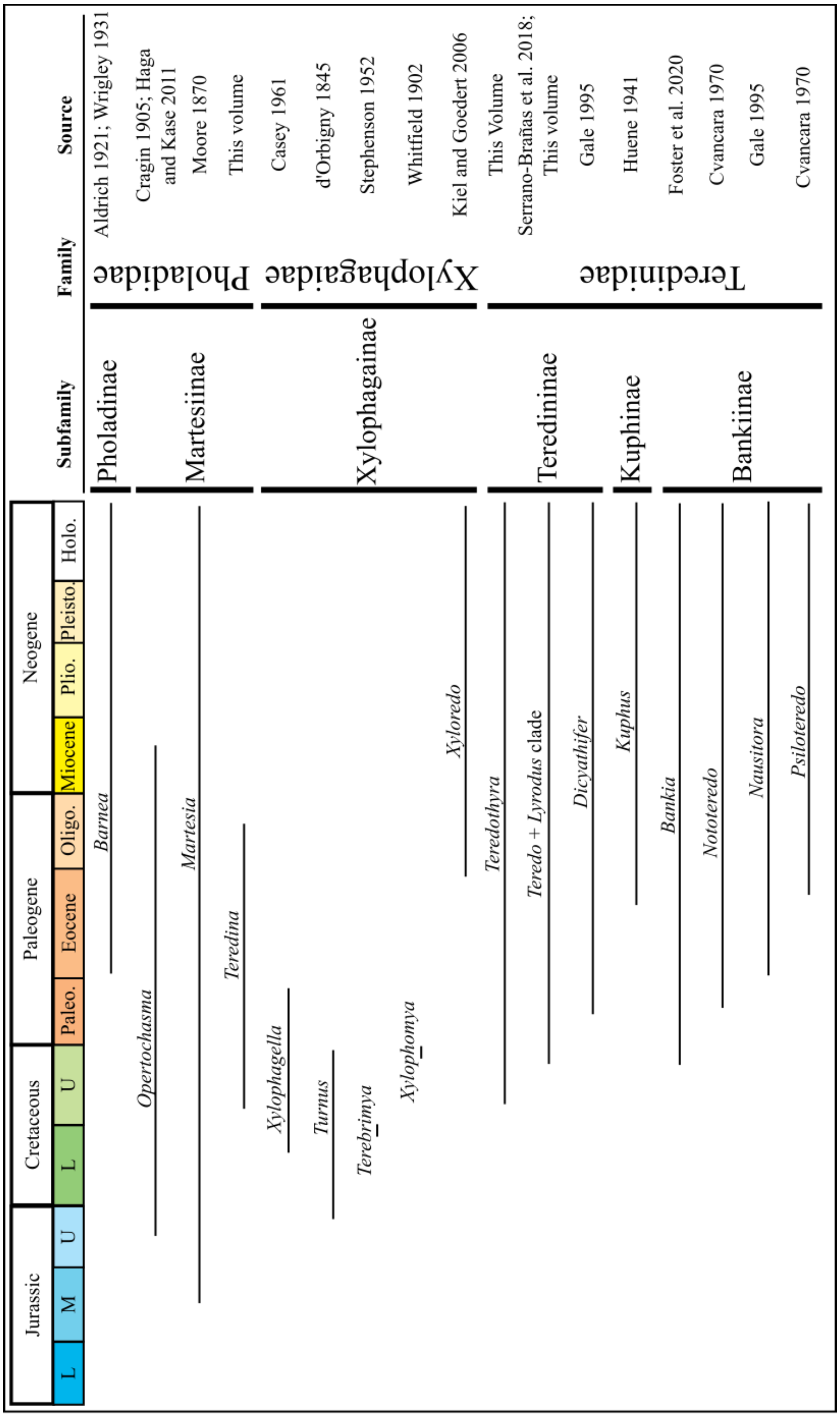
TABLE 5.—Facies associations, coding key, and relative contribution to the dataset used in this study.

TABLE 6.—Descriptive statistics of *Teredolites* boring diameters with respect to woodground preservation types.

TABLE 7.—One-Way ANOVA summary reporting of factors in the fossil dataset.

TABLE 8.—Factorial ANOVA summary reporting of Teredolites boring diameter and the interaction between ichnospecies and woodground preservation type.

TABLE 9.—Percent contribution of *Teredolites* ichnospecies and woodground preservation types with respect to systems tract.


Jurassic
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Paleogene
Paleo.
Eocene
Oligo.
Neogene
Miocene
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Pleisto.
Holo.
Subfamily
Family
Source
Barnea
Opertochasma
Martesia
Teredina
Xylophagella
Turnus
Terebrimya
Xylophomya
Xyloredo
Teredothyra
Teredo + Lyrodus clade
Dicyathifer
Kuphus
Bankia
Nototeredo
Nausitora
Psiloteredo
Pholadinae
Martesiinae
Xylophagainae
Teredininae
Kuphinae
Bankiinae
Pholadidae
Xylophagaidae
Teredinidae
Aldrich 1921; Wrigley 1931
Cragin 1905; Haga and Kase 2011
Moore 1870
This volume
Casey 1961
d'Orbigny 1845
Stephenson 1952
Whitfield 1902
Kiel and Goedert 2006
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Cvancara 1970
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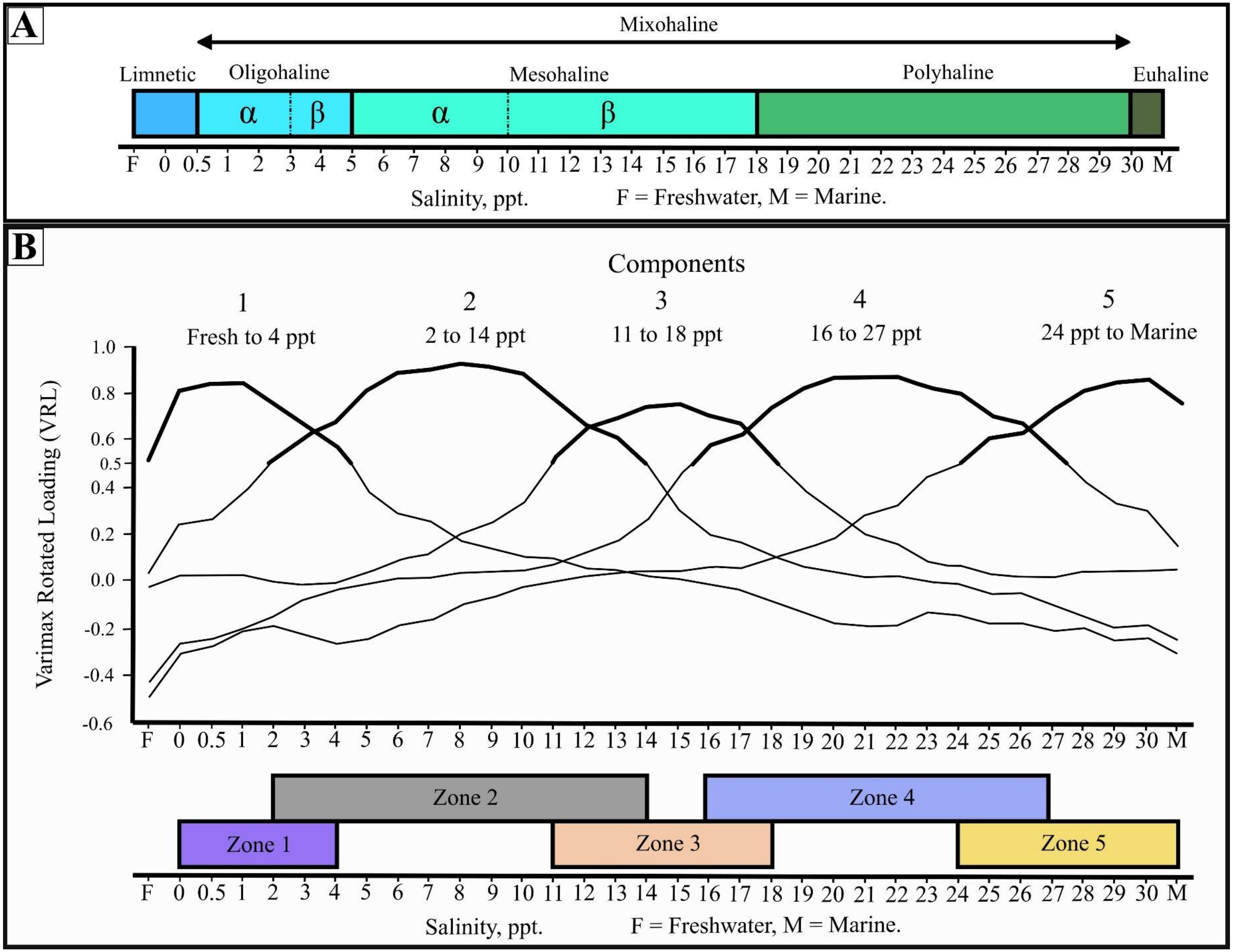
A
Mixohaline
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Polyhaline
Euhaline
α
β
α
β
F 0 0.5 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 M
Salinity, ppt.
F = Freshwater, M = Marine.
B
Components
1
Fresh to 4 ppt
2
2 to 14 ppt
3
11 to 18 ppt
4
16 to 27 ppt
5
24 ppt to Marine
Varimax Rotated Loading (VRL)
1.0
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-0.4
-0.6
F 0 0.5 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 M
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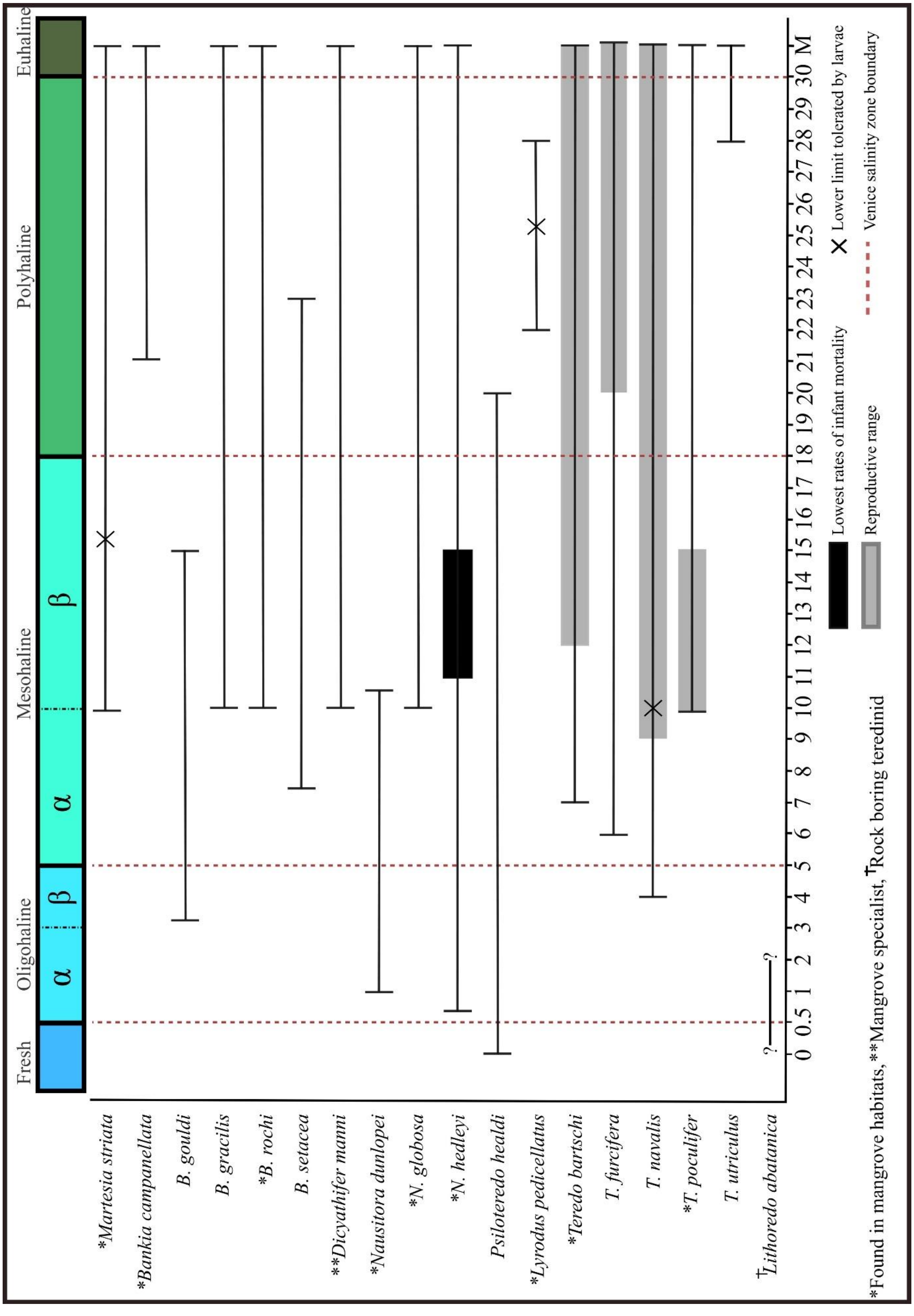
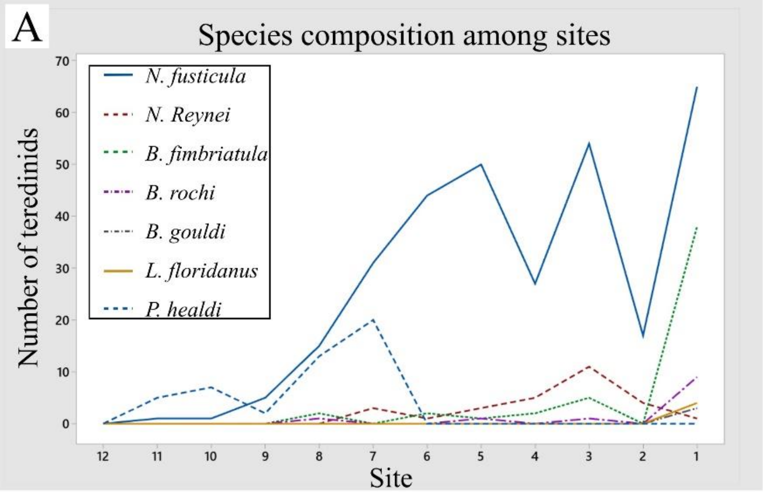
Salinity, ppt.
F = Freshwater, M = Marine.



*Found in mangrove habitats, **Mangrove specialist, †Rock boring teredinid


A
Species composition among sites
N. fusticula
N. Reynei
B. fimbriatula
B. rochi
B. gouldi
L. floridanus
P. healdi
Number of teredinids
0
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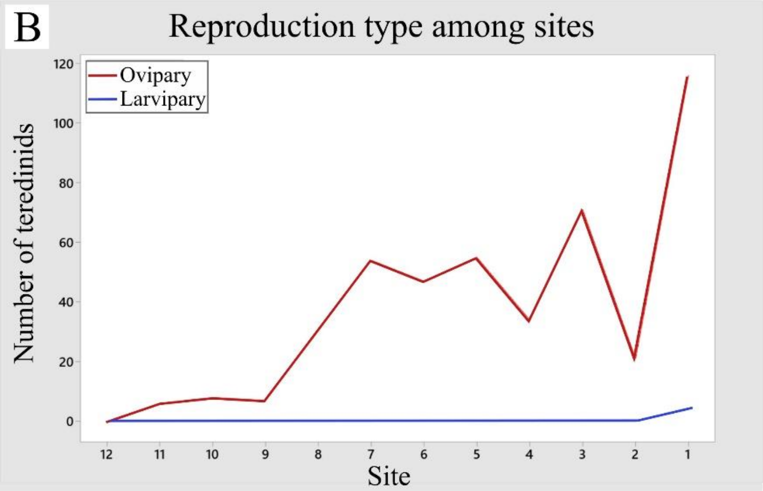
Site


B
Reproduction type among sites
Ovipary
Larvipary
Number of teredinids
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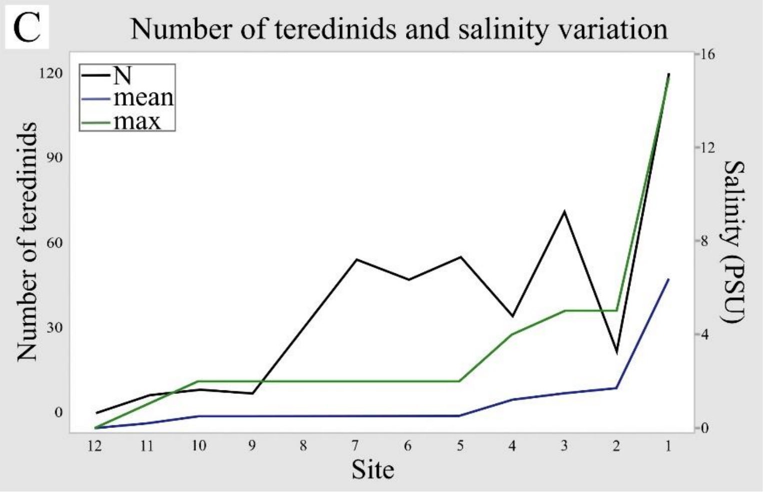
Site


C
Number of teredinids and salinity variation
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Number of teredinids
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Salinity (PSU)
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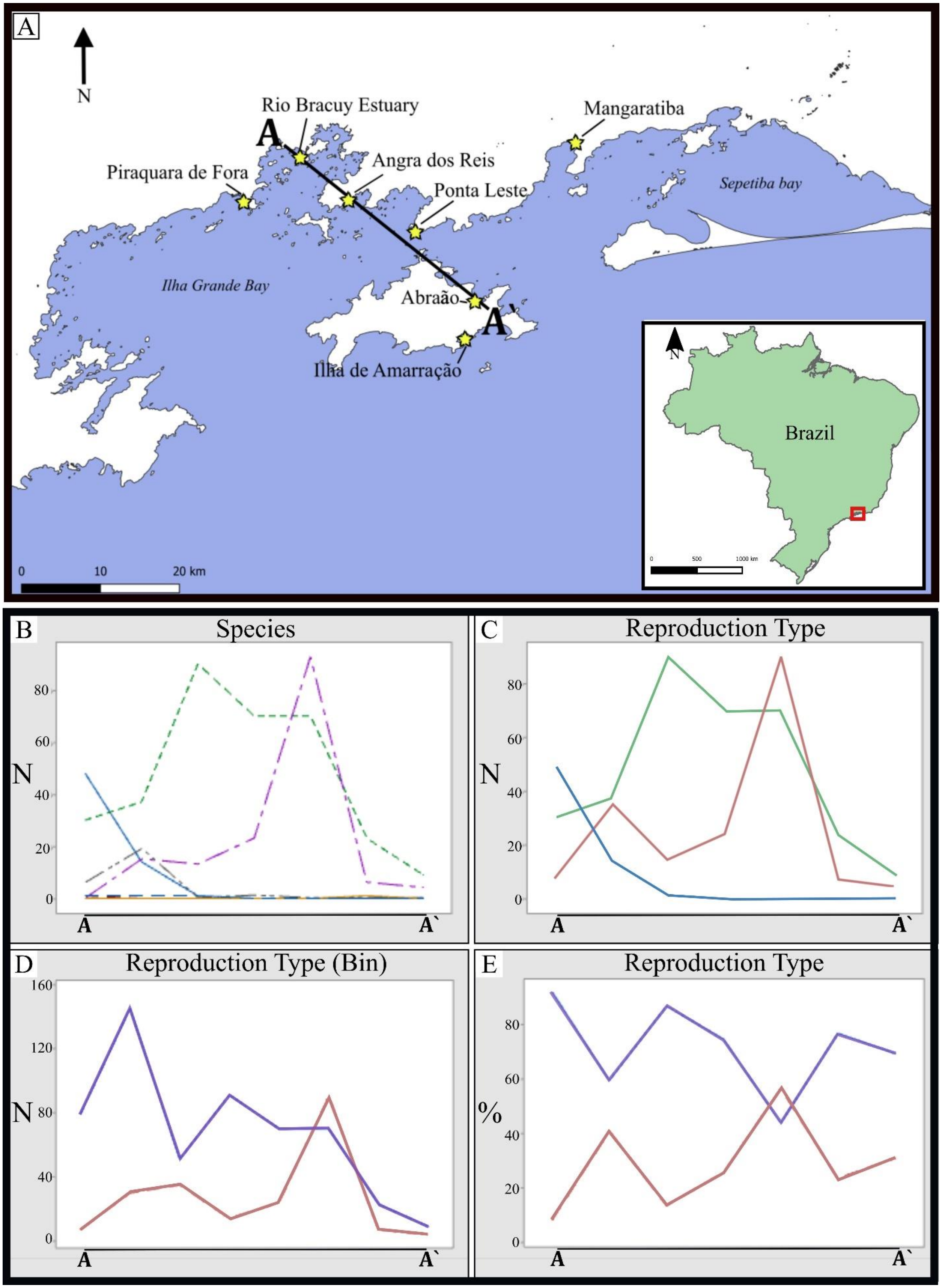
A
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Rio Bracuy Estuary
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Angra dos Reis
Piraquara de Fora
Ponta Leste
Sepetiba bay
Ilha Grande Bay
Abraão
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Ilha de Amarração
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Species
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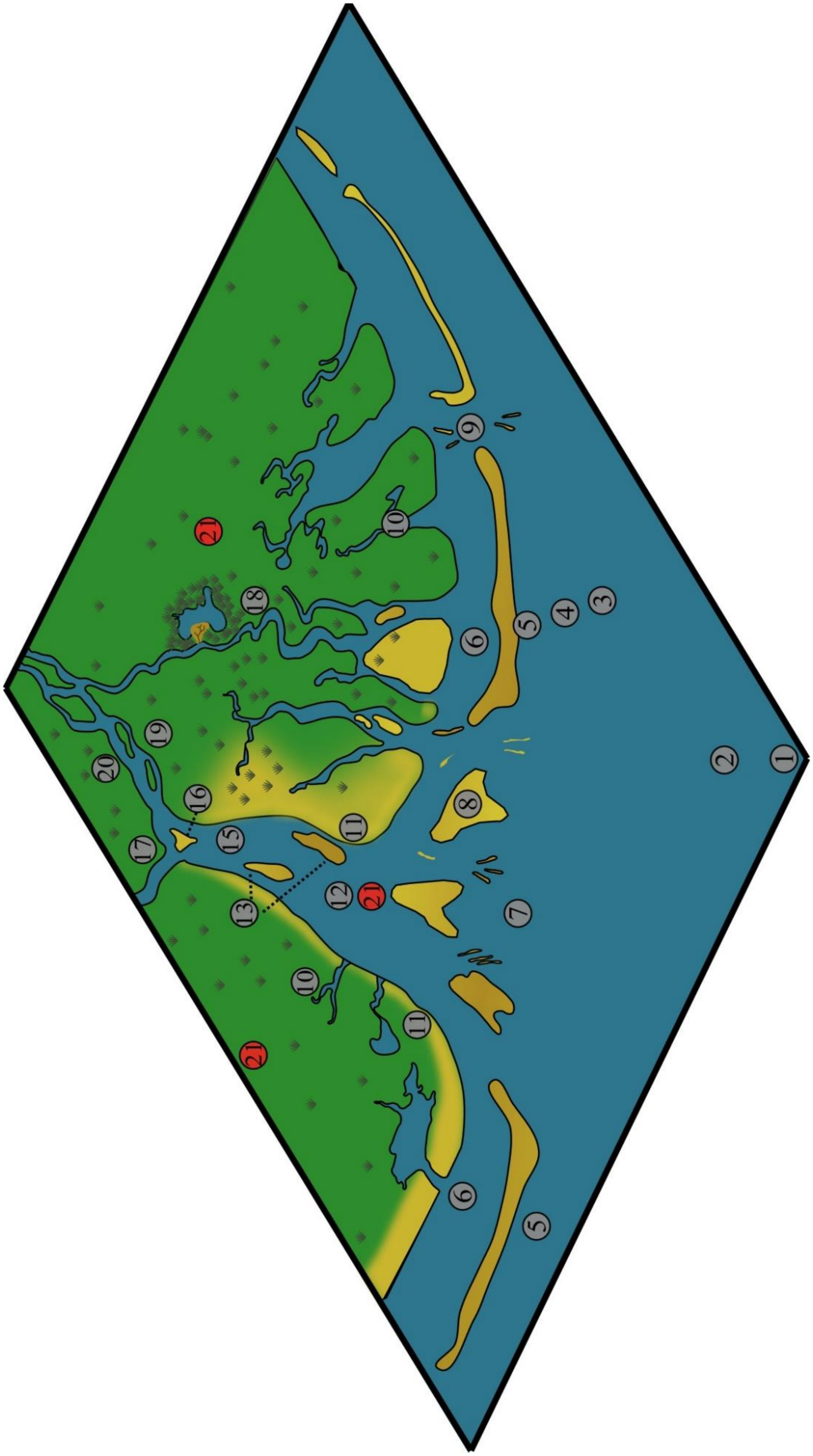
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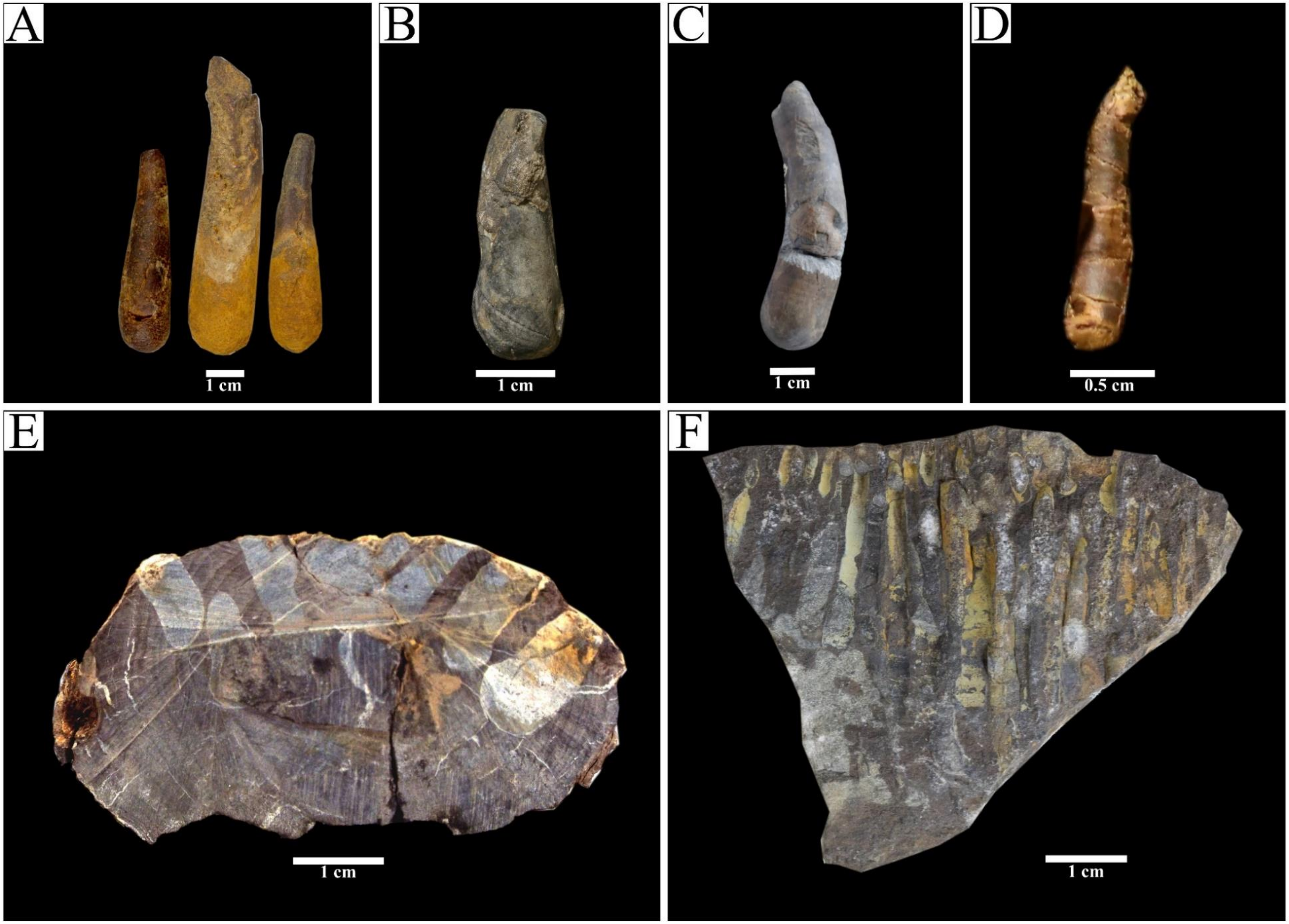
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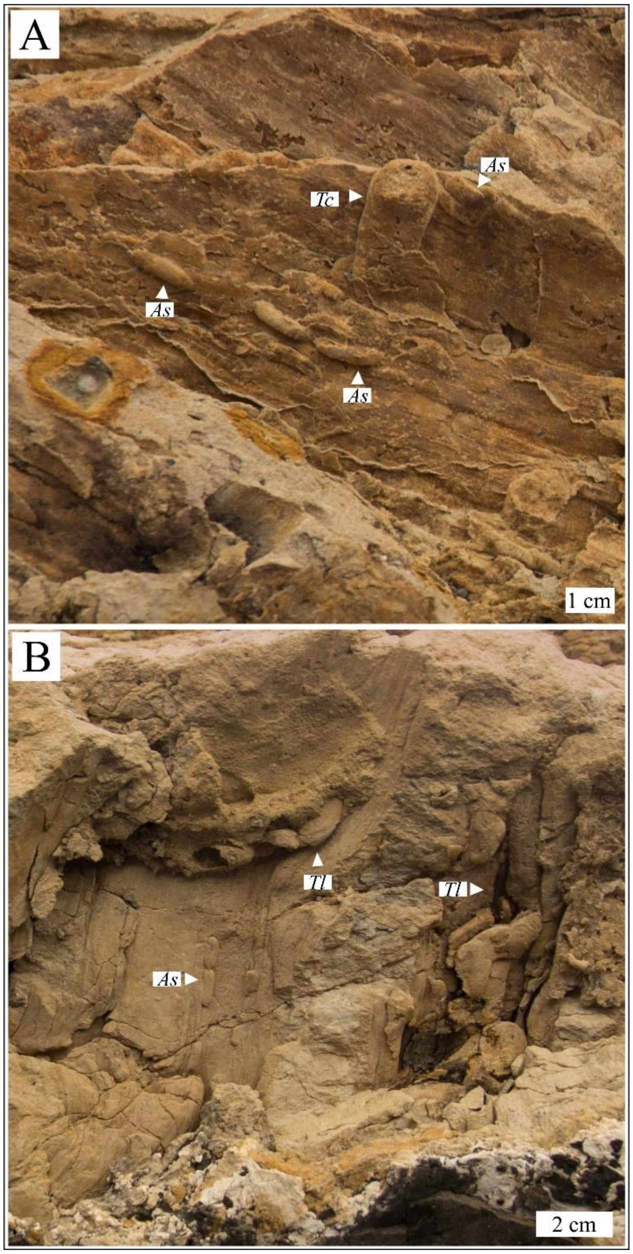
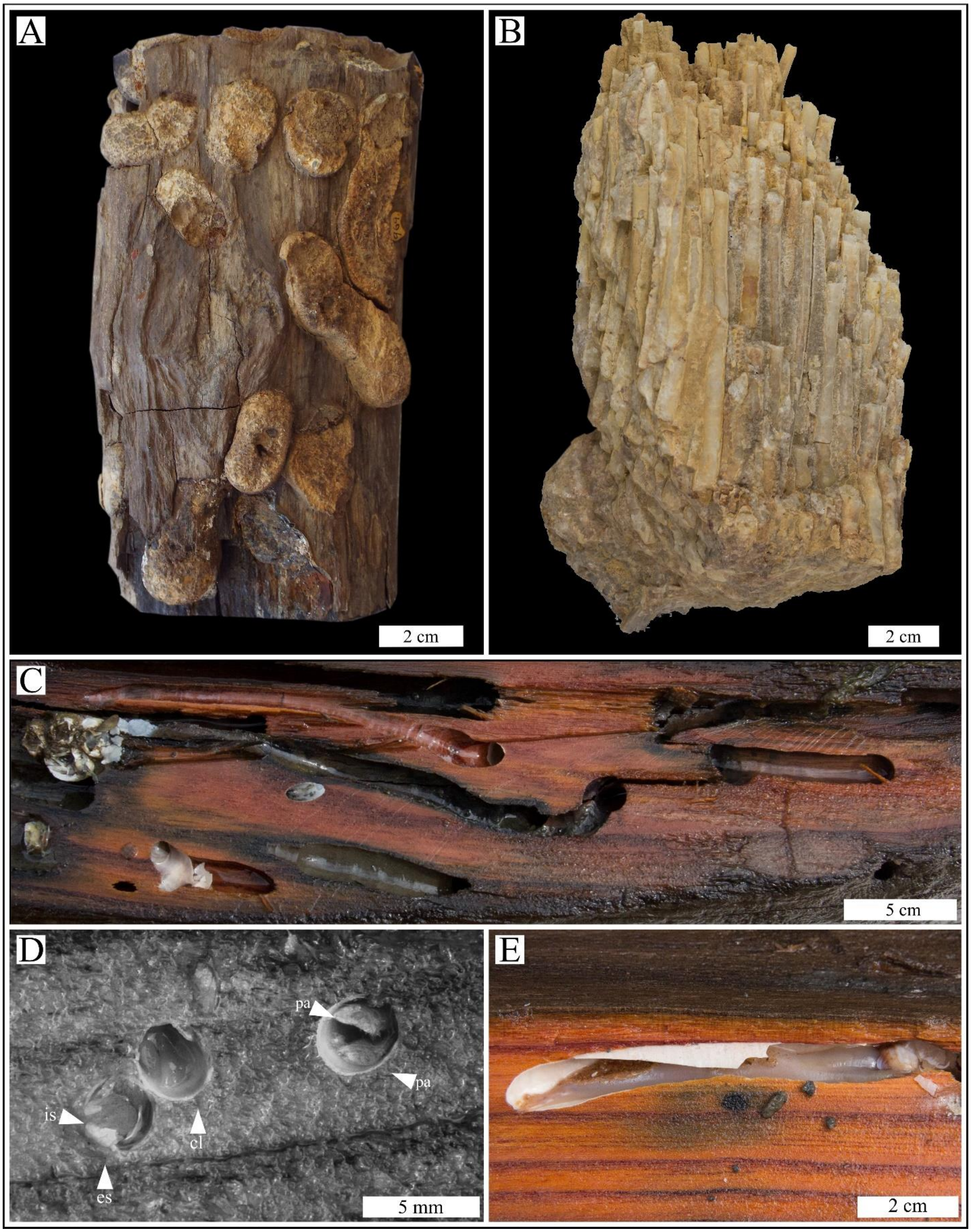
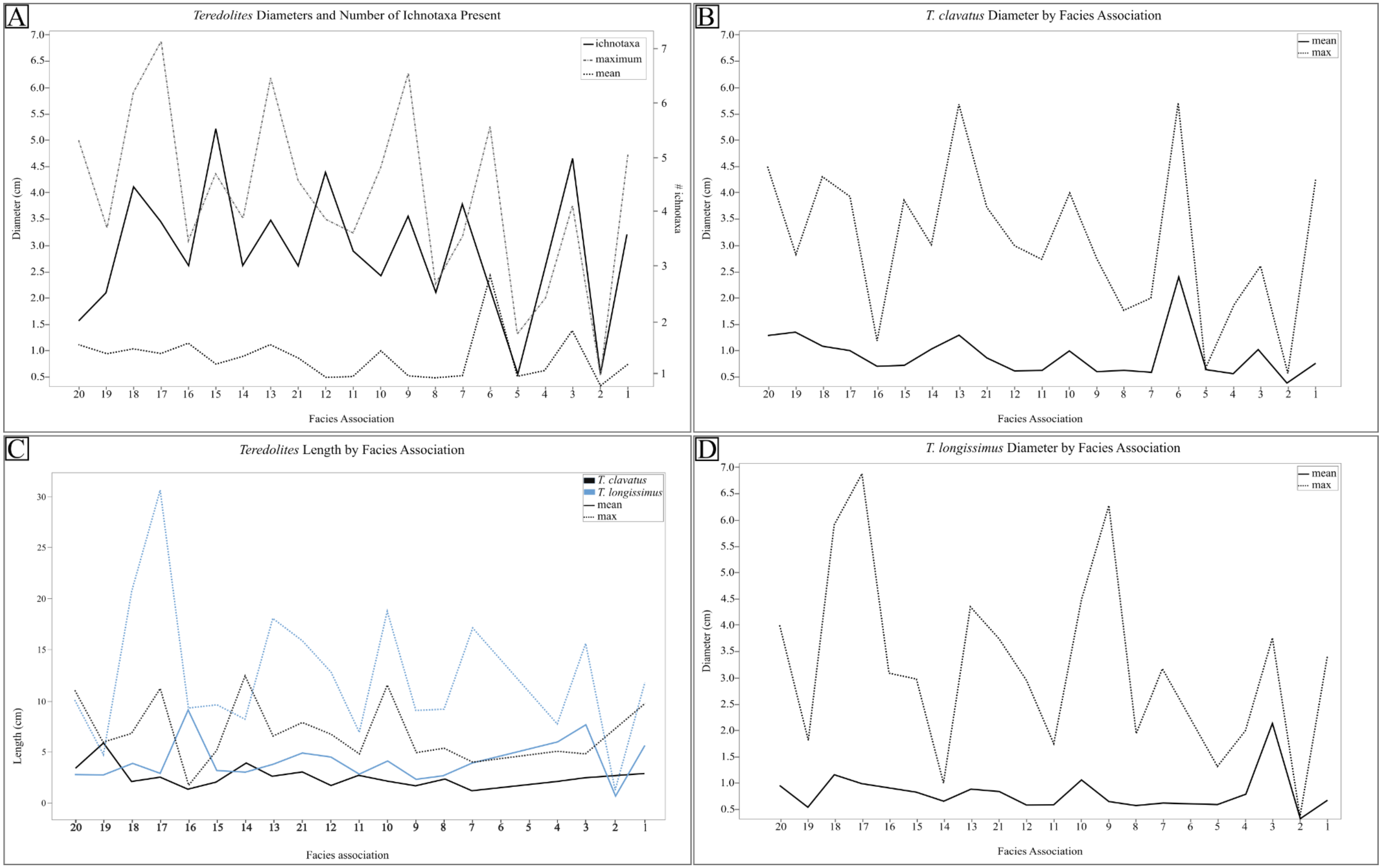
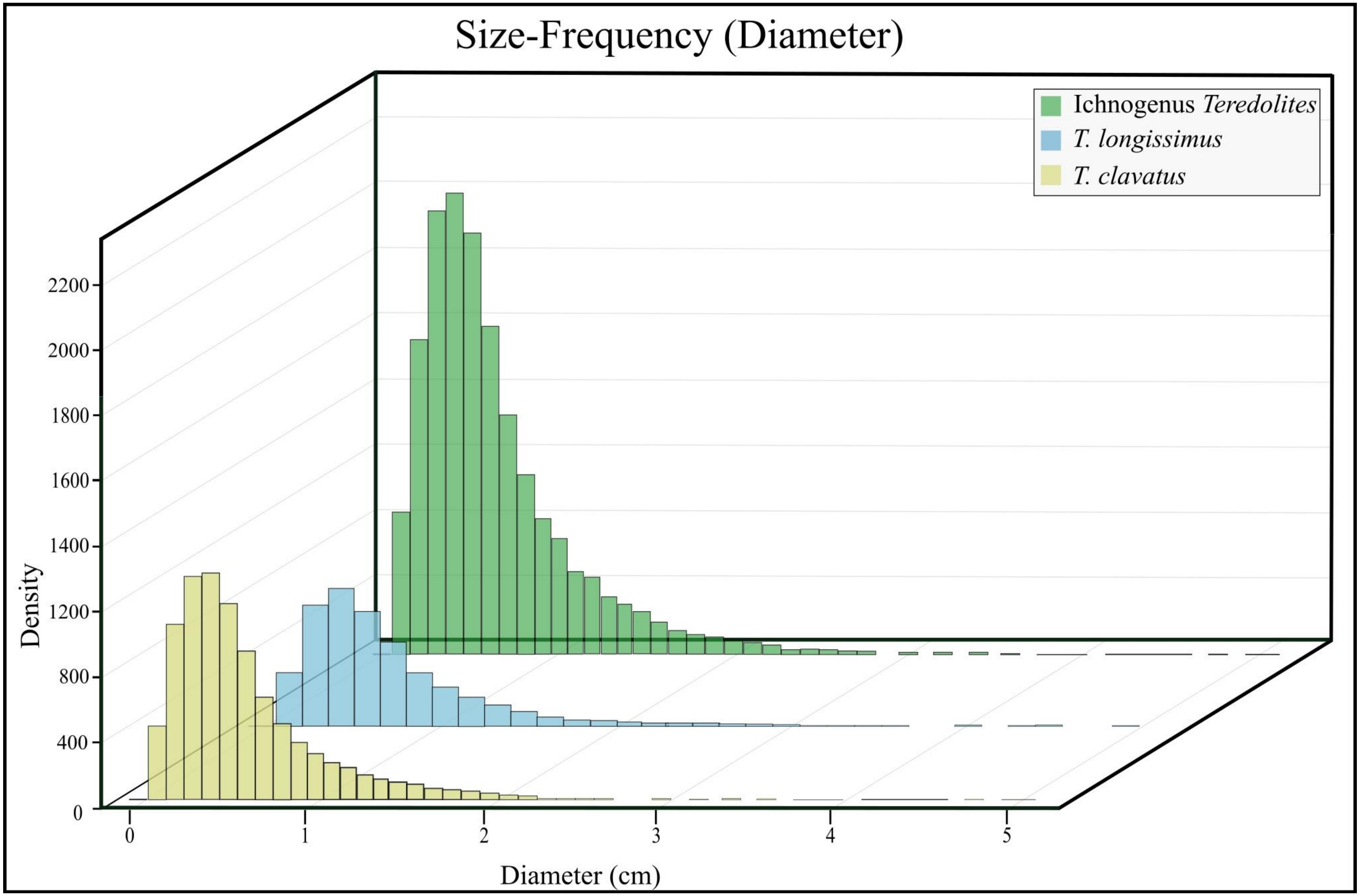
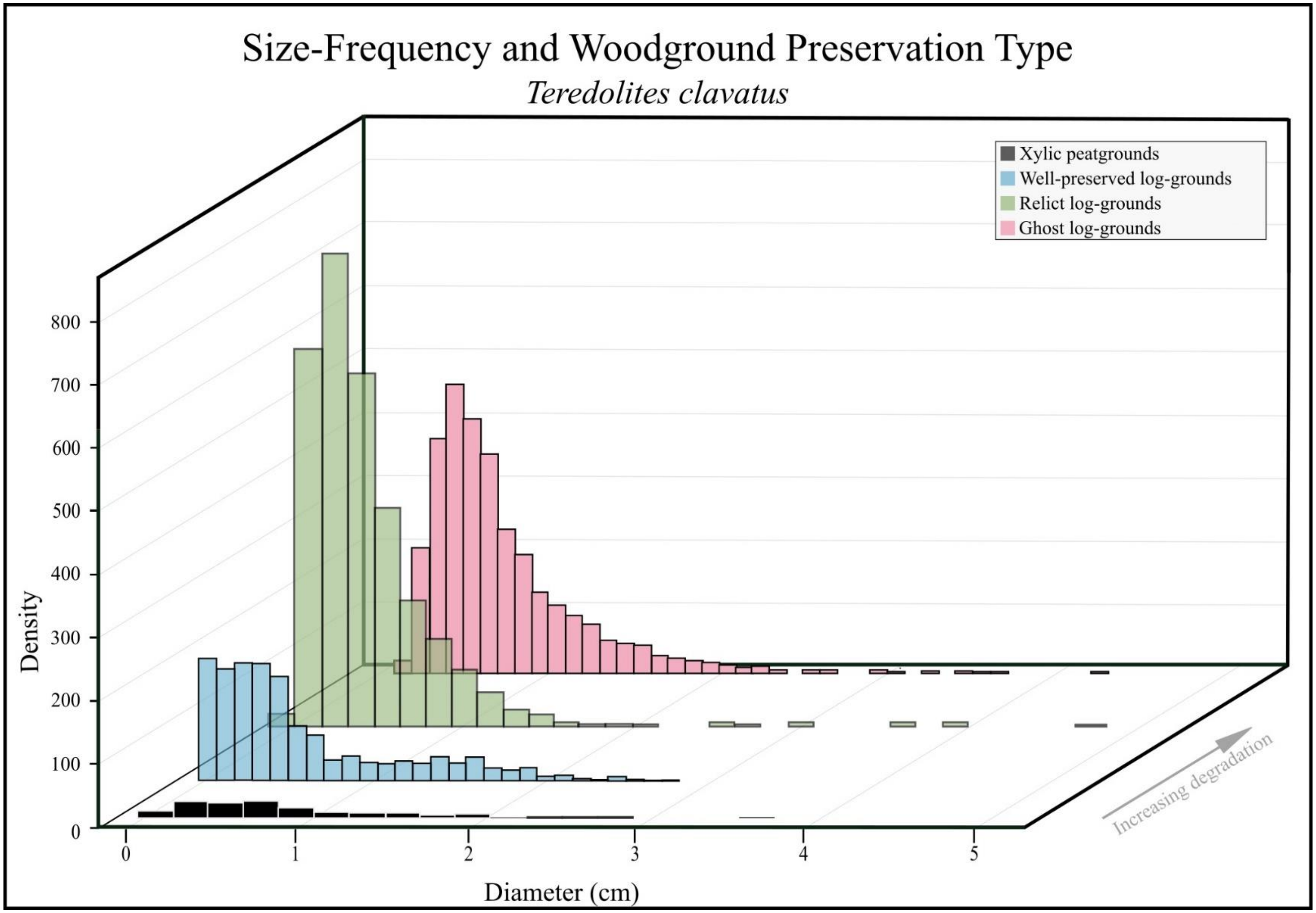
C
1 cm
D
0.5 cm
E
1 cm
F
1 cm

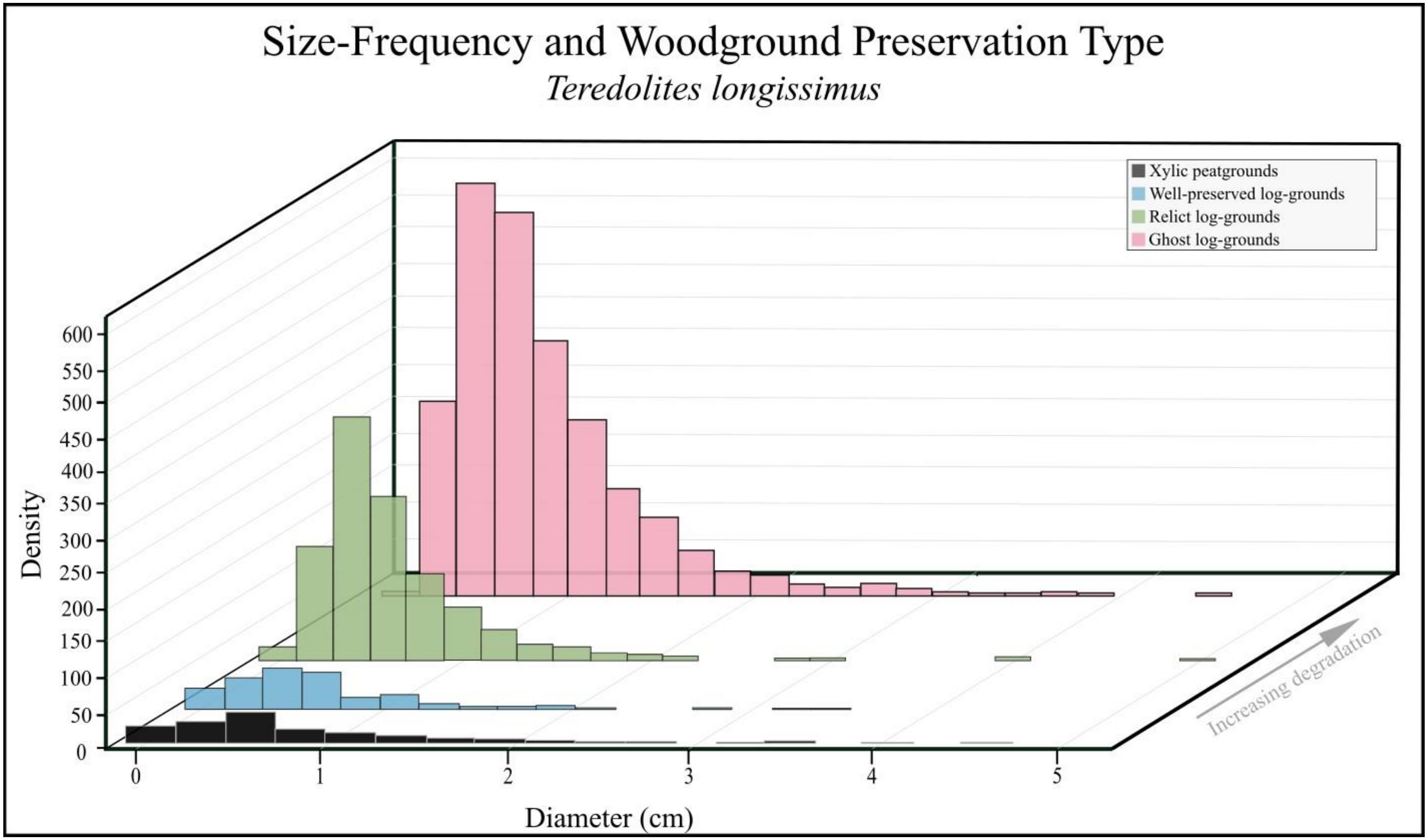

A
As
Tc
As
As
1 cm
B
Tl
Tl
As
2 cm

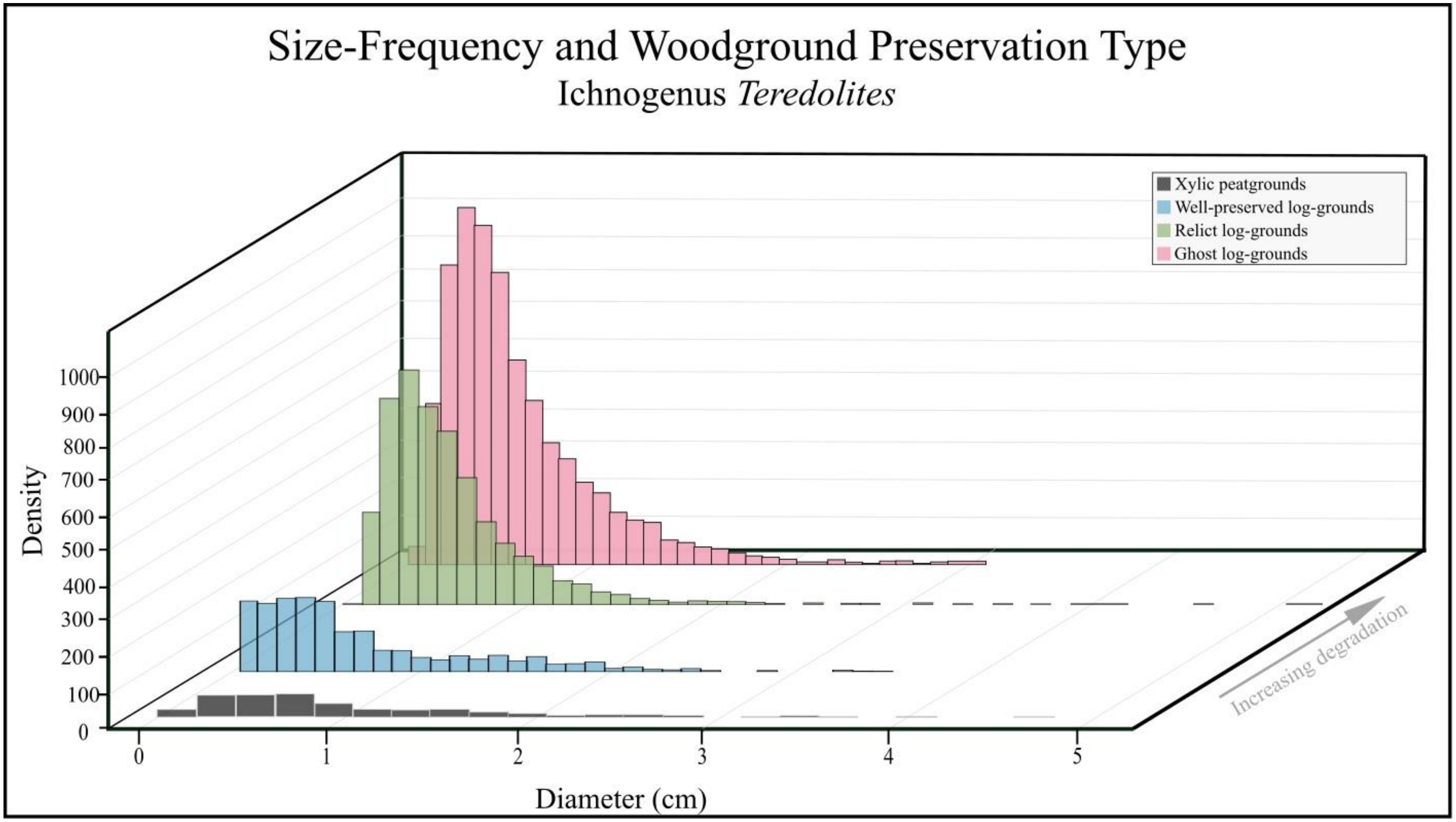

A
2 cm
B
2 cm
C
5 cm
D
pa
pa
is
cl
es
5 mm
E
2 cm


A
Teredolites Diameters and Number of Ichnotaxa Present
Diameter (cm)
ichnotaxa
ichnotaxa
maximum
mean
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
7
6
5
4
3
2
1
20 19 18 17 16 15 14 13 21 12 11 10 9 8 7 6 5 4 3 2 1
Facies Association
B
T. clavatus Diameter by Facies Association
Diameter (cm)
mean
max
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
20 19 18 17 16 15 14 13 21 12 11 10 9 8 7 6 5 4 3 2 1
Facies Association
C
Teredolites Length by Facies Association
Length (cm)
T. clavatus
T. longissimus
mean
max
30
25
20
15
10
5
0
20 19 18 17 16 15 14 13 21 12 11 10 9 8 7 6 5 4 3 2 1
Facies association
D
T. longissimus Diameter by Facies Association
Diameter (cm)
mean
max
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
20 19 18 17 16 15 14 13 21 12 11 10 9 8 7 6 5 4 3 2 1
Facies Association


Size-Frequency (Diameter)
🟩 Ichnogenus *Teredolites*
🟦 *T. longissimus*
🟨 *T. clavatus*
Density
2200
2000
1800
1600
1400
1200
800
400
0
0
1
2
3
4
5
Diameter (cm)

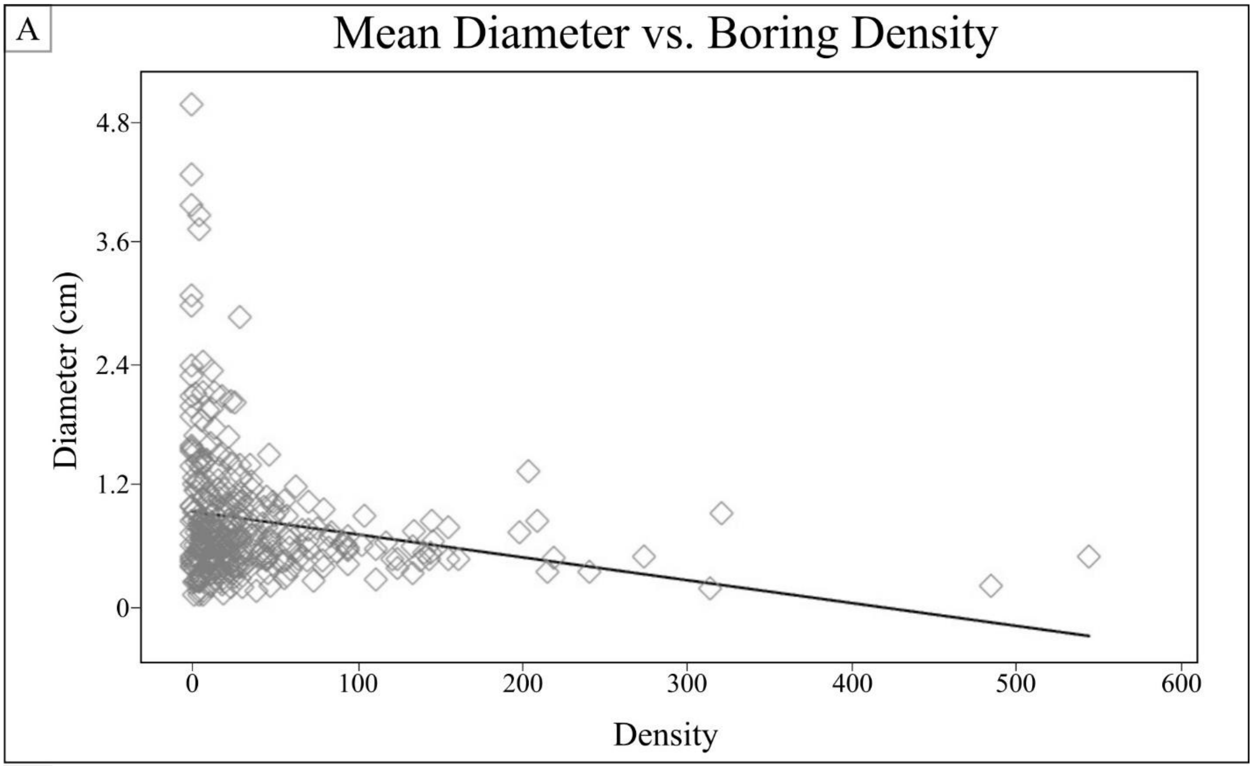

Size-Frequency and Woodground Preservation Type
Teredolites clavatus
Xylic peatgrounds
Well-preserved log-grounds
Relict log-grounds
Ghost log-grounds
Density
0
100
200
300
400
500
600
700
800
0
1
2
3
4
5
Diameter (cm)
Increasing degradation

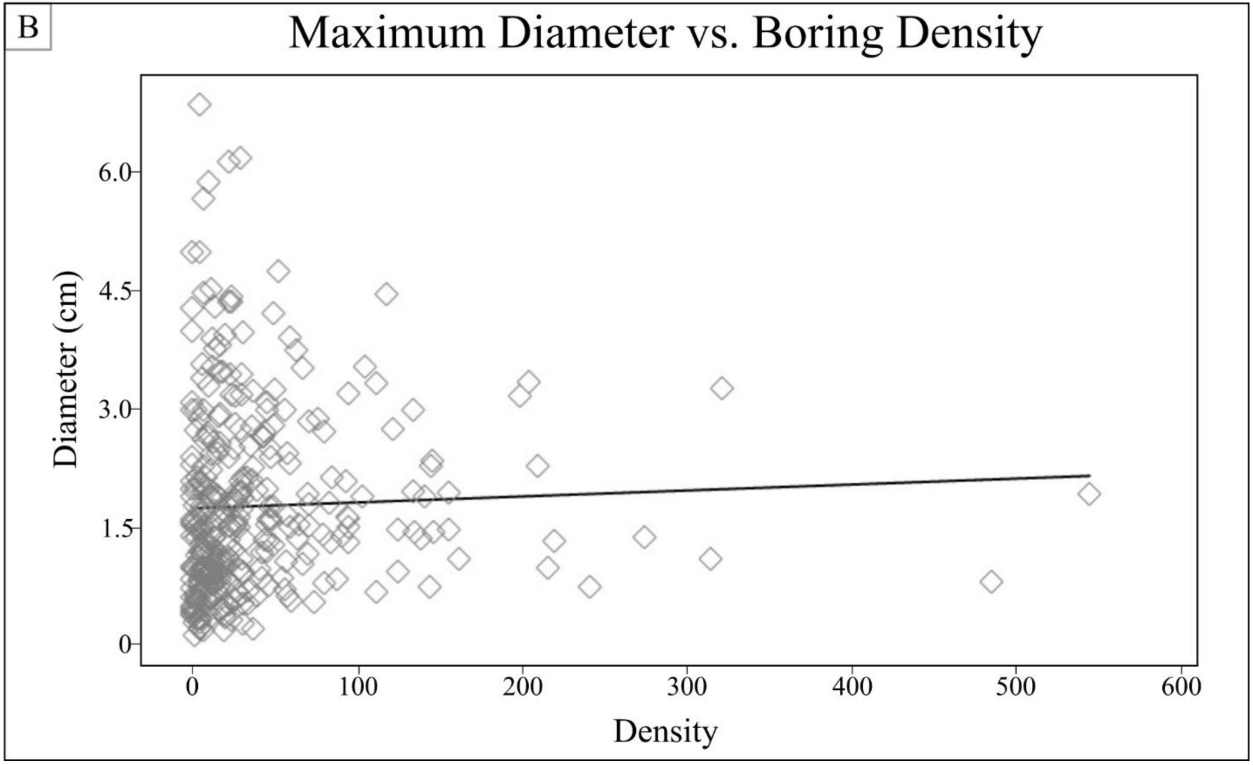

Size-Frequency and Woodground Preservation Type
Teredolites longissimus
Xylic peatgrounds
Well-preserved log-grounds
Relict log-grounds
Ghost log-grounds
Density
600
550
500
450
400
350
300
250
200
150
100
50
0
0
1
2
3
4
5
Diameter (cm)
Increasing degradation

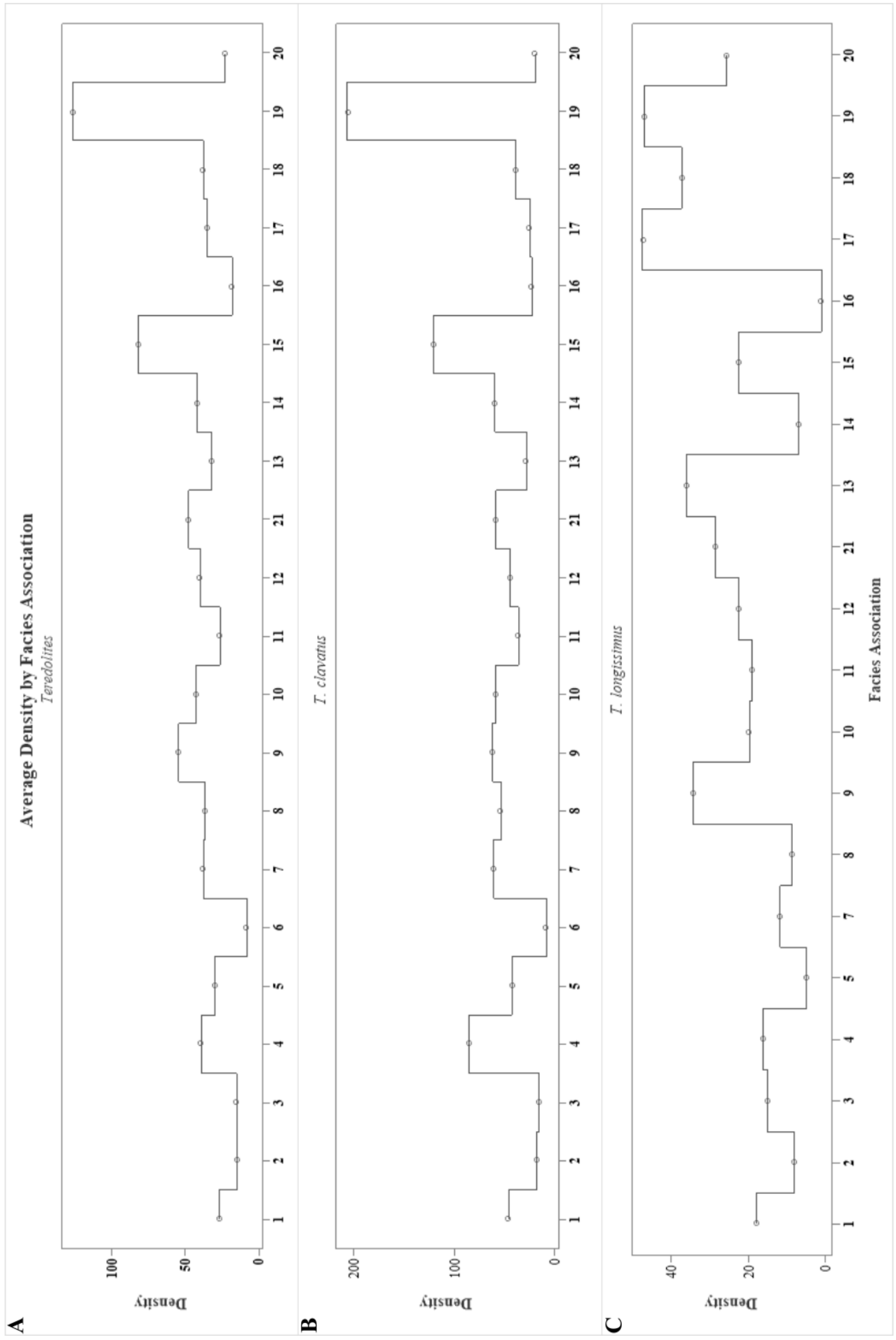


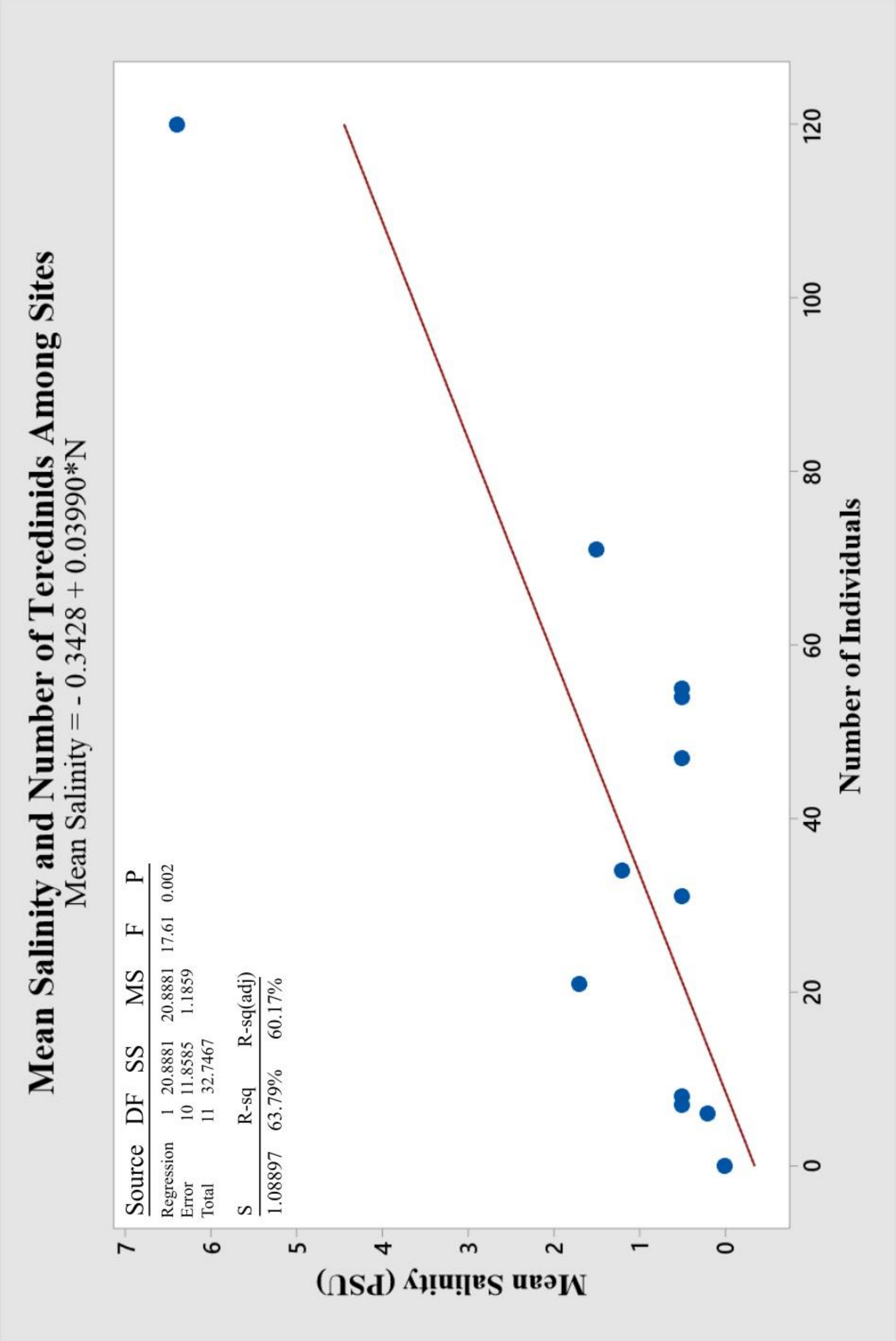
Size-Frequency and Woodground Preservation Type

Ichnogenus *Teredolites*


A
Mean Diameter vs. Boring Density
Diameter (cm)
4.8
3.6
2.4
1.2
0
0
100
200
300
400
500
600
Density


B
Maximum Diameter vs. Boring Density
Diameter (cm)
6.0
4.5
3.0
1.5
0
0
100
200
300
400
500
600
Density


A
Average Density by Facies Association
Teredolites
Density
100
50
0
1
2
3
4
5
6
7
8
9
10
11
12
21
13
14
15
16
17
18
19
20
B
T. clavatus
Density
200
100
0
1
2
3
4
5
6
7
8
9
10
11
12
21
13
14
15
16
17
18
19
20
C
T. longissimus
Density
40
20
0
1
2
3
4
5
7
8
9
10
11
12
21
13
14
15
16
17
18
19
20
Facies Association

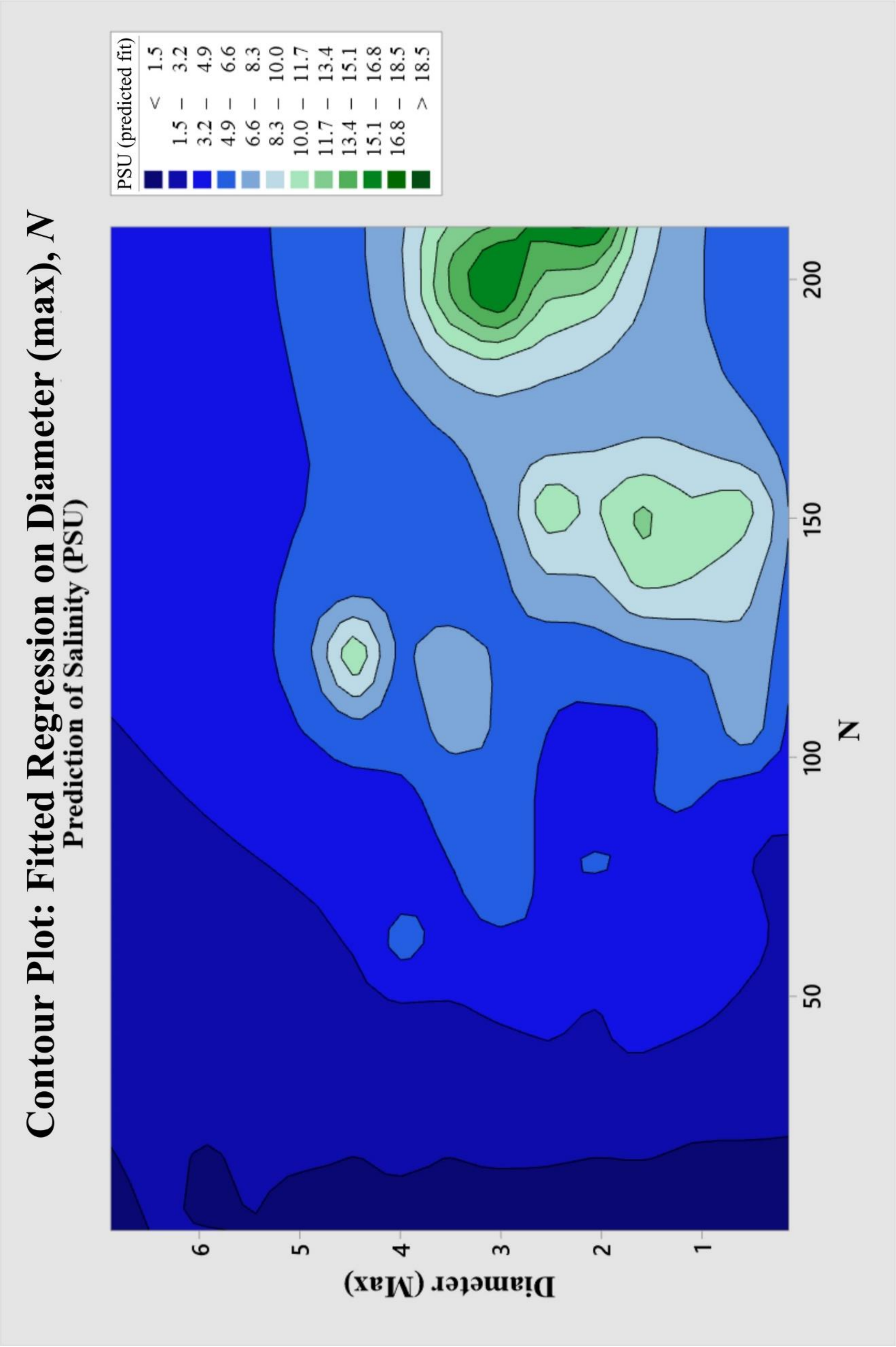


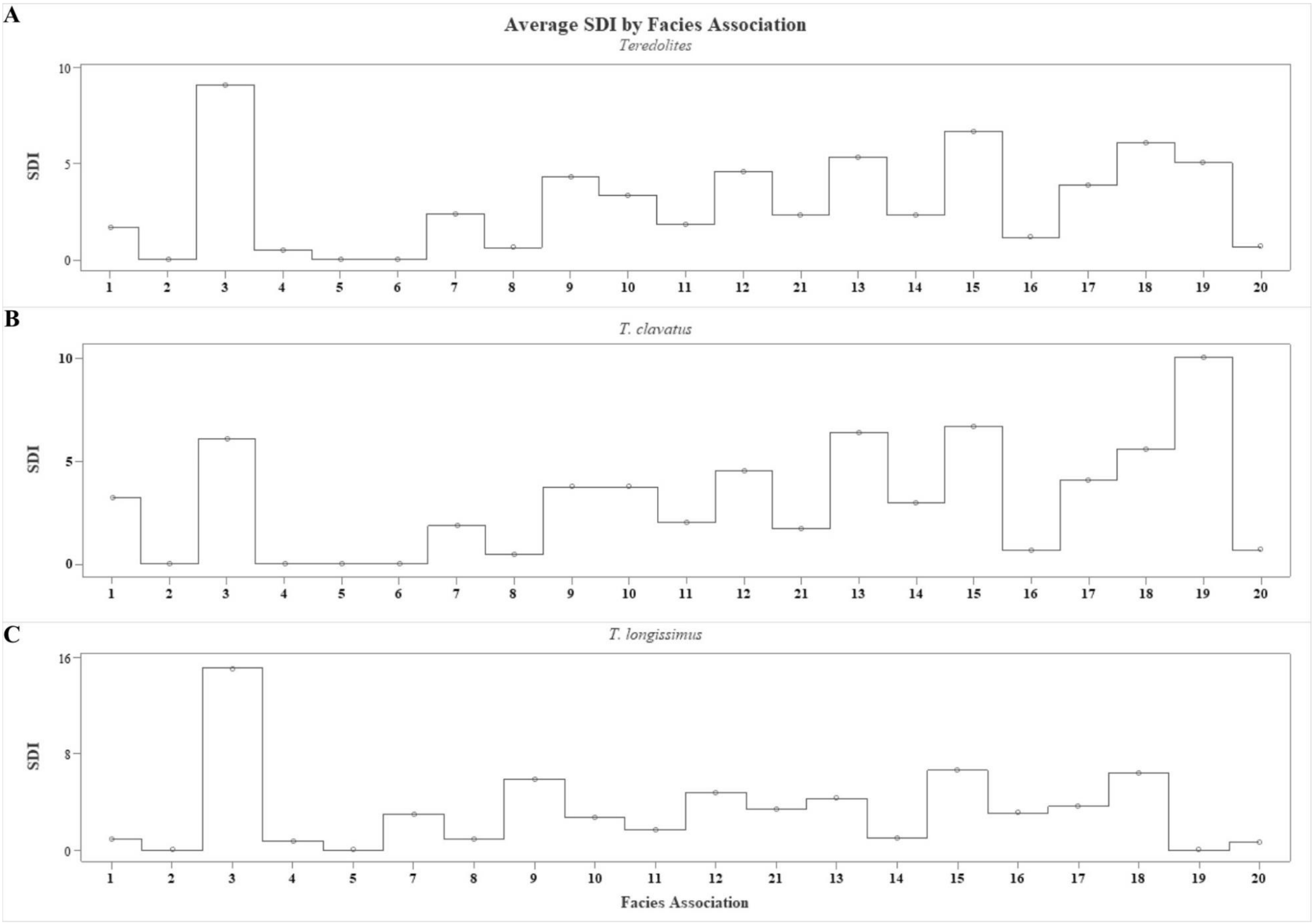
Mean Salinity and Number of Teredinids Among Sites

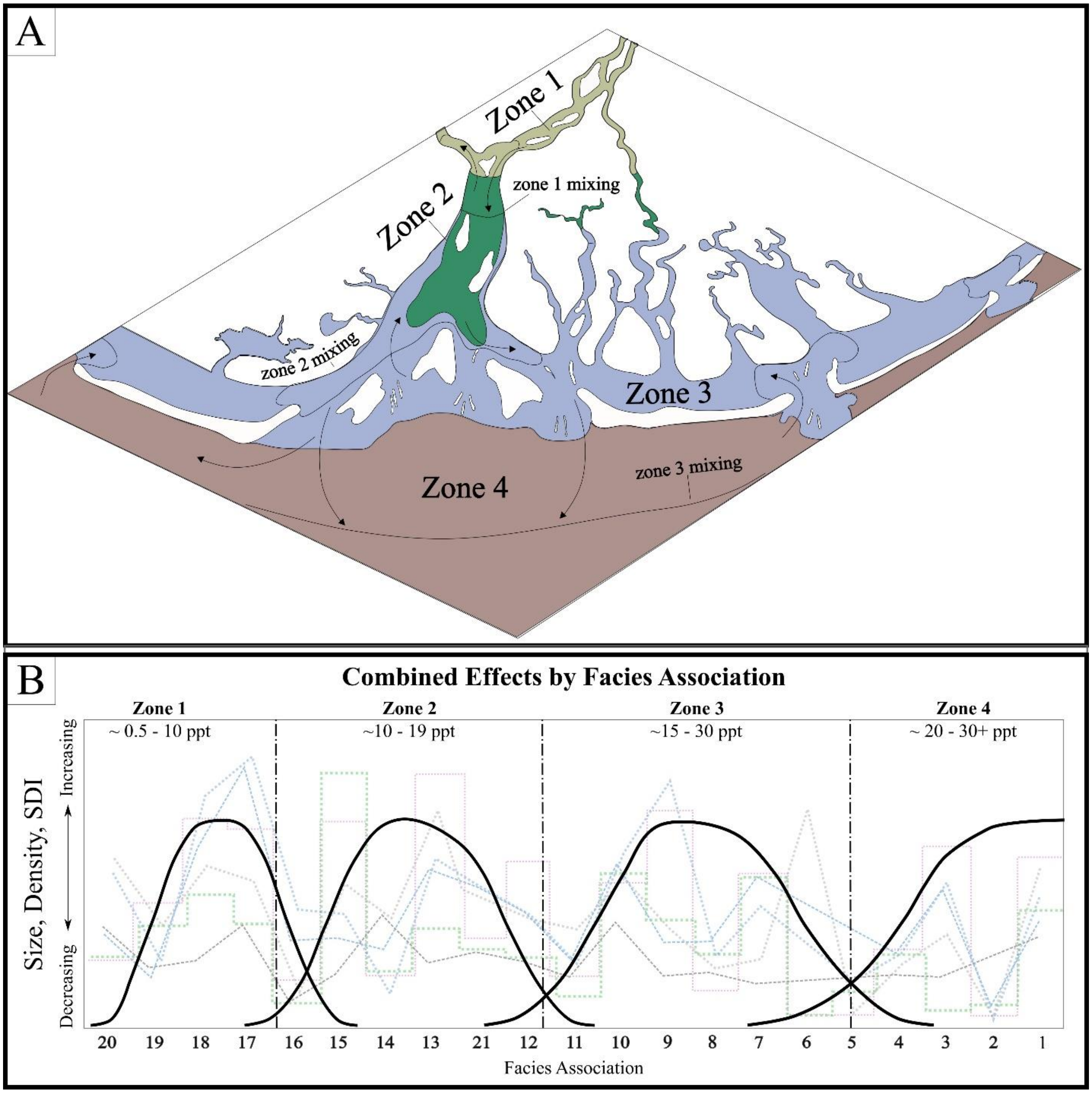
Mean Salinity = - 0.3428 + 0.03990*N

Source	DF	SS	MS	F	P
Regression	1	20.8881	20.8881	17.61	0.002
Error	10	11.8585	1.1859		
Total	11	32.7467			

S	R-sq	R-sq(adj)
1.08897	63.79%	60.17%


Contour Plot: Fitted Regression on Diameter (max), N
Prediction of Salinity (PSU)
PSU (predicted fit)
< 1.5
1.5 – 3.2
3.2 – 4.9
4.9 – 6.6
6.6 – 8.3
8.3 – 10.0
10.0 – 11.7
11.7 – 13.4
13.4 – 15.1
15.1 – 16.8
16.8 – 18.5
> 18.5
Diameter (Max)
6
5
4
3
2
1
N
50
100
150
200


A
Average SDI by Facies Association
Teredolites
SDI
10
5
0
1 2 3 4 5 6 7 8 9 10 11 12 21 13 14 15 16 17 18 19 20
B
T. clavatus
SDI
10
5
0
1 2 3 4 5 6 7 8 9 10 11 12 21 13 14 15 16 17 18 19 20
C
T. longissimus
SDI
16
8
0
1 2 3 4 5 7 8 9 10 11 12 21 13 14 15 16 17 18 19 20
Facies Association


A
Zone 1
zone 1 mixing
Zone 2
zone 2 mixing
Zone 3
Zone 4
zone 3 mixing
B
Combined Effects by Facies Association
Zone 1
~ 0.5 - 10 ppt
Zone 2
~10 - 19 ppt
Zone 3
~15 - 30 ppt
Zone 4
~ 20 - 30+ ppt
Size, Density, SDI
Decreasing
Increasing
20
19
18
17
16
15
14
13
21
12
11
10
9
8
7
6
5
4
3
2
1
Facies Association

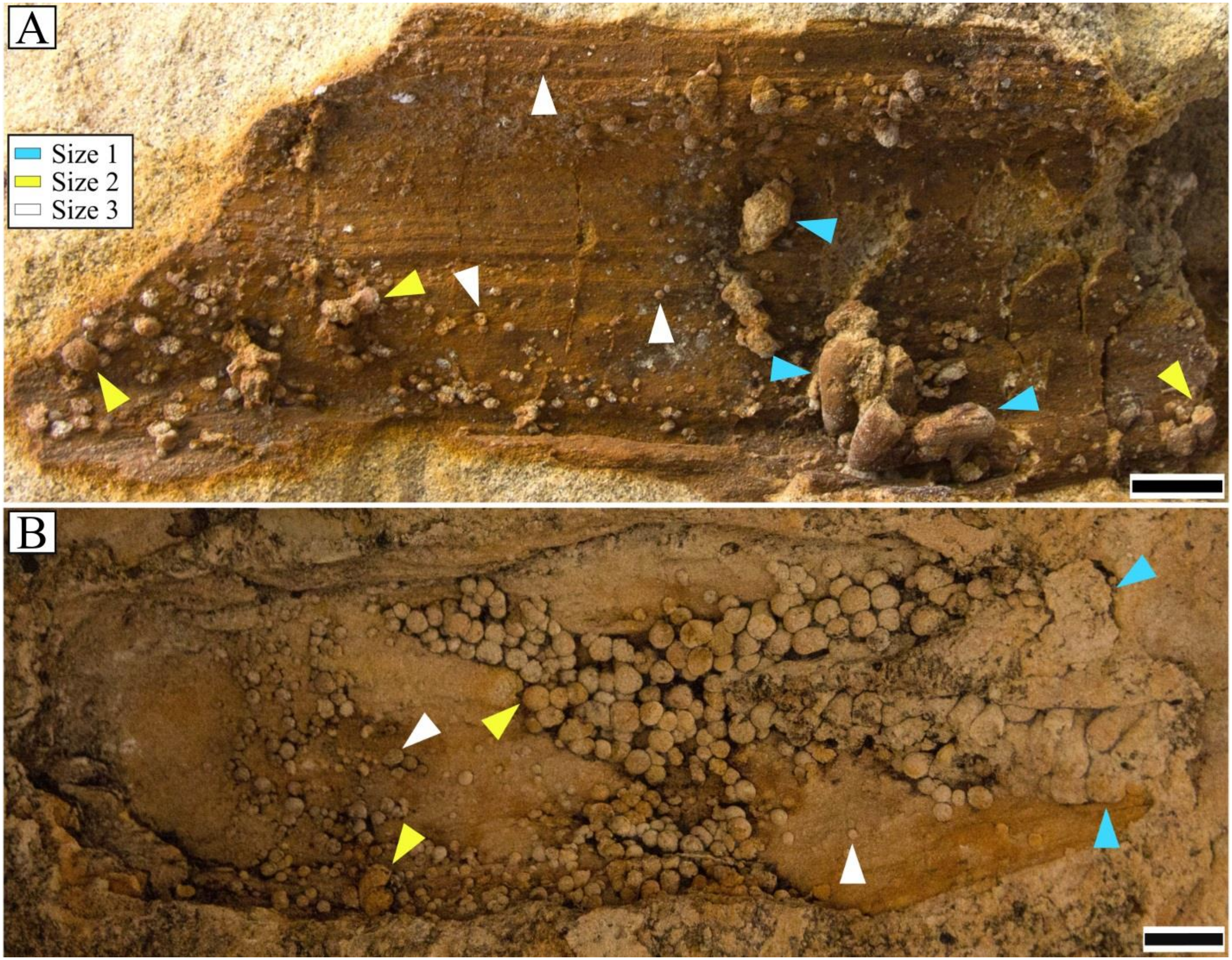
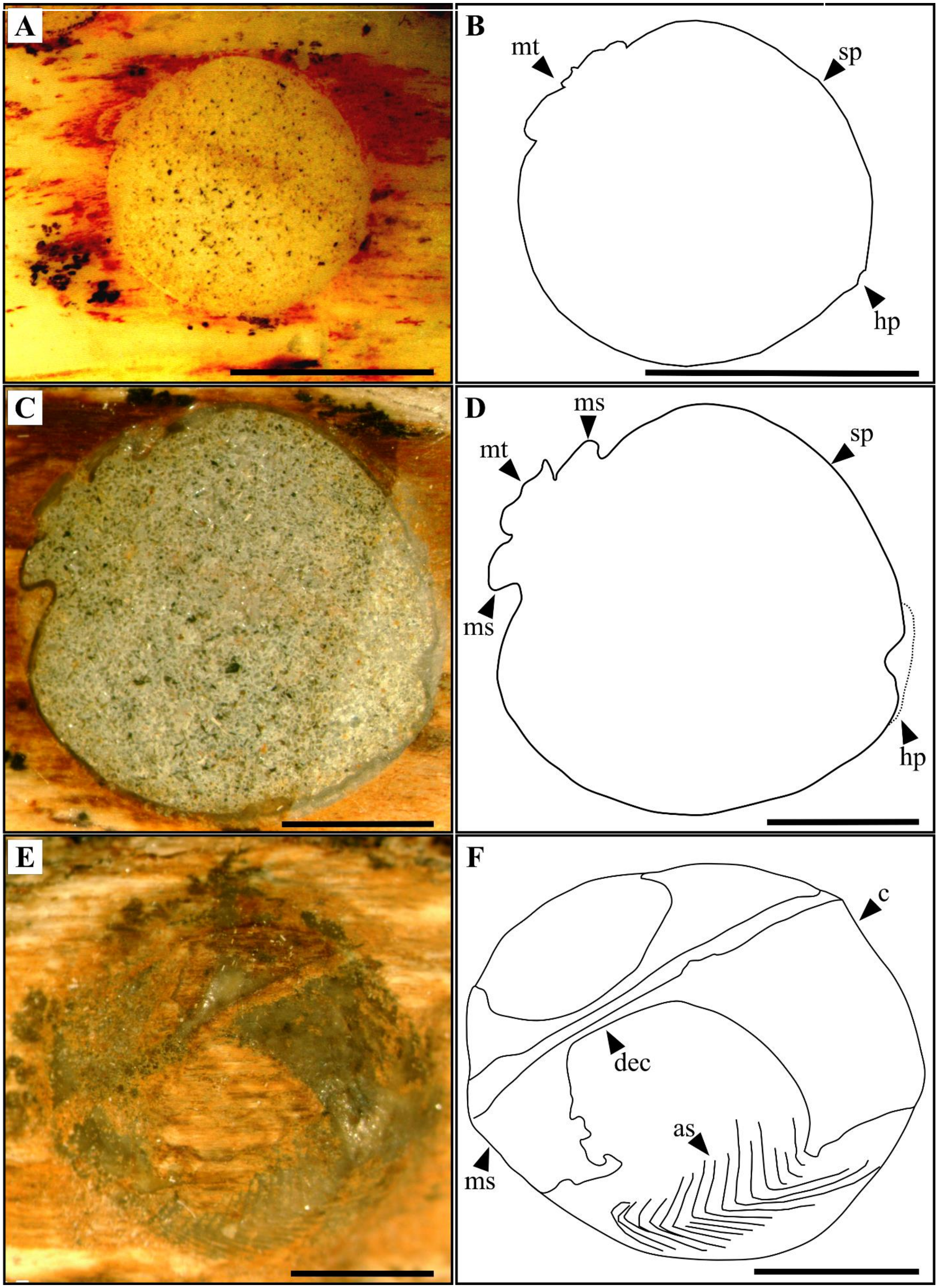
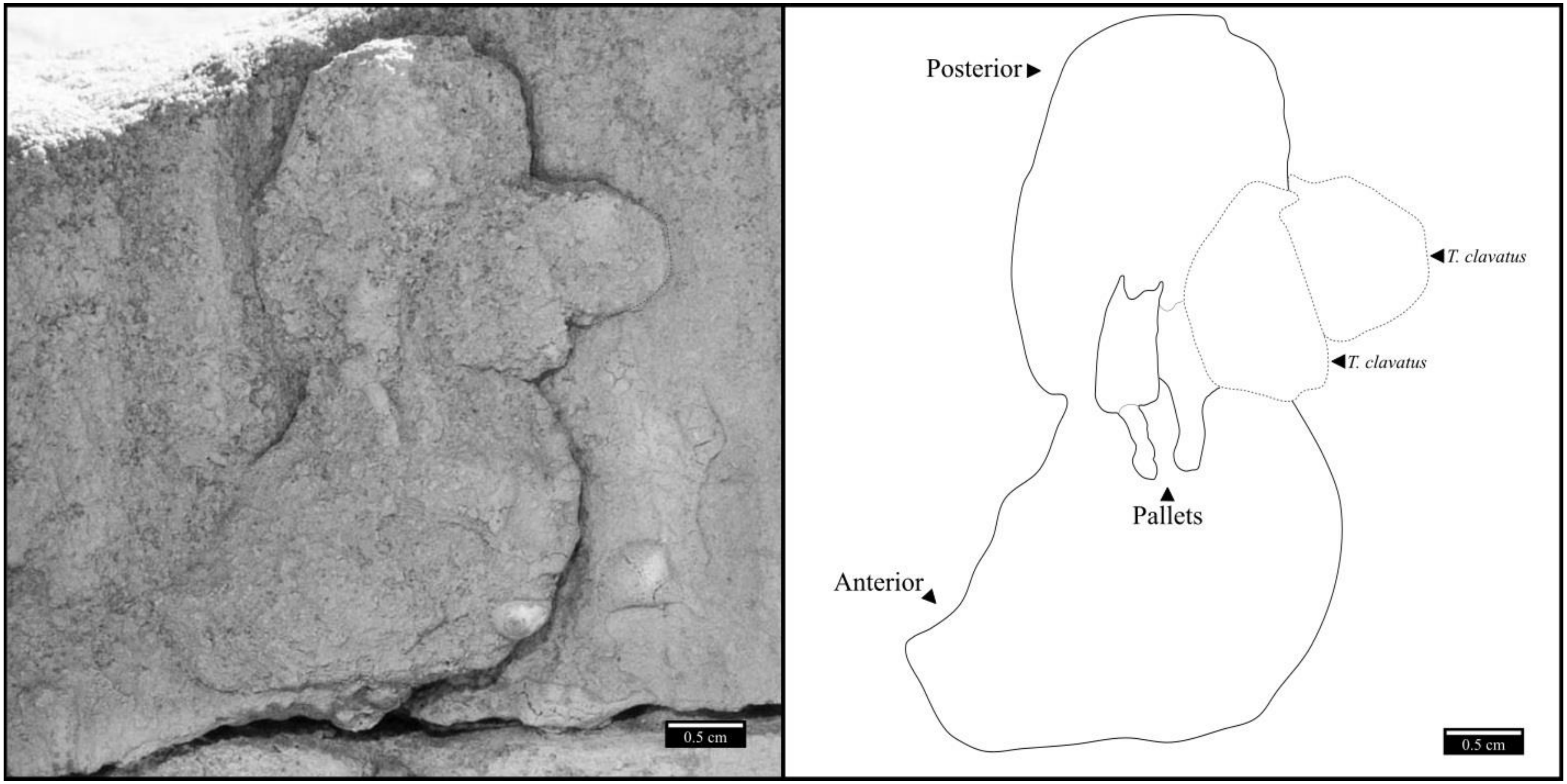
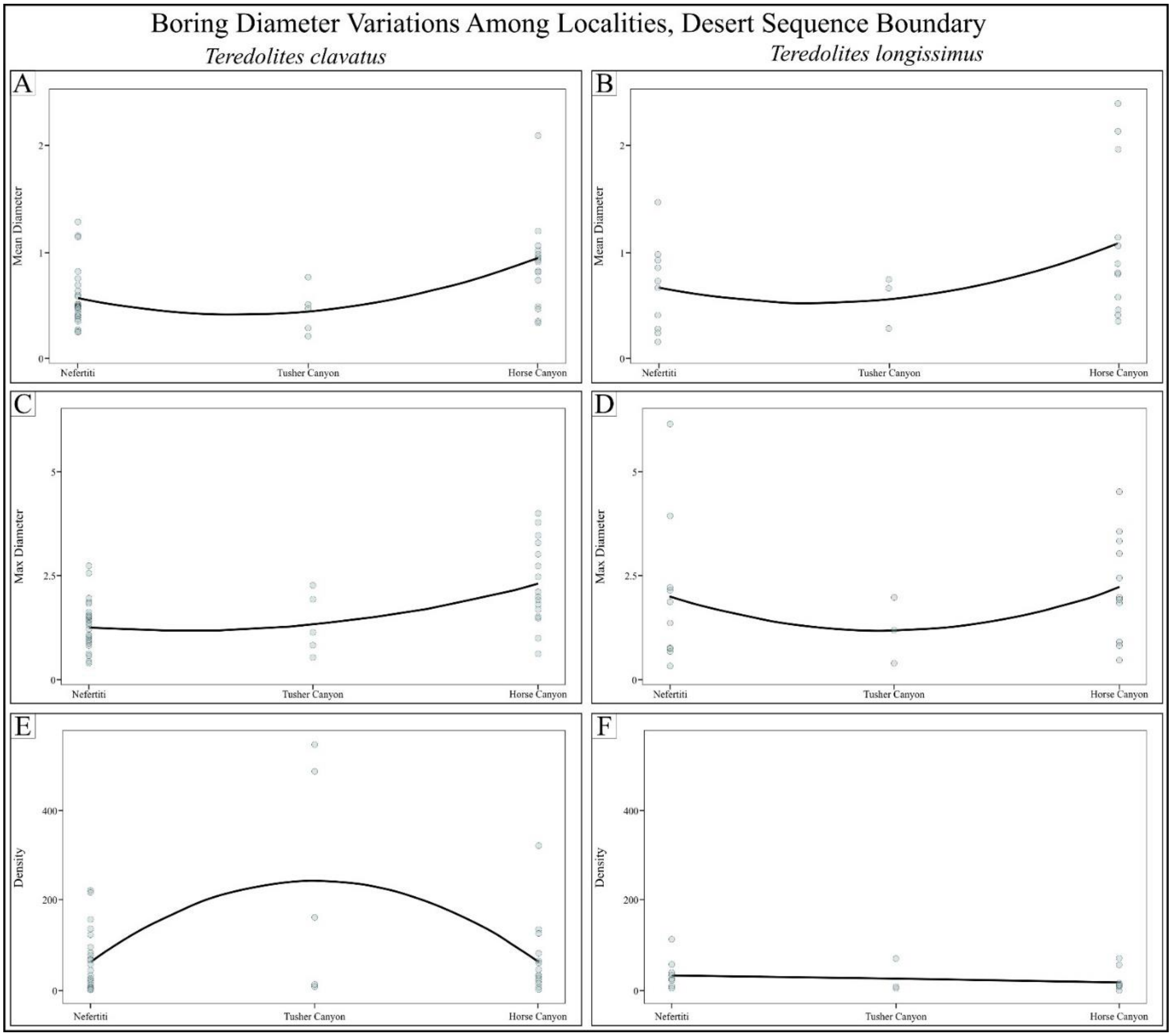

A
Size 1
Size 2
Size 3
B

Fig. 22: *Teredina jeffersoni*.




0.5 cm
Posterior
T. clavatus
T. clavatus
Pallets
Anterior
0.5 cm

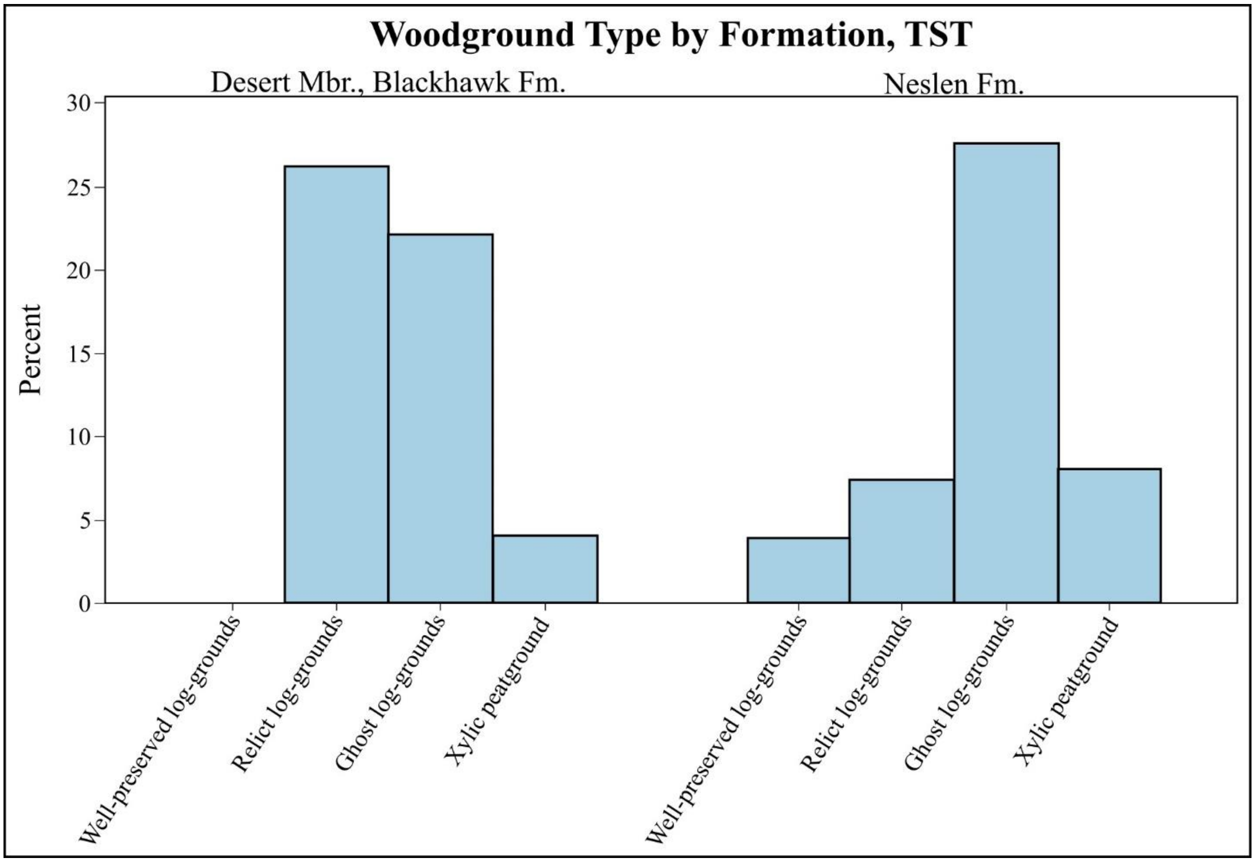

A
KU MIP 82136
B
KU MIP 82135
C
YPB IP 393493
D
KU IBGS CB-TC-030
E
YPB IP 393493
F
KU PB "K-5-L"
G
YPB IP 393493

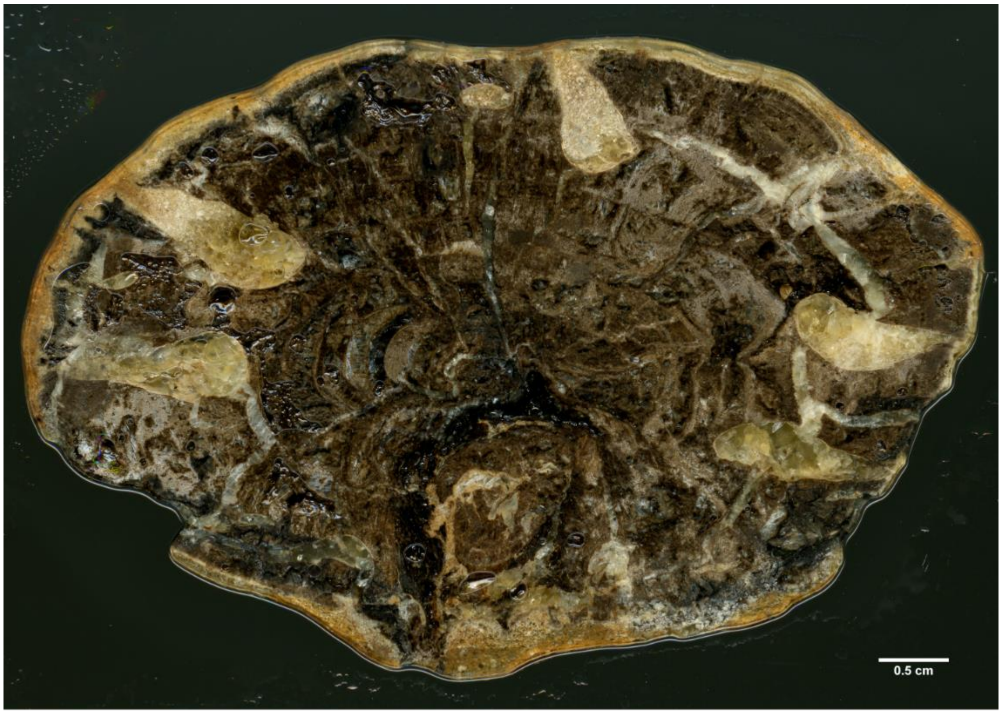


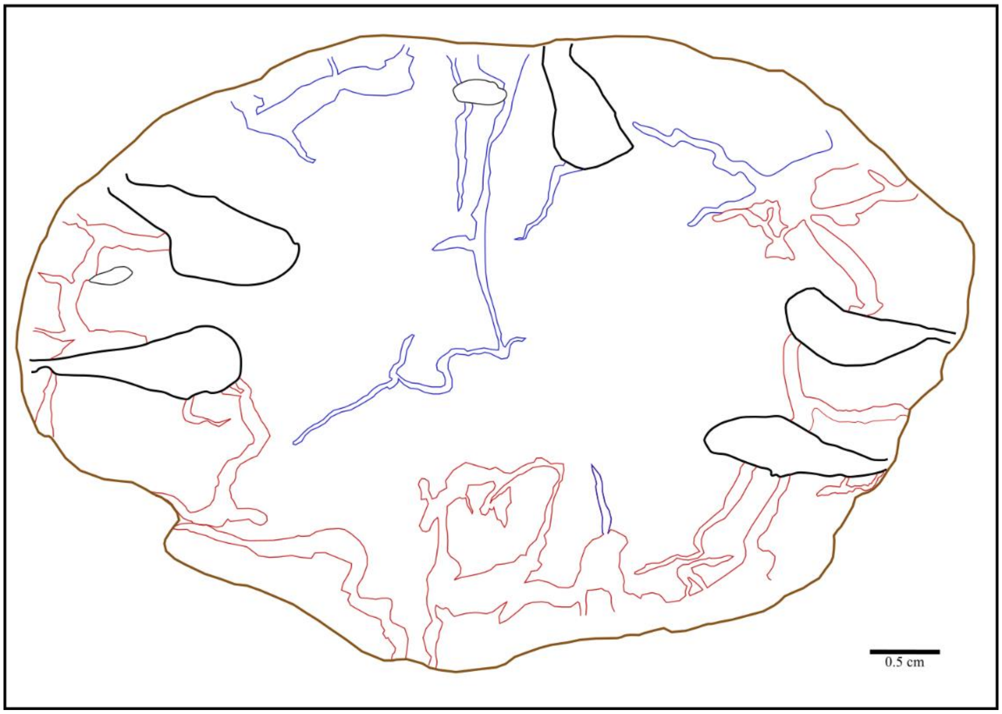
Boring Diameter Variations Among Localities, Desert Sequence Boundary

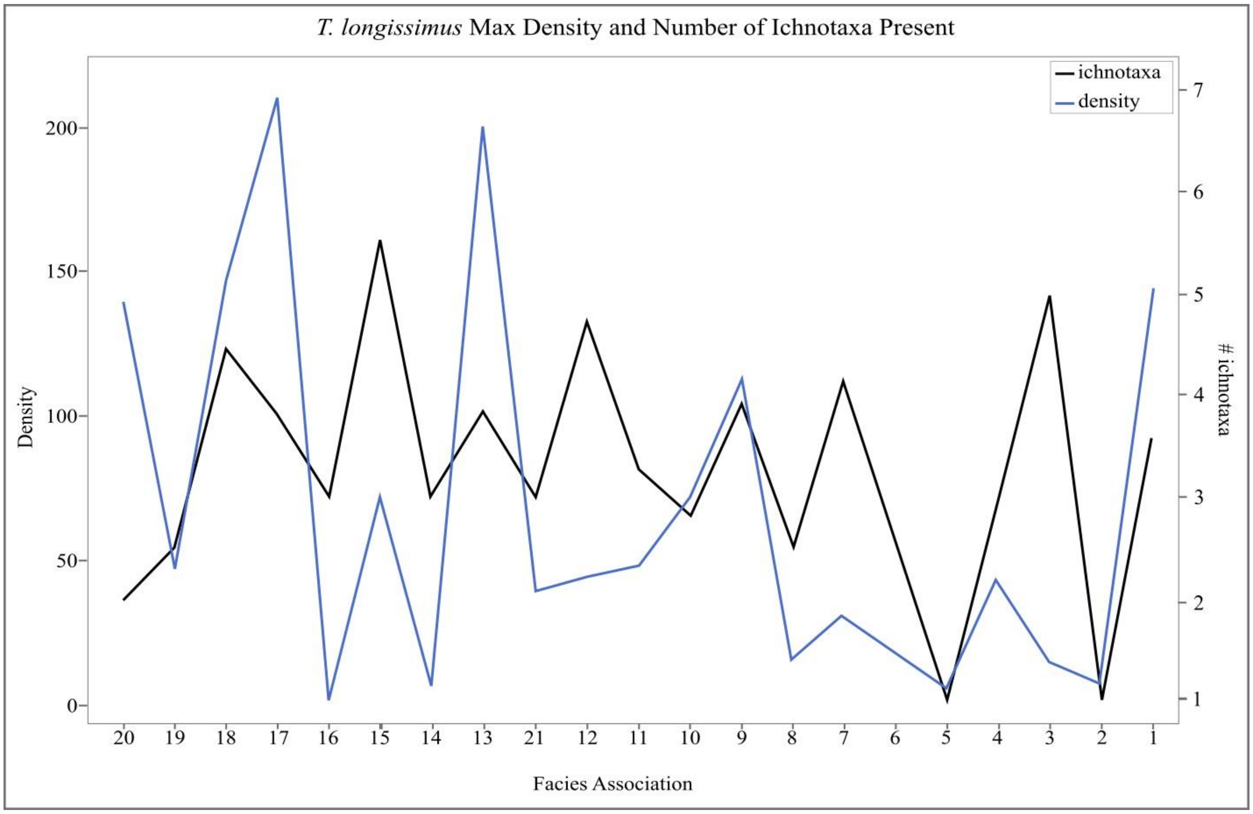
Teredolites clavatus

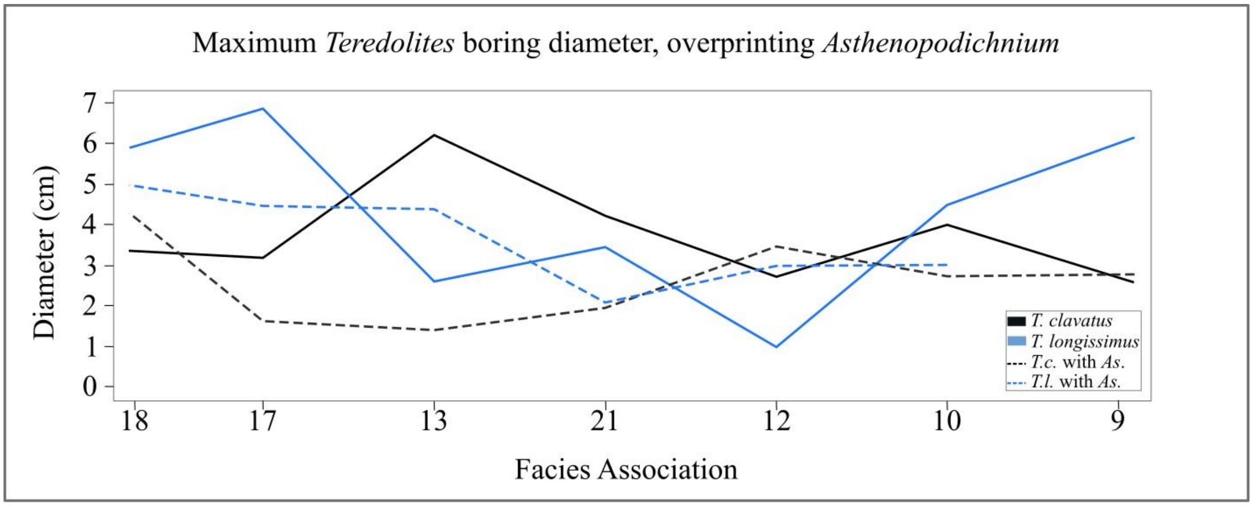
Teredolites longissimus

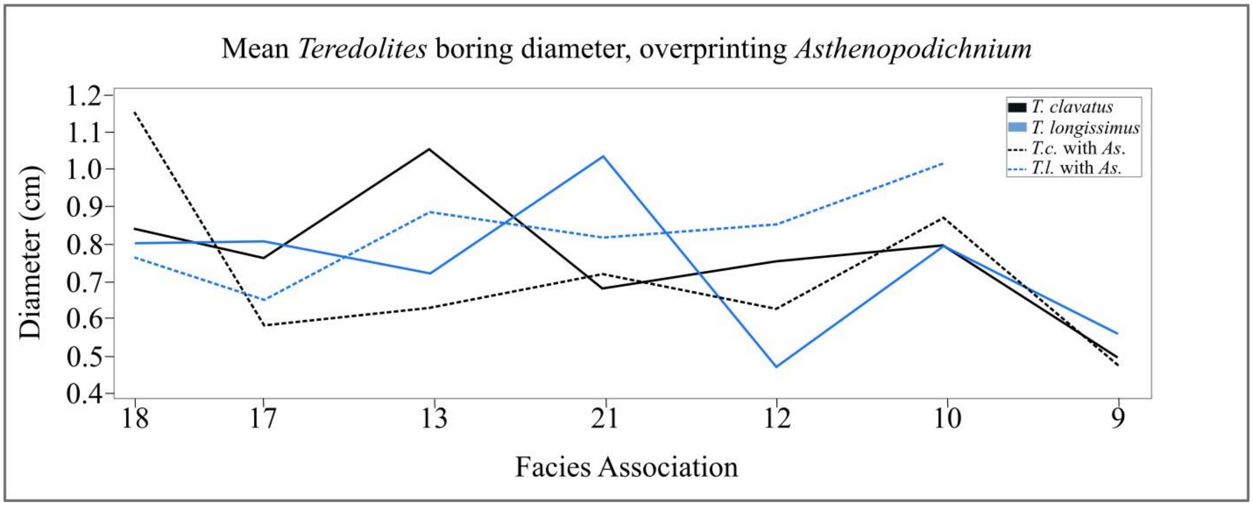

Woodground Type by Formation, TST
Desert Mbr., Blackhawk Fm.
Neslen Fm.
Percent
0
5
10
15
20
25
30
Well-preserved log-grounds
Relict log-grounds
Ghost log-grounds
Xylic peatground
Well-preserved log-grounds
Relict log-grounds
Ghost log-grounds
Xylic peatground


0.5 cm


0.5 cm


T. longissimus Max Density and Number of Ichnotaxa Present
ichnotaxa
density
Density
0
50
100
150
200
ichnotaxa
1
2
3
4
5
6
7
Facies Association
20
19
18
17
16
15
14
13
21
12
11
10
9
8
7
6
5
4
3
2
1


Maximum *Teredolites* boring diameter, overprinting *Asthenopodichnium*


Mean *Teredolites* boring diameter, overprinting *Asthenopodichnium*

Environmental Factors
Temperature
Salinity
Oxygen Tension
Turbidity
Pollutants
Presence and intensity of fouling organisms
Nature of the medium (species, softness, grain orientation)
Medium immersion period
Presence-absence of preservatives used on medium
Location of medium in relation to tidal changes
Possible exposure to dessication
Orientation with respect to depth
Nature of bottom
Mechanical effects of currents
Current velocity
Illumination
Interaction with other wood borers
Availability of suitable media at time of settlement
Effectiveness of local larvae sources
Presence-absence of predators and parasites

Parameters of Palichnologic Dataset	
Field ID	
Locality	Sampling locality
Age	Epoch, Series age if available.
Age Rank	Ranking assigned to sample age from oldest (smallest value) to youngest (highest).
Facies Association	Interpreted EOD of lithofacies associations.
Facies Association Code	Rank given to facies association from most distal (seaward) to most proximal (basinward)(1 - 22).
Ichnospecies	*Teredolites clavatus*, *T. longissimus*
Ichnospecies Code	Ranked coding for ichnospecies: 1= *T. clavatus*; 2= *T. longissimus.*
Density	Number of borings in a given sample.
Maximum Diameter	Maximum boring diameter in a given sample.
Mean Diameter	Mean boring diameter within a given sample.
Ichnocoenoses	Ichnofossils found associated with xylic media or along the same bedding plane as those which occur *Teredolites.*
Diveristy Rank	Rank assigned by the sum of traces found alongside a *Teredolites* occurrence.
SDI	The product of the maximum boring diameter in a given sample and the number of observed traces co-occurring with the same sample.
Systems Tract	Systems tract in which a sample is interpreted to have occurred.
Woodground Preservation Type	Woodground preservation type of a given teredolites sample per Bromley et al. 1984 and Savrda et al. 1993.
Woodground Preservation Code	Ranked value of woodground preservation type: 1 = xylic peatgrounds; 2 = well-preserved log-grounds; 3 = relict log-grounds; 4 = ghost log-grounds; 5 = reworked *Teredolites.*

Parameters of Modern Dataset	
Family	-
Subfamily	-
Genus	-
Species	-
Describer	-
Salinity Minimum	Minimum salinity tolerated
Salinity Maximum	Maximum salinity tolerated
Location	Collection Location
Substrate Specialist	For species requiring specific medium (i.e. seagrass, mangroves)
Reproduction Type	-
Breeding Season	-
Growth Rate Length	Growth rate (cm/month)
Growth Rate Width	Growth rate (cm/month)
Mean W:L shell ratio	-
Notes	i.e. breeding salinty ranges
Length	Length of boring (cm)
Width	Width of boring (cm)
Ichnospecies	-
Ratio	W:L ratio of boring
EOD	Environment of collection or deployment
Source	Sources for all above parameters

Teredolites Measured by Formation

Anchor Mine Tongue	8
Arroyo Escobar*	32
Bhuban Fm.*	23
Burket Quran	145
Blackhawk Fm.	
Desert Mbr.	463
Kennilworth Mbr.	11
Budden Canyon Fm.	
Lower Chickabilly Mbr.	246
Carlile Shale	306
Fairport Chalk Mbr.	46
Castlegate Sandstone	8220
Ceru di Cueba Fm.*	17
Chatton Fm.*	22
Dakota Sandstone	
D Sandstone	90
Expedition Fjord*	4
Ferron Sandstone*	53
Greenhorn Limestone	302
Horseshoe Canyon Fm.*	33
Jagua Fm.*	37
Kaiparowits Fm.*	20
Lias y/∂ Iron-Limestone Bank*	32
Loyd Sandstone	7
Niobrara Chalk	
Smokey Hill Chalk Mbr.	9
Neslen Fm.	2193
Noije Hill Bum Site*	32
Nunsplingen Plattenkalk*	12
Quiriquina Fm.*	61
Qsar al Sagha Fm.	
Dir Abu Lifa Mbr.	11
Rio Mayer Fm.*	20
Sego Sandstone	873
Star Point Fm.	
Panther Tongue Mbr.	292
Straight Cliffs Fm.*	
John Henry Mbr.*	48
Tallahatta Fm.*	134
Wangaloa Fm.*	132

*Measured from scaled photographs in the literature.

Facies Association	Lithology	Contacts	Diagnostic Features	Ichnology	Occurrence	Interpretation	Contribution (%)
1	Thickening-upwards succession of thinly bedded (5 - 10 cm) structureless bioturbated mudstone and structureless to planar-laminated siltstone. Overlain by wavy bedded carbonaceous mudstone with *Te*. *Ch* occurring within and around *Pl*.	Base: sharp. Top: sharp.	Heavily bioturbated siltstones and mudstones.	*Be, Ch, Pl, Op, Ta*	Desert Mbr., Blackhawk Fm. (Sagers Canyon)	Open Marine/ shelf.	10.24%
2	Interbedded sandy siltstone and fine-grained sandstone. Sandstone intervals 5 - 40 cm thick containing planar lamination and minor bi-directional ripples. Siltstone intervals contain wood chips with *Te* and leaf fragments.	Base: sharp. Top: sharp.	Heterolithics thickening-upwards.		Kennilworth Mbr., Blackhawk Fm.	Offshore transition.	0.81%
3	Interbedded siltstone and sandstone with hummocky cross-stratification, wave ripple and planar lamination. Sandbodies 10 - 50cm thick. Mud drapes common bounding sandbodies which occasionally contain pebble to cobble-sized siderite concretions.	Base: Sharp. Top: Sharp to gradational.	Hummocky cross-stratified sandstones and interbedded siltstones.	*Op, Phy, Pl, Rz, Th*	Castlegate Ss. (Sagers Canyon); Desert Mbr., Blackhawk Fm.	Distal lower shoreface.	0.81%
4	Interbedded siltstone and sandstones (1 - 3 m) with hummocky and swaley cross-stratification, wave ripple lamination, and planar-lamination.	Base: sharp. Top: sharp.	Hummocky and swaley cross-stratification.	*Be, Op, Pl, Th*	Castlegate Ss. (Sagers Canyon); Desert Mbr., Blackhawk Fm.	Lower shoreface.	3.50%
5	Very fine- to fine-grained sand with flaser bedding containing tidal rhythmites. Well-developed ridge and runnel systems contain sigmoidal cross-bedding, mega ripples, and small-scale interference ripples with accumulation of heavy minerals and fecal peloids in toughs on stoss side.		Sigmoidaly bedded, tidally modified sands.	*Dipatra* tubes, *Op, Pi*	Sapelo Is., GA; Virginia Beach, VA.	Foreshore/ upper shoreface.	1.35%
6	Very fine to fine-grained, parallel-laminated sheet to wedge-shaped sandstone. Current ripples and trough cross bedding uncommon. Wood fragments containing *Te* occur at bases of beds.	Base: gradational. Top: sharp.	White-stained, wedge-shaped sandbodies.		Desert Mbr., Blackhawk Fm.; Broad Bay, VA	Backshore.	0.27%
7	Coarsening-upward succession of ripple-laminated carbonaceous mudstone and very fine- to fine-grained sandstone. Heterolithic intervals commonly contain 2 m lenticular barforms cross-stratified at foresets. Coarsens into fine- to medium- grained tabular cross-stratified and herringbone cross-laminated sandstone with FWL bedding, mud clasts, and wood fragments.	Base: sharp. Top: sharp.	Coarsening-upward hetero-lithics with barforms and tidal structures.	*Lim, Op, Pi, Ro*	Castlegate Ss. (Rangely, CO), Sego Ss.	Tidally modified delta.	4.04%

Facies Association	Lithology	Contacts	Diagnostic Features	Ichnology	Occurrence	Interpretation	Contribution (%)
8	Fine to medium-grained structureless to planar laminated sandstone. Mud and coal rip-up clasts Common at base. Sandbodies grade laterally into heavily bioturbated mudstone and siltstone.	Base: sharp to erosional. Top: sharp.	Massive sandstones with tool marks and isolated logs at bases of beds..	*As, Op*	Panther Tongue Mbr., Star Point Fm.	Mouth Bar.	2.16%
	Very fine to fine-grained, structureless sandstone and interbedded coarse siltstone. Heavily bioturbated with organics-rich drapes and commonly contains coal clasts.	Base: sharp. Top: sharp.	Bioturbated heterolithics	*Cy, Pa, Pl, Sk, Tei, Th*	Panther Tongue Mbr., Star Point Fm.		
9	Fine to medium-grained wave and current rippled sandstone. Isolated channel bodies 5 - 10 m wide with 10 - 50 cm lenticular bedsets or 0.5 - 1 m wedge-shaped beds. Mud and carbonaceous drapes encase bedsets. Sandbodies planar-bedded with low-angle trough cross-bedding. Rip up clasts, wood and bone fragments abundant.	Base: erosional. Top: sharp.	Incisional sandbodies with abundant carbonaceous, argillaceous, and skeletal material.	*As, Ro, Tei*	Desert Mbr., Blackhawk Fm.	Tidal inlet channel.	10.78%
10	Fine to medium-grained structureless to sigmoidal bedded sandstone. Common mud drapes along foresets; mud rip-ups and bone fragments at base of sigmoids. Log-grounds containing *Te* and small *As* common at base of succession.	Base: sharp. Top: sharp.	Small-scale, isolated sandbodies overlying coals and carbonaceous mudstones	*As, Tei*	Castlegate Ss.	Tidal Channel.	7.82%
11	Upward-coarsening succession of carbonaceous, structureless mudstone and siltstone with FWL bedding. Overlain by structureless very fine- to fine-grained structureless, planar laminated, or sigmoidal cross-bedded sandstone. Mud chips common sandbody bases and sporatically within bed foresets. Mud drapes uncommon along foresets. *Te*-bored wood and *Op* common. Large, vertically penetrating rhizoliths and *Si* uncommon in structureless sandstone.	Base: sharp. Top: sharp.	Coarsening-upwards heterolithics.	*Op, Rz, Rhi, Si*	Sego Ss., Neslen Fm.	Sandy tidal flat.	1.89%
12	Heterolithic 2 - 5 m succession of carbonaceous mudstone with discontinuous very-fine silty- and fine to medium-grained sandstone beds. Mudstone weakly planar laminated and heavily bioturbated, rarely contains log-grounds with *Te*. Sandstone beds contain trough and sigmoidal cross-bedding. Mud rip-up clasts and dinosaur tracks common at erosional bases.	Base: sharp or gradational. Top: sharp or erosional .	Heterolithics at uppermost Lower Castlegate Ss.	*As, Be, Co,* Dt, *Lim, Phy, Tei*	Castlegate Ss.	Estuary.	7.28%

Facies Association	Lithology	Contacts	Diagnostic Features	Ichnology	Occurrence	Interpretation	Contribution (%)
13	Coarsening-upward succession of interbedded carbonaceous, current rippled mud and siltstone with wavy and lenticular bedding and occasional rhythmic laminations. Coarsens into fine-grained, sigmoidal cross-bedded sandstone with mud drapes and skeletal material. *Op*, *Th*, and *Te*-bored log-grounds are abundant.	Base: sharp. Top: sharp.	Coarsening-upward, cross-bedded heterolithics.	*As, Be, Pl, Op, Tei, Th*	Sego Ss.	Estuarine tidal sand bars.	5.12%
14	High-relief (25 - 30m), incisional, channel-form fine-grained sandstone with tabular and trough cross-stratification. Erosional, basal beds of stacked channels contain concentrated lags of *Te*-bored wood fragments and occasional mud rip-up clasts.	Base: erosional. Top: sharp.	High relief channel-form sandbodies.	*Op*	Sego Ss.	Tidally influenced valley fills.	0.81%
15	Fine to coarse-grained sandstone with large scale sigmoidal cross-bedded barforms, current ripple lamination, mud drapes, tidal bundles, and clay rip-up clasts. Mud drapes contain coarse and to pebble-sized carbonaceous material. Occasionally interbedded with with 10 cm beds of carbonaceous siltstone.	Base: sharp. Top: sharp.	Cross-bedded channel-form sandstone.	*As, Co, Di,* Dt, *Gf, Lim, Op, Rz, Sk, Tei*	Castlegate Ss.	Upper estuary.	5.39%
16	Fine to medium-grained limonite-stained sandstone with planar and rare ripple lamination. Sandbodies 0.5 - 2m thick with a sheet-like geometry overlying steeply dipping carbonaceous mudstone. Log-grounds common as cobble-sized clasts with *Te*.	Base: sharp. Top: sharp.	Limonite-stained planar bedded sandstone overlying mudstone.		Dakota Ss.	Bayhead delta.	1.35%
17	0.5-10 m succession of erosionally based, very-fine to fine-grained sandstone, fining upward into very fine to upper fine-grained sheet sandstone. IHS and trough cross-stratification or combined-flow ripples common with abundant mud chips, wood fragments at base, occasionally containing skeletal fragments of bivalves, gastropods, and fish. Succession fines-upward containing very-fine to upper very fine grained cross-laminated sandstone and capped by very fine grained planar-laminated sandstone, structureless siltstone, and occasionally carbonaceous shale.	Base: sharp to erosional. Top: sharp.	Erosionally based, fining-upward sheet sandstone with tidal indicaors and high ichnodiversity.	*As, Au, Lo, Gl, Pe, Pl, Rz, Sa, Si, Un*	Neslen Fm.	Distal tidal-fluvial channels.	10.24%

Facies Association	Lithology	Contacts	Diagnostic Features	Ichnology	Occurrence	Interpretation	Contribution (%)
18	Medium to coarse-grained sandstone interbedded with rhythmically bedded, current rippled mudstone and siltstone 0.5 - 3m thick. Sandstone contains trough cross-bedding, planar lamination, and carbonaceous drapes, double mud drapes containing silt to sand sized carbonaceous material. Large log-grounds with *As* and *Te*.	Base: sharp. Top: sharp.	Interbedded carbonaceous heterolithics with coarse carbonaceous material and large wood fragments	*As*, Dt, *Gl*, *Pi*, *Ps*, *Rhi*, *Si*, *Th*	Castlegate Ss.	Tidally influenced fluvial channel.	12.94%
19	Fine to very-fine grained, incised channel fill sandstones and siltstone 10s of m thick. Convolute bedding, trough cross-bedding, planar lamination, and wave-rippled lamination occurring in bedsets 5 - 50 cm thick. Mud drapes and double mud drapes common containing carbonaceous material. Isolated wood fragments rarely contain *Te*. Overlain by thin (1m) coal bed.	Base: sharp to erosional. Top: sharp.	Scoop-shaped channelforms with convolute bedding, mud drapes, overlain by coal.		Castlegate Ss.	Fluvial channel.	0.54%
20	Erosionally based fine to very-fine grained sandstone 0.5 - 20m thick frequently containing IHS, trough cross-bedding, combined-flow ripple cross-lamination, and planar lamination 10s to 100s m wide. Siderite and mud chips common. Succession fines upward into structureless to cross-laminated siltstone with common FWL bedding or very fine-grained structureless to sigmoidal-bedded sandstone. Soft sediment deformation, siderite, mud chips, and mud rip-up lags common. Isolated plant debris uncommon.	Base: Sharp. Top: Sharp to gradational.	Fining-upward sandstone to siltstone with trough cross-bedding, cross lamination, sigmoidal bedding, soft sediment deformation, siderite, and mud rip-up lags.	*Op*, *Rhi*, *Si* Beetle borings, Bird tracks, *Ca*, *Di*, *Rad*	Neslen Fm., Lafayette R., VA.	Proximal tidal-fluvial channels.	8.62%
21	Fine-grained wavy to planar bedded sandstones with FWL bedding and mud drapes between beds. Interbedded with thin coal beds (10 - 50 cm).	Base: sharp. Top: sharp to erosional.	Sandstones with small-scale coal beds, FWL bedding, plant fragments, and coalified compressions.		Desert Mbr., Blackhawk Fm.	Swamp/ coastal plain.	3.77%
	Packages of coal and carbonaceous shale 0.2 -1.5 m thick, laterally continuous 10 - 100s m. Coals occasionally containing plant impressions and small flecks of amber. *Teredolites* common penetrating tops of coals and in log-grounds. *As* rare in log-grounds.	Base: sharp. Top: sharp to erosional.	Laterally continuous coals and carbonaceous shale	*As*	Castlegate Ss. (Sagers Canyon), Neslen Fm.		

Statistical Summary by Woodground Preservation Type

	Teredolites					*T. clavatus*					*T. longissimus*				
Woodground Preservation	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Density	324	1592	3877	7255	21	160	1340	2792	4709	15	164	252	1085	2546	6
Mean	9.92	6.53	5.24	7.46	11.73	9.64	6.30	4.83	7.17	11.46	10.36	7.75	6.32	8.00	12.40
Minimum	1.03	0.59	0.34	0.33	4.93	1.03	0.59	0.34	0.33	4.93	1.34	1.16	0.66	0.82	10.12
1st quartile	5.34	2.68	2.67	3.98	8.83	4.88	2.54	2.42	3.86	6.92	5.53	4.60	3.52	4.25	11.00
Median	7.98	4.82	4.26	5.86	12.70	7.99	4.43	3.90	5.63	13.17	7.94	6.81	5.08	6.30	12.60
3rd quartile	12.87	8.69	6.48	9.12	14.42	12.10	8.25	6.00	8.61	15.04	13.25	9.16	7.54	9.98	13.85
Maximum	45.28	34.05	56.80	68.80	17.89	35.00	32.59	56.80	61.93	17.89	45.28	34.05	50.00	68.80	14.02
Interquartile range	7.52	6.01	3.81	5.14	5.59	7.21	5.79	3.57	4.75	8.12	7.72	4.56	4.02	5.72	2.85
Mode (*n*)	6.5, 6.52, 8.6, 10.0 (3)	3.0 (9)	4.0 (32)	4.0 (67)	—	2.56, 2.6, 3.3, 3.5 (2)	3.0 (8)	4.0 (14)	5.0 (53)	—	3.46, 3.64, 5.04, 5.7 (2)	8.15, 12.0 (3)	1.0 (12)	1.0 (19)	—

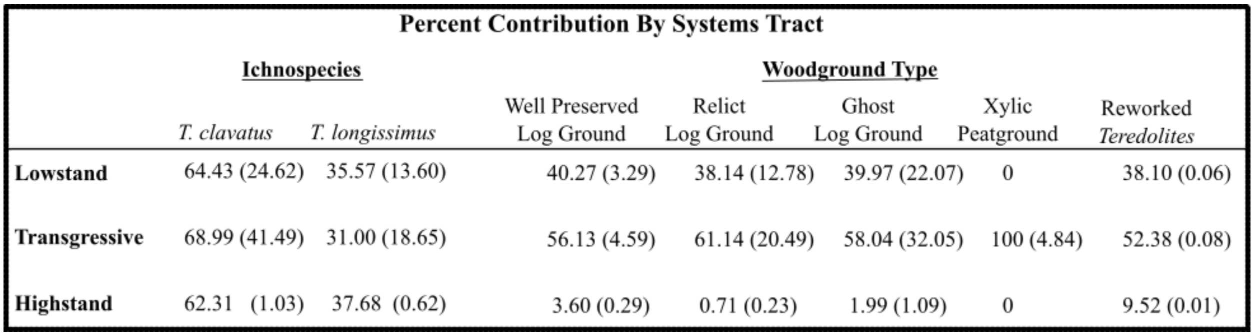
Teredolites boring diameter metrics with respect to woodground preservation type: 1 = Xylic peatgrounds; 2 = Well-preserved log grounds; 3 = Relict log grounds; 4 = Ghost log grounds; 5 = Reworked Teredolites. Measurements in mm.

One-Way ANOVA Summary

Response	Causal Variable	DF	F ratio	p - value	Welch's DF	Welch's F	Welch's p - value
Density	Ichnocoenoses	5, 304	1.67	0.141	5, 76.77	1.59	0.172
	Ichnospecies	1, 327	13.91	**0.000**	4, 264	11.90	**0.001**
	Facies Association	19, 319	1.62	0.051	19, 33.91	1.53	0.137
	Woodground Preservation	4, 326	5.24	**0.000**	4, 31.79	7.59	**0.000**
Diameter	Ichnospecies	1, 13936	215.93	**0.000**	1, 8999.07	227.93	**0.000**
	Facies Association	20, 12654	133.32	**0.000**	20, 383.75	124.18	**0.000**
Length	Ichnospecies	1, 2350	358.42	**0.000**	1, 2349.39	362.49	**0.000**
	Facies Association	19, 2323	13.01	**0.000**	19, 99.54	15.96	**0.000**
	Woodground Preservation	4, 2317	43.41	**0.000**	4, 35.63	57.03	**0.000**
Mean Diameter	Density	100, 240	0.97	0.559			
	Ichnocoenoses	25, 282	1.94	**0.005**	20, 29.71	1.65	0.104
	Ichnospecies	1, 353	2.45	0.118	1, 352.18	2.53	0.122
	Facies Association	19, 344	3.55	**0.000**	19, 36.03	3.22	**0.001**
	Systems Tract	3, 309	1.44	0.231			
	Woodground Preservation	4, 350	11.63	**0.000**	4, 34.42	12.83	**0.000**
Max Diameter	Density	100, 239	0.78	0.922			
	Ichnocoenoses	23, 276	1.79	**0.016**	20, 29.57	1.53	0.142
	Ichnospecies	1, 328	2.45	0.874	1, 299.71	0.02	0.886
	Facies Association	21, 308	4.04	**0.000**	19, 33.64	5.18	**0.000**
	Systems Tract	3, 309	3.10	**0.027**	3, 27.93	3.36	**0.033**
	Woodground Preservation	4, 325	7.25	**0.000**	4, 31.78	7.25	**0.000**
Facies Association	Ichnocoenoses	5, 311	7.50	**0.000**	5, 77.60	7.23	**0.000**
	Ichnospecies	1, 362	0.83	0.363	1, 308.66	0.79	0.374
	Woodground Preservation	4, 348	29.94	**0.000**	4, 31.91	21.66	**0.000**
Systems Tract	Density	3, 309	2.96	**0.032**			
	Ichnocoenoses	3, 309	8.79	**0.000**	3, 37.26	39.63	**0.000**
	Woodground Preservation	3, 309	7.86	**0.000**	3, 31.24	9.80	**0.000**

Heirarchical ANOVA Summary

Response	Causal Variable	DF	F ratio	p - value	Type
Density	Ichnospecies (Mean Diameter)	1, 327	53.28	**0.000**	Nested with Covariate
	Ichnospecies (Max Diameter)	1, 327	2.56	0.111	Nested with Covariate
Mean Diameter	Facies Association (Woodground Preservation)	37, 296	2.61	**0.000**	Nested
	Facies Association (Ichnocoenoses)	38, 255	1.69	**0.010**	Nested
Max Diameter	Facies Association (Ichnocoenoses)	30, 258	1.49	0.055	Nested
	Facies Association (Ichnospecies)	20, 288	0.89	0.600	Nested
	Facies Association (Woodground Preservation)	37, 271	1.06	0.390	Nested
Facies Association	Ichnospecies * Woodground preservaion	4, 345	3.02	0.018	Factorial



Percent Contribution By Systems Tract

	Ichnospecies		**Woodground Type**				
	T. clavatus	*T. longissimus*	Well Preserved Log Ground	Relict Log Ground	Ghost Log Ground	Xylic Peatground	Reworked *Teredolites*
Lowstand	64.43 (24.62)	35.57 (13.60)	40.27 (3.29)	38.14 (12.78)	39.97 (22.07)	0	38.10 (0.06)
Transgressive	68.99 (41.49)	31.00 (18.65)	56.13 (4.59)	61.14 (20.49)	58.04 (32.05)	100 (4.84)	52.38 (0.08)
Highstand	62.31 (1.03)	37.68 (0.62)	3.60 (0.29)	0.71 (0.23)	1.99 (1.09)	0	9.52 (0.01)