Shallow-Marine Carbonates

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1. INTRODUCTION

Carbonates comprise only 20–25% of the total volume of all sedimentary rocks (Boggs, 2009). This fact is reflected in the relatively small number of ichnological studies of carbonates compared with siliciclastics, although other aspects (such as sedimentology or diagenesis) are roughly equally covered. Given the importance of carbonates as oil and gas reservoirs and aquifers (about 50% of the world’s total proven hydrocarbon reserves are held in carbonate reservoirs), the ichnology of carbonate sedimentary systems has much potential for future investigations.

This chapter deals with the ichnology of shallow-marine carbonates, ranging from marginal-marine (peritidal) environments to the shelf. Trace fossils in carbonate rocks were previously reviewed by Kennedy (1975) and Ekdale et al. (1984), and ichnocoenoses specific to Quaternary, Bahamian-style carbonate environments by Curran (1994, 2007).

A review of literature with significant studies on the ichnology of shallow-marine carbonates shows an unequal representation of different time periods (studies focused solely on individual ichnotaxa are disregarded). Precambrian to Cambrian systems with their microbial mat-related, early bilaterian lifestyles are generally poorly covered (e.g., Weber et al., 2007). In the Phanerozoic, Paleozoic carbonate ichnology is strongly underrepresented, whereas the Mesozoic is relatively well documented. This is especially true for the Silurian to Permian (e.g., Archer, 1984; Knaust, 2009, 2010a; Narbonne, 1984), compared to the relatively intensively studied Ordovician (e.g., Dronov et al., 2002; Fei and Zhang, 2002; Osgood, 1970; Pickerill and Forbes, 1979; Pickerill et al., 1984). In the Mesozoic, several studies deal with the ichnology of Triassic carbonate platforms and ramps (e.g., Diedrich, 2008 and references therein; Knaust, 1998, 2007a,b, 2009, 2010a,b; Knaust and Costamagna, 2012; Rodríguez-Tovar et al., 2007; Twitchett and Wignall, 1996), but many are dedicated to the Jurassic (e.g., Avanzini et al., 1997; de Gibert, 1996; de Gibert
Following their main morphological characteristics, carbonate systems can broadly be classified into rimmed carbonate shelf, carbonate ramp (homoclinal and distally steepened), and isolated platform (Read, 1985). Each system has a different position for the carbonate factory and sediment transport pathways, giving reason to the classification into T factory (tropical), C factory (cool-water), and M factory (mud-mound) (Schlager, 2005).

2. ICHNOLOGICAL CHARACTERISTICS OF SHALLOW-MARINE CARBONATE SYSTEMS

The presence, distribution, and quality of trace fossils in shallow-marine carbonates are controlled by a number of criteria which can be grouped into three major categories (Table 1): (1) the faunal composition and distribution of benthic organisms as potential tracemakers, (2) the sediment type and its alteration, and (3) the early-diagenetic history. The interaction of these three criteria can create and convey a specific trace-fossil record which represents only a fraction of the full range of possible outcomes. According to which category played the most important role in the fossilization process, distinct ichnofaunas and trace-fossil associations may represent the same paleoenvironment in different settings. To facilitate evaluation of the trace-fossil record and to employ it for interpretation of paleoenvironments, each category is discussed in more detail before turning to characteristic ichnofacies of shallow-marine carbonates.

2.1 The Composition and Distribution of Benthic Organisms

The location of a given carbonate depositional system in relation to the equator is an important factor controlling its development and the fauna available for modification of the sediment. Warm waters of tropical systems generally contain a higher diversity of organisms than non-tropical, cool-water systems, which may have an effect on the kind and the amount of substrate modification that can occur. Most trace-fossil forms occur in both carbonate and siliciclastic environments, with only a few exceptions of carbonate-specific ichnotaxa that result
from particular burrowing or boring techniques adapted to early consolidated substrates such as firmgrounds and hardgrounds. For instance, some borings are driven by chemical means, such as *Trypanites* and *Entobia*, and are typical in carbonate substrates. In general, climatic control has an influence on the distribution of some trace-fossil groups. Decapod crustaceans are important burrowers and are most abundant in carbonate substrates from tropical and subtropical zones (Dworschak, 2000). As such, burrows like *Ophiomorpha*, *Thalassinoides*, *Spongeliomorpha*, *Psilonichnus*, *Pholeus*, and *Macanopsis* may be more common in carbonates than in siliciclastics.

Evolution is an important aspect in the generation of trace fossils, as different tracemakers change throughout the Phanerozoic. A relevant example is the occurrence of crustacean burrows in Mesozoic and Cenozoic deposits, whereas similar trace fossils such as *Thalassinoides* in Paleozoic strata were constructed by trilobites (e.g., Cherns et al., 2006) or unidentified animals. Other trace fossils (e.g., *Zoophycos*) are known from shallow-marine carbonates until the Jurassic but migrate to deeper environments during the Cretaceous and Cenozoic (Seilacher, 2007). On an ichnospecific level, *Rhizocorallium commune* (herein regarded as a senior synonym of *R. irregulare*) occurs from the Cambrian through Holocene and apparently is the product of polychaetes, whereas *R. jenense* (sensu stricto) characterizes Triassic and younger deposits and may be the product of arthropods. Radular bite traces known as “*Radulichnus*” are common in Proterozoic and Cambrian matgrounds (Seilacher, 2007) but also appear in the Triassic, where similar environments prevailed after the end-Permian mass extinction (Knaust, 2010b). In contrast, Cretaceous to modern *Radulichnus* occurs in hard substrates (Bromley, 2004).

Given the simple case of a homoclinal ramp, general trends can be observed from proximal (backshore, supra- to intertidal) to distal (shelf, subtidal) settings, although exceptions may occur. These trends include an overall decrease of burrow size and depth, an increase in ichnodiversity and bioturbation intensity, and a change from predominantly horizontal to vertical burrows (Laporte, 1969). The distribution of potential tracemaker benthic organisms is mainly controlled by the availability of organic matter within the substrate as food resource. Suspension feeders (e.g., many bivalves, sponges, brachiopods) prefer a stabilized (firm and hard) substrate in a proximal position (supratidal to shallow subtidal), whereas deposit feeders (e.g., some worms, some echinoids, some bivalves, many gastropods) thrive on and in more distal silty and muddy bottoms where they find a higher organic content.

### 2.2 Sediment Types

Carbonates differ from siliciclastics in some important ways. Carbonates are predominantly biogenic sediments and as such are mainly generated by organisms and their reworked skeletal components. Such deposits are also more prone to bioerosion by means of chemical dissolution than are siliciclastics.
TABLE 1 Relevant Differences Between Carbonates and Siliciclastics with Respect to Formation and Preservation of Trace Fossils. Modified from Curran (1994)

<table>
<thead>
<tr>
<th>Infaunal distribution</th>
<th>Carbonates</th>
<th>Siliciclastics</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Favored trace fossils (e.g., crustacean burrows, <em>Thalassinoides</em>, <em>Ophiomorpha</em>, <em>Psilonichnus</em>, <em>Macanopsis</em>, and <em>Pholeus</em> ) due to preferential occurrence of various benthic organisms in tropical and subtropical zones where shallow-marine carbonate environments dominate.</td>
<td>A wide range of ichnotaxa commonly occurs.</td>
<td></td>
</tr>
<tr>
<td>2. Carbonate platforms and ramps comprise broad and very shallow facies belts, often with restricted environments that are favorable for intense bioturbation.</td>
<td>Differentiated depositional systems with relatively small facies belts, heterogeneous bioturbation patterns, and intense bioturbation in offshore sediments.</td>
<td></td>
</tr>
<tr>
<td>3. Given their very low-gradient, carbonate platforms are commonly subject to wide-ranging subaerial exposure, resulting in the development of peritidal ichnofauna and trace fossils formed by plant roots (rhizomorphs or rhizoliths) and prostrate stems.</td>
<td>Rhizomorphs (rhizoliths) can occur, but are not nearly so common.</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Nature of sediment</th>
<th>Carbonates</th>
<th>Siliciclastics</th>
</tr>
</thead>
<tbody>
<tr>
<td>4. Bioerosion is common and related to reefs, bioherms, biostromes, and reworked skeletal components.</td>
<td>Bioerosion is subordinate because organic buildups are much less dominant, and relatively few organisms bioerode non-carbonates.</td>
<td></td>
</tr>
<tr>
<td>5. Borings driven by chemical means dominate (<em>Trypanites</em>, <em>Entobia</em>).</td>
<td>Borings with a mechanical or combined mechanical/chemical method occur.</td>
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</tr>
<tr>
<td>6. Hardgrounds and firmgrounds common and form rapidly, both have significant degrees and diversity of borer and burrower forms of the <em>Glossifungites</em> and <em>Trypanites</em> ichnofacies.</td>
<td>Hardgrounds rare, firmgrounds less common.</td>
<td></td>
</tr>
<tr>
<td>7. Preferential preservation of trace fossils (including fecal pellets) due to fine-grained lime mud in combination with microbial mats,</td>
<td>Delicate traces or parts of them are rarely well preserved due to the clastic nature of sediment, reworking, compaction, and late-diagenetic cementation.</td>
<td></td>
</tr>
</tbody>
</table>
Marine siliciclastic deposition commonly takes place on a well-defined gradient from the shoreline to the shoreface, across the shelf, and down the slope to a basin floor. In contrast, warm-water carbonate systems are chiefly controlled by the growth of organisms with prime dependence on available light. Consequently, their platforms have low-gradient geometries resulting in a shelf and ramp sea-floor with very low relief and facies development as broad belts.

Given the overall geometry of carbonate platforms with broad facies zonation, favorable conditions for the preservation of traces occur when different factors come together. Many shallow-marine carbonate rocks consist of fine-grained carbonate (micrite) generated from a degradation of skeletal material combined with in-situ precipitation which covers extensive areas in tropical and subtropical zones with abundant benthic life. The fine-grained and homogeneous sediment within peritidal facies is typically subject to periodic subaerial exposure, which leads to gradually changing substrate consistencies from soft to stiff and firm over short time intervals (e.g., diurnally). This prograding
change in substrate consistency may be documented by continuously changing trace-fossil morphologies and their excellent and detailed preservation, even of meiobenthic trace fossils less than 1 mm in shortest dimension (Knaust, 2007a, 2010b).

Another contribution comes from the microbial mats and biofilms, which are typical in such environments. They cover the sediment surface (including fresh animal traces) and prevent subsequent destruction, creating a slightly reducing microenvironment and in some cases even preventing the oxidization of the tracemakers, in which case they are preserved together with the traces. Rapid coverage by a new layer of fine-grained sediment (obrution) together with early-diagenetic cementation further increase the chance to preserve the traces in an optimal way.

Specific carbonate particles in combination with early-diagenetic cementation and alteration are another aspect of carbonates. A diverse worm and crustacean fauna contributes with major sediment-feeding organisms to bioturbate and rework the sediment, in many places completely, and results in a considerable production of fecal pellets. Such accumulations of microcoprolites are subject to early lithification and may turn into carbonate rocks. Fecal pellets are regarded as trace fossils and provide valuable information about the paleoenvironment (e.g., Knaust, 2008). Moreover, broken shells, ooids, and lithoclasts are commonly affected by microboring organisms that partly or completely destroy the structure of the grains while generating peloids (Wisshak, 2012).

### 2.3 Early Diagenesis

Taphonomic processes are important for trace-fossil preservation in siliciclastics, especially the casting of traces due to contrasting lithotypes such as sand and mud, whereas grain-size contrasts (e.g., arenite or rudite on carbonate mud) typically play only a minor role in the preservation in carbonates. However, the taphonomic history of trace fossils in carbonates differs from that in siliciclastics by the importance of diagenetic processes that lead to preferential preservation and trace-fossil selection (Narbonne, 1984). The reason for this is sea-floor lithification, and therefore less compaction than in siliciclastics, and a better preservation of sedimentary and biogenic structures. In other circumstances, carbonate cementation and recrystallization are able to alter trace fossils in carbonates, which can lead to a poor level of preservation.

Diagenetic processes on carbonate platforms and ramps play an important role in the transition of sediments to rocks. The different stages of substrate consistency and the timing of the inherent processes are often reflected by significant trace-fossil assemblages (including borings in hardgrounds) and thus can be utilized in the recognition of the kind of substrate, duration of sedimentation, omission, discontinuity surfaces, etc. (Bromley, 1975; Ekdale and Bromley, 2001; Goldring and Kaźmierczak, 1974; Hölder and Hollmann, 1969; Kobluk
et al., 1977; Lukasik and James, 2003; Wilson and Palmer, 1994). The taphonomy of trace fossils is controlled by the chemical microenvironment around the burrows and borings, which act as open conduits to the sediment/water interface and facilitate diagenetic processes such as the precipitation of calcite, dolomite, celestite, or pyrite (Bertling, 1999; Gingras et al., 2004).

Furthermore, diagenesis is capable of total alteration of the deposits as well as the development of secondary porosity. Because of common early-diagenetic consolidation of carbonate sediment, burrow-related porosity is an even more important aspect for the quality of hydrocarbon reservoirs and aquifers than in siliciclastic deposits (Cunningham et al., 2009, 2012; Knaust, 2009; Pemberton and Gingras, 2005).

3. ICHNOFACIES

Following the gradient on a carbonate platform (or ramp) from a relative proximal (landward) to distal (seaward) position, there are three ichnofacies of importance for the reconstruction of paleoenvironments (Fig. 1): (1) Psilonichnus Ichnofacies, (2) Skolithos Ichnofacies, and (3) Cruziana Ichnofacies. During periods with strongly reduced or no deposition (condensation, omission) and progressing lithification, each of the before-mentioned ichnofacies can be overprinted by the substrate-controlled (4) Glossifungites Ichnofacies, or the (5) Trypanites Ichnofacies.

FIGURE 1 Conceptual model of a carbonate ramp with characteristic depositional environments and related ichnofacies (see text for explanations). Note the complexity and resulting variation in ichnofacies occurrence.
3.1 Psilonichnus Ichnofacies (Frey and Pemberton, 1987)

The most landward, coastal dunes and supratidal to upper intertidal facies zone is dominated by the Psilonichnus Ichnofacies, which characterizes transitional marine/terrestrial environments, particularly the backshore, coastal dunes, washover fans, and supratidal flats (Frey and Pemberton, 1987; Frey et al., 1984; MacEachern et al., 2007, 2012). The ichnogenus Psilonichnus comprises predominantly vertical, cylindrical burrows with short horizontal or oblique side branches, with an upper part that is commonly Y-shaped (Fürsich, 1981).

Burrows formed by amphibious ghost crabs (Ocypodidae) typify the Psilonichnus Ichnofacies. They must not be confused with similar burrows of the mud shrimp Upogebia (Upogebiidae) containing turning chambers in the upper part of the burrow, attributed to the ichnogenus Parmachnus Pervesler and Uchman, 2009, and occurring in intertidal and subtidal areas (Nesbitt and Campbell, 2006; Radwański et al., 2012; see Knaust, 2012). Ichnospecies relevant to the Psilonichnus Ichnofacies include P. upsilon Frey, Curran and Pemberton, 1984 and P. tubiformis Fürsich, 1981 (P. quietis Myint, 2001 is probably a junior synonym to P. tubiformis).

Other constituents of this ichnofacies include root structures (e.g., rhizomorphs or rhizoliths, overprinting existing invertebrate burrows), various arthropod trace fossils (mainly occurring as reichnia), and vertebrate tracks. The deeply penetrating dwelling burrows of Psilonichnus are mainly known from Jurassic and younger deposits. Although the Psilonichnus Ichnofacies can be regarded as a softground ichnofacies, carbonate systems are prone to substrate modifications with superimposition of firmground ichnocoenoses of the Glossifungites Ichnofacies (Rhizocorallium jenense and Balanoglossites ichnospecies).

3.2 Skolithos Ichnofacies (Seilacher, 1967)

Adjacent to the Psilonichnus Ichnofacies (typical of low- to moderate-energy settings), the Skolithos Ichnofacies characterizes higher-energy sandy deposits from the beach (intertidal) to environments situated more distally on the platform or ramp (subtidal). Beach foreshore and sandy shoals on the platform margin are predestined as the Skolithos Ichnofacies. Opportunistic colonization of event beds (e.g., storm deposits) was referred to the Arenicolites Ichnofacies by Bromley and Asgaard (1991).

A low ichnodiversity but high burrow density indicates rapid colonization of sediment surfaces. Vertically oriented or steeply inclined shafts dominate, mainly produced by suspension-feeding organisms, for example, shrimp, polychaetes, and bivalves. Skolithos ichnospecies vary in size and comprise simple tubular shafts with or without lining. Skolithos linearis is the most common ichnospecies occurring in the Skolithos Ichnofacies. The obvious low number of attributes and therefore the broad diagnosis of Skolithos lead to the uncomfortable situation that it can
be produced by a range of higher organism taxa and even plant roots, a fact that clearly weakens the environmental value of Skolithos (Gregory et al., 2006).

Depending on the climate zone, kind of sediment and age, the following ichnotaxa may dominate within the Skolithos Ichnofacies or are part of the ichnocoenoses: Altichnus, Arenicolites, Diplocraterion, Lingulichnus, Macaronichnus, Ophiomorpha, Polykladichnus, Piscichnus, Psilomicnhus tubiformis, rhizomorphs, escape and equilibrium traces.

3.3 Cruziana Ichnofacies (Seilacher, 1967)

The Cruziana Ichnofacies is probably the most common and extensive among carbonate systems. It occurs in shallow-marine environments between the fair-weather wave base and the storm-wave base, commonly in a moderate- to low-energy system. The resulting deposition rate is low with the dominant deposition of fine sand to soft lime mud, occasionally punctuated by moderate to high-energy event deposition (e.g., storms).

The trace-fossil association mainly encompasses horizontally oriented burrows and traces produced by deposit-feeding and crawling organisms, accompanied by vertical structures. Given favorable conditions in terms of salinity, oxygen, currents, etc., the ichnodiversity and bioturbation is moderate to high and includes traces of different trophic groups of organisms (mainly arthropods and worms).

Common trace fossils of the Cruziana Ichnofacies are Archaeonassa, Arthropycus, Asterosoma, Cruziana, Curvolithus, Diplocraterion, Gyrochorte, Ophiomorpha, Palaeophycus, Phycoes, Planolites, Protovirgularia, Rhizocorallium commune, Teichichnus, Thalassinoides, and Zoophycos (in part).

3.4 Glossifungites Ichnofacies (Seilacher, 1967)

The substrate-controlled Glossifungites Ichnofacies occurs in semiconsolidated carbonate sediment with stable substrate properties forming stiff- to firmgrounds, which only allow specialized organisms to burrow into it. It is related to omission or erosion surfaces and generally occurs in different environments (Frey and Seilacher, 1980). However, preferred loci for substrate dewatering and consolidation on carbonate ramps and platforms are given in shallow subtidal and intertidal to supratidal environments, such as lagoons, beaches, and shoals (Pemberton and Frey, 1985).

Vertical burrows (dwelling structures) of suspension feeders are predominant and occur in moderate to high density, although the ichnodiversity is limited. Numerous burrowing organisms are adapted to colonize omission surfaces, for instance different species of polychaetes, nemerteans, and crustaceans. Given the cohesive stage of the substrate, burrow outlines are sharp and clearly defined if not blurred subsequently by diagenetic processes. The burrows are commonly passively infilled from above with sediment unrelated to the host
rock. Early cementation is important and is aided by the chemical microenvironment around the burrows, resulting in the crystallization of calcite, celestite, dolomite, goethite, or pyrite.

The name-bearer trace fossil of the Glossifungites Ichnofacies is now regarded as a junior synonym of Rhizocorallium jenense (Uchman et al., 2000). Other characteristic trace fossils are Balanoglossites, Gastrochaenolites, Pholeus, Spongeliomorpha, and Thalassinoides. The former two ichnogenera include both firmground burrows and borings, whereas other tracemakers are capable of burrowing into soft and firm substrates to produce, for instance, Chondrites, Palaeophycus, Siphonichnus, Lingulichnus, and Zoophycos.

A special expression of the Glossifungites Ichnofacies is a firm matground substrate, resulting from the development of algal or microbial mats on the sediment surface. Such conditions are well known from Precambrian and Early Cambrian units, but similar conditions repeatedly occur through the Phanerozoic. The related ichnofauna comprises surface traces of crawling and rasping organisms, which benefit from the organic matter as mat scratchers and digesters, mat stickers, or undermat miners (Seilacher, 2007).

### 3.5 Trypanites Ichnofacies (Frey and Seilacher, 1980)

The substrate-controlled Glossifungites and Trypanites ichnofacies are intimately associated, as the former has the potential to develop gradually into a hardground of the latter (Bromley, 1975). In contrast to the Glossifungites Ichnofacies, the Trypanites Ichnofacies is more restricted in its distribution to areas with rapid cementation. Such conditions are common in subtidal and intertidal environments, where this process may lead to an extensive pavement by hardgrounds or beachrock, but the Trypanites Ichnofacies also occurs on rocky shores or in reefs. Rapid lithification preferentially takes place in front of sand-shoal complexes (including the shelf break), where the sediment is exposed to wave sweeping and reworking.

Bromley and Asgaard (1993) proposed to replace or subdivide the Trypanites Ichnofacies with the Entobia Ichnofacies for deep-tier borings with high preservation potential and the Gnathichnus Ichnofacies including superficial sculptures resulting from short-term bioerosion. However, Entobia and Gnathichnus are probably better treated as ichnocoenoses within the Trypanites Ichnofacies (MacEachern et al., 2007).

Hardgrounds are often well defined by a clear top surface colonized by epibenthic organisms (e.g., oysters, serpulid polychaetes) and mineral staining. Bioerosion takes place on the hardground surface or from its top, marginal, or undercut surface into the substrate. It comprises a variety of borings mainly produced by suspension-feeding organisms. Trypanites weisei from its type area in the Middle Triassic of Germany occurs in micritic limestone assignable to the Glossifungites Ichnofacies, where it superimposes a Balanoglossites ichnofabric (Knaust, 2008). Its stratigraphical position, sedimentological and ichnological
context, and early-diagenetic dolomitization indicate an origin in the lower intertidal zone.

Important trace fossils of the *Trypanites* Ichnofacies are *Caulostrepsis*, *Entobia*, *Gastrochaenolites*, *Gnathichnus*, *Maeandropolydora*, *Rogerella*, and *Trypanites*, as well as numerous microborings.

4. **CASE STUDIES**

4.1 **Ordovician Cool-Water Carbonates:**
**St. Petersburg Region, Russia**

During the Ordovician, the Baltic paleocontinent migrated from a subpolar to a subequatorial position within the southern hemisphere (Cocks and Torsvik, 2005). This is reflected in the succession of facies from predominantly siliciclastics (sand and black shale) in the Tremadocian, through cool-water bioclastic wackestones in the Floian to Sandbian, to tropical sabkha dolomites and pelmicrites in the Katian to Hirnantian (Dronov and Rozhnov, 2007). The Ordovician carbonates of the St. Petersburg region (Floian to Katian) reach a thickness of 20–160 m and belong to the relatively shallow-water part of the epicontinental basin of Baltoscandia. The rocks are typically rich in bryozoans, brachiopods, trilobites, ostracods, echinoderms, and conodonts. Shells of gastropods, bivalves, cephalopods, and sponge spicules are locally abundant. In this chapter, cool-water carbonates of Volkhovian (Dapingian) age are described (Fig. 2), which are best exposed and most extensively studied in natural outcrops and quarries in the St. Petersburg region.

Basic ichnological features of these carbonates were described by Dronov et al. (2002) and Dronov and Mikuláš (2010). In general, the ichnodiversity of the Dapingian ramp is relatively low but due to the condensed character of the section, the trace-fossil density can be very high at some levels. The main ichnogenera are *Balanoglossites*, *Bergaueria*, *Chondrites*, *Gastrochaenolites*, *Palaeophycus*, *Thalassinoides*, and *Trypanites*. Major portions of the succession belong to the *Cruziana* Ichnofacies with numerous omission surfaces demarcated by the *Glossifungites* and *Trypanites* ichnofacies.

The well-bedded Dapingian limestone has been extensively quarried for building purposes since the foundation of the town of St. Petersburg in 1703 (Fig. 3). The basements and staircases of most buildings in the historical part of the city are made from certain beds of the “Glaucanite Limestone”. There is an old tradition among the local quarrymen to give names to distinctive beds and bedsets as well as to some bedding surfaces (Fig. 2). Regional conformity of this nomenclature reflects the lateral persistence of these lithological units. Objectively, this informal terminology is related to some distinctive lithological and ichnological features, such as hardness and homogeneity of the rock, mode of intercalation, distribution of colors as well as intensity of bioturbation, and specifically the ichnotaxa content of each bed. This informal terminology has
FIGURE 2  Detailed stratigraphy and interpreted sea-level changes in the Volkovian (Dapingian) of the St. Petersburg region, Russia. (1) Bioclastic wackestone with iron ooids; (2) bioclastic packstone; (3) marlstone with Thalassinoides ichnofabric; (4) carbonate mudstone to wackestone; (5) terrigenous siltstone; (6) quartz sandstone; (7) quartz sandstone enriched with glauconite; (8) black shale; (9) hardground surface pitted with Trypanites; (10) hardground surfaces with Balanoglossites (“Karandashi”); (11) hardground surface with superimposed Gastrochaenolites, Balanoglossites, and Trypanites; (12) hardground surface with well-developed Gastrochaenolites oelandicus (“Steklo” surface); (13) marine red bed with Thalassinoides and Chondrites; (14) Bergaueria at the base of the beds; (15) marine red bed with Chondrites.
been adopted for subdivision of the succession into numerous elementary units that, to a significant degree, are traceable over the eastern part of the Baltic-Ladoga Glint (a Holocene coast cliff) over a distance of more than 300 km (Jaanusson, 1976; Männil, 1966; Dronov et al., 1996, 2000; Fig. 4). In total, 29 lithostratigraphic units (parasequences) can be recognized in the Volkhov Formation (Figs. 2 and 3).

The Volkhov Regional Stage is interpreted as a single depositional sequence bounded by distinctive erosional surfaces with associated stratigraphic gaps. Sequence boundaries coincide with the hardground surfaces at the base and the top of that sequence (Fig. 2). The lowermost part of the Dikari Limestone

FIGURE 3 Sawn section through the Middle Ordovician Dikari unit in the Babino quarry, approximately 150 km east of St. Petersburg, Russia. The bed numbers correspond to the bed nomenclature of Fig. 2.

FIGURE 4 Bed-by-bed correlation of sections of the Middle Ordovician Volkhov Formation (Dapingian) along the Baltic-Ladoga Glint Line (Estonia-Russia).
is interpreted as a highstand systems tract of the underlying Latorp sequence. The upper part of the Dikari Limestone represents a lowstand systems tract, whereas the Zheltiaki Limestone and the Frizy Limestone represent transgressive and highstand systems tracts, respectively (Dronov and Holmer, 1999; Dronov et al., 2002).

4.1.1 **Highstand Systems Tract of the Underlying Latorp Sequence**

The lowermost part of the Dikari Limestone is represented by four distinctive beds (Fig. 2). The succession of the beds demonstrates a shallowing-upward trend and is interpreted as a highstand systems tract. On top of the Beloglaz Bed (bed 4 in Fig. 2) rests the Zeliony Bed (bed 5) with a prominent flat hardground surface covered by a thin glauconite veneer. It marks the base of the Middle Ordovician and is interpreted as a transgressive surface and sequence boundary (Fig. 5). The surface is pitted by so-called Amphora-like burrows and/or borings (Orviku, 1960; Vishnjakov and Hecker, 1937), corresponding to *Gastrochaenolites oelandicus* Ekdale and Bromley, 2001 (Fig. 6 A and B).

The hardground surface at the base of the Volkhov depositional sequence occurs not only in the Syas River area (“Steklo” surface) but also in Estonia (“Pustakkiht”), on the island of Öland in Sweden “Blommiga Bladet”, and in

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**FIGURE 5** Development of the “Steklo” transgressive surface mainly bioeroded with *Gastrochaenolites oelandicus*. Modified after Posamentier and Allen (1999).
the Oslo region in Norway. Everywhere it is recognizable by *G. oelandicus* pits usually filled with glauconite grains.

### 4.1.2 Lowstand Systems Tract, Upper Part of the Dikari Limestone (*BIIa*)

The upper part of the Dikari Limestone consists of 10 distinctive beds (Figs. 2 and 3). The Butina Bed is the most remarkable one, comprising 1–5 cm of relatively soft red marlstone with thin *Thalassinoides* forming a network typical for the Central Baltoscandian Confacies belt. This bed is the best marker and may be interpreted as a short-term invasion of relatively deep-water conditions. The Dikari are predominantly of gray bioclastic packstone or grainstone with numerous scattered glauconite grains. Distinctive hardground surfaces, emphasized by yellow goethite impregnation, are abundant at some levels (e.g., the Krasny, Zhelty, Nadzhelty, and Konoplasty beds). Some of these surfaces are pitted with *Balanoglossites* and, more rarely, *Trypanites*. These beds usually consist of four to eight elementary layers, each 3–4.5 cm thick. Most of the layers are distinctly graded. Brachiopods, echinoderms, bryozoans, ostracods, and trilobites are the main fossils. The uppermost bed of the Dikari Limestone (Butok) has a distinctive hardground non-depositional surface at the top, marked by an extensive yellow impregnation down to 2 cm. It is penetrated by shallow vertical borings attributed to *Trypanites* (Fig. 6C) and a complex *Balanoglossites* ichnofabric augmented by the weathering/dissolution of the surface prior to its hardening (Fig. 6D–F). The hardground is interpreted as a transgressive surface. Other ichnogenera of this unit include *Thalassinoides*, *Bergaueria*, and *Palaeophycus*.

### 4.1.3 Transgressive Systems Tract, Zheltiaki Limestone (*BIIb*)

The Zheltiaki Limestone differs from the underlying rocks of the Dikari Limestone in having more argillaceous material within the carbonate rock, the appearance of numerous clay layers, and the variegated, mostly red and yellow, color of the rocks. Glauconite is rare or absent. The faunal assemblages recovered from interbeds of clay are dominated by brachiopods, ostracods, and echinoderms, whereas those from the limestone beds are rather different and contain many trilobites. These differences can be explained by the tempestite origin of the limestone beds. The yellow and red colors of the rocks and the smaller grain size in comparison with the underlying and overlying strata point to a relatively deep-water origin. The Zheltiaki Limestone is subdivided into seven informal lithostratigraphic units (Fig. 2). The units bear rich ichnocomplexes dominated by *Thalassinoides* and *Chondrites* (Fig. 6G). Washed-out surface trace fossils are rare (e.g., *Rusophycus*; Dronov et al., 2002).

### 4.1.4 Highstand Systems Tract, Frizy Limestone (*BIIg*)

The Frizy Limestone consists of intercalations of greenish gray bioclastic limestone and bluish gray clay, both containing scattered glauconite grains. It can be subdivided into seven informal lithostratigraphical units (Fig. 2).
FIGURE 6 Common trace fossils from the Volkhovian (Dapingian) of the St. Petersburg region, Russia. Scale bars = 1 cm. (A) Vertical section of the “Steklo” hardground (Zeliony Bed) with Gastrochaenolites oelandicus filled with glauconite grains, Putilovo quarry. (B) G. oelandicus penetrating carapaces of the trilobite Megistaspis estonica, Zeliony Bed, Kingisepp quarry. (C) Hardground surface in the Zhelty Bed (Dikari unit) with grooves and openings of Balanoglossites triadicus (arrows) and Trypanites isp. on the ridges, Babino quarry. (D) Vertical section with the same hardground as in C, revealing a complex B. triadicus ichnofabric, Babino quarry. (E) Vertical section between the Krasnenky and Melkotsvet beds displaying a firm- to hardground with U- and Y-shaped
A proximal-to-distal trend is clearly recognizable in these storm deposits. The most distal facies are closer to the shore than the red-colored tempestites of the Zheltiaki Limestone. The individual units of the Frizy Limestone contain, in specific colonization horizons, *Thalassinoides* (various patterns and sizes of networks and boxworks), *Palaephycus* (simple, rarely branched, lined tunnels), *Bergaueria* (Fig. 6H), and rarely *Gastrochaenolites*. Inside the upper unit of intercalation, a “patchy hardground”, composed of hardened *Thalassinoides* tunnels, is bioeroded with *Trypanites*. The top of the Koroba Bed is marked by a prominent hardground surface pitted with *Trypanites* and is interpreted as the upper sequence boundary.

### 4.1.5 Sea-Level Fluctuations

The sediments of the Dapingian succession in the St. Petersburg region were deposited on a cool-water carbonate ramp within a shallow-marine, storm-dominated environment (Dronov, 1998). These conditions reflect short-term sea-level fluctuations where even minor changes in depth can cause an abrupt shift of facies. About eight lithofacies can be discriminated based on their lithology and ichnological content and can be arranged according to the relative depth of their deposition on the carbonate ramp. A sea-level curve has been reconstructed on the basis of the shift of these facies along the storm-dominated ramp profile (Dronov, 1999).

Major rises of relative sea level occurred at the following levels (with reference to the traditional bed nomenclature): (1) Krasnenky, (2) Butina, and (3) Krasnota. All of these events are marked by the appearance of red-colored deposits accumulated in the central part of the basin under relatively deep-water conditions. Important relative sea-level drops occurred at the following levels: (1) “Steklo” surface (base of Volkov), (2) Butok, (3) Tolstenky, and (4) Koroba. Overall, the sea-level curve is comparable to the one constructed by Nielsen (2004) for the Komstad Limestone in Scania, except for the Middle Volkov interval, where the data from Russia support the interpretation of a greater water depth than in the Lower Volkov. As a consequence, the B_{II}/B_{IIB} boundary in the shallow-water model (Dronov, 1999) is interpreted as a deepening (transgressive) event, whereas the same boundary in the deep-water model (Nielsen, 2004) is interpreted as a shallowing (regressive) event. This discrepancy is related to a different interpretation of facies and stratigraphy; further ichnological studies have the potential to assess the interpretation of these sea-level changes.
4.2 Triassic Epicontinental Carbonates: Germany

The Middle Triassic (Anisian-Ladinian), epicontinental carbonates and evaporites of the Muschelkalk Group in the Germanic Basin were deposited between continental siliciclastics of the Buntsandstein and Keuper groups. The carbonates of the Lower and Upper Muschelkalk contain a moderate to rich ichnofauna, whereas the evaporitic Middle Muschelkalk is principally devoid of trace fossils, except in its lower and upper transition zones (Knaust, 2007b). In contrast to the storm-dominated homoclinal carbonate ramp of the Upper Muschelkalk, the Lower Muschelkalk resulted from deposition on a partly detached and distally steepened carbonate ramp with influence of synsedimentary tectonics along the basin axis (Knaust, 2000). Sedimentation of the Lower Muschelkalk Group (Anisian) took place in a restricted, dysoxic, and evaporitic environment with starved basin conditions. Its ichnology is briefly outlined below.

The vast portion of the low-energy, lime-mud-dominated Lower Muschelkalk Group belongs to the *Cruziana* Ichnofacies, with intercalated high-energy skeletal and Oolite Beds of the *Skolithos* Ichnofacies, and omission surfaces demarcated by the *Glossifungites* Ichnofacies and more rarely *Trypanites* Ichnofacies. Ichnodiversity is moderate, but only a few ichnotaxa repeatedly occur throughout the succession.

The Lower Muschelkalk is built of numerous stacked depositional sequences, most of them showing a shallowing-upward trend (e.g., Knaust, 1998). Such an idealized sequence is typically between 0.5 and 10 m thick and shows a generally upward-decreasing amount of bioturbation from high/moderate to low or zero. It consists of characteristic lithofacies and trace-fossil assemblages reflecting different depositional environments on a prograding carbonate ramp. Depending on the stratigraphic and regional position within the Germanic Basin, different variations of carbonate ramps can be recognized, such as a homoclinal ramp with a very low gradient and siliciclastic influx in parts, a distally steepened ramp with a considerable amount of deformed and reworked sediment, and a detached carbonate ramp with a low gradient and two or more belts of shoals. Taking the detached ramp as an example (as it occurs in the region of central Germany), five lithofacies and related trace-fossil associations occur from the top of the sequence downward (Figs. 7 and 8).

4.2.1 Grainstone/Packstone (Rudite, Arenite): Rare Bioturbation

Beds of bioclastic (bivalves, brachiopods, echinoderms), intraclastic (flat-pebble conglomerates), or oolitic limestone occur on top of shallowing-upward cycles and may contain elements of the *Skolithos* Ichnofacies. These regional marker beds occur above lagoonal or intertidal deposits. Large-scale cross-bedding and vadose diagenetic fabric indicate an origin as high-energy
FIGURE 7 The Lower Muschelkalk Group (Middle Triassic, Anisian) in central Germany. (A) Idealized shallowing-upward sequence with the occurrence of characteristic trace-fossil associations. (B) Cartoon with an interpretation of the depositional system following the concept of a detached ramp (Schlager, 2005) with a basinward progradation barrier 1, subsequent minor flooding, and progradation of barrier 2 (inspired by Burchette et al., 1990).
FIGURE 8  Common trace fossils from the Lower Muschelkalk Group (Middle Triassic, Anisian) of Thuringia, central Germany, in bedding plane expression (except B and D, which show vertical sections). For localities and stratigraphical positions see Knaust (2007b). Scale bar = 1 cm. (A) Openings of *Lingulichnus verticalis* in a grainy packstone (arenite) with incipient firmground conditions. *Skolithos* Ichnofacies. Upper *Terebratula* Bed, Plaue quarry. (B) Steeply inclined and dolomite-filled burrows (*Altichnus* isp.) in a bioclastic and intraclastic (rudstone) limestone bed (event bed). *Skolithos* Ichnofacies. f-3 Bed, Jena-Steudnitz quarry. (C) Omission surface on a mudstone (micrite) with abundant openings of steeply inclined and open *R. jenense* burrows. *Glossifungites* Ichnofacies. Upper Wellenkalk, Rittersdorf quarry. (D) Mudstone (micrite) with a firmground
shoals in a shallow subtidal to intertidal environment. Because of the continued redeposition of sediment, bioturbation is rare and encompasses vertically oriented trace fossils such as *Lingulichnus verticalis* (Fig. 8A), *Skolithos* isp., and *Altichnus* isp. (Fig. 8B). Marginal regions of the shoal bodies merge into firm- or hardgrounds and may contain *Balanoglossites triadicus* and *Trypanites weisei*. Minor cycles typically preserve an event bed on the top.

### 4.2.2 Lime Mudstone (Micrite): B. triadicus-T. weisei Assemblage

Discontinuity surfaces with firm- and hardground features are common throughout the Lower Muschelkalk but are best developed as ravinement surfaces just below the grainstone/packstone beds (e.g., Upper Oolite Bed, Lower *Terebratula* Bed). Thus, they occur either in front of the shoals in a very shallow-subtidal to intertidal environment or in the back-shoal lagoon (subtidal). In front of the shoals, intense lithification with the development of thick and multiple hardground layers took place, whereas slightly deeper areas farther offshore and back-barrier lagoonal environments typically contain numerous thin firmground layers. The bioturbation and bioerosion of such lime mudstone layers is moderate to high with a low ichnodiversity, typically with few main components. The continuous spectrum of burrows and borings with sharp margins demarcates firmgrounds with *B. triadicus* and *R. jenense* (*Glossifungites* Ichnofacies, Fig. 8C), which progressively grade into hardgrounds with *T. weisei* (*Trypanites* ichnofacies, Fig. 8D; Knaust, 2008). They are passively filled by marly dolomite and probably originated on a lower tidal flat.

### 4.2.3 Marly Limestone with Horizontal Bedding: R. commune-Thalassinoides suevicus Assemblage

The lower and upper portion of the Lower Muschelkalk succession, where the facies shift from supratidal to inter- and subtidal conditions and back, is characterized by platy limestone. This facies also occurs in the upper part of major

shallowing-upward cycles, below and between the grainstone/packstone beds (e.g., the Oolite and Schaumkalk Beds). The marly limestone can be dolomitic and contain features of subaerial exposure (e.g., desiccation cracks), thus documenting deposition on low-energy tidal flats. Where dolomitization and exposure features are lacking, rocks of the same texture can be interpreted as shallow subtidal deposits. Inter- and subtidal environments can be differentiated on the basis of the ichnofauna. Bedding planes of the dolomitic marly limestone (intertidal) are covered by large and winding *R. commune* together with the fecal pellets *Coprulus oblongus* (*Cruziana* Ichnofacies, Fig. 8E), resulting from feeding activity, probably by polychaetes. Desiccated parts of the tidal flat were apparently visited by crustaceans, preferably following the weakened cracks between the desiccation polygons and producing *T. suevicus* (*Glossifungites* Ichnofacies). In contrast, the subtidal marly limestone contains more ichnotaxa and is dominated by short and oblique *R. commune* (Fig. 8F) accompanied by *Protovirgularia* isp.

4.2.4 Marlstone with Flaser Bedding: *Protovirgularia* isp.-*Pholeus abomasofomis* Assemblage

This lithofacies mainly occurs in the middle part of the cycles (outer ramp) and within the lagoonal facies (inner ramp). Its texture results from undulating and flaser-like micrite layers separated by thin seams of marl. Although belonging to the *Cruziana* Ichnofacies, the local and patchy occurrence of a firm substrate indicates overprinting by the *Glossifungites* Ichnofacies. Bioturbation is moderate to high, dominated by elongated bivalve burrows *Protovirgularia* isp. (with only weakly pronounced chevron ornament due to the stiff to firm substrate, Fig. 8G), the supposed polychaete feeding trace *R. commune* (small, inclined), the crustacean dwelling burrow *P. abomasofomis*, and more rarely, other ichnospecies of *Pholeus* (Fig. 8H; Knaust, 2002).

4.2.5 Marlstone with Nodular Bedding: *Planolites montanus*-*R. commune* Assemblage

This lithofacies occurs in the lower part of shallowing-upward cycles and consists of thinly bedded and alternating mudstone and marlstone. Various disruptions of the bedding result from synsedimentary deformation, reworking, or diagenetic overprint. Many units contain reworked sediment in the form of debris- and mud-flow deposits, where bioturbated sediment became unstable and subject to reworking. Consequently, many reworked clasts are actually disrupted burrows (ichnoclasts). All in all, a distal, outer ramp facies on a distally steepened carbonate ramp can be inferred. Many intervals are highly bioturbated and mainly contain *Planolites montanus*, *R. commune* (small, inclined), and *Protovirgularia* isp. (*Cruziana* Ichnofacies). Intergradations between *P. montanus* and *Protovirgularia* isp. suggest that they were produced by bivalves burrowing in soft versus firm substrate.
Each of the three Lower Muschelkalk units contains shallowing-upward cycles and terminates with two or three major carbonate sand bodies at the top. Facies patterns from outer to inner ramp suggest a prograding shoreline, of which the bioclastic *Terebratula* Beds in the middle unit represent shoal deposits in a relatively distal position, whereas the Oolite Beds of the lower unit and the Schaumkalk Beds of the upper unit are proximal. Because the inner ramp facies between the coupled shoal deposits is more restricted (and partly lagoonal) than the mid-ramp facies, it is concluded that drowning of the first barrier resulted in subsequent deposition of lagoonal and tidal deposits, before the now proximally positioned second barrier prograded over the system again (cf. Burchette et al., 1990; see Knaust, 1997).

5. NEOICHNOLOGICAL APPROACHES

5.1 Rimmed Carbonate Platforms: Quaternary of the Bahamas

The islands and shallow subtidal platforms of the Bahama Archipelago are geologically world famous as a natural laboratory for the study of the sedimentology and paleontology of Quaternary carbonate rocks and sediments (see Curran and White, 1995 on Bahamian terrestrial and shallow-marine geology, and Ginsburg, 2001 on Bahamian carbonate platform evolution). Pleistocene and Holocene rocks cap these islands, and their diverse modern carbonate sedimentary environments contain a commonly diagnostic ichnological signature.

The purpose of this section is to provide a brief, informative overview of the ichnology of the Bahamas; in-depth coverage can be found in Curran (1994, 2007) and references therein. A principal benefit gained from study of Bahamian ichnology is insight regarding the modern-to-fossil transition. Given that rocks of the Bahama Islands are geologically young, in many cases one can match modern tracemaker activity to analogs found in the fossil record. Trace fossils discussed here all fall within either the *Skolithos* or the *Psilonichnus* Ichnofacies that characterize the predominately grainstone lithofacies. Bioerosion is an important aspect in reef destruction and rocky-shore erosion and was recently reviewed by Bergman et al. (2010).

Modern carbonate environments and their counterpart units in the Bahamian rock record range from shallow-subtidal, commonly reefal settings, to beach and dune environments, as found along grainy, windward, or leeward island coasts. More protected environments that might exist marginal to coastal embayments, such as tidal flat–lagoon complexes, also are included. Figure 9 illustrates two hypothetical Bahamian islands and the spatial distribution of these coastal environments, with the side panel illustrating five ichnocoenoses recognized by Curran (2007), and each keyed to its respective depositional environment. In addition, Garrett (1977) described several invertebrate communities (nearshore, pond, and levee) from the extensive, mud-dominated tidal flats on the west side of Andros Island that could be regarded as a separate ichnocoenosis.
An ichnocoenosis represents an ecologically pure assemblage of traces or trace fossils derived from collective activities of a single endobenthic community (Bromley, 1996). In Bahamian-style settings, most trace-fossil assemblages are true ichnocoenoses; the exception is the occurrence of rhizomorphs (or rhizoliths) formed by plant roots. Rhizomorphs are typically an integral, and sometimes dominant part of eolian complexes, but they also can result from plant roots penetrating any preexisting lithofacies during an extended period of subaerial...
exposure with lowered sea level. Therefore, to at least some degree, rhizomorphs are ubiquitous in Quaternary Bahamian lithofacies.

5.1.1 The *Skolithos* Ichnofacies

In Bahamian and similar tropical carbonate settings, the *Skolithos* Ichnofacies, as defined and summarized by Bromley (1996), Pemberton et al. (2001), and McIlroy (2004), includes subtidal to intertidal ichnocoenoses dominated by bioturbation and fossil burrows of callianassid shrimp. Here callianassids commonly have created complex and robust burrow systems that result in distinctive, often maximum intensity ichnofabrics (Fig. 10).

As one continues seaward on the platform shelf, an increase in trails and tracks typically occurs with increasing water depth, suggesting transition to a *Cruziana* Ichnofacies assemblage. This transition has not yet been documented in the Bahamian rock record because of the abrupt shelf-to-slope break at the edges of Bahamian platforms. Accordingly, little is currently known about the deeper-water ichnology of the offshore areas.

Domination by the burrowing activities of endobenthic thalassinidean shrimp, particularly callianassids, of carbonate-sand substrates in tropical,

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**FIGURE 10** *Ophiomorpha* ichnofabrics in Bahamian Late Pleistocene grainstones keyed to the scale of Droser and Bottjer (1989).
shallow subtidal environments is important to both sedimentologists and ichnologists because “they often occur in high densities and influence the whole sedimentology and geochemistry of the seabed” (Dworschak, 2004). With respect to geochemistry, some studies, mostly by marine biologists (e.g., Webb and Eyre, 2004), support this statement, but data are limited. What has been clearly documented is the many effects callianassids have on surrounding carbonate sediments (Tudhope and Scoffin, 1984), including the total transformation of original lithofacies by burrowing activity (Curran, 1994; Tedesco and Wanless, 1991; Fig. 10). Nonetheless, ichnologists and sedimentologists should be mindful that overall knowledge of tropical callianassids remains poorly known with respect to species identification, burrow morphology, and general ecology and sedimentary environment effects.

There are many species of thalassinideans, and the families Callianassidae and Upogebiidae are cosmopolitan, with decreasing species numbers toward the poles. In a survey of extant thalassinidean diversity, Dworschak (2000) recorded 155 species of callianassids and 139 species of upogebiids (species numbers have increased to more than 200; Dworschak, 2010: personal communication) with subsequent new discoveries. Furthermore, most thalassinidean species are found in shallow-marine waters, living at depths of less than 20 m, with by far the highest numbers of species found at tropical to subtropical latitudes.

In the light of these numbers, it is no surprise that the bioturbation and burrows of callianassids (Ophiomorpha) dominate the ichnocoenoses of the Skolithos Ichnofacies as it occurs in the shallow-subtidal Quaternary grainstones of the Bahamas, south Florida, and other similar tropical carbonate settings. This is important because Ophiomorpha ichnofabrics commonly create high levels of permeable ichnogenic macroporosity, permitting host strata to have significant potential as carbonate aquifers and reservoirs (Cunningham et al., 2009, 2012).

The dominant ichnotaxon occurring in Late Pleistocene shallow-subtidal grainstones of the Bahamas and south Florida is Ophiomorpha (Ichnocoenosis 1). Bahamian Ophiomorpha burrow systems are commonly robust and well preserved (Fig. 10) and have been described in detail (Curran, 1994, 2007; Curran and White, 1991 and references therein). Ophiomorpha-bearing grainstones can occur in association with fossil coral reefs and intervene with coral rudstone (Curran, 1994). S. linearis is always present but secondary to Ophiomorpha, occurring in greatest densities in grainstones formed in the shallowest parts of shallowing-upward sequences.

Ichnocoenosis 2 includes Conichnus conicus and Planolites in addition to Ophiomorpha and Skolithos linearis. In Late Pleistocene rocks, C. conicus occurs most commonly in grainstones characterized by tabular and trough cross-bedding and interpreted as representing relatively rapid sediment accumulation under shallow-subtidal, shoaling conditions influenced by nearshore and/or tidal currents (Curran and White, 1997; Fig. 11A). Planolites typically is less abundant than
C. conicus, but specimens can be well formed and are common. C. conicus is generally attributed to the escape-burrowing activities of sea anemones (Shinn, 1968). However, a mechanical origin for C. conicus cannot be ruled out, based on the study of Buck and Goldring (2003). Further discussion of the possible modes of origin and significance of C. conicus was given by Curran (2007). Planolites in Bahamian grainstones and the Miami Limestone can be attributed to the deposit-feeding activity of balanoglossid worms (Curran, 2007).

Ichnocoenosis 3 is characteristic of the intertidal zone of semi-enclosed, tidally influenced, slightly hypersaline lagoonal areas, commonly referred to as “creeks”. An example is Pigeon Creek, on San Salvador Island, where the margins of a lagoon are bordered by mangroves that commonly give way to extensive carbonate flats of muddy sand. The ichnology of these intertidal flats and possible trace-fossil analogs and rock-record implications were investigated by Curran and Martin (2003). These flats and other similar areas throughout the Bahamas display a distinctive topography of mounds and craters formed by the callianassid shrimp Glypturus acanthochirus (Fig. 11B).

This deep-tier burrower profoundly modifies the intertidal and shallow-subtidal areas that it inhabits and is a true ecosystem engineer (Berkenbusch and Rowden, 2003). G. acanthochirus burrows are large, well lined and have a distinctive, downward-spiraling morphology (Curran and Martin, 2003; Dworschak and Ott, 1993). Deep, spiraling burrows from Florida, the Bahamas, and the Caicos Platform and generically attributed to “Callianassa” almost certainly also were formed by G. acanthochirus and indicate a distribution for this species throughout the wider Caribbean (Shinn, 1968; Tedesco and Wanless, 1991). Farther afield, Farrow (1971) and Braithwaite and Talbot (1972) described casts of large, spiraling callianassid-burrow systems from modern carbonate substrates in the Seychelles Archipelago, Indian Ocean, with the indication being that downward-spiraling morphology is widespread for callianassids in tropical, intertidal, and shallow-subtidal carbonate settings.

With the development of thin “Schizothrix” microbial mats, the surfaces of large, coalesced mounds formed by G. acanthochirus become stabilized and colonized by other burrowers (Curran and Martin, 2003). The most distinctive and complex burrows are those of the shrimp Upogebia vasquezi, which penetrate 10–15 cm into the mound surfaces; they are thickly lined, and have smooth interior and coarsely knobby exterior surfaces (Fig. 11F). Also present on mound surfaces are numerous fiddler crabs burrows. The larger burrows are formed by adult Uca major, with burrow openings commonly surrounded by scratch traces and numerous excavation and feeding pellets. Smaller openings indicate juvenile U. major burrows and/or other unidentified Uca species.

In an island interior facies of the Late Pleistocene Grotto Beach Formation on San Salvador, Curran and Martin (2003) described trace fossils identified as U. vasquezi burrows in association with the tops of presumed G. acanthochirus burrow shafts. Although not yet formally named, fossil U. vasquezi burrows, as characteristic of intertidal, mounded surfaces, should be geologically useful
FIGURE 11  Bahamian ichnology. (A) Cross sections of *Conichnus conicus* in cross-bedded Late Pleistocene grainstone (horizontal surface), Harry Cay, Little Exuma. Scale bar = 7 cm. (B) Mounded topography created by the deep-burrowing callianassid *Glypturus acanthochirus* on the wide intertidal zone of Pigeon Creek lagoon, San Salvador. (C) *Ocypode quadrata* burrow opening with radiating trackways, East Beach, San Salvador. Scale bar = 12 cm. (D) Mature *O. quadrata* ghost crab, same locality as C. About 10 cm from side to side. (E) Casts of typical *O. quadrata* burrows made by K. Seike, same location as C. Scale bar = 10 cm. (F) Casts of the complex burrow of the shrimp *Upogebia vasquezi*. One shrimp occupies each tube, a male in one and a female in the other, and the tubes are surrounded by a thick, unified, lining with large pellets on the exterior. (G) Dense occurrence of rhizomorphs in a Late Pleistocene regressive
as indicators of past sea-level position. Fossil fiddler crab burrows have not been reported from Pleistocene carbonate rocks, but, if they should be discovered in the future, they also would be good sea-level position markers.

5.1.2 The Psilonichnus Ichnofacies

The beach and coastal dune ichnocoenoses of the Bahamas fall within and conform fully to the definition of the Psilonichnus Ichnofacies, as conceived by Frey and Pemberton (1987, originally termed the Psilonichnus Ichnocoenose). The holotype specimen of *P. upsilon* (Frey et al., 1984) is a burrow likely formed by the ghost crab, *Ocypode quadrata* (Fig. 11C and D), and preserved within Holocene carbonate grainstones of backshore beds on San Salvador.

Ichnocoenosis 4 (Fig. 9) is characteristic of carbonate sand beaches of the Bahamas and elsewhere in the wider Caribbean and beyond, as well as equivalent Holocene strata in the Bahamas and the Pleistocene of Bermuda (Curran, 1994, 2007). This ichnocoenosis is dominated by the distinctive modern burrows of ocypodid crabs (e.g., ghost crabs) and *P. upsilon* (Fig. 11E). In the Bahamas, the analog relationship between *O. quadrata*, its modern burrows, and *P. upsilon* is well established (Curran, 1994; Curran and White, 1991; Frey et al., 1984). The typical range of vertical oblique, J-, U-, and Y-shaped morphologies for *P. upsilon* occurs in the Holocene beach-backshore beds in the Bahamas. Vannini (1980) and De (2005) illustrated an even wider range of morphologies for burrows constructed by species of *Ocypode* in modern siliciclastic beaches.

Beaches in the Bahamas tend to be relatively steep and narrow and usually are backed with heavily vegetated dunes. Burrowing activity of *O. quadrata* is effectively confined to the beach backshore zone. Unlike its distribution in coastal siliciclastic settings, where ghost crabs commonly range well back into the dunes, Bahamian *O. quadrata* normally does not inhabit dunes, owing to the thick vegetation cover which impedes its mobility, and possibly also because of abundant presence of the common land crab, *Gecarcinus lateralis*, within dunal areas (Curran 1994; Curran and White, 1991).

*P. upsilon* is widespread in Holocene upper foreshore and backshore successions throughout the Bahamas. In contrast, the backshore zone is not well represented in Pleistocene beach to dune sequences, and *P. upsilon* has not been reported from these rocks (Curran, 2007). However, *P. upsilon* is common in a carbonate beach to primary dune coastal exposure of the middle Pleistocene Belmont Formation on Bermuda (Curran, 1994: Fig. 3.11), where its occurrence has real value as a sea-level position indicator. This utilitarian aspect of *P. upsilon* likely can be applied to other similar tropical carbonate settings elsewhere.

eolianite, near Whale Point, North Eleuthera. Hammer length = 28 cm. (H) Large cluster burrow in Holocene eolianite, Hanna Bay, San Salvador. Height of burrow complex = 1.4 m. (I) Cross sections of stellate burrows (shafts with radiating short tunnels) exposed on horizontal surface of Holocene eolianite, same location as H. Scale bar = 10 cm.
The original definition of the *Psilonichus* Ichnofacies included trace-fossil assemblages of coastal eolian dunes (Pemberton and Frey, 1985). A distinctive suite of trace fossils occurs in Bahamian coastal-carbonate eolianites (Ichnocoenosis 5; Curran and White, 2001). In the past, eolianites were thought to contain only sparse ichnofauna at best, usually rare vertebrate trackways. With establishment of the *Entradichnus* Ichnofacies to characterize sparsely vegetated to unvegetated eolian dune fields in arid settings (Ekdale et al., 2007; and/or the *Octopodichnus* Ichnofacies of Hunt and Lucas, 2007, featuring arthropod trackways) and recognition of the Bahamian eolian ichnocoenosis, it is clear that eolianites can have a very real and diverse ichnologic signature (see Ekdale and Bromley, 2012).

Rhizomorphs (or rhizoliths) are a ubiquitous aspect of Bahamian eolianites, with prolific occurrences reaching maximum ichnofabric level and completely obscuring original bedding and textures, particularly in Late Pleistocene eolian sediments deposited during sea regression (Fig. 11G). In Holocene eolianite sequences throughout the Bahamas, thin caliche (micritic) crusts with well-developed rhizomorphs parallel to bedding are common and represent short breaks in the buildup of dunal sands. These horizontal rhizomorphs can be distinctive enough to be attributed to the activity of some common coastal plant species (Curran and White, 2001; White and Curran, 1988).

Various types of arthropods are the likely tracemakers for all five of the animal trace fossils previously described from Bahamian eolianites (Curran, 2007 and earlier references). The largest and most distinctive trace fossils in these eolianites are cluster burrows and stellate burrows (Fig. 11H and I), attributed respectively to brooding and hatching activities of sphecid (digger) wasps and nesting activities of halictid (sweat) bees. Stellate burrows likely can be assigned to the ichnogenus *Cellicalichnus* Genise, 2000. Both forms are common and can be well preserved in Holocene beds throughout the Bahamas and, although less common, also in Late Pleistocene eolianites.

5.2 Homoclinal Carbonate Ramp: Quaternary of the Southern Arabian Gulf

Modern carbonates of the southern region of the Arabian (Persian) Gulf comprise one of the best studied and understood carbonate systems of the world. Although they have been widely used as a key analog for homoclinal carbonate ramps encountered elsewhere (see Alsharhan and Kendall, 2003), care must be taken before rigorous applications are made (e.g., Knaust, 1997; Walkden and Williams, 1998). Despite its well known sedimentology and diagenesis, the ichnological aspect of the Arabian Gulf has been only marginally studied and a comprehensive treatment is still missing. In this section, an overview of the ichnology in relationship to established facies zones is given. A more detailed characterization of the area can be found in Purser (1973) and Riegl et al. (2010).
The well-oxygenated conditions of the Gulf permit abundant benthic life at all depths that are responsible for a relatively high degree of bioturbation and destruction of lamination. Only hypersaline lagoons have local anaerobic conditions within the sediment, as indicated by sulfate reduction and organic-rich layers with pyrite. Al-Ghadban et al. (1998) discussed the amount of bioturbation in the Gulf in relation to water depth (water circulation), light, sedimentation rate, and grain size. They concluded that bioturbation dominates in coarse-grained sediments deposited mainly in the shallow south-western part of the Gulf, where high water agitation, good light penetration, favorable hard substrate, and coarse-grained sediment provide adequate supplies of oxygen and food which allow for growth of various epifaunal and infaunal (burrowing) communities. Benthic organisms with a burrowing behavior include foraminifers, cnidarians, crustaceans, bivalves, echinoderms, sponges, and a diverse worm fauna (Basson et al., 1977; George, 2005; John and George, 2005).

The modern facies pattern along the southern Arabian Gulf consists of a barrier-island system (mainly microtidal) and a coastal plain with sabkha deposits (Evans, 1995). Several localities along the coastline of the United Arab Emirates offer insight into different aspects of modern carbonate deposition (Alsharhan and Kendall, 2002, 2003), of which the facies belts in the area south of Al Aryam Island (Kirkham, 1997, 1998) illustrate well the related traces. On a S-N transect, the five facies belts detailed below can be recognized from the land to the sea.

5.2.1 Supratidal Flat (Sabkha) with Beach Ridges
This broad zone consists of a polygonally cracked halite surface (upper supratidal), a convoluted halite crust (middle supratidal), and a moist carbonate mud and gypsum mush (lower supratidal, cf. Alsharhan and Kendall, 2002). It is relatively barren of traces except for some traces of terrestrial animals, mainly arthropods (ants, termites, spiders, scorpions, and other insects) and vertebrates, concentrated on local, slightly elevated areas with sand accumulation. Stranded Pleistocene beach ridges as a result of the Flandrian transgression (approximately 5000 years BP) build such topographic highs (Kirkham, 1998) and run parallel to the coast in an upper supratidal position (some 2–4 km inland). Weak and patchy lithification of the bioclastic carbonate sand allows some organisms to excavate open burrows. Most obvious are the shallow subterranean nests of termites, about 5 cm in diameter and packed with plant material from the sparse shrub cover (Fig. 12A). The nests are associated with elongated pathways, which emerge from the central chamber and run along the surface. This habitat is also occupied by desert geckos of the genus *Stenodactylus*, which comprise ground-dwelling species. A low level of bioturbation becomes more common in the lower supratidal zone, where sandy and muddy layers originate due to storm washover events.
FIGURE 12 Modern ichnology of the tidal flat complex south of Al Aryan Island (southern Arabian Gulf, UAE). Scale bars = 1 cm. (A) Stranded Pleistocene beach ridges with abundant shells of cerithid gastropods on a supratidal flat (sabkha). The two larger burrows were made by termites, whereas the smaller one in between results from ant activities. (B) Upper intertidal sand flat with a groove-like surface trace of the sand-dwelling crab *Scopimera crabricauda* and its pseudo-pellets. (C) Soft mud surface at the margin of a lower intertidal pool with minute trails produced by foraminifers. (D) Firmground surface of a mud-bank in the lower intertidal with intense bioturbation by worms. (E) Margin of a lower intertidal channel (cliff height = approximately 0.3 m). The channel floor shows abundant trackways of birds, whereas the bank acts as a stiff- to firmground and is
5.2.2 Upper Intertidal Microbial/Sand Flats

A broad coastal zone is occupied by microbial (cyanobacterial) mats with different morphologies (Alsharhan and Kendall, 2003; Kendall et al., 2002). Such microbial flats with a leather-like surface develop in a harsh and hypersaline environment, which is uninhabitable for most burrowing organisms and therefore very few traces can be found here. Terrestrial arthropods are temporary visitors of this transition zone and burrow underneath the mats while feeding on decomposing mat material. Sand-filled shrinkage cracks along the margins of mat polygons are preferred sites of moisture and weakness for entering the substrate. Marine colonization by crustaceans and worms occurs in parallel with diurnal inundation of seawater, resulting in a patchy distribution of sand or sandy beaches. Volcano-like mounds, approximately 10 cm high and 4 cm wide and with a 1–3 mm diameter axial canal, occur in the vicinity of tidal channels. The columnar structures consist of alternating biolamination and pellet layers and result from the work of polychaetes within the polygonal algal zone (Shinn, 1972). Amphipods and ghost crabs (Ocypode saratan) are marine animals with a semiterrestrial lifestyle and move up from the water and cross the high-tide line to burrow into lower supratidal deposits. Amphipods are known to produce Skolithos-, Arenicolites-, or Diplocraterion-like traces (Gingras et al., 2008), whereas ghost crabs excavate large J-, U-, Y-shaped or complexly branched burrows like Macanopsis and Psilonichnus (e.g., De, 2005). Besides scavenging, the ghost crabs may also rework organic-rich sand (deposit-feeding) and produce pellets (Fig. 12B). Trackways and resting traces may have a slight chance to become preserved, but this is unlikely for the up to 30 cm high sand towers build by some male ghost crabs to mark their territory (Basson et al., 1977).

5.2.3 Lower Intertidal Sand/Mud Flats with Tidal Channels and Beachrock

The substrate of this zone is extensively reworked by a diverse fauna, dominated by elements of the meiofauna (e.g., foraminifers, nematodes, copepods, polychaetes, and turbellarians; Fig. 12C), several kinds of worms (e.g., polychaetes, nemerteans, and sipunculids; Fig. 12D), molluscs (gastropods, bivalves), crustaceans (e.g., amphipods, isopods, and decapods), insects (e.g., beetles), and birds. Aragonite-cemented coastal sand, composed of cerithid gastropod shells, may turn into well-developed beachrock (Alsharhan and Kendall, 2003;
Kendall et al., 1994). These crusts have a patchy cement distribution with numerous crevices, which provide shelter and food supply for a diverse fauna. Semiconsolidated substrate is bioeroded by cyanobacteria, bivalves (Botula, Lithophaga, and Gastrochaena) and the shrimp Alpheus (cf. Asgaard et al., 1997; Fischer and Meyer, 1985). Muddy and firm substrate along eroding channel margins is intensively burrowed by crustaceans, polychaetes, echiurans, and other worms (Fig. 12D and E). Lower intertidal mud flats host burrows of deposit-feeding ocypodid crabs (mainly Macrophthalmus depressus, see Basson et al., 1977) producing Macanopsis-, Psilonichnus-, Skolithos-, and Gyroolithes-like burrow morphologies (Fig. 12F), with the echiuran Ikeda taeenioides leaving deep subvertical burrows (Hornby, 2005), and with bivalves. A rich association of avifauna traces is present, including trackways of herons, flamingo, plovers, sandpipers, gulls, and terns. On protected mud flats, the Greater Flamingo (Phoenicopterus roseus) leaves extensive feeding traces when sifting through the silt while turning its body slowly around (Allen, 1956). The circular and semicircular structures are approximately 1.2–1.6 m in diameter and comprise a central pedestal surrounded by a feeding trough (Fig. 12G). The surface of tidal pools and soupy channel mud banks is covered with minute trails produced by foraminifers and abundant trails of cerithid snails with orientation toward the water.

5.2.4 Subtidal Lagoon with Sand Bars

The lagoonal areas between barrier islands and the tidal flat are mainly sandy and subordinately muddy. Subaqueous cementation is common and leads to the synsedimentary development of extensive hardgrounds, which become bioeroded by algae, grazing snails, endolithic sponges (Entobia-like borings), bivalves (Gastrochaenolites-like borings), crabs, and stomatopods. Patch reefs consisting of corals and algae grow where a suitable hard substrate is available and are subject to bioerosion not only by the same kinds of organisms but also by sea urchins, polychaetes, sipunculids, and fish. A complex system of tidal currents within the lagoon gives rise to the accumulation of various sand bodies such as bars, spits, and ebb-tidal deltas consisting of ooids. This sandy bottom is inhabited by a diverse meiofaunal fauna in the interstices as well as by macrobenthic animals with a burrowing behavior. Different snails and sea urchins (sand dollars and heart urchins) leave their trails on the sediment surface or dig slightly deeper. Bivalves, crustaceans, and worms all bioturbate the sand, but their burrows are poorly known. Common features are sand cones up to 1 m in height, produced by callianassid shrimp, while excavating an extensive burrow system—known from the fossil record as Ophiomorpha, Spongeliomorpha, and Thalassinoides (see Section 5.1). Burrows made by alpheid shrimp are frequently inhabited by gobies, a small commensal fish. Larger fish (e.g., soles) hide in the sand while waiting for prey, whereas rays form deep plug-shaped feeding excavations due to hydraulic jetting. If fossilized, such traces are known
as *Piscichnus*, and numerous of such depressions are nicely exposed on a Pleistocene bedding plane along the northern coast of Futaysi Island (Kirkham and Evans, 2008). The muddy substrate is burrowed by different species of bivalves, gastropods, worms, echinoids, crabs, and shrimp.

### 5.2.5 Barrier Islands with Sabkha and Leeward Spit–Bar Complexes

The exposed seaward sides of the barrier islands are often fringed with coral reefs, which build similar habitats as the patch reefs in the lagoon. In addition to the above-mentioned fauna, the beach sands are periodically visited by breeding sea turtles, especially the Green Turtle (*Chelonia mydas*, Fig. 12H). The turtles come onshore to lay their eggs in pits and leave impressive trackways in the sand which have potential for preservation.

### 5.3 Holocene Along the Mussafah Channel near Abu Dhabi

In addition to patchy Pleistocene outcrops (e.g., Evans et al., 2002), the Pleistocene–Holocene sections along the man-made Mussafah Channel SW of the city of Abu Dhabi offer good outcrops for studying the facies zones described in Section 5.2 (Kirkham, 1997, 1998) and their trace fossils. The about 2-m-thick section shows lateral and vertical facies variations but in general consists of the three units described below (Strohmenger et al., 2010).

#### 5.3.1 Pleistocene Reworked Dune Deposits (Eolianites)

The massive to cross-bedded carbonate-rich sandstone crops out at the base of the succession. This rock is affected by high-tide currents and contains numerous modern borings made by crustaceans (crabs and/or shrimp, Fig. 13A). This evidence implies that ancient crustacean structures similar to *Psilonichnus* and *Macanopsis* not only derive from the burrowing activity in sediment but sometimes also could be bioerosion features (cf. Asgaard et al., 1997; Fischer and Meyer, 1985).

#### 5.3.2 Holocene Transgressive Unit (Intertidal to Subtidal)

Above an unconformity, the carbonate succession starts with a thin layer of microbial mat deposits (intertidal) with weak bioturbation, locally over lain by a consolidated and cemented, cerithid-rich grainstone. The latter is a firm- to hardground that builds the lag of a compound channel cutting down into the eolianite. The eroded top surface of the firm- to hardground reveals various cross sections of burrows/borings, many of them with a dumb-bell shape suggesting pouch-shaped excavations similar to the ones of modern *Polydora* (Fig. 13B). Above it follows bioclastic pack-, grain-, and rudstone of tidal channel origin, which interfingers laterally with extensive lagoonal deposits (subtidal) consisting of mud-rich packstone with oxidized rootlets.
FIGURE 13  Ichnology of Pleistocene (A) and Holocene (B–H) deposits from the Mussafah Channel SW of the city Abu Dhabi. (A) Reworked dune deposits (eolianites) with modern crustacean borings in the upper intertidal zone. Cliff height = approximately 0.6 m. (B) Cerithid-rich firm-to hardground (channel lag deposit) with an eroded top surface and numerous cross sections of burrows/borings, probably produced by polychaetes. Scale bar = 1 cm. (C) Lower bedding plane of a beach sand layer (intertidal) with an extensive burrow system of Thalassinoides paradoxicus, probably produced by crustaceans. Scale bar = 1 cm. (D) Lagoonal packstone with large lenticular gypsum crystals (L, subtidal), bioturbated beachrock (B, lower intertidal) and microbial mats with gypsum crystals (M, upper intertidal). Scale bar = 20 cm. (E) Top of the lagoonal packstone with
Sections in a most landward position commonly contain beach deposits, some of which are intensively bioturbated. The burrows are about 5 mm in diameter and build a comprehensive system of *Thalassinoides paradoxicus*, maybe the product of crustaceans (Fig. 13C). The burrows promote a selective cementation which creates an ichnofabric in hypichnial preservation.

### 5.3.3 Holocene Regressive Unit (Subtidal to Supratidal)

The lagoonal, peloidal–skeletal packstone with large lenticular gypsum crystals of the transgressive unit continues into the upper part of the succession. Its sharp top surface exhibits many irregular shafts to crudely Y-shaped burrows (*Parmaichnus* isp.), penetrating deep into the substrate (Fig. 13D and E). They were likely produced by thalassinidean decapods (like *Upogebia*) and indicate lower intertidal conditions (Pervesler and Uchman, 2009). The colonization surface is covered by a 10- to 20-cm-thick rudstone/grainstone with cerithid gastropods and cross-bedding (Fig. 13D). This loosely consolidated sediment in places contains an irregularly branching burrow system (*Balanoglossites ramosus*, Knaust, 2008; Fig. 13F and G); the sediment is interpreted as high-energy tidal channel and beach deposit. Its top surface is locally covered by a thin firm- to hardground representing beachrock (Fig. 13H). The bioclastic packstone/grainstone locally continues toward the top of the section, where it results from extensive beach spit and bar deposition (intertidal), but is less bioturbated and subsequently overprinted by large gypsum crystals (supratidal).

### 6. CONCLUSIONS

The ichnology of carbonate sedimentary systems is less well studied compared to that of siliciclastic systems. Published ichnological/sedimentological studies of shallow-marine carbonates are biased toward the Mesozoic (especially Jurassic), whereas Precambrian, Paleozoic, and Cenozoic systems are underrepresented.

Shallow-marine carbonates differ from their siliciclastic counterparts by a number of criteria which can be grouped into three categories: (1) The composition and distribution of trace-fossil associations is controlled by the preferential abundance of various benthic organisms in tropical and subtropical zones where shallow-marine carbonate environments are common. This results in favored trace fossils such as crustacean burrows. (2) Given their specific

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*a dense accumulation of Parmaichnus* isp., interpreted as the burrows of thalassinidean decapods (e.g., *Upogebia*) in a lower intertidal environment. Scale bar = 1 cm. (F) Cerithid-rich rudstone/grainstone (lower intertidal) with an irregularly branching burrow system of *Balanoglossites ramosus* (vertical section), interpreted as the burrows of polychaetes. Scale bar = 1 cm. (G) As figure F, bedding surface. Scale bar = 1 cm. (H) Top surface of a firm- to hardground (intertidal beachrock) with a *Balanoglossites* ichnofabric below it. Scale bar = 20 cm.
morphology, carbonate ramps and rimmed shelves comprise broad and very shallow facies belts favorable for intense bioturbation, subaerial exposure, and development of peritidal ichnofauna and trace fossils formed by plant roots. (3) Carbonate sediments and their high diagenetic potential have a strong impact on the ichnological signature, resulting in the common occurrence of bioerosion, chemically etched borings, abundance of firm- and hardgrounds, and preferential trace-fossil preservation. Early-diagenetic processes can lead to rapid lithification with trace-fossil accentuation, but can also result in little to no sediment color contrast between burrows and matrix and bears a high potential for diagenetic alteration of trace fossils and hosting rocks.

Three ichnofacies are important for the reconstruction of paleoenvironments on carbonate shelves (or ramps): the *Psilonichnus* Ichnofacies, the *Skolithos* Ichnofacies, and the *Cruziana* Ichnofacies. In addition, the substrate-controlled *Glossifungites* Ichnofacies and the *Trypanites* Ichnofacies can overprint the former ones during periods with stagnant or low net-sediment accumulation (condensation, omission).

The value of ichnological analysis in shallow-marine carbonates is demonstrated in two case studies, the Middle Ordovician cool-water carbonates of the St. Petersburg region in Russia and the Middle Triassic epicontinental carbonates in Germany. Furthermore, neoichnological approaches can set a focus on rimmed carbonate platforms exemplified on the Quaternary of the Bahamas, and on homoclinal carbonate ramps such as the Quaternary of the southern Arabian Gulf. These examples, with their distinctive ichnocoenoses, are similar to other carbonate systems elsewhere and may serve as a comparative model for future investigations around the world.

Ichnological studies of modern carbonate environments and their rock-record equivalents are far from complete and have much potential for fruitful future research. Carbonates should not be viewed as the object of a separate subdiscipline of ichnology. Rather, ichnological information from carbonates should be combined with that of siliciclastics to achieve a better, more comprehensive understanding of depositional environments and the sedimentary rock record.

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