A HIGHLY DIVERSE ICHNOFAUNA IN LATE TRIASSIC DEEP-SEA FAN DEPOSITS OF OMAN

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ABSTRACT

We encountered a highly diverse ichnofauna within the deep-sea fan deposits of the Upper Triassic Al Ayn Formation in Oman. It comprises 32 ichnogenera: 18 ichnogenera represent predepositional graphoglyptids and other trace fossils that are preserved as casts on turbidite soles, and 14 ichnogenera represent postdepositional trace fossils that penetrate turbidite beds. The relatively large size of the area studied certainly favors encountering a high number of ichnogenera. The diversity we found approximately doubles the value that has often been stated in the literature and contradicts the paradigm that the Triassic represents a time of low ichnodiversity in the deep sea. Although the data are limited, in general the recovery of deep-sea tracemakers has been very slow owing to environmental disturbances that resulted from cold-bottom-water circulation after the Carboniferous–Permian glaciation. The high ichnodiversity in the Al Ayn Formation is explained by its paleogeographic position and locally formed warm bottom waters. The Al Ayn deposits accumulated adjacent to wide evaporitic and carbonate shelves, indicating continuous warm conditions. The Al Ayn clastic system was likely influenced by dense, salt-rich, warm water flowing back to the ocean from the carbonate and evaporitic shelf area. The downwelling water may have reduced the effects of cold water that formed during the Late Paleozoic glaciation and the Permian–Triassic anoxia, and, thus, it may have provided a refuge habitat. Despite the global trend of low-diversity deep-sea ichnocoenoses, refuge habitats may have been established in areas less affected by the otherwise harsh conditions.

INTRODUCTION

The purpose of this paper is to describe and analyze a trace-fossil community preserved in turbiditic deep-sea deposits of the Upper Triassic Al Ayn Formation in Oman (Fig. 1), which accumulated along the southern passive continental margin of the Tethys. The trace-fossil taxa have been compared with ichnocoenoses described in the literature for the Permian–Middle Jurassic. We discuss the implications on the long-term diversity trend found in deep-sea trace fossil associations.

The trace-fossil record for the deep sea is affected by a considerable gap in knowledge from the Permian until the Middle–Late Jurassic (e.g., Crimes, 1974; Seilacher, 1974; McCann, 1990; Uchman, 2003, 2004). Most of deep-marine ichnocoenoses are assigned to the *Nereites* ichnofacies (Seilacher, 1967). The high diversity within the *Nereites* ichnofacies during the late Mesozoic and early Cenozoic is largely attributed to the occurrence of complex-patterned, surface, and near-surface trace fossils commonly referred to as graphoglyptids (Fuchs, 1895).

The diversity trend of deep-marine trace fossils through time is still a matter of contention. Crimes (1974) counts the total number of ichnotaxa for a geologic period and detects a slight increase in diversity through most of the Phanerozoic, with a strong increase in diversity from the

Cretaceous to the Paleogene. He realizes, however, that data for some of the periods within the Phanerozoic are sparse. Simultaneously, Seilacher (1974) describes a steady increase during the Phanerozoic, accentuated by a peak in diversity during the Late Cretaceous. This analysis was based on the diversity of individual assemblages. McCann (1990) tests these observations and finds that the increase in diversity was neither as dramatic nor as consistent during the Phanerozoic as originally suggested. Buatois et al. (2001) reviews those works, suggesting that the former reflects global diversification patterns and that the latter provides information about the structure of individual communities. Uchman (2004) provides a detailed evaluation of deep-sea ichnodiversity and suggested a relative maximum during the Early Carboniferous, a marked decrease at the end of the Carboniferous, a minimum during the Permian and Early Triassic, and then a stepwise increase—interrupted by a short decline in the Albian—toward the Eocene maximum, followed by a decline in the Oligocene. Uchman (2004) invokes oceanographic events that interrupted the long-term evolutionary trend toward increasing diversity.

In spite of many differences, several studies of diversity trends of deep-sea ichnocoenoses through time share some similarities. Major crises as interpreted from the body-fossil record are not so clearly reflected by deep-sea trace fossils; however, data from trace-fossil associations within the *Nereites* ichnofacies are sparse for those times. The strong decrease in ichnodiversity during the Late Paleozoic occurred before the Permian–Triassic mass extinction. Uchman (2004), therefore, suggests that the formation of oxygenated cold deep water during the Permo–Carboniferous glaciation (e.g., Frakes et al., 1992) led to increased oxygenation of bottom waters. This strongly affected the deposition of organic matter in the deep sea, which, in turn, had severe consequences for deep-sea biota. It is possible, however, that the causal factors of the biotic crisis were initiated earlier than previously thought and did not spread to shallow-water successions until the Late Permian (J.-P. Zonneveld, personal communication, 2006).

The very low ichnodiversity within the *Nereites* ichnofacies during the Permian and the slight increase during the Triassic and Early and Middle Jurassic described by all authors have not been analyzed in detail because few turbiditic deep-sea deposits from this time span have been studied. Only nine deep-sea ichnofossil occurrences have been analyzed for a time interval covering more than 120 Ma.

MATERIAL AND METHODS

We logged four sections in detail in the central and eastern Oman Mountains (see Fig. 1), and we give locations for the individual sections in Universal Transverse Mercator (UTM) grid data using the World Geodetic System 84 (WGS; see Table 1). The biostratigraphy of the sections we studied is based on radiolarians, sponge spiculae, foraminifers, and corals (Blechschmidt et al., 2004).

Trace fossils have been classified by comparing them with previously described material to ascertain accurate identification (e.g., Uchman, 1995a, 1998). To minimize taxonomic artifacts owing to many unresolved
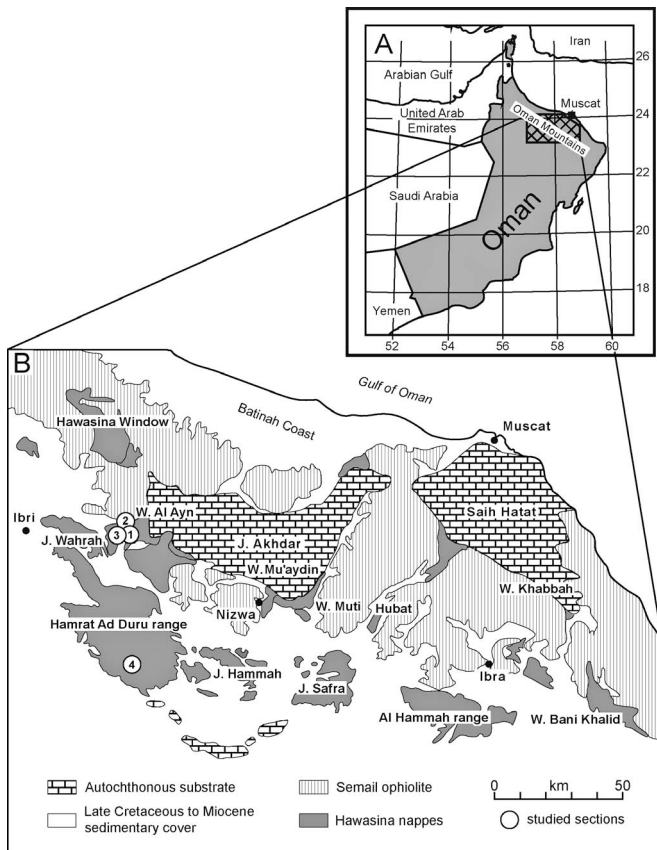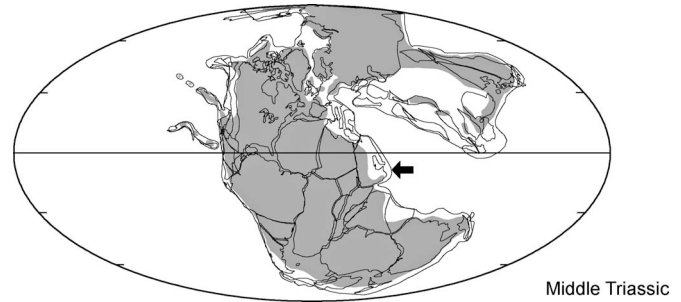
FIGURE 1—Study area. Inset shows location of the Sultanate of Oman. Numbers refer to sections analyzed in detail; their exact positions are listed in Table 1.

FIGURE 2—Paleogeographic map for the Middle Triassic (240 Ma; Scotese, 1997); arrow points to the study area. Continental areas are shaded; marine realms in white.

problems in ichnotaxonomy, we restricted long-term diversity analysis to the ichnogenus level (e.g., Uchman, 2004).

GEOLOGICAL BACKGROUND

During the Early Permian, a rift system developed between Gondwana, including the Arabian Plate, and the Cimmerian blocks to the east (Ziegler and Stampfli, 2001). Subsequent spreading starting in the Late Permian led to the formation of the Neo-Tethyan Hawasina Basin along the Arabian Platform (Fig. 2). The passive continental margin deposits comprise the Hamrat Duru Group (Fig. 3; Blechschmidt et al., 2004). Continuous Middle–Late Triassic extension led to a subdivision of the Hawasina Basin by the formation of the Misfah Platform, which separated the proximal Hamrat Duru Basin from the Umar Basin (Béchennec et al., 1990). During the Late Cretaceous, ocean floor and Hawasina strata were dissected and thrust onto the Arabian Platform (Allemann and Peters, 1972; Glennie et al., 1973; Watts and Blome, 1990).

The Mesozoic Hamrat Duru Group is subdivided into six formations based on the proportion of carbonates and siliciclastics and two distinct phases of high radiolarian content (Blechschmidt et al., 2004; Fig. 3). Sea-level fluctuations, particularly second and third order, affected de-

position within the basinal settings. In this basin, Blechschmidt et al. (2004) interpret carbonate dominance as indicative of high sea level, whereas siliciclastics indicate falling or low sea level. During the Late Triassic, a siliciclastic-dominated succession accumulated on a deep-sea fan. These deposits make up the Al Ayn Formation (Fig. 4). The sedimentology is described in detail by Blechschmidt (2002) and Blechschmidt et al. (2004), and we briefly summarize that description here.

The Al Ayn Formation exhibits two major progradation phases, which correspond to third-order fluctuations of relative sea level. The Al Ayn Formation consists primarily of quartz arenites and locally variable proportions of carbonate-calcareous sandstone, quartz-bearing calcarenite, and limestone conglomerate. Terrigenous clastics eroded from cratonic crystalline basement and local sediment cover were transported across the Arabian Platform carbonate shelf to the Hamrat Duru Basin. Paleoflow directions imply that sediment was transported from sources in the south and southwest to the north in the proximal areas and toward northwest or east to southeast in the distal regions of the Hamrat Duru Basin. The paleocurrent pattern and facies relationships suggest the development of several radial fans along the Arabian passive continental margin. Sediments of the Al Ayn Formation were deposited predominantly by submarine sediment-gravity flows in base-of-slope and abyssal-plain settings.

The architecture of the lithofacies associations provides insights into the development of the Al Ayn deep-sea fan system (Fig. 5). It can be adequately described by a sand-prone, radial submarine fan model (e.g., Mutti and Ricci Lucchi, 1972; Mutti 1992; Stow et al., 1996). In the proximal fan areas, channeled and amalgamated thickly bedded sandstone and conglomerate strata are organized predominantly into fining- and thinning-upward successions representing submarine channels. Cyclically stacked, coarsening-upward sandstone lobes grade into sandy-silty distal lobes of a middle fan and finally into a lower fan to basin-plain distal facies, indicating a retreat of the fan. We discuss the ichnology of the mainly centimeter-to-decimeter-thick, middle-to-lower-fan sandstone beds here.

RESULTS AND INTERPRETATION

The Upper Triassic Al Ayn Formation contains 32 ichnogenera. Eighteen ichnogenera, mostly graphoglyptid trace fossils, are predepositional and cast by turbidites (Fig. 6; Table 2). Fourteen ichnogenera are postdepositional with respect to turbidite deposition and penetrate them (Fig.

TABLE 1—Studied outcrops.

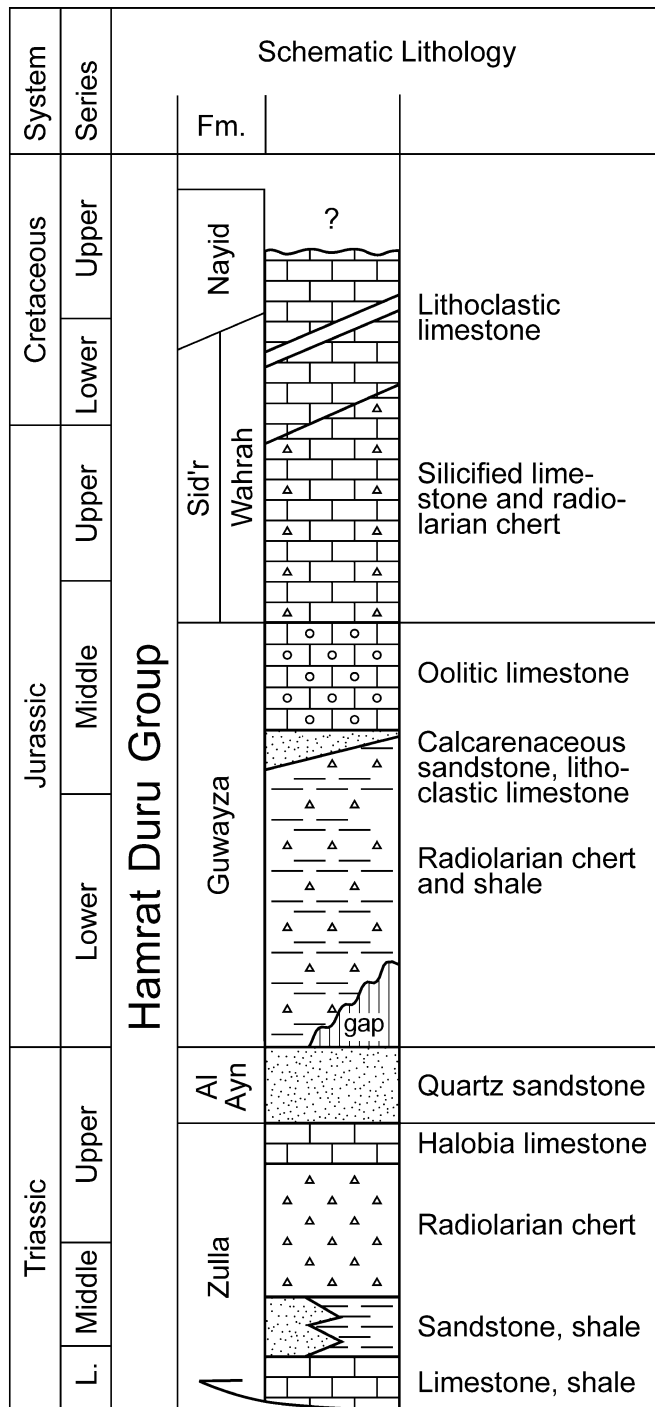|	Location	Coordinates		Depositional environment	Distance to outcrop no. (km)			
No.	Name	(UTM/WGS 84)			1	2	3	4
1	Tawi Shannah	498805	2568647	depositional lobe to fan fringe	—	~3	~5	~40
2	Al Jil	503500	2571500	depositional lobe to fan fringe	~3	—	~6	~45
3	Tawi Shu'ah	482100	2564346	upper midfan to depositional lobe	~5	~6	—	~40
4	Wadi Sal	490011	2523209	midfan to depositional lobe	~40	~45	~40	—

FIGURE 3—Compound lithologic log of the Hamrat Duru Group (from Blechschmidt et al., 2004). The studied interval of the Al Ayn Formation is dominated by siliciclastics.
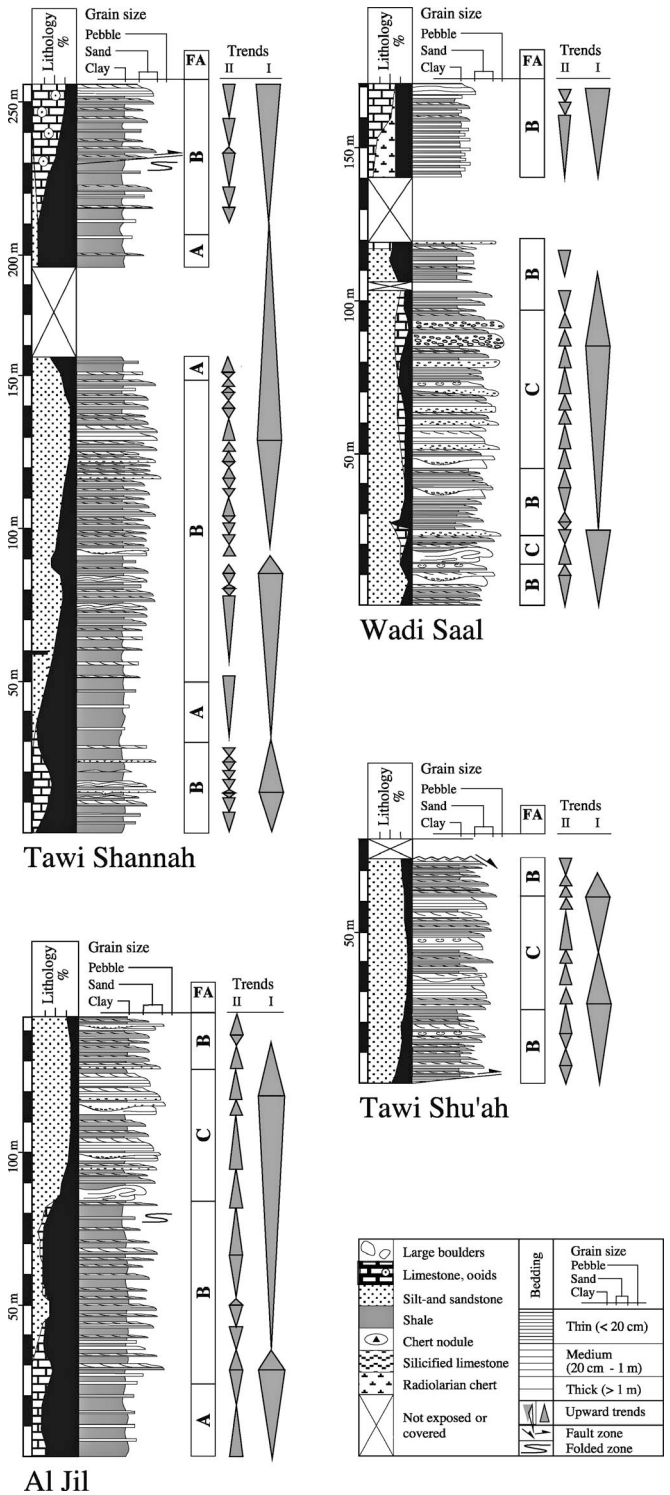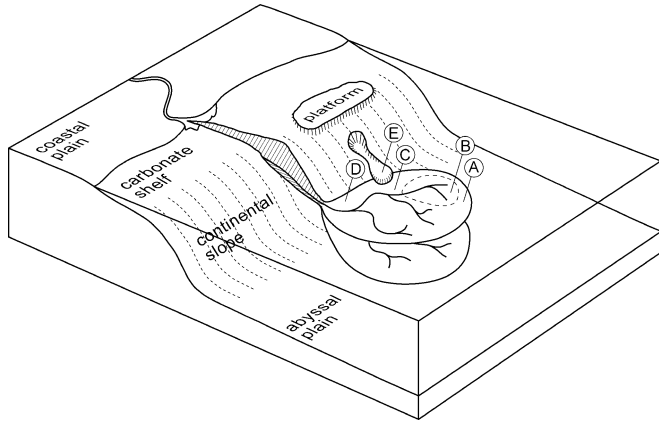

FIGURE 4—Schematic lithologic logs of the outcrops studied (from Blechschmidt, 2002). Facies associations represent areas shown in Figure 5. Small-scale and large-scale trends in bedding indicate coarsening- and thickening-upward and fining- and thinning-upward of beds, respectively. FA = facies associations; A = distal turbidites and hemipelagites in an outer-fan-to-fan fringe setting; B = medium-to-high concentrated turbidity current deposits on a sandy lobe with minor channels in a middle-to-outer fan setting; C = high-density turbidity current and debris-flow deposits in a channelized upper-to-middle fan setting.

7; Table 3). The very high ichnodiversity within the Al Ayn Formation becomes evident in comparison to other Permian–Middle Jurassic trace fossil assemblages belonging to the *Nereites* ichnofacies (see Supplementary Data[1]). The contribution of graphoglyptid traces to ichnodiversity is 56%, and hence is relatively high when compared with other ichnocoenoses within the *Nereites* ichnofacies for the time interval from the Permian to the Jurassic (15%–66%; Uchman, 2004) or for the Phanerozoic (10%–70%; Uchman, 2004). The ichnocoenoses of the Al Ayn For-

FIGURE 5—Schematic representation of the Al Ayn depositional system during the Late Triassic (from Blechschmidt et al., 2004). Letters refer to depositional environments: A = fan fringe; B = depositional lobe; C = mid-fan; D = upper fan; E = continental slope with slumps.

mation are more diverse than previously described Paleozoic ichnocoenoses (a maximum of 27 ichnogenera; Uchman, 2004) but less diverse than those described from the Late Cretaceous to Paleogene (a maximum of 50 ichnogenera; Uchman, 2004). Among the trace fossils encountered in the Al Ayn Formation, we distinguish those that (1) are known to occur continuously in the fossil record, (2) are known to occur only in rocks younger than Triassic, (3) are known to occur only in Paleozoic rocks, or (4) are restricted to the Al Ayn Formation (new ichnotaxa).

Predepositional Trace Fossils

Long-Term Occurrence in Deep-Sea Deposits.—Thirteen graphoglyptid ichnogenera have been reported from Late Triassic to Middle Jurassic deep-sea strata (see Supplementary Data[1]; Uchman, 2003): *Belorhaphe*, *Buthotrephis*, *Circulichnis*, *Cochlichnus*, *Desmograpton*, *Glockerichnus*, *Gordia*, *Helminthopsis*, *Lorenzinia*, *Megagrapton*, *Paleodictyon*, *Strobilorhaphe*, and *Treptichnus*. With the exception of *Buthotrephis* and *Cochlichnus*, all these ichnogenera are in the Al Ayn Formation.

Glockerichnus, *Helminthopsis*, *Megagrapton*, *Paleodictyon*, and *Strobilorhaphe* are known from both late Paleozoic and early Mesozoic successions. *Lorenzinia* may have occurred continuously through the Early Mesozoic but thus far has only been reported from Lower Triassic and Lower–Middle Jurassic deposits (see Supplementary Data[1]). *Desmograpton pamiricus*, found in Triassic–Jurassic deposits, has a typical geometry and size (for details, see Uchman, 2003). The specimens reported from the Eocene by Buatois et al. (2001) are smaller and more sharply bent up than the Mesoczoic ones and, hence, can be clearly distinguished.

Belorhaphe and *Gordia* are known from the Paleozoic and Late Permian, respectively, and then from Early and Late Jurassic deep-sea deposits; however, they have not yet been recorded in the Late Permian–Triassic. Specimens from Oman either fill an observational gap or they document a recovery of deep-sea faunas represented by these animal behaviors. The observational gap appears to be even longer for *Agrichnium*, *Circulichnis*, and *Helminthoidichnites*. *Agrichnium* is known from Upper Paleozoic and Permian flysch (Uchman, 2004) and has been described from Paleogene flysch (Plička, 1984); the observational gap equals this time interval. *Circulichnis* is known from Ordovician, Early and Middle Jurassic, and younger deep-sea deposits (see Uchman, 2004). It has been reported, however, in Carboniferous marginal-marine deposits (e.g., Buatois et al., 1998). *Helminthoidichnites* occurs for the first time in the Early–Middle Ordovician in Norway (Uchman et al., 2005) and is absent apparently until the Early Cretaceous in Bulgaria (Uchman and Tchoumatchenco, 2003). *Helminthoidichnites*, however, is a simple tube and abundant that the most likely explanation for the stratigraphic gap is a lack of observations. *Treptichnus* is known from the Paleozoic as well as the late
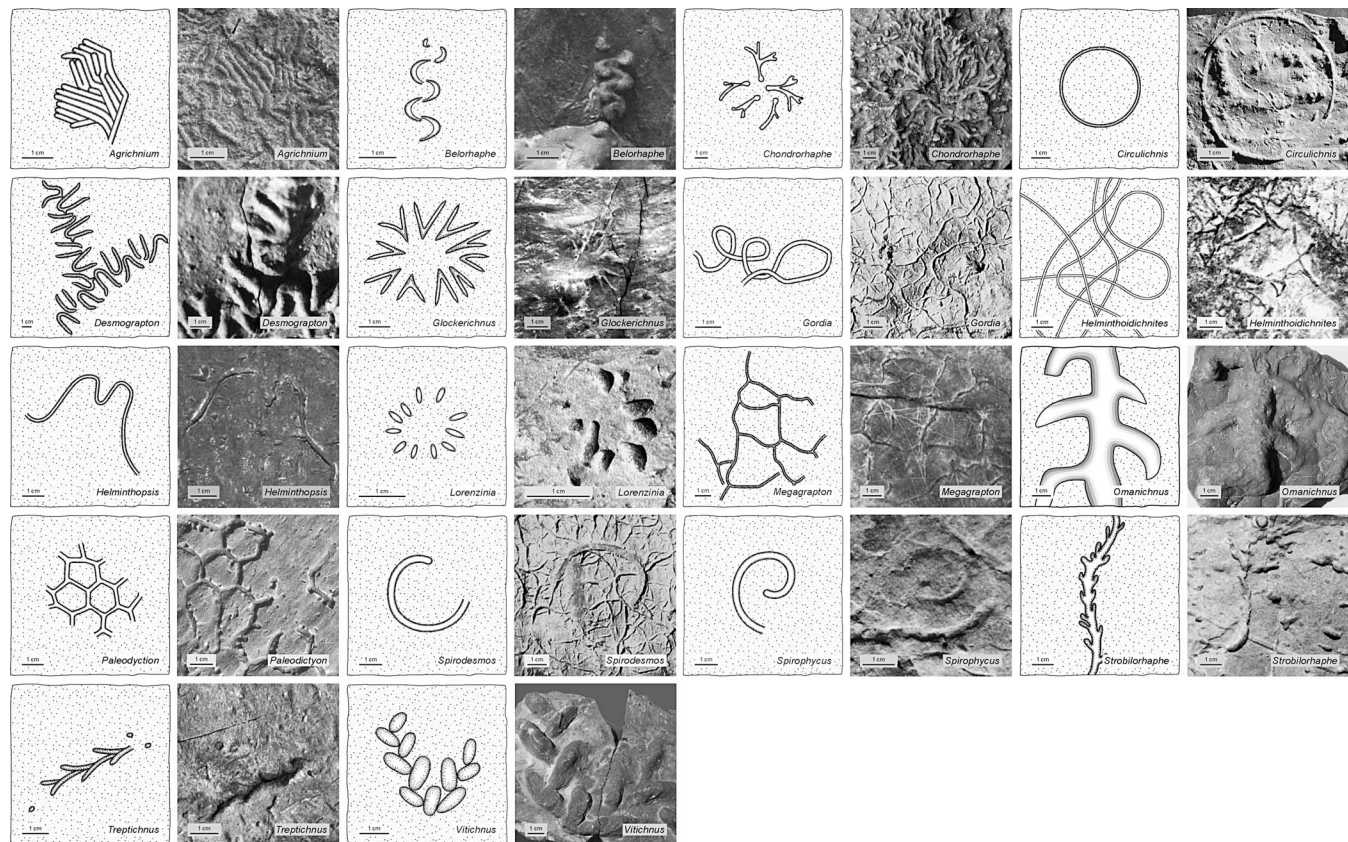
FIGURE 6—Schematic drawings and photographs of predepositional burrows encountered in the Al Ayn Formation. Short descriptions are given in Table 2.

TABLE 2—Short description of predepositional ichnogenera (shown on Fig. 6).

Ichnogenus	Short description
Agrichnium Pfeiffer, 1968	Small, closely spaced furrows of unequal length arranged in groups, initiating either from a branching point or by repeated branching.
Belorhaphe Fuchs, 1895	Wide 1st order meanders formed by zigzag 2nd order meanders, sometimes with protrusions. A piece was classified as cf. *Belorhaphe* isp.
Chondrorhaphe Seilacher, 1977	Radial dichotomously branching strings having knoblike structures at most of the bifurcations. *C. bifida* has been observed.
Circulichnis Vialov, 1971	Ring-shaped, smooth trace, almost circular or slightly ellipsoidal. *C. montanus* has been found.
Desmograpton Fuchs, 1895	Double row of U- or J-shaped, inwardly bent, in alternating modules; opposite modules joined by short bar. *D. pamiricus* was found.
Glockerichnus Pickerill, 1982	Usually dichotomously branched strings radiate from a central point or hollow central area.
Gordia Emmons, 1844	Unbranched, horizontal, winding, or irregularly meandering trace fossil, predominantly horizontal, tending to form loops.
Helminthoidichnites Fitch, 1850	Horizontal, thin, unbranched, straight or curved to circular burrow. *H. tenuis* was found.
Helminthopsis Heer, 1877	Unbranched, cylindrical tube with curves, windings, or irregular open meanders. *H. hieroglyphica* and *H. tenuis* were found (see Wetzel and Bromley, 1996).
Lorenzinia Gabelli, 1900	Simple short, smooth, hypichnial ridges regularly arranged in a circular row, radiating from a round central area; *L. apenninica* has been found.
Megagrapton Książkiewicz, 1968	Irregular net with meshes bordered by slightly winding strings that branch at nearly right angles. *M. irregulare* has been found.
Omanichnus Wetzel et al., 2007	Tubular central axis and regular, lateral, simple branches. Branches turn nearly rectangular after a short distance. *O. virgatus* was found.
Paleodictyon Meneghini, 1850	Horizontal net composed of hexagonal meshes having vertical outlets. *P. goetzingeri*, *P. maximum*, *P. arvense* were identified.
Spirodesmos Andree, 1920	Simple spiral tube having one or a few windings. The found part of a spiral shows an increasing curvature, thus classified as *S.* isp.
Spirophycus Häntzschel, 1962	Horizontal string bent at one end in a spiral. *Spirophycus involutissimus* has been found.
Strobilorhaphe Książkiewicz, 1968	Horizontal central tube and numerous lateral short, blunt, clavate branches. *S. clavata* has been found.
Treptichnus Miller, 1889	Simple or zigzag, straight or curved segments associated with vertical or oblique tubes. *Treptichnus* isp. has been found.
Vitichnus Wetzel et al., 2007	Overall V-like structure composed of short tubes arranged in tresslike pattern; both open to the same side. *V. nizwaensis* was found.

Mesozoic (Uchman, 2004). Also in this case an observational gap is invoked.

Occurrence in Post-Triassic Deep-Sea Deposits Only.—Prior to discovery in Oman the earliest occurrence of *Chondrorhaphe* is Late Cretaceous (Uchman, 2003). The Oman specimens may represent the activity of ancestors with the same animal behavior or other organisms that had a similar ethology early in the Mesozoic.

Occurrence in Paleozoic Deep-Sea Deposits Only.—*Spirodesmos* and *Spirophycus* are common in Paleozoic flysch; both have been reported from the Permian and, therefore, represent a continuation of the record. *Spirodesmos* is only known from Upper Paleozoic and Lower Triassic deposits (Uchman, 2003).

New Ichnogenera.—Two trace-fossil forms observed in the Oman material share some characteristics with *Saerichnites* and *Agnodipodas*. They exhibit diagnostic features distinguishing them from these and other ichnogenera, however. These new forms represent new ichnotaxa, *Omanichnus* and *Vitichnus* (Wetzel et al., 2007).

Postdepositional Trace Fossils

Several ichnogenera are thought to occur continuously in deep-sea settings since the Paleozoic. We describe the less-common trace fossils in some detail but only list the other traces (see Supplementary Data[1]). Because of their environmental significance, we deal with *Arenicolites* and *Protovirgularia* briefly here. In addition, we discuss *Ophiomorpha*, *Thalassinoides*, and *Zoophycos* as they represent the earliest deep-sea occurrences of these ichnogenera so far.

Arenicolites.—*Arenicolites* is found within a distal channel on a deepsea fan. Larval or adult animals might have been carried within the nepheloid layer or by turbidity currents down canyon, and they could have colonized sediment similar to that which they inhabited in the source area (e.g., Crimes, 1977; Wetzel, 1984; Grimm and Föllmi, 1994). *Arenicolites*, therefore, may indicate down-canyon current flow, even in times without turbidity current activity.

Protovirgularia.—As the main habitats of the *Protovirgularia* producers are shallow-marine environments (e.g., Seilacher and Seilacher, 1994), it is very likely that adults or larvae of the *Protovirgularia* producers have been transported to deep sea in a similar way as those of *Arenicolites* by suspension currents or within a nepheloid layer. It is also possible that *Protovirgularia* producers inhabited deep-sea environs more or less continuously while being repeatedly imported from shallow-water areas. The first abyssal *Protovirgularia* was reported from Silurian flysch (e.g., Crimes and Crossley, 1991).

Thalassinoides and Ophiomorpha.—The stratigraphic record of these ichnogenera has been analyzed by Carmona et al. (2004). *Thalassinoides* and *Ophiomorpha* can belong to the same burrow system in deep-sea deposits found intercalated with muddy and sandy sediments (Kern and Warme, 1974); therefore, they are considered together here. The earliest shallow-marine *Ophiomorpha* were reported from Middle Pennsylvanian strata in Utah (Driese and Dott, 1984). The first deep-marine *Ophiomorpha* was described from Upper Jurassic flysch (Tchoumatchenco and Uchman, 2001). The finds in Oman, therefore, indicate an earlier occurrence in such an environment. The occurrence of *Ophiomorpha* in Triassic deep-sea fan deposits is not unexpected because the corresponding ichnogenus *Thalassinoides* has been reported from Lower to Middle Triassic flysch (Zhang and Li, 1998). Consequently, the occurrence of *Ophiomorpha* and *Thalassinoides* in the Upper Triassic Al Ayn Formation suggests that the colonization of the deep-sea by *Thalassinoides*- and *Ophiomorpha*-producing animals started earlier than previously thought, possibly during the Early Triassic (see Supplementary Data[1]).

Zoophycos.—The specimens found in the Al Ayn Formation represent the oldest so far described occurrences from deep-sea fan deposits characterized by the *Nereites* ichnofacies. Note that the Paleozoic deep-water *Zoophycos* of Bottjer et al. (1988) do not match the criteria of the *Nereites* ichnofacies (e.g., Frey and Pemberton, 1984). Similarly, the deep-water *Zoophycos* reported by Pek and Zapletal (1990) from the Early Carboniferous is not associated with graphoglyptids and, hence, was later placed by these authors in the *Zoophycos* ichnofacies (Zapletal and Pek, 1999).

The *Zoophycos* producers were assumed to have initially colonized deep-sea turbiditic environments during the late Mesozoic (e.g., Seilacher, 1986; Chamberlain, 2000). The Oman specimens, however, document that colonization of the deep sea started at least by the Late Triassic. The
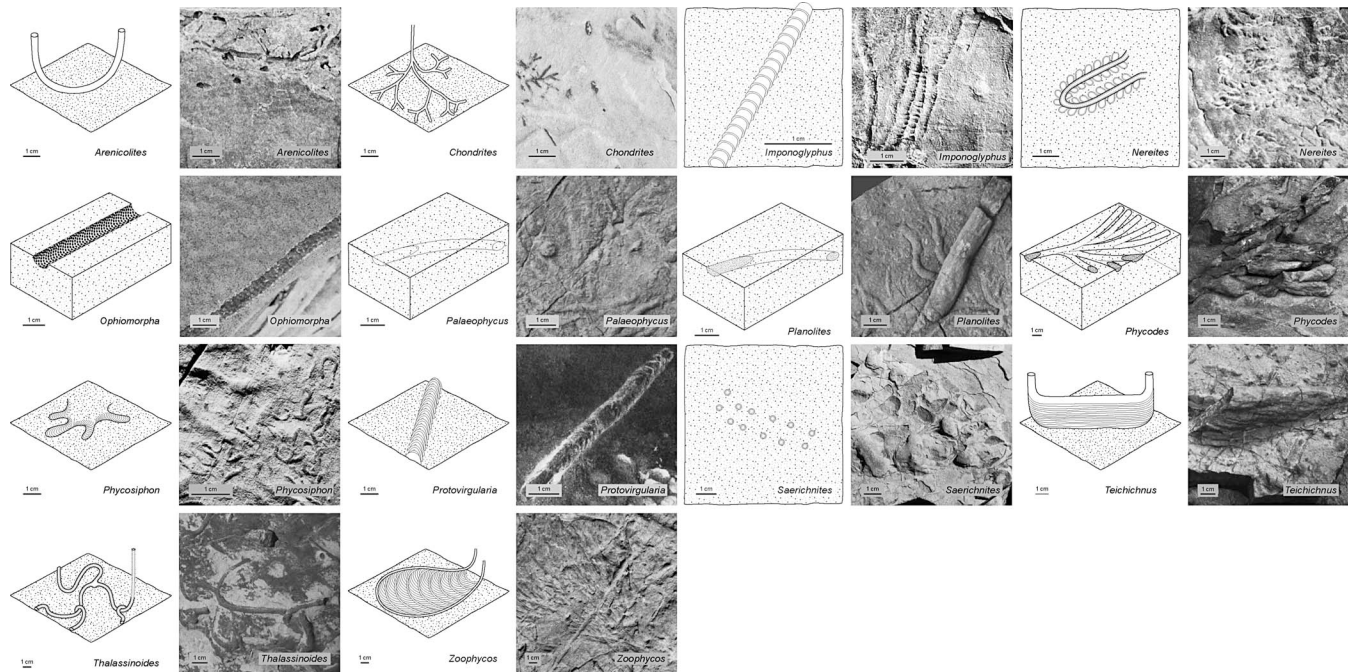
FIGURE 7—Schematic drawings, photographs and short descriptions of postdepositional burrows encountered in the Al Ayn Formation. Short descriptions are given in Table 3.

simple, rooster-tail-like *Zoophycos* are penetrated by simple tubes like *Planolites* and *Paleophycus* and hence, were probably produced at a shallow depth within the sediment (Fig. 8).

Zoophycos moved from shallow-water to deeper-water habitats through time (e.g., Seilacher, 1986; Bottjer et al., 1988; Olivero, 2003). In addition, *Zoophycos* changed from a simple, rooster-tail-like form (also with incomplete coiling; see Knaust, 2004) in Paleozic shelf deposits to geometrically complex, coiled, and lobate forms in Upper Cretaceous–Eocene flysch deposits (e.g., Seilacher, 1986; Chamberlain, 2000). From the Toarcian to Cenomanian, Olivero (2003) found that simple forms in shallow-water deposits evolved into increasingly advanced forms when the *Zoophycos* producers migrated into deep basinal deposits. At this time, coiling became complicated, and the spreite-production program increasingly variable, resulting in lobate forms. The Oman *Zoophycos* demonstrates that its morphology did not become increasingly advanced when the *Zoophycos* producers moved from bathyal to abyssal environments and does not confirm the linkage of behavioral change and colonization of a new environment proposed by Seilacher (1986) and Olivero (2003). Instead, the Oman *Zoophycos* suggests that behavioral evolution of simple forms was delayed after colonization of a new environment.

DISCUSSION

The ichnodiversity of the Al Ayn Formation is the highest reported so far from Permian–Triassic *Nereites* ichnofacies deposits. It is similar to or slightly higher than the Paleozoic maximum but below that for Late Cretaceous deep-sea deposits (Fig. 9). The extraordinary high diversity has important implications for understanding Late Paleozoic–Early Mesozoic deep-sea trace-fossil communities. Two aspects are of major importance for evaluating the significance of the ichnodiversity of the Al Ayn Formation: (1) area-size effects—because of the patchiness of the fauna, the number of ichnogenera observed should increase with the size of the area investigated (Fürsich, 1975)—and (2) paleogeographic position of the investigation area—in this case, we infer continuous warm conditions adjacent to wide evaporitic and carbonate shelves.

To some extent, there is a positive correlation between the amount of section available for examination and ichnodiversity encountered (Für-

sich, 1975). This effect is not as important within the context of the present study because a wide area was investigated. For comparison with other ichnocoenoses and analysis of the ichnodiversity, there are severe consequences when exposures of varying sizes have been compared; in particular, the smaller areas are subject to underestimated real ichnodiversity. With respect to the Al Ayn Formation, the size effect may influence the ichnodiversity in two ways. First, the size effect can be more pronounced in the deep-sea (compared to shallow-water) ichnocoenoses that were analyzed by Fürsich (1975) because of the high patchiness of the deep-sea fauna (e.g., Gage and Tyler, 1991). Second, the larger the area investigated within a deep-sea fan setting, the higher the probability of sampling an increasing number of subenvironments with varying ichnofaunas.

The studied outcrops of the Al Ayn Formation were up to 45 km away from each other (Fig. 1). In the outcrop with the highest ichnodiversity, we found 22 ichnogenera, representing 71% of all ichnotaxa. Within 40 km, we encountered the total ichnodiversity (Table 4). The number of postdepositional ichnogenera increases by 20%, and that of predepositional ichnogenera by 35%, when the size of the study area is increased. We did not observe identical trace-fossil assemblages at any two localities. These findings in the Al Ayn Formation are similar to the sparse data in literature, in particular, the study of the Lower Eocene Gurnigel Flysch in Switzerland by Crimes et al. (1981). In that study, 42 ichnogenera were observed in one outcrop. The number of postdepositional ichnogenera increased by increasing the size of the area investigated by about 20%; the number of predepositional trace fossils increased by 72% (Table 4).

An increase in diversity with increasing area sampled is more pronounced for the predepositional trace fossils and, hence, implies a stronger patchiness of their producers than for postdepositional trace fossils. This is not unexpected because the postdepositional fauna partially consists of trace-fossil producers living permanently within the habitat, especially multilayer colonizers (Uchman, 1995b), that can survive turbidite erosion and deposition. Examples of this ability include the producers of *Ophiomorpha*, *Thalassinoides*, *Teichichnus*, and *Zoophycos*. In addition, some postdepositional trace fossils were produced by animals that recol-
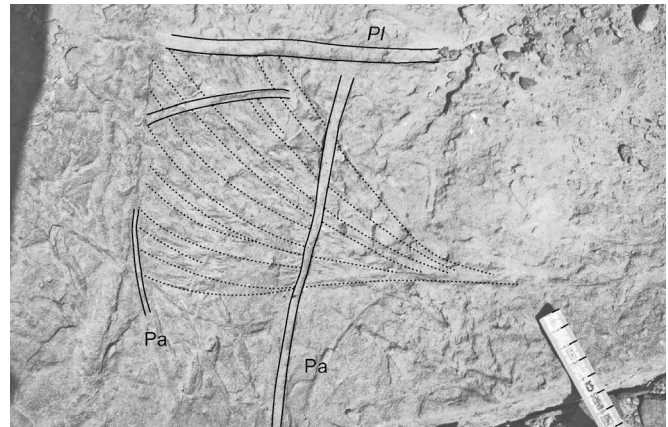
TABLE 3—Short description of postdepositional ichnogenera (shown on Fig. 7).

Ichnogenus	Short description
Arenicolites Salter, 1857	Vertical U-tube without a spreiten, tube diameter 2 and 3 mm, limbs 2–6 cm apart.
Chondrites Sternberg, 1833	From a master shaft, tubes regularly ramify at depth to form a dendritic network; *C. intricatus*, *C. targionii*, and *C.* isp. have been encountered.
Imponoglyphus Vialov, 1971	Invaginated, regularly spaced cones form ridges on a slightly winding burrow. *I. torquendus* is nearly straight.
Nereites MacLeay, 1839	Winding to meandering, central back-filled tunnel enveloped by even to lobate zone of reworked sediment. *N. irregularis* has been found.
Ophiomorpha Lundgren, 1891	Simple to complex burrow systems lined at least partially with pelletoidal sediment. *O. recta* has been found.
Palaeophycus Hall, 1847	Branched or unbranched, lined, cylindrical burrow, fill structureless, of the same lithology as host rock. *P. striatus* and *P.* isp. have been found.
Phycodes Richter, 1850	Palmately to laterally branched, flabellate burrow system; partially preserved burrows could not be assigned to an ichnospecies.
Phycosiphon Fischer-Ooster, 1858	Repeated narrow, U-shaped tubes enclose spreiten at mm to cm scale, branching from an axial spreiten. *P. incertum* has been found.
Planolites Nicholson, 1873	Unlined, rarely branched, straight to tortuous, tubular burrow; structureless fill differs from host rock. *P. beverleyensis* was found.
Protovirgularia McCoy, 1850	Tube, almond-shaped or triangular in cross section, internally having successive pads that form ribs on the exterior. *P.* isp. has been found.
Saerichnites Billings, 1866	Two parallel rows of round, more or less regularly distributed pits or pustules on bedding plane. *Saerichnites* isp. has been found.
Teichichnus Seilacher, 1955	Long, wall-shaped burrow consisting of a pile of gutter-shaped laminae. *T. rectus* is straight, unbranched with a retrusive spreite.
Thalassinoides Ehrenberg, 1944	Three-dimensional burrow system composed of smooth, cylindrical tubes branching at Y- to T-shaped, enlarged points. *T. suevicus* has been found.
Zoophycos Massalongo, 1855	U- or J-shaped protrusive elements of variable length and orientation form a spreiten structure. Simple rooster-tail–like specimens have been found.

FIGURE 8—*Zoophycos* (spreite structure indicated by stippled lines) cross-cut by *Planolites* and *Palaeophycus* tubes implying shallow burial depth of the Zoophycos producer; scale with cm marks; outcrop Tawi Shu'ah. *Pl = Planolites*; *Pa = Palaeophycus*.

onized the sediment after an event, indicated by sequential cross-cutting relationships and sediment fill (e.g., Wetzel and Uchman, 2001); among them are the producers of *Chondrites*, *Nereites* or *Phycosiphon*.

In contrast, the producers of graphoglyptids belong to the equilibrium fauna (Ekdale, 1985) and, hence, need time to reestablish within an event bed. Within a given environment, therefore, the patchiness of the fauna is likely to be inversely related to the recurrence time of turbidity currents. In the case of prolonged intervals between events, patchiness is balanced to some degree by the long interval between events during which time animals may migrate through an area and produce traces. Short-time intervals between events favor the preservation of patchiness and do not allow the full reestablishment of a highly diverse fauna. The local or regional conditions may be important, however; the benthic food content, currents, substrate consistency, and other factors affect the diversity as in modern deep-sea settings (e.g., Gray, 2002).

The evaluation of area size leads to the question of whether ichnodiversity depends only on area size or if it also depends on sampling a potentially larger number of subenvironments. It is important that most graphoglyptids are preserved in low-erosive turbidites deposited primarily

in distal settings (e.g., Seilacher, 1977). Consequently, in good outcrops exposing >100-m-thick sections, several subenvironments of a middle-to-lower deep-sea fan can be identified, as each one is represented by bed packages up to some tens of meters thick (e.g., Stow et al., 1996; Blechschmidt et al., 2004). For instance, in the outcrop with the highest ichnodiversity of the Lower Eocene Gurnigel Flysch (Zollhaus, Switzerland), Crimes et al. (1981) recognizes three subenvironments within proximal-to-distal outer fan settings (channel, interchannel, and depositional lobe). Similarly, Blechschmidt et al. (2004) identifies the same three subenvironments for the Al Ayn Formation in the Tawi Shannah section. Consequently, as the thickness of exposed section exceeds several tens of meters, several subenvironments are likely to be represented.

The size of a sampling area has a major effect on the ichnodiversity encountered, even if the exposed section is sufficiently long and covers a variety of subenvironments. These findings imply a patchiness of the deep-sea fauna; with respect to the available data, the faunal patches may be in the order of some square kilometers, or more.

Another aspect of late Paleozoic–middle Mesozoic deep-sea ichnodiversity is that, at the end of the Permian and the beginning of the Triassic, the marine fauna heavily suffered from widespread, if not worldwide, anoxia because oceans became stratified (e.g., Wignall and Twichett, 2002). The strongest decrease in ichnodiversity within the *Nereites* ichnofacies during the Late Paleozoic, however, occurred before the severe end-Permian environmental crisis. Uchman (2004), therefore, suggests that the decrease in deep-sea ichnodiversity was related to the onset of the Permo–Carboniferous glaciation. This glaciation oceanographically is believed to have led to initiation or intensification of the thermohaline circulation in the world's oceans by formation of cold, oxygenated water in polar regions mainly in the southern hemisphere (e.g., Frakes et al., 1992). Coincident with the onset of the Paleogene glaciation, deep-sea ichnodiversity decreased from the Eocene to the Oligocene because of similar processes (Uchman, 2004). During the Late Paleozoic, such cold-water masses affected Panthalassa and the southeastern parts of the Paleotethys. In contrast, warm-to-temperate climates surrounded the western parts of the Paleotethys (e.g., Scotese, 1997). The prevailing cold, deep water led to an increased formation of deep-marine cherts, which declined in abundance during the Early–Middle Triassic (e.g., Beauchamp and Baud, 2002). At this time, around the Ladinian-Carnian boundary, the climate returned to a so-called warm mode, which persisted until the Middle Jurassic (Frakes et al., 1992). The reasons for the low ichnodiversity within the *Nereites* ichnofacies are not really known, however, as the database for this time interval is very small.

If Uchman's (2004) assumption is correct, then the post-Permian recovery of trace-fossil-producing fauna could have started from shelf and
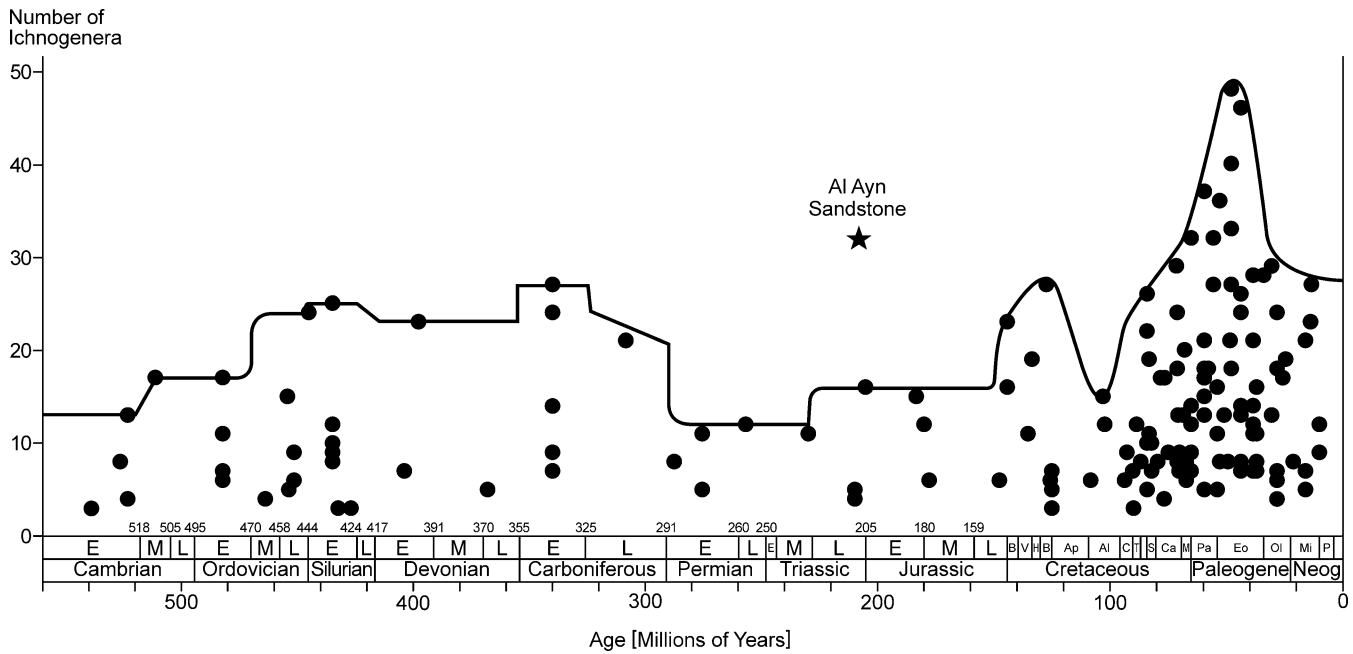
Number of
Ichnogenera

FIGURE 9—Variation of ichnodiversity in the *Nereites* ichnofacies on the ichnogenus level versus time. Line represents the long-term variation found by Uchman (2004) based on 103 studies; star marks the extraordinary high ichnodiversity of the Al Ayn Formation.

continental slope areas or other refuge habitats located in warm climates. Within this context, investigations in the recent show that shallow-water fauna attempting to colonize deep-water settings appear to be strongly affected by water temperature (e.g., Tyler and Young, 1998).

Potential refuge habitats might have been located on the shelves and continental margins of the Neotethyan Realm having warm water, for instance, along the equator or low latitudes during the Triassic (e.g., Scotese, 1997). Such conditions are met at the Triassic continental margin of the Arabian Peninsula, which could have acted as a nearly ideal refuge habitat. As a passive continental margin, the Arabian Peninsula has had a wide, open-marine carbonate shelf (e.g., Ziegler, 2001; Blechschmidt et al., 2004) and an extensive continental slope because of its gentle

inclination (compared to active continental margins). Furthermore, the Al Ayn deep-marine clastic system within the Hamrat Duru Basin was partly incised into the carbonate shelf (e.g., Ziegler, 2001), and oceanward some ridges might have affected the deep-marine circulation (Blechschmidt et al., 2004). During the Late Paleozoic, the Cimmerian blocks to the east (e.g., Ziegler and Stampfli, 2001) might have restricted the influence of cold deep-marine circulation. In addition, evaporites accumulated on a wide shelf to the north of the study area from the Late Permian to the Late Triassic (e.g., Ziegler, 2001), producing warm saline shelf waters that could have flowed back to the ocean, affecting at least the local oceanographic conditions and replacing anoxic (e.g., Kump et al., 2005) or cold deep water. If the assumption holds true that organisms can re-

TABLE 4—Ichnodiversity in relation to size of study area.

Outcrop	1. Tawi Shannah		2. Al Jil		3. Tawi Shu'ah		4. Wadi Sal	
Al Ayn Formation (Triassic, Oman)								
Distance to outcrop 1 (km)	0		3		5		40	
	ichnogenera		ichnogenera		ichnogenera		ichnogenera	
	total	total	not found in outcrop 1	total	not found in outcrops 1–2	total	not found in outcrops 1–3	
Postdepositional	11	8	1	8	0	9	2	
Predepositional	11	9	3	4	0	8	3	
Total	22	17	4	12	0	17	5	
Outcrop	1. Zollhaus		2. Fälli Hölli		3. Höllbach		4. Fayaux	
Gurnigel Flysch (Eocene, Switzerland)								
Distance to outcrop 1 (km)	0		8		10		40	
	ichnogenera		ichnogenera		ichnogenera		ichnogenera	
	total	total	not found in outcrop 1	total	not found in outcrops 1–2	total	not found in outcrops 1–3	
Postdepositional	19	6	0	11	1	12	3	
Predepositional	11	7	0	3	1	16	7	
Total	30	13	0	14	2	28	10	

colonize the habitats of their ancestors from refuge habitats, the general but interrupted evolutionary trend toward increasing ichnodiversity could have continued during the Triassic at the same or a somewhat lower level than before the Late Paleozoic crisis in the deep sea.

CONCLUSIONS

Thirty-two ichnogenera found within the turbiditic deposits of the Al Ayn Formation in Oman represent the most diverse deep-sea ichnofauna observed thus far from the Cambrian until the Early Cretaceous. Post-depositional burrows provide about half of the diversity, graphoglyptids the other half. The richness in graphoglyptids is very high compared to other Paleozoic and Early Mesozoic deep-sea ichnocoenoses.

The analysis of the ichnofauna data from the Al Ayn Formation and from literature clearly shows that the size of the investigated area affects the ichnodiversity found. The area size certainly affects the comparison with other trace-fossil assemblages if the size of the area studied differs. Within an area of a few kilometers, about two-thirds to three-quarters of all ichnogenera were encountered; however, additional ichnotaxa often are found in outcrops tens of kilometers away. The increase in ichnodiversity with size of area studied may reflect the patchiness of trace-producing fauna rather than the number of subenvironments investigated. As graphoglyptids are preserved best in low-erosive, distal turbidite subenvironments that form bed packages a few meters to a few tens of meters thick, in good outcrops numerous subenvironments are consequently encountered.

The highly diverse ichnofauna in the Al Ayn Formation contradicts the post-Paleozoic diversity minimum from the Late Paleozoic–Late Jurassic. The high ichnodiversity of the Al Ayn Formation is explained by its paleogeographic position and the understanding that times of high ichnodiversity in *Nereites* ichnofacies coincide with periods characterized by warm bottom water in the oceans. The Al Ayn sands accumulated adjacent to wide evaporitic and carbonate shelves since the Late Paleozoic, indicating continuous warm conditions. So the Al Ayn clastic system may have been influenced by dense, salt-rich warm water flowing back to the ocean from the carbonate and evaporitic shelf area. The downwelling water may have reduced the effects of cold water formed during the Late Paleozoic glaciation and the Permian–Triassic anoxia, and, thus, provided a refuge habitat. In spite of a global trend to low-diversity, deep-sea ichnocoenoses within refuge habitats could have been less affected by the otherwise harsh conditions.

ACKNOWLEDGMENTS

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