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SCRATCH TRACES OF LARGE EDIACARA BILATERIAN ANIMALS

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ABSTRACT—Ediacara fan-shaped sets of paired scratches *Kimberichnus teruzzii* from the Ediacara Member of the Rawnsley Quartzite, South Australia, and the White Sea region of Russia, represent the earliest known evidence in the fossil record of feeding traces associated with the responsible bilaterian organism. These feeding patterns exclude arthropod makers and point to the systematic feeding excavation of seafloor microbial mats by large bilaterians of molluscan grade. Since the scratch traces were made into microbial mats, animals could crawl over previous traces without disturbing them. The trace maker is identified as *Kimberella quadrata*, whose death masks co-occur with the mat excavation traces in both Russia and South Australia. The co-occurrence of animals and their systematic feeding traces in the record of the Ediacara biota supports previous trace fossil evidence that bilaterians existed globally before the Cambrian explosion of life in the ocean.

INTRODUCTION

THE CO-OCCURRENCE of Ediacara body fossils and trace fossils in South Australia (Glaessner, 1969, 1984; Jenkins, 1995), Namibia (Germs, 1972; Crimes and Germs, 1982), Russia (Fedonkin, 1977, 1992, 2003; Grazhdankin, 2004; Grazhdankin et al., 2005), and northwestern Canada (Narbonne and Hofmann, 1987; Narbonne and Aitken, 1990) distinguishes these assemblages from the older and deeper water fossils assemblages of largely sessile organisms in eastern Newfoundland, Canada, and Leicestershire, United Kingdom (Narbonne, 2005; Howe et al., 2012) where trace fossils are either very rare (Liu et al., 2010; Menon et al., 2013) or entirely absent. Ediacaran successions with trace fossil assemblages, but few body fossil taxa, include Finnmark in north Norway (Banks, 1970; Farmer et al., 1992), the White-Inyo Mountains in western U.S.A. (Alpert, 1975), the Dengying Formation in south China (Weber et al. 2007; Chen et al., 2013), central Australia (Walter et al., 1989), and central Spain (Vidal et al., 1994; Cortijo et al., 2010). Bilobed trace fossils from Uruguay, described as early Ediacaran by Pecoits et al. (2012), and resembling Phanerozoic traces from freshwater sediments, were more-likely part of Permian sediments disconformably overlying granitic rocks rather than intruded by them (Gaucher et al., 2013). The similarity in diversity and form shared by Ediacara trace fossil assemblages suggests common patterns of behavior and similar environmental settings (Crimes, 1987, 1992; Buatois and Mangano, 2010). Although the bilaterian affinities of body fossils in the Ediacara biota have been questioned (Seilacher, 1984, 1989, 1992), there is broad agreement that trace fossils herald the beginning of integrated sensory-muscular activity of true animals with bilateral symmetry (Seilacher, 1984, 1989; Bergström, 1990; Valentine et al., 1999; Jensen et al., 2005; Erwin et al., 2011). Ediacara trace fossils are almost exclusively two-dimensional and restricted to partings beneath very thin sandy beds (Glaessner, 1969; Seilacher, 1999; Jensen et al., 2005, 2006). They record furrowing within microbial mat-bound sandy substrates (Gehling, 1999; Gehling and Droser, 2009; Droser et al., 2006). Arguably such Ediacara furrows and shallow, intrastratal burrow traces represent the activities of small coelomate animals with well-developed muscles and sensory capacity. While motile acoelomate organisms (e.g., anemones and flat worms) are capable of making similar trace patterns (Collins et al., 2000), the chances of preserving such locomotive traces are limited (but see Liu et al., 2010; Menon et al., 2013). Although a diverse array of trace fossils has been claimed in the Ediacara Biota, Jensen et al. (2005) regard true trace fossils as represented by relatively few ichnotaxa, the most common being levee-bearing furrow traces referable to *Helminthoidichnites* (Jensen, 2003). The most unusual Ediacara trace fossils are serial "resting traces" of the mat-like forms, *Dickinsonia* and *Yorgia* (Ivantsov and Malakhovskaya, 2002) interpreted as a mode of saprophytic feeding (Gehling et al., 2005; Sperling and Vinther, 2010). Claims for regular contact meander burrows and fecal pellet trails in these assemblages (Glaessner, 1969; Fedonkin, 1977; Jenkins, 1995) are less convincing. Serial, arcuate forms, such as *Palaeopascichnus*, *Neonereites uniseriali* and *Nenoxites* (with affinities to *Shaanxilithes ningqiangensis* from South China and India), have been variously interpreted as trace fossils (Fedonkin, 1977; Haines, 2000; Rogov et al., 2012) megascopic algae (Seilacher, 1998; Gehling et al., 2000), a form of protozoan (Ancliffe et al., 2011) convergent on modern xenophyophorans (Seilacher et al., 2003), and annulate, tubular body fossils (Meyer et al., 2012; Brasier et al., 2013; Tarhan et al., 2013).

Although the production of the South Australian arrays was previously attributed to arthropods (Jenkins et al., 1983; Gehling, 1991; Jenkins, 1992, 1995; Crimes, 1994), examination of a large number of specimens has shown that the general arrangement and variations in form are not consistent with that expected from the action of arthropod legs. Specimens from South Australia and the White Sea region of Russia (Gehling, 1996; Seilacher, 1999; Martin et al., 2000; Fedonkin, 2003) represent some of the first published examples of Ediacara trace fossils preserved with the body fossils of their likely makers. We attempt to reconstruct the feeding behavior, the physiology of the feeding animal, and the taphonomy of this association of maker and trace fossil.

STRATIGRAPHY

The South Australian scratch traces occur in the same sedimentary facies as body fossil impressions of the Ediacara biota, in the upper part of the 300-m-thick Ediacara Member of

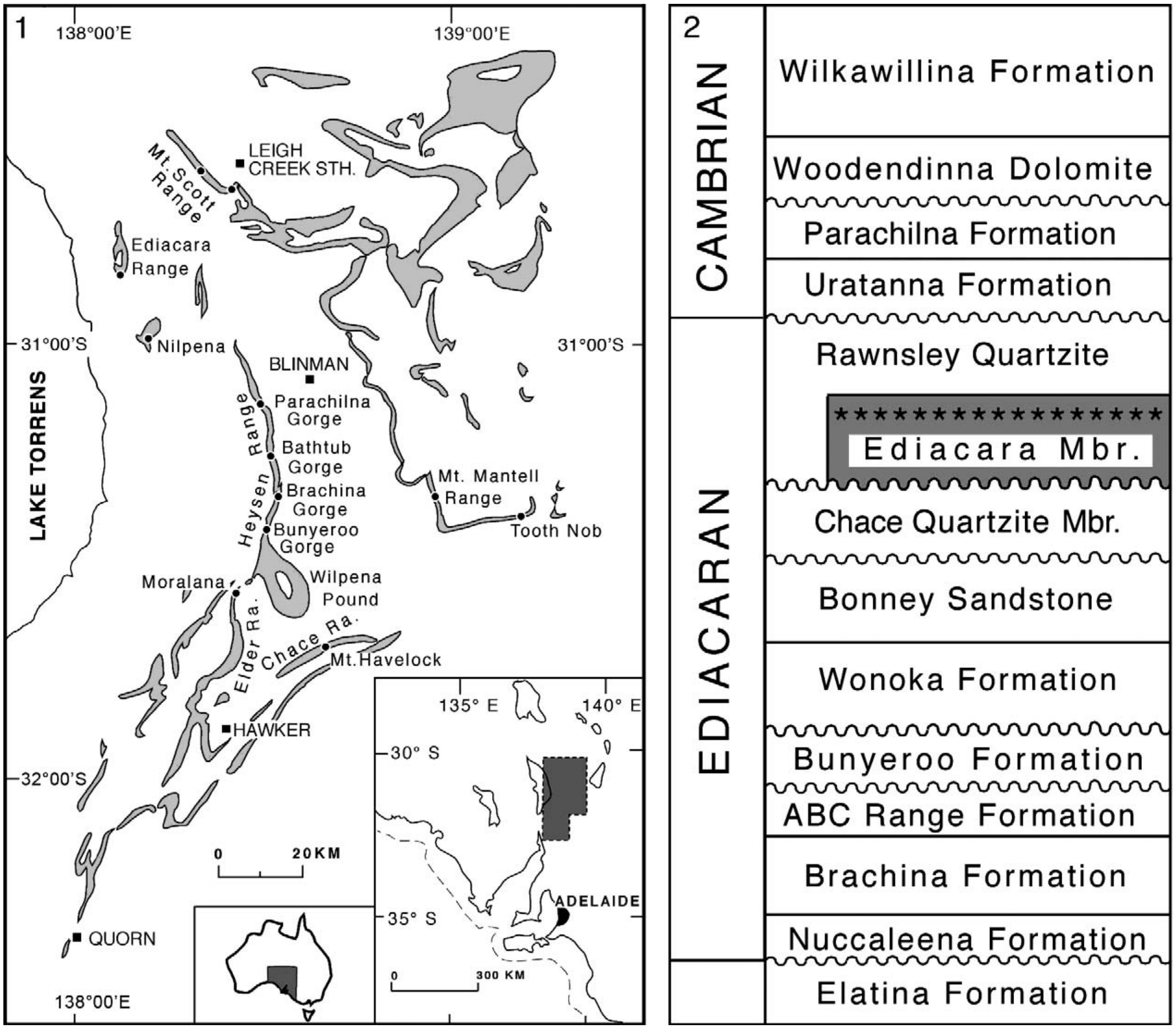


FIGURE *1*—*1*, distribution of the Pound Subgroup (Rawnsley Quartzite and Bonney Sandstone) in the Flinders Ranges South Australia, with marked localities of numbered specimens of *Kimberichnus teruzzii* Ivantsov, 2013; *2*, stratigraphic context of the fossil bearing Ediacara Member in relation to the Ediacaran and early Cambrian formations in the Flinders Ranges, South Australia.

the Rawnsley Quartzite (Fig. 1.2; Jenkins et al., 1983; Jenkins, 1995; Gehling, 2000; Gehling and Droser, 2012). Outcrops of the Rawnsley Quartzite are preserved in the northern part of the Adelaide Geosyncline, 350–500 km north of Adelaide (Fig. 1.1). Ediacara fossils occur on the soles of sandy event beds, commonly with corresponding counterparts on the tops of underlying sandstone beds. Fossiliferous beds span some 200 m of the Ediacara Member in its thickest developments (Gehling, 2000; Gehling and Droser, 2012). The early Cambrian Uratanna Formation disconformably overlies the Rawnsley Quartzite (Fig. 1.2). The base of the Cambrian is, by definition, marked by the first appearance of *Treptichnus pedum* and *Phycodes coronatum*, 230 m above the base of the Uratanna Formation. Distinctive Cambrian trace fossils, including *Treptichnus pedum*, *Phycodes coronatum, Taphrhelminthopsis,* and *Rusophycus,* occur throughout the upper third of the Uratanna Formation (Daily, 1973; Mount and McDonald, 1992; Jensen et al., 1998; Droser et al., 1999). Frond-like fossils discovered by Jensen et al. (1998), about 100 m above the first *Treptichnus pedum* in the Uratanna Formation (Fig. 1.2), represent early Cambrian holdovers of Ediacara-like fossils. Comparisons of taxonomic diversity in the Ediacara Member (Gehling and Droser, 2013), as demonstrated at the National Heritage Ediacara Site at Nilpena, south of the Ediacara Conservation Park on the western flanks of the Flinders Ranges (Fig. 1.1), enable tentative correlations with the Ediacaran successions of the White Sea region of Russia (Martin et al., 2000; Grazhdankin, 2004) and Namibia (Grotzinger et al., 1995; Saylor et al., 1995). Thus the Ediacara scratch arrays in the Ediacara Member may date from 560–545 Ma.

LOCALITIES AND REPOSITORIES

Localities for the South Australian scratch traces include: 1) Mt. Scott Range, S 30°37′25″, E 138°21′21″; 2) Mt. Scott Range, S 30°39′35″, E 138°25′15″; 3) Ediacara Range, S 30°50′14″, E 138°08′10″; 4) Bath Tub Gorge, S 31°14′48″, E 138°32′14″; 5) Heysen Range, 2 km south of Brachina Gorge S 31°22′06″, E 138°33′33″; 6) Heysen Range, 2 km south of Bunyeroo Gorge, S 31°25′25″, E 138°32′12″; 7) Moralana Creek, S 31°33′48″, E 138°26′45″; 8) Mt. Mantell Range, S 31°21′43″, E 138°58′58″; 9) Tooth Nob, S 31°21′48″, E

139°13′49″; 10) Mt. Havelock, Chace Range, S 31°40′06″, E 138°44′37″; 11) Nilpena, S 30°58′51″, E 138°12′43″ (Fig. 1.1).

The Ediacara specimens of *Kimberichnus teruzzii* Ivantsov, 2013, held in the South Australian Museum paleontological collection (prefix SAM), include P35651a (hyporelief cast) and corresponding counterpart P35651b (Bathtub Gorge); P35656 (Heysen Range south of Bunyeroo Gorge), P35657 (south of Brachina Gorge), P35653 (Bathtub Gorge); P35654 (Mt. Mantell Range), P35652 (Tooth Nob), P35655 (Moralana), P35662, P35663, P35696 (Mt. Scott Range), P35691 (unfigured), P35696 (Mt. Scott Range), and P35693, P35699, P48936 (Nilpena National Heritage Site).

SYSTEMATIC ICHNOLOGY

Ichnogenus Kimberichnus Ivantsov, 2013

Type ichnospecies.—*Kimberichnus teruzzii* Ivantsov, 2013 by original designation.

Diagnosis.—Arrays of shallow, bifid ridges, in arcuate sets, with progressive increase in radius and width of arc (emended from Ivantsov, 2013).

Etymology.—The generic name is for *Kimberella quadrata*, the Ediacara body fossil consistently associated with these traces (emended from Ivantsov, 2013).

Kimberichnus teruzzii Ivantsov, 2013
Figures 2–7

1983 "fan-shaped patterns of arthropod scratch marks" Jenkins et al., p. 113.
1991 "Sets of paired hypichnial ridges" Gehling, p. 215, pl. 6, fig. 3.
1992 "scratch marks made by feeding arthropods" Jenkins, p1. 58, fig. 10G.
1995 "cf. *Monomorphichnus*" Jenkins, p. 58, pl. 1C.
1996 "Troctichnus flabellatus" *nomen nudum* Gehling, p. 181–222.
1997 "arthropod feeding scratches" Grazhdankin and Bronnikov, fig. 1.
2000 "Structures interpreted as radular scratches" Martin, Grazhdankin, Bowring, Evans and Kirschvink, fig. 4E.
2003 "radular scratches (*Radulichnus*)" Seilacher, Grazhdankin, and Leguota, p. 44, fig. 3.
2003 "Enigmatic scratch marks" Fedonkin, p. 33, fig. 15.
2003 "grazing tracks" Fedonkin, p. 34, fig. 16.
2004 "*Radulichnus*" Dornbos et al., fig. 5.
2005 "*Radulichnus*" Seilacher, Buatois and Mangano, p. 330, fig. 5.
2008 "*Radulichnus*" Peterson, Cotton, Gehling, and Pisani, fig. 2a.

Diagnosis.—Emended: equal pairs of parallel grooves made in the substrate but most commonly preserved as sharp positive (hyporelief) casts on the sole of the overlying bed; offset or touching; some are blunt or merge at proximal ends, being sharpest and slightly splayed at distal ends; isolated longer pairs simple, parallel; mostly ranked in arcuate or obliquely staggered sets, with adjacent pairs sub-parallel; within each array, more proximal sets tend to overlap and erase more distal sets; some overlap between laterally adjacent fans. The focal point of fanned sets, preserves no bifid scratches, but may be over-printed by clusters of sand pellets, 2–4 mm in diameter.

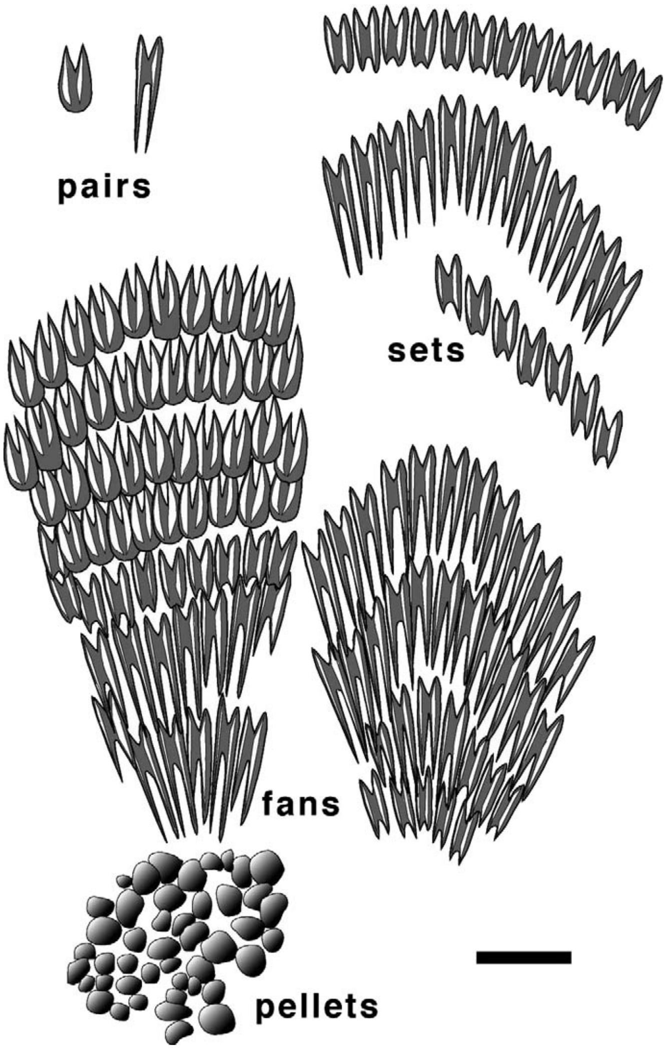
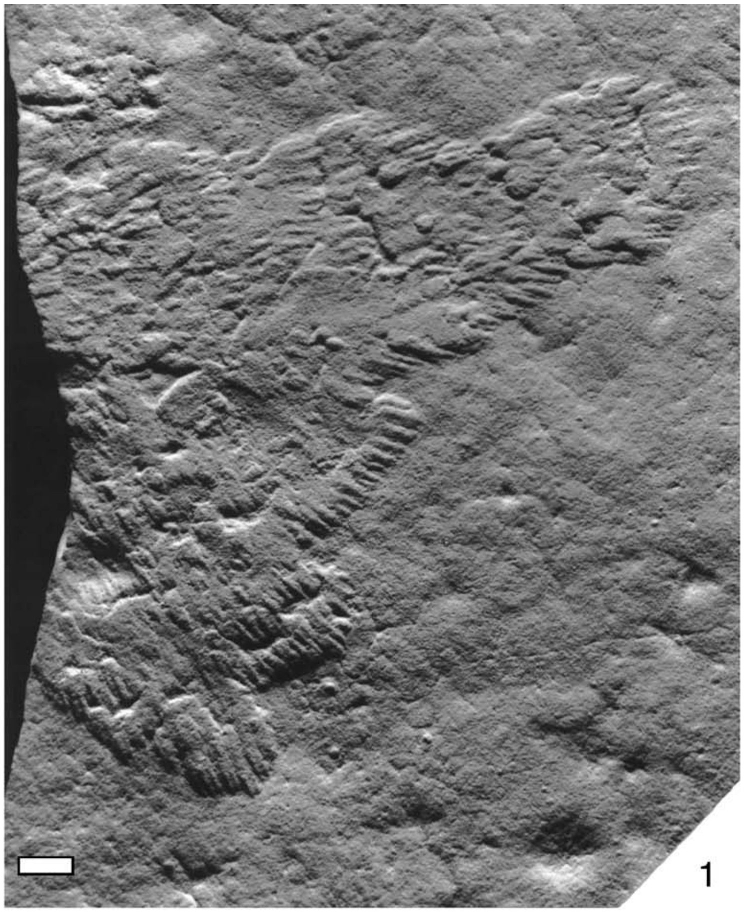


Figure 2—*Kimberichnus teruzzii*. Stylistic drawing of scratch pairs, arcuate sets and fans (in positive hyporelief) and sand pellets (in positive epirelief) that comprise arrays of scratch traces. Scale bar=1 cm.

Description.—The hypichnial ridges are natural bed-sole casts corresponding to epirelief grooves on counterpart surfaces. Arrays are composed of the following elements: "pairs" of equal, touching grooves; "sets" being pairs arranged in concentric or *en echelon* rows; "fans" being nested or partly overlapping sets of paired grooves, progressively increasing in radius and width of arc (Fig. 2). The convex edges of arcuate sets are described as distal, and the concave edges, proximal. Bifid grooves are sub-parallel within each set, and radially arranged within each fan. Some pairs are amalgamated at their blunt proximal ends; deeper comb-like sets may be formed by adjacent amalgamated pairs. In other cases, shallow pairs of fine grooves have constant depths and widths of separation. Distal sets, or pairs within sets, tend to truncate more proximal sets. Neighboring fans with different foci either interfere or the last-made fan erases the overlapped portions

→

Figure 3—*Kimberichnus teruzzii*, Ediacara Member, Rawnsley Quartzite, Flinders Ranges, South Australia; all specimens are in positive hyporelief, being natural casts of scratch undertraces. *1*, overlapping arrays of bifid ridges, SAM P35651a, Bathtub Gorge; *2*, widely spaced pairs in single fan, SAM P35652, Tooth Nob; *3*, irregular sets and fans, SAM P35653, Bathtub Gorge; *4*, elongate pairs in overlapping sets, SAM P35654, Mt. Mantell Range; *5*, widely spaced pairs in *en echelon* sets, SAM P35655, Moralana. Scale bars=1 cm.



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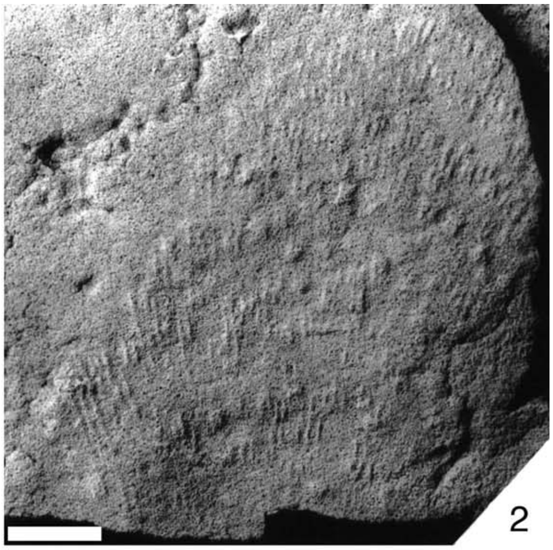

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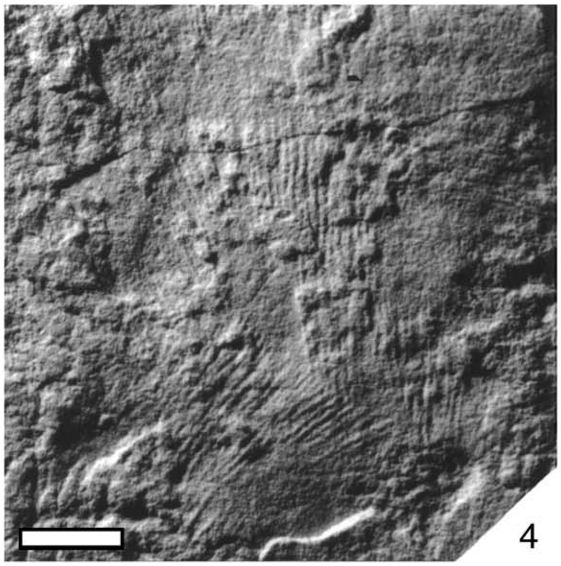

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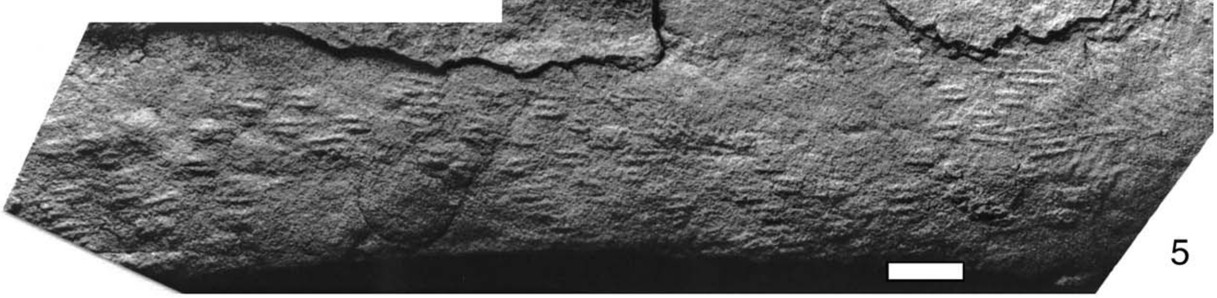

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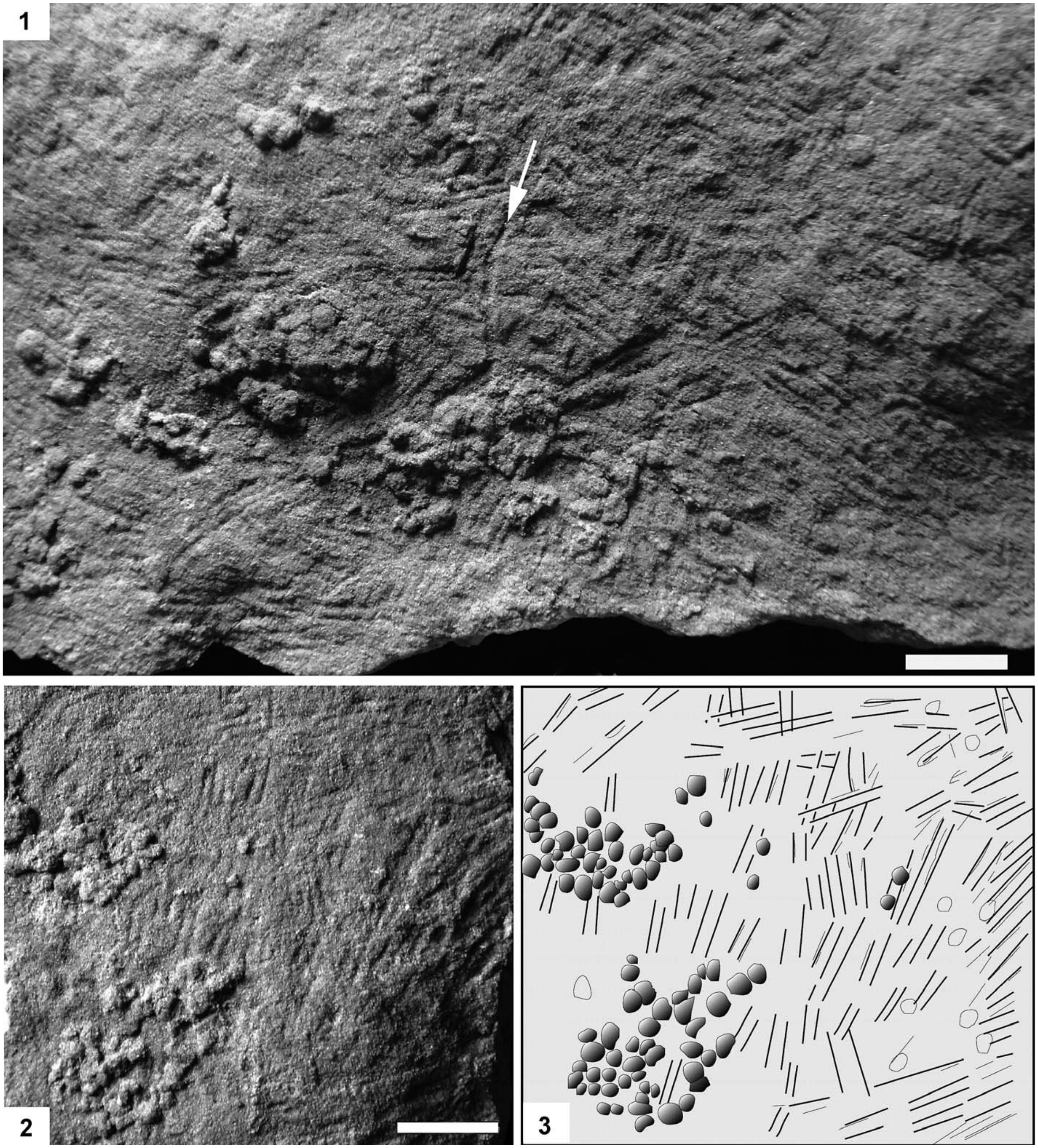

FIGURE 4—*Kimberichnus teruzzii. 1,* paired scratches made on bed top (epirelief) with pellets of sand adhering to the surface representing presumed organic rich sediment raked up by an inferred trace maker; fine-medium grained sandstone bed, 0.5–1.2 cm thick, from the Ediacara Member, Mt. Scott Range, SAM P35662; note a single groove trace, *Helminthoidichnites*, cutting the same surface (arrow) after scratch traces; *2,* epirelief sample; *3*, sketch of *K. teruzzii* with sand pellets and hollows from the same bed, SAM P35663. Scale bars=1 cm.

of an earlier one. Interference occurs where paired grooves are sharp and shallow, and erasure where pairs are spatulate and deep. For most arrays, distinct individual grooves are about 1 mm wide; the majority of pairs are 2–4 mm wide and 5–25 mm long. Within each fan, the width of pairs is constant and sets have a common focus if projected proximally. Fans have a 15°–45° arc of spread, being 25–50 mm wide. The radius of the most distal arc is 45–80 mm from the reconstructed focus of the fan. However, sets never extend all the way into the focus. The most proximal sets begin at least one-quarter the total radial length away from the focal point.

FIGURE 5—*Kimberichnus teruzzii*, SAM P35657, positive hyporelief (natural cast of excavations) aligned with the resting trace of *Kimberella,* SAM P35661, and negative hyporelief of *Dickinsonia costata,* SAM P35660; Ediacara Member, south of Brachina Gorge. Scale bar=1 cm.

In some cases, oblong sets project distally beyond the main fan. The mean radial length of 63 fans is 55 mm. Clusters of sand pellets, 2–4 mm in diameter are found in association with *K. teruzzii* on top surfaces where scratch traces are preserved in negative epirelief (Figs. 2, 4) and also as clusters of hollows (external molds) on bed soles where *K. teruzzii* is cast in positive hyporelief.

Remarks.—These traces consist of fans of bifid radial scratches, arranged in concentric sets. In most specimens, the bifid grooves tend to be shallower and consequently slightly splay in the distal direction, while being more deeply impressed, and often merging, at their proximal ends. This is interpreted as the result of a distal to proximal excavation stroke, opposite to the radular motion of modern gastropods. Fans with the deepest relief are typically composed of comb-like, arcuate or oblique sets of short, amalgamated bifid grooves with steep proximal margins (Fig. 3.1, 3.3, 3.5). The least distinct fans consist of shallow, elongate pairs of fine grooves (Fig. 3.2, 3.4, 3.5). Thus deeper excavation resulted in less distinct individual grooves and greater merging of individual strokes. This effect has been observed in shallower versus deeper undertraces made by trilobites (Seilacher, 1970; Goldring and Seilacher, 1971; Goldring, 1985). Each arcuate set was apparently constructed as a horizontal pendulum-like sweep made up of repeated individual sub-parallel scratch pairs. At the end of an arc, the action was interrupted and a more distal arc began with a greater radius of swing in the opposite direction. Because sets are so closely spaced, no clear meander loops can be distinguished; but as distances between sets remain constant, it may be assumed that the radius changed stepwise at the end of each transverse row. Fans made up of arrow-head sets (Fig. 3.1), or oblique, *en echelon* sets (Fig. 3.2, 3.5), with irregular spacing and variable length of pairs, suggest that the more common pattern of nested arcuate sets was not obligatory. However, mechanical limits to the radial and lateral scope of excavation are indicated by the fan shape. Scratch fans never have a proximal confluence; however the imaginary focal point, reconstructed by proximal projection of the groove pairs in a fan, is interpreted as the stationary pivot for lateral, pendulum-like excavational movements, because arcuate sets within fans are essentially con-focal. The tendency for more proximal sets to be truncated by more distal sets indicates a centrifugal order of excavation.

The associations of sand pellets with arrays of *K. teruzzii* are most obvious on epirelief preservations (Fig. 4). Like other Ediacara fossils, arrays of *K. teruzzii* are most commonly preserved as bed-sole casts, the underlying counterpart (bed top) usually being a very thin sandstone layer, too fragile to be found in locations where slabs are part of the talus. These clusters of pellets appear to be the result of scratch excavation of the mat-coated, sandy substrate at or near the focal point of scratch arrays. As such, they partly resemble sand pellets arrayed by a variety of modern tropical, intertidal sand bubbler crabs, including the genera *Dotilla* and *Scopimera* (Bulcao and Hodgson, 2012).

The reconstruction of *Kimberella* proposed by Ivantsov (2009, fig. 4; 2010, fig. 1; 2013, fig. 3) involved a spatulate extension of the body, armed with multiple spikes enabling each fan array to be made in a single stroke. This is not consistent with the fan-shaped sets of scratches observed on many surfaces in the fossiliferous facies of the Ediacara Member where parallel pairs are the rule. Fan-shaped sets vary in shape and internal arrangement of rows. Single pairs of scratches are common (Fig. 3.2, 3.4, 3.5); in many cases these pairs crisscross previously made sets (Fig. 4). Associated sand pellets, preserved on smooth, epirelief surfaces with paired grooves, are more likely the products of single strokes by a narrow proboscis.

In conclusion, each fan appears to have been constructed by a more or less stationary excavator with an extensible head or proboscis armed with a pair of stylets or "teeth" that made radial probes on the substrate with widening arcs. Each new fan represents a shift in location, or rotation of the whole body. Fans may be regular, with simple, con-focal arcuate sets, or composed of more random scratches of variable length. On most surfaces, such shifts of focus have produced multiple fans that partly overlap and interfere with previous ones. In some cases, several fans are radially arranged about a common pivotal zone.

Kimberichnus teruzzii has some similarity to arrays of radular scratch traces included in the ichnogenus *Radulichnus* Voigt 1977, originally described from the inner surfaces of Mesozoic oysters by the radular action of mollusks feeding on microbial coatings. Voigt (1977) compared them with almost identical scratch traces made by the modern docoglossid limpet, *Patella vulgata*. The similarity to *K. teruzzii* is confined to the pairing of scratches. Although *Radulichnus* can be confidently attributed to a molluscan radula organ, there is no unequivocal evidence that *Kimberichnus* had the same origin. The shape of *K. teruzzii* pairs of scratches is most consistent with strokes beginning distally and ending proximally, the opposite to radular movement on mollusks. Moreover, the association of body fossil impressions of *Kimberella quadrata* with casts of *K. teruzzii* suggests that the maker was able to move in reverse (Figs. 6, 7.3–7.6), a behavior unknown in extant gastropods that utilize a mucus gland on the anterior end of the foot to facilitate pedal muscular waves over terrestrial substrates (Lai et al., 2010).

Genus KIMBERELLA Wade, 1972 emended from Glaessner and Wade, 1966

Type species.—*Kimberella quadrata*.

Diagnosis.—Revised: oval to spatulate body outline, with or without a neck; one end always rounded and the other truncated

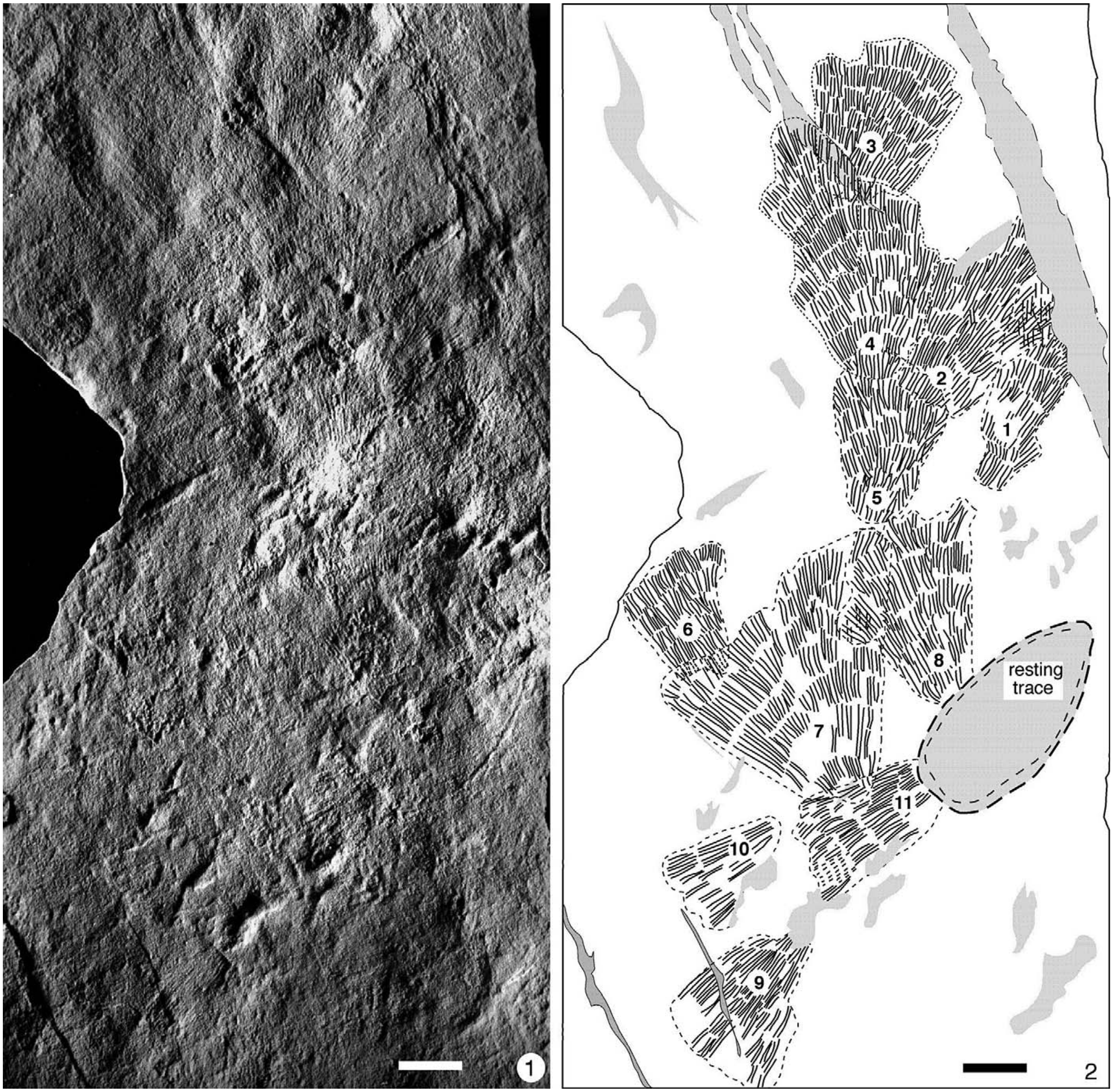

FIGURE 6—*1*, *Kimberichnus teruzzii*, SAM P35656, array of overlapping fans preserved in positive hyporelief (natural cast); Ediacara Member, Rawnsley Quartzite, south of Bunyeroo Gorge; *2*, sketch of trace arrays showing overlapping fans numbered in order of excavation, as determined by overlap of previously made scratch fans; preserved outline and faint pedal impression of the possible maker (center right), at the end of the staged, rearward and forward movements. Scale bar=2 cm.

or narrow and extended. Body sides oval or near parallel; sometimes slightly bent. Ovoid centre variously high relief in small specimens, flat or with sharp medial, sinuous to asymmetrical ridge in others; crossed by fine transverse grooves in largest specimens. Bordering rim tripartite with crenulated, median zone. Neck variable in length in smaller specimens, and short or absent in larger specimens.

Description.—The oval shaped body may include a neck-like projection. In the larger specimens, where the neck is absent, this margin is diffuse or straight. Most specimens, less than 1 cm long, are preserved on bed soles in high relief as external molds with a simple ornamented border confined to the oval body. In specimens larger than 5 cm long, the body is either preserved in shallow relief as a composite external mold, or as an asymmetric external mold. The rim consists of a regularly divided or frilled zone, bordered by distinct inner and outer grooves. In shallow composite molds the ovoid central region, inside the rim, is divided by regular transverse grooves being much finer than the outer frills. The neck is absent in many large specimens, but common in smaller specimens where it bears a terminal bulge with two short projections in some small specimens.

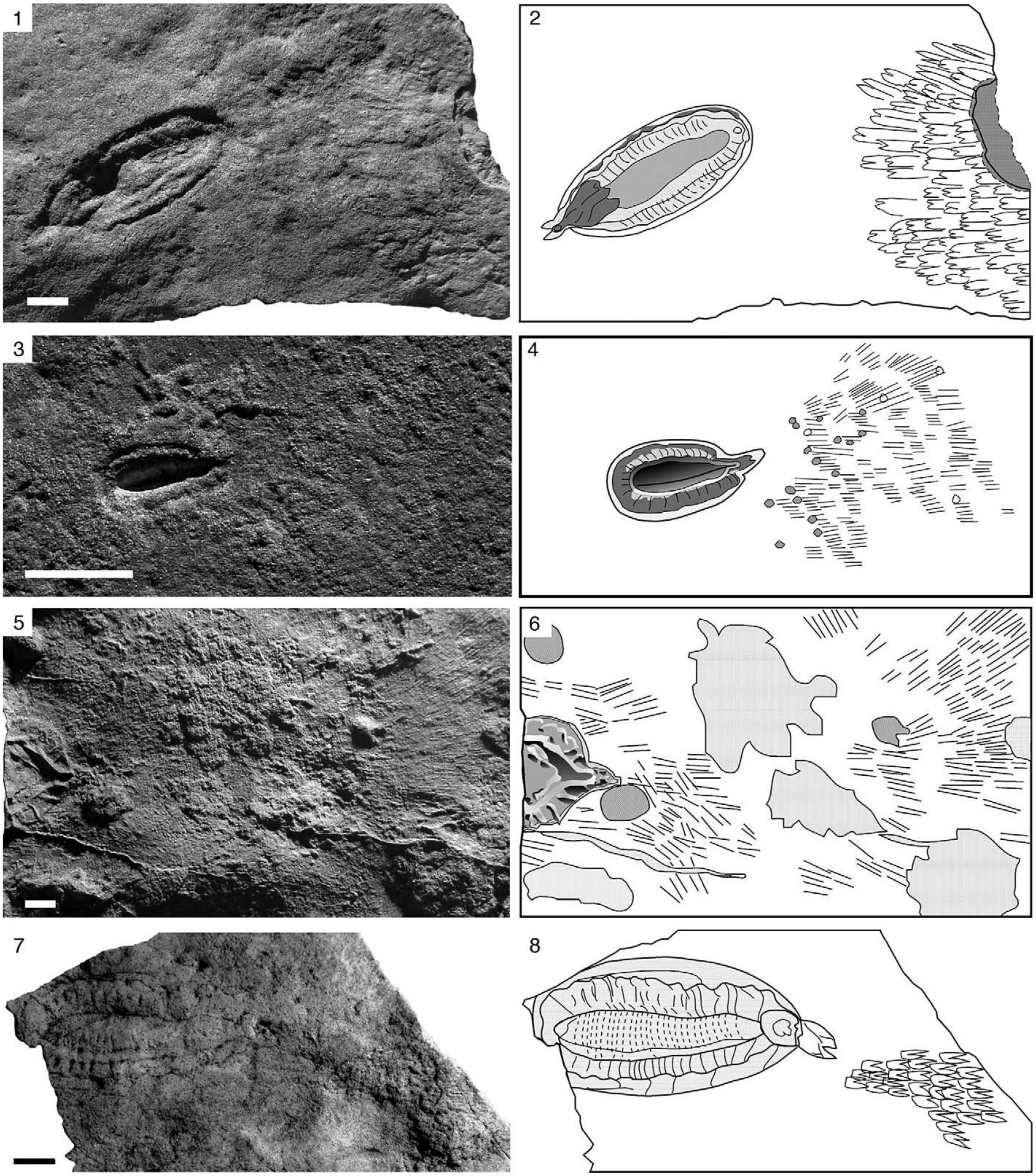

FIGURE 7—*1,* hyporelief of *Kimberella quadrata,* SAM P35692, preserved as a composite external mold with partly everted proboscis-like organ (presumed anterior end) on same surface as an array of *Kimberichnus teruzzii*, SAM P35693, a likely previous feeding position, indicated by the orientation of fanned array of scratch casts; Nilpena (National Heritage Ediacara Fossil Site), wave-base sandstone facies, Ediacara Member, Rawnsley Quartzite; *2,* corresponding sketch; *3,* hyporelief external mold of a small, high relief specimen of *Kimberella* , SAM P35698, positioned with everted proboscis at proximal end of faint casts of fanned-arrays of *K. teruzzii,* SAM P35699, and molds of presumed sand pellets; delta-front facies, Ediacara Member, Nilpena; *4,* corresponding sketch; *5,* latex cast of one-third of *Kimberella* (left side), SAM P35697, with partly everted proboscis and arrays of *K. teruzzii*, SAM P35696, wave-base sandstone facies, Ediacara Member, Mt. Scott Range; *6,* corresponding sketch indicating eroded areas of the weather hyporelief specimen; *7*, natural external mold of *Kimberella,* SAM P48935a, with proboscis and a fan array of paired casts of *K. teruzzii*, SAM P48935b, wave-base facies, Ediacara Member, Nilpena; *8*, corresponding sketch. Scale bars=1 cm.

Type.—Holotype, SAM P12734; paratype, P12739 Glaessner and Wade, 1966 (pl. 97, figs. 6, 7).

Occurrence.—Ediacara Member, Rawnsley Quartzite; Ediacara Conservation Park, South Australia.

Remarks.—Many specimens were preserved on surfaces with *Kimberichnus teruzzii* arrays, and may or may not be aligned with fans of scratches. *Kimberichnus teruzzii* is rare in association with specimens of *Kimberella* less than 15 mm in length, due apparently to the smaller size of the scratching appendage in relationship to the sediment grain size (Fig. 7.3, 7.4). Previously, in keeping with the original consensus that the Ediacara biota represented beach or tidal-flat strandings dominated by pelagic cnidarians (Sprigg, 1947, 1949; Glaessner and Daily, 1959; Glaessner, 1984), *Kimberella* was interpreted as a Carybdeida-like cubomedusoid (Glaessner and Wade, 1966; Wade, 1972; Jenkins, 1984, 1992). The asymmetrical preservation of the frilled zones in a few larger specimens of *Kimberella* was considered evidence of a tubular, bell-shaped body wall with partial preservation of four sets of gonads (Wade, 1972).

ANALYSIS OF *KIMBERICHNUS*

In *Kimberichnus* each pair of grooves is interpreted as corresponding to a single excavation, produced by a rasping action on the substrate. Due to a pendulum-like movement of the presumed proboscis, the scratch marks in each arcuate set are radially oriented and ascribed to a single focal point on the concave side of each set. *Kimberichnus teruzzii* scratches vary in relief, depending on their position in the fan, but tend to be slightly deeper on their proximal ends. The rasping motion appears to have been directed back toward the focal point in *K. teruzzii*. However, interpretation of the direction of each rasping action depends on the motion of the head as well as the attitude of the rasping organ with respect to the substrate.

Previously, specimens of *K. teruzzii* from South Australia have been informally referred to as *Monomorphichnus* Crimes, 1970 (Jenkins et al., 1983; Jenkins, 1995), and are likely the traces that Crimes (1987, 1992, 1994) offered as evidence of arthropods in the Ediacaran of South Australia. However, unlike the probable trilobite trace, *Monomorphichnus*, the scratches of *Kimberichnus* are not parallel, but are radially arranged. The scratches in *Monomorphichnus* (often unequal in pairs) are generally considered to have been made by arthropod limbs with biramous appendages (Martinson, 1965; Crimes, 1970). Unlike *Monomorphichnus*, where the sets of grooves are generally parallel due to the raking of limbs on the trailing side of a grazing trilobite (or in *Dimorphichnus*, where the push marks of legs on the leading side are also preserved), in *Kimberichnus* they fan in a manner that suggests repeated probing by a single organ with a pair of "teeth".

The first specimens of *K. teruzzii* discovered in South Australia were casually referred to as "spicular sets". However, unlike the spicular meshwork of *Palaeophragmodictya reticulata* Gehling and Rigby (1996) and *Coronacollina acula* (Clites et al., 2012), arrays of *K. teruzzii* are not preserved as external molds, as would be expected for mineralized spicules. Superficially, the larger fanned scratch arrays do resemble certain laterally flattened conical sponges. However *K. teruzzii* fans always lack an apex, unlike true radial spicular arrays, such as in the Cambrian sponge, *Choia* (Walcott, 1920).

In contrast to *Helminthoidichnites* furrow traces, the scratch marks were clearly made by an epibenthic rather than an infaunal organism. Of the *K. teruzzii* examined (some with part and counterpart slabs) none show any evidence of a burrow opening at or near the foci of the fans. In most cases, the geometry and overlap of successive fans reflect ordered, periodic shifts of the focal point, combined with systematic radial and lateral movements; such a pattern of rasping could only be achieved by a mobile trace maker with an effective and firm foothold on an established biomat (Figs. 4–7).

ASSOCIATION OF *KIMERELLA* AND SCRATCH TRACES

The preservation of mortichnia (Seilacher, 2007), being trace fossil arrays together with a record of the maker, is not common in the fossil record. Firstly, although a single animal can produce enormous numbers of traces, the chance of the maker being preserved in conjunction with its traces is small. Secondly, the taphonomy of trace fossil preservation requires that trails, feeding and resting traces are preserved rather than erased by the preservational event (see below). Although animals may occasionally be buried at the end of a trail or burrow, later bioturbation, physical reworking, and other taphonomic processes, conspire to limit the chances of preserving such associations. In Ediacara assemblages, the preservation of both trace and body fossils appears to have been due to parallel taphonomic pathways (Gehling, 1999). However, trace fossils like *Helminthoidichnites,* as interpreted by Droser et al. (2005), represent the activities of organisms that were too small to allow easy identification from death masks in medium grained sand. *Kimberichnus teruzzii* is one of the few Ediacara trace fossils produced by an animal large enough for the maker to be preserved as a death mask.

Kimberichnus teruzzii is far more common in the sedimentary facies of the Ediacara Member than impressions of *Kimberella*, let alone examples of specimens aligned with these distinctive trace-fossil arrays. However, several examples are documented in South Australia where *K. teruzzii* arrays are associated with appropriately oriented body fossil impressions of *Kimberella quadrata* (Figs. 5–7). The clearest example is a slab (Fig. 5) with six scratch fans associated with a pedal impression or resting trace of *Kimberella* aligned with the last-made fan. A specimen of *Dickinsonia costata*, preserved nearby, provides evidence that this surface was relatively typical of Ediacara body fossil preservation. However, the ovoid impression aligned with the last made *K. teruzzii* specimen and shaped like *Kimberella,* but without the usual composite internal structures, is interpreted as a resting trace. The scratch fans, preserved in positive hyporelief, overlap in the order of excavation (Fig. 5, from middle-left to upper-right). The 45 mm wide and 90 mm long resting trace of *Kimberella* is preserved as a composite cast with a sharp, double-edged border. Near the anterior end, the border is interrupted by impressions of more resistant structures. A central bulge outlined by depressions on each side (in hyporelief) lies along the midline, and branches into two irregular lobes that extend beyond the expected position of the border. The remainder of the ovoid body is almost entirely smooth, apart from faint longitudinal structures parallel to the axis. There is a ribbon-like sinuous impression, just inside one margin, and extending for half the body length. A sharp groove extends from the medial posterior end to the other end, where it bifurcates above the anterior lobes. The detail in these resting traces is matched by the precision the *K. teruzzii* array and the complex multi-stage impression of *Dickinsonia* (see Gehling et al., 2005, fig. 8).

Re-examination of other specimens of *Kimberella* has revealed previously unnoticed *K. teruzzii* arrays on the same slabs. A weathered talus specimen from Nilpena preserves an external mold of *Kimberella,* with partly everted proboscis (Fig. 7.1, 7.2). Its position on the distal side of an arcuate array of *K. teruzzii* is interpreted as an association where *Kimberella* had moved over its last feeding trace before the burial event. A third example from Nilpena is a smaller specimen of *Kimberella,* less than 1 cm long, preserved opposite a faint array of paired scratch traces, less than 1 mm apart, which were cast on the base of a very fine-grained sandstone layer (Fig. 7.3, 7.4). Thus the reason that proportionately-sized sets of *K. teruzzii* have not been found with the other known specimens of *Kimberella,* less than 1 cm long, is because the molding sediment is not sufficiently fine-grained to record scratch arrays of pairs less than 1 mm. Larger, but less well preserved specimens of *Kimberella* with anterior ends proximal to fans of *K. teruzzii* confirm the association (Fig. 7.5–7.8).

INTERPRETATION

The trace fossil arrays of *Kimberichnus teruzzii* are interpreted as rasping excavations by benthic organisms feeding on biomats. Dornbos et al. (2004) described epirelief impressions of scratch fans similar to *Kimberichnus*, associated with circular hollows, from the lower Cambrian, Meishucun Formation of southwest China. In this case, the arrays consist of extremely wide arcs, suggesting that the circular hollows were resting traces made as the organism swiveled in place on the substrate. However, the inferred biomats from Ediacaran and early Cambrian substrates preserve no locomotive traces unless the animal was able to disrupt the mat surface. The association of *K. teruzzii* and *Kimberella* provides a good model for elucidating behaviors and taphonomy in the Ediacara biota.

A comparison of *K. teruzzii* with more modern scratch traces is suggestive of a motile bilaterian maker. However, although the association of *K. teruzzii* with *Kimberella* could be used as supporting evidence that *Kimberella* was a mollusk, as interpreted by Fedonkin and Waggoner (1997), closer examination of the *K. teruzzii* arrays provides some contrary evidence. Our study of the overlapping patterns of *K. teruzzii* scratch fans in large arrays (Figs. 5, 6) shows that the maker had the capacity to move in reverse as well as pivoting and moving forward. Fedonkin et al. (2007, figs. 20–22) provide evidence of retreat traces of *Kimberella* in response to live burial. Such behavior is not within the known repertoire of gastropod mollusks.

Biomechanics of epibenthic mat grazing.—The rows of paired scratches in *K. teruzzii* are comparable to scratch traces that gastropods leave when grazing on cyanobacterial coatings on various hard substrates (Voigt, 1977; Hickman, 1983). Observations made with the marine limpet, *Patella*, show that the arc of each meander lobe in a grazing trace approximately equals the width of the body. Grazing traces of the planispiral, fresh water gastropod *Gyraulus,* on biofilms of an aquarium wall, are made up of a sinuous array of arcuate sets, each composed of 6–12 deltoid shaped scratches in which individual tooth marks cannot be distinguished (Fig. 8). The sets have amplitudes that approximately equal the width of the foot, representing the limit of lateral movement of the head as it grazes the surface. Importantly, the foot of the modern gastropod left no trace on the microbial film that coated the glass aquarium.

Considering the associations of *K. teruzzii* and *Kimberella*, it is reasonable to calculate the approximate body dimensions of the trace maker as a function of the radius and width of the arcuate scratch sets. Allowing for the fact that a gastropod foot is highly variable in size, its length is normally about twice the focal length of a scratch set, and its width almost exactly the same as the width of the set. This predicts that *Kimberella* as 40 mm wide by at least 110 mm long in *K. teruzzii*, which is consistent with the specimens preserved in place

The *K. teruzzii* scratch fans appear to have been executed by an extensible organ capable of three components of movement. Each pair of scratches involved a radially directed scratch stroke, like that in living gastropods. Arcuate sets of scratches were made by stepwise lateral shifts between strokes. The arcuate swings began with sets close to the anterior end of the animal. At the end of each set the head end extended to make the next set, with a wider arc. The fan was completed when the proboscis reached its limit of distal extension. Having grazed a pie-shaped area of the biomat, the overlapping of scratch fans shows a variety of behaviors. From specimens with evidence of *Kimberella* in place (Figs. 5–7), the animal appears to have first advanced over its previous excavations to a new stationary locus and then retreated, or rotated in place, before grazing a new sector of mat. As far as can be judged by field observations of extant marine and terrestrial gastropod grazing behavior, all movement is forward in the direction of convexity of the scratch fans (Fig. 8) or rotational, but never backward.

Taphonomy of mat grounds.—Unlike modern radular traces on intertidal rock platforms or aquaria walls, the Ediacara ones were made and preserved on a sedimentary substrate. In soft sediment,

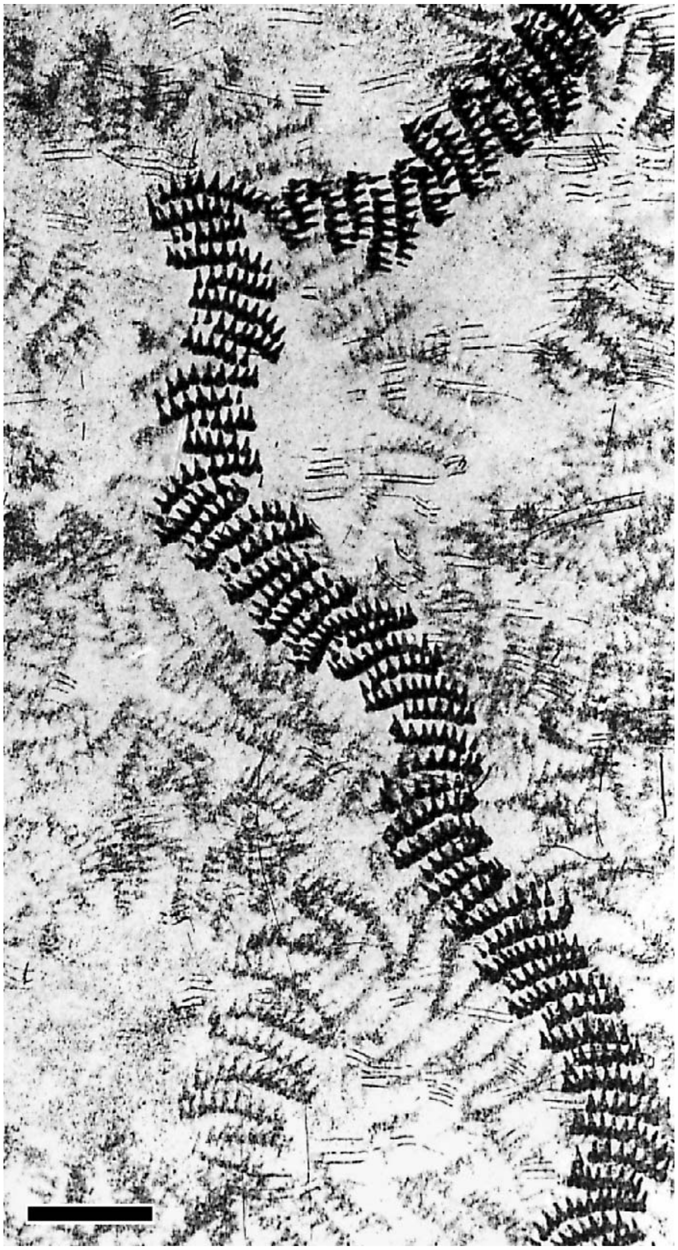

FIGURE 8—Radular grazing traces of a fresh-water gastropod (*Gyraulus*) on microbial mats coating an aquarium wall. Scale bar=1 cm.

the advance of the muscular foot would be expected to smudge radular markings. In Ediacaran low-energy marine environments, however, the absence of diverse and efficient grazing and burrowing organisms allowed microbes to bind the upper few millimeters of soft sediment into a coherent biomat (Gehling, 1999; Seilacher, 1999). With the evolution of more diverse and increasingly effective infauna in the early Phanerozoic (Droser et al., 2002a; Droser et al., 2002b) such biomats gradually disappeared and became restricted to hostile sedimentary environments (Hagadorn and Bottjer, 1999; Pflüger, 1999; Bottjer et al., 2000). Thus in the Ediacaran, biomats were sufficiently tough to carry the load of the animal's body, without leaving a trail that erased previous radular markings. The evidence for biomats in ancient siliciclastic sediment includes wrinkled surface textures (Hagadorn and Bottjer, 1999), "petee" structures (Gehling, 1999, 2000), rollup structures (Schieber, 1999), impressions of reworked biomat clasts (Pflüger, 1999), and pyritized filaments (Grazhdankin and Gerdes, 2007, fig. 3A, 3B). Distinctive sole marks ("old elephant skin" and wrinkle textures) identify the presence of microbial mats that protected substrates from erosion and produced effective partings between serial sandstone beds in the absence of clay (Gehling, 1986, 1999; Fedonkin, 1992; Gehling and Droser, 2009). Bacterial decay and formation of a mineral "death-mask" over the sand-smothered animals and biomats, proposed as the mechanism for the preservation of microbial textures and body-fossil impressions (Gehling, 1999), has been confirmed by the discovery of unweathered pyritic "death-masks" in Ediacara fossil beds from the White Sea region of Russia (Grazhdankin and Gerdes, 2007). Firstly, the preservation of trace fossils required that mat grounds be scratched, furrowed or degraded by an organism resting on the mat, to be recorded on bed-soles. Secondly, pyrite produced by anaerobic decay of the sand-smothered organic matter fixed the sole-veneer of the smothering sand before both mats and buried organisms had completely decayed. Counterpart casting by the underlying uncemented sediment then conformed to the "death-mask" impression, so that both part and counterpart impressions could be preserved during diagenesis. In the Australian weathering profile of outcrops, these fossil surfaces have oxidized to leave resilient ferric cement on the bed sole-veneer. Sandstone casts of feeding excavations or long-term resting traces on mats, as well as external molds of organisms that happened to be caught in feeding positions on these biomats, are the best-preserved specimens.

That *K. teruzzii* occurs in conjunction with the impressions of skeletonless organisms emphasizes the uniqueness of the environments and of the taphonomic conditions that were responsible for this preservational window into the Ediacaran biosphere. In the Ediacara Member of South Australia, fossils preserved in positive hyporelief are rarely found on the same surfaces as others preserved in negative hyporelief. The properties of the microbial mats underlying these organisms, the thickness of the smothering sand, and the time between storm events, appear to have determined the preservation potential of organisms of different construction or lifestyle. Fossils preserved in positive hyporelief are generally the buried undermat holdfasts of frond-like organisms, benthic polyps, some reclining vendobionts, and collapsed trace fossil galleries that penetrated the biomat before a mineralized "death mask" was formed over decaying organic mats and buried bodies (Gehling, 1999; Droser et al., 2006). Conversely, tougher organisms were preserved as external molds, where the "death masks" were sand-cast from below as the bodies decayed. A third category of preservation includes weak positive casts or "resting traces" of animals like *Dickinsonia* and *Yorgia*. Body-shaped depressions in the substrate mark the places where these mat-like organisms, lying on the microbial mats, had caused decay of the mat, possibly as an adjunct to absorbing the released nutrients (Gehling et al., 2005.). In contrast, rare casts of *Kimberella* pedal resting traces (Figs. 5, 6; described above), suggest that this animal moved more frequently as demonstrated by the shifting focus of more prominent casts of scratch fans.

Ediacara basal crown group bilaterians.—Following the initial interpretation of large specimens of *Kimberella* as a cubozoan cnidarian (Glaessner and Wade,1966; Wade, 1972; Jenkins, 1984), the discovery of smaller specimens (3–20 mm) with a strong, median keel in South Australia, provided a growth series that includes the type material. A number of these small, high relief specimens have a serially patterned outer flange and a proboscis-like organ projecting from the non-convex end (Gehling et al., 2005, fig. 12a, 12b). It is now apparent that the asymmetric groove, parallel to the body axis in some of the type material, was a product of collapse and flattening of a bilateral animal with high relief. As best preserved in small specimens, the prominent, median dorsal keel, rounded at one end and open or more pointed at the other, is regarded as a flexible, unmineralized outer integument. The serrate zone has been interpreted as a corrugated mantle frill overlying a wider central muscular foot. After studying a large collection of well-preserved specimens from the White Sea coast of Russia, Fedonkin and Waggoner (1997), Fedonkin et al. (2007) and Ivantsov (2009, 2010, 2013) reinterpreted *Kimberella* as a mollusk-like animal with bilateral symmetry. The closed or rounded end of the impression was designated as anterior (rather than posterior) by Fedonkin and Waggoner (1997). Since then, large collections of specimens from the White Sea region, and lesser numbers of specimens from South Australia, demonstrated that a proboscis-like structure aligned axially, lay within, or extended from, the opposite and least well defined end of the organism (Fig. 7). The less-frequent preservation of this organ is typical of the differential preservation of structures at various levels within three-dimensional Ediacara organisms. Since both Australian and Russian specimens of *Kimberella* show alignment of the open end (previously termed "posterior") proximal to scratch fans, it is now apparent that this was the anterior end where the feeding apparatus projected.

Fedonkin and Waggoner (1997) and Fedonkin et al. (2007) argued that *Kimberella* possessed a shell. However, Ivantsov (2009, 2010) recognized the lateral flexibility of *Kimberella* as evidence that a rigid "shell" was not a possibility, preferring instead to interpret the tessellate pattern of some Russian specimens as evidence of mineralized sclerites. External molds of *Kimberella* generally show higher relief in comparison with other similar-sized body fossils in the Ediacara biota. Although originally, Glaessner and Wade (1966), Wade (1972) and Jenkins (1984) had interpreted *Kimberella* as a cubomedusoid with an elongated bell-shaped body, a bilaterian grade body plan (Fig. 9) is more in keeping with the preserved morphology. Evidence from arrays of overlapping scratch fans in the South Australian material indicates that *Kimberella* was able to make retrograde body movements. Such behavioral characteristics are unknown in extant terrestrial gastropods (Brusca and Brusca, 2003).

The lack of evidence for retrograde movement by extant gastropods could be reason to consider priapulids, echiurids and sipunculids as possible analogues for *Kimberella*. The early Cambrian palaeoscolecid from Kangaroo Island, South Australia, *Wronascolex antiquus* (Garcia-Bellido et al., 2013), which exhibits, a spinose introvert, is possibly a stem-group priapulid. Dzik (2007) and Vannier et al. (2010) suggested priapulid-grade animals were the likely makers of early Cambrian burrow traces such as *Psammichnites* (referred to as *Mattaia*) and *Treptrichnus pedum* that are part of the assemblage that defines the base of the Cambrian in siliciclastic sedimentary sequences (Landing, 1994). Considering the near universal distribution of *Treptichnus pedum*

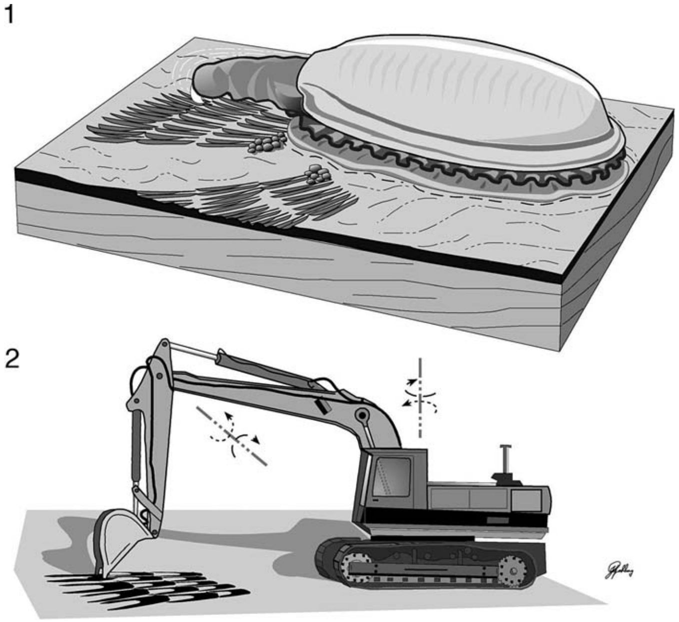

FIGURE *9—1*, diagrammatic representation of hypothetical molluscan grade organism, such as *Kimberella quadrata* Glaessner and Wade, 1966 producing fanned scratch traces of *Kimberichnus teruzzii* on a sandy biomat; *2,* a modern mechanical excavator mimics the feeding style of the Ediacara mollusk; the excavator arm moves around two axes: a vertical axis for the swing of the arm (probe), and a horizontal axis for radial movement of the bucket (head).

burrow traces at the base of the Cambrian, an Ediacaran origin for the maker is possible. Unlike gastropods, priapulids are capable of advancing and retreating. However, the preserved structures in *Kimberella* cannot readily be attributed to composite molding of any living clades of tubular organisms. Furthermore, no feeding traces like *K. teruzzii* have been reported in association with feeding by living priapulids.

Ivantsov (2013, pl. 2, fig. 2) illustrated a specimen of *Kimberella* with an extensible anterior "head" bearing structures interpreted as a set of "teeth". In the absence of preserved evidence for a mineralized or resilient radula in *Kimberella*, molluscan affinities are uncertain. However, from the taphonomic analysis of their soft parts, extant monoplacophorans (Trusler et al., 2007) and polyplacophorans (Seilacher, 1999) are useful analogues for composite external molds of *Kimberella*.

RECONSTRUCTION

Following Fedonkin and Waggoner (1997), *Kimberella* has been reconstructed as a "soft-limpet" with an unmineralized dorsal shield. There is now evidence of an extensible excavation organ or proboscis (Fig. 7; Gehling et al., 2005, fig. 12; Fedonkin et al., 2007, figs. 14–17; Ivantsov, 2009, 2010, 2013); however, in most specimens this organ is not readily distinguishable. This is inferred to be a result of its retraction within the circumference of the body. The bifid and slightly splayed grooves that make up the fans of *Kimberichnus teruzzii* imply a flexibly mounted scratching organ. The orientation of the bifid grooves, with respect to *K. teruzzii* fans, represents movement parallel to the body axis. Differences in the lengthwise profile of grooves, from one part of an array to another in *K. teruzzii*, reflect changes in the reach of the proboscis between subsequent sets. From the paired scratches in *K. teruzzii,* it is apparent that there was a simple pairing of stylets or "teeth" in the cutting organ. The profile of any given pair of grooves on a thick mat-surface would depend on the pivot point of the "teeth" in relation to the substrate. The stylized reconstruction of *Kimberella* in feeding position, with a proboscis that could extended well beyond the margin of the body, combines the characters preserved in various body fossils that suggest how it may have produced fan-shaped scratch excavations of the substrate (Fig. 9).

Deformed molds of large specimens of *Kimberella,* and high relief molds of small specimens, indicate considerable relief on the body. This reconstruction of *Kimberella* includes an inferred stiff but flexible unmineralized shield that enclosed internal organs over a mantle frill and a muscular foot (Fig. 9). It is supported by the preserved positions of the body fossil or its resting traces relative to the orientation of *K. teruzzii* fans. However, unlike the inferred molluscan radular trace fossil, *Radulichnus inopinatus,* preserved on the surfaces of fossil shells (Voigt, 1977), arrays of *K. teruzzii* suggest more complex feeding patterns. With respect to resting traces the arrays of scratch fans suggest that *Kimberella* was capable of retrograde movement between successive arrays. This is a behavior unknown in extant gastropods. Furthermore, in gastropods, the movement of the radular membrane over a cartilaginous odontophore in grazing gastropods results in a forward directed radular stoke. However, the pattern of individual scratches is far more complex in those families where the radular organ is made up of rows with several teeth set in a radular membrane (Hickman and Morris, 1985). In archaeogastropods, the result of the outward radular stroke is a distal narrowing of the scratches on a hard substrate (Fig. 8).

Although the interpretation of the body fossil impressions of *Kimberella* in both Russia and Australia aligned with trace fossil arrays of paired scratch marks appear to support a stem-group mollusk interpretation for *Kimberella*, the evidence of the style of scratching stroke, the apparent rearward motion of *Kimberella* both when feeding (Figs. 5, 6) and in response to burial (Fedonkin, 2007), renders the affinities of *Kimberella* uncertain.

ENVIRONMENTAL SETTINGS OF *KIMERICHNUS*

In the Flinders Ranges of South Australia, the most fossiliferous facies of the Ediacara Member consist of thin- to medium-bedded, wave-rippled, storm sands. They were deposited between storm and fair-weather wave-base during the cyclic progradation of a tidally influenced delta complex over a previously incised and flooded land surface (Gehling, 2000; Gehling and Droser, 2013). Previously, Jenkins et al. (1983) and Nedin and Jenkins (1991) assigned these beds to intertidal settings, on the basis of flaser bedding and sun desiccation cracks. Restudy of the claimed mud cracks, however, shows them to be variously, the products of syneresis in microbial mats sandwiched between sand layers, tension cracks in ball and pillow sand, or pull-apart cracks formed after partial cementation of bed soles over organic rich substrates (Gehling, 2000, fig. 10c). The Ediacara fossils in South Australia occur on the bases of storm beds that correspond to a sharp change from laminated clayey siltstone to thin- and medium-bedded sandstones with rippled tops (Gehling, 2000). In the absence of efficient burrowing organisms, microbial mats thrived not only in upper-intertidal environments, but also subtidally, below the zone of daily wave agitation. While mat-grounds are obvious in carbonates, as algal laminites and stromatolites, their original presence in Proterozoic siliciclastic sediments can be inferred from textured organic surfaces (TOS) and microbially induced sedimentary structures (MISS) (Horodyski, 1993; Seilacher and Pflüger, 1994; Pflüger and Gresse, 1996; Gehling, 1999; Hagadorn and Bottjer, 1999; Seilacher, 2008; Gehling and Droser, 2009; Noffke, 2009).

If, as postulated by Retallack (2013), the Ediacara biota was of terrestrial or intertidal origin, the Chace Quartzite Member that underlies the Ediacara Member of the Rawnsley Quartzite should be replete with body fossils. In practice, no body or trace fossils have been identified on any bed surface of the Chace Quartzite Member. The association of *Kimberichnus* with sand pellets and body fossil impressions of *Kimberella* in the Ediacara Member of the Rawnsley Quartzite cannot be reconciled with the claim of Retallack (2013) that the fanned scratch arrays represent preservation of ice crystals in a sandy substrate. It is inconceivable that paired arrays of ice crystals would have been preferentially preserved with *Kimberella*. For taphonomic and structural reasons, *K. teruzzii* cannot be interpreted as casts of structural elements such as spicules or organic fibers.

Ediacara trace fossils, other than resting traces of *Dickinsonia* and *Yorgia* and the excavation trace, *K. teruzzii*, were the products of shallow-furrowing activities of organisms confined to biomat horizons, whether beneath a thin blanket of sediment, or within biomats at the sediment-water interface. The invention of effective appendages and intensive grazing, surface churning, and penetrative burrowing resulted in the disruption of the physical integrity of membranous and sediment-binding microbial mats at the beginning of the Cambrian (Seilacher and Pflüger, 1994; Jensen et al., 1998; Seilacher, 2008). Bioturbation continued to increase in depth, intensity, and effectiveness throughout the early Paleozoic (Bottjer and Droser, 1994; Droser et al., 2002a, 2002b), which also facilitated the escape of gases and decay products and the invasion of buried organic layers by oxygen-rich water (Aller, 1983; McIlroy and Logan, 1999).

SUMMARY

The Ediacara scratch-like excavations were made as sharp pairs of grooves into mat-coated sandy substrates and best preserved as casts on bed soles sandy event beds. By association on the same surfaces, *Kimberichnus teruzzii* is interpreted as the grazing trace of *Kimberella quadrata* armed with a proboscis bearing two “teeth”. This relatively large organism advanced across a mat veneer without obliterating previous scratch patterns. However, the feeding trace evidence of distal to proximal scratching stokes and reverse movement by *Kimberella* are not characteristic of extant gastropods. A comparison with bilaterians such as priapulids, for which there is a plausible fossil record in the Cambrian, has been considered and negated by the preserved body plans of numerous specimens of *Kimberella* from both Russia and Australia that cannot be explained by a tubular body. Consequently, *Kimberella* and its feeding scratches are best explained as evidence of basal crown group bilaterians with lophotrochozoan affinities.

Microbial mats played a crucial role in preserving the impressions of soft-bodied organisms as well as trace fossils. Such mats were ubiquitous on subaqueous bottoms prior to the invention of bioturbation during the Cambrian diversification of marine animal life. Whether their disappearance was a response to, or a trigger for, ecological changes accompanying the Cambrian explosion of animal life, remains uncertain.

Kimberichnus teruzzii is a common trace fossil in the Ediacara Member of the Rawnsley Quartzite in South Australia and the Zimney Gory Formation on the White Sea coast of Russia. Most other Ediacara trace fossils record the activity of endostratal organisms feeding below or within a microbial mat horizon. In contrast, *Kimberichnus teruzzii* and *Kimberella quadrata* represent the first record of systematic grazing by an epifaunal metazoan of bilaterian grade in the geological record.

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